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Factors Influencing Biodiversity, Ecosystem functioning and Ecosystem services in Oil Palm Landscapes

by

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Thesis for the degree of Doctor of Philosophy

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Abstract

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In the face of huge biodiversity loss due to agriculture and associated loss of ecosystem function, it is imperative to elucidate factors that contribute to or alleviate this problem, in order to improve management of agricultural landscapes. My meta-analysis, along with a large body of previous research has identified the impact that forest conversion to oil palm plantations can have on biodiversity and ecosystem function. In this thesis, I identify factors which influence biodiversity and ecosystem functioning within oil palm dominated landscapes, both positively and negatively. I first explore the conservation value of oil palm landscapes to forest and generalist birds and assess associated ecosystem services provided by them. I sample bird species richness, abundance and diet using traditional bird sampling methods and next-generation sequencing techniques (Chapter 2). Then, I determine how large-scale replanting of oil palm may affect agricultural sustainability and biodiversity by sampling indicators of soil quality and soil macrofauna communities along an oil palm replanting chronosequence. I use structural equation modelling to explore drivers of soil degradation (Chapter 3) and mixed models and multivariate community composition analysis to evaluate biodiversity change (Chapter 4) after replanting. Finally, I explore how within-plantation soil biodiversity and ecosystem functioning can be improved, by examining the effect of enhancing understory vegetation complexity (Chapter 5). This body of work can inform wildlife conservation practices and sustainable management practices in landscapes containing oil palm.

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Research Thesis: Declaration of Authorship

Print name:	Adham John Ashton-Butt

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I declare that this thesis and the work presented in it are my own and has been generated by me as the result of my own original research.

I confirm that:

1. This work was done wholly or mainly while in candidature for a research degree at this University;
2. Where any part of this thesis has previously been submitted for a degree or any other qualification at this University or any other institution, this has been clearly stated;
3. Where I have consulted the published work of others, this is always clearly attributed;
4. Where I have quoted from the work of others, the source is always given. With the exception of such quotations, this thesis is entirely my own work;
5. I have acknowledged all main sources of help;
6. Where the thesis is based on work done by myself jointly with others, I have made clear exactly what was done by others and what I have contributed myself;
7. Parts of this work have been submitted for publication, all chapters were produced as part of collaborative work. However, in all cases, I collected the data, analysed the data and wrote the thesis. I will be first author on all publications that are accepted from this thesis. All chapters are presented in the format that they have or will be submitted for publication.

Signature:		Date:	

Acknowledgements

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Chapter 1: General Introduction

As a result of human activities there has been a drastic, global decline of biodiversity over the last 50 years. Monitored vertebrate populations have declined by 60% since 1970 (Barrett et al., 2018), with invertebrates declining on a similar scale (Hallmann et al., 2017). Agriculture has been the leading cause of biodiversity loss, due to encroachment of natural habitats and intensification of agricultural practices (Barrett et al., 2018; Gámez-Virués et al., 2015; Gibbs et al., 2010; Potts et al., 2010). However, biodiversity sustains many ecosystem functions and services that are vital to agricultural landscapes such as pollination, maintenance of soil quality and natural pest-control (Mace et al., 2012). Agricultural intensification results in the simplification of landscapes as the proportion of crop area increases and crop diversity decreases, driven by the focus on the most economically viable crop within a region (Landis, 2017). The loss of ecosystem functioning and services supported by biodiversity due to landscape simplification (Cardinale et al., 2012; de Vries et al., 2013) has resulted in the need for increased anthropogenic inputs to sustain yield, thus, creating major doubts over the sustainability of food production (Robertson, 2015; Tscharntke et al., 2012).

In recent years, the tropics have experienced the worst declines in biodiversity (Barrett et al., 2018), likely due to their inherently high taxonomic diversity (Myers et al., 2000) and the vast amounts of natural habitat conversion to agricultural areas (Newbold et al., 2015). High rates of biodiversity loss are expected to continue in the tropics as market demand for cash crops places further pressure on natural environments (Vongvisouk et al., 2016). This has led to the proposal of the land sparing approach to conservation, where primary forests are kept intact by intensifying agricultural practices in other areas to meet market demand (Phalan et al., 2011); as opposed to a land sharing approach which aims to promote less intensified agricultural landscapes with higher biodiversity, at the expense of lower yields (Karanth et al., 2016). However, intensification does not guarantee land sparing; as the profitability of agriculture grows, often so does demand for land (Lambin & Meyfroidt, 2011; Yan, 2017). Furthermore, intensive agricultural landscapes may not be sustainable in the long-term (Landis, 2017). A more balanced approach to agriculture in tropical landscapes (and in general) has been proposed, that incorporates both land sparing and land sharing and that allows for both biodiversity conservation and the maximising of ecosystem service provision (Fischer et al., 2014; Tscharntke et al., 2012).

Oil palm agriculture is one of the fastest expanding crops in the tropics, currently covering about 22 million ha (FAOSTAT, 2016). Global demand for oil palm is growing rapidly and palm oil currently accounts for 35% of the world's vegetable oil production (Meijaard et al., 2018). Oil palm products are used globally, with Indonesia, India, China, the European Union and North America all major consumers (USDA-FAS, 2017). Palm oil products are used in roughly 50% of all supermarket items in Europe (WWF, 2009). Most oil palm is grown in Malaysia and Indonesia, which produce 85% of the world's palm oil (USDA-FAS, 2017) and are both major consumers and exporters of palm oil (Byerlee et al., 2017). However, oil palm agriculture is expanding in Latin America and Africa and is predicted to grow in the coming years (Furumo & Aide, 2017; Henders et al., 2015; Pirker et al., 2016).

Oil palm production has serious ramifications for biodiversity and climate change due to the impacts of forest conversion to plantations. Direct forest conversion accounted for over 55% of oil palm expansion in Indonesia and Malaysia between 1990 and 2005 (Koh & Wilcove, 2008). Oil palm is also replacing other habitats such as grasslands and cattle pastures, particularly in Latin America, with varying effects on biodiversity depending on the initial state (Meijaard et al., 2018; Prescott et al., 2016). Furthermore, there is a worry that ecosystem services have been compromised in oil palm landscapes due to the degradation of ecosystem function and biodiversity caused by large-scale land use change (Dislich et al., 2016). Dislich *et al.*, (2016) found that out of 14 ecosystem functions reviewed, 11 showed a net decrease after forest conversion to oil palm. The authors only report one function that increases with oil palm cultivation: the production of marketable goods. Information on biological control and pollination after forest conversion was deemed to be too data poor to assess whether the impact was positive or negative.

Despite the negative environmental impacts, oil palm is the most productive vegetable oil crop per unit area (Zimmer, 2010) and is a crucial part of the economy for developing countries such as Indonesia and Malaysia (Koh & Wilcove, 2007). Therefore, palm oil production is likely to continue to expand in the foreseeable future (Meijaard et al., 2018), particularly in Latin America and Africa (Furumo & Aide, 2017; Ordway et al., 2017). According to a recent report by the International Union for Conservation of Nature (IUCN), the best way to protect biodiversity is to prevent further deforestation for oil palm through a land sparing approach of forest conservation and agricultural intensification of oil palm plantations (Meijaard et al., 2018). Thus, protecting hyper-diverse rainforests and the biodiversity within them. However, intensively grown oil palm is often planted in monocultures that can cover a considerable proportion of the landscape (Azhar et al., 2017). Simplification of landscape structure due to intensive agriculture degrades ecosystem functioning and biodiversity on which agricultural ecosystem services depend (Landis, 2017) and although highly intensified landscapes often support high yields, this has been found to be unsustainable in the long term in other agricultural systems (Liebman & Schulte, 2015). This is typified by problems such as: pollinator decline (Potts et al., 2010); soil degradation (Koch et al., 2013); and reduction of biocontrol (Chaplin-Kramer & Kremen, 2012). Thus, industrial agriculture has come to rely on increasing anthropogenic inputs that can come at a huge environmental and economic cost (Huang et al., 2018; Sobota et al., 2015). Therefore, it is surely vital to improve current practices in order to maintain biodiversity, ecosystem functioning and ecosystem services to make oil palm more sustainable in addition to conserving natural forest. Pressure on existing forest to be converted to oil palm should be lessened if existing plantations remain viable and productive. If ecosystem multifunctionality and soil quality is maintained on plantation land, this will also act as a safeguard for growing future crops or regeneration of natural or semi-natural habitat.

Current sustainability in oil palm: The RSPO

The Roundtable on Sustainable Palm Oil (RSPO) is a privatised governing body that regulates palm oil certification and aims to make the entire commodity chain more sustainable (Schouten & Glasbergen, 2011). Currently about 20% of global palm oil production is certified sustainable (RSPO, 2017), which has risen from < 4% in 2009 (Laurance et al., 2010). The RSPO has taken a step forward in addressing biodiversity conservation by banning all clearing of primary forest, for oil palm, by its members (RSPO, 2017). Furthermore, certification requires concession owners to avoid establishing plantations on substandard land (Roundtable on Sustainable Palm Oil, 2013), hopefully resulting in less low yielding plantations that result in agricultural abandonment. The RSPO has 8 principles that growers have to fulfil in order to be certified, with 3 that focus on environmental sustainability. These include stipulations on maintaining soil quality, biodiversity, water quality etc. However, these stipulations are very general and open to interpretation. They also include very little detail on how to achieve sustainable practices or when they should be implemented; e.g. “Techniques that minimise soil erosion are well known and should be adopted, where appropriate. These should include practices such as ground cover management, biomass recycling, terracing, and natural regeneration or restoration instead of replanting.” (Roundtable on Sustainable Palm Oil, 2013). The RSPO stresses the importance of conserving areas of natural vegetation and the benefits that these areas bring to biodiversity are assumed to present in nearby plantations (Azhar et al., 2015). However, relatively few certified plantations actually contain natural forest patches (Carlson et al., 2018) and where they do, forest patches are often managed ineffectively, not of sufficient size, or are too degraded to contain higher diversity than an oil pam plantations (Azhar et al., 2015; Lucey et al., 2017). There is no guidance or promotion from the RSPO to increase within-plantation biodiversity by improving management of plantations or restriction of the homogenisation of oil palm landscapes with large-scale monoculture plantations (Azhar et al., 2015). It is maybe not a surprise, therefore, that major criticisms on the legitimacy and efficacy of the RSPO (Carlson et al., 2018; Schouten & Glasbergen, 2011) have arisen.

There has only been one comprehensive case study, to my knowledge, on the efficacy of the RSPO compared to business as usual (Morgans et al., 2018) although there have been other studies that have considered the impact of certification on biodiversity conservation (Carlson et al., 2018; McCarthy & Zen, 2010). Morgans *et al.* (2018) assess the impacts of certification on six of the eight central pillars of the RSPO Principles and Criteria (P&C): conservation of biodiversity; responsible development of new plantings; responsible consideration of communities; consideration of social impacts; economic viability; and commitment to best practice. The authors used as a case study, Indonesian Borneo (Kalimantan), which is a major producer of palm oil and has undergone considerable deforestation for oil palm agriculture (Austin et al., 2015). The environmental sustainability metrics in this the study were limited to Orang-utan presence and density and number of fire incidences in non-certified and RSPO certified plantations. The authors concluded that certification was inadequate in order to improve environmental sustainability and certified plantations performed no better than business than usual, in agreement with other studies (Carlson et al., 2018; Meijaard et al., 2018). Currently, there is limited evidence that the RSPO's certification for sustainable oil palm has had a positive impact on the environmental sustainability of oil palm. However, the RSPO is currently the main hope for the wide scale improvement of oil palm sustainability (Fitzherbert et al., 2008; Morgans et al., 2018; Wilcove & Koh, 2010). In order for this to be effective, it is necessary for the RSPO to develop more specific guidelines for stakeholders regarding sustainable agricultural practices (Morgans et al., 2018), guided by the increasing amount of scientific research on how to oil palm improve management practices (Ashraf et al., 2018; Spear et al., 2018b; Tohiran et al., 2017; Yahya et al., 2017). Furthermore, the baseline conditions of the plantations should be considered when the RSPO audit the efficacy of plantation management practices. Currently, there is a "one size fits all" approach with regards to environmental practices such as limiting deforestation, where oil palm concessions that had no forest to begin with are assessed the same way as areas with high forest cover. Whether roundtable members improve the stringency of criteria for certified plantations and additional aspects of sustainability are considered and incorporated in their guides for agricultural practice will determine oil palm certification's contribution to sustainability. Under its current guise, RSPO certification might be doing more harm than good, as environmentally conscious consumers and companies are misled by the sustainable label.

Biodiversity and ecosystem functioning in oil palm landscapes

Eight years ago, Foster *et al.* (2011) identified the need and potential for maintaining biodiversity and ecosystem functioning within oil palm landscapes. They identified three main ecosystem functions under threat from loss of biodiversity: pollination; biocontrol; and decomposition/soil fertility (of which latter two are addressed in this thesis); and the need for evidence of impacts of biodiversity on these functions, in an oil palm context. Foster *et al.* (2011) stressed the importance of approaching this problem at both a landscape and local scale and proposed several potential solutions in the absence of proper evidence. Potential landscape-scale strategies to enhance biodiversity and ecosystem function included: maintaining forest fragments and native vegetation and installing riparian strips within the oil palm landscape. Local-scale strategies included: enhancing understory vegetation; beneficial plants for biocontrol and maintaining palm epiphytes within oil palm plantations. Since 2011, research on biodiversity and ecosystem functioning within oil palm landscapes has grown rapidly, including on many of the solutions proposed by Foster *et al.* (2011). However, there are still many research gaps, some of which are addressed in the research chapters of this thesis.

Landscape-scale impacts on biodiversity and ecosystem functioning

Perhaps the largest body of research on landscape-scale impacts of oil palm on biodiversity and ecosystem functioning is coming from the Stability of Altered Forest Ecosystems Project (SAFE) in Malaysian Borneo (Ewers et al., 2011). This large-scale project investigates the impacts of forest fragmentation by oil palm on biodiversity and ecosystem functioning both in forest fragments and oil palm plantations and the effects of increasing oil palm cover at the expense of forest. Much of the output so far has been concentrated on the effects of conserving riparian strips (also called riparian zones, fragments or corridors) in oil palm landscapes (Gray et al., 2015; Gray et al., 2014; Mitchell et al., 2018). Riparian strips are uncultivated patches of often natural

vegetation, which surround rivers in oil palm landscapes to reduce flood risk, soil erosion and maintain water quality (Luke et al., 2017). However, they have been proposed as a tool to conserve biodiversity, aid connectivity and boost ecosystem functioning in oil palm landscapes (Gray & Lewis, 2014; Mitchell et al., 2018). Research from the SAFE project suggests that indeed riparian strips can hold significant amounts of forest-associated biodiversity (Gray et al., 2014; Mitchell et al., 2018) but probably fail to boost ecosystem functioning within the plantation due to lack of spillover effects, at least in terms of insect pest-control by birds or dung removal by dung beetles (Gray et al., 2016; Gray et al., 2014). However, riparian strips do provide benefits to ecosystem functions regarding water quality (Luke et al., 2017). The effect of riparian zones on landscape connectivity has yet to be rigorously tested in the SAFE project or otherwise.
Landscape effects on biodiversity have also been explored in other projects, primarily focussing on the impact of forest cover on biodiversity within oil palm dominated landscapes (Gilroy et al., 2015; Koh, 2008b; Prescott et al., 2016a), with the conclusion that increasing forest cover improves species richness of most taxa, particularly forest-associated species. However, there is scant knowledge on how landscape structure i.e. heterogeneity affects biodiversity related ecosystem functions in landscapes dominated by oil palm, although one study suggests possible benefits to pest-control services, based on predation rates in plantations, due to increased habitat heterogeneity (including forest cover) (Nurdiansyah et al., 2016). I systematically investigate the delivery of biocontrol ecosystem services with proximity to forest in chapter 3 of this thesis.

Local scale impacts on biodiversity and ecosystem functioning

Recent research on the impact of management of oil palm plantations on biodiversity and ecosystem functioning at a local scale has been particularly prevalent in Peninsular Malaysia (Ashraf et al., 2018; Asmah et al., 2017; Syafiq et al., 2016; Yahya et al., 2017). Much of this research has focussed on the comparison of industrial plantations with smallholder plantations. Industrial plantations are usually owned by big companies and cover large areas, often thousands of hectares, whereas smallholder plantations are owned by individuals, families or communities and usually cover < 50 ha (Azhar et al., 2014, 2015). Smallholders make up about 40% of the global palm oil production system (RSPO, 2017). Smallholder plantations have been found to contain greater biodiversity than industrial plantations for the majority of taxa studied, due to more “environmentally friendly” practices such as polyculture, reduced use of herbicides and having greater landscape heterogeneity due to their small size situated in a mosaic of other land-use types (Azhar et al., 2015). However, although the positive impact of this biodiversity on ecosystem function has been alluded to (Syafiq et al., 2016; Yahya et al., 2017) it has not been directly tested. There are also potential management regimes that can boost biodiversity within plantations for both smallholders and large-scale plantations. These include alley-cropping (the intercropping of oil palm with a different crop), which can benefit arthropod biodiversity (Ashraf et al., 2018) and cattle grazing as an alternative to herbicides for controlling the oil palm understory, which can increase avian species richness (Tohiran et al., 2017). The authors of these studies allude to potential benefits of increasing biodiversity for ecosystem functioning; however, this was not directly tested. The Biodiversity and Ecosystem Function in Tropical Agriculture programme (BEFTA) (Foster et al., 2014) has a remit that intends to explore the effect of understory vegetation on above and belowground biodiversity and ecosystem function (see chapter 6). This research could provide important and practicable evidence for management of plantations to improve agricultural sustainability.

Bridging the gap

The Experimental Biodiversity Enrichment in Oil-Palm-Dominated Landscapes in Indonesia (EFForTS-BEE) project (Teuscher et al., 2016) is working on bridging the gap between landscape and local scale biodiversity and ecosystem function improvement in oil palm landscapes. They are exploring the potential of increasing habitat heterogeneity in oil palm dominated landscapes by native and non-native tree planting within plantations. The end goal being: improved biodiversity; ecosystem function; and ecosystem services within the plantation and landscape, while minimising economic loss. Early results show benefits to biodiversity (birds and invertebrates), although no change to ecosystem functioning. However the authors expect to see benefit to biodiversity associated ecosystem functions in later results.

Important ecosystem functions remain understudied

Foster *et al.* (2011) identified soil fertility and decomposition as one of the main biodiversity related ecosystem functions under threat in oil palm plantations. Nevertheless, soil biodiversity and ecosystem functioning is largely understudied in oil palm agriculture (Bessou et al., 2017). There is considerable impact upon soil quality and biodiversity after forest conversion to oil palm (Fayle et al., 2010; Guillaume et al., 2015, 2018; Tripathi et al., 2016). However, after initial land conversion, oil palm agriculture is often described as a low input and sustainable crop with regards to soil health (Khasanah et al., 2015; RSPO, 2017). Oil palm plantations actually do need considerable inputs of fertiliser, particularly nitrogen and potassium for plant growth and alkaline inputs to counteract the natural acidity of tropical forest soils (Corley & Tinker, 2016). There are large bodies of research on fertiliser management and regimes under different soils, seasons, elevations and management types (Corley & Tinker, 2016), but these are rarely related to the soil biota. Soil fauna can have large direct and indirect benefits on soil quality and agricultural yield (Bardgett & van der Putten, 2014) and are vital for many ecosystem functions such as nutrient retention, carbon cycling and maintaining plant diversity (de Vries et al., 2013; Wagg et al., 2014). Soil biodiversity is vital in ecosystem multifunctionality in natural and agricultural systems (Bender et al., 2016) and provides many ecosystem services that contribute to human health (Wall et al., 2015). Indeed, enriched levels of soil biota have been found to enhance agricultural sustainability by improving crop yield, nutrient uptake and reduce nitrogen leaching (Bender & van der Heijden, 2015). Furthermore, activity and abundance of soil fauna has been found to positively correlate with other soil characteristics that are beneficial to oil palm yield (increased soil moisture and pH) (Tao et al., 2018). In addition, both soil biodiversity and soil quality in oil palm plantations have been shown to be affected by different management practices and spatial heterogeneity within the plantation (Carron *et al.*, 2015; Carron *et al.*, 2015), however, these have not been explicitly linked. There is urgent need for further research into soil biodiversity and ecosystem function in oil palm plantations in order to ensure sustainability of oil palm plantations

(Bessou et al., 2017). In Paper 2 and 3 of this thesis I investigate the effect of replanting, a ubiquitous management practice in oil palm cultivation on both soil quality and biodiversity.

Biocontrol was also identified by Foster *et al.* (2011) as being an ecosystem function under threat from biodiversity loss. Oil palm plantations are affected from a variety of pests e.g. rats, caterpillars or fungi that can either inhibit plant growth or directly feed on oil palm fruit (Wood, 1971). Barn owls are perhaps the most well-known biocontrol agents in oil palm plantations, but are actually a vagrant species, whose abundance is increased by human intervention to control rats (Puan et al., 2011). However, for the purpose of this thesis I will just discuss natural agents of biocontrol, focussing on insect pests. Oil palm is attacked by a number of insect pests, with bagworms (of the moth family Psychidae), nettle caterpillars (Limacodidae) and the rhinoceros beetle (*Oryctes rhinoceros)* probably being the most economically damaging (Wood, 2002). Biocontrol of insect pests is an environmentally friendly alternative to using insecticides and can result in better long-term pest suppression as natural insect predators are not harmed by the spread of insecticides (Wood, 1971). However, so far, most studies on biocontrol have focussed on the introduction of exotic biocontrol agents rather than factors affecting the efficacy of natural predators as biocontrol agents (Nurdiansyah et al., 2016). Studies investigating natural pest suppression or the influence of predator biodiversity on biocontrol have been somewhat inconclusive or show contradictory findings (Denmead et al., 2017; Koh, 2008a). Insectivorous birds are often described as important agents of pest-control in scientific literature (Pejchar et al., 2018). However, they are negatively affected by forest conversion to oil palm and by intensive oil palm agricultural practices and are of conservation concern (Azhar et al., 2011; Srinivas & Koh, 2016; Yahya et al., 2017). Therefore, birds are an interesting study taxon when exploring factors affecting biodiversity and ecosystem functioning in oil palm landscapes. Two studies have explored the role of birds as insect pest-control agents in oil palm plantations, with one finding a large positive effect (Koh, 2008a) and the other, no effect (Denmead et al., 2017). However, both studies measured suppression of oil palm herbivores by exclusion studies. A large drawback of both these methods is the potential to be confounded by the exclusion of other insectivorous animals (reptiles, mammals), which could play a role in pest suppression. Furthermore, neither can address the potential for birds to suppress pests at a plantation level. Exclusions only cover a limited area, therefore, excluded branches or palms could still benefit from larger-scale pest suppression from birds elsewhere in the plantation. In chapter 3 of this thesis, I carry out the first study, to my knowledge, which directly explores if birds consume oil palm pests and the effect of nearby forest cover on this ecosystem service.

Research objectives and chapter outline

My meta-analysis (Ashton-Butt *et al.* in review), along with a considerable body of previous research has identified the impact that forest conversion to oil palm plantations can have on biodiversity and ecosystem function (Dislich et al., 2016; Foster et al., 2011; Koh & Wilcove, 2008; Savilaakso et al., 2014). In this thesis, my aim is to identify factors which influence biodiversity and ecosystem functioning within oil palm dominated landscapes, both positively and negatively. I have conducted research on five facets of this overarching aim and have presented this research as five independent research articles. These five facets are: species richness and abundance loss after forest conversion to oil palm; the diet of forest-associated and generalist birds and associated pest-control service provision in oil palm plantations; the effect of oil palm replanting on soil quality; the effect of replanting on soil biodiversity; and the effect of understory vegetation on soil biodiversity and ecosystem function. To conclude the introduction to this thesis, I will lay out the background and objectives behind these five research facets.

Background, chapter 2: Although attempts have been made to quantify average losses of species richness and abundance after conversion of forest to oil palm, previous efforts have been hampered by low sample sizes (Saavilakso et al., 2014).

Objective, chapter 2: To quantify average change in species richness and abundance after primary forest conversion to oil palm plantation through a meta-analytic approach. Furthermore, to quantify number of papers published on biodiversity in oil palm plantations and describe global forest loss to oil palm plantations.

Background, Chapter 3*:* Forest conversion to oil palm results in a loss of species richness, with birds suffering a heavier loss than some other taxa (chapter 2). Furthermore, forest biodiversity can be negatively affected by the impacts of the surrounding landscape i.e. oil palm plantations (Luskin et al., 2017; Scriven et al., 2015; Sodhi et al., 2010). Despite much research into the effects of oil palm and related landscape factors (including forest cover) on bird species richness, abundance and community composition (Gilroy et al., 2015; Hawa et al., 2016; Yahya et al., 2017), to my knowledge, there has been no study investigating the diet of forest and non-forest birds in oil palm landscapes. In addition, the potential pest-control services that forest-associated and generalist birds may bring and the effect of proximity to forest, is still under debate. Proximity to forest can aid bird-mediated pest-control services in other agricultural systems, such as coffee, probably due to spillover effects of forest birds (Karp et al., 2013; Milligan et al., 2016).

Objective, Chapter 3: To assess the diet and ecosystem service provision of forest and generalist birds in oil palm landscapes and the extent to which plantations act as a barrier to forest bird movement.

To investigate this, I set up 33 transects to sample birds from the edge of a large peat-swamp forest bordering oil palm plantations to 1.5km away from forest. Bird diet and insect pest-control services of forest-associated and non-forest birds were assessed by mist-netting birds and taking faecal samples at the forest/plantation edge, 100m and 300m inside the plantation. Oil palm pests were also collected systematically and opportunistically in plantations to identify the common pests located in the study site. In addition, birds were sampled by point counts at the forest/plantation edge, 100m, 300m and 1.5km inside the plantation to elucidate the extent to which oil palm plantations form a barrier to forest birds. Bird diet and associated pest-control services was investigated by DNA extraction and next-generation sequencing of bird faecal samples. Similarity of bird species' diet and bird diet with distance to forest was assessed by Bayesian correlated-response models and pure latent-variable models (Hui, 2016). Overall bird species richness, abundance and forest-associated bird abundance from distance to forest was explored by mixed models (linear and generalised mixed models).This research advances our understanding on diet, niche differentiation, pest-control services and connectivity for birds in oil palm landscapes.

Background, Chapter 4: Replanting occurs roughly 25 years after oil palm is initially planted, because of a drop of yield and the difficulty of harvesting the fruit bunches due to the increasing height of the palm (Corley & Tinker, 2016). 12 million ha of oil palm could potentially be replanted by 2028. Replanting involves removing all vegetative coverage by heavy machinery causing soil compaction and leaving soil bare (Goh & Chew, 2000). After deforestation, which negatively impacts soil quality (Guillaume et al., 2015), the soil of first generation oil palm planted on mineral soils is relatively stable throughout its 25 year lifetime (Khasanah et al., 2015). However, the effects of replanting on soil quality has not been investigated on mineral soils and therefore, the long-term sustainability of oil palm agriculture, with regards to soil, is not known.

Objective, Chapter 4: To quantify the effect of oil palm replanting on soil quality.

To investigate this, I collected soil quality data from a plantation in Sumatra, Indonesia over a 7-year chronosequence from non-replanted oil palm (converted directly from logged forest) to freshly cleared, 1-year-old, 3-year-old and 7-year-old replanted oil palm. I collected soil from plantations at each stage in the chronosequence and measured 9 indicators of soil quality: SOC, soil water content (SWC), total nitrogen (N), C/N ratio, available phosphorous (P), pH, cation exchange capacity; aggregate stability and soil macrofauna diversity. With this data I used mixed models and structural equation modelling to investigate the effect of replanting on soil quality and the driving factors behind this change. The findings of this work have implications for oil palm and soil sustainability, climate change and future oil palm management.

Background, Chapter 5: Oil palm replanting is likely to impact upon biodiversity due to the large-scale changes in vegetation structure and microclimate (Kurz et al., 2016; Luskin & Potts, 2011). Soil biodiversity could be particularly badly affected due to physical and microclimatic perturbations to the soil. Furthermore soil biodiversity is key for soil functioning (Wurst et al., 2012) and could play an important role in soil rehabilitation (Bardgett & van der Putten, 2014).

Objective, Chapter 5: To quantify effect of oil palm replanting on soil biodiversity

To investigate this, I collected soil macrofauna biodiversity (ordinal richness and abundance) data from a plantation in Sumatra, Indonesia over a 7-year chronosequence from non-replanted oil palm (converted directly from logged forest) to freshly cleared, 1-year-old, 3-year-old and 7-year-old replanted oil palm. I collected invertebrates from soil monoliths, using a modified method from the handbook of tropical soil biology (Bignell et al., 2008) from each stage in the chronosequence and counted and identified invertebrates to order (or other relevant taxonomic status). Mixed models (linear and generalised mixed models) were used to assess the effect of replanting on ordinal richness and abundance. Furthermore, predictive models for multivariate abundance data were used to assess difference in soil macrofauna community composition before and after replanting. The findings of this work has implications for conservation of soil biodiversity and for agricultural and soil sustainability in oil palm landscapes.

Background, Chapter 6*:* Better management of oil palm plantations is needed to improve soil biodiversity and ecosystem functioning within plantations. However, research on how management impacts upon this is scant (Bessou et al., 2017). Understory vegetation can be rather diverse in oil palm plantations due to long lived and perennial nature of the crop (Foster et al., 2011). However, herbicide use in oil palm plantations is common in order to keep plantations “clean” (Tohiran et al., 2017). Herbicide use can be variable with plantations completely free of understory vegetation, just paths and the area around the palms (weeded circle) cleared or no herbicides used.

Objective, Chapter 6: To quantify the effects of understory vegetation on soil biodiversity and ecosystem function

In order to investigate this, I sampled soil macrofauna ordinal richness and abundance, abiotic indicators of soil quality and litter decomposition rates in three understory vegetation treatments.

These treatments were installed as part of the BEFTA project (Foster et al., 2014) and consisted of 3 replicate blocks of each of a reduced understory treatment (heavy herbicide use), normal understory treatment (intermediate herbicide use clearing the paths and weeded circle of vegetation) and enhanced understory treatment (no herbicide use and some manual clearance of understory vegetation from the paths and weeded circle). Soil macrofauna ordinal richness and abundance was sampled using a modified soil monolith method from the handbook of tropical soil biology (Bignell et al., 2008) and litter decomposition rates were investigated by installing bags filled with a known mass of oil palm fronds and measuring mass loss after a fixed period of time. Mixed models (linear and generalised mixed models) were used to assess the effect of understory vegetation on ordinal richness and abundance, in addition to, soil abiotic variables and litter decomposition rates. Furthermore, predictive models for multivariate abundance data were used to assess difference in soil macrofauna community composition between treatments. The findings of this work have important implications for management and herbicide use in oil palm plantations for the conservation of soil biodiversity, soil function and soil sustainability.

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Chapter 2: Impact of forest conversion to oil palm on species richness and abundance: a meta-analysis

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ABSTRACT

Research into the biodiversity decline associated with forest cover loss due to oil palm expansion has greatly increased in the last ten years. However, current rates of deforestation remain high, despite the growing attention from scientists, governments, NGOs and the media. Here we present the most up to date analysis on the ability of oil palm plantations to support tropical biodiversity, by meta-analysis. The results show that across all studies, regions and taxa, forest conversion to oil palm plantation results in a loss of total species richness and abundance by 45% and 38%, respectively. Species composition was also largely different in oil palm compared to forest with at least 60% of forest bird 70% of bat, 80% of small mammal and 85% of primate species being absent in oil palm. These results highlight the profound changes that occur across all taxonomic groups when forest is converted to oil palm. The change in species composition and richness is more marked than abundance, likely due to more disturbance-tolerant species showing hyper-abundant populations within oil palm plantations. These results emphasise the limited ability of oil palm plantations to support tropical biodiversity and conserve forest species and the vital importance of protecting remaining forest habitats.

Keywords: Biodiversity; deforestation; oil palm; sustainability; meta-analysis

Introduction

Oil palm cultivation remains one of the dominant drivers of forest loss across the tropics, with many countries experiencing over 75% increase in land area under oil palm since 2006 (Table 1). It is only in recent years that detailed estimates on the role that oil palm expansion has had on rainforest loss have been made. Southeast Asia is the most affected region: in Indonesia, Malaysia and Papua New Guinea alone, palm oil production contributed to an average of 0.3 million $ha^{-1-}y^{-1}$ of deforestation from 2001 to 2011 [1]. Oil palm expansion in the Neotropics has seemingly resulted less from direct forest loss, but conversion from other land use types. Furumo and Aide (2017) report that 270,205 ha (79%) of the total area planted with oil palm (342,032 ha) in Latin America between 2000 and 2014, was situated on non-forested land (mainly cattle pastures). This means that 21% (71,828 ha) of this expansion has still come at the expense of forests, particularly in the Amazon and northern Guatemala [2]. Peru, specifically, experienced the highest rate of deforestation in the Neotropics due to oil palm cultivation (76% from direct forest loss), amounting to 15,685 ha [2,3].

Table 1. FAO data of land area under oil palm production in 2006 and 2017 by country or region [4]

Country or Region	**Area under oil palm production in 2006 (ha)**	**Area under oil palm production in 2017 (ha)**	**Change in area under production (%)**
Angola	23000	23269	1
Benin	22000	39149	78
Brazil	96509	111233	15
Burundi	5500	8750	59
Côte d'Ivoire	219233	354236	62
Cambodia	13636	14732	8
Cameroon	72000	170169	136
Central African Republic	3000	650	-78
China	45000	50826	13
Colombia	165000	280344	70
Congo	10800	11876	10
Costa Rica	48406	72856	51
Democratic Republic of the Congo	169654	178998	6
Dominican Republic	19480	30880	59
Ecuador	143348	260292	82
Equatorial Guinea	3500	3508	0
Gabon	4000	4460	12
Gambia	3500	3509	0
Ghana	333000	364595	9
Guatemala	45000	151000	236
Guinea	310000	315053	2
Guinea-Bissau	9500	9620	1
Honduras	80000	180000	125
Indonesia	4110000	9277690	126

Liberia	17000	18135	7
Madagascar	1800	1812	1
Malaysia	4165215	5110713	23
Mexico	22033	65805	199
Nicaragua	2500	7430	197
Nigeria	3075000	3037291	-1
Panama	6800	4374	-36
Papua New Guinea	92000	177779	93
Paraguay	13130	14840	13
Peru	10906	58951	441
Philippines	31444	60069	91
Sao Tome and Principe	1600	1931	21
Senegal	7000	12035	72
Sierra Leone	24000	27478	14
Solomon Islands	10000	20000	100
Suriname	550	593	8
Thailand	379872	756630	99
Togo	14100	18109	28
United Republic of Tanzania	4500	5460	21
Venezuela	25252	37191	47
Eastern Africa	11800	16022	36
Middle Africa	287554	394861	37
Western Africa	4034333	4199210	4
Central America	204739	481465	135
South America	454695	763444	68
Oceania	102000	197779	94
Eastern Asia	45000	50826	13
South-Eastern Asia	8700167	15219834	75
World	13859768	21354320	54

There remains very little quantitative research on deforestation for oil palm agriculture in Africa. West Africa and Central Africa have shown a recent rise in oil palm cultivation, a trend which also coincided with a rise in forest losses in Sierra Leone, Cote d’Ivoire, Congo, Liberia and Cameroon, amongst others [5]. Vijay et al. (2016) suggest that, since 1989, only a small proportion of area of oil palm was planted on previously forested land in five African countries (Cameroon, Ivory Coast, Ghana, Democratic Republic of Congo and Nigeria). However, less than 5% of the oil palm harvested area in these countries was cross-checked for deforestation, making it possible that a higher proportion of oil palm was planted on forested land. Based on a survey of 546 oil palm farms in Cameroon, 73% of producers admitted to clearing forest to plant oil palm, especially large-scale plantations employing a more commercialised system [6]. Unless there is strong and sustained opposition by governments, NGOs, large palm oil buyers or consumers, a considerable deforestation in Africa to make way for oil palm cultivation in the coming years is expected [6–8]. Mosnier *et al.*, (2015) predict that 15% of all deforestation in Central Africa between 2020 and 2030 will be due to oil palm expansion. Interestingly, discrepancies among studies [7,10] suggest that the scientific community still struggle to assess accurately, previous land-use types for newly developed oil palm areas, due to lack of land-use data in some regions.

Forest conversion to oil palm has a detrimental effect on biodiversity [11–14]. This has long-term implications for the future resilience of tropical ecosystems; biodiversity can sustain ecological processes [15,16], underpins the delivery of ecosystem services [17], contributes to global food security, environmental sustainability and supports greater ecosystem resilience against environmental change [18–20].

Here, we assess publication trends on biodiversity research relating to oil palm plantations from 1970 to 2017 by quantifying papers published per country in order to identify global research hotspots and gaps. We also provide the most recent and comprehensive analysis of species richness, abundance and community composition change when forest is converted to oil palm. Although a number of reviews have been carried out, the rapid recent expansion in the oil palm literature across a broad range of taxonomic groups makes this a timely moment to re-examine findings and assess the overall impact of oil palm expansion on biological communities. Furthermore, due to the greater number of publications available, we are able to analyse change in biodiversity for more specific faunal groups than was previously possible, i.e. Birds, Invertebrates, Herpetofauna and Mammals.

Results and Discussion

Malaysia and Indonesia are oil palm biodiversity research hotspots

Prior to 2008, when Fitzherbert *et al.*(2008) published the first full review of biodiversity loss after forest conversion to oil palm, there were only 27 papers relating to oil palm's impact on biodiversity. From 2008-2017 an additional 143 papers were published on the subject. The majority of these studies took place in Malaysia (72) and Indonesia (21) (Fig. 1). However, there has been a considerable increase of publications from the Neotropics, perhaps in response to the recent boom in oil palm agriculture. The biodiversity research associated with Neotropical oil palm has not only focussed on the conversion of forest to oil palm but also on the impacts of conversion from other land use types such as grazing pastures [22,23], reflecting the nature of land use change in that region. Despite the increase in oil palm area in Africa, research on only four published, primary research papers was conducted on the biodiversity impacts of oil palm agriculture in Africa since 2008 [24–27]. This may reflect the slower growth of the oil palm industry in region or underlying global biases in biodiversity research and literature [28].

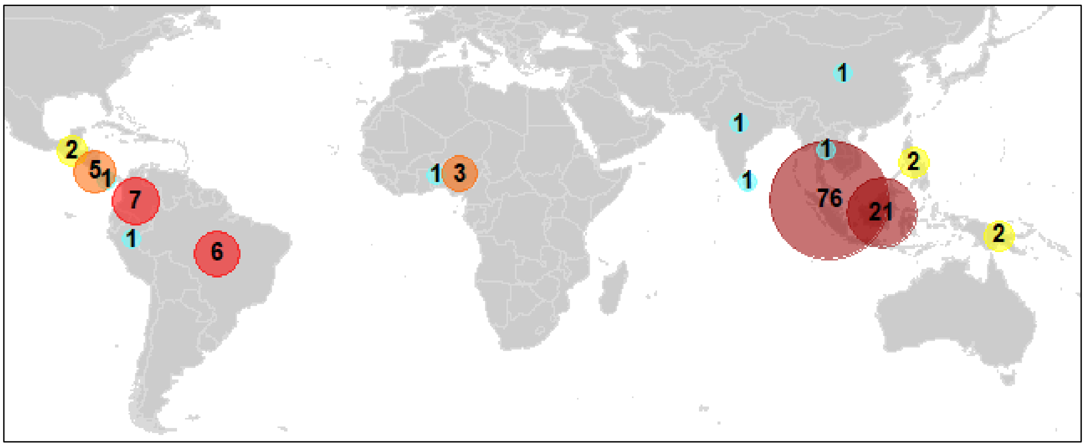

Figure 1. Research hotspots of oil palm biodiversity research. Number of published studies investigating biodiversity in oil palm plantations, per country of data collection, from 2008-2017 (studies that span regions or multiple countries are not shown). Figure designed in R [29] *using the packages: "ggmap"* [30]*and "ggplot2"* [31]

In terms of the taxonomic focus the diversity of taxa investigated has broadened, with studies focussed on bats, microbes and fungi amongst others published between 2008 and 2017. By far the most common taxa studied were Birds (33 papers) and ants (23 papers), whereas we only identified one study that assessed plant diversity [32].

Tropical forest conversion to oil palm plantation reduces biodiversity

After initial screening there were 59 studies that reported species richness, abundance or community composition in primary forest and oil palm. From these studies 24 were suitable for comparing species richness, contributing 43 samples, as different taxa from the same study were counted as different data points. Eight studies were suitable for comparing abundance, totalling 21 samples. For species composition change after forest conversion to oil palm plantations, there were 28 studies that published species list or composition change between habitats. It should be noted that many studies failed to report plantation age when sampling, which can affect levels of biodiversity [33] (see SI).

Species Richness

The overall mean LRR of species richness compared between primary forest and oil palm plantations was -0.598 (95% CiLb = -0.753, CiUb = -0.443); indicating that on average, species richness is 45% lower in oil palm plantations than primary forest (Fig.2). For subgroup analyses, species richness was lower in oil palm for all taxa studied, with an average 57% decline in bird species richness (LRR = -0.84, K=6), an average 45% decline in mammalian species richness (LRR=-60, K=6), an average 47% decline in invertebrate species richness (LRR = -0.63, K=23) and an average 32% decline in herpetofauna species richness (LRR=-0.38, K=6).

Abundance

Overall, mean abundance was 38% lower in oil palm than forest (LRR = -0.563 CiLb = -1.06 , CiUb = -0.065) (Fig.3). However, neither mean abundance in vertebrates or invertebrates decreased significantly after subgroup analysis. This suggests that although overall, mean abundance is lower in oil palm plantations than in forest, there is considerable variation, with some studies reporting increases in abundance of groups such as Collembola and Diptera [34]. In addition, between some studies, both declines and increases in abundance of the same taxa are shown. Possible reasons for these differences are heterogeneity between sites thorugh management of plantations or geographic location, difference in sampling methods and/or the hyper-abundance of some disturbance tolerant taxa [35].

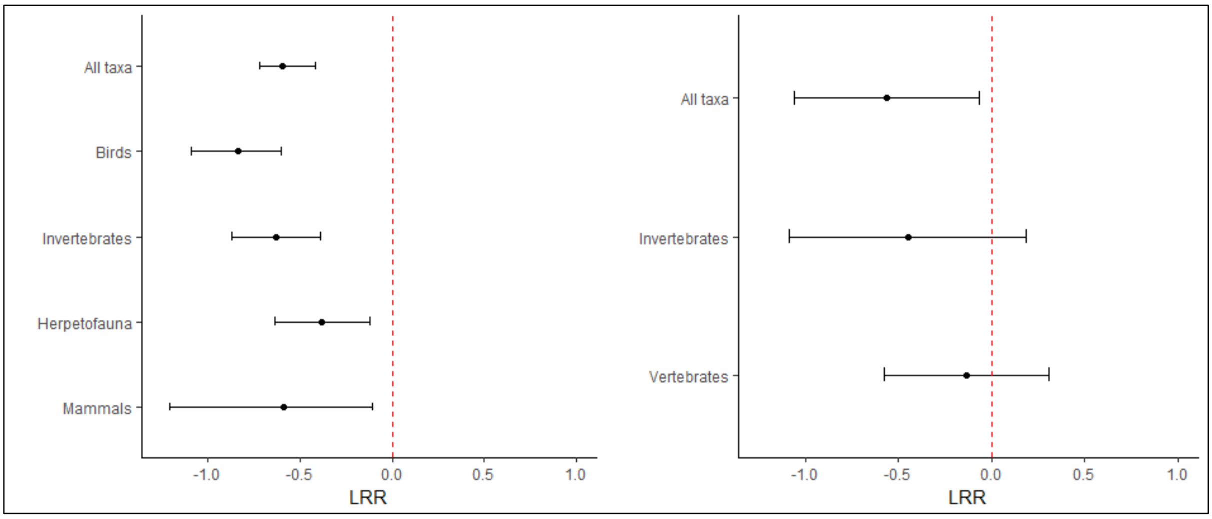

Figure 2. Forest plots of species richness (left) and abundance (right) change between primary forest and oil palm. LRR is the log ratio response, where 0 represents no change in species richness or abundance. All taxa is the mean effect size for all samples.

Species composition

In all studies, bar one (on mosquitos [36]), species composition was different in oil palm plantations to forest (Fig. 3). Vertebrate species composition seemed to be particularly affected: 60% of bird, 70% of bat, 80% of small-mammal and 85% of primate forest species were lost in oil palm plantations. Ant species composition change was much more variable, ranging from 20-80% of forest species lost, likely reflecting the sampling method and microhabitat sampled for the individual studies [37–40], in addition to some ant species' tolerance to disturbed habitats [41].

Figure 3. Species composition change between primary forest and oil palm. The figure shows the proportion of forest only species, oil palm only species and species shared between both habitats, recorded in each study (one bar represents one study).

Our results clearly demonstrate that oil palm plantations are able to support considerably lower species richness and abundance compared to forest, across the majority of taxa studied. Species richness was clearly reduced in taxonomic groups that could be modelled separately: birds, mammals, herpetofauna and invertebrates. However, despite the rapid increase in oil palm biodiversity literature, plants and fungi remained understudied. Oil palm plantations also have a profoundly different species composition to forest. The change in species composition between forest and oil palm highlights the unsuitability of oil palm plantations for the majority of forest species [13,21,42]. This likely explains the more mixed effects on faunal abundance in oil palm plantations after forest conversion; where forest species are replaced by disturbance tolerant, hyper-abundant and often invasive species such as the ant, *Tetramorium bicarinatum* (Nylander) [38] and the earthworm, *Pontoscolex corethrurus* (Müller, 1857) [43]. Furthermore, this highlights that the detrimental effects on biodiversity found in this study are conservatively estimated, as we could not show the likely severe ecological changes due to forest conversion to oil palm with the data available to us.

Our findings corroborate those of previous studies that state oil palm agriculture is one of the highest contributors to biodiversity loss per unit area, globally [44]. Worryingly, there is growing evidence that remaining forests continue to be degraded by ecological impacts that cross the boundaries of agricultural land of adjacent oil palm plantations [45].Therefore, it is essential to adopt a landscape approach in efforts to conserve biodiversity in areas containing oil palm, that promotes forest conservation and connectivity alongside long-term agricultural sustainability.

Methods

To assess the current state of biodiversity research associated with oil palm plantations we conducted a literature search for studies published between 1970 and 2017) using systematic review guidelines [46] (see supplementary info for a detailed methodology). The databases and search engines used were: ISI Web of Science; Scopus; Google Scholar; CIFOR; CIRAD-Agritrop; and sustainablepalmoil.org. To assess publication trends since the first major oil palm biodiversity review in 2008 [21]publications were quantified as papers published between 2008 and 2017, per country, based on location of research site.

Meta-analysis on the biodiversity loss of forest conversion to oil palm

From the literature search; studies that addressed the question: “What is the impact of primary forest conversion to oil palm plantation on species richness and abundance?” and met the inclusion criteria were selected for meta-analysis. The criteria for inclusion were: The ability to access (either from the paper itself or from the author) the actual mean values (not rarefied values), the sample number, and standard deviation for species richness and abundance for both primary forest (control) and oil palm (treatment).

The log response ratio (LRR) was chosen as the metric to calculate effect size. LRR is an intuitive effect size measure for these data as the effect size of the treatment (e.g. species richness of oil palm plantations) is calculated as a ratio of the control (e.g. species richness of primary forest). This allows for an overall percentage change in species richness or abundance to be calculated from the control (primary forest) to the treatment (oil palm). The LRR also does not require the calculation of a standardised mean difference, which can be problematic when calculating an effect size for biodiversity data. This is because the method assumes that any differences in standard deviations among studies are in the scale of measurement and not differences in variability amongst study populations [47]. LRR can be biased when sample size is small, however, when the control is larger than the treatment the effect size is likely to be underestimated resulting in any negative effect size estimates being robust but conservative [48].

All analyses were carried out in R (version 3.3.1), using the package “Metafor” [49]. A random-effects model (REML) was chosen to estimate effect size. This assumes that the true effect size differs between experiments and that the estimated summary effect is an average of effects across samples. Different taxa from the same study were treated as independent samples, as were the same taxa collected by different methods. Along with the effect size, 95% confidence intervals (CI) were estimated. If the upper and lower confidence intervals did not intersect zero then the estimated effect was considered to have a true effect. Log responses were back transformed to the LRR, allowing for the effect size to be described as percentage change. Two models were run for the species richness data set: A REML on all samples and a REML with subgroup analysis running mammals, birds, invertebrates and herpetofauna in their own analyses. These groups were chosen as there was sufficient data to run separate analyses on these taxonomic divisions. For abundance, owing to fewer studies recording abundance and a resulting reduced sample size, a REML was run on all samples and subgroup analyses was carried out on vertebrates and invertebrates only. Funnel plots and a plot of study sample size against effect were conducted to check for publication bias against positive results. If publication bias exists there should be a negative relationship between sample and effect sizes [50]. There was no trend between sample size and effect size indicating no publication bias. In addition, a funnel plot of log ratio of means showed no clear selection bias either way.

Species composition was compared between forest and oil palm plantations for studies that reported the species list sampled in forest and oil palm or the species richness in each habitat along with species number found in both habitats. Species were classified as forest only, shared (present in both habitats) and oil palm only species and plotted on a study by study basis as a proportion of the total number of species per taxa reported in the three habitats.

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Data Availability

All data generated or analysed during this study are included in this published article (and its Supplementary Information files).

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Author contributions

A.A-B designed and conducted the study and wrote the paper. K.S-H.P and J.L.S discussed the results and directed the study. E.C.T helped with study design and discussion of results. S.S. provided data and helped with study design. B.A. and G.M.P were involved in formulating the study question and all authors read and were involved in writing the final manuscript.

Competing Interests

The authors declare no competing interests.

Chapter 3: Spillover and ecosystem service provision of forest birds in oil palm plantations: evidence from DNA metabarcoding

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Abstract

Currently, over 13 million ha of oil palm cover the tropics, with this area predicted to expand in the coming years. Oil palm expansion has had a huge impact on biodiversity and ecosystem functioning because of deforestation. Birds are of particular conservation concern, due to the large decline of species richness in plantations, in particular, forest-associated birds. However, the reasons behind this are poorly understood. In order to assess the conservation value of oil palm plantations to forest birds: we conduct the first study to systematically sample forest and generalist birds in oil palm plantations with increasing distance to forest; and the first metabarcoding of insectivorous forest-associated and non-forest bird diet in oil palm plantations. Furthermore, we examine whether birds provide an insect pest-control service in oil palm plantations. We find that oil palm plantations act as a significant barrier to forest birds, with only some individuals from few species penetrating beyond 100 m into plantations. In addition, forest, forest-edge and non-forest bird species have large dietary overlap in plantations, likely because of low niche-space for birds due to lack of resource complexity; one of the probable mechanisms responsible for the exclusion of many bird species from oil palm plantations. Furthermore, we found no evidence for any insect pest-control service by forest or non-forest birds in oil palm plantations. Our findings show that oil palm plantations have little conservation value for forest birds and connectivity between remaining forest patches is likely inhibited by the presence of oil palm plantations. The simplification of tropical landscapes by plantations forces a generalist dietary approach on insectivorous birds, leading to the exclusion of more specialist, forest-associated species.

Introduction

Between 1990 and 2017, the area of land under oil palm cultivation has expanded from 6 million ha to over 21 million ha (FAOSTAT, 2017). Much of this land was converted directly or indirectly from forest. This conversion has had a devastating impact on tropical-forest biodiversity as many animals and plants associated with these forests are unable to survive in oil palm plantations (Meijaard et al., 2018). Birds are one of the most affected taxa, experiencing an average 57% decline in species richness, after forest conversion to oil palm (Ashton-Butt et al. in review). Forest-associated birds are less likely to be found in oil palm plantations (Azhar et al., 2011; Gilroy et al., 2015; Senior et al., 2013) and decline in abundance with distance to forest (Azhar et al., 2013; Prescott et al., 2016a). Further conservation concerns have arisen due to the increased fragmentation of declining bird populations because of expanding oil palm plantations (Edwards et al., 2013; Gilroy et al., 2015), causing isolation of forest patches (Edwards et al., 2010; Fitzherbert et al., 2008). Landscape connectivity in fragmented habitats is necessary for maintaining gene flow between populations; providing foraging habitats for wide ranging animals; and maintaining ecosystem resilience under climate change (Braaker et al., 2014; Jiguet et al., 2007; Şekercioğlu et al., 2015; Stork et al., 2009). Native biodiversity in remaining forest patches can also be degraded by proximity to oil palm plantations; a recent study found that the hyper-abundance of wild pigs in oil palm plantations can spillover to neighbouring forest and cause a decline in seedling survival (Luskin et al., 2017).

Due to these negative consequences of oil palm plantations, there has been a large recent push for sustainable palm oil certification by consumers, non-governmental organisations (NGOs) and large companies (Lim et al., 2015), particularly with regards to conserving natural habitat, to protect biodiversity (Meijaard et al., 2018). Furthermore, it has been suggested that enhancing biodiversity in the oil palm landscape could improve yield and lower production costs by providing ecosystem services, such as biological control (Foster et al., 2011). However, the contribution of palm oil certification to protecting biodiversity, has been heavily criticised due to lack of positive impact (Carlson et al., 2018; Morgans et al., 2018). Partly due to lack of guidance and incentives for the plantation owners to implement better management, in order to protect biodiversity (Azhar, Saadun, Prideaux, & Lindenmayer, 2017)

To assess the effects of oil palm plantations on forest species and prevent further erosion of biodiversity, within oil palm landscapes, it is vital to know how both forest and non-forest species utilise the landscape (Bennett et al., 2014; Haas, 1995). However, little is known on this subject, particularly with regards to the ability of forest birds to utilise oil palm and the feeding strategy and diet of birds in plantations. The capacity of a novel, converted habitat to supplement the diet of species of conservation concern is often used to assess the conservation value of a landscape (Capmourteres & Anand, 2016). For example, non-forest bird species proliferate in oil palm plantations, probably due their ability to utilise the resources more effectively than more specialist forest-associated species (Prescott et al., 2016b; Srinivas & Koh, 2016). Insectivorous birds species richness is particularly low in oil palm plantations (Azhar et al., 2013; Peh et al., 2005), possibly due to the reduced diversity of insects after forest conversion to oil palm plantations (Gilroy et al., 2015; Wang & Foster, 2015). However, the diet of insectivorous birds in oil palm has been little studied.

The diet of birds that forage in oil palm plantations could also be important for biological-control (Nurdiansyah et al., 2016). Pest-control services, particularly of insect pests, are widely cited as an ecosystem service that birds provide in agricultural settings which can be enhanced by proximity to natural habitat (Pejchar et al., 2018). However, the importance of pest-control services by birds and the impacts of nearby forest on pest-control in agriculture is disputed (Pejchar et al., 2018). Indeed, the net result is often context-dependent, as in the case of coffee plantations, which can experience differing levels of benefit from bird-mediated pest control depending on proximity to forest, plantation type and landscape factors (Milligan et al., 2016; Railsback & Johnson, 2014). Gray and Lewis, (2014) found that although over 20% of artificial, insect pest baits were attacked by birds, this was not affected by the presence of small, riparian forest fragments. Studies investigating bird-mediated pest-control of insects in oil palm plantations, using exclusion experiments, have reached contradictory conclusions; either finding that birds offer a significant pest-control service (Koh, 2008), or that birds offer minimal protection against insect herbivores (Denmead et al., 2017). Furthermore, these studies cannot differentiate between forest and generalist species and can be conflated by the impact of other predators (e.g. mammals , reptiles) on insect pests.

Here, we systematically sample bird communities in oil palm plantations with increasing distance to the forest edge. Using this method, we quantify the spillover distance of forest-dependent birds in oil palm plantations. Furthermore, using DNA metabarcoding, we investigate the diet of birds in oil palm landscapes and how this differs in generalist and forest-associated bird species with proximity to forest, using Bayesian latent variable models (Hui, 2016). We also explore whether birds consume insect pests in oil palm plantations, and any spillover effects of forest birds. We hypothesise that forest bird abundance will decline with distance to forest, particularly less mobile understory specialists. Furthermore, we predict that insectivorous bird diet will become less diverse with distance to forest, due to the reduction in forest-associated insect species in the birds' home range.

Methods

Study area

We conducted our study on the west coast of Selangor, Peninsular Malaysia in oil palm plantations adjacent to the North Selangor Peat Swamp Forest (NSPSF). The NSPSF covers ~78,000 ha of logged mixed peat swamp forest (95%) and lowland dipterocarp forest (<5%). Commercial logging in the NSPSF ceased 25-40 years ago, but pockets of the forest remain pristine and have never been logged. The NSPSF is the second largest peat swamp forest on the peninsula. The oil palm estates covered a mixture of smallholder and large-scale plantations, established in the area between 3 and 40 years ago. Fieldwork took place from April to August 2018, during the dry season. We established 33 transects around the NSPSF. Each transect was 1500 m long, started at the forest/plantation boundary and went directly away from the forest into oil palm plantations. We sampled at points four points along the transect: 0 m (the plantation edge nearest the forest), 100 m, 300 m and 1500 m away from the plantation edge (Fig. 1). The start of transects was selected by randomly choosing from grid squares along the NSPSF edge, on either the North or South side of the NSPSF. The Western edge was surrounded by paddy fields and the Eastern edge was inaccessible. A road and a man-made waterway or river (total approximately 10–50 m wide) were always present between the forest edge and plantation; typical features of oil palm plantations bordering peat-swamp forest, for vehicular access and water drainage, respectively.

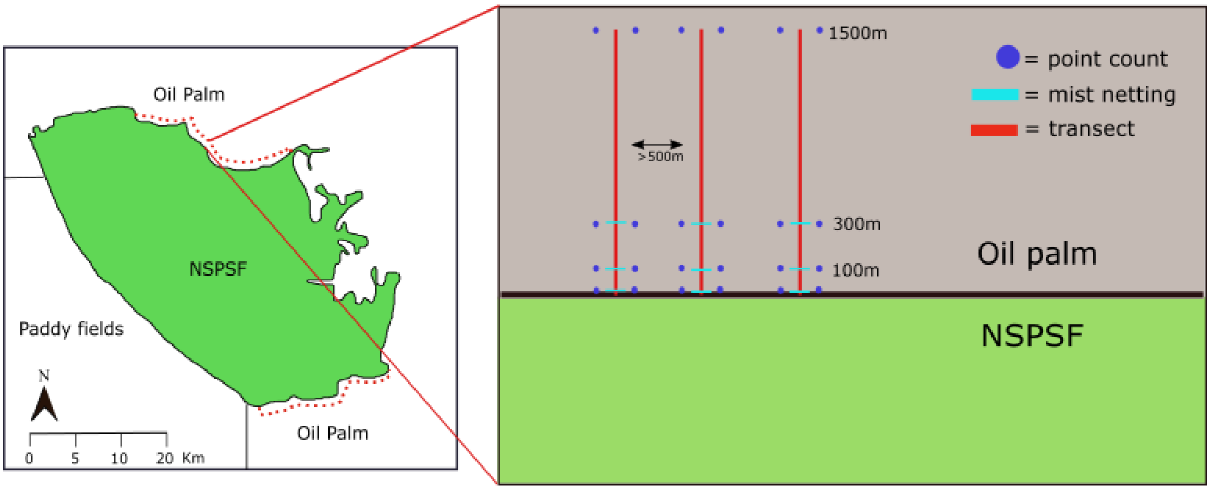


Figure 1: Sampling and transect design of the study. Red dotted lines on the map signify the extent of the forest/oil palm boundary sampled.

Bird Sampling

Bird were counted on all 33 transects at each of the four points along the transect (0 m, 100 m, 300 m and 1500 m) by 10-minute duration point counts (Bibey et al.2000). Two point counts were taken 100m west and 100m east of each transect, 200m apart from each other (see Pearman, 2002; Whitman et al., 1998), resulting in a total of 264 point counts. Transects were 500m apart from each other. All point counts were conducted from 07:00 hours to 10:00 hours. Birds were detected visually or acoustically within a 50 m radius of each sampling point were recorded and distances checked by a Bushnell laser range finder, if necessary. The same researcher conducted all point counts. Vegetation structural data was also recorded, including: palm height, ground vegetation percentage cover (estimated by eye), ground vegetation height (measuring 3 vegetation points by the point count start with a tape measure and averaging height), number of dead palms and number of non-oil palm trees. Birds were classified as forest-associated and non-forest species using published species lists from two studies in Peninsular Malaysia (including one from the NSPSF) (Azhar et al., 2011; Peh et al., 2005). Forest-associated birds were further classified into forest-edge and forest-interior species based on the same literature.

Bird faecal sample collection

Mist netting was used to trap birds in order to collect faecal samples, along 25 of the 33 point count transects at 0 m, 100 m and 300 m; 75 mist netting points in total. At each sampling point mist nets were placed perpendicular to the plantation edge in a 100m long continuous netting line where possible; where immovable obstructions occurred to the line of mist-nets the line was continued at the next possible point. A combination of high (3-6 m) and low (0-3 m) nets was used to maximise capture diversity. Nets were opened at dawn and closed at 12:00. We did not reopen the nets in the late afternoon as bird activity remained low throughout this time period. Birds were identified and placed in clean holding bags for a maximum of 10 minutes. Faecal samples collected from holding bags were preserved in 100 % ethanol. We handled the faecal samples with forceps that were flamed with ethanol before use to prevent any contamination.

Sample selection and DNA extraction

We selected species for diet analysis if we had faecal samples from > 15 individual birds. Three DNA extraction kits (Norgen, Qiagen and Biotech) were tested for the extraction of DNA from the bird faecal samples. The Norgen Stool DNA Isolation Kit (Norgen BIOTEK, Thorold, ON, Canada) was chosen due to higher DNA yields from the test samples.

PCR, sequencing and bioinformatic analysis

Amplification of a 157-bp fragment of the mitochondrial cytochrome c oxidase subunit 1 was performed using primers ZBJ-ArtF1c and ZBJ-ArtR2c (Zeale et al., 2011) adapted to include Fluidigm tags CS1 and CS2. Each 10 µl PCR contained 5 µl of Qiagen multiplex PCR (Qiagen, CA) master mix, 3 µl of water, 0.5 µl of each 10 µM primer, and 1 µl of eluted DNA. PCR amplification was as follows: 95 °C, 15 min; 50 cycles of 95 °C, 30 s; 52 °C, 30 s; 72 °C, 30 s, and 72 °C, 10 min. Amplicon QC was performed using a DNA D1000 TapeStation (Agilent Technologies), and quantification was performed using Qubit dsDNA HS Assay Kit (Invitrogen, Life Technologies). Sequencing was performed bidirectionally with 10-bp Fluidigm indexes following manufacturer's protocols, and sequencing was run on the MiSeqv2 Chemistry using a 2 × 150 bp run with 300 cycle run (Illumina). Reads were merged in Mothur (Schloss et al., 2009) and then processed using the Galaxy platform (Blankenberg, Von Juster, & Coraor, 2010; Giardine et al., 2005; Goecks, Nekrutenko, Taylor, & Galaxy Team, 2010). Primer sequences were removed and all sequences that were longer or shorter than the target amplicon length of 157 bp were filtered out. Sequences were collapsed into unique haplotypes, and then, singleton sequences were excluded from further analyses.

Sequences were clustered into molecular operational taxonomic units (MOTU; Floyd, Abebe, Papert, & Blaxter, 2002). Because accurate identification of DNA sequences requires a complete or relatively complete reference database we employ the MOTU concept (Floyd et al. 2002) which does not equate to a specific taxonomic level but refers to pools of equal genetic diversity which can be compared and quantified across sampling units (Floyd, Abebe, Papert, & Blaxter, 2002).

A representative sequence of each MOTU was picked for analysis with the QIIME pick otu and uclust methods (http://qiime.sourceforge. net; Caporaso et al., 2010). MOTUs were clustered using a similarity threshold of 92% to minimize spurious OTU generation (Clare *et al.*, 2016). MOTUs were also clustered using a 94% and 96% similarity threshold in order to compare results and ensure that resulting ecological analysis was not dependent on threshold choice. Our data suggest there was no difference in the overall conclusions using the other thresholds (Table 2 and Fig. 1-9 in SI). We identified MOTUs to order level using BLAST analyses and a reference database of > 600,000 DNA barcodes extracted from GenBank with a wider taxonomic profile (including potential contaminants bacteria, fungi, vertebrates as well as arthropods, the target of interest). MEGAN version 5.6.3. (Huson, Mitra, Ruscheweyh, Weber, & Schuster, 2011) was used to screen out unknowns, unidentified sequences and those not resolved to order with the LCA parameters recommended by Salinas-Ramos, Herrera Montalvo, León-Regagnon, Arrizabalaga-Escudero, and Clare (2015). A technical PCR replicate of all samples was sequenced. MOTUs identified in each replicate were combined to form the final MOTU library for each sample. MOTUs which could be classified to an arthropod order reliably were used for statistical analysis of diet (unclassifiable MOTUs were excluded).

Pest sampling

We conducted both opportunistic and systematic sampling for herbivorous insects in our study sites. We randomly chose five of the bird sampling transects, from each of the North and South side of the NSPSF and searched three fronds from three oil palms at least 10 m away from each other, at the edge of the plantation, 100m, 300m and 1.5km away from the plantation edge. A total of 360 fronds from 120 palms were searched. Pests were collected and stored in ethanol for later identification by an expert entomologist in oil palm pests. In addition, while conducting bird sampling in plantations, if oil palm pests were seen, they were also collected and stored in ethanol for later identification.

Statistical analysis

All statistical analysis was performed in R 3.4.4 (R Core Team, 2018). Species richness and abundance of birds from distance to forest was examined by mixed effects models using the “lme4” package (Bates et al., 2014). Linear mixed effects models (LMMs) were used for species richness as the response variable, with distance to forest and side of the forest sampled fitted as categorical fixed effects. The transect number sampled was fitted as a random effect. Generalised mixed effects models (GLMMs) were used for bird abundance with a poisson distribution (as count data should not be modelled using a Gaussian distribution) with the same model structure as for bird species richness. Model selection was conducted based on Akaike Information Criteria (AIC) (Burnham et al., 2011) and p-values were computed by Kenward-Rodger approximation

(Luke, 2017). Model estimates for GLMMs were presented as incidence rate ratios (Tripepi et al., 2007) as these are more intuitive than the transformed model estimates.

“True” bird species richness was also calculated using the “vegan” package (Oksanen et al., 2013) at each distance from forest, based on the average of four nonparametric richness estimators first order jackknife richness estimator (JACK1), jackknife 2 richness estimator (JACK2), Chao 1 richness estimator (CHAO1), and BOOTSTRAP. These estimators quantify the number of bird species that were not detected by point counts but may have been present in the habitat. Beta diversity of birds was also calculated for each distance to forest using the Sorenson dissimilarity (Anderson et al., 2006).

MOTU richness in bird diet was also examined using LMMs with MOTU richness fitted as the response variable and bird species fitted as a categorical fixed effect. Distance from forest nested within transect number were fitted as random effects. The model selection criteria and p-value computation methods used were the same as the other LMMs in this study.

Co-occurrence patterns were estimated via pure latent variable and correlated response models using Bayesian Markov chain Monte Carlo (MCMC) methods in the boral package in R (Hui, 2016). This approach partitions pairwise associations into an environmental-based component, which reflects shared responses to environmental gradients, and a residual component, which captures unmeasured species relationships after accounting for environmental conditions (Warton et al., 2015). The environmental variable included in the correlated response model was the species of bird the sample came from. We included distance to forest during model selection, however, this did not explain any of the species co-occurrence when comparing the differences in the trace of the estimated residual covariance matrix between models (Hui, 2016). The resulting residual correlation matrix (given by the latent variables) was used to estimate separate pairwise MOTU associations for all MOTUs, and the environmental correlation matrix (given by the MOTU-specific regression coefficients) was used to estimate co-occurrence between MOTUs in bird species’ diet. We used a burnin length of 10000 iterations and a total number of 40000 iterations for the MCMC. The MCMC burnin period was evaluated by trace plots. Separate models using the same methods as above were run with distance to plantation edge as the environmental variable for species that have > 15 samples per sampling distance to investigate whether this had an effect on bird diet.

Results

Use of oil palm plantations by forest and farmland birds

Across the 264 sites, 2507 birds were counted, of 81 species. The most common birds were oriental magpie-robin (*Copsychus saularis*), yellow-vented bulbul (*Pycnonotus goiavier)*, common tailorbird (*Orthotomus sutorius*), Javan myna (*Acridotheres javanicus*), spotted dove (*Spilopelia chinensis*), zebra dove (*Geopelia striata*) and ashy tailorbird (*Orthotomus ruficeps*), all with over 100 sightings. These species are all generalist bird species, not usually present in forest (Azhar et al., 2011; Peh et al., 2006). We found further evidence of habitat separation between oil palm and forest-associated birds with no individuals of these common oil palm species sampled during 15 days of mist-netting (data unpublished). Thirty six species of forest-associated birds were observed in plantations, most of which were observed at the edge of plantations nearest to forest (Table 1 in SI). We recorded 83% of bird species according to the average estimated “true” species richness (mean of chao, jack1, jack2 and bootstrap estimators). Species richness, Shannon diversity and abundance of birds were all higher at the edge of plantations near the forest than at 100 m, 300 m and 1500 m away from forest, with the other distances exhibiting no difference from one another (Table 1 and Fig 2.). Furthermore, abundance of forest-associated birds was higher at the edge of plantations, near the forest than at 100 m, 300 m and 1500 m away from forest (Table 1.), with the other distances exhibiting no difference from one another. In contrast, there was no difference in abundance of non-forest (open country) birds in plantations with distance to forest (Table 1.). Species richness and abundance of birds was lower on the south side of the forest than the north side (Table 1.), possibly due to the lower height of understory vegetation in oil palm plantations situated there (model estimate = - 80 cm, $P = < 0.001$). Mean beta diversity of birds was highest at the edge of plantations, near the forest

(0.64) and declined with increasing distance from the forest: 100 m (0.62), 300 m (0.55) and 1500 m (0.57).

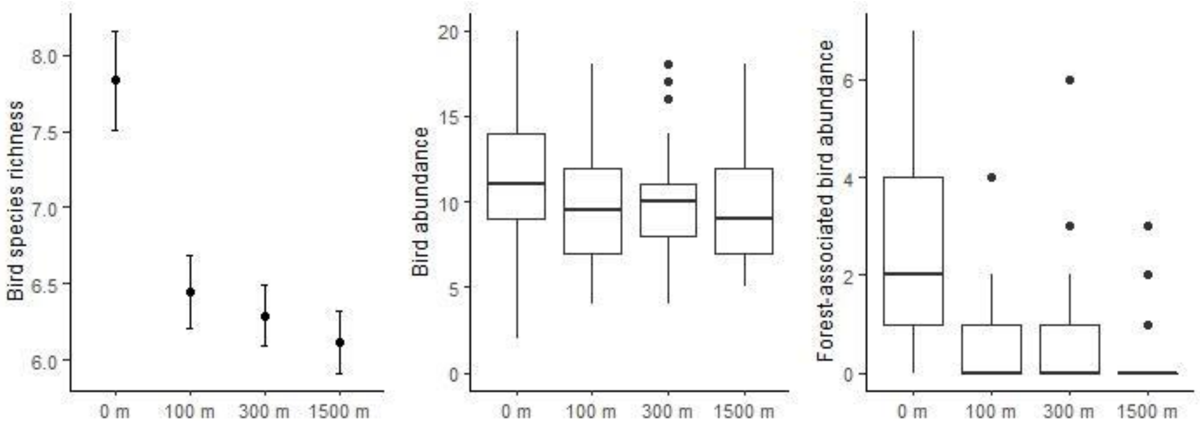


Figure 2. Plots of bird species richness, total bird abundance and forest-associated bird abundance against distance from forest

Diet of birds in oil palm plantations

We sequenced 269 faecal samples in total; from three forest-associated bird species: olive-winged bulbul (*Pycnonotus plumosus*) (45); orange-bellied flowerpecker (*Dicaeum trigonostigma*) (20); and cream-vented bulbul (*Pycnonotus simplex*) (17). In addition to six non-forest bird species: oriental magpie robin (59); yellow-vented bulbul (53); ashy tailorbird (25); common tailorbird (16); plain-throated sunbird (*Anthreptes malacensis*) (20); and pied fantail (*Rhipidura javanica*) (15).

165 unique MOTUs were found across all bird faecal samples, comprised of nine different insect orders and one crustacean (Isopoda). Lepidoptera, followed by Diptera were by the far the most abundant orders in bird faecal samples across all bird species, with these two orders making up 87-96 % of the diet of all bird species (Table 2). A large proportion of MOTUs were rare, with 68 MOTUs present in two or less samples. Only 59 MOTUs were present in five or more samples and 17 MOTUs in over 20 or more samples.

Common tailorbird had the highest MOTU richness per sample in its diet, followed by ashy tailorbird, oriental magpie-robin, plain-throated sunbird and pied fantail, although there was no statistical difference between these species. The common tailorbird and the ashy tailorbird had higher MOTU richness per sample, than the orange-bellied flowerpecker, olive-winged bulbul and yellow-vented bulbul (Table 3; Fig. 3).

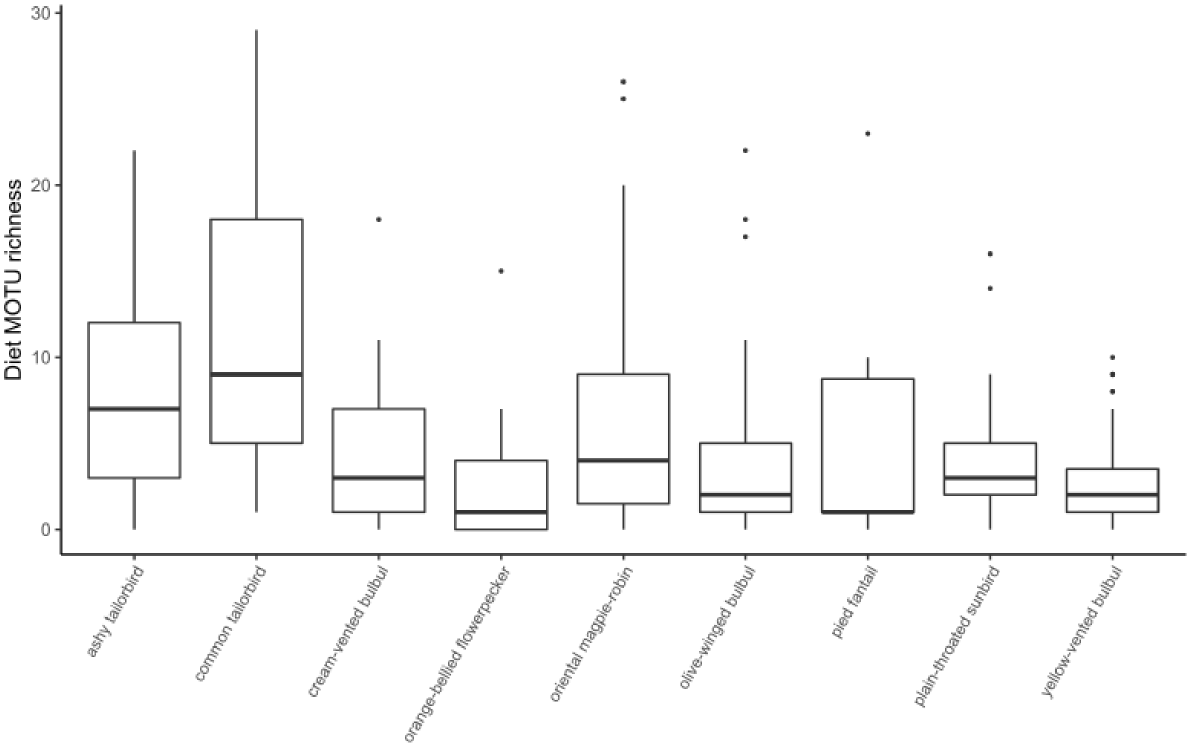


Figure 3. MOTU richness of bird diet per species

There were several dominant MOTUs that were found in a large number of samples of all species, showing a high dietary overlap between all bird species in the oil palm plantations sampled (Fig. 4 and Fig. 5). The most abundant MOTU (Lepidoptera.62) was present in over 30% of the faecal samples of all bird species and was in over 50% of the samples for five of the nine bird species.

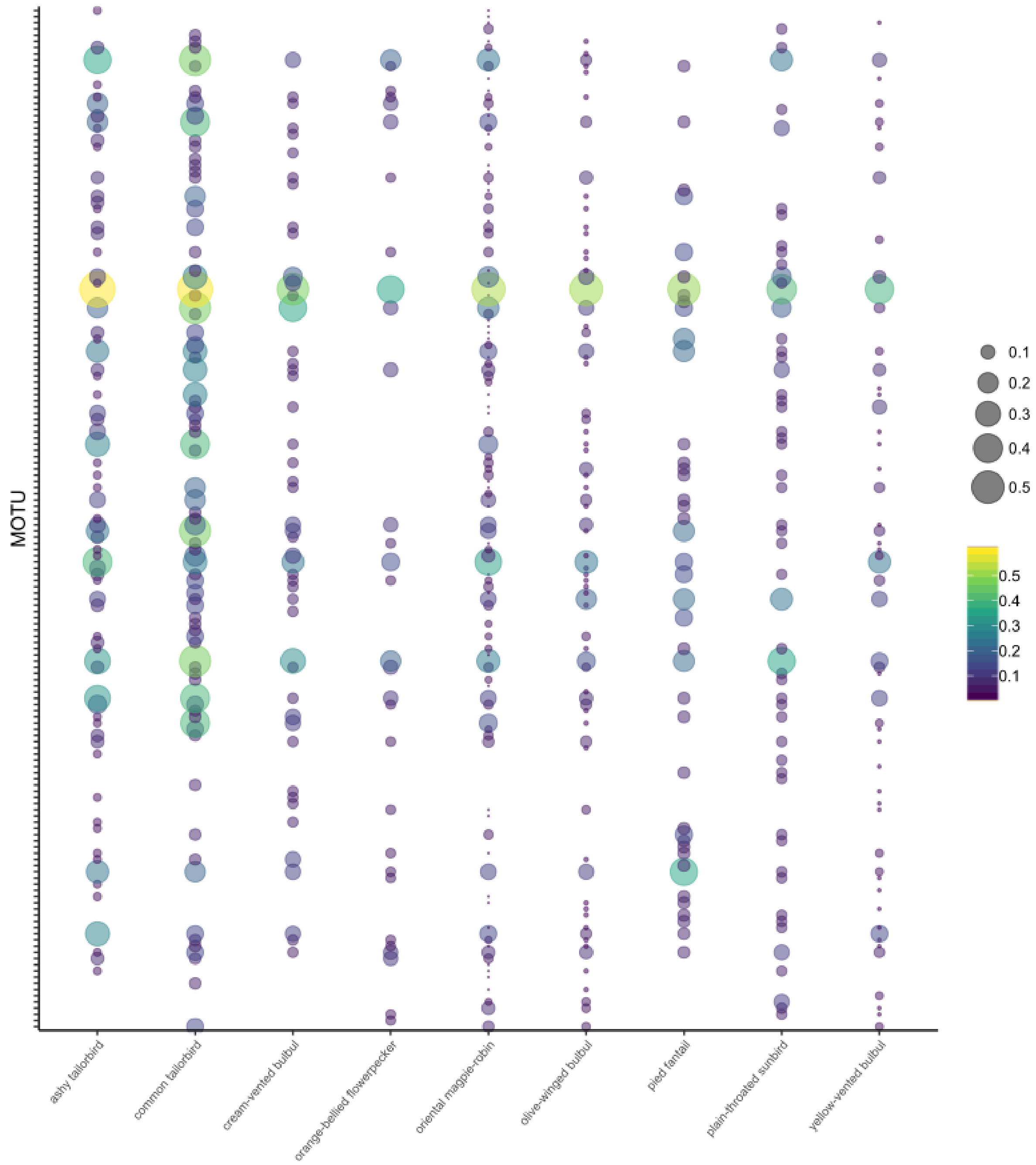


Figure 4. Proportion of occurrence of each MOTU generated from faecal sampled per bird species. Larger circles indicate a higher presence of MOTUS e.g. a circle corresponding to the 0.5 size means an MOTU was present in 50% of faecal samples from that bird species.

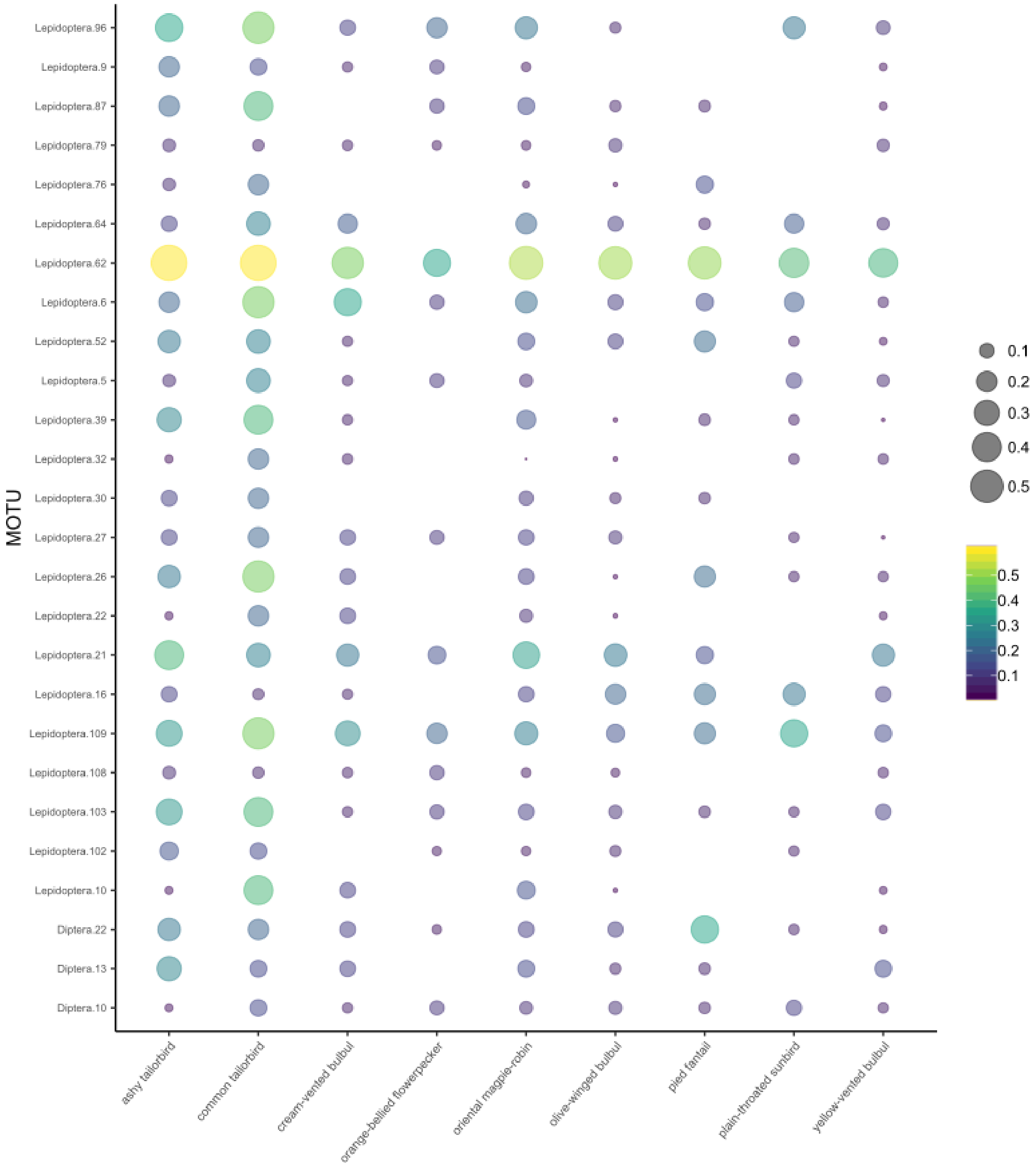


Figure 5. Proportion of occurrence of MOTUs in faecal per bird species for MOTUs occurring in more than 5% of total samples. Larger circles indicate a higher presence of MOTUS e.g. a circle corresponding to the 0.5 size means an MOTU was present in 50% of faecal samples from that bird species.

Based on the comparison of the trace of the estimated residual covariance matrix induced by the latent variables between the pure latent variable model and the correlated response model (model with covariates), bird species explained 31% of the covariation between MOTUs and 69% was explained by the latent variables, showing little dietary separation between species. We also ran a model with distance to forest as a covariate, however, this did not explain any of the covariation between MOTUs, so did not play a significant role in bird diet. In addition, we analysed the diet composition of yellow-vented bulbul and oriental magpie-robin separately with distance to forest due to their large respective sample sizes at each sampling distance. The diet of either species did not change with distance to forest, with the correlated-response model (containing distance to forest as a covariate) explaining less covariation than the pure latent variable model for both bird species.

The correlated response model showed that the majority of co-occurrence between abundant MOTUs (present in >20 samples) could not be explained by bird species (Fig. 6). However, there was widespread co-occurrence of abundant MOTUs explained by the latent-variables (residual variation). A similar relationship was found between rare MOTUs (present < 20 samples): the majority of co-occurrence of MOTUs could not be explained by bird species but was explained by the latent variables (Fig. 7). This highlights the large dietary overlap between all the bird species we sampled in oil palm plantations. There was no clustering of samples in the model-based unconstrained ordination, based on the model posterior median estimates and this was very similar to the residual ordination that takes into account variation explained by bird species, showing little difference in diet between bird species (Fig.8). If there was dietary separation between bird species, there would be expected clustering in the unconstrained plot, with clustering being removed in the residual ordination plot. In addition, the posterior medians of each MOTU corresponding to each bird species showed there were few MOTUs that were positively associated with individual bird species' diet and there was only one MOTU that was negatively associated with the diet of a bird species (pied fantail) (Fig S10 in SI). Pied fantail (10), plain-throated sunbird (10) and cream-vented bulbul (6) had the highest amount of MOTUs that were associated more positively with their diet than other species. Olive-winged bulbul had no MOTUs associated more with their diet than in the diet of other bird species oriental magpie robin, yellow-vented bulbul and orange-bellied flowerpecker had just one.

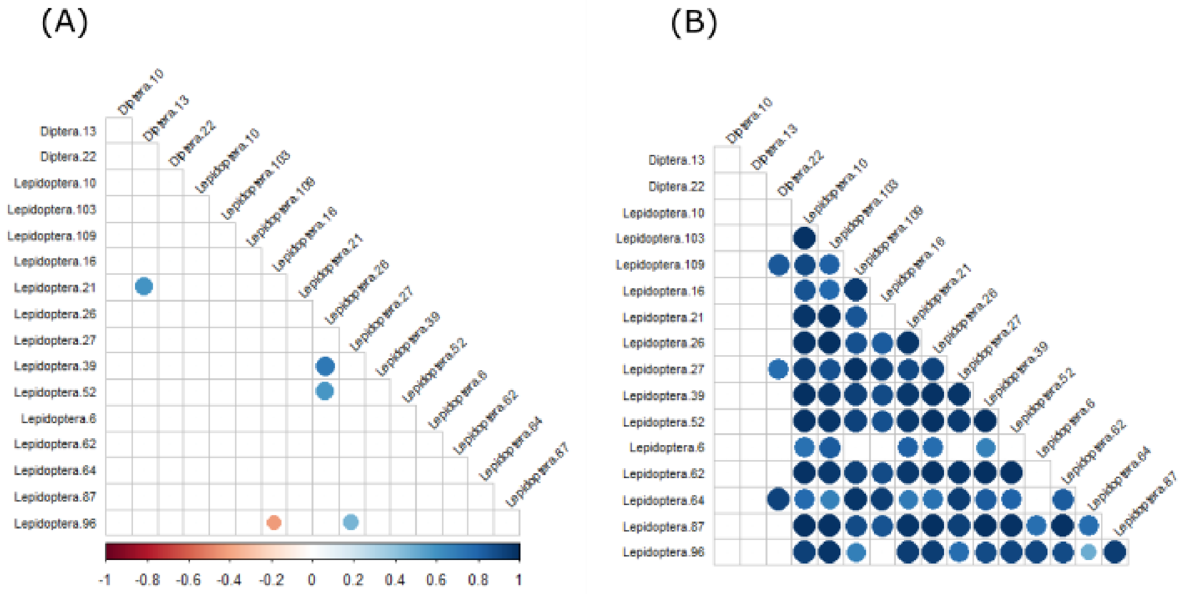


Figure 6. Co-occurence of common MOTUs (present in > 20 samples) explained by the bird species that consumed them (environmental covariate in the model) (A) and co-occurence explained by latent variables (residual correlation) (B).

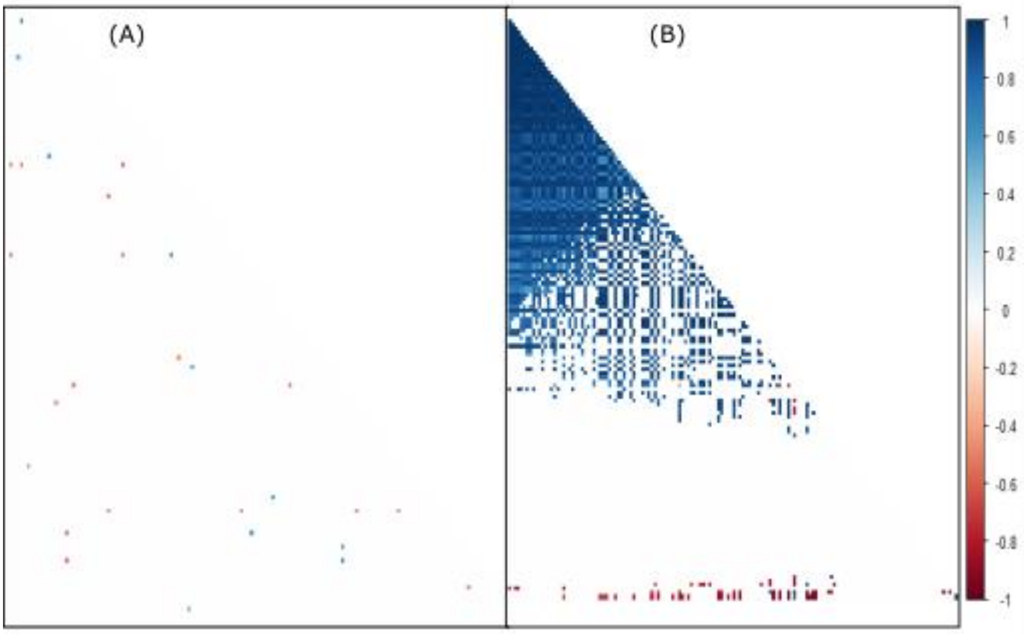
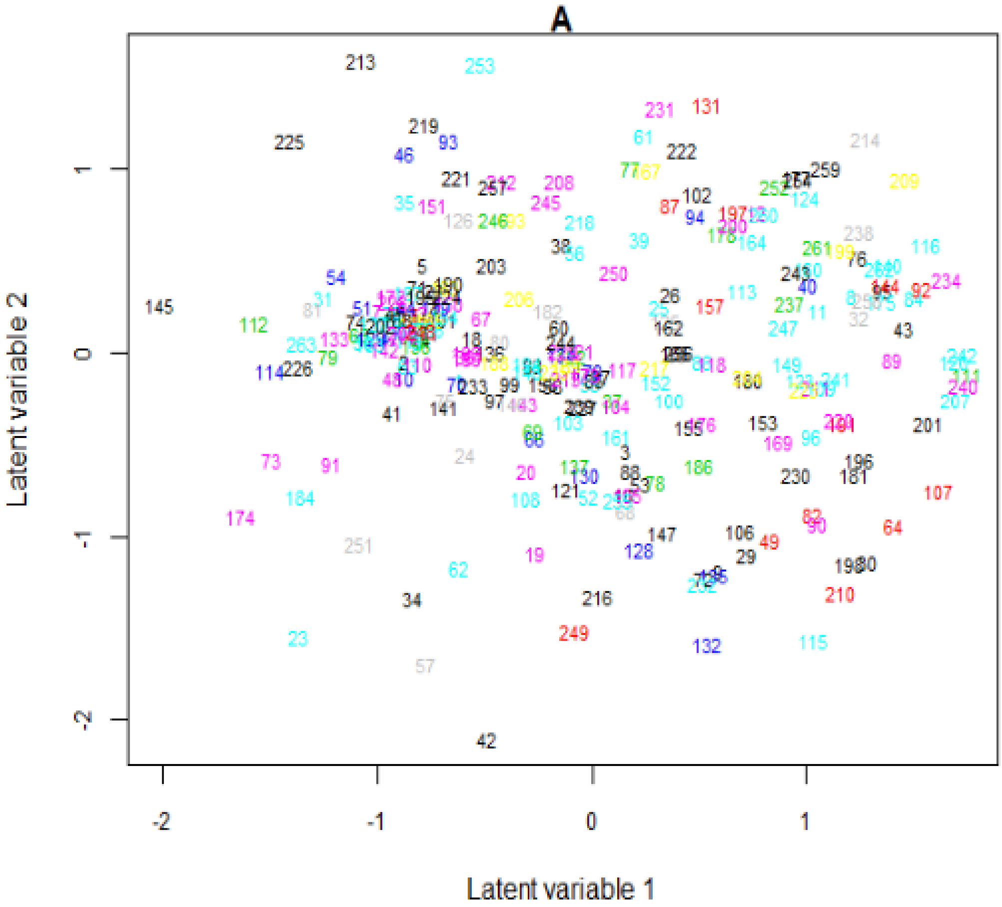


Figure 7. Co-occurence of rare MOTUs (present in < 20 samples) explained by the bird species that ate them (environmental covariate in the model) (A) and co-occurrence explained by latent variables (residual correlation) (B).


A
Latent variable 2
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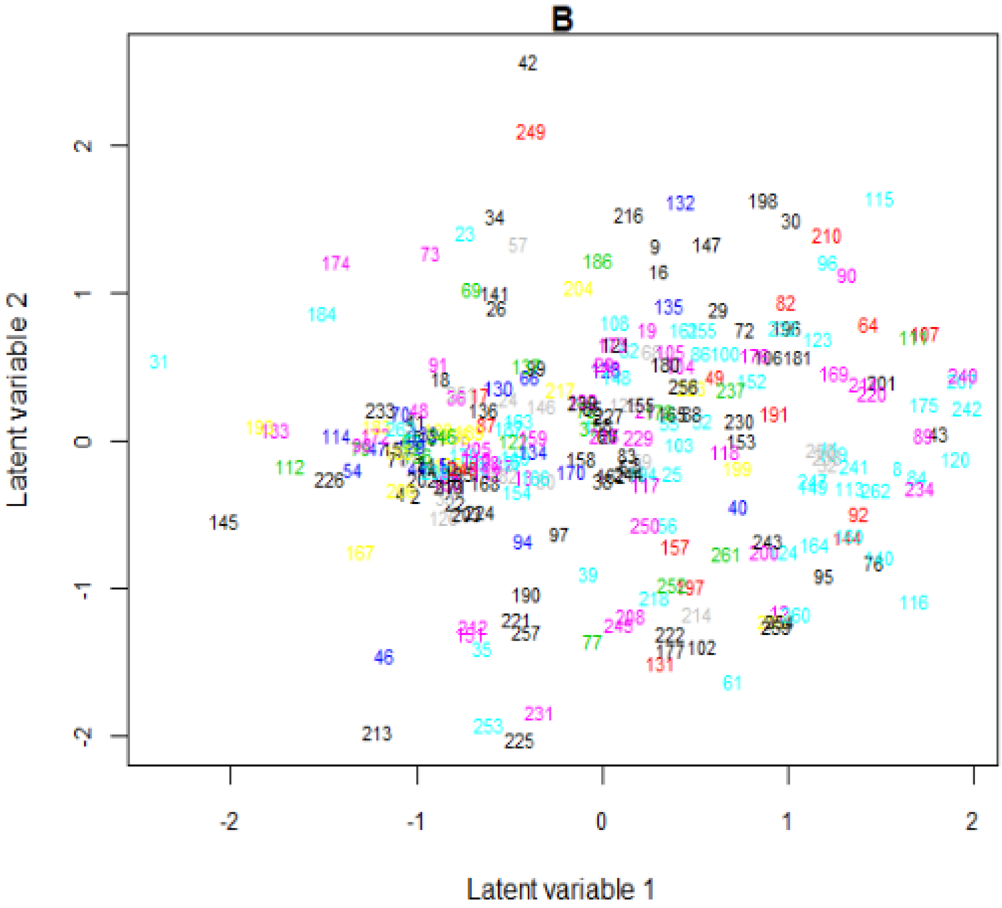
B
Latent variable 2
Latent variable 1
-2
-1
0
1
2
-2
-1
0
1
2

Figure 8. Model-based unconstrained ordination not taking into account variation explained by bird species (A) and residual ordination accounting for variation explained by bird species (B) biplots based on posterior median estimates. Each number is a separate faecal sample and each colour represents a different bird species. Both plots show no obvious clustering and are similar in pattern, showing the similarity of diet between bird species.

Presence of oil palm pest species in bird diet

Bagworms of the family Psychidae (including the species: *Pteroma pendula, Mahasena corbetti, Metisa plana, Clania spp* and an unknown species) were found in all plantations we sampled from. In addition to bagworms, the hemipteran pest: the pineapple mealybug (*Dysmicoccus brevipes*) was commonly sampled along with various species of nettle caterpillar from the family Limacodidae. After screening all the sequences for our MOTUs in BOLD from the faecal samples, we found no matches with any of these pests, or from their respective taxonomic families, in the top 100 matches for each sequence. We conclude, that the metabarcoding data provides no evidence for consumption of these common oil palm pest species by any of the bird species sampled, in our study.

Discussion

Our findings show that oil palm plantations are rarely utilised by forest-associated birds and that there is a very limited spillover of true forest birds, with species richness declining rapidly as distance to forest increases. Due to this low amount of spillover, the diet of only one species of true forest bird could be assessed (cream-vented bulbul), in oil palm plantations, along with two forest-edge species (olive-winged bulbul and orange-bellied flowerpecker). All the bird species sampled had considerable dietary overlap, feeding largely on a few lepidopteran and dipteran MOTUs. This indicates that there is little niche differentiation in regards to the insect diet of birds in oil palm plantations.

Furthermore, we found no evidence of predation of any of the main insect oil palm pests by six of the most common non-forest bird species, two forest-edge species and one true forest species, in the sampled plantations. Although this may be the result of biases associated with primer selectivity, PCRs or the high throughput sequencing process, it raises questions regarding the contribution of birds (forest-associated or farmland) to insect pest-control service in oil palm plantations, at least in our study area. In addition, the homogeneity of bird diet across the distance gradient suggests that prey availability does not change with proximity to forest and/ or that our birds were generalists..

Oil palm plantations were a significant barrier to forest birds with very few forest-associated birds penetrating into oil palm plantations. This is of great conservation concern because there are often considerable tracts of oil palm plantation between forest patches, which forest birds, in particular, small-medium sized passerines, are likely unable to cross. Whole taxonomic groups of forest-associated birds were completely excluded from our study site inside oil palm plantations (further than 100m) and 20 of the 35 species of forest-associated birds we sampled were only encountered at the edge of plantations. This included five species of babblers, which are abundant at the edge and interior of the adjacent forest (Azhar et al., 2011). The white-chested babbler (*Trichastoma rostratum*) and black-throated babbler (*Stachyris nigricollis*), two species of conservation concern (IUCN, 2018), were entirely absent from oil palm plantations, but were observed in the forest interior (data unpublished). The barrier that oil palm plantations form to forest birds, could result in limited or complete absence of connectivity between forest patches and leave many forest-associated bird populations vulnerable to local extinction (Turner, 1996). One possible method of increasing connectivity for forest-associated birds, could be the widespread introduction of riparian strips, which can hold good numbers of forest-associated birds in oil palm plantations, if large enough (Mitchell et al., 2018). These riparian reserves could provide corridors for forest-associated birds to move between existing forest patches. Riparian reserves can also benefit many other taxa e.g. dung beetles, mammals and ants (Gray et al., 2015, 2014; Lees & Peres, 2008), as well as providing ecosystem services to oil palm landscapes, such as improving water quality (Luke et al., 2017).

Oil palm plantations may be particularly inhospitable to forest birds due to their simple vegetation structure, resulting in poor foraging habitat and cover from predators (Azhar et al., 2013). Understory, insectivorous forest birds are particularly negatively affected by reduced understory vegetation, which has been found to be the main reasons for their decline in simplified habitats (Peh et al., 2005). Many of the plantations in our study area, used herbicides to control or completely clear understory vegetation, which has been shown to reduce bird diversity (Tohiran et al., 2017). In addition, fruiting trees are generally scarce in oil palm plantations resulting in a lack of food for frugivorous birds commonly found in forest habitats (Azhar et al., 2013). The oil palm microclimate may also be unsuitable for many bird species (including forest-associated birds); plantations are much hotter than forests (Hardwick et al., 2015), particularly young plantations (Luskin & Potts, 2011). We caught few birds in the afternoon (when temperatures peak) while mist-netting, indicating that bird abundance or activity was particularly low during these periods. Furthermore, the diet of all bird species sampled in oil palm plantations was dominated by a few insect MOTUs. This may indicate a low diversity of suitable prey for insectivorous birds in oil palm plantations, resulting in the low diversity of insectivorous birds (Tohiran et al., 2017).

Dietary overlap of birds in oil palm plantations was high, with a small number of MOTUs being present in all of the bird species sampled. This low separation, is likely because of the lack of resource complexity of oil palm plantations (Azhar et al., 2011), resulting in a low diversity of bird species (Eisenhauer et al., 2013; Langenheder et al., 2010). The homogeneity of oil palm plantations is the likely explanation for the lack of forest-associated birds found in oil palm plantations, as they are out-competed by more generalist species, due to the constricted set of foraging opportunities (Holmes & Schultz, 1988). Interestingly, the four bird species we sampled that are considered to be largely frugivorous (cream-vented bulbul, olive-winged bulbul, yellow-vented bulbul and orange-bellied flowerpecker), three of which are forest-associated species, all frequently had the same insect MOTUs in their diet as the truly insectivorous birds (common tailorbird, ashy tailorbird, pied fantail and oriental magpie robin). This could indicate oil palm plantations support a high density of a limited number of insect species.

Distance to forest had no effect on the diet of birds, suggesting that oil palm plantations may also be a barrier to forest-associated insect species. The lack of spillover of insects from forest to oil palm has been reported in previous studies (Gray et al., 2014; Lucey & Hill, 2012). Further research on diet differentiation between birds in the forest and oil palm plantations would elucidate differences in diet preference and availability for birds in these two habitats. However, due to the minimal overlap of insectivorous bird species in oil palm plantations and forest (Azhar et al., 2011; Srinivas & Koh, 2016), same-species comparisons would be limited to species such as the orange-bellied flowerpecker.

Our study contributes to the limited evidence on the role of birds as predators of insect pests, in oil palm plantations. Although the potential for birds as biocontrol agents of insect pests is widely discussed, there are few papers that provide direct evidence. The two previous major studies on this matter used bird exclusion experiments to measure the effect on the herbivory of oil palm by insects (Denmead et al., 2017; Koh, 2008). A critical drawback of exclusion experiments is the potential to be confounded by the exclusion of other insectivorous animals (reptiles, mammals), which could play a role in pest suppression. Furthermore, neither can address the potential for birds to suppress pests at a plantation level. Exclusions only cover a small area (usually a branch or a single tree) and therefore could still benefit from pest suppression from birds, outside of the exclusion. We found no evidence of any major oil palm pests in the diet of the nine bird species tested, including from the common insectivorous gleaners (common and ashy tailorbird). This is despite all three abundant species of bagworm in Peninsular Malaysia (Sankaran, 1970; Wood, 1968) being present in our study plantations. This included outbreaks in two of our sampling transects of *Metisa plana* which had densities of > 40 individuals per oil palm frond, thus providing ample potential for predation. Bagworm larvae could be unsuitable prey for birds due to their protective casing made out of tough silk, leaves and twigs (Barlow, 1982) that may make them unpalatable. Furthermore, the lack of spillover of forest birds into oil palm plantations also leads to the inability of forest birds to provide pest-control services in oil palm plantations, as they have been reported to do in other agricultural systems, e.g. coffee and cacao (Karp et al., 2013; Maas et al., 2015).

There is a possibility that the methods we employed to analyse bird diet, did not pick up the presence of oil palm pest species due to: primer selectivity; DNA extraction/PCR bias; or the sequencing process; and we cannot be certain that there was a complete absence of these pest species. However, the primers we used amplify lepidopteran DNA particularly well (Zeale et al., 2011) and were successful in amplifying other lepidopteran and hemipteran DNA in this study. Furthermore, other molecular diet studies using NGS were able to successfully identify pests (including lepidopteran and hemipteran pests) in bird and bat diets, using the same primers (Aizpurua et al., 2018; Crisol-Martínez et al., 2016; Razgour et al., 2011). Therefore, we suggest that efforts to enhance biocontrol of insect pests be focussed on other taxa. However, we stress that this should not come at the expense of making oil palm plantations more bird-friendly. Indeed, efforts to enhance other biocontrol agents of pests (e.g. bats, parasitoid wasps and predatory beetles), such as enhancing beneficial plants, understory vegetation and landscape heterogeneity are likely to also enhance bird biodiversity.

In conclusion, our study show that birds utilising oil palm plantations all share a similar diet. This low niche partitioning, due to lack of habitat complexity (Eisenhauer et al., 2013), is a likely reason that most forest-associated birds are absent from plantations. Oil palm plantations, therefore, currently hold little conservation value for forest birds. To enhance avian biodiversity within oil palm landscapes, habitat heterogeneity will need to be increased, by practises such as improving understory vegetation or planting of native trees within the monocrop (Teuscher et al., 2016; Tohiran et al., 2017). Furthermore, because of the barrier that oil palm forms to forest birds, there is an urgent need to increase connectivity for forest-associated birds between forest patches, in order to prevent population isolation and local extinctions of forest species. Future research should focus on practicable means of increasing connectivity between forest patches in oil palm landscapes.

Table 1. LMM and GLMM outputs for species richness, total bird abundance, forest bird abundance and non-forest bird abundance at each sampling distance away from forest, with confidence intervals (CI) and p-values (p). All p-values that are < 0.05 are presented in bold.

	Species richness			**Total bird abundance**			**Forest bird abundance**			**Non-forest bird abundance**		
Predictors	*Estimates*	*CI*	*p*	*Incidence Rate Ratios*	*CI*	*p*	*Incidence Rate Ratios*	*CI*	*p*	*Incidence Rate Ratios*	*CI*	*p*
0 m	8.62	8.11 – 9.14	**<0.001**	13.26	12.19 – 14.44	**<0.001**	2.56	2.04 – 3.19	**<0.001**	8.75	7.99 – 9.59	**<0.001**
100 m	-1.51	-2.11 – -0.92	**<0.001**	0.82	0.74 – 0.92	**<0.001**	0.31	0.21 – 0.46	**<0.001**	0.98	0.87 – 1.10	0.742
300 m	-1.60	-2.18 – -1.03	**<0.001**	0.81	0.73 – 0.90	**<0.001**	0.19	0.12 – 0.28	**<0.001**	1.00	0.89 – 1.12	0.950
1500 m	-1.76	-2.35 – -1.17	**<0.001**	0.84	0.75 – 0.93	**0.001**	0.11	0.06 – 0.19	**<0.001**	1.05	0.94 – 1.18	0.372
South side	-1.53	-2.07 – -0.99	**<0.001**	0.76	0.69 – 0.83	**<0.001**						

Table 2. Percentage of insect order contribution to total bird diet per species

Bird species	**Araneae**	**Blattodea**	**Coleoptera**	**Decapoda**	**Diptera**	**Hemiptera**	**Hymenoptera**	**Isopoda**	**Lepidoptera**	**Neuroptera**	**Orthoptera**
Ashy tailorbird	0	0	0	0.52	10.94	1.04	0.52	1.04	85.42	0	0.52
Common tailorbird	1.13	0	0.56	0	6.78	0.56	0	0	90.4	0.56	0
Cream-vented bulbul	0	0	0	0	10	5	0	1.25	83.75	0	0
Orange-bellied flowerpecker	3.77	0	0	0	16.98	1.89	0	1.89	75.47	0	0
Oriental magpie-robin	1.11	1.94	0.55	0.28	9.42	0.55	0	1.11	83.38	0	1.66
Olive-winged bulbul	1.18	2.37	0.59	0.59	11.24	1.18	0.59	1.78	80.47	0	0
Pied fantail	0	0	0	0	26.09	1.45	0	0	72.46	0	0
Plain-throated sunbird	1.27	3.8	0	1.27	11.39	2.53	1.27	1.27	75.95	0	1.27
Yellow-vented bulbul	2.05	2.05	0	0	13.7	2.05	0.68	0.68	78.08	0	0.68

Table 3. LMM output of log MOTU richness per faecal sample for each bird species

Predictors	*Estimates*	*CI*	*p*
Ashy tailorbird	1.81	1.46 – 2.16	**<0.001**
Common tailorbirds	0.46	-0.09 – 1.02	0.098
Cream-vented bulbul	-0.36	-0.90 – 0.18	0.194
Orange-bellied flowerpecker	-0.80	-1.33 – -0.27	**0.003**
Oriental magpie-robin	-0.24	-0.64 – 0.16	0.243
Olive-winged bulbul	-0.61	-1.03 – -0.19	**0.004**
Pied fantail	-0.42	-0.99 – 0.15	0.151
Plain-throated sunbird	-0.32	-0.85 – 0.20	0.227
Yellow-vented bulbul	-0.73	-1.15 – -0.31	**0.001**

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Chapter 4: Replanting of first-cycle oil palm reduces soil quality

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Abstract

Soil quality and soil carbon is reduced after conversion of forest to oil palm plantations, but remains relatively stable during the lifetime of the plantation. However, oil palm is replanted after 25-30 years of growth due to an inaccessibility to harvesters and a reduction in yield. Over 13 million ha of first-generation oil palm is estimated to be replanted by 2030. Therefore, it is vital to know the effects of replanting on soil quality, including soil organic carbon (SOC), so that the long-term sustainability and climate change impacts of oil palm agriculture can be assessed. In this study, we investigated the effects of oil palm replanting by clear cropping on soil quality, over a 7-year chronosequence, until oil palm reached maturity in the second growing cycle. After replanting, there was a drop in key indicators of soil quality and impactors on oil palm yield: SOC; soil water content; soil nitrogen; cation exchange capacity; and soil biodiversity. Soil quality remained low in second-cycle, mature oil palm. SOC was 50% (95% CI: 28-65%) lower than in first-cycle oil palm, 7-years after replanting. This percentage SOC loss is similar or higher than reductions in SOC after forest conversion to oil palm. Due to these serious impacts on soil quality, we state that under current practices, oil palm agriculture may not be sustainable in the long term. The effects of replanting need to be mitigated if climate change impacts are to be reduced and soil quality levels are to be maintained.

Introduction

Oil palm agriculture has greatly expanded since 1990, with the area under production increasing from 6 million ha to over 21 million ha (FAOSTAT, 2017). Much of this area has come at the expense of tropical forest. Subsequently, there has been a considerable amount of research focussed on the negative environmental effects of the first-cycle of oil palm, after forest conversion. These include: reductions in soil quality (Guillaume *et al.*, 2015, 2018); increased carbon emissions (Carlson *et al.*, 2013); and loss of biodiversity and ecosystem functioning (Fitzherbert *et al.*, 2008; Savilaakso *et al.*, 2014; Dislich *et al.*, 2016).

Land-use change in tropical ecosystems can negatively impact on soil quality and more specifically soil organic carbon (SOC) (Post and Kwon, 2000; Klinge *et al.*, 2004; Don *et al.*, 2011). Soil degradation after forest conversion to oil palm plantations is particularly high when compared to some other agricultural land use types such as rubber plantations, due to greater soil erosion and lower carbon inputs (Guillaume *et al.*, 2015). However, degradation is slowed during the 25-year life cycle of the plantation by the development of closed canopy and understory vegetation as the palms mature and chemical or organic nutrient inputs (Chiti *et al.*, 2014). The preservation of soil quality is vital in maintaining agricultural sustainability and food security (Verhulst *et al.*, 2010). Furthermore, preserving the long-term viability of existing oil palm landscapes is important for conserving remaining natural habitat by avoiding the need for additional deforestation due to losses in yield. However, there is a lack of research on soil sustainability beyond the first-generation of oil palm plantations and therefore, the long-term effects of oil palm agriculture on the soil.

With the boom in oil-palm cultivation beginning in the mid-1980s, large scale replanting of oil palm plantations is currently taking place in Southeast Asia (Snaddon *et al.*, 2013). Oil palm (*Elaeis guineensis*) yield peaks when palms are between 7 and 18 years old, after which yield begins to drop and palms can become increasingly difficult to harvest due to their increase in height. This results in a commercial lifespan of about 25 years (Corley and Tinker, 2016). Based on data from the Food and Health Organisation (FAOSTAT, 2017), over 7.5 million ha of oil palm has potentially already been replanted and around 5.4 million ha could be replanted by 2030.

Oil palm plantations are usually prepared for replanting by clear felling of existing palms using heavy machinery (Goh and Chew, 2000), resulting in considerable soil disturbance and large tracts of land left bare, after having vegetative coverage for the last 25 years. Newly replanted oil palms show an increase in diurnal ambient temperatures of 6 °C compared with old (25-30 years) plantations (Luskin and Potts, 2011); this along with the loss of vegetation structure may have marked immediate impact on biodiversity and ecosystem processes (Kurz *et al.*, 2016). Replanting could also have potential long-term effects on soils. A study on peat soils found that soil organic carbon (SOC) in 8-year old replanted plantations continued to reduce at a high rate (Matysek *et al.*, 2018). In contrast, another study on mineral soils suggested that SOC stocks recovered, to some extent, after replanting (Rahman *et al.*, 2018). However, to our knowledge no study has investigated the effect of oil palm replanting on overall soil quality.

To assess the long-term sustainability of oil palm agriculture, we quantify the impact of oil palm replanting on soil quality. To determine whether large-scale replanting affects soil quality, we measured physical, chemical and biotic soil properties from mature oil palm blocks (converted directly from forest) and replanted oil palm blocks, on mineral soils, along a 7-year chronosequence. Nine commonly used physical, chemical and biotic indicators of soil quality were measured and the direct and indirect effects of replanting on these indicators explored using structural equation modelling (SEM).

Methods

Study Area

The study was carried out across four oil palm estates located in the Siak regency of Riau province, Sumatra, Indonesia (0°55′56″ N, 101°11′62″ E), which have been certified by the Roundtable for Sustainable Palm Oil (RSPO). The study area was logged in the

1970s, with the resulting logged forest converted to oil palm from 1985–1995 and is currently undergoing replanting The climate of this region is tropical humid, with a mean temperature of 26.8 °C and an average rainfall of 2400 mm (Tao *et al.*, 2016). The soil type is ferralitic with gibbsite and kaolinite (Ferric Acrisol according to the FAO classification). All the plots chosen for the study were located on flat terrain. The plantation was arranged on planting blocks 300 m by 1000 m, with roads or drainage ditches in between blocks. We used a space-for-time substitution approach, sampling five age classes along a 7-year chronosequence: mature (21-27 years old); first-cycle oil palm (12 sites in 6 blocks, 2 sites per block); replanted (second-cycle) sites of <1-month (5 sites, one site per block); 1-year (8 sites, one site per block); 3-years (9 sites, one site per block); and 7-years (10 sites, one site per block) (Fig.1). Oil palm begins to be productive after two years, and after seven years oil palm is classified as mature, with peak production between 7 and 18 years (Corley and Tinker, 2015).

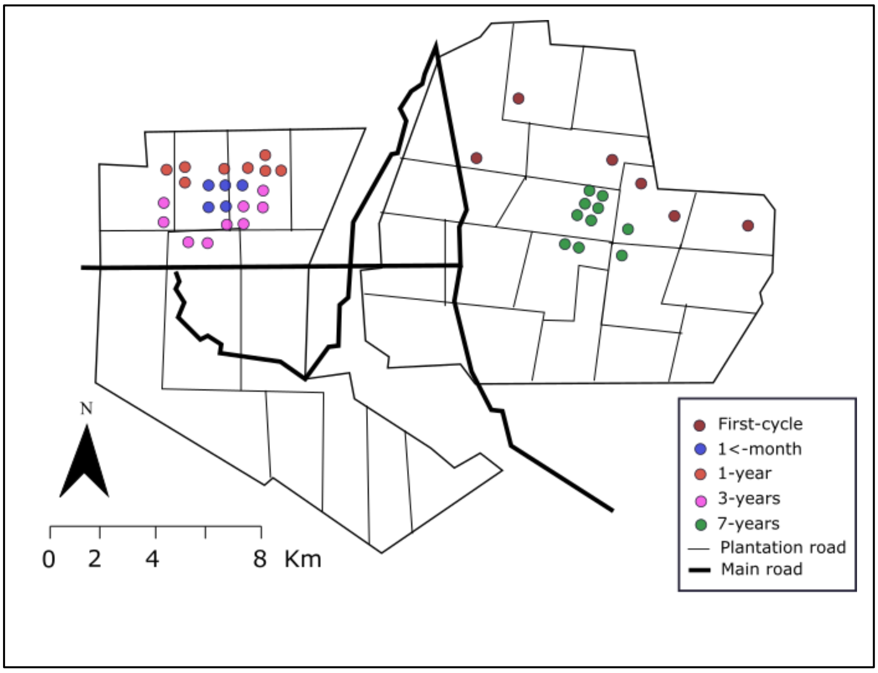

Figure 1. Map of sampling sites, with coloured circles representing the sampled blocks of oil palm from both first-cycle and second-cycle sites.

The uneven sampling design was due to availability of blocks from different ages. The oil palms were planted in a staggered design with triangular spacing of 9 m between palms, with three typical management zones. The weeded circle, a circular zone with a radius of 1.8 m directly around each palm trunk, which is kept “clean” by chemical weed control to facilitate the collection of fruit bunches. The windrow, the zone where the pruned palm fronds (approximately 18 fronds palm^{-1} year^{-1}) are placed on the ground in a windrow of consecutive U-shapes around each palm. This zone is kept free from major disturbances during the entire cropping cycle, with understory vegetation (predominantly ferns (*Nephrolepis biserrata* (Sw.) Schott) allowed to grow. The alternate rows are cleared harvesting paths are used for agriculture-related traffic, resulting in tracks of largely bare soil.

In the replanted sites, removal of first-generation oil palms was conducted by heavy equipment vehicles. The trunk was removed from the plantations and the bole, roots and dead understory vegetation were shredded and dispersed over the plantation. New palms and a leguminous cover crop (*Mucuna brachteata*) were planted within a month of old palms being cleared.

Across the sites, chemical fertilisers: (1.75 kg palm^{-1} yr^{-1} urea (46% N); 0.5 kg palm^{-1} yr^{-1} triple super phosphate (45% P_2O_5, 15% Ca); 2.5 kg palm^{-1} yr^{-1} muriate of potash (61% K_2O, 46% Cl); and 0.5 kg palm^{-1} yr^{-1} Kieserite (16% Mg, S: 22%)) were applied. Increased amounts of N, P and K fertilisers are applied to young palms, after replanting, due to their relatively high needs of these nutrients in the developments of young palms (Khalid *et al.*, 2000). These are applied in line with the development of the root system, i.e. close to the bulb (trunk) for the first year of development, moving progressively further away from the palms as the palms age i.e. at 1, 2, and 3 years old (Pardon *et al.*, 2016).

Soil quality sampling

Soil and vegetation sampling

Sampling took place from April to June 2016. The sampling sites were centred on randomly selected palms within each block, where samples were collected from both the weeded circle and the windrow of each palm. The windrow and weeded circle have been found to have different physical, chemical and biological properties (Tao *et al.,* 2016, Carron *et al.*, 2015) and thus were kept separate.

In total, samples were collected from 44 palms, with two samples (weeded circle and windrow) taken at each site; resulting in a total of 88 samples. All sampled palms were at least 50m apart. Soil samples were taken using a soil Dutch auger from a depth of 0-15 cm. At each sample site, soil samples were taken three times from each of the weeded circle and windrow. The three samples from each zone were bulked to form one sample from each zone.

At each site, the percentage vegetation cover and the percentage of bare ground were estimated for both weeded circle and windrow and all plants were identified to species level.

Indicators of soil quality

Nine soil quality indicators were measured according to common indicators of soil quality set out by Bünemann *et al.*, (2018). These included a mixture of chemical, physical and biotic indicators. The nine indicators were: soil pH, SOC, SWC (carbon and water availability are thought to be two of the key variables affecting oil palm yield along with climate (Tao *et al.*, 2017; Zhao *et al.*, 2017), total N concentration, C/N ratio, cation exchange capacity (CEC), available P concentration, aggregate stability and macrofauna order richness. The soil pH was determined using a pH meter with a soil to water ratio of 1:1. The concentration of SOC was measured by loss on Walkley–Black method (Nelson and Sommers, 1982). SWC was measured by the oven drying method at 75 °C for 48 hours. The total N was determined by the Kjeldahl method (McGill and Figueiredo, 1993).The available P concentration was measured by Bray 1 and CEC by extraction with ammonium acetate at pH 7. The soil aggregate stability was measured on 3-5 mm aggregates according to the method proposed by Le Bissonais (1996).

Soil Macrofauna sampling

Soil Macrofauna were sampled from the same sample sites as the soil abiotic indicators, according to the standard Tropical Biology and Fertility Institute soil monolith method (Bignell *et al.*, 2008) using a 25 cm × 25 cm quadrat and sampling to a depth of 20 cm. Macrofauna were characterised as fauna visible to the naked eye (Kevan, 1968). Worms were placed immediately into formalin and all other invertebrates were stored in 70% ethanol for later identification. The invertebrates were sorted to ordinal level with the exception of some taxonomic groups that were further categorised i.e. Isoptera within the order Blattodea; Formicidae within Hymenoptera and Lumbricidae to family level; Chilopoda and Diplopoda to class level; and Hirudinae to subclass, hence forth referred to as “order”.

Statistical analysis

Linear mixed effects models

All statistical analysis was performed in R 3.4.4 (R Core Team, 2018). We built linear mixed effects models using the “lme4” package (Bates *et al.*, 2014) to examine the effect of replanting age, vegetation cover and species richness on soil quality: pH, SOC, SWC, total N, C/N ratio, available P, CEC, aggregate stability and macrofauna order richness. Vegetation species richness and total cover were included in the model building process as fixed effects, however they were removed from the models after model selection by Akaike Information Criteria (AICc) (Burnham *et al.*, 2011); and the model fit. Replanting age (<1-month, 1-year, 3-years and 7-years and first-cycle) and sampling zone (windrow or weeded circle) were fitted as categorical fixed effects for models of SOC and macrofauna order richness. However, sampling zone was removed from all other models of soil variables after model selection by AIC. Sampling point nesting within sampling block were fitted as random effects to account for the nested sampling design in first-cycle blocks. The linear mixed effects models were *y~ replanting age + (1| block/ oil palm)* and *y~ replanting age + sampling zone + (1| block/ oil palm)* for SOC and macrofauna order richness. To meet model assumptions; C, N, available P, CEC and water content were log-transformed, C/N ratio, aggregate stability, pH and order richness fitted a normal distribution. Significant overall effect of replanting age on soil variables were explored via best linear unbiased predictions (BLUP) and p-values computed by Kenward-Rodger approximation (Luke, 2017).

Piecewise structural equation modelling

Piecewise structural equation modelling (SEM) (Lefcheck, 2016) was performed to examine the effects of oil palm replanting on soil quality and summarise the soil parameters in a single casual network based on a priori knowledge and model selection (AICc using Linear Mixed Effects models). Among the nine indicators, soil pH was not included in the model as it did not show a significant response to replanting based on the linear mixed effects model. C/N ratio was not included due to it being a calculation from two of the other variables included in the model. Although aggregate stability did not show significant response to replanting, it showed a significant response to SOC, and hence was included in the model. From the remaining seven indicators (SOC, SWC, total N, available P, CEC, macrofauna order richness and aggregate stability) a model was built *a priori*, with potential causal relations between variables based on theoretical knowledge and hypotheses. These were: 1) replanting reduces SOC content due to increased soil erosion due to removal of vegetative cover and compaction of soil by heavy machinery (Polyakov and Lal, 2004; Guillaume *et al.*, 2015). 2) Reduction in SOC would then lead to a reduction in all other indicators of soil quality due to the associated properties of soil organic matter (SOM) that stabilise nutrients, hold water and provide food for soil macrofauna (Franzluebbers, 2002; Polyakov and Lal, 2004; Wall *et al.*, 2012).

Subsequently, we built a component model with each of the seven indicator variables in the form of a linear mixed effects model, incorporating fixed effects based on the hypothesised causal pathways in the *a prior* model and a random effect of the sample number nested within sampling point. SOC, total N, SWC, CEC and available P were log-transformed. From prior data exploration and the results of the linear mixed effects models, the responses of the indicators of soil quality did not change between replanting ages, therefore we assigned treatment type as a categorical variable with two levels: First-cycle and second-cycle oil palm. Assumptions of normality and homogeneity of variances of the residuals of each component model of the global path model were met. During the model selection process, new causal relationships between the soil variables which were not included in the *a prior* model appeared and were further included for examination (see SI for an example). The most parsimonious model was selected where deleting any variables generated an AICc < 3 (Shipley, 2013). The model goodness-of-fit was examined by the Shipley's test of d-separation, using Fisher's C statistics with X2 distribution (Lefcheck, 2016). The structural equation modelling was performed using the piecewiseSEM package (Lefcheck, 2016).

Results

After replanting SOC, total N, SWC and CEC were reduced in all replanting ages when compared to first-cycle oil palm (Table 1 and Fig. 4). There was no difference of SOC, total N, SWC or CEC between replanting ages (*P* >0.05). There was a marginal difference between SOC content in the zone of oil palm sampled, with SOC slightly higher in the windrow than in the weeded circle (*P* = 0.052). There was no difference between windrow and weeded circle for total N, SWC and CEC. There was no difference of aggregate stability between replanting ages. However, aggregate stability increased with SOC (*P* = 0.022).

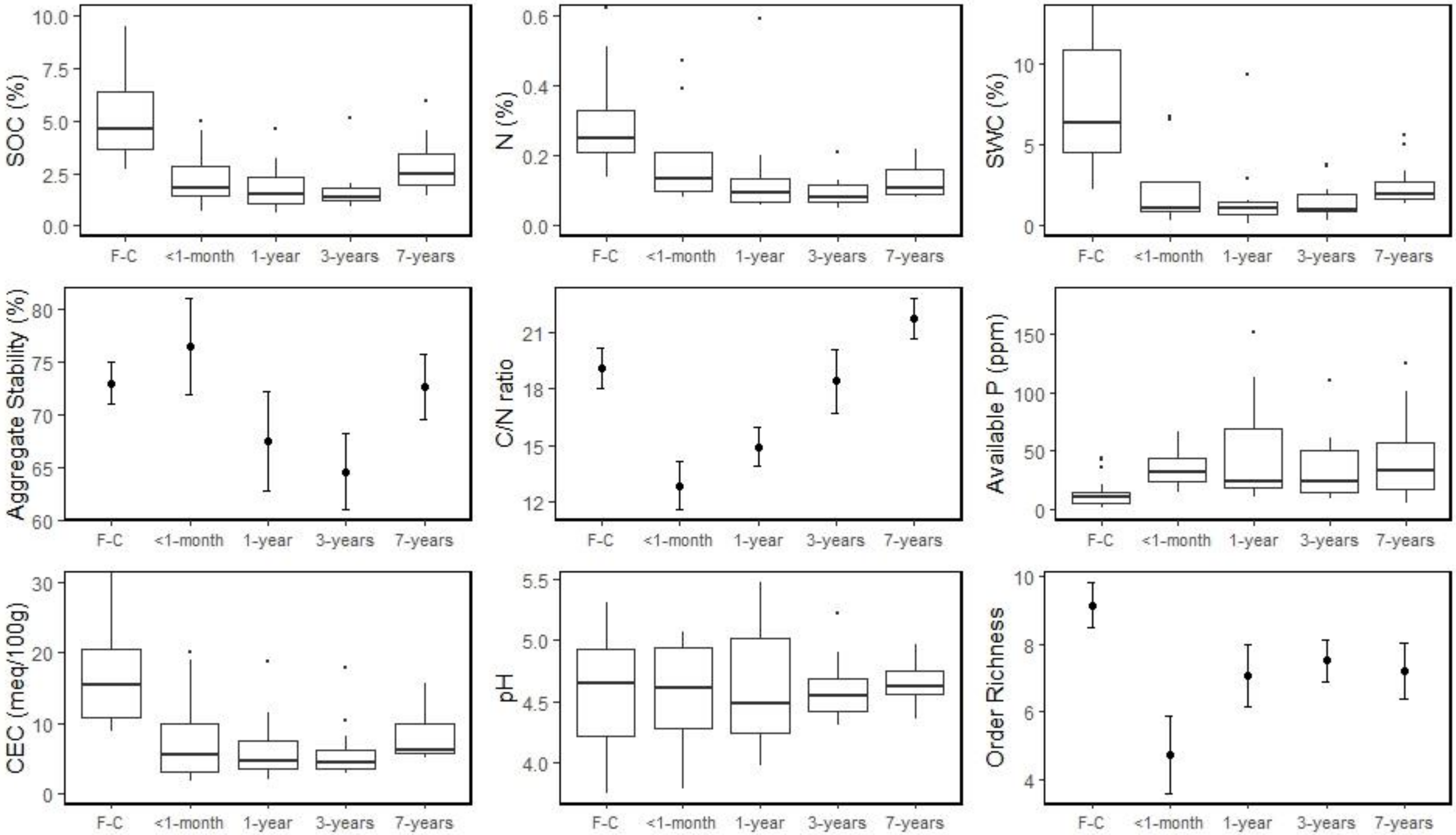

Figure 2. SOC, total N, SWC, aggregate stability, C/N ratio, available P, total K , pH and macrofauna order richness of soil in first-cycle (F-C) oil palm soil and second-cycle oil palm ages: <1-month, 1-year, 3-years and 7-years. Box and whisker plots are presented all variables

that had a non-normal distribution, with horizontal lines representing 25, 50 and 75% quantiles and whiskers representing range within 1.5 x of the lower or upper quantile. Data outside this range are plotted as individual points. Mean and standard error were plotted for variables with a normal distribution, filled circles indicate means and bars indicate standard errors.

The soil C/N ratio was lower in the <1-month (*P* = 0.018) and 1-year-old (*P* = 0.048) second-cycle oil palm than first-cycle sites (see Table 1 and Fig. 4). C/N ratio was not discernibly different between 3-year-old and first-cycle oil palm and was higher in 7-year-old second-cycle oil palm than in first-cycle although this was not significant (*P* = 0.157). C/N ratio was noticeably higher in 7-year-old oil palm than in <1-month and 1-year-old oil palm. Available P was higher in second-cycle oil palm than in first-cycle oil palm of all ages and there was no difference between replanting ages. There was no clear difference between pH in second-cycle and first-cycle soil (see Table 1).

In total, 36 soil macrofauna orders were recorded from all samples. Soil macrofauna order richness was lower in all replanting ages than in first-cycle oil palm (Table 1) although this was not statically significant for 3-year-old replanted oil palm (*P*=0.083). The order richness of the windrow was on average 3.8 higher across all ages than the weeded circle according to the model estimate (*P*<0.001)

Ground vegetation cover was completely removed after replanting (<1month), however plant cover (model estimate= + 22.4%, *P* <0.001) and plant richness (model estimate= +4.7, *P* <0.001) increased beyond first-cycle levels 1 year after replanting and then returned to first-cycle levels 3 years after replanting with no difference between vegetation cover (*P* = 0.31) or plant richness (*P* = 0.064) between 3, 7-years old second-cycle and first-cycle age groups (Fig. 4.). Vegetation cover was more extensive in the windrow (model estimate= +25%, *P*<0.001) than weeded circle whereas plant richness was the same in both windrow and weeded circle.

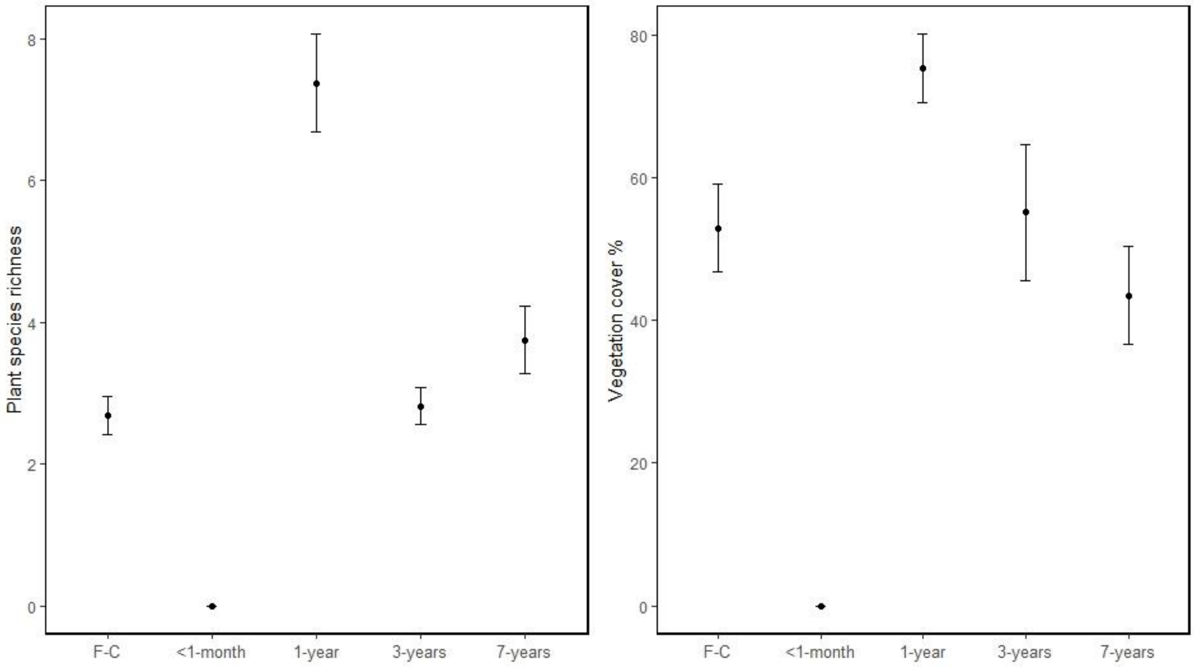

Figure 3. Plant species richness and plant cover of in first-cycle (F-C) oil palm soil and second-cycle oil palm ages: <1 month, 1 year, 3 years and 7 years with standard error bars.

The SEM models provided a good fit to the data and were well supported by the Fisher's C test (Fisher's C = 48.132, df = 48, *P*= 0.468). Replanting had a strong negative effect on SOC (*P* <0.001) and soil macrofauna order richness (*P* <0.001) (Fig. 4). The reduction in SOC, by replanting, was the driver behind all of the other indicators (apart from macrofauna richness, which showed no link to other soil quality indicators). SOC had a direct positive influence on total N (*P* <0.001) and CEC (*P* <0.001). CEC had a direct positive influence on SWC (*P* <0.001), which in turn had a direct positive influence on soil aggregate stability (*P* <0.005). Available P was positively and directly affected by replanting (*P* <0.001).

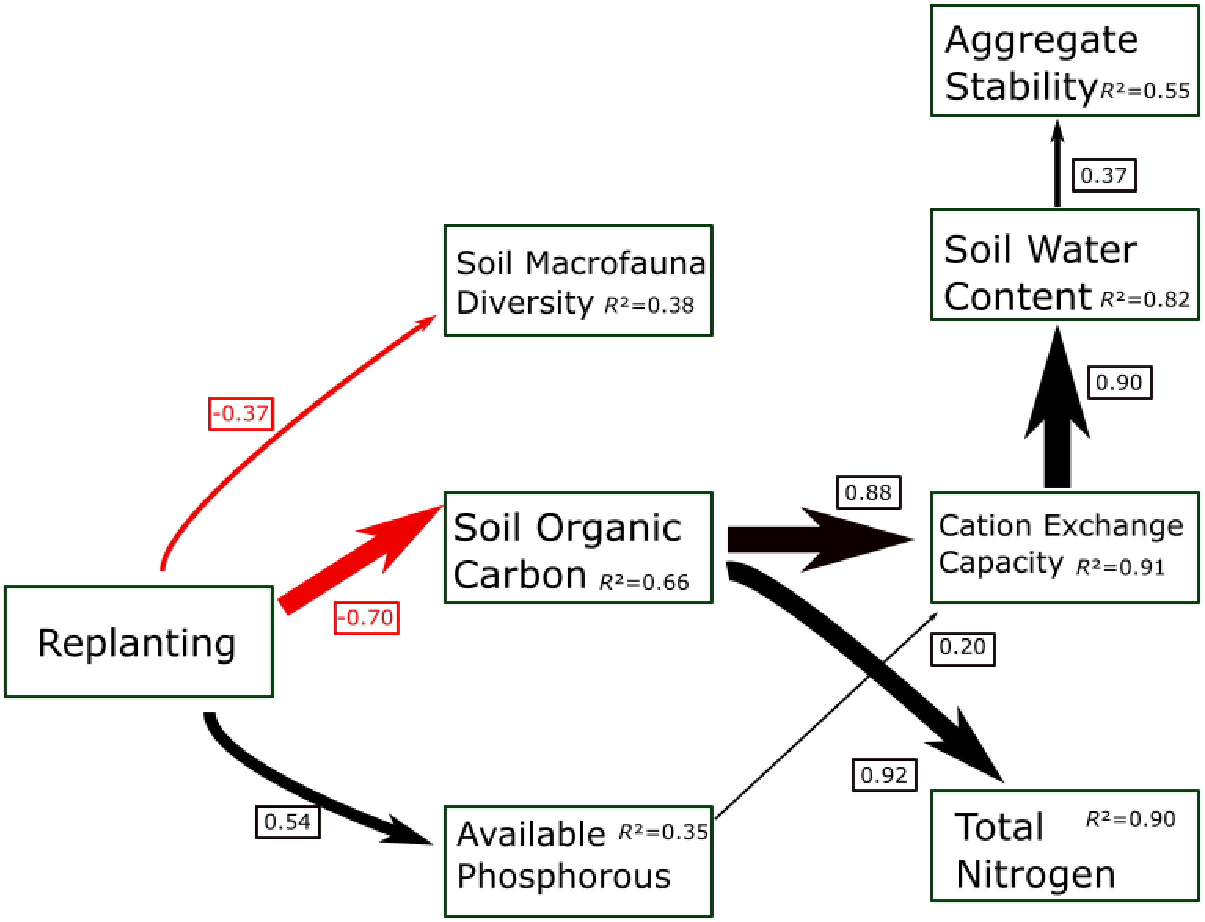

Figure 4. Structural equation models (SEM) exploring the effects of replanting on indicators of soil quality. Arrows represent unidirectional relationships between the variables and arrow thickness the strength of the relationship (standardised estimate of model). Black arrows denote positive relationships, and red arrows negative. An absence of an arrow between variables indicates no direct relationship. All relationships were statistically significant. The conditional R^2s for component models are given in the box of the response variable.

Discussion

Here, we show the first evidence that replanting of first-cycle oil palm causes a marked reduction in overall soil quality and that soil quality showed no significant recovery when plantations reach maturity, seven years after the replanting process.

Soil Organic Carbon

Soil organic carbon was lower in all replanting ages than in the first-cycle blocks and was still 50% (95% CI: 28-65%)) lower seven years after replanting. This reduction of SOC after replanting is similar to or higher than the reported initial percentage drop in SOC after forest conversion on mineral soils (Chiti *et al.*, 2014; Guillaume *et al.*, 2015; Shanmugam *et al.*, 2018). SOC in first-cycle oil palm plantations (after forest conversion) has been found to remain relatively stable or suffer a slight decline throughout the 25-year commercial lifespan of the plantation (Guillaume *et al.*, 2015, 2018; Khasanah *et al.*, 2015). Thus, our finding is the first evidence of a substantial reduction of SOC beyond the establishment of oil palm plantations for mineral soils. Over 13 million ha could be replanted by 2030 (FAOSTAT 2016). Given the scale of this issue, the huge amounts of carbon potentially released has considerable implications for soil sustainability and climate change. Our findings contradict those by Rahman et al. (2018), who found some recovery of SOC stocks after replanting, however, the percentage of C in their soils was initially much lower than in our sites and soil from only six palms was collected from replanted sites. However, this discrepancy highlights the need for further research conducted on different soil types and regions, on the effect of replanting on SOC and soil quality in oil palm plantations.

Soil erosion after clear cropping of mature oil palm is likely to be the primary contributor to the loss of SOC; soil is left bare (percentage cover of vegetation dropped to zero immediately after replanting) and subject to heavy tropical rains that can lead to not only soil and water loss but leaching of SOC (Polyakov and Lal, 2004). This could lead to further losses in SOC by erosion as soil erodability increases as SOC decreases (Van Noordwijk *et al.*, 1997; Berhe *et al.*, 2007). SOC was slightly lower in the weeded circle than the windrow, possibly due to the lower amount of root matter and decomposing vegetation from the understory vegetation, which is largely removed from the weeded circle.

An increase in the rate of SOC loss by microbial respiration relative to SOC formation from organic matter could also contribute to SOC decline. Possibly explained by increased temperatures after replanting, due to the removal of the canopy (Luskin and Potts, 2011). Higher temperatures result in increased microbial decomposition of soil organic matter (SOM) of which SOC is the main component (Davidson and Janssens, 2006). In addition, steady inputs of organic matter from oil palm roots, fronds and understory plants are removed as plantations are prepared for replanting which could lead to a reduction in SOC sequestration. Decomposition of SOM may be enhanced by rapid nutrient release of dead biomass and by labile organic matter released when soil aggregates are disturbed during replanting, similar to the effect of forest conversion to plantation (Guillaume *et al.*, 2015). Loss of SOC after replanting was the driver influencing the drop in other soil quality indicators, shown by the SEM.

Soil Nitrogen and C/N ratio

Total N in soil was lower in all replanting ages than in first-cycle oil palm and was still 57% (95% CI: 39-70%) lower seven years after replanting. The SEM indicated that the drop in total N was a direct result of a decrease in SOC. Higher N levels are associated with levels of SOC and SOM as N can be immobilised in the SOM structure (Drinkwater *et al.*, 1998).In addition, microbial N accrual is positively linked to high levels of SOC due to the reliance of these microbes on SOM as a food source (Taylor and Townsend, 2010). Furthermore, denitrification rates by soil microbes may increase in second-cycle oil palm as soil aeration and infiltration is reduced due to the reduction in SOC; although SWC was lower in replanted oil palm, denitrification can occur rapidly when soils are wetted after rainfall, particularly in compacted soils (Smith and Tiedje, 1979).

Soil C/N ratio initially dropped after replanting and was still lower than in first-cycle soil one year after replanting, likely because of the loss of SOC to erosion. However, C/N ratio then returned to first-cycle levels 3 years after replanting. This corroborates the SEM findings that SOC is reduced by replanting (thus the initial drop in C/N ratio) which then drives N loss (balancing out of C/N ratio). Reduction in total N could potentially prevent the recovery of SOC as additional N is required to support terrestrial C accumulation as a result of stoichiometric relationships in both vegetation and soil (Hungate *et al.*, 2003). If terrestrial C sequestration is not accompanied by a simultaneous N gain, the system will become increasingly N limited or will undergo progressive N limitation (Li *et al.*, 2012).

CEC and available P

CEC dropped in all replanting ages compared to first-cycle oil palm and was 54% (95% CI ± 26%) lower 7 years after replanting. CEC is a major controlling agent of stability of soil structure, nutrient availability for plants and the soil’s reaction to fertilisers (Hazelton and Murphy, 2016). Soils with a low CEC have poor resistance to changes in soil chemistry due to land-use change (Hazelton and Murphy, 2016). CEC was directly and positively influenced by SOC content, which aligns with theory as organic matter has a high CEC (Moore, 2001). Available P actually increased in second-cycle oil palm, however, this is likely because of increased inputs of mineral fertilisers containing P added after replanting. Mineral P inputs are increased due to the high P needs of young palms (Corley and Tinker, 2016).

Soil water content

SWC was much lower in all replanting ages than in first-cycle oil palm. Similarly to SOC it remained over 64% (95% CI: 29-70%) lower after seven years, despite a small recovery between 3 and 7-year-old second-cycle oil palm. In agreement with the literature (Hudson, 1994; Rawls *et al.*, 2003; Manns and Berg, 2014) the SEM indicated that the drop in soil water was a direct result of reduction in CEC. This is unsurprising as SWC can be used as a proxy for measuring CEC (Arthur, 2017) and soil's capacity for water adsorption is strongly linked with its CEC (Lambooy, 1984). Soil perturbation then subsequent compaction by machinery in the first stage of replanting leaves the soil vulnerable to erosion as infiltration capacity is reduced (Hamza and Anderson, 2005). This could lead to a further reduced infiltration capacity of the soil. Reductions in SWC due to replanting is likely to increase erosion as dry soils experience higher erosion rates under heavy rain (Le Bissonnais and Singer, 1992) causing a positive feedback of soil degradation as SOC and SWC are reduced further.

Soil pH and aggregate stability

There was no difference in soil pH between first-cycle and second-cycle oil palm. Soil pH in oil palm plantations is artificially raised by liming due to the highly acidic nature of tropical forest soils (Tripathi *et al.*, 2012). Therefore, the application of fertilisers rich in calcium and magnesium is continued throughout the life-cycle of the plantation, likely balancing out the acidifying effects of acidifying fertilisers, leaching of nutrients from high amounts of rainfall and the planting of leguminous cover crops (Goulding, 2016).

Aggregate stability was not different between second-cycle and first-cycle oil palm and there was large variability within age groups. However, aggregate stability did improve with increased SOC, driven directly by increased SWC. Effects of replanting on aggregate stability may have been confounded by soil compaction by machinery during the replanting event (Keller *et al.*, 2013).

Macrofauna diversity

Replanting of oil palm had a negative impact on soil macrofauna richness. This may reduce ecosystem functions such as litter incorporation, decomposition, water infiltration and primary production by influencing soil processes (Wurst *et al.*, 2012). SOC can support soil biodiversity through SOM (Wall *et al.*, 2012), however, reduced SOC in second-cycle oil palm was not picked up as the initial driver of loss of macrofauna diversity which was independent of other indicators of soil quality and driven by the disturbance of the replanting event itself. In the future, as the sites mature, we predict there will be a positive feedback where reduced SOC levels inhibit soil biodiversity and this in turn slows down the process of soil formation and SOC sequestration, delaying recovery of soils after replanting. There has been no studies on microbial diversity or functioning after replanting; both of which are key in SOM formation and decomposition (Brussaard, 2012). Both soil biotic and abiotic factors need to be considered and protected through the replanting process to avoid the major degradation.

Impacts of SOC loss in soil quality

SOC in second-cycle oil palm is likely to remain low as SOC accumulation in oil palm plantations is poor; SOC levels in first-cycle plantations either decline or remain stable as they age (Chiti *et al.*, 2014; Khasanah *et al.*, 2015). SOC can act as a biomembrane that filters pollutants, reduces sediment load in rivers, degrades contaminants, and is a major sink for atmospheric CO2 and CH4 (Lal, 2004). An increase in SOC can raise crop yield even in high-input agriculture (Johnston, 1986; Bauer and Black, 1994) and has been strongly linked with improved yield in oil palm (Tao *et al.*, 2017). SOC content is directly linked to SOM content: SOM provides nutrients to plants and improves water availability, both of which enhance soil fertility and ultimately improve food productivity. The persistence of SOM is affected by SOC stabilization in the soil matrix through its interaction and association with soil minerals (Schmidt *et al.*, 2011). Therefore, SOC and SOM recovery after replanting are going to be severely hampered unless mitigation measures are put in place.

The benefits of increased SOC levels was shown in this study as SOC had a direct positive impact on total N, and CEC. N is one of the major limiting plant nutrients; a drop in N is likely to cause a drop in yield resulting in the need for increased anthropogenic N inputs. The increased use of chemical N fertilisers would have negative impacts on greenhouse gas emissions (Crutzen *et al.*, 2016) and water quality (Azrina *et al.*, 2006). Furthermore, available P increased after replanting, likely due to the increased of P fertilisers, this could cause further water pollution and eutrophication as P is leached from soils increasingly vulnerable to erosion (Sharpley *et al.*, 1994). The reduction of the ability of the soil to hold water is also likely to decrease yields. Reduced water availability was reported as one of the leading causes of drop in yield in the same study area (Tao *et al.*, 2017) and seasonal changes in rainfall can explain 55% of yield variations in Malaysian oil palm (Chow, 1992). Furthermore, with climate change and reduced rainfall in areas of oil palm production, water availability is likely to become an increasingly limiting factor in oil palm agriculture, highlighting the need to maintain the soils capacity for water retention by maintaining SOC and mitigating other deleterious effects of replanting.

SOC is one of the major carbon sinks and loss of SOC through replanting is likely to lead to considerable emissions of CO2 as large swathes of oil palm are replanted. This needs to be taken into account when conducting life cycle assessments (LCAs), considering the viability of oil palm as a biofuel and evaluating oil palm agriculture’s contribution to climate change. Furthermore, this study was conducted on mineral soils; much of the world's oil palm is planted on peat soils (18.2% of Indonesia's peat swamp forest loss between 2000 and 2010 was in oil palm concessions [Abood *et al.*, 2015]) that are likely to suffer more drastic decreases in SOC after replanting. Peat soils that are exposed to higher temperatures, erosion and reduced water content emit large amount of C due to oxidative decomposition (Carlson *et al.*, 2013).

Mitigation

Results from our SEM show that loss of SOC was the driver behind the degradation of soil quality, thus retaining SOC during the replanting process should be the focus of mitigation strategies. Variable retention is a method that may be considered when replanting to reduce loss of SOC; this involves maintaining strips of mature palms while other strips are replanted (Luskin and Potts, 2011). This could reduce soil erosion by maintaining a canopy, understory vegetation and plant roots in addition to ameliorating extreme microclimates and providing habitat for wildlife (Luskin and Potts, 2011). Furthermore, the understory could be left unmanaged (no weeding or herbicide application) for the last years of the oil palm before replanting. Higher plant diversity and cover is associated with more accumulation of SOC (Lange *et al.*, 2015), improved understory vegetation could allow for an increased build-up of SOC and provide protection for the soil after the removal of mature oil palms (Ashton-Butt et al 2018). Our study was conducted on level ground, rates of soil loss are likely to be exacerbated for replanting of oil palm on steeper slopes which are more prone to erosion (Nigel and Rughooputh, 2010). Oil palm grown on steep slopes already have a substantially lower yield than flat plantations (Balasundram *et al.*, 2006); this yield may be further reduced after the effects of replanting, therefore the sustainability of oil palm grown on steep slopes should be questioned.

Conclusions

We show that oil palm replanting can cause a severe loss of soil quality, particularly driven by SOC loss. Our analysis shows that soil quality remains highly degraded seven years after the replanting event. This is likely to impact upon oil palm yield (Tao *et al.*, 2017) raising questions about oil palm's long-term sustainability under current practices. In addition, mass replanting of oil palm could lead to a considerable release of previously stored carbon into the atmosphere, raising further climate change concerns about oil palm agriculture. This study highlights the need for more research into mitigating soil degradation after replanting and the need to factor loss of SOC into LCA's and assessments of oil palm's use as a biofuel over the long term.

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Table 1. Model outputs of LMMs comparing SOC, N, SWC, C/N ratio, Aggregate stability, available P, CEC and macrofauna order richness between first-cycle and second-cycle oil palm ages: <1 month, 1 year, 3 years and 7 years. First-cycle oil palm weeded circle is the model intercept; all other model estimates are compared to this value.

	log(SOC)			**log(N)**			**log(SWC)**			**C/N ratio**		
	Estimates	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
First-cycle	1.55	1.29 – 1.81	**<0.001**	-1.31	-1.57 – -1.05	**<0.001**	1.85	1.48 – 2.21	**<0.001**	18.24	15.57 – 20.90	**<0.001**
<1month	-0.99	-1.46 – -0.53	**<0.001**	-0.59	-1.06 – -0.13	**0.012**	-1.47	-2.17 – -0.76	**<0.001**	-6.12	-10.95 – -1.29	**0.013**
1 year	-1.17	-1.56 – -0.77	**<0.001**	-0.92	-1.32 – -0.52	**<0.001**	-1.75	-2.35 – -1.15	**<0.001**	-4.31	-8.42 – -0.20	**0.040**
3 years	-1.23	-1.61 – -0.86	**<0.001**	-1.19	-1.56 – -0.81	**<0.001**	-1.59	-2.16 – -1.02	**<0.001**	-0.77	-4.66 – 3.12	0.696
7 years	-0.70	-1.06 – -0.33	**<0.001**	-0.85	-1.21 – -0.49	**<0.001**	-1.02	-1.56 – -0.47	**<0.001**	2.78	-0.98 – 6.54	0.147
windrow	0.19	0.01 – 0.37	**0.044**	0.10	-0.10 – 0.30	0.321				1.52	-0.13 – 3.17	0.071

	Aggregate stability			**log(CEC)**			**log (available P)**			**pH**		
	Estimates	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
First-cycle	72.79	66.12 – 79.45	**<0.001**	2.79	2.51 – 3.07	**<0.001**	2.35	1.96 – 2.75	**<0.001**	4.61	4.40 – 4.81	**<0.001**
<1month	3.65	-9.15 – 16.44	0.577	-1.06	-1.60 – -0.52	**<0.001**	1.11	0.35 – 1.87	**0.004**	-0.07	-0.46 – 0.32	0.726
1 year	-4.21	-15.08 – 6.66	0.448	-1.13	-1.59 – -0.66	**<0.001**	1.17	0.51 – 1.83	**<0.001**	0.11	-0.22 – 0.44	0.503
3 years	-7.64	-17.94 – 2.66	0.146	-1.16	-1.60 – -0.72	**<0.001**	0.99	0.38 – 1.61	**0.002**	-0.03	-0.34 – 0.28	0.850
7 years	-0.16	-10.11 – 9.80	0.975	-0.77	-1.19 – -0.35	**<0.001**	1.09	0.49 – 1.68	**<0.001**	0.02	-0.28 – 0.32	0.887

	Macrofauna Order Richness		
	Estimates	*CI*	*p*
First-cycle	11.05	9.71 – 12.38	**<0.001**
<1month	-4.39	-6.42 – -2.35	**<0.001**
1 year	-2.07	-3.94 – -0.21	**0.035**
3 years	-1.64	-3.44 – 0.17	0.083
7 years	-1.94	-3.69 – -0.18	**0.037**
WC	-3.82	-4.93 – -2.70	**<0.001**

Chapter 5: Replanting of first-cycle oil palm results in a second wave of biodiversity loss

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Abstract

1. Conversion of forest to oil palm plantations results in a significant loss of biodiversity. Despite this, first-cycle oil palm plantations can sustain relatively high biodiversity compared to other crops, however, the long-term effects of oil palm agriculture on flora and fauna are unknown. Oil palm has a 25-year commercial lifespan before it needs to be replanted, due to reduced productivity and difficulty of harvesting. Replanting is likely to cause impacts on the local ecosystem as the complex vegetation structure of this perennial crop is removed. However, the effect of replanting on biodiversity is little known.
2. Here, we investigate the effects of oil palm replanting on soil macrofauna communities. We assessed diversity, abundance and community composition of soil macrofauna in first-cycle (25-27-years-old), freshly cleared, 1-year-old, 3-year-old and 7-year-old mature second-cycle oil palm.
3. Macrofauna abundance and richness drastically declined immediately after replanting. Macrofauna order richness showed some recovery 7-years after replanting, but was still 19% lower than first-cycle oil palm. Soil macrofauna abundance recovered to similar levels to that of first-generation oil palm plantations, 1-year after replanting. This was mainly due to high ant abundance, possibly due to the increased understory vegetation as herbicides are not used at this age. However, there were subsequent declines in macrofauna abundance 3 and 7-years after replanting; resulting in a 59% drop in macrofauna abundance in second-cycle mature oil palm compared to first-generation levels. Furthermore, soil macrofauna community composition in all ages of second-cycle oil palm was different to first-generation plantations, with decomposers suffering particular declines.
4. After considerable biodiversity loss due to forest conversion for oil palm; belowground invertebrate communities suffer a second wave of biodiversity loss due to replanting. This is likely to have serious implications for the conservation of soil invertebrates in oil palm

landscapes and agricultural sustainability due to the vital ecosystem functions that soil macrofauna provide.

Keywords: Macrofauna, soil, invertebrate, agriculture, sustainability, belowground

Introduction

Oil palm plantations currently cover more than 21 million ha of the tropics (FAO (Food and Agriculture Organization of the United Nations), 2017). Conversion of forests to oil palm has resulted in huge biodiversity losses, especially in Southeast Asia where 85% of palm oil is produced (Koh & Wilcove, 2008; Savilaakso et al., 2014). Changes associated with this forest conversion has been the focus of considerable research within the last 10 years. However, the long-term effects of oil palm cultivation on biodiversity are understudied, with the majority of studies focussing on the immediate impacts after forest conversion (Savilaakso et al. 2014; Kurz et al., 2016). Oil palm has a 25 year commercial lifecycle, after which it needs to be replanted because of a decrease in yield and difficulty in harvesting due to the increased height of palms (Corley & Tinker, 2016). In large-scale oil palm plantations, replanting usually involves the clear cropping of palms by heavy machinery. This involves the pushing over mature palms with a bulldozer or digger and uprooting them. The boles of the felled palms (and sometimes the trunks) are then shredded and distributed on the soil surface on which a leguminous cover crop and the young oil palms are planted (Corley & Tinker, 2016). By 2030 over 13 million ha of first-cycle oil palm plantations could potentially have been replanted (FAO (Food and Agriculture Organization of the United Nations), 2017).

Although oil palm has much lower biodiversity than rainforest, it is a perennial crop, with a relatively complex vegetation structure and can support a considerable range of species (Foster et al., 2011). Furthermore, agricultural landscapes are becoming increasingly important for biodiversity conservation, in their own right, due to loss of natural habitat (Fahrig et al., 2011; Tscharntke et al., 2012). However, current methods of replanting where large swathes of plantations are simultaneously removed could lead to a loss of biological complexity and significantly reduce habitat for flora and fauna (Luskin & Potts, 2011).

Agricultural intensification and land-use change have been found to have negative effects on soil biodiversity and ecosystem functioning (Creamer et al., 2015; de Vries et al., 2012; de Vries et al., 2013). Loss of soil biodiversity has been identified as one of the major issues facing soil security and named as a key factor in the six existential global environmental challenges facing humanity (McBratney et al., 2014). Soil is home to the largest genetic and species diversity of any habitat (Lavelle et al., 2006). This biological diversity is important for ecosystem functions such as nutrient retention, carbon cycling and maintaining plant diversity (de Vries et al., 2013; Wagg et al., 2014) and provides many ecosystem services that contribute to human health (Wall et al., 2015) e.g. provision of food, carbon sequestration, water retention (Adhikari & Hartemink, 2016) . Indeed, enriched levels of soil biota have been found to enhance agricultural sustainability by improving crop yield, nutrient uptake and reduce nitrogen leaching (Bender & van der Heijden, 2015). Furthermore, activity and abundance of soil fauna has been found to positively correlate with other soil characteristics that are beneficial to oil palm yield (Tao et al., 2018). However, the impact of oil palm agriculture on soil biodiversity is largely understudied (Bessou et al., 2017).

Here, we investigate how oil palm replanting affects soil macrofauna diversity, abundance and community composition < 1 month, 1-year, 3-years and 7-years after the replanting event, using a space for time approach By using a 7-year chronosequence, we couldsecond-cyclequantify temporal fluctuations in soil diversity or abundance,over this period. We predicted that diversity and abundance of soil macrofauna would be negatively affected by the disturbance of oil palm replanting, in addition to change in community composition. However, we expected some recovery of soil macrofauna communities after 7-years, in young, mature oil palm, due to the restoration of understory vegetation and oil palm canopy.

Methods

Study area

The study was carried out across four oil palm estates located in the Siak regency of Riau province, Sumatra, Indonesia (0°55′56″ N, 101°11′62″ E). The oil palm plantation at the sites were established in 1987 and has been certified by the Roundtable for Sustainable Palm Oil (RSPO). The study plots are located in an industrial plantation belonging to PT-Smart (Golden Agri-Resources). The climate of this region is tropical humid, with a mean temperature of 26.8 °C and an average rainfall of 2400 mm (Tao et al., 2016). The study area was logged in the 1970s and the resulting logged forest was converted to oil palm from 1985–1995. At the regional scale, between 1990 and 2012 tropical forest cover in Riau declined from 63 percent to 22 percent mainly due to oil palm expansion (Ramdani & Hino, 2013). The soil type is ferralitic with gibbsite and kaolinite (Ferric Acrisol according to the FAO classification). In our study site, removal of first-cycle oil palms for replanting was conducted by large diggers. The trunk was removed from the plantations and the bole, roots and dead understory vegetation were shredded and dispersed over the plantation. New palms and a leguminous cover crop (*Mucuna brachteata*) were planted less than a month after old palms were cleared.

Sampling Strategy

Sampling took place from April to June 2015. Oil palm blocks were sampled in the first cycle of growth and after a replanting event in a 7-year chronosequence: mature oil palm (~25 years old) was sampled in the first cycle; 7-year-old, 3-year-old, 1 year-old and freshly cleared (<1-month) oil palm blocks were sampled after replanting.

Soil macrofauna was sampled according to the standard Tropical Biology and Fertility Institute soil monolith method (Bignell et al., 2008) using a 25 cm x 25 cm quadrat and sampling to a depth of 20cm. Macrofauna were characterised as fauna visible to the naked eye (Kevan, 1968). Worms (Annelida) were placed immediately into formalin and all other invertebrate taxa were stored in 70% ethanol for later identification. The invertebrates were sorted to ordinal level with the exception of some taxonomic groups i.e. Isoptera to infraorder within the order Blattodea; Formicidae (ants) and Lumbricidae to family level; Chilopoda and Diplopoda to class level; and Hirudinae to subclass. Soil monoliths were taken from both the weeded circle and the windrow (see Ashton-Butt et. al,. 2018. Carron et al., 2015). The weeded circle is a zone around the oil palm trunk, with a radius of approximately 2 m, which is kept clear of vegetation by spraying with herbicides, in order to allow unhindered access to harvesters. The windrow zone is a crescent around the palm, on the outside of the weeded circle that is relatively undisturbed and where pruned fronds are also placed throughout the oil palm lifecycle (Corley & Tinker, 2016). The weeded circle and windrow are known to hold different soil macrofauna abundance and composition (Carron et al., 2015) . The sample plots were centred on individual palm trees, with one randomly selected tree sampled for each of eight different blocks of oil palm from the 1-year-old second-cycle oil palm, one tree from each of nine different blocks of 3-year-old replanted oil palm, one tree from each of ten different blocks of the 7-year-old second-cycle oil palm and 2 trees from each of 6 different blocks from the mature age and one tree from each of six different blocks of <1-month-old second-cycle oil palm. All palms sampled were at least 50m apart from each other. The uneven sampling design was due to the availability of blocks from different ages. Only six blocks of <1-month-old oil palm were available at the time of sampling and time constraints allowed for only one tree to be sampled at each block. Blocks of oil palm were 150m by 300m rectangles, with roads or drainage ditches in between blocks and are the way in which oil palm plantations are commonly organised, in order to facilitate access to plantation workers. Thus, macrofauna were sampled from 45 palms, with two samples taken from each palm (weeded circle and windrow); resulting in a total of 90 soil monoliths.

Ground vegetation surveys were conducted at all 45 palms. Where a 1 m x 1 m quadrat was placed randomly, 4 times, within both the weeded circle and windrow and the ground cover and bare ground estimated. The values used for both vegetation and bare ground covers were the average of estimates obtained by two observers. In addition, within each quadrat, plants were identified to species level and the number of individuals recorded.

Statistical analysis

All statistical analyses were performed in R 3.4.4 (R Core Team, 2018). We used linear mixed effects models in R package ‘lme4’ (Bates et al., 2014) to examine the effect of replanting and replanting age on order richness (as the data followed a Gaussian distribution) and generalised linear mixed effects models (GLMM) to examine the effect of replanting on soil macrofauna abundance. We used a negative-binomial distribution to fit the GLMM to account for overdispersion and non-normal distribution of the data (Warton et al., 2016). Replanting age (<1-month, 1-year, 3-year and 7-year and first-cycle oil palm) and sampling zone (windrow or weeded circle) were fitted as categorical fixed effects. Sample plots were nested within oil palm block and fitted as random effects, to account for the nested sampling design of first-cycle plots. Plant species richness and ground cover were also tested as fixed effects in the model building process for both macrofauna abundance and macrofauna order richness. However, after model selection by Akaike Information Criteria (AICc) (Burnham et al., 2011) and assessment of the model fit, they were not included in the final model. Significance of replanting age on macrofauna order richness were explored via best linear unbiased predictions (BLUP) and p-values computed by Kenward-Rodger approximation (Luke, 2017).

To determine whether replanting affected soil macrofauna community composition, we fitted multivariate generalized linear models to the macrofauna abundance data using R package ‘mvabund’ (functions ‘manyglm’ and ‘anova.manyglm’) (Wang et al., 2012). We used this model-based method to analyse community composition because, unlike distance-based methods (e.g. PRIMER), multivariate generalized linear models can account for the confounding mean–variance relationships that often exist in ecological count data by modelling multivariate abundance data with a negative binomial distribution (Warton et al., 2016). Model terms were tested for significance with a likelihood ratio test and a Monte Carlo resampling scheme with 999 iterations; we simultaneously performed tests for univariate (single-order) responses to treatment, adjusting these univariate p-values to correct for multiple testing, using a step-down resampling procedure (Wang et al., 2012). A significance level of 0.05 was used.

A model-based approach was used to visualise change in soil macrofauna community composition. A pure latent variable model was fitted using Bayesian Markov Chain Monte Carlo (MCMC) estimation in the R package boral (Hui 2016). Default model parameters were used. Posterior latent variable medians from the model were plotted in an ordination in order to visualise potential clustering of first and second-cycle oil palm sites based on soil macrofauna composition, where the first two axes represents the two most important axes of macrofauna variation (Hui 2016).

A separate linear mixed effects model with plant species richness and plant cover was fitted with replanting age (<1-month, 1-year, 3-year and 7-year and first-cycle oil palm) and sampling zone (windrow or weeded circle) fitted as categorical fixed effects to examine the effect of replanting age on plant species richness and plant cover.

Results

Soil Macrofauna

We sampled a total of 6679 soil arthropods from 37 different orders and taxonomic groups. Ants made up over 50 % of all macrofauna (3817 individuals). Other common groups were Lumbricidae (673), Isoptera (304), Aranae (264), Blattodea (222), Dermaptera (221), Isopoda (219), Chilopoda (209), Coleoptera (193), Diplopoda (191) and Diplura (102). These groups contributed to 39 % of all macrofauna, and with ants totalled to over 95 % of all individuals sampled. Soil macrofauna order richness was lower in all replanting ages than in first-cycle oil palm (Fig. 1, Table 1) although this was marginally statistically significant for 3-year-old second-cycle oil palm (*P* = 0.083). There was an average of 3.8 more orders in the windrow than the weeded circle according to the model estimate (P < 0.001).

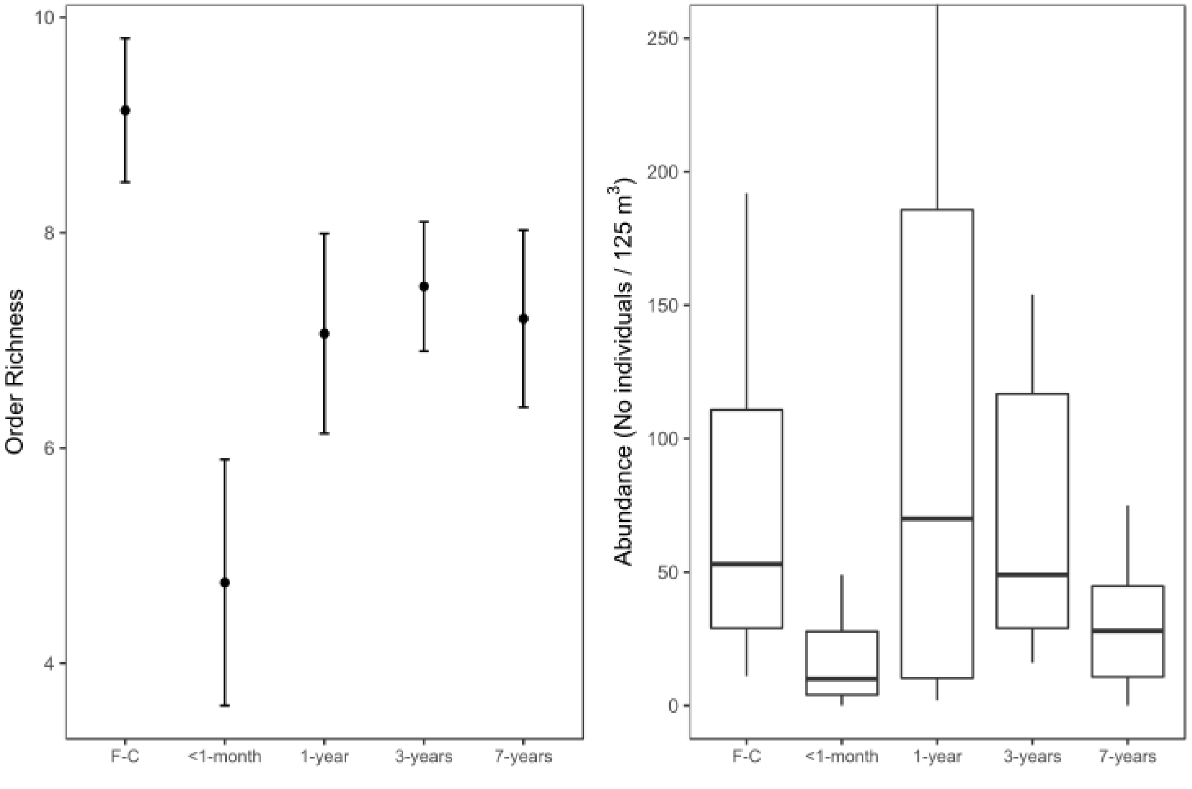

Figure 1: Soil macrofauna ordinal richness and abundance in first-cycle (F-C) oil palm and second-cycle oil palm ages: <1 month, 1-year, 3-years and 7-years. Box and whisker plots are presented for abundance due to the non-normal distribution of the data, with horizontal lines representing 25, 50 and 75% quantiles and whiskers representing range within 1.5 x of the lower or upper quantile. Data outside this range are plotted as individual points. Mean and standard error were plotted for order richness as data were distributed normally, filled circles indicate means and bars indicate standard errors.

Soil macrofauna abundance was lower in < 1-month-old (IRR = 0.22, *P* < 0.001), and 7-year-old (IRR = 0.41, *P* < 0.05) replanting ages compared to first-cycle oil palm (Fig. 1 and Table 1). Abundance of soil macrofauna was similar between first-cycle, 1-year-old (IRR = 0.97, *P* = 0.947) and 3-year-old (IRR = 0.96, *P* = 0.925) second-cycle oil palm. The abundance of macrofauna was 3.51 times higher in the windrow than the weeded circle (*P* < 0.001) for all age ranges according to the model estimate.

Soil macrofauna order composition changed between first and second-cycle oil palm sites (LR = 490.4, $P < 0.001$) and all replanting ages were different from first-cycle oil palm. Of the most abundant eleven orders, ten had adjusted univariate *P* values that were significant at the 0.005 level and showed difference in abundance between replanting ages: ants, Blattodea, Chilopoda, Coleoptera, Isopoda, Lumbricidae, Dermaptera, Hemiptera, Diplopoda and Diplura. Only Aranae abundance was not different between second-cycle and first-cycle oil palm. Dermaptera, Diplura and Isopoda abundance was reduced in all ages of replanting compared to first-cycle oil palm (Fig. 2). The latent variable model-based ordination showed clear clustering of the first-cycle sites when compared to the second-cycle sites (fig.3). Macrofauna composition of second-cycle sites of different ages were more similar to each other than first-cycle sites, however, clustering within age groups was still evident.

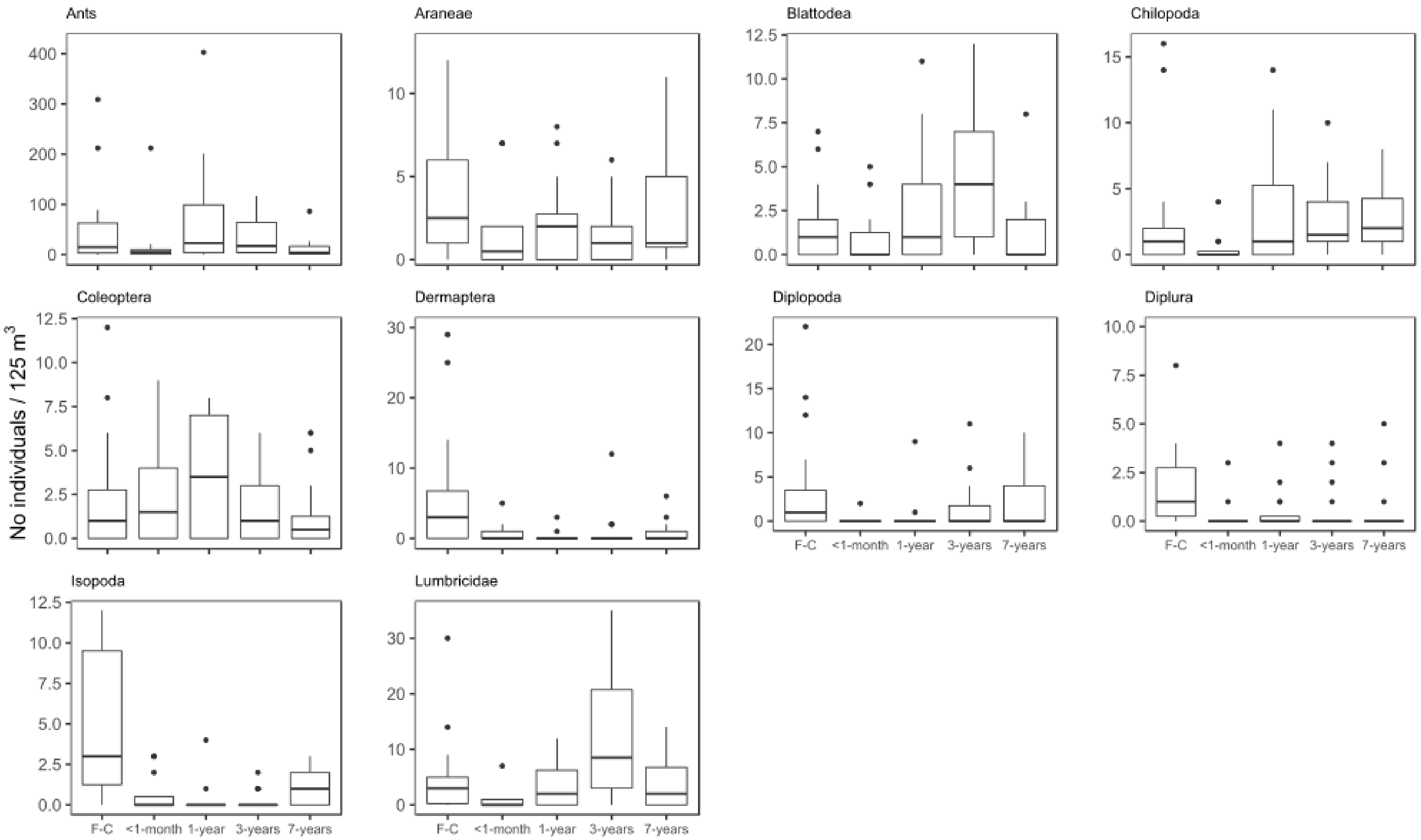

Figure 2: Box and whisker plots of soil macrofauna abundance for the ten most abundant orders in first-cycle (F-G) oil palm and second-cycle oil palm ages: <1 month, 1-year, 3-years and 7-years. Horizontal lines represent the 25, 50 and 75% quantiles and whiskers represent the range within 1.5 x of the lower or upper quantile. Data outside this range are plotted as individual points.

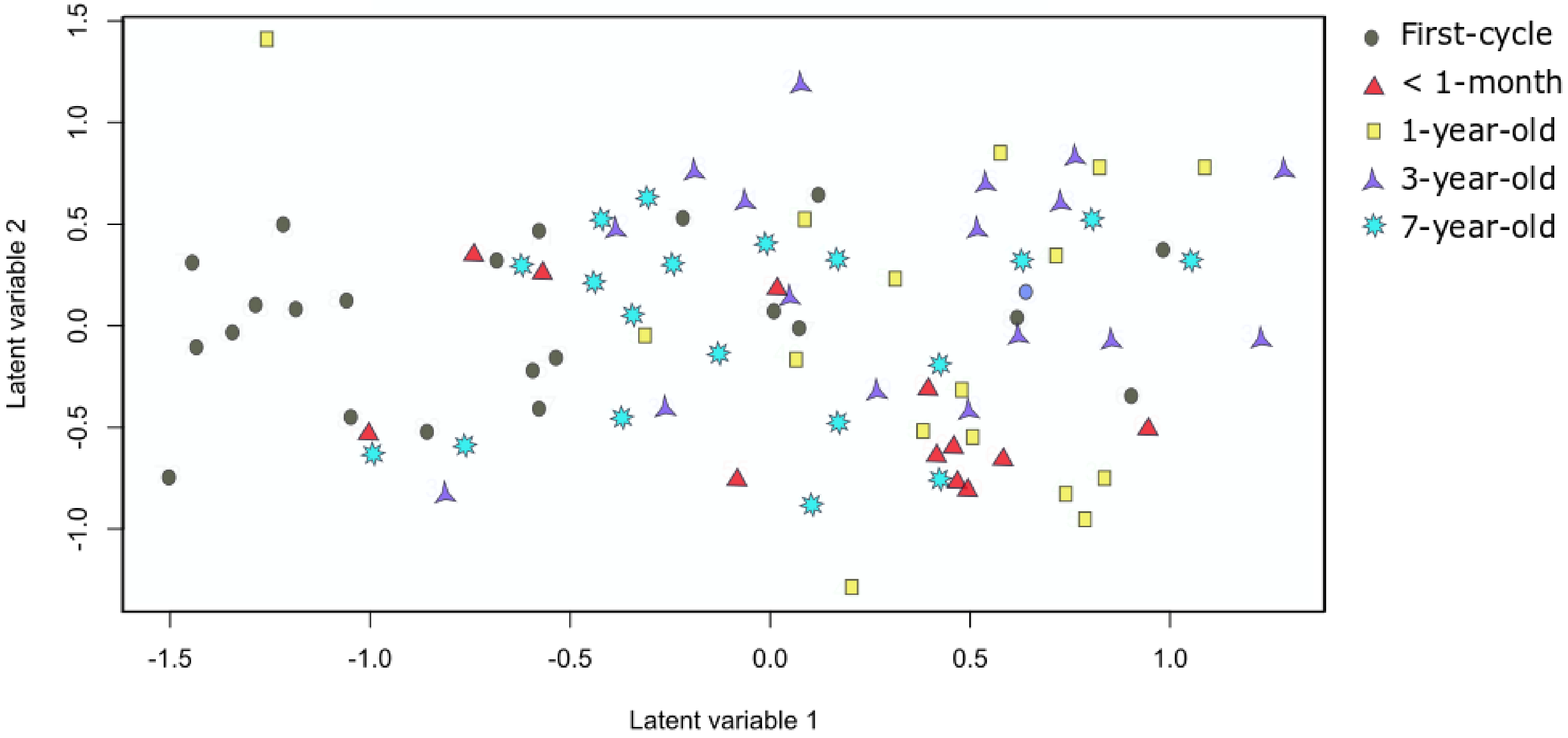

Figure 3: Latent variable model-based ordination of soil macrofauna composition of first-cycle and second-cycle (<1-month, 1-year, 3-year and 7-year old) oil palm sites.

In addition, soil macrofauna composition was different between the windrow and weeded circle (LR = 181.4, $P < 0.001$) (Table. 2). The abundance of ants (LR = 13.287, $P < 0.005$) Aranae (LR = 18.6, $P < 0.001$, Dermaptera (LR = 21.42, $P < 0.001$), Diplopoda (LR = 14.49, $P < 0.001$), Diplura (LR = 14.01, $P < 0.001$) Hemiptera (LR = 14.96, $P < 0.001$) and Isopoda (LR = 19.64, $P < 0.001$) were all lower in the weeded circle of second-cycle oil palm when compared to the weeded circle of first-cycle oil palm. Coleoptera, Hemiptera and ants had a higher abundance in the windrow, but not the weeded circle of 1-year-old second-cycle oil palm than in the other replanted ages and first-cycle oil palm.

Vegetation

Ground vegetation cover was completely removed after replanting (< 1month), however cover (model estimate= + 22.4%, $P < 0.001$) and plant richness (model estimate = + 4.7, $P < 0.001$) increased beyond first-cycle levels 1-year after replanting and then returned to first-cycle levels 3-years after replanting. There was no difference between vegetation cover or plant richness between first-cycle, 3-year and 7-year-old oil palm (Fig. 4, Table 1).Vegetation cover was much more extensive in the windrow (model estimate = + 25%, $P < 0.001$) than weeded circle, whereas plant richness was the same in both windrow and weeded circle.

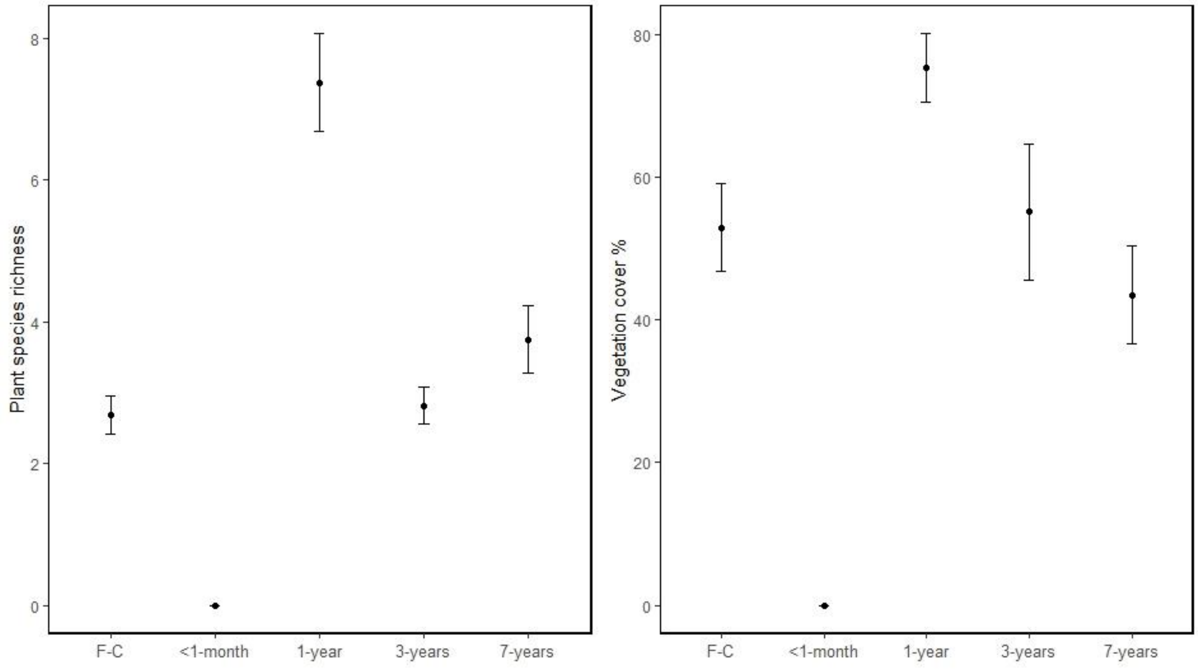

Figure 4: Plant species richness and vegetation cover in first-cycle (F-G) oil palm and second-cycle oil palm ages: <1-month, 1-year, 3-years and 7-years. Filled circles indicate means and bars indicate standard errors.

Discussion

Reduction in macrofauna abundance and order richness after replanting

Our study shows that replanting causes a marked decrease in soil macrofauna diversity and abundance. Worryingly, diversity and abundance of soil macrofauna were still lower in second-cycle oil palm, when plantations reached maturity (i.e. 7-years after replanting) and macrofauna community composition differed from first-cycle oil palm.

These negative impacts on soil macrofauna corroborate our recent findings that soil quality is severely degraded after oil palm replanting (Ashton-Butt et al in preparation). A primary reason for the decline in macrofauna could be the loss of soil organic matter (SOM). SOM is a key food resource for many soil invertebrates (Brussaard *et al.*, 2007). During the replanting process, soil is left completely denuded of vegetation and undergoes disruption and compaction by heavy machinery. This leaves the soil vulnerable to heavy tropical rains and likely results in large amounts of erosion which removes habitat and nutrients for soil macrofauna (Pimentel & Kounang, 1998). Furthermore, initial erosion is likely to leave the soil increasingly vulnerable to future erosion by reducing the stability of soil and the capacity for infiltration (Berhe et al., 2007; Hamza & Anderson, 2005). This is likely to further impact on soil macrofauna abundance and diversity during the years after replanting by further removing suitable habitat. Soil quality remains degraded 7-years after replanting (Ashton-Butt et al. in preparation), likely inhibiting the ability of soil macrofauna populations to recover and recolonise. There is also a reduction in soil inputs after replanting, that soil macrofauna feed on or inhabit, such as: rotting vegetation; undergrowth; root matter; and decaying trunks. Physical disturbance caused by large machinery used to cut down mature oil palms during replanting could also impact negatively upon soil macrofauna as soil microhabitats are disrupted (Tsiafouli et al., 2015)Large bodied and relatively long-lived soil fauna have been shown to be particularly sensitive to disturbance by agriculture (Postma-Blaauw et al., 2010; Tsiafouli et al., 2015).

In addition to physical disturbance of the soil medium, there is a large change in microclimate because of loss of canopy cover and understory vegetation, when the palms and undergrowth are removed during replanting. Soil is therefore exposed to higher temperatures than in mature plantations (Luskin & Potts, 2011). Hot and dry conditions can be unsuitable for many soil macroinvertebrates that are suited to cool, moist conditions,and tropical invertebrates can be particularly sensitive to rises in temperature (Fayle *et al.*, 2010; Robinet and Roques, 2010; Kingsolver *et al.*, 2011). Furthermore, soil water content (SWC) is reduced in second-cycle oil palm (Ashton-Butt et al. in preparation). This likely exacerbates the effect of increased temperatures on soil macrofauna. There are few studies on the impacts of disturbance and land-use change on soil fauna in oil palm plantations. However, species richness and abundance of litter dwelling ants substantially decrease after forest conversion to oil palm, likely due to a change in microclimate, increase in disturbance and reduction in habitat complexity (Fayle, *et al.*,2010; Foster *et al.* 2011). We suggest that the disturbance caused by replanting of oil palm are similar to those of land use change or intensive agricultural practices, as the complex habitat and diverse vegetation structure of perennial palms and undergrowth are removed.

Interestingly, abundance of soil macrofauna recovered to first-cycle levels in 1 and 3-year-old replanting oil palm, however it dropped to 41% of first-cycle levels when the plantation reached maturity (7-years of age). This temporary recovery of macrofauna abundance could possibly be due to the increase in vegetation richness and cover, a year after replanting. Herbicides use is reduced within the first year, which led to a rapid colonisation of plant species and therefore, a large resource of food and habitat for disturbance tolerance insects. Ants were found in extremely high abundance in this age class with a relative contribution per sample of over 55% of invertebrate individuals. Some ant taxa, particularly non-native species, have been found to be very tolerant to disturbance and extreme microclimates and are found in very high abundance in oil palm plantations (Fayle *et al.*, 2010). Furthermore Hemiptera were found in much higher abundance in this age class than any other; Hemiptera are primarily herbivorous and the increase in vegetation cover and plant species richness is a likely driver of their increase in abundance. When vegetation cover and plant richness dropped in the 3 and 7-year second-cycle age group, abundance of Hemiptera declined to levels below that of first-cycle oil palm.

Change in soil macrofauna composition after replanting

Macrofauna composition changed between first-cycle and second-cycle oil palm ages. Of the eleven most abundant groups, eight (Ants, Araneae, Blattodea, Coleoptera, Dermaptera, Diplopoda, Diplura and Isopoda) were more abundant in first-cycle oil palm than 7-years after replanting. This reduction of the majority of the most abundant groups in our study likely reflects the habitat degradation caused by replanting. Reduction of these orders after habitat disturbance and degradation has been found in studies in other habitats (Barnes et al., 2014; Parfitt et al., 2010; Tsiafouli et al., 2015). Abundance of some orders including, ants, Blattodea and Coleoptera, actually increased between 1 and 3-years after replanting, likely due to the increase in plant diversity and cover due to the halting of herbicide usage, but then fell again between 3 and 7-years when plant diversity and cover dropped. This suggests that reduction of diversity and abundance of soil macrofauna due to replanting could be buffered by using lower levels of herbicides and increased vegetation could prevent soil degradation and aid regeneration of SOM ((Ashton-Butt et al., 2018)) as seen in other crops (Keesstra et al., 2016; Parfitt et al., 2010). We recognise that due to the relatively coarse level of identification of soil macrofauna in this study, more nuanced relationships of diversity and community composition change between oil palm ages may have been missed. Thus, we predict that our findings on the negative impacts of replanting on soil biodiversity are likely conservative. Due to the staggering diversity of soil macrofauna and the poor understanding of tropical soil fauna taxonomy, further identification was out of the scope of this study. However, we did endeavour to include orders such as diplura, which are often ignored in tropical soil biota studies (Carron et al., 2015; Franco et al., 2016).Isoptera were found in low abundances in all oil palm ages, similar to findings from previous studies (Carron et al., 2015; Luke et al., 2014). Isoptera provide important ecosystem functions in tropical ecosystems such as decomposition of wood and soil and thus play important roles in nutrient cycling and are considered ecosystem engineers (Lavelle, 1997). Isoptera are found in very high abundances in the natural habitat in this region (tropical forest) but require humid conditions to avoid desiccation and soils rich in organic material for colony building and food (Eggleton, 1997; Hassall et al., 2006). Replanting causes a hotter and drier microclimate (Luskin & Potts, 2011) and reduces organic material in soil (Ashton-Butt et al. 2018), therefore, Isopteran abundance, especially for soil feeding species, is likely to be severely impacted in areas with high densities of oil palm plantations, possibly causing local and even regional extinctions of these species.

Influence of oil palm zone on abundance and richness

Macrofauna abundance was 70% lower and order richness was 35% lower in the weeded circle than in the windrow, according to our model estimates and in agreement with a previous study (Carron et al., 2015). The weeded circle is relatively devoid of vegetation, receives higher levels of chemical fertilisers and herbicides and is exposed to more disturbance by oil palm workers than the windrow (Carron et al., 2015). This finding highlights the importance of understory vegetation for soil biodiversity in oil palm plantations. Simplified understory in oil palm has been linked with lower above and below-ground invertebrate densities and decreased ecosystem functioning (Spear *et al.*, 2018; Ashton-Butt et al. 2018); an increased understory could provide protection and refuge for soil organisms during and after the replanting event. Vegetation cover and plant species richness were not good predictors of abundance or order richness in our models, however. There may have been an interaction effect that vegetation had with replanting age. However, these effects could not be included in our model due to insufficient sample sizes.

Potential impacts on ecosystem function

Reductions in soil biodiversity and abundance has been found to have negative effects on ecosystem functions such as nutrient retention, litter decomposition, carbon sequestration, SOM formation and plant diversity (de Vries et al., 2013; Handa et al., 2014; Lavelle et al., 2006; Wagg et al., 2014). It is likely that after oil palm replanting, there will be a synergistic effect from the degradation of soil biodiversity and soil quality, slowing or preventing soil rehabilitation. Loss of soil functionality could have a negative effect on oil palm yield and the soil's future viability as a medium for growing crops (Brussaard et al., 2007). Of the more abundant macrofauna groups, decomposers were badly affected; with abundance of Diplopoda, Diplura and Isopoda decreasing substantially after replanting and remaining low when plantations reached maturity. This could have a knock on effect on nutrient cycling; Diplopoda and Isopoda are considered functional keystone species in the soil habitat (Hättenschwiler et al., 2005) and transform the soil habitat by processing large amounts of litter (Heemsbergen et al., 2004; Jean-Francois & Gillon, 2002) and influence the composition of microbial decomposers and smaller soil fauna (Hättenschwiler et al., 2005). Diplura are understudied but nonetheless are thought to play key roles in litter decomposition and nutrient cycling (Wall et al., 2012). High abundances of these orders have been linked with greater decomposition rates in oil palm plantations (Ashton-Butt, et al., 2018.).

Conclusions

Soil macrofauna abundance, order richness and community composition are adversely affected by replanting of oil palm. This has worrying implications for the conservation of soil biodiversity in areas with large concentrations of oil palm plantations. Furthermore, this loss of soil biodiversity is likely to impact on ecosystem functioning; threatening the sustainability of oil palm beyond the first cycle of growth. A considerable loss of soil quality has been recorded following oil palm replanting (Ashton-Butt et al., in preparation; Matysek et al., 2018). The recovery of soil quality is likely to be severely inhibited by the reduction in key ecosystem engineers. In addition, we found that soil macrofauna temporarily recovered in abundance after replanting, possibly explained by a temporary rise in vegetation diversity,before falling considerably. This demonstrates the importance for future studies to investigate impacts on soil biodiversity, from perturbations, several years beyond the event.

Table 1. Model outputs of LMMs and GLMM comparing macrofauna order richness, abundance, plant species richness and vegetation cover between first-cycle and second-cycle oil palm ages: <1 month, 1-year, 3-years and 7-years. First-cycle oil palm weeded circle is the model intercept, all other model estimates are compared to this value.

	Macrofauna order richness			**(Log) Macrofauna abundance**			**Plant species richness**			**Vegetation cover**		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
First-cycle	7.22	5.84 – 8.60	**<0.001**	3.62	3.05 – 4.18	**<0.001**	3.05	2.18 – 3.92	**<0.001**	41.20	28.21 – 54.19	**<0.001**
<1 month	4.38	-6.45 – -2.31	**<0.001**	-1.52	-2.40 – -0.63	**0.001**	-3.06	-4.36 – -1.76	**<0.001**	-56.07	-76.56 – -35.58	**<0.001**
1-year	-2.07	-3.97 – -0.17	**0.033**	-0.02	-0.83 – 0.79	0.964	4.48	3.33 – 5.63	**<0.001**	23.62	5.27 – 41.98	**0.012**
3-years	-1.63	-3.47 – 0.21	0.083	-0.03	-0.80 – 0.73	0.930	-0.12	-1.27 – 1.03	0.836	5.23	-13.12 – 23.59	0.576
7-years	-1.93	-3.72 – -0.14	**0.035**	-0.90	-1.65 – -0.15	**0.019**	0.88	-0.27 – 2.03	0.135	-7.80	-26.15 – 10.56	0.405
Windrow	3.82	2.70 – 4.93	**<0.001**	1.25	0.86 – 1.65	**<0.001**	0.01	-0.76 – 0.79	0.974	23.74	14.80 – 32.68	**<0.001**

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Author Contributions

A.A-B. collected the data, analysed the data and wrote the paper. S.W helped with the study design and contributed to the writing of the paper. D. P helped with study design and conducted the vegetation surveys. S, A A.K.A, R.W, A.S.C.H helped with study design and data collection. G.M.P helped conceive the study. J-P Caliman helped with study design and contributed to writing the paper. K.S-H. P and J.L.S were principal investigators on the project and were involved in all stages of the study and manuscript preparation.

Date accessibility statement: All data from this study is available on Dryad.

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Chapter 6: Understory vegetation in oil palm plantations benefits soil biodiversity and decomposition rates

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Abstract

Oil palm is the most productive vegetable oil crop per unit area and is crucial to the economy of developing countries such as Malaysia and Indonesia. However, it is also highly controversial due to the impact it has on biodiversity. Inputs of herbicides to control understory vegetation in plantations are high, which is likely to harm native biodiversity, but may be unnecessary in protecting oil palm yield. In this study we investigate the effects of understory manipulation using herbicides on soil fauna, litter decomposition rates and soil abiotic variables: pH, soil organic carbon, soil water content, nitrogen, carbon/nitrogen ratio, potassium and phosphorous. Understory vegetation was manipulated in three treatments: enhanced understory complexity (no herbicides, developed understory), normal understory complexity (intermediate herbicide use with some manual removal) and reduced understory complexity (heavy herbicide use, no understory vegetation). Two years after treatment, soil macrofauna diversity was higher in the enhanced than the normal and reduced understory treatment. Furthermore, both macrofauna abundance and litter decomposition was higher in the enhanced than the reduced understory treatment. By contrast, soil fertility did not change between treatments, perhaps indicating there is little competition between oil palms and understory vegetation. The reduction of herbicide use should be encouraged in oil palm plantations, this will not only reduce plantation costs, but improve soil biodiversity and ecosystem functioning.

Introduction

Oil palm is the most productive vegetable oil crop per unit area (Zimmer, 2010) and is a crucial part of the economy in developing countries such as Indonesia and Malaysia (Koh & Wilcove, 2007). However, with over 21 million ha of plantations covering the tropics (FAOSTAT, 2016) oil palm cultivation is also one of the most controversial land uses. This is primarily due to the negative impacts on biodiversity and climate change caused by forest conversion to plantations (Carlson et al., 2013; Savilaakso et al., 2014). Therefore, improving the management of oil palm plantations to protect existing biodiversity and ecosystem functions is vital for agricultural sustainability and biodiversity conservation (Foster et al., 2011). Furthermore, it is in the interest of plantation managers to develop and apply sustainable practices, as this can lead to economic gain (Woittiez et al., 2017) and there is considerable market demand for palm oil to be certified as sustainable by the Round Table on Sustainable Palm Oil (RSPO) (Tayleur et al., 2018). Oil palm has the potential to implement relatively long-term sustainable management practices as it is a perennial crop with a ~25 year commercial lifespan. One of the core management criteria for plantations to be certified as sustainable by the RSPO is to improve soil sustainability (Roundtable on Sustainable Palm Oil, 2013).

Soil biodiversity plays a large part in the ecosystem functions that help maintain soil sustainability (Bardgett & van der Putten, 2014). Soil biota are important for many vital ecosystem functions such as: nutrient cycling; carbon sequestration; and nutrient uptake by plants. However, soil biodiversity is threatened by land use change and agricultural intensification (Franco et al., 2016; Tsiafouli et al., 2015) which can reduce ecosystem functioning (Bardgett & van der Putten, 2014; de Vries et al., 2013). For example, reductions in decomposer functional diversity has been shown to reduce decomposition rates and carbon and nutrient cycling (Handa et al., 2014), which are important ecosystem functions for soil formation and fertility (Nielsen et al., 2011).

While there has been a recent upsurge in research investigating the effects of oil palm plantation management on aboveground biodiversity and ecosystem function (Nurdiansyah et al., 2016; Syafiq et al., 2016; Teuscher et al., 2016), belowground biodiversity and soil functioning has been severely neglected (Bessou et al., 2017). Recent studies have found large declines in soil fertility and, in particular, soil organic carbon (SOC) in oil palm plantations after forest conversion, with continued declines as plantations age (Ashton-Butt et al., in review.; Guillaume et al., 2018; Matysek et al., 2018). There are also changes to belowground biodiversity after forest conversion to oil palm; with termites and litter feeding ants showing severe declines (Luke et al., 2014); and soil microbial communities have been found to alter in community composition and functional gene diversity (McGuire et al., 2015; Tripathi et al., 2016). However, the effect of these changes in biodiversity on ecosystem functioning is little known (Dislich et al., 2016). Recent research has found that the application of organic matter to the soil can improve soil quality and related biotic functions (Carron et al., 2016; Tao et al., 2016, 2018) and different zones around the palm hold varying amounts of soil fauna and nutrients as a result of standard management regimes (Carron *et al.*, 2015).

Soil communities and their functioning are largely impacted by the diversity and abundance of plant communities (Eisenhauer et al., 2011; Thakur & Eisenhauer, 2015). Oil palm plantations can have a reasonably diverse plant understory (Foster et al., 2011). However, these plants are often seen as weeds thought to compete with oil palms for nutrients by some plantation managers and although understory vegetation management varies widely between different plantations, complete removal by herbicides and weeding is common (Tohiran et al., 2017). A typical plantation uses up to 90% of its pesticide budget on herbicides such as paraquat, glufosinate ammonium and glyphosphate (Page & Lord, 2006; Wibawa et al., 2010). This extensive use of herbicides can pollute water sources and pose a threat to natural ecosystems and human health (Comte et al., 2012; Schiesari & Grillitsch, 2011). Herbicides are also economically costly, especially to small-scale farmers (Lee et al., 2014). Furthermore, the use of pesticides in agriculture has been linked with mass biodiversity declines around the world (Beketov et al., 2013; Geiger et al., 2010) without consistent benefits to agricultural yield (Lechenet et al., 2017). In oil palm plantations, reduction in herbicide use and a greater coverage of understory vegetation has been shown to improve avian biodiversity (Nájera & Simonetti, 2010; Tohiran et al., 2017). Furthermore, a greater developed understory benefits aboveground invertebrate communities, by providing additional habitat and food resources (Ashraf et al., 2018; Chung et al., 2000; Spear et al., 2018). However, it is not known how the understory vegetation in oil palm plantations influences belowground invertebrate communities and related ecosystem functions.

In this study, we investigate the effect of experimentally manipulating understory vegetation in oil palm plantations on soil macrofauna abundance, diversity and community composition, and litter decomposition rates and soil abiotic properties in oil palm plantations. We hypothesised that macrofauna abundance and diversity would be positively affected by the amount of understory vegetation and that this would have correspondingly positive effects on soil processes. Our findings will have important implications for the sustainable management of oil palm plantations.

Methods

Study area

Fieldwork took place in Sumatra, Indonesia, as part of the Biodiversity and Ecosystem Function in Tropical Agriculture (BEFTA) Programme. The BEFTA Vegetation Project is a large-scale, long-term ecological experiment testing the influence of different understory vegetation management strategies on oil palm biodiversity, ecosystem functioning and yield (Foster et al. 2014). The project is located in oil palm estates owned and managed by Pt Ivo Mas Tunggal, a subsidiary of Golden Agro Resources (GAR) and with technical advice from Sinar Mas Agro Resources and Technology Research Institute (SMARTRI, the research and development centre of GAR). The estates are located in the Siak regency of Riau Province, Sumatra (0°55′56″ N, 101°11′62″ E) (see Foster *et al.*, (2014)). This area receives an average rainfall of 2400 mm/yr, with the natural landscape characterized by wet lowland forest on sedimentary soils. The soil type is ferralitic with gibbsite and kaolinite (Ferric Acrisol according to the FAO classification). Our study area was logged in the 1970s and the resulting logged forest was converted to oil palm from 1985–1995. The plantations included in this study were on average 25 years old (between 29 and 23 years old). The majority of the area around these estates is used to cultivate oil palm. There is no natural forest and few other crops are grown.

Standard fertiliser treatment of oil palm in our study site includes: 1.75 kg tree^{-1} yr^{-1} urea (46% N); 0.5 kg tree^{-1} yr^{-1} triple super phosphate (45% P_2O_5, 15% Ca); 2.5 kg tree^{-1} yr^{-1} muriate of potash (61% K_2O, 46% Cl); and 0.5 kg tree^{-1} yr^{-1} Kieserite (16% Mg, S: 22%).

Understory treatments:

Eighteen study plots were established in October 2012. Oil palms on all plots were planted between 1987 and 1993, and so were mature at the time of the study. Plots were 150 m x 150 m and are located on flat ground between 10 and 30 m above sea level and without adjacent human habitation. The plantations have a typical zonation of soil and vegetation management leading to 3 distinct zones, weeded circle, harvesting path and windrow (Fig 1). The plots were arranged adjacently in triplets, with one plot in each triplet randomly assigned one of three understory vegetation management treatments (Fig. 2). Treatments were implemented in February 2014, and involved the following management:

1) Normal understory complexity: standard company practice, consisting of intermediate understory vegetation management using herbicides and some manual removal. The weeded circle (a circular zone around the palm) and harvesting paths were sprayed, and woody vegetation (shrubs and trees) was removed manually.

2) Reduced understory complexity: all understory vegetation was removed using herbicides.

3) Enhanced understory complexity: understory vegetation was allowed to grow with limited interference except for minimal manual clearance in the weeded circle and harvesting paths.

The herbicides used in the establishment of the plots were Glyphosate (Rollup 480 SL), Paraquat Dichloride (Rolixone 276 SL), metsulfuron-methyl (Erkafuron 20 WG) and Fluroxypyr (Starane 290 EC).

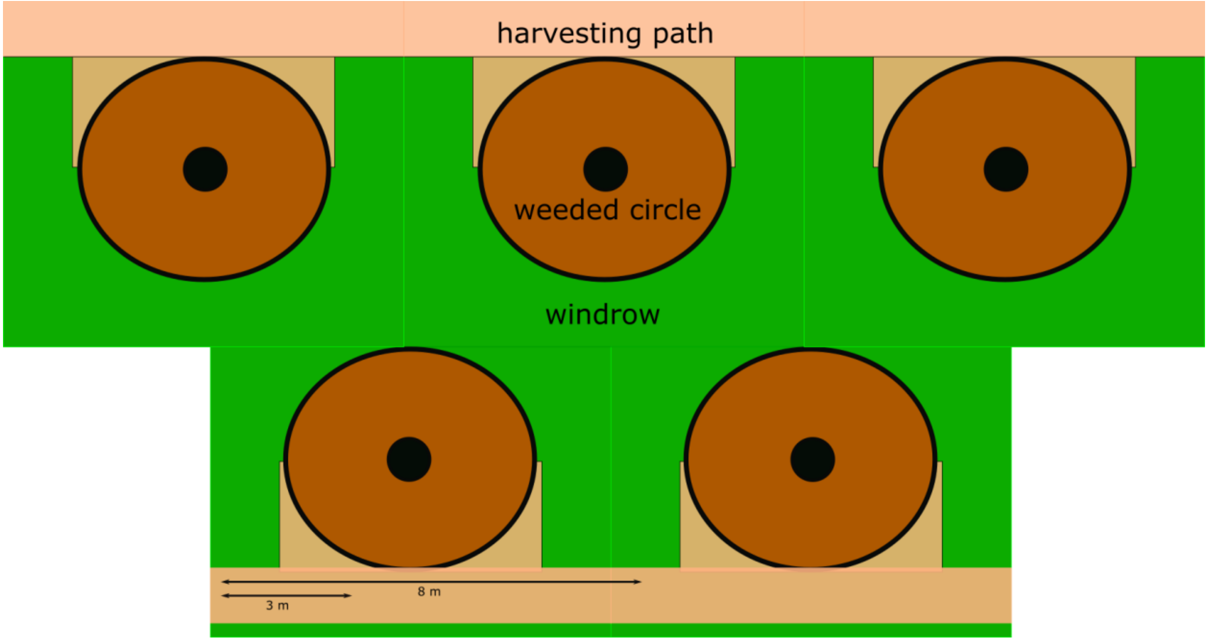

Figure 1. Diagram representing different management zones. The oil palms are the filled circles. The weeded circle is a circular zone with a radius of 1.8 m directly around the palm trunk, which is normally kept "clean" by chemical weed control to facilitate the collection of fruit bunches. The windrow is the zone where the palm fronds pruned during harvest (approximately 18 fronds palm−1 year −1) are placed on the ground forming a U-shaped windrow around the palm. The harvesting path is a zone cleared for access in the alternate rows, with the windrows in-between.

Figure 2. Photographs of the three understory treatments: Reduced complexity; Normal complexity; and Enhanced complexity (from left to right). Photographs courtesy of Edgar Turner.

Vegetation sampling

Ground vegetation surveys were conducted (between April and June 2016, two years after the treatments were established)within each of the 6 replicate treatment blocks,at two sampling points (two palms) (12 palms from each treatment), totalling 36 points. At each sampling point, a 1 m x 1 m quadrate was placed randomly, 4 times, within both the weeded circle and windrow zones and the ground cover and bare ground estimated from an average of two observers. In addition, within each quadrat plants were identified to species level and abundance of each species recorded.

Soil macrofauna sampling

Soil macrofauna was sampled at the same points as the vegetation surveys, with samples being taken from both the circle and the windrow, as these have been shown to hold different soil macrofauna abundance and composition (Carron *et al.*, 2015). The harvesting path was not sampled, as this is known to contain a very low abundance of soil macrofauna (Carron *et al.*, 2015). We used a standard Tropical Biology and Fertility Institute soil monolith method to sample invertebrates (Bignell et al., 2008), which involved excavating a 25 cm x 25 cm quadrat to a depth of 20 cm. All macrofauna, characterised as fauna visible to the naked eye (Kevan, 1968), were removed from soil samples in the field by hand-searching. Worms were placed immediately into formalin and all other arthropods were stored in 70% ethanol for later identification. Invertebrates were sorted to order, with the exception of termites and ants, which were separated from Blattodea and Hymenoptera, owing to their abundance and distinct ecology, and Diplopoda and Chilopoda, which were identified to class.

Soil abiotic sampling

Soil abiotic samples were taken from the same sample locations as the vegetation and soil macrofauna surveys. Soil was collected from the weeded circle and windrow from 0-15cm depth using a soil Dutch auger. At each sampling point, three samples were taken and bulked from each of the weeded circle and windrow. The weeded circle and windrow have been found to have different soil nutrient contents in previous studies (Carron *et al.*, 2015; Tao *et al.*, 2016) and thus were kept separate.

The following soil chemical properties were measured: soil pH, soil organic carbon content (SOC), total nitrogen (N) content, carbon/nitrogen ratio (C/N ratio), total phosphorous content (P) and total potassium content (K). The soil pH was determined using a pH meter with a soil to water ratio of 1:1. The SOC concentration was measured by loss-on-ignition, using the Walkley–Black method (Nelson & Sommers, 1982). The total soil P concentration was analysed using the hydrogen chloride extraction method. The total N was determined by the Kjeldahl method (McGill & Figueiredo, 1993). In addition to the chemical properties, soil aggregate stability (the ability of soil particles to resist disintegration) was measured on 3-5 mm aggregates according to the method proposed by Le Bissonais (1996) and soil water content were measured by the oven drying method.

Litter decomposition rates

We used litter decomposition bags, made of fine mesh, to calculate litter mass loss over time. Bags (10 cm x 10 cm) were filled with 4 g of freshly-cut oil palm fronds that had been dried to a constant weight in the oven. Bags were subject to two treatments: closed bag with no holes, excluding invertebrates, and open bags that had eight 1cm holes cut into them, allowing access to invertebrates. Open bags were placed with the holes facing upwards, in order to prevent leaf litter from falling out of the bags. Closed bags represent decomposition from microbes only and open bags decomposition from microbes and invertebrates. Both closed and open bags were stapled together and placed in each weeded circle and windrow at all sampling points (a total of 144 bags). Bags were left in the field for 30 days after which they were collected, dried at 70°C to a constant weight and weighed to measure mass loss.

Statistical analysis

All statistical analysis was performed in R 3.4.4 (R Core Team, 2018). We used linear mixed effects models (LMM) in R package ‘lme4’ (Bates et al., 2014) to examine the effect of understory treatment on order richness and general linear mixed effects models (GLMM) to examine the effect on soil macrofauna abundance (as count data should not be modelled using a Gaussian distribution). We used a negative-binomial distribution to fit the GLMM to account for overdispersion. Understory treatment and sampling zone (weeded circle or windrow) were fitted as categorical fixed effects. Interaction effects were explored between sampling zone and understory treatment for both LMMs and GLMMs and were introduced into the GLMM based on model selection by the AICc value (Brewer et al., 2016). Sampling zone (weeded circle or windrow) was nested within the oil palm sampled and fitted as random effects. Model estimates for GLMMs were presented as incidence rate ratios (Tripepi et al., 2007) as these are more intuitive than the negative binomially transformed model estimates.

A separate linear mixed effects model with plant species richness and vegetation cover was fitted with understory treatment and sampling location (windrow or weeded circle) as interacting categorical fixed effects to examine the effect of understory treatment on plant species richness and plant cover.

To determine whether understory treatment affected soil macrofauna community composition, we fitted multivariate generalized linear models to the macrofauna abundance data using R package 'mvabund' (functions 'manyglm' and 'anova.manyglm') (Wang et al., 2012). We used this model-based method to analyse community composition because, unlike distance-based methods (e.g. PRIMER), multivariate generalized linear models can account for the confounding mean–variance relationships that often exist in ecological count data by modelling multivariate abundance data with a negative binomial distribution (Warton et al., 2016). Model terms were tested for significance with a likelihood ratio test and a Monte Carlo resampling scheme with 999 iterations. Tests were simultaneously performed for univariate (single-order) responses to treatment, adjusting these univariate p-values to correct for multiple testing (Wang *et al.*, 2012).

To explore the effect of understory treatment on soil abiotic properties, LMMs were used with the same model structure as macrofauna order richness. C/N ratio, aggregate stability and pH fitted a normal distribution, however, soil variables: C, N, P, K and water content were log-transformed to correct for a non-normal distribution.

To determine the effect of understory treatment on decomposition rates we used a LMM. The model included understory treatment, sampling zone (weeded circle or windrow) and decomposition bag treatment as categorical fixed effects. Interaction effects were explored during model selection between the fixed effects, but were not included based on AICc values (Brewer et al., 2016). Sampling zone (windrow or weeded circle) was nested within the oil palm sampled and fitted as random effects. The model was: *decomposition rate~ understory treatment + sampling* *zone + bag treatment (1| oil palm/sample number)*. Significance of all LMMs and GLMMs were explored via p-values computed by Kenward-Rodger approximation (Luke 2017).

Results

Vegetation

Vegetation cover did not differ between normal and enhanced understory treatments (estimate = -9.23, *P* = 0.306), but was higher than the reduced treatment for both weeded circle and windrow (Table 1 and Fig. 2). Forty-five plant species were identified in the plantations. *Asystasia micrantha* was the most abundant species followed by *Nephrolepis biserrata, Peperomia pellucida* and *Asplenium longissimum.* Plant species richness did not differ between normal and enhanced understory treatments, but was higher than the reduced treatment for both weeded circle and windrow (estimate = -2, *P* = 0.003) (Fig 3). Sampling zone had an interaction effect within treatment; the windrow of the enhanced understory treatment had a lower species richness than the weeded circle (estimate = -1.31, *P* = 0.035), whereas there was no difference between plant species richness of the weeded circle and windrow in the normal and reduced treatment.

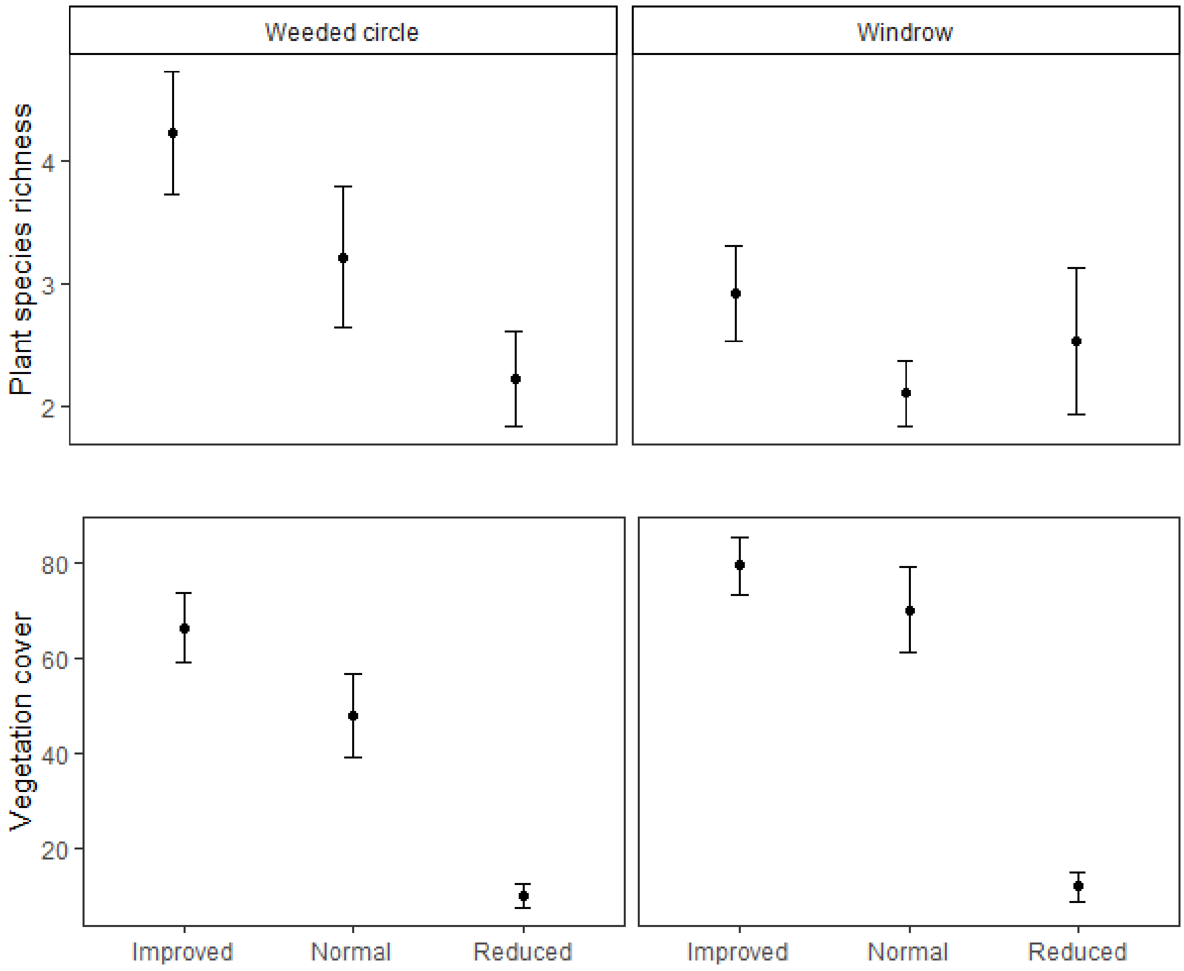

Figure 3. Plant species richness and vegetation cover of the weeded circle and windrow of the Enhanced, Normal and Reduced understory treatments. Filled circles indicate treatment means and bars standard errors.

Macrofauna richness and abundance

For the macrofauna survey, we sampled 6417 individuals from 34 orders and taxonomic groups. Ants were the most abundant group found followed by: Dermaptera, Lumbricidae, Aranae, Isopoda, Diplopoda, Chilopoda, Blattodea, Diplura, Coleoptera and Diptera. Order richness was higher in the enhanced understory treatment compared to the normal (estimate = -1.51, $P < 0.05$) and reduced understory treatments (estimate = -2.46, $P < 0.001$) (Table 1 and Fig. 3). Order richness was also higher in the windrow (estimate = +3.11, $P < 0.001$) than the weeded circle in all treatments (Fig. 4). Macrofauna abundance was higher in the weeded circle (but not the windrow) in areas with an enhanced understory than both areas with normal (IRR = 0.22, *P* < 0.005) and reduced understory (IRR = 0.3, *P* < 0.01) (Fig. 4). In addition, abundance was higher in the windrow than the weeded circle of the normal (IRR = 4.64, *P* < 0.005); and reduced understory treatments (IRR = 3.37, *P* < 0.01). However, in the enhanced understory treatment, the windrow had a lower macrofauna abundance than the weeded circle, although, this was marginally non-significant (IRR = 0.53, *P* = 0.053).

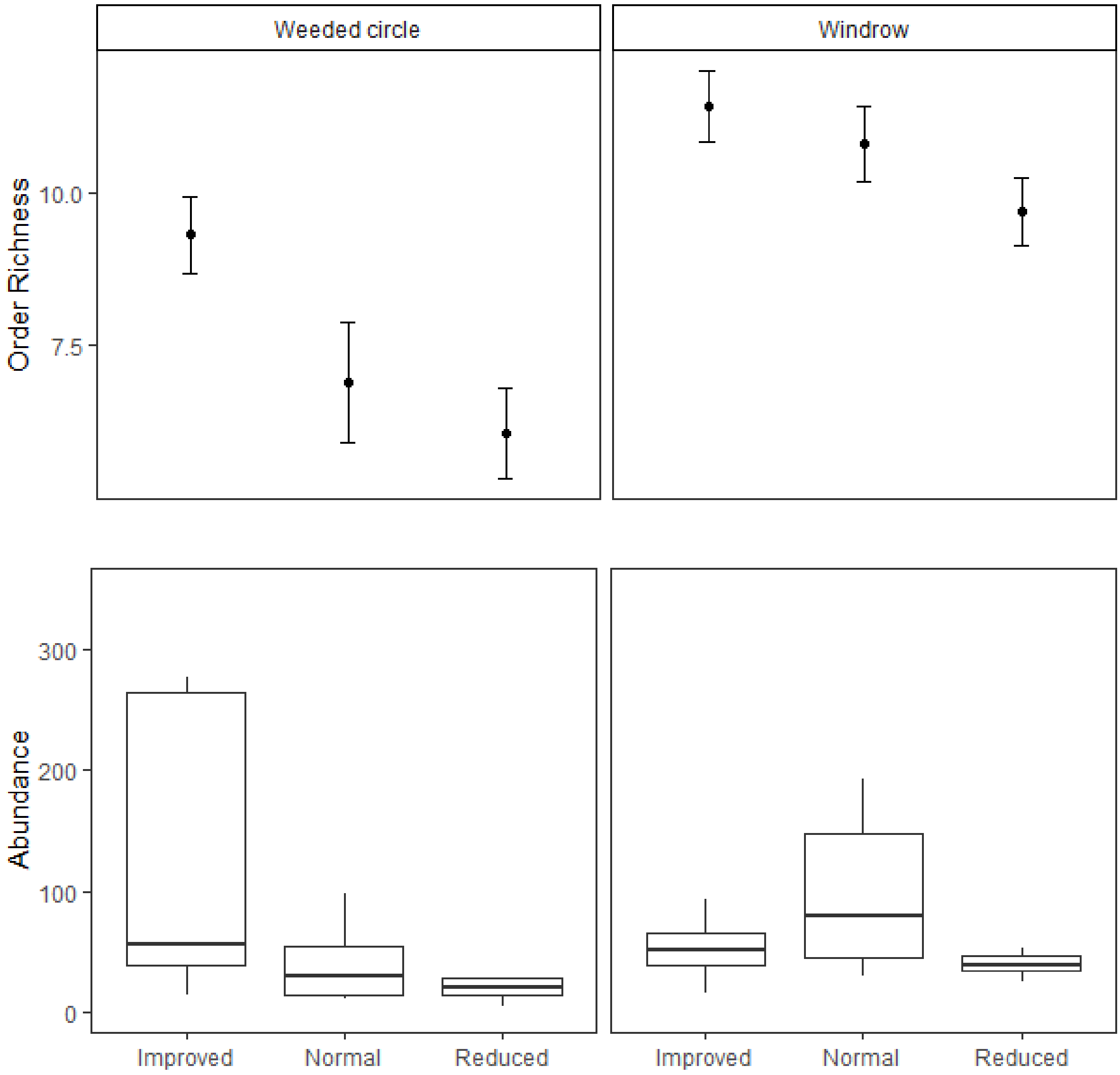

Figure 4. Soil macrofauna abundance and order richness in the weeded circle and windrow of the Enhanced, Normal and Reduced understory treatments. Filled circles indicate treatment means and bars standard errors.

Macrofauna Composition

Understory treatment had an effect on macrofauna composition (LR = 144.4, $P < 0.001$). The normal (LR = 52.69, $P < 0.001$) and reduced understory treatment (LR = 115.49, $P < 0.001$) differed in soil macrofauna composition from the enhanced treatment. The reduced understory treatment exhibited a larger difference in macrofauna composition from the enhanced treatment than the normal understory treatment. Zone of oil palm sampled (weeded circle or windrow) also had an interaction effect with treatment on macrofauna composition in the enhanced (LR = 69, $P < 0.001$), normal (LR = 38.93, $P < 0.01$), and reduced (LR = 115.49, $P < 0.001$) understory treatments. Ant (LR = 13.32, $P = 0.02$) Coleoptera (LR = 12.55, $P = 0.038$), Dermaptera (LR = 13.93, $P = 0.012$), Diplopoda (LR = 11.93, $P = 0.048$), Isopoda (LR = 13.8, $P = 0.013$) abundances were all affected by treatment, with lower abundances present in the reduced understory treatment than the enhanced or normal treatments (Fig. 5).

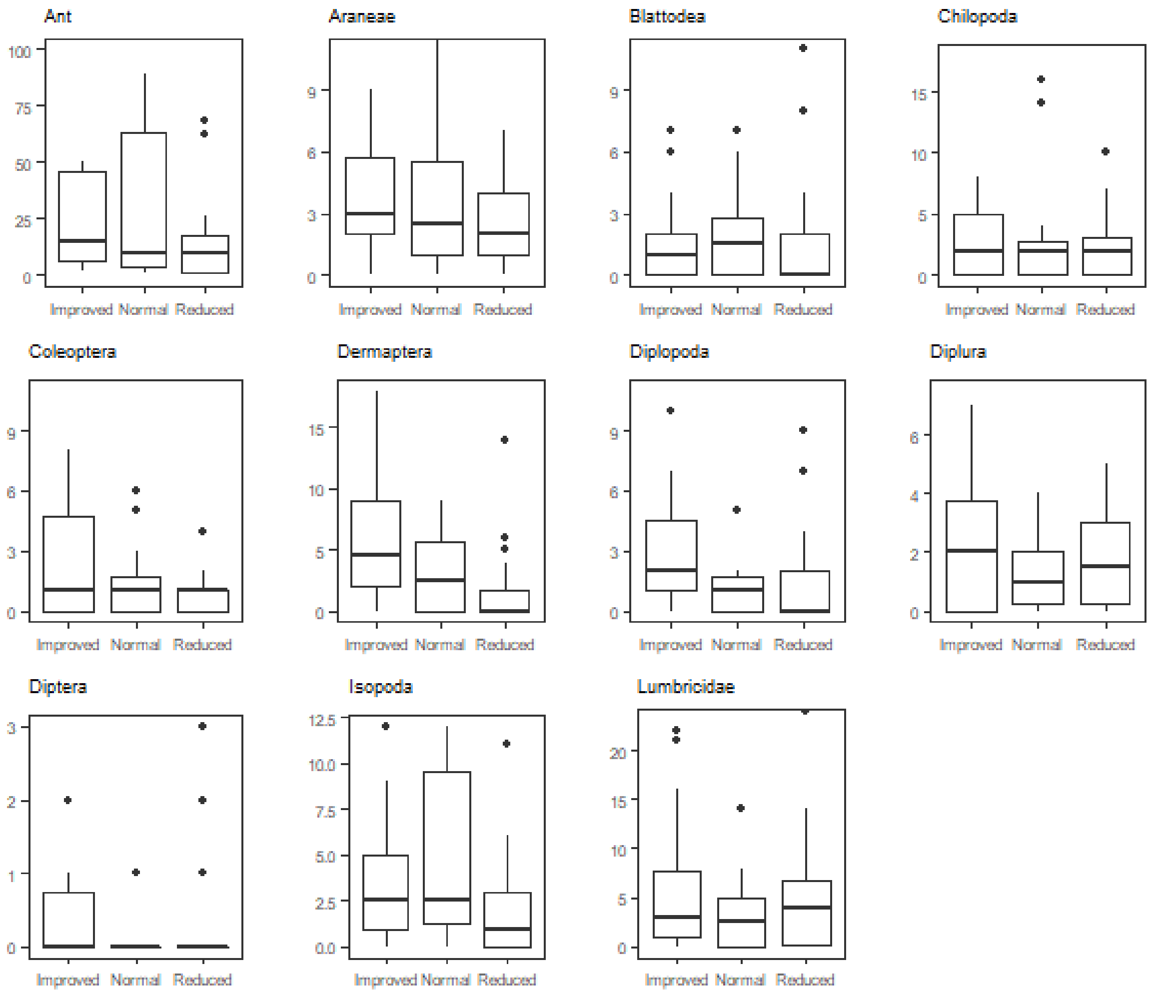

Figure 5. Abundance of the 11 most abundant orders found in the Enhanced, Normal and Reduced understory treatment.

Abiotic variables

Understory treatment had no effect on SOC, N, P, K, SWC, C/N ratio, aggregate stability or pH (Fig. 6 and Table 2). The zone of the oil palm sampled also had no effect on these variables apart from C/N ratio, where the windrow had a slightly higher C/N ratio than the weeded circle (model estimate = +2.65, *P* = 0.018) and total phosphorous where the windrow had a slightly lower total phosphorous level in the soil than the weeded circle (model estimate = -0.40, *P* = 0.045).

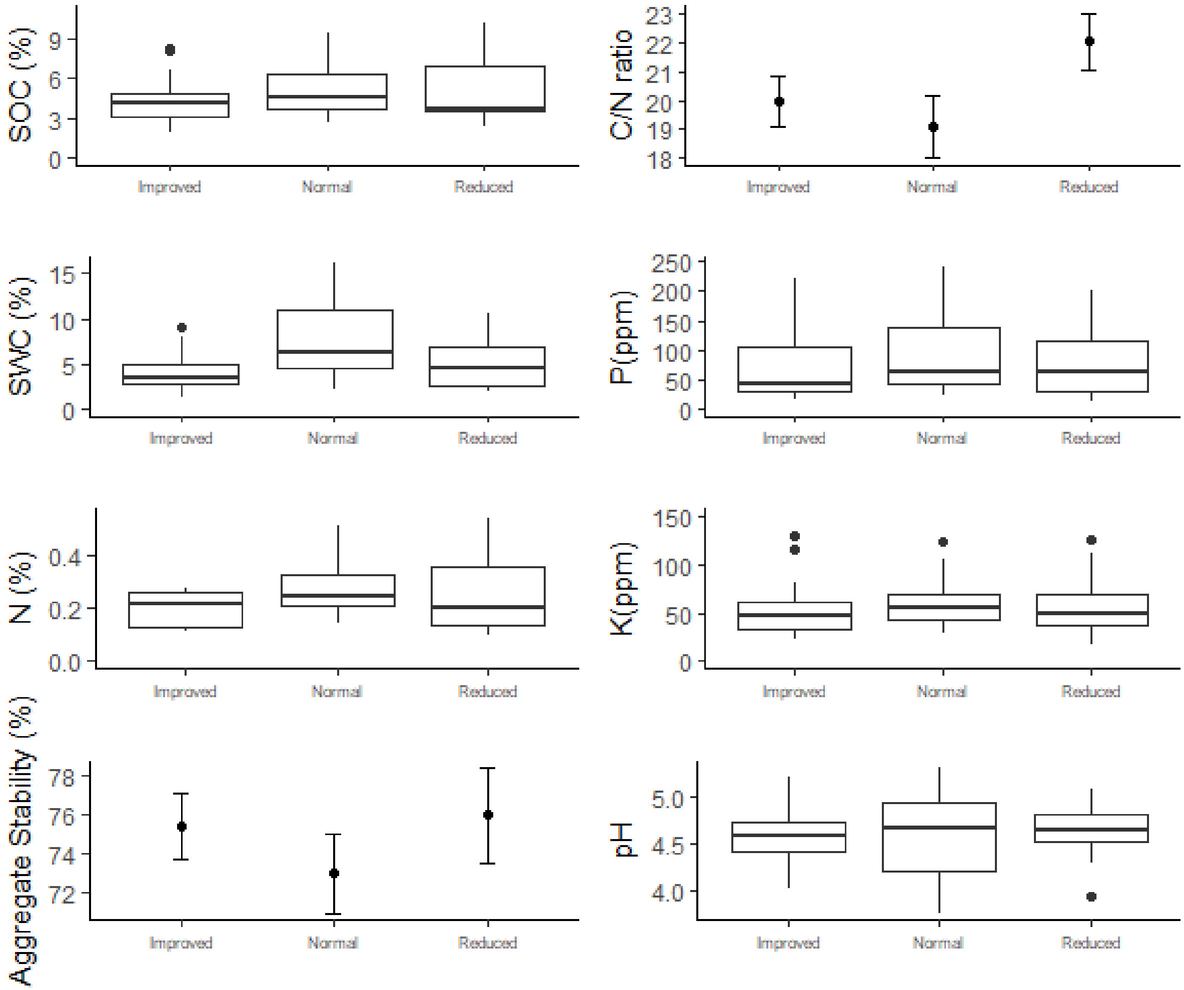

Figure 6. Soil abiotic properties of the Enhanced, Normal and Reduced understory treatments. Box-and-whisker plots present data with a non-normal distribution. Filled circles indicate treatment means and bars standard errors for normally distributed data.

Decomposition

Decomposition rate was higher in the enhanced treatment compared to the reduced understory treatment (estimate = -0.0068 g$^{/}$day, *P* = 0.003) (Table 3 and Fig. 7) and in the normal treatment compared to the reduced treatment (estimate = -0.0054 g$^{/}$day, *P* = 0.028). Decomposition rate was marginally lower in the normal understory treatment compared to the enhanced understory treatment, although this was not statistically significant (estimate = -0.0014 g/day, *P* = 0.548). Bag treatment also had an effect on decomposition: open bags experienced a higher decomposition rate than closed bags (estimate= 0.0031 g/day, *P*=0.042). Sampling zone also had a large effect on decomposition with bags in the windrow experiencing a higher decomposition rate than those in the weeded circle (estimate=0.0074 g/day, $P<0.001$).

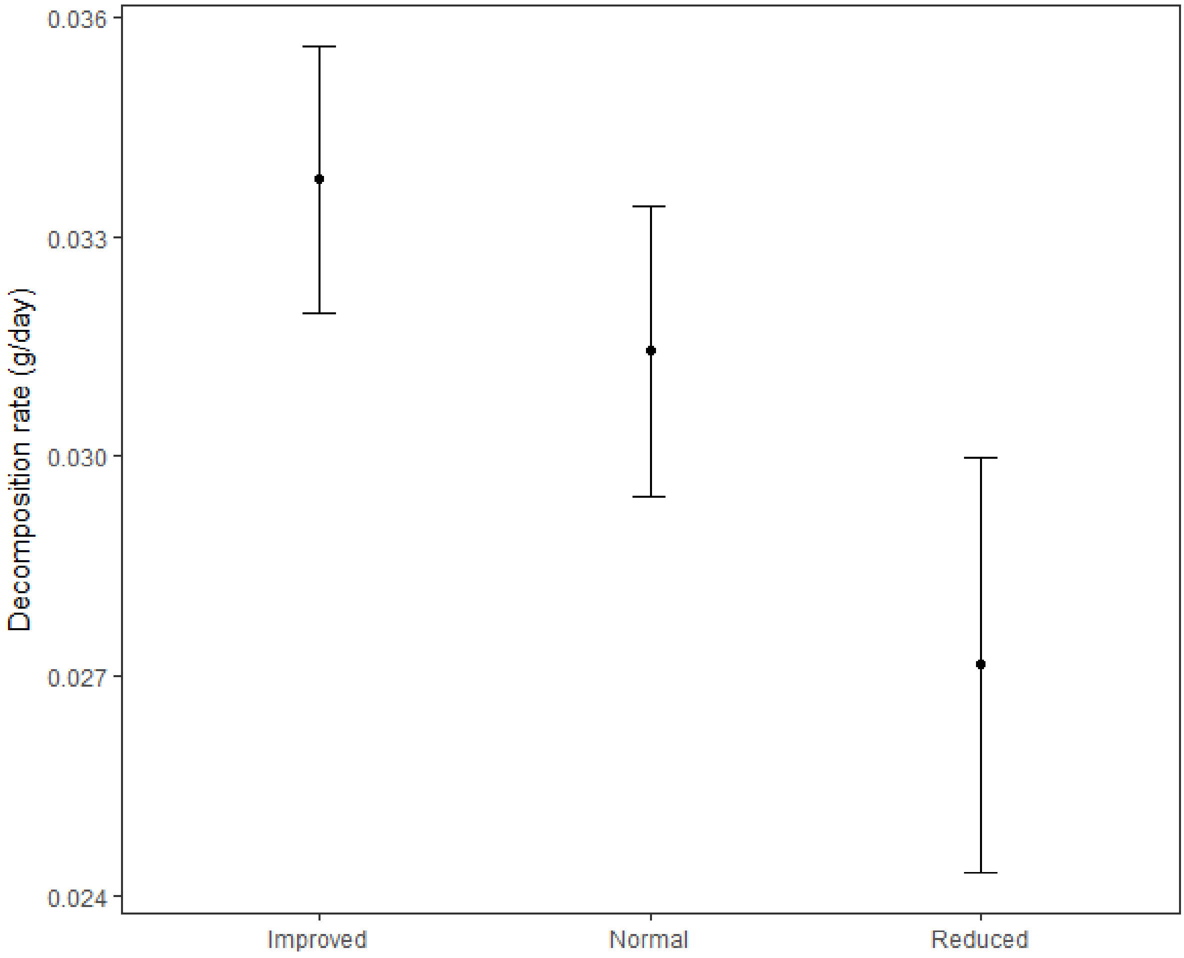

Figure 7. Decomposition rate of litter bags in the Enhanced, Normal and Reduced understory treatment. Filled circles indicate treatment means and bars standard errors.

Discussion

Our findings show that diversity and abundance of soil macrofauna along with belowground ecosystem functioning can be improved in oil palm plantations by reducing herbicide applications and enhancing understory vegetation. Furthermore, soil nutrient levels were the same in the enhanced understory treatment compared to the other treatments, adding to evidence that understory vegetation is unlikely to compete for nutrients with oil palms.

Soil macrofauna

Soil macrofauna order richness and abundance were higher in enhanced understory plots than the reduced plots and order richness (but not abundance) was higher in plots with an enhanced understory compared to normal understory plots. Increased plant diversity (characteristic of the enhanced understory plots) has been found to benefit soil biota in other systems (Scherber *et al.*, 2010; Eisenhauer *et al.*, 2011, 2012) and increased understory complexity can increase aboveground invertebrate abundance and food web complexity in oil palm plantations by providing greater resources (Spear et al., 2018). Furthermore, oil palm plantations suffer from hotter and drier microclimates than the natural habitat in the region (Luskin & Potts, 2011), which native soil invertebrates can be sensitive to (Fayle et al., 2010). An increased understory is likely to ameliorate this microclimate by preventing exposure of the soil to direct sunlight and by increasing water infiltration, thus benefitting soil invertebrates (Ashraf et al., 2018; Belsky et al., 1993). Soil macrofauna composition was different in the three understory treatments; taxa that include litter feeding organisms: Dermaptera; Diplopoda; Coleoptera; and Isopoda, all increased in abundance in the enhanced compared to the reduced understory treatment. This is likely due to the greater biomass and diversity of decaying vegetation and root matter provided by the understory plants (Wardle et al., 2004). These fauna are considered ecosystem engineers and are key in breaking down leaf litter and creating a wider availability of resources for microbial decomposers (Brussaard, 2012). Furthermore, the reported positive effects of the understory on soil biodiversity may be conservative in our study; benefits of plant diversity on soil biota can have a significant time delay (Eisenhauer et al., 2012). The enhanced understory treatment had only been installed for two years at the time of sampling, therefore, increased positive effects on the soil macrofauna community and associated ecosystem functions can be expected over time. This is extremely pertinent in oil palm plantations, as they have a long commercial lifespan of more than 25 years. This study was conducted in mature plantations; enhanced understory vegetation could be even more important in young plantations where soil erosion and microclimate is more severe, as there is a reduced canopy cover and less organic matter available from decaying fronds (Guillaume et al., 2015; Luskin & Potts, 2011).

Soil abiotic properties

Our results show there was no impact of either treatment on soil fertility. This indicates that the changes in soil macrofauna community were caused by the direct impacts of vegetation. Furthermore, it suggests that the understory vegetation has little impact on nutrient availability for the oil palm, as there was no difference in nutrient levels between the treatments. If enhanced understory vegetation is maintained for an extended period of time, positive effects on soil fertility could be seen as undergrowth is likely to prevent soil erosion, loss of SOM and leaching of other nutrients (Li et al., 2007; Lieskovský & Kenderessy, 2014).

Decomposition

Litter decomposition rates were substantially lower in reduced understory than in the normal and enhanced understory plots. Decomposition influences carbon storage and underlies soil formation (Swan & Kominoski, 2012). It is also a good indicator of the sensitivity of ecosystem processes to change in species richness (Hooper et al., 2012). The slowed rate of decomposition with reduced understory vegetation corresponds to the loss of macrofauna diversity and abundance (particularly litter feeders) in the reduced understory treatment. Bags that were closed to invertebrates also showed slower decomposition rates in all treatments. This is likely to be explained by a reduction in microbial litter decomposition. This could be a result of reduced macrofauna litter decomposition resulting in a lower availability of pre-digested material for microbes (Brussaard, 2012) and/or that the enhanced understory provides a more favourable microhabitat and microclimate for microbial fauna, due to the increased soil cover and greater plant diversity. This could increase both microbial diversity and function (Eisenhauer, 2016). These findings have important impacts on soil sustainability and recovery after forest conversion to oil palm plantations and after replanting events, when soils lose large amounts of SOC (Guillaume et al., 2015; Matysek et al., 2018). Increased understory could help ameliorate these negative effects by biologically enhancing SOC sequestration, providing physical protection from soil erosion and drying and providing a more amenable microclimate.

Conclusions

This study shows that a reduction in herbicide usage and the resulting improvement in understory vegetation diversity and coverage can be a key tool in improving within-plantation belowground biodiversity and ecosystem functioning. Furthermore, we stress that the reduced understory management scheme, that many oil palm plantations employ, has negative impacts on biodiversity and ecosystem functioning. Reducing herbicide application can also benefit plantation owners by lowering operating costs and reducing health risks to plantation workers that are exposed to herbicides, sometimes without being equipped with the necessary protective equipment.

The improved soil quality realised by increasing understory vegetation in oil palm plantations could improve yield (Balasundram et al., 2006). It is thought that understory plants could compete for nutrients and water with oil palms and cause difficulty in harvesting fallen fruit, thus negatively impacting upon yield (Tohiran et al., 2017). However, we found no evidence for nutrient competition in this study. The impacts on yield are a priority for future research and are being addressed in the larger BEFTA project. However, as environmental conditions can take some time to effect yield, these findings are not published here. Further research into the long-term effects of understory management in oil palm plantations may also realise further benefits to soil sustainability. To support soil biodiversity and ecosystem functioning, increasing understory vegetation should be encouraged by certification schemes, such as the Round Table of Sustainable Palm Oil and other advisors of oil palm agriculture best practice.

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Table1. *Model outputs of LMMs and GLMM comparing macrofauna order richness, abundance, vegetation cover and vegetation richness between Enhanced, Normal and Reduced treatment. Table A is the model output with the windrow as the intercept, table B is the model output with the weeded circle as the intercept; Enhanced treatment is the intercept for both table A and B. * denotes an interaction effect.*

(A)	**Order Richness**			**Macrofauna Abundance**			**Vegetation cover**			**Vegetation richness**		
Predictors	*Estimates*	*CI*	*p*	*Incidence Rate Ratios*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
Enhanced treatment	11.90	10.85 – 12.95	**<0.001**	70.62	41.54 – 120.04	**<0.001**	79.23	67.93 – 90.53	**<0.001**	2.92	2.04 – 3.81	**<0.001**
Normal treatment	-1.51	-2.92 – -0.10	**0.036**	1.33	0.59 – 3.02	0.495	-9.23	-26.90 – 8.43	0.306	-0.81	-2.19 – 0.57	0.249
Reduced treatment	-2.46	-3.74 – -1.18	**<0.001**	0.72	0.34 – 1.50	0.377	-67.15	-83.13 – -51.18	**<0.001**	-0.38	-1.63 – 0.87	0.546
Weeded circle	-3.11	-4.18 – -2.05	**<0.001**	1.87	0.99 – 3.54	0.053	-12.92	-26.21 – 0.36	0.057	1.31	0.14 – 2.47	**0.028**
Normal*weeded circle				0.22	0.08 – 0.56	**0.002**	-9.30	-30.07 – 11.47	0.380	-0.20	-2.01 – 1.62	0.832
Reduced*weeded circle				0.30	0.12 – 0.72	**0.007**	11.00	-7.79 – 29.79	0.251	-1.62	-3.26 – 0.03	0.054

(B)	**Order Richness**			**Macrofauna Abundance**			**Vegetation cover**			**Vegetation richness**		
Predictors	*Estimates*	*CI*	*p*	*Incidence Rate Ratios*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
Enhanced treatment	8.79	7.74 – 9.84	**<0.001**	132.24	76.07 – 229.90	**<0.001**	66.31	55.01 – 77.61	**<0.001**	4.23	3.35 – 5.11	**<0.001**
Normal treatment	-1.51	-2.92 – -0.10	**0.036**	0.29	0.12 – 0.66	**0.003**	-18.53	-36.19 – -0.87	**0.040**	-1.01	-2.39 – 0.37	0.153
Reduced treatment	-2.46	-3.74 – -1.18	**<0.001**	0.21	0.10 – 0.46	**<0.001**	-56.15	-72.13 – -40.18	**<0.001**	-2.00	-3.25 – -0.75	**0.002**
Windrow	3.11	2.05 – 4.18	**<0.001**	0.53	0.28 – 1.01	0.053	12.92	-0.36 – 26.21	0.057	-1.31	-2.47 – -0.14	**0.028**

Normal*windrow	4.64	1.78 – 12.08	**0.002**	9.30	-11.47 – 30.07	0.380	0.20	-1.62 – 2.01	0.832
Reduced*windrow	3.37	1.39 – 8.15	**0.007**	-11.00	-29.79 – 7.79	0.251	1.62	-0.03 – 3.26	0.054

Table 2. *Model outputs of LMMs soil abiotic variables between Enhanced, Normal and Reduced treatment with the weeded circle as the model intercept.*

	water			**N**			**C**			**K**		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
Enhanced treatment	1.39	1.03 – 1.74	**<0.001**	-1.56	-1.82 – -1.29	**<0.001**	1.34	1.10 – 1.57	**<0.001**	3.96	3.69 – 4.22	**<0.001**
Normal treatment	0.47	-0.02 – 0.96	0.058	0.34	-0.02 – 0.70	0.066	0.27	-0.05 – 0.59	0.093	0.11	-0.22 – 0.45	0.502
Reduced treatment	0.16	-0.34 – 0.65	0.541	0.07	-0.30 – 0.44	0.699	0.17	-0.15 – 0.50	0.296	-0.01	-0.35 – 0.33	0.948
Windrow	-0.03	-0.27 – 0.21	0.791	-0.07	-0.26 – 0.13	0.485	0.08	-0.06 – 0.23	0.272	-0.07	-0.34 – 0.20	0.618

	P			**stability**			**C N**		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
Enhanced treatment	4.22	3.82 – 4.62	**<0.001**	76.11	71.45 – 80.77	**<0.001**	18.63	16.56 – 20.71	**<0.001**

Normal treatment	0.28	-0.23 – 0.79	0.280	-2.46	-8.60 – 3.68	0.432	-0.93	-3.56 – 1.69	0.485
Reduced treatment	0.09	-0.42 – 0.61	0.728	0.55	-5.69 – 6.79	0.863	2.09	-0.57 – 4.75	0.123
Windrow	-0.40	-0.79 – -0.01	**0.045**	-1.44	-5.46 – 2.58	0.483	2.65	0.58 – 4.73	**0.012**

Table 3. *Model outputs of LMM comparing litter decomposition rates between Enhanced, Normal and Reduced treatment with the weeded circle as the intercept.*

	Decomposition rate g/day		
Predictors	*Estimates*	*CI*	*p*
Enhanced treatment	0.0271	0.0234 – 0.0309	**<0.001**
Normal treatment	-0.0014	-0.0061 – 0.0033	0.548
Reduced treatment	-0.0068	-0.0113 – -0.0024	**0.003**

Windrow	0.0074	0.0042 – 0.0105	<**0.001**
Open to invertebrates	0.0031	0.0001 – 0.0061	**0.042**

Synthesis

Main findings and importance

In this thesis, I investigated factors influencing biodiversity, ecosystem function and ecosystem services in oil palm landscapes. In chapter 1, I provide the most up-to-date assessment of species richness and abundance loss after conversion of forest to oil palm. Furthermore, I provide an assessment of global land use change for oil palm, including the relatively recent trend of grassland conversion to oil palm in Latin America. I also show bird species richness is particularly impacted by forest conversion to oil palm, providing justification for conducting the research in chapter 2 of this thesis.

In chapter 2, I explore some of the mechanisms behind the decline in bird species richness. I showed that the conservation value of oil palm is low for forest birds as a dietary resource. The use of oil palm plantations by forest birds is extremely limited (even directly adjacent to forest), but when it does occur, these forest birds consume the same insects as farmland birds. Indeed, all birds that were sampled in oil palm plantations had little dietary separation with regards to insect prey. It is vital to boost landscape connectivity between forest patches to conserve forest bird biodiversity.

Furthermore, I examined the contribution of birds to pest-control in oil palm plantations; a subject that has had conflicting outcomes in past research (Denmead et al., 2017; Koh, 2008). I systematically investigated whether there is a spillover effect of forest birds to pest-control. These potential benefits have been proposed in oil palm plantations adjacent to forest but previous research has been inconclusive (Gray & Lewis, 2014). Through analysing both forest-associated and generalist bird diet, I found no evidence of any insect pest-control service. Potential spillover effects are greatly reduced by the lack of forest-associated birds that penetrate beyond the edge of oil palm plantations.

In chapters 3 and 4, I investigated the impact of replanting on biodiversity and factors influencing soil sustainability. Replanting could act as a second major perturbation to the landscape after initial forest clearance for oil palm (Snaddon et al., 2013). I showed that soil is severely degraded by the replanting of oil palm and that this degradation is largely driven by loss of soil organic carbon. This could have a large impact upon yield and agricultural sustainability. I also show a reduction in soil macrofauna species richness and abundance, in addition to a change in community composition after oil palm replanting. This reduction may have serious implications for soil functioning and recovery after the replanting event. Abundance of soil macrofauna fluctuated throughout the experimental chronosequence, possibly due to plant-arthropod interactions. This highlights the need to sample soil biodiversity over an extended time period.

Finally, in chapter 5, I investigated how standard oil palm management practices can influence soil biodiversity, ecosystem function and provide a possible mitigation strategy for the effects of replanting. I showed that soil biodiversity and ecosystem functioning in oil palm plantations can be improved by increasing understory vegetation complexity through the reduction of herbicide application. This research can provide a practicable management tool to increasing within-plantation biodiversity and ecosystem functioning as well reducing the use of environmentally damaging herbicides.

Research in a wider context

Due to the serious global issue of biodiversity loss and associated erosion of ecosystem function, studies that identify drivers of degradation or mitigation strategies are crucial for both wildlife conservation and agricultural sustainability. The research chapters in this thesis present an important step forward regarding these issues, especially in an oil palm context. They highlight considerable issues that need to be solved in order to prevent further negative impacts of oil palm agriculture. In addition, they offer some practicable solutions to mitigate these impacts.

Evidence from chapter 3 shows a lack of dietary separation of birds in oil palm plantations could have serious ramifications for food web stability as birds are sharing much of the same resource. This work also suggests connectivity, especially for passerines, is severely limited by oil palm plantations. Research should now be conducted on how to mitigate this effect. Possible avenues include the wide-scale implementation of riparian strips. These strips of native forest not only provide ecosystem services in oil palm landscapes by reducing erosion and increasing water quality (Luke et al., 2017), but also can contain a diverse range of forest-associated birds (Mitchell et al., 2018). Riparian strips show promise as corridors between forest patches, however, their efficacy at providing connectivity needs to be tested. Native tree islands within oil palm plantations have also been proposed as a method to improve biodiversity in the landscape (Foster et al., 2011; Teuscher et al., 2016). These may also enhance connectivity for forest-associated birds, although this is probably more limited to larger, more mobile, forest birds, such as hornbills and parrots, which are able to cross periods of open ground.

This chapter of research (and that of chapter 1) highlights the difficulty of balancing biodiversity conservation with a food production landscape and shows the importance of preserving natural habitat for native biodiversity in landscapes dominated by agriculture. Even with the RSPOs moratorium on deforestation and the advice against draining peat soils for oil palm, the forest that was sampled in chapter 3 is under threat by oil palm agriculture and is slowly disappearing. This is likely to have a devastating impact on local wildlife.

In addition, I provide evidence that a biocontrol ecosystem service provided by spillover of forest birds is in reality, unlikely in oil palm landscapes. However, this experiment was only conducted in one of the countries that oil palm is cultivated and different biocontrol relationships may occur elsewhere. Furthermore, proximity to forest and increased landscape heterogeneity could enhance biocontrol other organisms not tested in this study (Nurdiansyah, Denmead, Clough, Wiegand, & Tscharntke, 2016). It is important that findings from this study do not cloud the evidence from multiple recent studies in oil palm and other agricultural land-uses showing that landscape heterogeneity is vitally important for the delivery of ecosystem services (Nurdiansyah et al., 2016;

Pywell et al., 2015; Rusch et al., 2016). Furthermore, recent unpublished work shows that high yielding oil palm smallholder plantations have higher bird species richness than lower yielding plantations, possibly indicating a greater delivery of ecosystem services in biodiversity rich plantations (Razak et al. *in preparation*).

In chapter 4 and 5 I demonstrate the huge impacts that replanting can have on soil quality and belowground biodiversity. In order to maintain the viability of the soil for future agriculture, mitigation strategies need to be developed to protect the soil from degradation. My work showed loss of soil organic carbon was the driver behind the decline in other soil nutrients. Therefore, mitigation strategies need to focus on protecting soil organic carbon during the replanting process. This could be achieved by ensuring stability of soil organic matter through preventing soil erosion and by maintaining inputs of soil organic carbon, such as roots from vegetation. Furthermore, replanting could be conducted using a staggered method (Luskin & Potts, 2011), leaving smaller areas of soil exposed to erosion and the effects of runoff. Rigorous experiments need to be conducted to ascertain the best methods for replanting of oil palm, that maintain soil quality while causing minimal inhibition to oil palm production.

This research was limited to one geographic region and style of plantation management. In order to expand upon and corroborate these findings it is vital to conduct similar studies across the geographic range and soil types of oil palm cultivation. One may expect relatively similar findings across its geographic range due to oil palm being restricted to tropical and subtropical regions that experience similar climates: high rainfall; and high levels of sunshine (Corley & Tinker, 2016). However, topography, microclimate and plantation management are all likely to influence the effect of replanting on soil quality, to some extent.

In chapter 6, I show the importance of understory vegetation for soil biodiversity and ecosystem functioning in oil palm plantations. Longer term results from this experiment could also see benefits to soil quality from maintaining a substantial understory. This research is an example of an easily implemented management change that improves within-plantation biodiversity and ecosystem functioning. This kind of approach will be valuable in convincing plantation managers to change their practices, hopefully benefiting biodiversity and agricultural sustainability within the sector.

Furthermore, there are possible benefits of increasing understory vegetation and botanical diversity of oil palm plantations beyond those found in this thesis. For example, plantations that manage their understory vegetation by cattle grazing as opposed to herbicides support greater bird diversity, attributed to the greater coverage and height of understory vegetation with cattle grazing, providing more habitat and foraging availability to birds (Tohiran et al., 2017). Increased predation rates of artificial herbivores by predatory arthropods in oil palm plantations have also been linked with greater understory vegetation (Denan et al., *in preparation*). This indicates that less intensive management of the understory can benefit ecosystem functions other than decomposition rates (chapter 6) and possibly provide an ecosystem service. Overall, the reduction of herbicide use across agricultural land-use types is likely to be beneficial to the long-term sustainability of food production (Landis, 2017).

The chapters in this thesis all strongly relate to the field of sustainable intensification (SI) in agriculture. SI can be defined as achieving high yields, without compromising the long term viability of land to produce food (Garnett et al., 2013; Tilman et al., 2011). In some areas higher yields will be compatible with environmental improvements, however, in others, land re-allocation or yield reductions are necessary to ensure sustainability and conservation of wildlife (Garnett et al., 2013). The results from chapters: 2; 3; 4; and 5 all indicate situations which may involve reductions in yield in order to reduce impacts on wildlife (2 and 3) or maintain agricultural sustainability (4 and 5). Whereas, chapter 6 offers the opportunity of a management practice that could both reduce inputs and improve long-term yield by environmental improvements.

Challenges

There has been a recent push for wildlife friendly agriculture due to massive declines in biodiversity, related ecosystem functions and services due to the results of agricultural intensification, particularly in Europe and North America. Furthermore, there is evidence that wildlife friendly farming can increase crop yields, due to increases in ecosystem service delivery (Pywell et al., 2015). Even if yields are moderately reduced in the short term, by implementing practices that boost biodiversity, ecosystem functioning and ecosystem service delivery, while decreasing the need for environmentally costly chemical inputs, the long term sustainability gains surely outweigh a short-term drop in yield? However, in the oil palm agricultural research community (and the wider tropical conservation community), there is still a major school of thought that promotes intensive farming in order to protect existing forest, through a land sparing approach (Meijaard et al., 2018; Phalan et al., 2011). The theory behind this is based on maximising oil palm yield in order to reduce pressure on natural habitats, by meeting demand for palm oil on the minimum amount of land possible. However, this may be a short-sighted approach, which ignores the pitfalls of intensive agricultural practices, such as declines in: soil fertility; pollinators; biocontrol; and biodiversity (Grab et al., 2018; Landis, 2017; Rusch et al., 2016; Tscharntke et al., 2012). Furthermore, intensive agricultural practices cause other problems to surrounding land uses, such as water pollution from fertilisers, erosion and flooding, and have been attributed to a decline in natural habitat biodiversity (Hallmann et al., 2017; Luskin et al., 2017). In order to conserve biodiversity and mitigate climate change impacts, sparing natural habitats has to be a priority. However to produce sustainable, high-yielding oil palm in the long-term, attention also needs to be given to increasing biodiversity and ecosystem functioning within oil palm and other agricultural landscapes. This may result in short-term drops in yield and capital gain, however, the long-term local, landscape and global benefits outweigh these costs (Grab et al., 2018). As part of this approach, oil palm production needs to be regulated in order to promote sustainable practices. Currently, the main palm oil regulation body is the RSPO (RSPO, 2017).

Although the RSPO has good policies on “no deforestation” and “zero burning”, it has been ineffective in changing agricultural practices for the better (Carlson et al., 2018; Morgans et al., 2018). Pressure needs to be put on oil palm growers in order that they uptake more sustainable practices, however, there is currently no evidence that certification provides any benefit to the environment (Carlson et al., 2018; Morgans et al., 2018).Therefore, consumer beliefs that certified palm oil is environmentally friendly may be misled. Furthermore, the prohibitive expense of becoming certified, often excludes small-scale plantation owners, whose practices may be more sustainable and environmentally friendly than their certified large-scale plantation counterparts (Azhar et al., 2017). Oil palm agriculture has the potential to be an incredibly sustainable crop. It is extremely high yielding compared to other oil crops (Zimmer, 2010), and is a long lived, perennial crop, that develops relatively high structural heterogeneity and biodiversity during its commercial lifecycle (Foster et al., 2011). Furthermore, oil palm growers have been receptive to introducing environmentally friendly practices, such as reducing carbon emissions by decreasing fertiliser input and recycling oil palm waste to use as an organic fertiliser (Tao et al., 2017), and are acutely aware of the negative perception that palm oil has gained. Smallholders, in particular, already use environmentally friendly farming practices in their plantations, such as the use of polyculture, even without technical advice and encouragement from policy (Azhar et al., 2017). Therefore, smallholdings often sustain greater biodiversity than large-scale plantations, which is inherently improved by their smaller size and more diverse crop types, leading to greater landscape heterogeneity (Azhar et al., 2013, 2011). Overall, there is great scope for improving the effectiveness of oil palm certification, providing policy is guided by scientific evidence and certification is made more accessible (Yan, 2017).

Oil palm, along with many other types of agriculture, faces big sustainability challenges due to current rates of biodiversity loss and the parallel degradation of ecosystem functions and services. Therefore, it is critical to identify areas that affect this degradation. By integrating research across taxa, trophic levels and below/above-ground systems, these research chapters form an important contribution to explicate factors behind these losses. They also highlight important environmental issues that need to be swiftly resolved and suggest some solutions to these pertinent problems.

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Appendices

Supplementary Information: Chapter 2

Conduct of literature review

Objective of review

The aim of the review was to create a reproducible and unbiased synthesis of literature that can address the question “What do we know about biodiversity and ecosystem function in oil palm landscapes?” The focus was not limited to studies that compare a natural habitat with an oil palm plantation but also sought to include comparisons with other anthropogenically modified habitats and varying managements of oil palm. **However, for the purposes of this review only the oil palm biodiversity section of the review was included.**

Search strategy

Literature sources

The available literature was searched by topic using the ISI Web of Science, Scopus, Google Scholar, CIFOR, CIRAD-Agritrop and sustainablepalmoil.org databases (searches were conducted on the 22/07/15 and redone on the 15/02/17).

Search terms

Search strings were created using two categories:

Intervention- Oil palm and Outcomes- a measurable variable or change in state. Boolean operators AND between categories and OR within categories were used along with a wildcard character, i.e. the asterisk, was used in the subject category to include alternative word endings .No specific search terms were used for the study population, i.e. faunal and floral species, as they are inherent in the outcome category. The final search string is presented below. Owing to the limitations of some of the search engines used, modified (shorter) search strings were used (also shown below). Final search string- web of science and scopus (conducted on the 22/07/15 and 15/02/17):

Publication database searches

oil palm AND biodiversity OR bird OR “species composition” OR “species richness” OR fung* OR mammal OR insect OR ant OR beetle OR “microb* diversity” OR arthropod OR butterfl* OR bees OR worm OR collembola OR millipede OR centipede OR “bacterial diversity” OR bat OR termite OR archaea OR nematode OR productivity OR “litter producti*” OR “wood producti*” OR “secondary metaboli*” OR biomass OR “organic carbon” OR “carbon storage” OR “ecosystem stability” OR resilience OR “temporal variability” OR “ecosystem relia*” OR “food web” OR trophic OR “nutrient cycl*” OR “life cycle” OR “carbon cycl” OR “nitrogen cycl*” OR “nitrogen retention” OR “nitrogen loss” OR “energy flux” OR biogeochemical OR “soil respiration” OR “soil erosion” OR “soil carbon” OR “soil structure” OR “plant respiration” OR “mass loss” OR “organic matter” OR predation OR pollinat* OR parasitism OR symbiosis OR herbivory OR “primary producer” OR prey OR decompos* OR “food chain” OR “seed dispersal”

OR “hydrological cycl*” OR interception OR transpiration OR watershed OR “water table” OR “run off” OR “water quality” OR “bioremediation” OR “biological control” OR replant* OR conservation OR rainforest OR riparian OR “rubber plantation” OR peat OR “stand age” OR “plantation age” OR “basal growth” OR “pest management” OR microclimate

Internet searches

Internet searches were conducted 27.7.2015 and redone 15.2.2017. For Google and CIFOR websites the first 100 most relevant hits were exported for review. The following search strings were used:

google scholar- oil palm AND biodiversity OR “ecosystem function” CIFOR- “oil palm

CIRAD-AGRITROP “oil palm”

In addition, The Sustainability Policy Transparency Toolkit website (http://www.sustainablepalmoil.org/-) was searched manually through environment category publications

Article screening

Study inclusion criteria for review

A set of inclusion criteria were developed according to the following:

- Relevant subject- **biodiversity**
- Relevant intervention- **presence of an oil palm plantation**

Relevant outcomes- **a metric of biodiversity** (species richness, abundance, diversity indices etc.)

Screening process

The first search of all databases resulted in a total 9461 articles (not checked for duplicates). This was reduced to 1037 after reading the title and abstract of the article following the above study inclusion criteria. This number was finally reduced to 143 articles that we were able to access and fit the study inclusion criteria.

Meta-analysis:

We aimed to answer the question: “what is the impact of conversion of primary forest to oil palm plantation on species richness and abundance?”

Study quality and inclusion for meta-analysis

For the meta-analysis, we categorised studies based on the methodology of the study and excluded any studies that had a poor methodical design according to the “quality of evidence” categories used in Savilaakso *et al.* (2014). Furthermore, we only included studies that had the ability to access (either from the paper itself or from the author) the mean actual species richness, or abundance (not rarefied species richness or relative abundance) for both control (primary forest) and treatment (oil palm), sample number and standard deviation.

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Supplementary Information: Chapter 3

Table S1. Table of bird species sampled by sampling method at each distance from forest.

Species		Sampling method	0m	100m	300m	1500m	Total
ashy tailorbird	*Orthotomus ruficeps*	mist-net	11	13	12	NA	36
ashy tailorbird	*Orthotomus ruficeps*	point count	40	29	46	15	130
asian glossy starling	*Aplonis panayensis*	mist-net	0	0	1	NA	1
asian glossy starling	*Aplonis panayensis*	point count	0	1	1	0	2
baya weaver	*Ploceus philippinus*	mist-net	4	1	3	NA	8
baya weaver	*Ploceus philippinus*	point count	7	3	0	7	17
black-capped babbler	*Pellorneum capistratum*	mist-net	1	0	0	NA	1
black-capped babbler	*Pellorneum capistratum*	point count	2	0	0	0	2
black-headed munia	*Lonchura malacca*	mist-net	1	1	0	NA	2
black-naped oriole	*Oriolus chinensis*	mist-net	2	0	1	NA	3
black-naped oriole	*Oriolus chinensis*	point count	2	6	5	7	20
blue-eared kingfisher	*Alcedo meninting*	mist-net	5	2	0	NA	7

Species		Sampling method	0m	100m	300m	1500m	Total
blue-eared kingfisher	*Alcedo meninting*	point count	6	1	4	0	11
brown shrike	*Lanius cristatus*	mist-net	1	1	1	NA	3
brown shrike	*Lanius cristatus*	point count	0	1	0	0	1
buff-necked woodpecker	*Meiglyptes tukki*	mist-net	2	0	0	NA	2
changeable hawk-eagle	*Nisaetus cirrhatus*	mist-net	0	1	0	NA	1
changeable hawk-eagle	*Nisaetus cirrhatus*	point count	0	1	0	0	1
chestnut-winged babbler	*Stachyris erythroptera*	mist-net	0	1	0	NA	1
chestnut-winged babbler	*Stachyris erythroptera*	point count	1	0	0	0	1
chestnut munia	*Lonchura atricapilla*	mist-net	4	0	3	NA	7
chestnut munia	*Lonchura atricapilla*	point count	2	1	3	0	6
common flameback	*Dinopium javanense*	mist-net	2	1	0	NA	3
common flameback	*Dinopium javanense*	point count	7	4	7	5	23
common tailorbird	*Orthotomus sutorius*	mist-net	9	4	5	NA	18
common tailorbird	*Orthotomus sutorius*	point count	38	63	70	57	228

Species		Sampling method	0m	100m	300m	1500m	Total
cream-vented bulbul	*Pycnonotus simplex*	mist-net	14	11	0	NA	25
cream-vented bulbul	*Pycnonotus simplex*	point count	25	6	2	0	33
crimson-breasted flowerpecker	*Prionochilus percussus*	mist-net	4	0	0	NA	4
crimson-breasted flowerpecker	*Prionochilus percussus*	point count	1	0	0	0	1
dark-necked tailorbird	*Orthotomus atrogularis*	mist-net	1	0	1	NA	2
dark-necked tailorbird	*Orthotomus atrogularis*	point count	9	0	0	0	9
emerald dove	*Chalcophaps indica*	mist-net	11	7	4	NA	22
emerald dove	*Chalcophaps indica*	point count	2	2	0	1	5
fluffy-backed tit-babbler	*Macronous ptilosus*	mist-net	1	0	0	NA	1
fluffy-backed tit-babbler	*Macronous ptilosus*	point count	7	0	0	0	7
Javan myna	*Acridotheres javanicus*	mist-net	0	1	0	NA	1
laced woodpecker	*Picus vittatus*	mist-net	1	0	0	NA	1
laced woodpecker	*Picus vittatus*	point count	1	0	0	2	3

Species		Sampling method	0m	100m	300m	1500m	Total
large-tailed nightjar	*Caprimulgus macrurus*	mist-net	2	2	0	NA	4
large-tailed nightjar	*Caprimulgus macrurus*	point count	4	2	7	0	13
little spiderhunter	*Arachnothera longirostra*	mist-net	3	2	3	NA	8
little spiderhunter	*Arachnothera longirostra*	point count	0	1	1	1	3
olive-winged bulbul	*Pycnonotus plumosus*	mist-net	53	25	16	NA	94
olive-winged bulbul	*Pycnonotus plumosus*	point count	67	24	8	0	99
orange-bellied flowerpecker	*Dicaeum trigonostigma*	mist-net	17	3	4	NA	24
orange-bellied flowerpecker	*Dicaeum trigonostigma*	point count	9	4	3	1	17
oriental magpie-robin	*Copsychus saularis*	mist-net	41	33	31	NA	105
oriental magpie-robin	*Copsychus saularis*	point count	75	91	97	81	344
pacific swallow	*Hirundo tahitica*	mist-net	4	0	0	NA	4
pacific swallow	*Hirundo tahitica*	point count	13	0	1	3	17
pied fantail	*Rhipidura javanica*	mist-net	9	6	4	NA	19

Species		Sampling method	0m	100m	300m	1500m	Total
pied fantail	*Rhipidura javanica*	point count	7	11	7	7	32
pin-striped tit-babbler	*Macronus gularis*	mist-net	6	1	2	NA	9
pin-striped tit-babbler	*Macronus gularis*	point count	31	2	0	5	38
plain-throated sunbird	*Anthreptes malacensis*	mist-net	3	10	7	NA	20
plain-throated sunbird	*Anthreptes malacensis*	point count	15	23	16	15	69
plaintive cuckoo	*Cacomantis merulinus*	mist-net	2	0	0	NA	2
plaintive cuckoo	*Cacomantis merulinus*	point count	7	4	1	0	12
purple-naped spiderhunter	*Hypogramma hypogrammicum*	mist-net	2	0	0	NA	2
red-eyed bulbul	*Pycnonotus brunneus*	mist-net	14	5	0	NA	19
red-eyed bulbul	*Pycnonotus brunneus*	point count	21	5	1	0	27
red junglefowl	*Gallus gallus*	mist-net	2	0	0	NA	2
red junglefowl	*Gallus gallus*	point count	27	13	12	12	64

Species		Sampling method	0m	100m	300m	1500m	Total
ruby-cheeked sunbird	*Chalcoparia singalensis*	mist-net	1	1	0	NA	2
ruby-cheeked sunbird	*Chalcoparia singalensis*	point count	1	0	0	0	1
rufescent prinia	*Prinia rufescens*	mist-net	1	0	0	NA	1
rufous-tailed tailorbird	*Orthotomus sericeus*	mist-net	2	0	0	NA	2
rufous-tailed tailorbird	*Orthotomus sericeus*	point count	4	0	0	0	4
rufous woodpecker	*Celeus brachyurus*	mist-net	1	4	3	NA	8
rufous woodpecker	*Celeus brachyurus*	point count	16	2	4	1	23
rusty-rumped warbler	*Helopsaltes certhiola*	mist-net	0	1	0	NA	1
scarlet-backed flowerpecker	*Dicaeum cruentatum*	mist-net	0	1	0	NA	1
scarlet-backed flowerpecker	*Dicaeum cruentatum*	point count	1	4	4	0	9
sooty-capped babbler	*Malacopteron affine*	mist-net	0	0	1	NA	1
sooty-capped babbler	*Malacopteron affine*	point count	5	0	0	0	5
spotted dove	*Spilopelia chinensis*	mist-net	1	2	1	NA	4

Species		Sampling method	0m	100m	300m	1500m	Total
spotted dove	*Spilopelia chinensis*	point count	29	48	65	47	189
white-headed munia	*Lonchura maja*	mist-net	0	0	3	NA	3
white-headed munia	*Lonchura maja*	point count	3	2	1	0	6
white-rumped shama	*Copsychus malabaricus*	mist-net	3	0	0	NA	3
white-rumped shama	*Copsychus malabaricus*	point count	5	0	0	0	5
white-throated kingfisher	*Halcyon smyrnensis*	mist-net	9	7	14	NA	30
white-throated kingfisher	*Halcyon smyrnensis*	point count	28	29	18	22	97
yellow-bellied prinia	*Prinia flaviventris*	mist-net	6	0	0	NA	6
yellow-bellied prinia	*Prinia flaviventris*	point count	22	3	2	5	32
yellow-breasted flowerpecker	*Prionochilus maculatus*	mist-net	2	0	0	NA	2
yellow-vented bulbul	*Pycnonotus goiavier*	mist-net	27	37	50	NA	114
yellow-vented bulbul	*Pycnonotus goiavier*	point count	50	54	75	53	232
zebra dove	*Geopelia striata*	mist-net	11	4	4	NA	19

Species		Sampling method	0m	100m	300m	1500m	Total
zebra dove	*Geopelia striata*	point count	14	22	45	51	132
BarredButtonquail	*Turnix suscitato*	point count	1	0	1	0	2
black and red broadbill	*Cymbirhynchus macrorhynchos*	point count	4	0	0	0	4
black and yellow broadbill	*Eurylaimus ochromalus*	point count	1	0	0	0	1
blue-crowned hanging parrot	*Loriculus galgulus*	point count	0	2	0	1	3
buff-necked woodpecker	*Meiglyptes tukki*	point count	0	0	1	0	1
buff-rumped woodpecker	*Meiglyptes tristis*	point count	0	0	0	1	1
bushy-crested hornbill	*Anorrhinus galeritus*	point count	1	3	0	0	4
cattle egret	*Bubulcus coromandus*	point count	0	0	0	2 0	2
collared kingfisher	*Todiramphus chloris*	point count	0	0	1		1
common iora	*Aegithina tiphia*	point count	0	1	0	1	2
common myna	*Acridotheres tristis*	point count	0	0	0	3	3

Species		Sampling method	0m	100m	300m	1500m	Total
coppersmith barbet	*Megalaima haemacephala*	point count	0	1	0	0	1
crested goshawk	*Accipiter trivirgatus*	point count	1	0	0	0	1
crested serpent-eagle	*Spilornis cheela*	point count	3	0	2	2	7
crimson-winged woodpecker	*Picus puniceus*	point count	3	0	0	0	3
dusky eagle-owl	*Bubo coromandus*	point count	1	0	0	0	1
edible-nest swiflet	*Aerodramus fuciphagus*	point count	47	19	21	35	122
eurasian tree sparrow	*Passer montanus*	point count	0	0	0	2	2
golden-bellied gerygone	*Gerygone sulphurea*	point count	1	3	1	1	6
greater coucal	*Centropus sinensis*	point count	10	12	10	5	37
greater racket-tailed drongo	*Dicrurus paradiseus*	point count	5	0	0	0	5
hill myna	*Gracula religiosa*	point count	5	0	1	0	6
house crow	*Corvus splendens*	point count	0	1	1	0	2

Species		Sampling method	0m	100m	300m	1500m	Total
Javan myna	*Acridotheres javanicus*	point count	47	35	39	101	222
large-billed crow	*Corvus macrorhynchos*	point count	4	0	2	4	10
long-tailed parakeet	*Psittacula longicauda*	point count	7	8	10	3	28
oriental dollarbird	*Eurystomus orientalis*	point count	2	3	0	0	5
oriental pied hornbill	*Anthracoceros albirostris*	point count	0	0	0	3	3
pink-necked pigeon	*Treron vernans*	point count	1	0	2	0	3
plain flowerpecker	*Dicaeum concolor*	point count	0	0	1	0	1
purple heron	*Ardea purpurea*	point count	0	2	1	3	6
raffles malkoha	*Rhinortha chlorophaea*	point count	1	0	0	0	1
red-wattled lapwing	*Vanellus indicus*	point count	0	0	3	1	4
rhinocerus hornbill	*Buceros rhinoceros*	point count	1	0	0	0	1
scaly breasted munia	*Lonchura punctulata*	point count	0	1	0	0	1

Species		Sampling method	0m	100m	300m	1500m	Total
short-tailed babbler	*Malacocincla malaccensis*	point count	1	0	0	0	1
stork-billed kingfisher	*Pelargopsis capensis*	point count	4	0	0	0	4
white-breasted waterhen	*Amaurornis phoenicurus*	point count	1	3	5	9	18
yellow-bellied bulbul	*Alophoixus phaeocephalus*	point count	1	0	0	0	1

Table S2. Model output for LMMs of MOTU richness of bird diet compared between MOTU clustering levels.

	92% clustering			**94% clustering**			**96% clustering**		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
Ashy Tailorbird (Intercept)	1.81	1.46 – 2.16	**<0.001**	1.95	1.59 – 2.30	**<0.001**	1.94	1.55 – 2.33	**<0.001**
Common tailorbird	0.46	-0.09 – 1.02	0.098	0.47	-0.09 – 1.03	0.098	0.59	-0.02 – 1.20	0.057
Cream-vented bulbul	-0.36	-0.90 – 0.18	0.194	-0.55	-1.10 – 0.00	0.050	-0.54	-1.14 – 0.06	0.078

Orange-bellied flowerpecker	-0.80	-1.33 – -0.27	**0.003**	-0.94	-1.48 – -0.41	**0.001**	-0.92	-1.51 – -0.34	**0.002**
Oriental magpie-robin	-0.24	-0.64 – 0.16	0.243	-0.39	-0.80 – 0.02	0.060	-0.26	-0.71 – 0.18	0.245
Olive-winged bulbul	-0.61	-1.03 – -0.19	**0.004**	-0.79	-1.22 – -0.36	**<0.001**	-0.77	-1.23 – -0.30	**0.001**
Pied fantail	-0.42	-0.99 – 0.15	0.151	-0.55	-1.14 – 0.03	0.064	-0.38	-1.02 – 0.26	0.244
Plain-throated sunbird	-0.32	-0.85 – 0.20	0.227	-0.41	-0.95 – 0.12	0.129	-0.34	-0.92 – 0.24	0.253
Yellow-vented bulbul	-0.73	-1.15 – -0.31	**0.001**	-0.86	-1.28 – -0.43	**<0.001**	-0.83	-1.29 – -0.36	**<0.001**

Figure S1. Biplot of residual ordination for the 92% clustering level

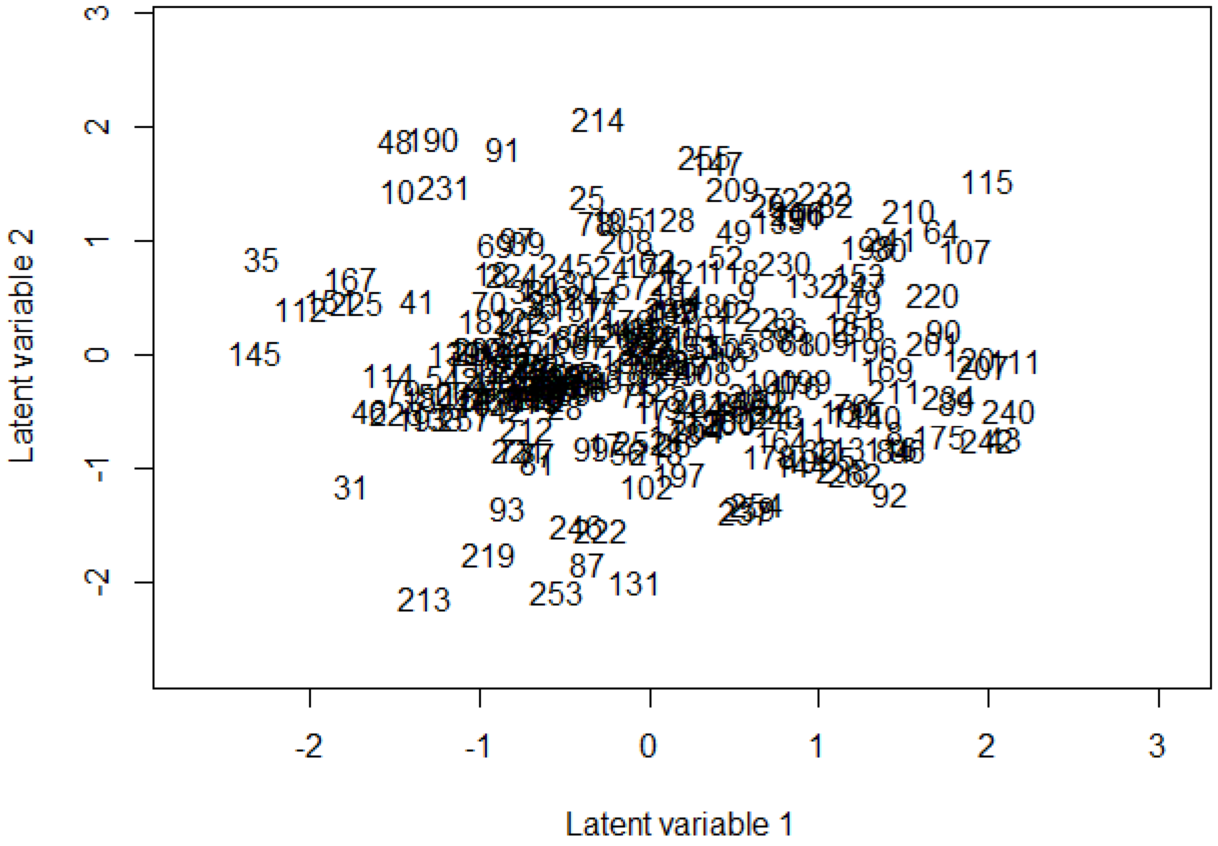


Figure S2. Biplot of residual ordination for the 94% clustering level

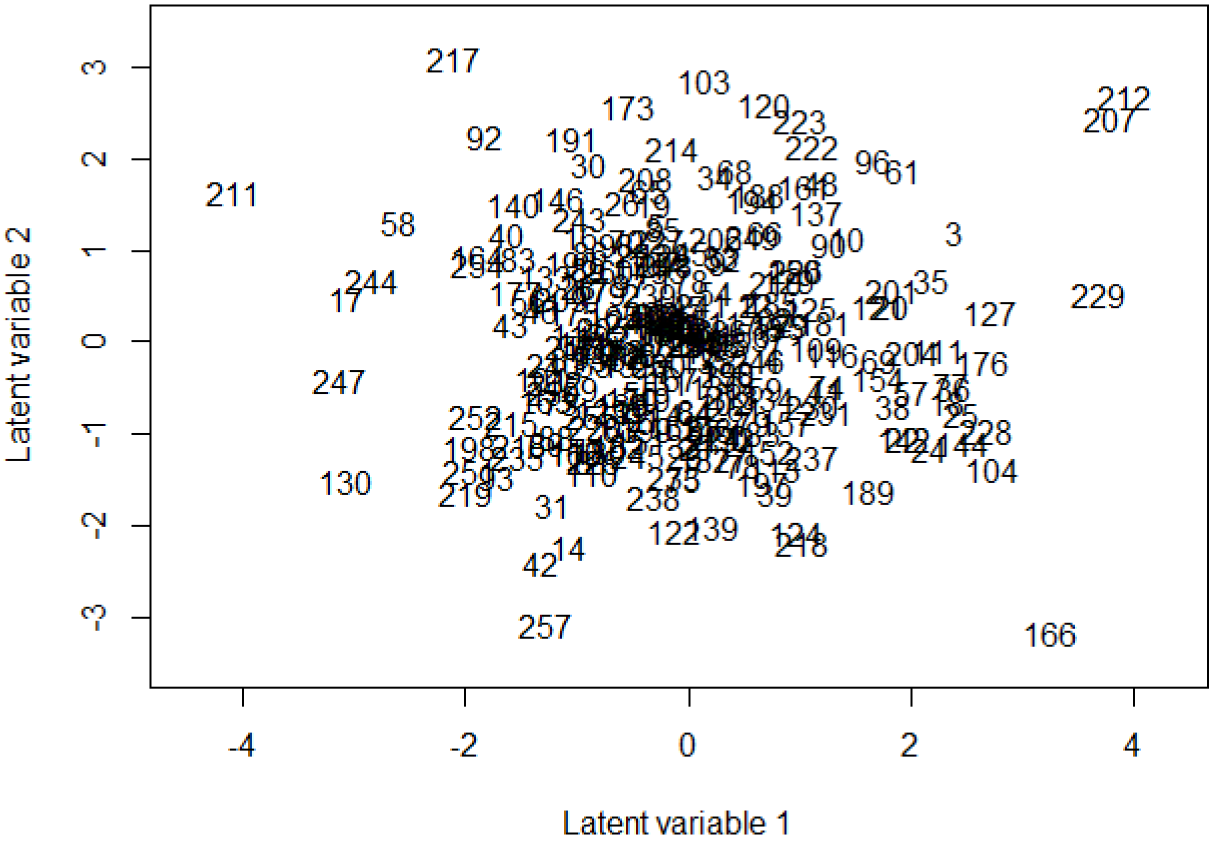


Figure S3. Biplot of residual ordination for the 96% clustering level

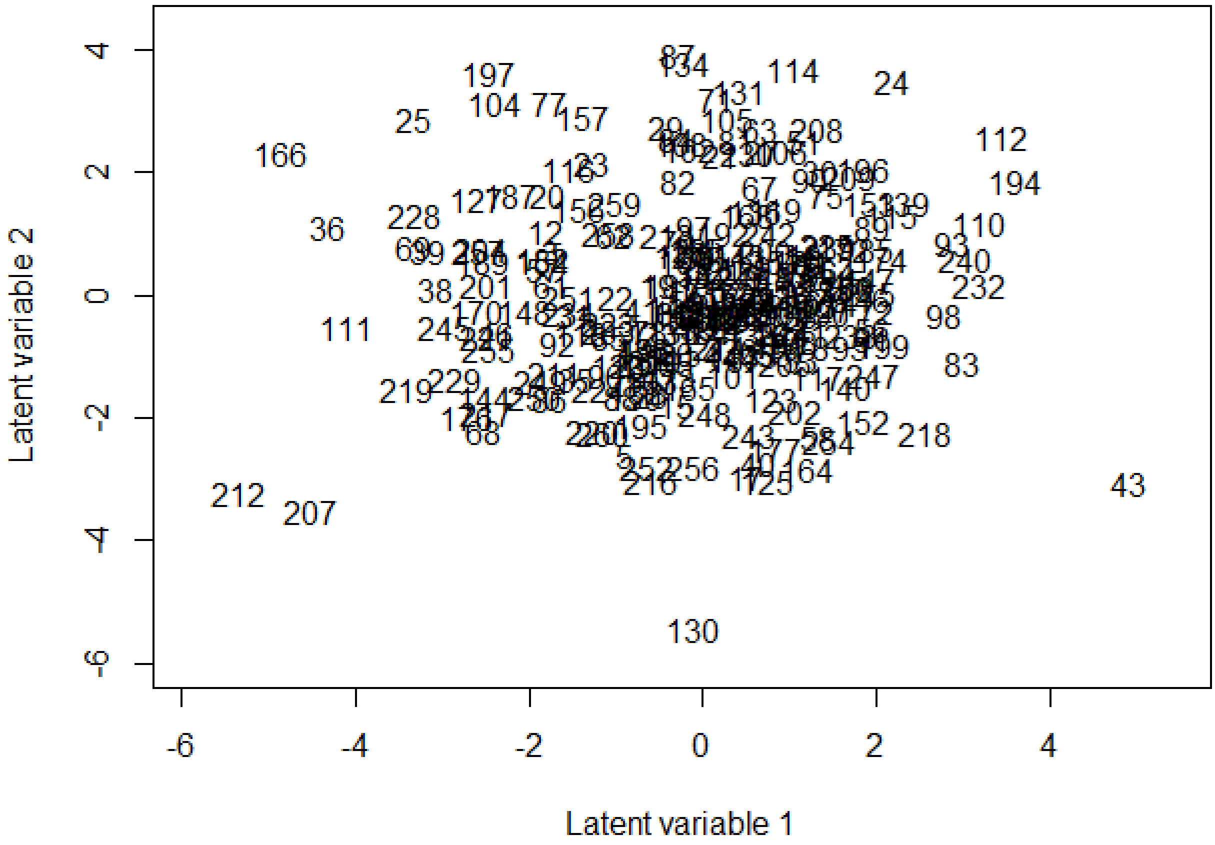


Figure S4. Biplot of constrained ordination for the 92% clustering level

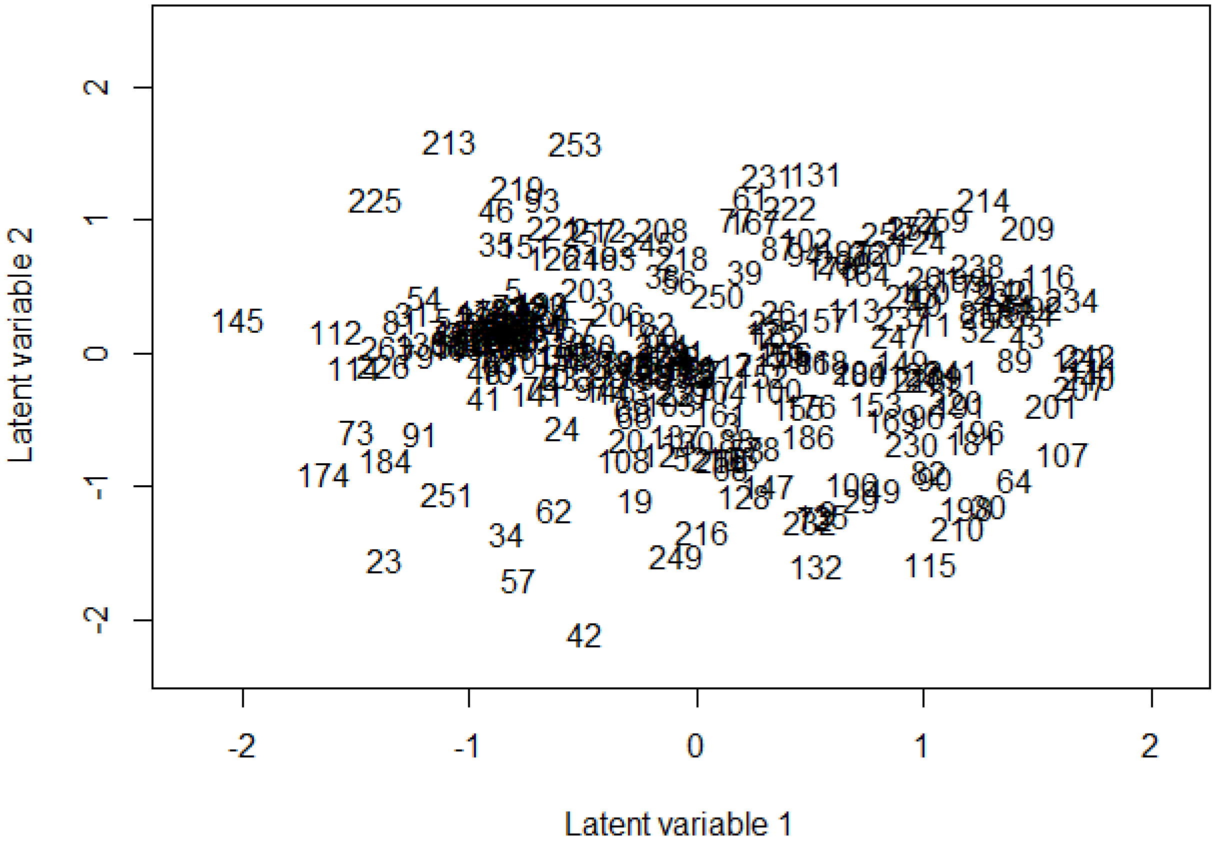


Figure S5. Biplot of constrained ordination for the 94% clustering level

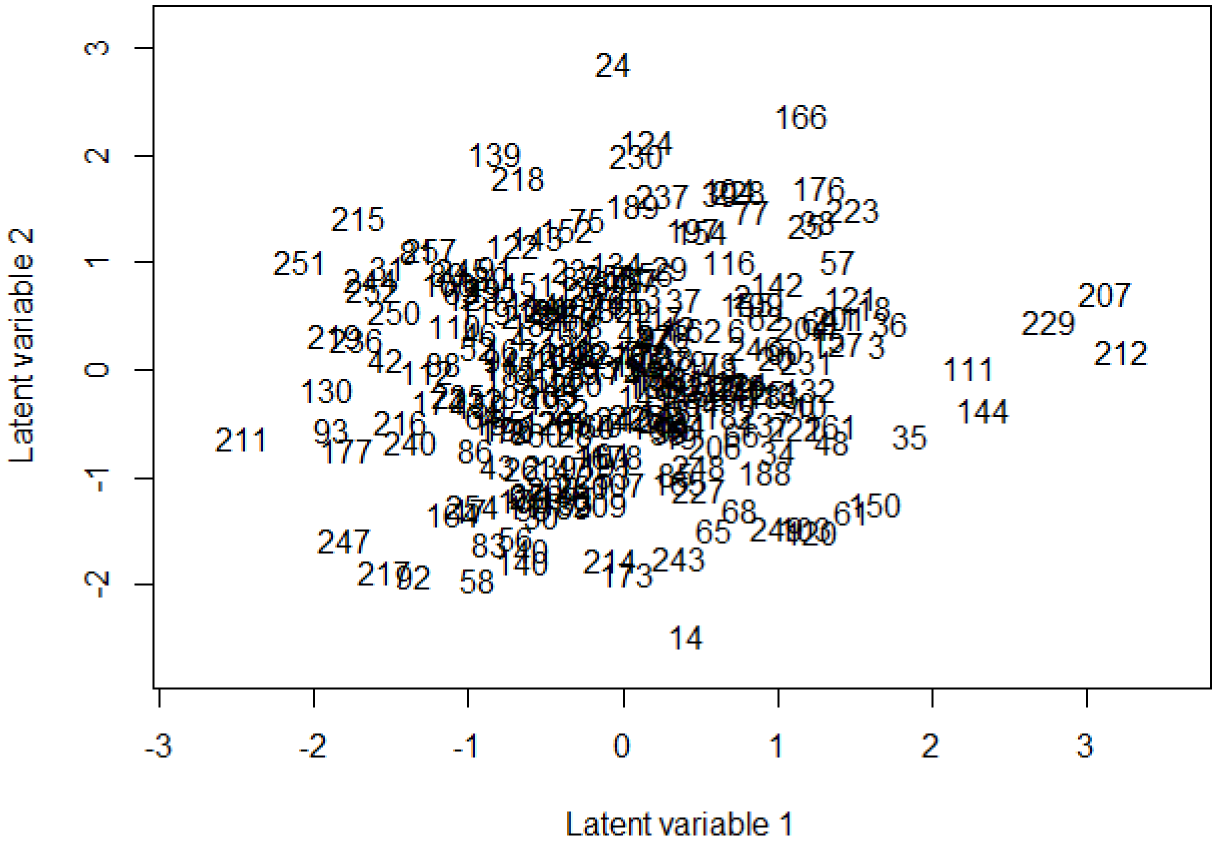
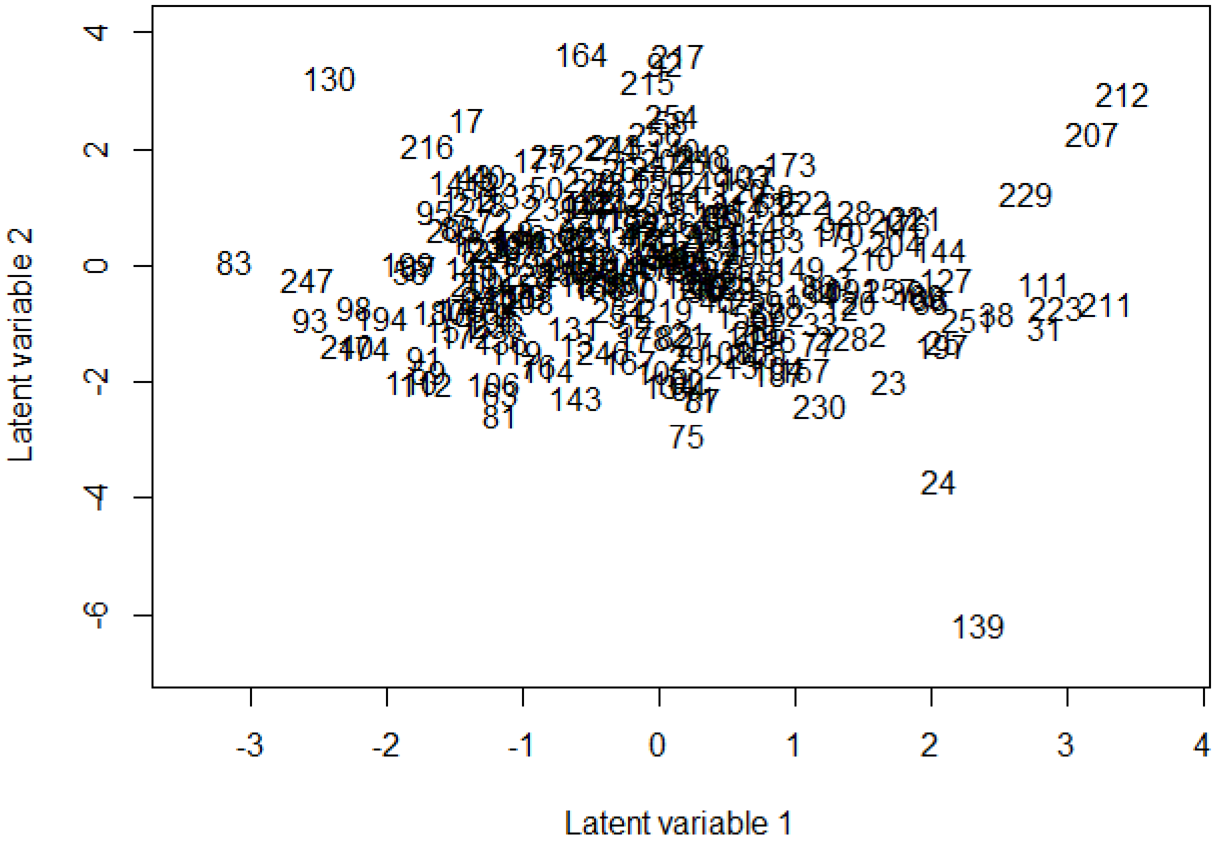


Figure S6. Biplot of constrained ordination for the 96% clustering level


Latent variable 2
Latent variable 1
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2
0
-2
-4
-6
-3
-2
-1
0
1
2
3
4
164
217
130
215
212
207
17
216
173
229
83
247
93
98
194
111
223
211
31
23
230
143
75
24
139

Figure S7. MOTU presence in bird diet for the 92% clustering level

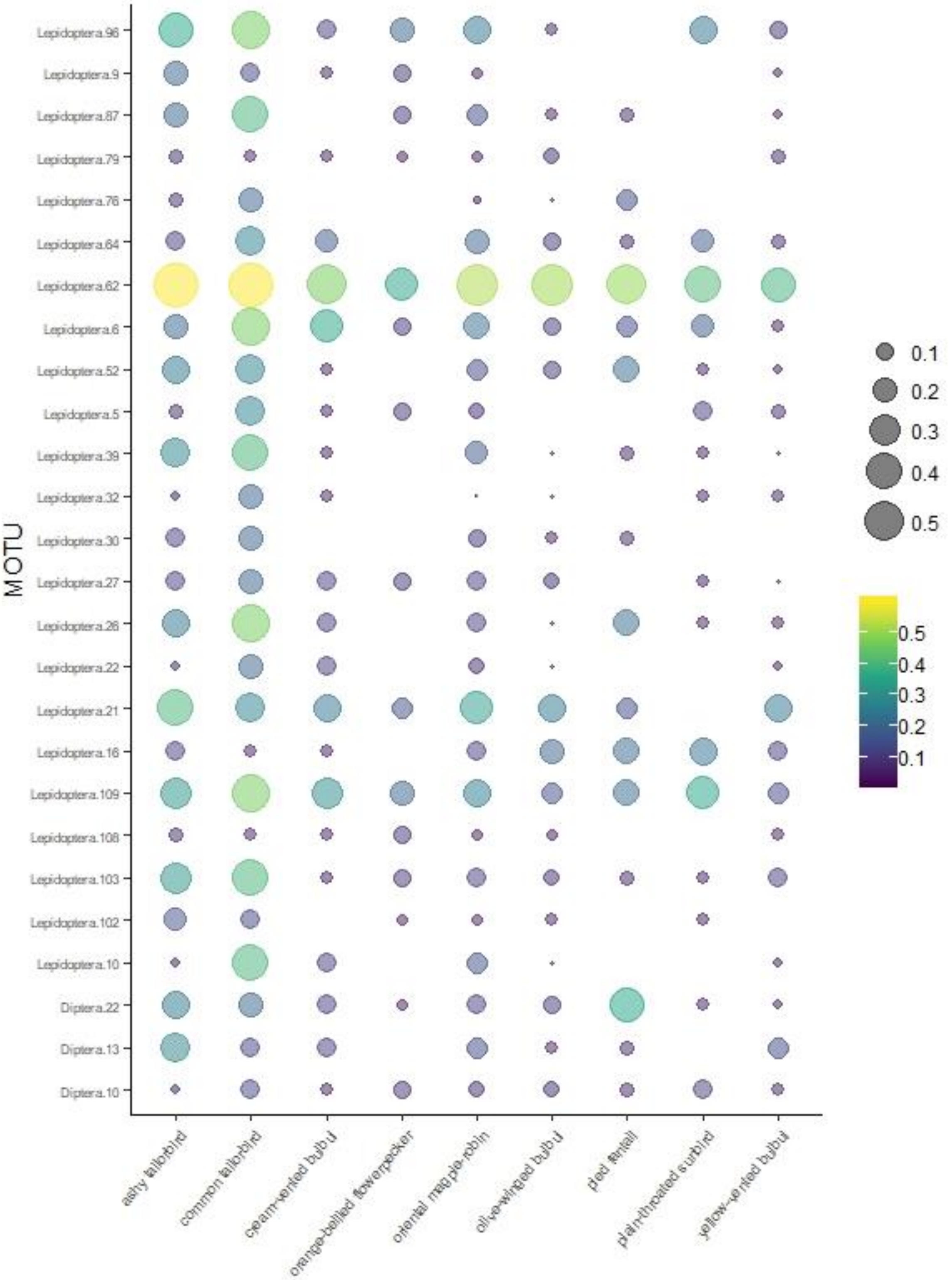


Figure S8. MOTU presence in bird diet for the 92% clustering level

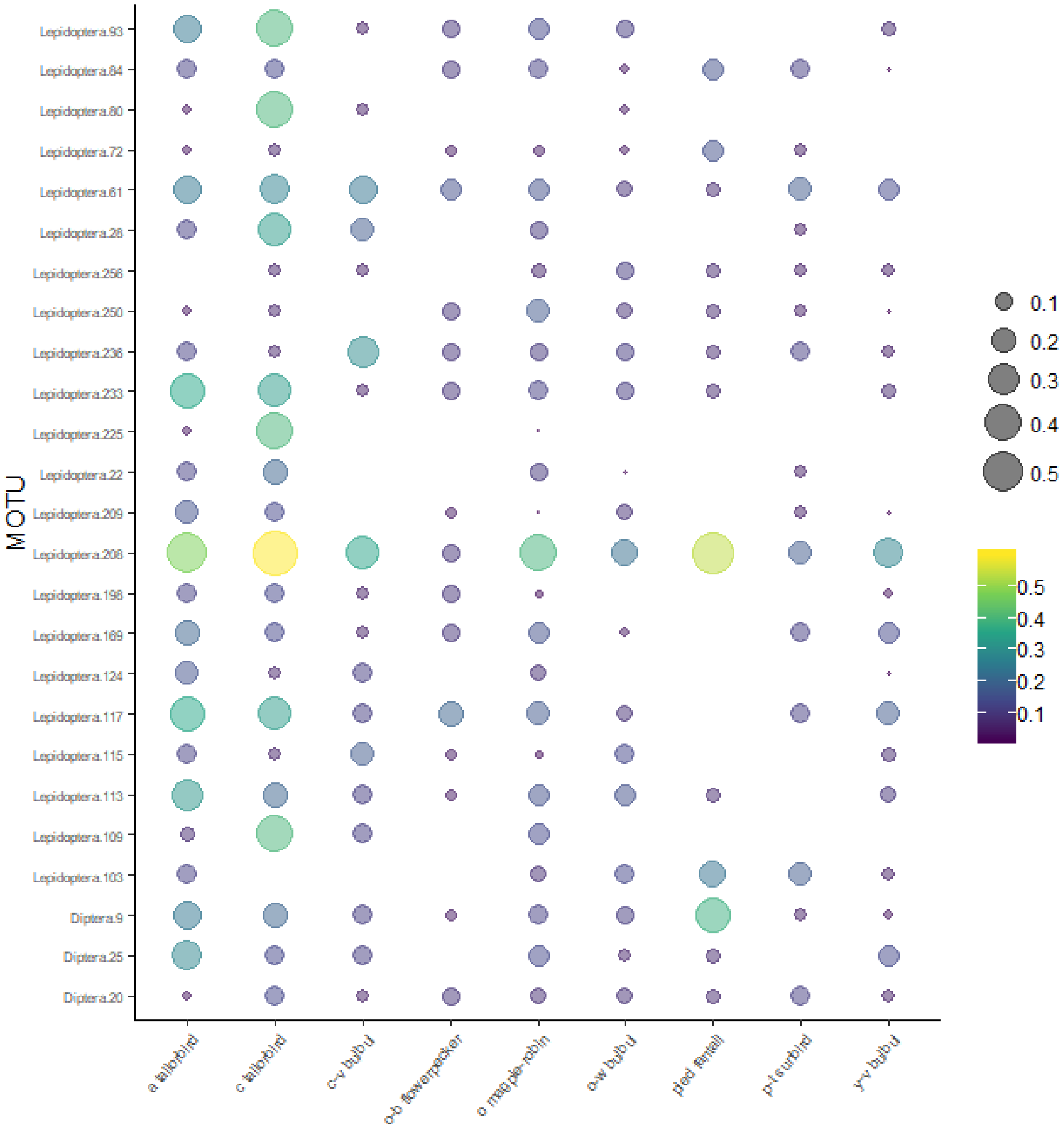


Figure S9. MOTU presence in bird diet for the 96% clustering level

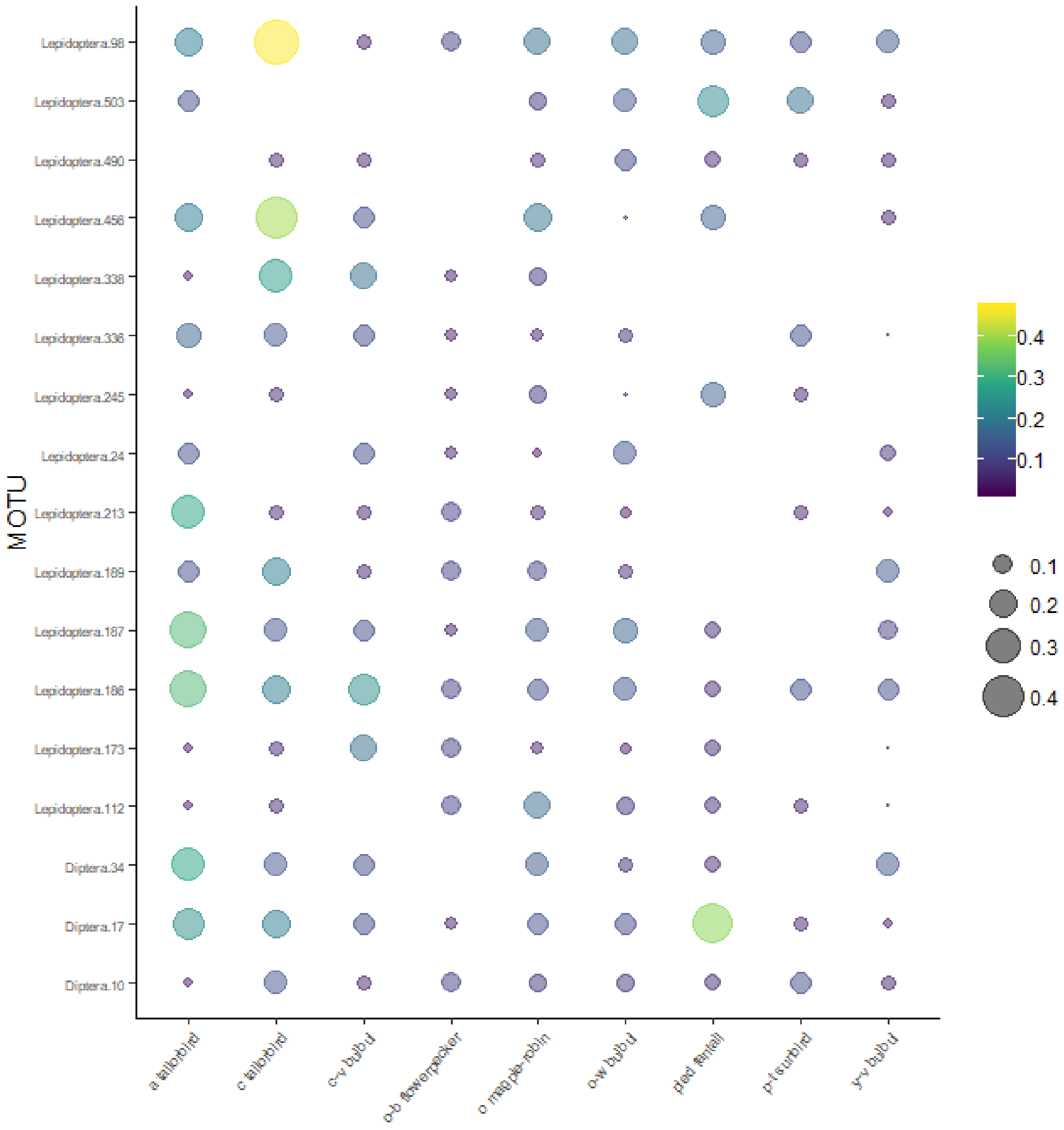
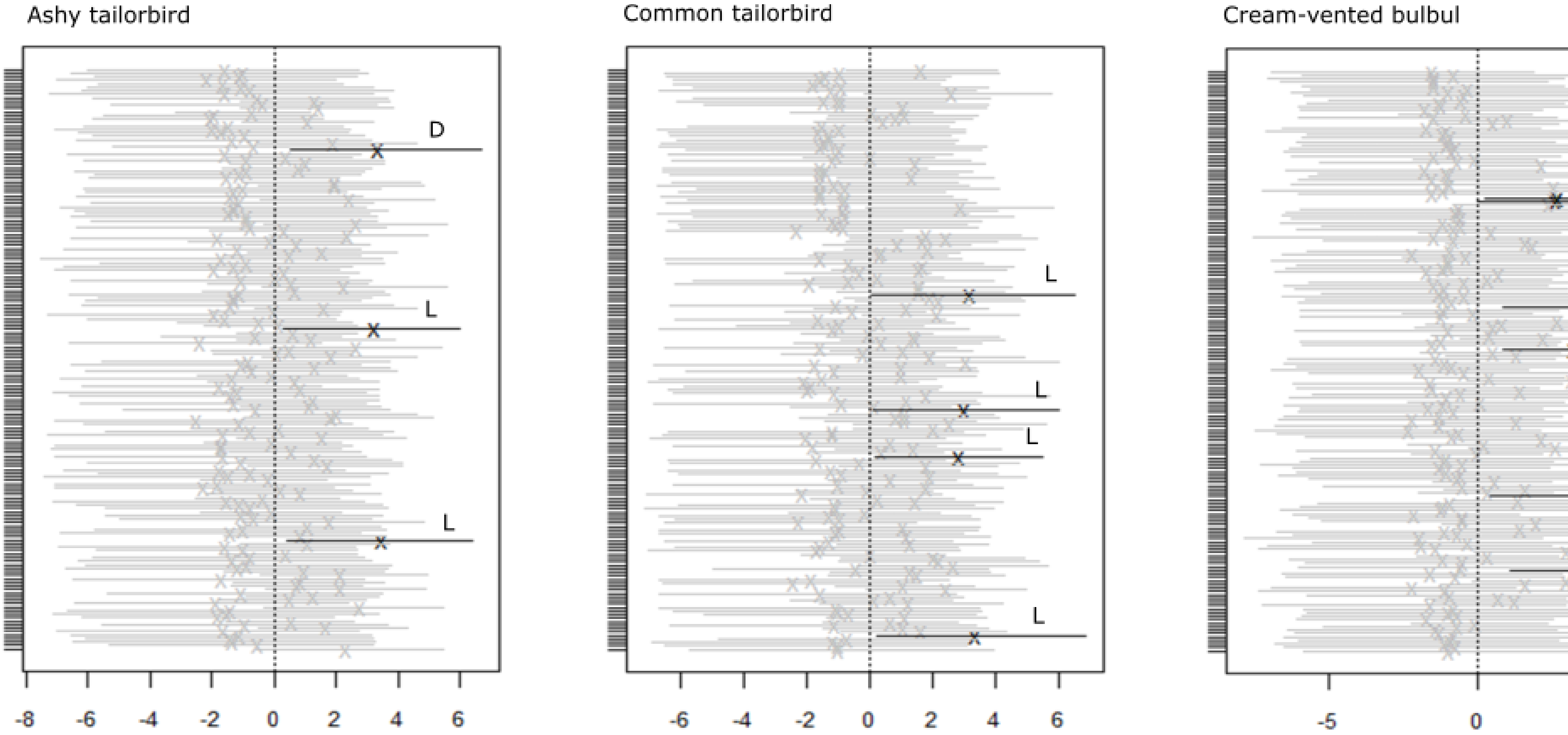
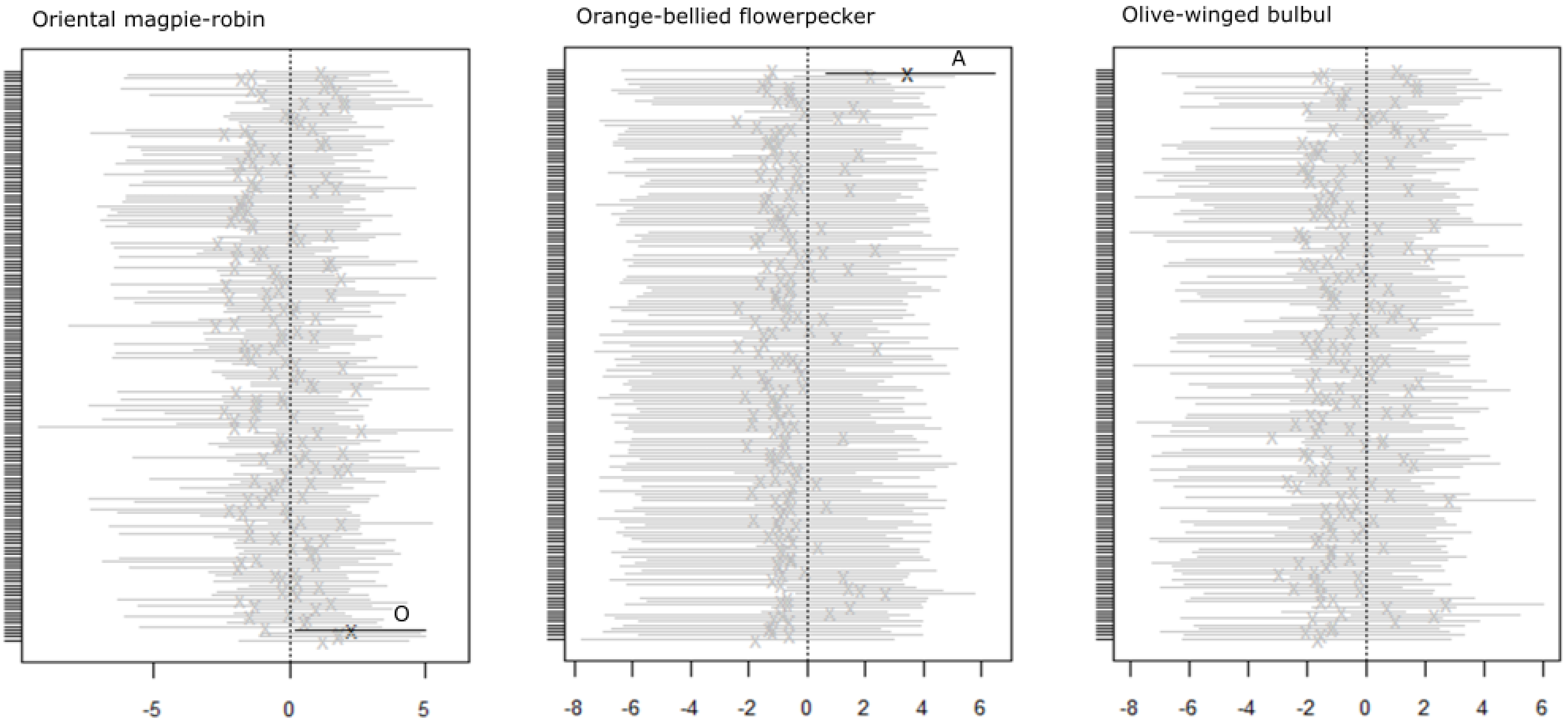
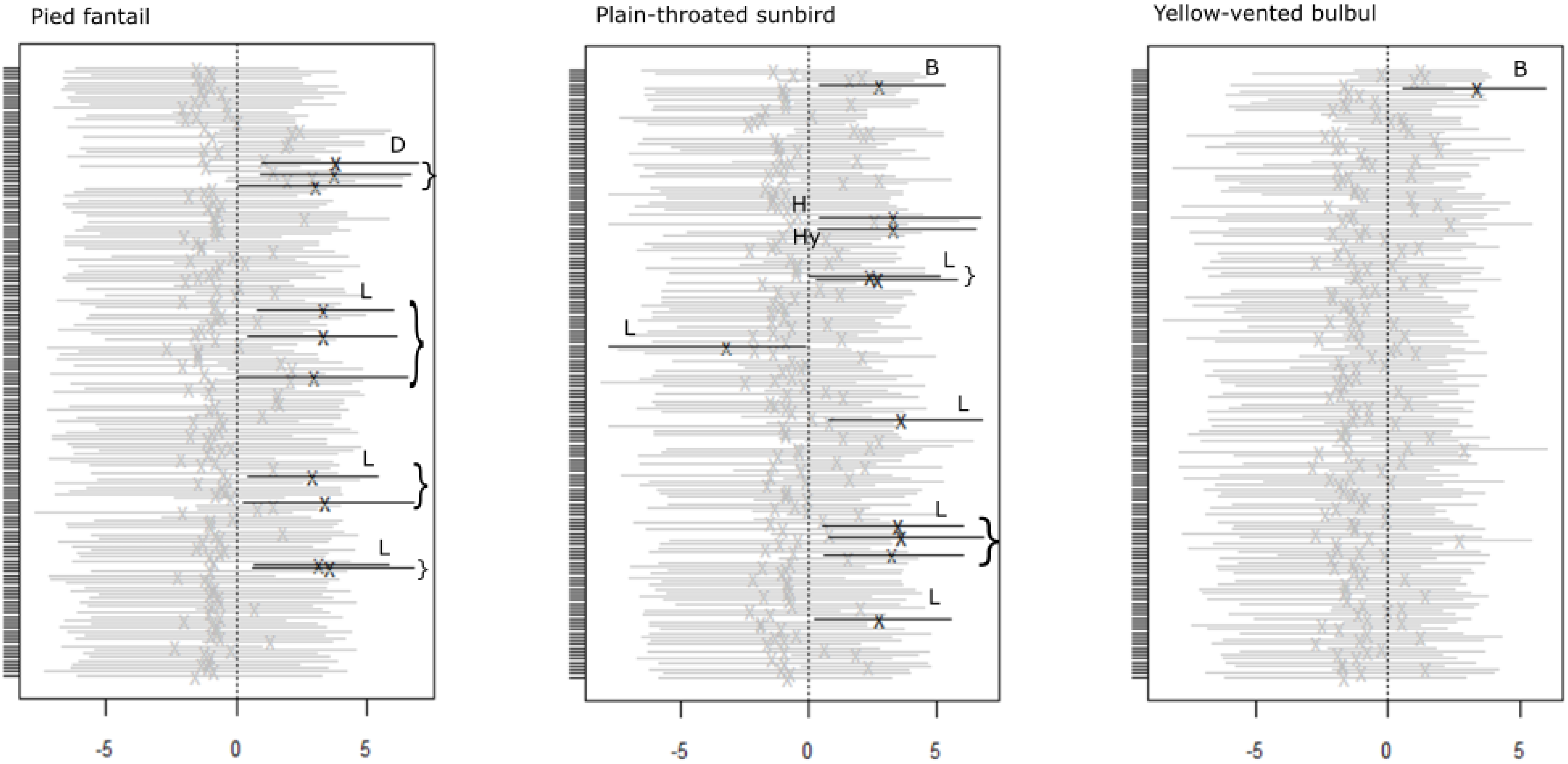


Figure S10. Posterior medians with 95% high posterior density intervals (HPD) of each MOTU corresponding to each bird species. HPDs that don't cross zero are in bold. The lettering signifies the ordinal assignment of the MOTU: L = lepidoptera, D = diptera, H = hemiptera, A = araneae, B = blattodea and HY = hymenoptera.




Oriental magpie-robin
O
-5
0
5
Orange-bellied flowerpecker
A
-8
-6
-4
-2
0
2
4
6
Olive-winged bulbul
-8
-6
-4
-2
0
2
4
6


Pied fantail
D
L
L
L
-5
0
5
Plain-throated sunbird
B
H
Hy
L
L
L
L
L
-5
0
5
Yellow-vented bulbul
B
-5
0
5

Supplementary Information: Chapter 4

Example of the process of piecewise SEM and model selection

Initial model based on theory and mixed models

[SOC ~ replanting +

P ~ replanting +

N ~ SOC +

SWC ~ SOC +

CEC ~ SOC +

Aggregate stability ~ SOC+

Macrofauna ~ SOC + replanting + sampling zone]

Suggested missing paths

N ~ P *p = 0.01*

Stability ~ SWC *p = 0.008*

SWC ~ replanting *p= 0.005*

Non-significant paths

Macrofauna ~ SOC *p = 0.32*

Aggregate stability ~ SOC *p = 0.16*

New model

[SOC ~ replanting +

P ~ replanting +

N ~ SOC + P +

SWC ~ SOC + replanting +

CEC ~ SOC +

Aggregate stability ~ SWC+

Macrofauna ~ replanting + sampling zone]