# Exploring the ecological resilience of smallholder oil palm landscapes

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# ABSTRACT

Employing more sustainable farming practices could enhance the ecological resilience of tropical oil palm smallholder farms. Concerns about the environmental impacts of oil palm cultivation has led the Roundtable on Sustainable Palm Oil (RSPO) to develop more sustainable management practices. However, it is unclear whether the uptake of such practices will enhance ecological resilience. My study focuses on oil palm smallholdings in Sabah, Malaysian Borneo. Using questionnaire-led interviews with farmers and ecological surveys of their farms, I examined inter-relationships between farm management practices, oil palm yields and the biodiversity, ecosystem functioning, and ecological resilience of farms. Oil palm yields varied widely across smallholder farms (6.9–37.4 t $ha^{-1}$ $yr^{-1}$), but there was little evidence that less intensive management reduced farm yields. I surveyed ground-dwelling ants on farms to assess species richness and functional diversity (richness and dispersion), and ant-mediated ecosystem functions (scavenging and leaf-litter decomposition). Ant species richness varied among farms (5-30 species), and there were positive associations between native and non-native species (which accounted for 0-40% of ant species on farms). Thus, native ant species persisting in oil palm habitats are resilient to invasion by non-native species, which maintain generalist ecosystem functions on farms. I used Structural Equation Models to investigate the inter-relationships between local factors (e.g., farm management) and wider landscape factors (e.g., proximity to roads and forest) on native and non-native species richness and functional diversity metrics, to make inferences about the ecological resilience of oil palm farms. Both local and landscape factors were important but native and non-native ant species were influenced by different factors. Compared with non-natives, native species contributed most to functional richness and dispersion, occurred on cooler farms, and were associated with higher oil palm yields. Thus, anthropogenic climate warming may reduce the ecological resilience of oil palm farms via its detrimental effects on native species, which may also impact crop yields. I conclude that more efforts should be made to enhance on-farm biodiversity and to develop management practices that support farmer livelihoods, enhance crop yields, and maintain the ecological resilience of oil palm landscapes.

Thomas Howells, Azlin Bin Sailim and me at a smallholder farm in Tampenau, near the Danum Valley Forest Reserve (photo credit, Jacob Anderson)

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## AUTHOR’S DECLARATION

I declare that this thesis is a presentation of original work and I am the sole author. This work has not previously been presented for an award at this, or any other, University. All sources are acknowledged as References.

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# CHAPTER 1

# General Introduction

Newly planted oil palm seedlings in an industrial plantation

Sabah, Malaysian Borneo

## 1.1 Abstract

Continued agricultural intensification and land-use changes could threaten the ecological resilience of tropical landscapes through the further loss of biodiversity and ecosystem functioning. In Southeast Asia, oil palm has played a major role in shaping tropical agricultural landscapes, but unfortunately this has come at a cost, with environmental and social issues such as deforestation, biodiversity and ecosystem functioning loss, and displacement of people. However, oil palm cultivation has also been a valuable source of income to smallholder farmers, which are estimated to make up over 30% of global palm oil production. Given this benefit, it is urgent that we find solutions to the management of oil palm landscapes that reduce environmental impacts whilst still maintaining farm yields and livelihoods. More sustainable management of oil palm landscapes could provide a solution, but there needs to be better understanding of the interactions between local farm yields, biodiversity and ecosystem functioning, and farm management. In this general introduction chapter, I outline the current understanding of the environmental impacts of oil palm agriculture; starting with an overview of the history and developments leading to the demand for sustainable oil palm, to an overview of the current management practices. I then focus on the potential factors that might be responsible for the large variation in oil palm yields, with a particular focus on smallholder oil palm landscapes. Finally, I consider how local oil palm management, together with features within the wider landscape, may interact to affect local farm biodiversity and ecosystem functioning, and hence influence the ecological resilience of farms to further environmental change. I introduce the overall aim of my thesis, which is to improve the understanding of what more sustainable and resilient tropical agricultural landscapes could look like. I also outline the main aims of each of my three data chapters, which are (1) to examine whether opting for sustainable farming practices results in trade-offs between oil palm yield and biodiversity, (2) to quantify the functional diversity of farms, and (3) to examine whether local farm management and wider landscape factors can improve the ecological resilience of oil palm communities through their effects on species richness and functional trait diversity.

## 1.2 Land-use change in tropical landscapes

The tropics are one of the most biodiverse regions in the world, but they are also experiencing significant pressures from agricultural expansion (Zeng et al., 2018), human population growth, urban development, and climate change (Edelman et al., 2014). Biodiversity in the tropics is thought to be particularly sensitive to climatic and land-use change (Newbold et al., 2020), and a significant amount of biodiversity has been lost through land-use change and habitat degradation (Giam, 2017; Ocampo-Peñuela et al., 2020). To minimise further biodiversity loss and environmental damage within these tropical regions, further consideration of the interlinkages between biodiversity and human livelihoods within these landscapes will be necessary under current and future land-use priorities (Defries et al., 2010).

Borneo is a biodiversity hotspot with high levels of endemism (Camacho-Sanchez et al., 2019; Neo et al., 2021; Salas et al., 2005), making it an especially important area for conservation (Angulo et al., 2022). However, Borneo has experienced high rates of deforestation over many decades due to urban development, commercial logging activities and oil palm cultivation (Gaveau et al., 2016, 2018). Whilst recent policies have been implemented in Malaysian Borneo to reduce deforestation and habitat degradation (Ng et al., 2022), remnant forest habitats still remain vulnerable to further land-use change from infrastructure development and agricultural expansion (Abram et al., 2022; Shirley & Kammen, 2015; Sloan et al., 2019; Spencer et al., 2023; Theresia et al., 2020). At the same time, agriculture is an important source of income that facilitates economic development and poverty alleviation in tropical regions (Alexandra Edelman et al., 2014; Kubitza et al., 2018). Therefore, it is important to understand how tropical landscapes, such as those on Borneo, can be managed so as to preserve biodiversity without detrimental impacts on the livelihoods of agricultural communities.

### 1.3 Resilience in the context of tropical palm oil landscapes

Resilience can be defined as the ability to resist and recover from pressures or change (Dakos & Kéfi, 2022; Hosseini et al., 2016). In an ecological context, the concept of resilience can be applied to understand whether species and ecological communities are able to withstand and recover from environmental changes and disturbance (Holling, 1973) (e.g., climate warming or land-use change), and the consequences that this has on the provisioning of ecosystem functions (Oliver et al., 2015). Assessing the resilience of ecological communities in tropical landscapes will be especially important for understanding where management and conservation actions may be required (e.g., to protect more vulnerable species), and the potential to mitigate the loss of ecosystem functions and services that people rely on.

A loss of ecological resilience could result in ecological communities that are more vulnerable to changes in their structure and functioning (Holling, 1973), and so reduce the provisioning of ecosystem services (Oliver et al., 2015). Agricultural production is a particularly important ecosystem service within tropical landscapes, contributing to 60% of global agricultural production (FAO, 2020). Hence, maintaining resilient tropical agricultural landscapes will be necessary to ensure global food security (Bullock et al., 2017). However, food security is a multi-faceted issue which needs to be addressed across the entire food-production supply chain. At a landscape-scale, this involves ensuring that agricultural production is able to withstand environmental pressures, such as climatic changes, introduction of pests and invasive species, and loss of soil fertility (Urruty et al., 2016). Biodiversity is central to reducing the impacts of some of these pressures (Martin et al., 2019; Waddell et al., 2020), which therefore requires a better understanding of the factors contributing to more resilient biodiversity and maintenance of ecological functions. Maintaining ecological resilience in agricultural landscapes requires inclusive practices that consider the needs and livelihoods of smallholder farmers. To achieve this, sustainable management practices must be both effective and affordable, so that farm yields are not negatively impacted. By prioritizing people's livelihoods and the biodiversity of agricultural landscapes, we can ensure that these landscapes continue to thrive over the long term (DeFries et al., 2016; Maleksaeidi & Karami, 2013).

## 1.4 Oil palm cultivation

### 1.4.1 Background: origins, arrival in SE Asia and growth of industry

Oil palm (*Elaeis guineensis* Jacq.) is an important vegetable oil crop with very high-yielding fruits, producing four times more oil per hectare of land (2.91 t ha$^{-1}$) compared to the next two highest oil-producing crops, sunflower (0.73 t ha$^{-1}$) and rapeseed (0.72 t ha$^{-1}$), and covering only 6% of the cultivated land used for all oil-producing crops (Ritchie & Roser, 2021). Due to the oil palm's high productivity per unit of land, palm oil and other oil palm fruit-derivatives (from the fruit pulp and kernel) are now extensively used in a wide range of products ranging from food and personal care products to cosmetics and biofuel. To meet growing consumer demands for oil-based products, the cultivation of oil palm has been expanding globally (particularly in Asia, Latin America, and central Africa), with the world's largest palm oil producers centred in Southeast Asia. Notably, Malaysia and Indonesia have been estimated to contribute to over 84% of global production in 2021 (~ 61,500 Mt; Ritchie & Roser, 2021). Despite oil palm only being introduced as a crop in these regions within the last 150 years (Byerlee, 2014), they have nonetheless become the world's most dominant producers due to the environmental suitability for high crop productivity, as well as the large economic development that oil palm production has facilitated in both countries.

Oil palm originates from western and central Africa, where it naturally occurs around swamps and along edges of forested areas (Robins, 2021). Historically, oil palm groves have held high cultural significance among communities in these regions, with the oil-rich fruits and other parts of the palm tree providing a valuable source of oil, wine, as well as medicinal products. Traditionally, oil palm was reported to have been harvested from wild and semi-wild managed groves occurring in cleared areas and along forest edges (Khatun et al., 2020). During the 18th and 19th centuries, there was a large increase in export of palm oil to European countries, where it became a valuable asset as an industrial lubricant, for soaps and as a biofuel (Robins, 2021). Colonialists wanting to capitalise on palm oil's commercial success in Europe then drove the transformation of oil palm cultivation from wild and semi-wild groves to more industrialised and commercialised plantations that aimed to maximise yield production for profits, and ultimately leading to the expansion of oil palm production into new regions within and beyond Africa (Robins, 2021). *Elaeis guineensis* was first introduced to Southeast Asia in the 1840s. However, due its dependence on hand pollination for fruit production, it was initially more popular as an ornamental plant. The first commercial estate was established in Sumatra in the 1900s, and the site was chosen for its fertile soils and favourable climate (e.g., well-draining soils with sandy to clays texture, high annual rainfall and, high temperatures; Corley & Tinker, 2016) that had previously been proven successful for the cultivation of rubber and other crops (Feintrenie & Levang, 2009). Expansion of oil palm plantations throughout Sumatra and Borneo continued during Dutch colonial rule (Baudoin et al., 2017), and oil palm was an alternative crop to replace natural rubber following the development of the first type of synthetic rubber in 1909 (Khoo Kay Kim, 1999). Oil palm became a crop that was once traditionally grown in less-forested areas in Africa, to one that was driving deforestation of SE Asian rainforests. Following independence of Malaysia and Indonesia, the palm oil industry has become important for supporting the economic development of Malaysia and Indonesia (Varkkey et al., 2018). With the introduction of the pollinating weevil in the 1980s (*Elaeidobius kamerunicus*), palm oil production boomed as labour was released from hand-pollinating palm tree flowers, resulting in much higher yields (Yousefi et al., 2020). Oil palm cultivation has resulted in an estimated clearance of 18.7 Mha of old-growth forest between 1973 and 2015 in Borneo alone (Gaveau et al., 2016).

Industrial plantations have driven deforestation in Malaysian landscapes (Gaveau et al., 2016), whereas smallholder oil palm producers have generally contributed to a smaller portion of land-use change (Lee, Abood, et al., 2014). Smallholders, defined as smaller-scale growers with farms less than 50 ha in size, and where the palm oil crop provides the main source of income (RSPO P&C, 2018), are estimated to contribute to over 30% of global palm oil production (Descals et al., 2020). However, there is a wide variety of smallholder producers and industry schemes (e.g., independent farmers, plasma schemes linked to multi-national companies; Jelsma et al., 2009, 2019), as well as differences in cultivation practices and policies, and forest protection (Cisneros et al., 2021; Varkkey et al., 2018; Wicke et al., 2011). This diversity results in large differences in the way that oil palm is cultivated within and between countries, resulting in varied impacts that oil palm cultivation has on human communities, biodiversity and ecosystem services within production landscapes (e.g., land-use change, carbon-emissions, livelihoods; (Furumo & Aide, 2017; Qaim et al., 2020; Quezada et al., 2019). For example, oil palm farming models within Ghana differ in the cropping systems used, with independent farmers sometimes following a mixed-crop system within oil palm farms during the initial stages of planting to support household incomes, whereas scheme-supported farmers that have contractual obligations to larger companies or mills typically follow an oil palm monoculture system (Proforest, 2014)**.** Moreover, cultivation of palm oil in Latin America is distinct from that in Southeast Asia, as the large proportion of oil palm plantations have expanded onto land-use that was previously used for agricultural production (e.g., 51% on cattle pastures, 30% on croplands, and only 16% on natural vegetation habitats; Furumo & Aide, 2017). In conclusion, this diversity of producers, cultivation practices, and regional contexts generates a wide spectrum of outcomes, in particular within smallholder landscapes, emphasizing the need for address the varying consequences of oil palm cultivation across different regions and communities.

### 1.4.2 Current management of oil palm in SE Asia: striving for higher yields and closing yield gaps

Oil palm in Southeast Asia is conventionally cultivated as an intensive monoculture, with plantations characterised by having little understorey vegetation cover as a result of wide-spread applications of herbicides. However, despite this intensive management, there is large variation in oil palm fruit production, particularly among smallholders (Euler et al., 2016). Hoffmann et al., (2015) estimate the potential average yield for large commercial plantations to be 35–40 t of fresh fruit bunches (FFB; ha$^{-1}$ yr$^{-1}$), but the Roundtable on Sustainable Palm Oil (RSPO) report much lower smallholder yields of an average of 18.9 t FFB ha$^{-1}$ yr$^{-1}$, half the estimated production for larger-scale plantations (RSPO, 2019). As such, there is a focus on closing yield gaps by intensifying management on smallholder farms, as well as on industrial plantations, with the aim to minimise further oil palm expansion into high carbon natural forest habitats (Fairhurst & Griffiths, 2014; Hoffmann, Donough, Oberthur, et al., 2015; figure 1).

**Figure 1.** Pictured left, oil palm Fresh Fruit Bunches (FFB). Pictured right, a smallholder farmer's harvest awaits collection for transport to a nearby mill (photograph credit Thomas Howells).

Many studies have investigated the factors influencing oil palm yields, which have identified climate (Oettli et al., 2018), soil properties (Balasundram et al., 2006; Paramanthan, 2013), and agricultural management as key factors (summary of key findings provided in Table 1). Climate affects fruit production at different development stages, from flower inflorescence to fruit development and ripening (Corley & Tinker, 2016). Important climate variables are rainfall, temperature, and light intensity (Oettli et al., 2018) as they determine the amount of energy that the plant can put towards fruit production (Corley & Tinker, 2016). Soil quality is a key factor influencing palm tree health and fruit production, and nutrient deficiencies can stunt palm tree growth, making them more susceptible to pests and disease, and so diminishing FFB production and quality (Corley & Tinker, 2016).

Agricultural management practices can address these issues to some extent, for example using terracing to prevent soil erosion and water run-off, reducing nutrient deficiencies through fertiliser application, reducing pests and diseases outbreaks with insecticides, suppressing weed cover with herbicides, pruning palm fronds to maximise light penetration, and optimising planting density to maximise soil nutrient uptake (Woittiez et al., 2017).

Given improvements in management practices, it is still unclear why large variation in smallholder yields still occur, and why yields are so much lower on smallholder farms compared to industrial-scale growers (Corley & Tinker, 2016; Euler et al., 2016). Thus, further investigations are needed to better understand drivers of yield variation, and the relative importance of management, soil, and/or climatic conditions. Previous studies have used experimental plots to test the impacts of management practices on yields (Bonneau et al., 2018; Tampubolon et al., 1990; Tao, Donough, et al., 2018), or have looked at the effects of soil and climatic variations (Oettli et al., 2018; Safitri et al., 2018; Sukarman et al., 2022), but few studies have considered these factors together. Studies considering multiple factors and whether increasing management intensity will be especially important for smallholder farmers in order to understand how climate, soil and management collectively impact oil palm yields, with the aim to sustainably increase oil palm production.

| **Factor limiting yield** | **Impact on yield** | **Reference** |
|---|---|---|
| **Abiotic** | | |
| Temperature | Fruit development (inflorescence development to fruit development). Optimum mean annual temperatures between 26-29$^{o}$C. | (Corley & Tinker, 2016; Fleiss et al., 2022) |
| Rainfall (water availability) | Fruit development (sex determination to fruit development). Optimum annual rainfall > 2000mm, without a clear dry season. | (Aji et al., 2022; Corley & Tinker, 2016; Gunawan et al., 2020; Fleiss et al., 2022) |
| Solar radiation | Fruit development (Inflorescence initiation to fruit development). Optimum sunshine of 5-7h/day evenly across the year. | (Corley & Tinker, 2016) |

|  |  |  |
|---|---|---|
| Nutrient deficiencies | Deficiency of key nutrient elements within soils, particularly N, P, K, Mg, Ca and S. Optimal growth in well-draining soils with sands to clay texture, and no gravel or stones. | (Corley & Tinker, 2016; Woittiez et al., 2018) |
| **Management** |  |  |
| Pruning activities | Frequent pruning of palm fronds to direct energy to flowering and fruiting. However, over-pruning can be damaging. | (Marcelino & Diaz, 2016; Rosenfeld, 2009; Soliman et al., 2016) |
| Nutrient application | Application of synthetic or organic fertilisers to address nutrient deficiencies or improve soil quality. Ensures nutrient availability to palm trees for fruit production. | (Woittiez et al., 2018) |
| Planting material | Type of planting material affects fruit bunch size fruit to kernel ratio. Three seed varieties: *tenera, dura* and p*sifera*, with *tenera* being the highest oil-yielding variety. | (Corley & Tinker, 2016; Soliman et al., 2016) |
| Planting density | Planting at optimum densities to prevent competition between palm trees. Increases nutrient availability and fruit production. | (Bonneau et al., 2018; Corley, 1973) |
| Crop recovery | Collection of fallen fruit to increase harvesting efficiency. | (Lee, Ghazoul, et al., 2014; Rhebergen et al., 2018, 2020) |
| Terracing | To prevent nutrient run-off and soil erosion on plantations established on steeper slopes. | (Afandi et al., 2017; Mohsen et al., 2014) |
| Ground-cover management. | Maintain ground-cover vegetation within plantations to reduce run-off, soil erosion and nutrient leaching. | (Satriawan et al., 2021) |
| **Biotic** |  |  |

| | | |
|---|---|---|
| Pests | Can contribute to crop reductions and tree mortality. | (Kamarudin et al., 2016; Ming et al., 2021) |
| Disease | Can lead to tree mortality and yield reductions, such as bud rot or *Ganoderma* infection. | (Kamarudin et al., 2016; Tupaz-Vera et al., 2021) |
| Pollination | Insufficient pollination can contribute to bunch failure and reduce fruit production. | (Yousefi et al., 2020) |
| Weeds | Reduce nutrient availability to palm trees and fruit production. | (Samedani et al., 2014; Soliman et al., 2016) |

**Table 1.** Overview of key abiotic, biotic and management factors shown to limit oil palm yield across various stages of fruit development.

### 1.4.3 Consequences of agricultural intensification to close yield gaps

Increasing agricultural intensity may improve oil palm yields on plantations, but this often comes at a cost to biodiversity and environmental sustainability (Clough et al., 2016; Teuscher et al., 2015). Trade-offs between management and biodiversity have been observed along gradients of agricultural land-use intensification, with more intensive oil palm monocultures supporting lower biodiversity and ecosystem functioning (e.g., soil nutrient retention), but higher crop productivity compared to less intensive plantations (i.e., 450% more harvested biomass compared to a less intensive agroforestry crop system) (Clough et al., 2016). These trade-offs probably occur because agricultural intensification exacerbates the detrimental environmental and social impacts of oil palm cultivation, such as greater biodiversity loss due to habitat degradation (Fitzherbert et al., 2008; Olivier et al., 2020), greater pollution of waterways from higher agrochemical inputs (Mercer et al., 2014), and lack of income diversification for smaller-scale farmers from the cultivation of monocultures (Santika et al., 2019). There is evidence that more intensive agrochemical inputs (e.g., herbicides) reduce understorey vegetation complexity and ground-vegetation cover in planted areas (Luke et al., 2019), which contribute to higher soil degradation (Borrelli et al., 2017) and loss of soil biodiversity and functioning (Ashton-Butt et al., 2018). Many plantations require high fertiliser inputs to maintain yields as land scarcity pushes oil palm cultivation to increasingly marginal land with nutrient-depleted soils (Guillaume et al., 2016). However, applying these intensive management practices is expensive, and are not always required to improve oil palm yields (Darras et al., 2019; Soliman et al., 2016). For example, reductions in fertiliser applications and herbicide applications in Sumatran oil palm plantations did not see a decline in oil palm yields over a two-year period (Darras et al., 2019). As such, agricultural intensification may not be an economically viable solution for smallholder farmers with less available capital to maintain long-term yields by using intensive practices (e.g., high chemical fertiliser application). Hence, it is important to explore ways to increase oil palm productivity that have fewer trade-offs with biodiversity and environmental sustainability, and that are able to address socio-economic issues within oil palm farming landscapes (e.g., Adolph et al., 2020; Garnett et al.; Rockström et al., 2017; Tilman et al., 2011; Yi et al., 2019).

## 1.5 Demand for sustainable solutions to oil palm agriculture

Growing public awareness of the environmental and social consequences of the palm oil industry (e.g., forest loss and degradation, land rights issues between local communities and large corporations over land ownership), has led to mounting pressures from boycotts and campaigns, and calls to reform or ban palm oil products (Fair, 2021; Teng et al., 2020). As a response, the Roundtable on Sustainable Palm Oil (RSPO) was set up in 2004, founded by NGOs and key players in the food-production industry, including WWF (World Wide Fund for Nature), the Malaysian Palm Oil Association (MPOA), Unilever (consumer goods company), AAK (vegetable fats and oil producer), and Migros (supermarket). The RSPO created a voluntary sustainability certification standard for industrial and smallholder growers, based on the RSPO's Principles and Criteria (P&Cs) (RSPO P&C, 2018). The P&Cs have developed over time and address three impact goals: (1) Prosperity, (2) People, and (3) Planet. Within the 'Planet' goal, RSPO specify that: "Ecosystems and their services are protected, restored and resilient, supported by sustainable consumption and production, and sustainable management of natural resources (in line with UN Sustainable Development Goal, SDG 15: sustainably manage forests, combat desertification, halt and reverse land degradation, halt biodiversity loss)." Hence, the RSPO emphasise the requirement of "resilient and restored" ecosystems, although they do not provide any definitions of 'resilience'. A major emphasis of RSPO's environmental guidelines is on protecting biodiversity within conservation set-asides, such as High Conservation Value (HCV) areas, High Carbon Stocks (HCS) sites, and riparian corridors, but make little reference to the contribution that within-farm biodiversity could make to the resilience of oil palm landscapes. Therefore, there are still many knowledge gaps that need to be addressed in order to understand what a resilient oil palm landscape looks like, which management practices contribute to ecological resilience, and the relationships between biodiversity, resilience and sustainable oil palm production.

The word 'sustainability' has many different meanings (Glavič & Lukman, 2007; Virtanen et al., 2020; Zhang et al., 2021), but the overall consensus is that sustainability should address three aspects: (1) environmental, (2) social, and (3) economic. Within the palm oil industry, sustainability is mainly focused on the practices outlined by the RSPO's P&C (Prosperity, People and Planet), where goals around 'Prosperity' and 'People' are more developed (e.g., increasing worker safety and inclusion of smallholders within the supply chain) than those for 'Planet'. The P&Cs linked to 'Planet' are focused on identifying and protecting conservation-set asides within oil palm landscapes and improving soil fertility on farms (e.g., through improved agricultural practices; RSPO P&C, 2018), but with limited recommendations on how to apply farm management to improve within-farm biodiversity. For example, there are a variety of tools and manuals to assess, manage and monitor biodiversity and carbon-stocks within High Conservation Value Areas (e.g., HCV-HCVA assessment manual; (HCVN, 2017). Approximately 20% of oil palm is RSPO-certified, with European consumers being the main market for sustainable palm oil (EPOA et al., 2022).

At a farm-scale, Best Management Practices (BMPs) are recommended to reduce environmental impacts whilst still maintaining oil palm yields through improved harvesting practices and fewer agrochemical inputs (Fairhurst & Griffiths, 2014; Rhebergen et al., 2020). BMPs are included within some RSPO recommendations to improve soil fertility (e.g., organic mulching, maintaining ground vegetation cover and palm frond stacking), but BMPs also cover management practices that aim to increase smallholder oil palm yields whilst maintaining lower agricultural costs (e.g., improving crop recovery and more frequent harvesting). Improved yields and soil organic carbon (SOC) have been reported on farms applying BMPs (Rahman et al., 2021) and so studies of BMPs are an important focus of research to improve the sustainable production of oil palm on smallholder farms. However, understandings of how BMPs can boost farm biodiversity are limited.

Current evidence shows mixed impacts of RSPO certification for achieving its sustainability goals. RSPO certification can improve crop yields (e.g., through improved nutrient management, planting material and harvesting frequency; De Vos et al., 2021) and community livelihoods within production landscapes (Santika et al., 2021). However, improvements in village socioeconomic and socioecological well-being (i.e., living conditions, infrastructure, and security) can be highly dependent on the village livelihood sector prior to development, whereby overall wellbeing of villages dependent on subsistence livelihoods (particularly socioecological indicators such as low wage agricultural labourers and prevalence of conflicts) are reduced after transition to RSPO-certified plantation villages (Santika et al., 2021). There are also studies on the ecosystem services and biodiversity benefits of RSPO certification and conservation set-asides of natural forest areas (e.g., improved carbon storage, plant and mammal diversity within HCVs; Deere et al., 2018; Fleiss et al., 2020), and how to improve HCV-HCSA practices and zero-deforestation commitments (Austin et al., 2021; Edwards et al., 2012; Scriven et al., 2019; Senior et al., 2015). However, fewer studies have examined how farm management and wider landscape factors influence on-farm biodiversity.

Evidence suggests that BMPs may improve on-farm biodiversity. For example, mulching through the application of empty oil palm fruit bunches (EFB) can enhance soil ecosystem functioning, including higher soil faunal feeding activity, as well as improved soil chemical properties and moisture conditions (Tao et al., 2016; Tao, Snaddon, et al., 2018). However, the benefits on soil fauna communities and carbon sequestration may be limited to the EFB application areas (Carron et al., 2016). Reduced fertiliser and herbicide use increases ground-vegetation cover (Luke et al., 2019), which can increase soil biodiversity (Ashton-Butt et al., 2018) and invertebrate abundance (Hood et al., 2020). Incorporating more non-palm trees on farms can boost diversity and abundance of birds and invertebrates (Razak et al., 2020; Teuscher et al., 2016), but can reduce yields (Hamer et al., 2021; Teuscher et al., 2015). Thus, studies examining factors that promote more biodiverse oil palm habitats need to consider trade-offs with crop yields and any negative consequences and disbenefits for smallholder livelihoods.

## 1.6 Biodiversity in oil palm landscapes

Oil palm landscapes are highly modified by people and support very different ecological communities to those within tropical forest habitats (Fitzherbert et al., 2008; Senior et al., 2013). Loss of tree canopy cover and understorey vegetation complexity, results in warmer temperatures (6.5$^{o}$C temperature difference; Hardwick et al., 2015) and reduced stability in micro-climatic conditions (i.e., greater differences in air temperature and humidity; Clough et al., 2016). These altered environmental conditions have large impacts on local biodiversity, with oil palm areas supporting fewer species than tropical forested areas (Clough et al., 2016; Dislich et al., 2017), and with few species shared (15-30% of species occurring in tropical forests; Fitzherbert et al., 2008; Lucey et al., 2017; Savilaakso et al., 2014) and so little overlap in community composition (Lee-Cruz et al., 2013; Savilaakso et al., 2014). These differences are mainly due to the loss of forest-dependent species and the arrival of non-native species in oil palm areas (Waddell, Chapman, et al., 2020). However, despite lower species diversity and altered community composition, biodiversity within agricultural landscapes contributes to important ecosystem functions (e.g., water management, carbon sequestration, pest control, decomposition, and nutrient cycling; Dislich et al., 2017), and so is vital to conserve. If biodiversity is maintained, it may provide farmers with more sustainable management options (e.g., reduced reliance on agrochemical fertilisers and pesticides).

Sustainable food production requires biodiversity so that food production, and the ecosystem functions that it relies on, are resilient to future environmental changes. Supporting biodiversity on oil palm farms will be key to developing more sustainable and resilient tropical agricultural landscapes, which requires a greater understanding of the abiotic and biotic factors influencing on-farm biodiversity, especially those factors contributing to native species richness. There is also a need to better understand whether non-native species contribute to ecosystem functions on oil palm farms, or if an increasing dominance of non-native species results in a loss of diversity and ecosystem functioning on farms. These topics are the focus of my PhD project.

Species that persist following the conversion to oil palm habitats tend to share particular traits, such as a smaller body size and lower trophic level, with consistent findings across several taxa (Barnes et al., 2014; Senior et al., 2013). The convergence in species traits could have implications for the resilience and provisioning of ecosystem functions. It is possible that the species that persist in oil palm habitats possess traits that confer high resistance to disturbances, such as dietary generalism and high thermal tolerance, which could enhance their ability to cope with further disturbance and environmental changes. As a result, these species may continue to perform important ecosystem functions without being significantly impacted by future disturbances. However, convergence in trait similarity implies a loss of trait diversity, which could indicate a loss of functional roles performed by species within oil palm habitats. Coupled with the loss in overall species richness, this could result in lower functional redundancy, reducing the buffering capacity of ecosystem functions against further loss of species and environmental changes (i.e., ‘insurance hypothesis’; Naeem & Li, 1997).

Increased abundance of non-native species in oil palm habitats may contribute to greater trait similarity between species (e.g., smaller body size). Non-native species generally share traits that facilitate dispersal and survival in novel habitats (Holway et al., 2002; McGlynn, 1999), which may contribute to reductions in trait diversity and ecosystem functioning in oil palm areas (Wong et al., 2020). Waddell et al., (2020) examined factors affecting the occurrence of non-native plants in oil palm landscapes, but did not consider their ecological impacts. Therefore, we still lack understanding of the factors that drive patterns in trait diversity on oil palm farms and the effects of non-native species on ecosystem functioning.

Local farm factors as well as factors in the wider landscape have been shown to affect species diversity and abundance on farms (e.g., Ashton-Butt et al., 2018; Teuscher et al., 2016), but the consequences for functional trait diversity and redundancy have not yet been explored. Less intensive farm management may boost biodiversity by creating more complex understorey environments, with a wider variety of niches for species to occupy, and by reducing inter-specific competition through resource partitioning (Gámez & Harris, 2022). For example, management practices that enriching vegetation, intercropping or maintain groundcover vegetation can boost farm biodiversity and related ecosystem functions (Ashton-Butt et al., 2018; Teuscher et al., 2016; Yahya et al., 2017)**.** These practices could also contribute to more functionally diverse communities, with increased functional redundancy and so potentially greater ecological resilience. Moreover, increasing habitat heterogeneity (Benton et al., 2003; Steckel et al., 2014) and connectivity (Brudvig et al., 2009) within the landscape surrounding oil palm habitats may also influence local farm biodiversity by facilitating species dispersal and meta-population dynamics, and so potentially contributing to more functionally diverse communities (Hatfield et al., 2018). Within oil palm landscapes, spillover of species from adjacent forest habitats can increase the occurrence of predatory and forest-dependent species and related ecosystem functions within oil palm plantations (Lucey & Hill, 2012; Nurdiansyah et al., 2016), but this can depend on factors such as forest patch size and quality (Gray et al., 2016; Lucey et al., 2014). Addressing these questions will be especially useful for understanding how adopting more environmentally sustainable management practices and landscape designs could help boost functional diversity and the ecological resilience of oil palm farms.

### 1.7 Quantifying the ecological resilience of oil palm farms

Quantifying ecological resilience can be challenging as it involves assessing the response of communities or ecosystem functioning to environmental change, specifically metrics such as resistance, adaptability to change, and recovery (Yi & Jackson, 2021). To achieve this understanding typically requires long-term surveys or experiments. However, several indicators and metrics have been proposed to make inferences about the underlying mechanisms of ecological resilience (e.g., Dakos & Kéfi, 2022; Oliver et al., 2015; C. Yi & Jackson, 2021; see table 2). In this thesis, I use metrics and focus specifically on species-level and community-level mechanisms hypothesised to influence the resilience of ecosystem functioning to environmental change (Oliver et al., 2015). Species-level mechanisms influence the ability of a species to resist or adapt to environmental change and disturbance, which I assess by measuring the sensitivity of species to environmental change based on morphological metrics. Community-level mechanisms relate to how a community is able to maintain its structure and functioning, which I assess by examining the extent of redundancy in communities, based on species that fill similar functional roles (i.e., functional redundancy; Oliver et al., 2015). The context of the wider landscape is also important when considering ecological resilience, because landscape factors can mediate species- and community-level responses to environmental change (Oliver et al., 2015). For instance, by influencing species dispersal and meta-population dynamics through connectivity and availability of natural habitats. Thus, in this thesis I also consider the role of landscape factors in influencing the local biodiversity on farms.

Species functional traits, which are morphological, physiological or phenological characteristics that relate to a species functional role (Petchey & Gaston, 2006), are useful tools for assessing species- and community-level mechanisms underpinning ecological resilience.  Functional traits provide information on which type of species are sensitive to environmental change (Oliver et al., 2015), and how environmental changes affect the structure and functioning of communities (e.g., functional diversity; Mammola et al., 2021). Functional diversity can be defined as “the range of things that organisms do in communities and ecosystems” (Petchey & Gaston, 2006), and it is useful to explore variation in species sensitivity and community composition based on species functional traits. Two particularly useful metrics of functional diversity are functional richness, which describes the amount of variety in functional traits, and functional dispersion, which describes the dissimilarity between species within a community according to their functional traits (Mammola & Cardoso, 2020). Together with measures of species richness, these metrics provide information on the diversity of functional roles within a community, as well as a community’s functional redundancy. The assumption is that higher species richness and functional redundancy contribute to higher ecological resilience because a community is able to buffer against some degree of species loss without changing its structure or functioning. Moreover, communities composed of species that show lower sensitivity to environmental change confer greater ecological resilience (Oliver et al., 2015). By examining the impacts of non-native species on functional structure and composition on oil palm farms, and considering the interactions between local farm management and the surrounding landscape, this approach can provide insights into the factors that influence local biodiversity on farms and contribute to ecological resilience.

## 1.8 The role of ants in measuring biodiversity impacts within oil palm habitats

### 1.8.1 The importance of ants

Despite their small size, ants (Formicidae, Hymenoptera) are one of the most abundant taxonomic groups in the world (Schultheiss et al., 2022), with a large impact on the environments that they inhabit (Ameixa et al., 2018; Folgarait, 1998). Ants, along with other invertebrates, have been described by E. O. Wilson as “the little things that run the world” (WIilson, 1987), because they provide a wide range of functional roles, including as carrion decomposers (Nooten et al., 2022), predators (Camacho & Avilés, 2019), and granivores (Pirk & Casenave, 2011), as well as interspecific interactions such as nectar-feeding mutalisms (Cagnolo & Tavella, 2015), fungus-farming symbioses (Mueller et al., 2004) and social parasitism (Huang & Dornhaus, 2008). As a consequence, ants contribute to key ecosystem processes such as nutrient re-distribution, seed dispersal and soil fertility (Folgarait, 1998; Frouz & Jilková, 2008).

Tropical regions hold the highest diversity and biomass of ants (Kass et al., 2022), with an estimated 31% of global ant abundance occurring within tropical moist forests (Schultheiss et al., 2022). On Borneo, a total of 793 species from 110 genera has been recorded (Antwiki, 2022), and ants are key contributors to ecosystem functions such as scavenging (Griffiths et al., 2018; figure 2). However, ant mediated ecological functions (Ewers et al., 2015) and their community interactions are sensitive to local disturbances (Floren et al., 2008; Gray et al., 2018). Ant traits reflect responses to environmental change, for example, relationships between body size and thermal tolerance (Boyle et al., 2021). Hence, ants are useful for assessing the impacts of environmental changes on functional composition and ecosystem functioning, and studies of ants have revealed relationships between ant response traits and provisioning of ecosystem functions (e.g., body size and decomposition; Nooten et al., 2022).

**Figure 2.** *"The little things that run the world"*. Left: Ants defending their foraging grounds on a tree sapling, Maliau Conservation Area. Top right: The not so little Giant forest ant, *Dinomyrmex gigas*, one of largest known ant species in the world, with workers reaching up to 3cm in size. Bottom right: Ground-foraging ants work collectively to carry a live earthworm back to their nest, Danum Valley Conservation Area. Photos taken by the author in Sabah, Malaysian Borneo.

### 1.8.2 Ants in oil palm habitats

Ants occur widely in tropical agricultural landscapes (Sanabria et al., 2014), but at much lower densities compared to more natural habitats (Schultheiss et al., 2022). The effects of forest conversion to oil palm have been well studied, with reported losses in ant species richness varying from 22-64% loss of species richness (Brühl & Eltz, 2010; Fayle et al., 2010; Gray et al., 2015; Lucey et al., 2014; Nazarreta et al., 2020). Land-use change not only causes a loss of species, but also changes to species composition (Gray et al., 2015) and functional structure (Luke et al., 2014), with few ant species shared with forest habitats (Brühl & Eltz, 2010; Fayle et al., 2010). Oil palm is characterised by a higher dominance of generalists species and a loss of more specialist ants from higher trophic positions (Kreider et al., 2021; Senior et al., 2015). However, despite this loss in species richness and altered community structure, ants still remain relatively abundant in oil palm habitats compared to other taxonomic groups (Barnes et al., 2014; Hood et al., 2020). In these novel habitats, ants contribute to ecosystem functions such as scavenging (Gray et al., 2015) and predation (Denmead et al., 2017), albeit at lower levels compared to forest. Hence, it is important to understand how variation in the management of agricultural landscapes affects ant communities and their ecosystem functions on farms.

Ants are successful invaders of novel habitats (Bertelsmeier, 2021; Holway et al., 2002). Fayle et al., (2010) report a loss of 81% of forest ant species following conversion of forest habitats to oil palm, but a much higher abundance of non-native ants on oil palm farms. This shift in ant species composition could potentially have negative consequences for the functional composition and diversity of ant communities, and consequently the provisioning of ecosystem functions on oil palm farms. Ants have been identified by the IUCN as being some of the world's worst invasive species (e.g., the Argentine ant, *Linepithema humile*, and the Yellow crazy ant, *Anoplolepis gracilipes*; Lowe et al., 2000), The effects of *Solenopsis invicta* are estimated to have cost $16.7 billion between 1960 and 2020, due to costs of invasion management and the economic damage to agriculture, infrastructure and human health, making this species one of the most economically damaging invasive species in the world (Cuthbert et al., 2022). Non-native ants can exhibit higher numerical and behavioural dominance over native species for resources and territories (Trigos-Peral et al., 2021), resulting in altered community composition and species diversity(Drescher et al., 2011; Lessard et al., 2009; Rahim & Ohkawara, 2019; Wong et al., 2020). Moreover, non-native ants tend share similar traits, such as a smaller body size (McGlynn, 1999) and an omnivorous diet (Holway & Cameron, 2021). Due to these trait similarities, communities that comprise a large number of non-native species could have reduced trait diversity (Wong et al., 2020), with potential consequences for functional diversity, and altered provisioning of ecosystem functions within habitats where they are common (Carney et al., 2003; Devenish et al., 2019; Milligan et al., 2022) .

However, non-native species do not always have negative effects (Milligan et al., 2016) and the impacts of non-native species can be highly context dependent (Sapsford et al., 2020; Thomas & Holway, 2005). Fayle et al., (2013) show that non-native ants can facilitate species co-existence on oil palm farms by reducing competitive exclusion between ant species, and contribute to generalist functions involving mutualisms with epiphytic ferns (Fayle et al., 2015). By contrast, negative effects of non-native species are more frequently observed in natural habitats (Drescher et al., 2011; Wong et al., 2022). Hence, in highly modified landscapes such as oil palm, non-native ants may contribute positively to community diversity and functioning (Castro-Díez et al., 2019; Jain et al., 2016; Schlaepfer et al., 2011). Understanding whether non-native species contribute positively to the ecological resilience of oil palm habitats is particularly important to investigate, especially because non-native species can exhibit higher resistance to human disturbances and environmental change (Meyer et al., 2021).

### 1.8.3 Current understanding of factors affecting ant communities in oil palm landscapes

There is considerable variation in estimates of ant species richness within oil palm habitats (Brühl & Eltz, 2010; Fayle et al., 2010; Gray et al., 2015; Lucey et al., 2014; Nazarreta et al., 2020), which could be due to many factors such as non-native occurrence, local farm management, or wider landscape factors. Many studies have described the impacts of land-use conversion on ant communities (Fayle et al., 2015; Kreider et al., 2021; Nazarreta et al., 2020; Wang & Foster, 2015), but fewer studies have examined the ecological mechanisms that are driving changes in local ant diversity among farms. Those studies reveal that at local farm scales, management of understory and epiphytic vegetation can increase ant abundance and diversity on farms (Ganser et al., 2017; Hood et al., 2020). Wider landscape factors have also been shown to influence community composition on farms, with adjacent forest fragments contributing to spillover of more forest-dependent native species into plantations (Lucey et al., 2014), while proximity to forest fragments reduces the occurrence of non-native ants on oil palm plantations (Rizali et al., 2021). These findings suggest that there may be nuanced differences in the responses of native and non-native ant species to local and landscape-level factors, highlighting the need for further investigation of the drivers of non-native ants within oil palm landscapes. Human-mediated dispersal, habitat degradation and climatic changes are recognised drivers of non-native ant colonisation and expansion (Warren et al., 2020, 2023; Wong et al., 2023). Thus, proximity to urban areas (McKinney, 2006) and road networks (Gippet et al., 2019) could contribute to ant community composition on oil palm farms, while increases in local temperature conditions on farms could favour smaller-bodied non-native ants (Boyle et al., 2021).

Taken together, the information presented in this chapter reveals the complexity of factors that influence ant local diversity on oil palm farms, including roles for local and landscape-level drivers, and the need for further research to understand the ecological mechanisms underlying these patterns. While some progress has been made in understanding the individual effects of local farm management and landscape factors, our understanding of the interactions among different factors and their impacts on native and non-native ant species is still lacking. Moreover, there is still little understanding of how variation in ant community composition relates to ecosystem functioning and ecological resilience. My thesis aims to address these knowledge gaps by investigating local and landscape-scale drivers of native and non-native ant species richness on oil palm farms, and examining evidence of trade-offs between smallholder yields, sustainable management practices and ecological resilience. Ultimately, my research will contribute to better-informed management practices in oil palm landscapes, that maintain smallholder livelihoods whilst minimising impacts on biodiversity.

## 1.9 Thesis aims and rationale

In this thesis, my main aim is to examine the impacts of local farm management and wider landscape factors on smallholder oil palm yields, ant biodiversity and ecosystem functions, in order to inform on the development of sustainable and more resilient oil palm landscapes. My thesis investigates oil palm smallholdings in Sabah, Malaysian Borneo, where I carried out fieldwork to quantify the impacts of farm management practices on oil palm yields and ant biodiversity. In chapter 2, I report findings from field surveys and farmer questionnaires which examined how farm management practices affect the environmental sustainability of smallholder oil palm farms, and any trade-offs with crop yields. From this chapter's findings, I conclude that applying sustainable management practices does not reduce crop yields. In chapter 3, I analyse field survey data from ground-dwelling ants to assess ant species richness and use morphological measurements to quantify the functional diversity of smallholder oil palm farms. I conclude that non-native ants have little impact on ant community structure and functioning on oil palm farms. In chapter 4, I bring together information from the previous two chapters to examine inter-linkages between local farm management, landscape factors, crop yields and ant biodiversity. I conclude that native and non-native species have differing effects on ecological resilience, with both local and landscape factors influencing ant biodiversity on farms. In chapter 5, my general discussion, I synthesise my findings and discuss the degree to which current oil palm practices are addressing the RSPOs aims to achieve "resilient and restored" oil palm landscapes and sustainable production without reductions in farm yields. I discuss how local factors and wider landscape changes affect the resilience of biodiversity and ecosystem functions on farms. I describe the key aims of each of these chapters below.

### Chapter 2: "Sustainable management practices do not reduce oil palm yields on smallholder farms on Borneo"

In this chapter, I carry out ecological surveys and use interviews with smallholder farmers to examine variation in yields on smallholder oil palm farms and the role of management intensity, understorey vegetation cover, climate, and soil properties on yields. I assess whether there are trade-offs between increasing yields versus enhancing environmental sustainability on farms through increased understorey vegetation cover and improved soil chemical properties. I use two methods to assess impacts of smallholder management: (1) an index of overall farm management intensity, synthesised from nine management practices, and (2) the number of Best Management Practices (BMPs) employed the farmer.

Key hypotheses:

(1) Trade-offs occur between oil palm yield, understory vegetation and soil properties on farms along a gradient of management intensity.
(2) BMPs influence understory vegetation and soil properties, without resulting in trade-offs with yield.

### Chapter 3: "Non-native ant species do not reduce functional diversity or ecosystem functioning on oil palm smallholdings"

In this chapter, I carry out field surveys to examine the occurrence of ground-dwelling ants on smallholder oil palm farms, and assess how non-native species affect overall ant species richness and functional diversity (measures of functional richness and dispersion based on morphological measurements), and the provisioning of two important ecosystem processes provided by ants: scavenging and leaf-litter decomposition. I also compare ant community composition on farms with those in nearby protected forest sites.

Key hypotheses:

(1) Farms and rainforest sites differ in ant species richness and the proportion of non-native species, with non-native species more common on farms.
(2) Non-native species differ in functional trait composition compared to native species.
(3) The proportion of non-native species influences farm-scale functional richness and functional divergence, with consequences for scavenging and decomposition rates on farms.

## Chapter 4: “Landscape-scale and local factors influence local ecological resilience of oil palm smallholdings.”

In this chapter, I use Structural Equation Models (SEMs) to examine the interlinkages and relative influence of local factors (e.g., farm management practices), and surrounding landscape characteristics (e.g., proximity to roads and forest) on native and non-native ant functional diversity in order to understand the ecological resilience of farms.

Key hypotheses:

(1) Native and non-native species differ in their association with local farm factors (management intensity, yield, understorey vegetation and temperature) and wider landscape factors (forest extent and proximity to roads).
(2) Native species contribute more to functional diversity metrics than non-native species.
(3) Local factors as well as wider landscape factors influence ecological resilience and functional redundancy (measures of species richness, functional richness and functional dispersion) of oil palm farms.

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# CHAPTER 2

# Sustainable management practices do not reduce oil palm yields on smallholder farms on Borneo

Smallholder oil palm farm with dense understory vegetation

Sabah, Malaysian Borneo

## 2.1 ABSTRACT

We assess the consequences of sustainable farming practices (“Best Management Practices”) on oil palm fruit production on 40 smallholder farms in Sabah, Malaysian Borneo, and whether maintaining vegetation cover, which is linked to environmental sustainability and higher biodiversity, results in a trade-off with oil palm production. We found considerable variation in yield among farms (6.9-37.4 t $ha^{-1}$ $yr^{-1}$), but little evidence for any trade-offs between yield and farming practices. This finding has important implications for livelihoods if farmers can minimise agricultural inputs, reducing costs and supporting the environmental sustainability of oil palm smallholder farms, whilst maintaining crop yields.

## 2.2. INTRODUCTION

Since the beginning of the 21st century, agricultural cultivation has been the main driver of forest conversion in Southeast Asia (Zeng et al. 2018). For example, in Malaysian Borneo, the oil palm industry has been a major contributor to deforestation and land-use change in the past four decades, mainly driven by the expansion of industrial plantations and smallholder farms (Gaveau et al. 2018). This agricultural expansion has resulted in widespread species declines across most taxa (Edwards et al. 2014; Savilaakso et al. 2014; Kwatrina et al. 2018). However, with careful management, agricultural landscapes could have the potential to conserve biodiversity and valuable ecosystem services (Tscharntke et al. 2005), thereby helping to ensure the environmental sustainability of oil palm landscapes, whilst also supporting high yields and farmer livelihoods.

Smallholder producers (< 50 hectares; RSPO 2021) are estimated to contribute up to 33% of global palm oil production (Descals et al. 2020), but the average smallholder yield reported by the Roundtable on Sustainable Palm Oil (RSPO) is only 18.9 tonnes of fresh fruit bunches (FFB; $ha^{-1}$ $yr^{-1}$), which is almost half of the estimated potential average yield for smallholders at 33.2t $ha^{-1}$ $yr^{-1}$ (Euler et al. 2016), and half of the estimated potential average yield for large commercial plantations (35-40t $ha^{-1}$ $yr^{-1}$; (Hoffmann et al. 2015). Studies of smallholder agriculture have been increasing (Euler et al. 2016; Kurniawan et al. 2018; Rhebergen et al. 2020), and the capacity to boost yields on current smallholdings has been highlighted as a potential solution to sustainably intensify palm oil production and increase farmer incomes (Hoffmann et al. 2017; Varkkey et al. 2018). This intensification may also reduce further conversion of natural habitat to agriculture, conserving biodiversity (Edwards et al. 2010; Lee et al. 2014). Variations in yield can occur due to climate (Oettli et al. 2018), soil characteristics and topography (Corley and Tinker 2016), and agricultural management practices (Euler et al. 2016; Hoffmann et al. 2017; Woittiez et al. 2017), which may explain the wide variations in smallholder yields that have been reported. The effects of certain management practices on FFB yields have been well studied, such as optimal palm planting density (Corley 1973; Bonneau et al. 2018), fertiliser inputs (Tengoua et al. 2015; Tao et al. 2017), frond pruning (Marcelino and Diaz 2016; Soliman et al. 2016), FFB harvesting frequency (Lee et al. 2014; Rhebergen et al. 2020), and weeding and ground cover management (Samedani et al. 2014; Soliman et al. 2016). However, the overall impact of farm management intensity on smallholder oil palm yields remains unclear.

There is a need to identify management practices that result in win-win scenarios for yield and environmental sustainability (Fischer et al. 2017; Tamburini et al. 2020). For example, ‘Best Management Practices’ (BMPs), are recommended by the RSPO as a way to sustainably intensify palm oil production by improving soil fertility and preventing soil degradation (RSPO P&C 2018). These BMPs include practices that minimise the use of inorganic pesticides and fertilisers (Sundram et al. 2019; Yi et al. 2019), techniques that reduce soil erosion and nutrient leaching by managing ground cover vegetation (Darras et al. 2019; Formaglio et al. 2020), and maintaining soil organic matter through the application of crop residues such as Empty Fruit Bunches (EFBs) and palm oil mill effluent (Tao, Snaddon, et al. 2018; Yi et al. 2019). The uptake of BMPs substantially increases FFB yields on some smallholdings (Pauli et al. 2014; Rhebergen et al. 2020; Rahman et al. 2021), as well as replenishing soil organic carbon (SOC) and nitrogen content (Tao et al. 2016; Rahman et al. 2021), but BMPs can be labour intensive. Hence it is important to assess whether application of BMPs affects yield and soil quality, and whether BMPs offer more environmentally sustainable management options.

Supporting greater structural complexity of ground vegetation could maintain soil fertility, a crucial factor for healthy palm growth and fruit production (Corley and Tinker 2016), and also reduce soil erosion and run-off (Zheng 2006; Sahat et al. 2016; García-Orenes et al. 2012). Understorey vegetation could also support biodiversity that improves the functioning of soil processes (Barnes et al. 2014). Thus, increasing understorey vegetation cover could improve yields, as well as improving the environmental sustainability of farms. However, high intensity management practices such as high herbicide inputs suppress understorey vegetation (Luke et al. 2019), with consequent negative effects on soil fauna (Ashton-Butt et al. 2018; Darras et al. 2019), which contributes to the degradation of SOC, a valuable indicator of soil fertility (Guillaume, Holtkamp, et al. 2016). These findings imply trade-offs between management practices to support ground vegetation cover and soil fertility, versus management to increase yields. Hence improved environmental sustainability might incur costs to farmers if it reduces yields, and so it is important to examine relationships between yield, management practices, and understorey vegetation cover on farms.

In this study, we examined variation in yield on smallholder oil palm farms (Fig. S1), and the role of management intensity, understorey vegetation cover, climate, and soil characteristics (soil type, SOC, total N, total P and available P) on yields. We used responses from face-to-face questionnaires of 40 smallholder farmers located across six governance zones in Sabah, Malaysian Borneo, to collect information about their management practices, including BMPs, and reported FFB yields. We also carried out field surveys on these farms to quantify understorey vegetation cover and soil characteristics (Fig. S2). We used this information to examine variation in reported FFB yields among farms, how yields varied in relation to management intensity and use of BMPs, and the effects of management intensity on understorey vegetation cover and soil chemical properties. We investigated whether there are trade-offs between increasing yields versus enhancing environmental sustainability on farms through increased understorey vegetation cover and improved soil chemical properties.

## 2.3 MATERIALS & METHODS

### 2.3.1 Study sites

We collected data between August to October 2019 from 40 smallholdings (defined as farms < 50 ha) across six governance areas in Sabah, Malaysia (Fig. S2a-c) of which 35 smallholders were part of a Smallholder Group Scheme organised by a local social NGO (WildAsia), and the remaining five were independent smallholders. In our analyses, we allocated smallholders to governance areas (n = 6) according to the village community the smallholder belonged to, on the assumption that smallholders within the same governance area would manage their farms in a similar way by following the guidance of the local community leader and WildAsia staff. Governance areas differed slightly in maximum temperature ($^{o}$C) and minimum rainfall (mm month$^{-1}$), as well as soil type (Table S1. Farms had been established between 8-27 years ago, ranged between 0.81 and 7.73 ha in size, and had either been established after conversion from commercial selectively-logged forest (n = 18 farms) or from agriculture other than palm oil (such as coffee, rice, vegetables or fruit crops; 22 farms) (Table S1). Smallholders were either oil palm monocultures (n = 19 farms) or mixed agriculture systems that included other crops (n = 21 farms), although non-palm tree crops grown on mixed agriculture farms were at very low densities because farmers were not relying on non-palm trees for income. Planting densities of palms were the same on monoculture farms (median = 136 trees ha$^{-1}$, n = 19) and mixed farms (median = 136 trees ha$^{-1}$, n = 21). Smallholder selection criteria for inclusion within our study were (i) crop age (to minimise variation in yields as a result of crop age, trees had to be mature fruiting trees i.e. > 8 years) (Hoffmann et al. 2017), and (ii) farm size (to be large enough to conduct ecological surveys using our standardised plot design i.e. > 0.5 ha). When farms had mature oil palm trees of multiple ages > 8 years old, we computed the average age of the oil palm crop according to the proportion of the farm area planted with each age group.

### 2.3.2 Smallholder questionnaires to assess management intensity and fruit bunch yields

Information about farm management practices was collected from interviews with smallholder farmers, following a standardised questionnaire of 29 questions, including questions on farm history and physical characteristics, palm fruit harvesting practices, and management inputs (for questions see SI3). The questionnaire was developed based on information about practices known to influence oil palm yields (Corley and Tinker 2016; Woittiez et al. 2017). Questionnaires with farmers were conducted in Bahasa Malay by ABS, SGA and a translator from WildAsia.

We developed an index of management intensity by synthesising the information on management practices that we collected from the interviews (applying multiple imputation methods for the very small number of incomplete responses; see SI4 for details). From the responses to the questionnaires, we derived nine management parameters per farm, and graded each parameter a binary score for intensity of either 0 (less intensive) or 1 (more intensive) (Table 1). Each management practice was graded as more intensive if it required more production inputs, either in labour or agricultural inputs. For example, there were two questions about fertiliser application, a score of 1 was assigned if the smallholder used fertilisers and 0 if they did not, and for those farms applying fertiliser, an input score of 0 if fertiliser inputs were below the median input level across farms ($ha^{-1}$ $yr^{-1}$) and a score of 1 if inputs were above the median value. To calculate the overall management intensity score for each farm, we computed the management intensity index (with a value between 0-1) by summing the intensity scores for all nine parameters and dividing by nine. To obtain a measure of yield for each farm, we used the reported monthly Fresh Fruit Bunch (FFB) harvest by each farmer or calculated yield from the reported monthly income and price per tonne of FFB issued by the mill. Depending on the information provided by farmers, data on reported average yields were either the most recently obtained single month or harvest yield, or an average yield per month or per harvest. We report the monthly FFB yield as annual yield in tonnes per hectare per year (t $ha^{-1}$ $yr^{-1}$) for comparison with published information, as well as yield in kilograms per tree per year (kg tree$^{-1}$ yr$^{-1}$) to account for variation in planting densities on farms.

| **Management Practice** | **Description** | **Management Intensity Score** |
|---|---|---|
| Planting density | The number of fruit-bearing palm trees planted per ha on the smallholding (median = 136 trees ha$^{-1}$) | Planting density < 136 trees ha$^{-1}$ = 0<br>Planting density > 136 trees ha$^{-1}$ = 1 |
| Pruning frequency | The number of times frond pruning takes place per month. | Once a month = 0<br>Twice a month = 1 |
| Harvest frequency | The number of times Fresh Fruit Bunches (FFB) are harvested, either once or twice a month. | Once a month = 0<br>Twice a month = 1 |
| Weeding frequency | Weeding frequency (median = 2 times yr$^{-1}$). | Frequency < 2 times yr$^{-1}$ = 0<br>Frequency > 2 times yr$^{-1}$ = 1 |
| Weeding method | Weeding method, either manual weeding (with a grass cutter) or herbicide spraying. | Manual = 0<br>Herbicide = 1 |
| Herbicide quantity | The quantity of herbicide applied in L of product ha$^{-1}$ year$^{-1}$ (median = 3.8 L ha$^{-1}$ year$^{-1}$). | Herbicide < 3.8 L ha$^{-1}$ year$^{-1}$ = 0<br>Herbicide > 3.8 L ha$^{-1}$ year$^{-1}$ = 1 |
| Fertiliser use | Whether the smallholder applies organic or inorganic fertilisers. | No fertiliser = 0<br>Fertilisers applied = 1 |
| Fertiliser quantity | The amount of fertiliser applied, measured in t per ha per year (median = 542 kg ha$^{-1}$ ya$^{-1}$) | Fertiliser < 542 kg ha$^{-1}$ ya$^{-1}$ = 0<br>Fertiliser > 542 kg ha$^{-1}$ ya$^{-1}$ = 1 |
| Pesticide use | Whether the smallholder applies pesticides. | No pesticides = 0<br>Pesticides applied = 1 |

**Table 1** Description of the management practices carried out by smallholder farmers, and how information on management practices was used to produce a management intensity index score for each farm. Information about the implementation of these management practices was collected from interviews with the smallholder farmers (n = 40 farms; see SI for details of questionnaires).

### 2.3.3 Identifying RSPO Best Management Practices

From the farmer questionnaires, we extracted information on the application of 'Best Management Practices' as outlined by the Roundtable on Sustainable Palm Oil (RSPO). The RSPO lists in its Principles & Criteria (P&C) number 7.4 (RSPO P&C 2018) that 'long-term fertility depends on maintaining the structure, organic matter content, nutrient status and microbiological health of the soil' and P&C 7.5 that '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'. We concluded that RSPO 'Best Management Practices' taken up by farmers in our study related primarily to nutrient recycling and ground cover management, including (i) application of crop residues, (ii) minimising use of herbicides, (iii) retaining areas of ground vegetation cover, and (iv) clearing a contour of vegetation around palms (Table 2). We assigned smallholders into four BMP groups according to the number of BMPs the smallholder farmer employed: 0, 1, 2 or 3 BMPs (no farmer did all four BMPs).

| **Best Management Practice (BMP)** | **Description** |
|---|---|
| ***Nutrient cycling*** | |
| 1. Application of crop residues | The application of crop residues such as Empty Fruit Bunches (EFB) or mill slush as an inorganic fertiliser to increase soil carbon content. |
| ***Ground cover management*** | |
| 2. Maintenance of ground vegetation cover | The restriction of weeding activities to paths to maintain ground vegetation cover in order to minimise soil degradation via run-off and soil erosion. |
| 3. Reduced herbicide use | The application of none or minimal (< 2 L $ha^{-1}$ $year^{-1}$ ) herbicide to the palm cultivated area, to promote greater vegetation cover within the farm. |
| 4. Vegetation clearing around palms | The clearing of vegetation around the palm stems (with 2m radius) to suppress growth of weeds around the palms and increase efficiency of fertilisers via palm nutrient uptake. |

**Table 2** Description of 'Best Management Practices' (BMPs) as defined by the Roundtable on Sustainable Palm Oil. Information about uptake of BMPs by farmers was collected from interviews with the smallholder farmers (n = 40 farms; see SI for details of questionnaires).

### 2.3.4 Field surveys of understorey vegetation structure

Surveys of understorey vegetation were conducted on each farm, measuring 18 vegetation parameters within a 0.28 ha circular plot (i.e. 30 m radius plot; Fig. SI2d) within each smallholding (see SI5 for further details). To quantify differences in understorey vegetation cover among farms, we then used principal component analysis (PCA) to identify which vegetation parameters were the most important for explaining variability in understorey vegetation structure across the smallholder farms (Table S4 and S5). The first principal component (PC1) accounted for 25% of the total variance, which was positively related to vegetation height and cover (> 10cm height) and palm contour vegetation cover, and was negatively related to leaf litter depth (Table S5). The second principal component (PC2) accounted for a further 15% of the total variance, and was positively associated with occurrence of non-palm large trees and saplings, leaf-litter depth and cover, and was negatively associated with bare ground cover (Table S5). We included PC1 and PC2 in our analyses as measures of understorey vegetation cover and structure.

### 2.3.5 Measuring soil chemical properties

In each 0.28 ha survey plot, we also collected soil samples (20 cm depth) to quantify soil carbon and nutrients (see SI6). In subsequent analyses, we omitted soil variables that were highly correlated (Pearson's $r > 0.9$; SI5; Table S6), and included soil organic carbon (%; SOC), total nitrogen, total phosphorus and available phosphorus, which are important for growth and yield of oil palm trees (Webb et al. 2013; Corley and Tinker 2016; Guillaume, Holtkamp, et al. 2016).

Oil palm yields are also affected by soil type, for example soils that are saline, acid sulphate, or poorly drained are less suitable for oil palm cultivation (Corley and Tinker 2016). We classified smallholdings according to soil type using 'The Soils of Sabah' base map (Panagos et al. 2011; see SI6), with most farms on mudstone, sandstone and miscellaneous rocks (soil type 2; n = 24 farms), nine farms on mudstone and alluvium (soil type 3), and five farms on alluvium (soil type 1; Table S1).

### 2.3.6 Effects of climatic conditions (rainfall and temperature)

To control for possible time-lagged effects of climatic variables on yield, we analysed rainfall and temperature variables from CRU TS 4.05 dataset ($0.5^{\circ} \times 0.5^{\circ}$ grid cells; 50 km resolution; Harris et al. 2020), averaged across 36 months prior to the study (i.e. between

November 2016 and December 2019, covering the period of inflorescence development; see SI7 for more details). Farms from our six governance regions occurred within four different CRU climate data grids (Table S1). We included monthly minimum rainfall (mm; a measure of drought and water stress, which is an important limiting factor to FFB yields in Sabah) and maximum monthly temperature (° C; linked to solar radiation which is important for oil palm growth (Oettli, Behera, and Yamagata 2018; Corley and Tinker 2016; Carr 2011) (see SI7).

### 2.3.7 Statistical Analyses

All data and statistical analyses were performed in the R statistical programming (R Core Team 2019). Prior to fitting all GAMM models, we standardised explanatory variables by transforming every value as the ratio of that value to the maximum value for that variable.

#### 2.3.7.1 Drivers of yield

To examine whether smallholder yields were influenced by management intensity (our management intensity index score, 0-1), understorey vegetation cover (PC1 and PC2 scores), soil type and chemical properties (SOC, total N, total P and available P), climate (average monthly maximum temperature and minimum monthly rainfall in the 36 months prior to the study), and farming system (monoculture or mixed agriculture), we fitted a Generalized Additive Mixed effect Model (GAMM) via restricted maximum likelihood (REML) using the gamm4 package (Wood and Scheipl 2017). GAMMs model both linear and non-linear relationships by using smoothing functions (i.e. splines) (Lin and Zhang 1999). We applied penalised cubic regression splines as the smoothing basis function, to remove non-influential explanatory variables from the model (Marra and Wood 2011). We applied the GAMM to the smallholder dataset excluding two yield outliers (n = 38 farms; see SI9), and included smoothing parameters for management intensity score, understorey vegetation cover (PC1 and PC2 scores), soil chemical properties (SOC, total N, total P and available P), minimum rainfall (mm month$^{-1}$) and monthly maximum temperature ($^{o}$C). We also included farm area with productive palms (ha; to control for differences in yield as a result of farm size), crop age (to control for possible variations in yield as a consequence of palm tree age; Hoffmann et al. 2017; Woittiez et al. 2017), and soil type. We fitted models with a Gaussian identity link function to obtain homoscedasticity and normality of residuals (see SI9 for further details of GAMMs).

To assess whether the use of BMPs influenced yields on farms, we examined the differences in yield across the four BMP groups (0, 1, 2 or 3 BMPs taken up by farmers). We fitted a GAMM with yield as a response variable, the number of BMPs employed, farming system (monoculture or mixed) and previous land-use as linear terms, and smoothing parameters (penalised cubic regression splines) for crop age, farm size and monthly minimum rainfall. Our main analyses used FFB yield per farm (t $ha^{-1}$ $yr^{-1}$), but we repeated analyses using mean data for yield in kilograms per tree per year (kg $tree^{-1}$ $yr^{-1}$), which did not alter our main conclusions (see SI9).

#### 2.3.7.2 Consequences of management intensity and BMPs

To examine the consequences of management intensity on understorey vegetation cover and soil chemical properties (SOC, total N, total P and available P) on farms, we fitted GAMMs similar to those for identifying drivers of yield. We fitted smoothing parameters to management intensity index, crop age, monthly minimum rainfall and maximum temperature, and included previous land-use (forested or agriculture) to control for the effect that land-use history may have on soil chemical properties on farms (Guillaume, Maranguit, et al. 2016). We fitted models using the full smallholder dataset (n = 40) to model the effects of management intensity on understorey vegetation cover (PC1 and PC2 scores), SOC, total soil N and total P. When modelling the effects of management intensity on available soil P, we used a reduced dataset excluding one outlier datapoint for available P (n = 39 farms) (see SI11). Models were fitted with an inverse gaussian log link function to the SOC, a gaussian log link function to the total N data, and a gaussian identity link function to the PC1, PC2, total P and available P data. Differences in soil chemical properties across the four BMP groups (0, 1, 2 or 3 BMPs taken up by farmers) are given in SI8 (Table S10).

## 2.4 RESULTS

### 2.4.1 Summary of yield and management variability across smallholder oil palm farms

Across the 40 farms, we found that reported yields (measured as FFB t $ha^{-1}$ $yr^{-1}$) varied widely, ranging from 6.9 to 37.4 t $ha^{-1}$ $yr^{-1}$ (median = 15.6 t $ha^{-1}$ $yr^{-1}$, sd = 7.3). This variation arose because smallholder yields varied among the six governance areas (median = 13.2 –

20.8 t $ha^{-1}$ $yr^{-1}$; Fig. 1a), and also among smallholders within the same governance area (Table S1).

Smallholders also varied considerably in the way that they managed their farms, and the management intensity scores (synthesised from nine management practices, index max/min score range = 0 – 1; Table 1) ranged from 0.25 to 1.00 (median = 0.69; Fig. 1b). Study farms were either oil palm monocultures (n = 19 farms) or mixed-crop farms (n = 21) cultivating fruit crops such as coconut (*Cocos nucifera*) or rambutan (*Nephelium lappaceum*) for household consumption. Some management practices were relatively consistent across farms, for example, most farms carried out palm frond pruning and there was little variation in FFB harvesting frequency (either once or twice a month). However, herbicide application rates (varying from 0 – 40 L $ha^{-1}$ $yr^{-1}$), and fertiliser inputs (varying from 0 – 1456 kg $ha^{-1}$ $yr^{-1}$, equivalent to 0 – 10 kg $tree^{-1}$ $yr^{-1}$) did vary widely (Table S1 and S9), as well as the types of fertiliser (e.g. borate, murate of potash, as well as relative composition of MPK and NPK) and herbicides applied (e.g. glyphosate, metsulphuron). The planting density of productive fruit-bearing palm trees (86-165 trees $ha^{-1}$) also varied, but the median value across study farms (136 trees $ha^{-1}$) was within the recommended optimal planting density (130-145; Corley and Tinker 2016). We obtained planting stock information from eight farmers: one of whom planted *dura*, one planted *pisifera* and six farmers planted *tenera* seed types. Smallholder farmers differed in the number of 'Best Management Practices' (BMPs) they employed (median = 2; ranging from two farms using no BMPs, to five farms using three BMPs, with the majority of farmers applying two BMPS, but no farmer using all four). Of the four types of BMPs, more than half of the farms cleared a contour of vegetation around palm trees (n = 23 farms), and about a third applied crop residues such as empty fruit bunches (n = 12 farms) or retained areas of ground vegetation cover (i.e. did not carry out blanket spraying) (n = 12); applying minimal amounts of herbicide was the least popular BMP (<2 L $ha^{-1}$ $yr^{-1}$; n = 9 farms) (Table S9).

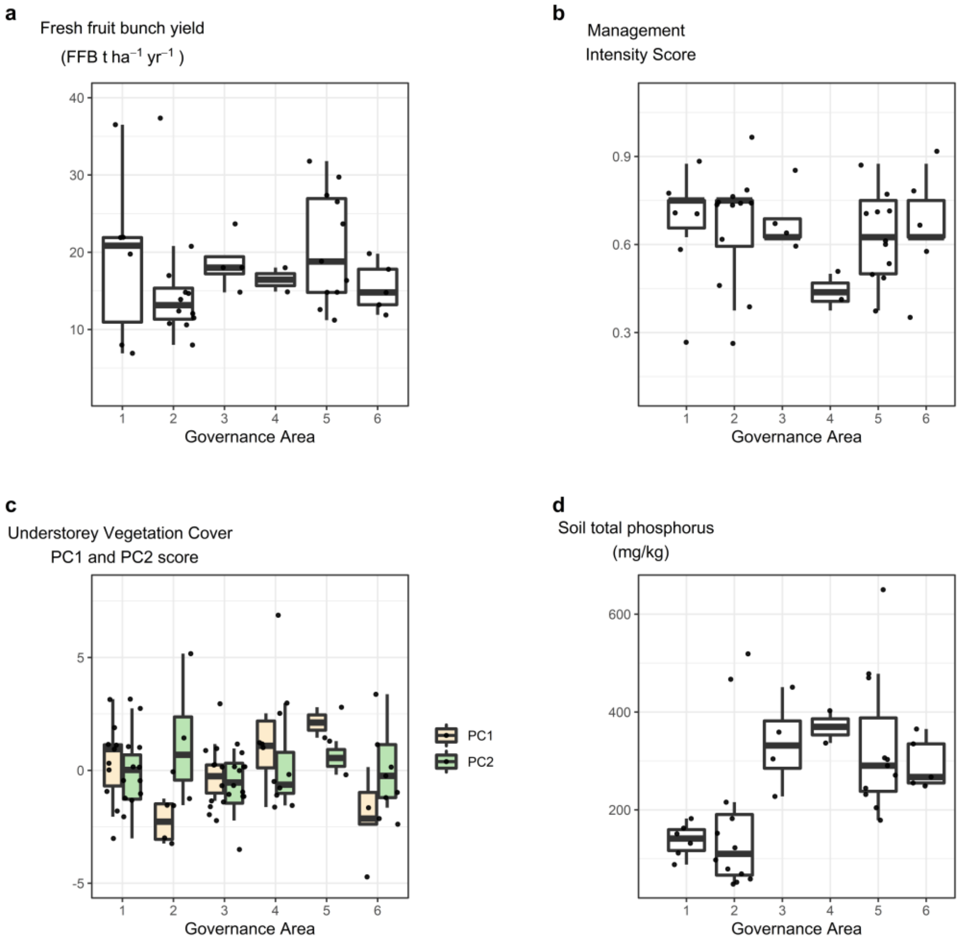

**Figure 1** Boxplots detailing variation in **(a)** fresh fruit bunch yield (FFB t ha$^{-1}$ yr$^{-1}$), **(b)** management intensity, **(c)** understorey vegetation cover, yellow boxplots correspond to PC1 scores and green boxplots to PC2 scores, and **(d)** total phosphorus content (mg/kg) on farms in six governance areas (n = 40 farms; governance area number corresponds to those shown in figure S2b). Data show the median (horizontal bar) and interquartile range (box), as well as the range of the largest and smallest values within 1.5 times the interquartile range (vertical line).

### 2.4.2 Drivers of variation in yields across smallholder farms

Despite wide variation in yields (t ha$^{-1}$ yr$^{-1}$) among smallholder farms, only 3% of this variation in yield was explained by management intensity, understorey vegetation cover (PC1 and PC2 scores), productive farm area (ha), oil palm tree age (years), soil chemical properties, or rainfall (adjusted $R^2$=0.007; see Table S12 and Fig. S3). Yield was not significantly influenced by farm productive area (n = 38 farms, F = 0.00, p = 1.00), crop age (F = 0.00, p = 1.00), or soil type (t = 0.80, p = 0.43; t = 1.89, p = 0.07). Our results show that 38/40 farmers employed at least one Best Management Practice (BMP) on their farm, but yields did not vary with the number BMPs employed by a farmer (0 – 3 BMPs; n = 40, Adjusted-R squared = 0.028; Fig. 2; see Table S14).

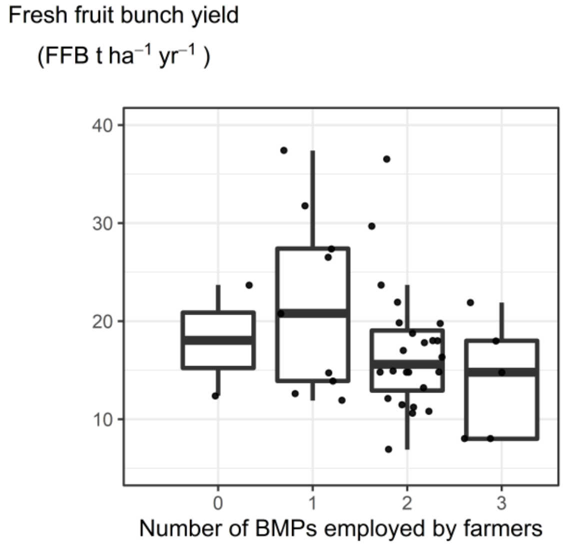

**Figure 2** Boxplots show fresh fruit bunch yields (FFB t $ha^{-1}$ $yr^{-1}$) across smallholders employing 0, 1, 2 and 3 'Best Management Practices' (BMPs; n = 40 farms). Data show the median (horizontal bar) and interquartile range (box), as well as the range of the largest and smallest values within 1.5 times the interquartile range (vertical line).

### 2.4.3 Impacts of management intensity

Our results showed that management intensity did not affect understorey vegetation cover (Fig. 3b; PC1 score, n = 40, F = 0.00, p = 1.00; PC2 score, F = 0.32, p = 0.13), SOC (n = 40, F = 0.00, p = 1.00, total N (n = 40, F = 0.00, p = 1.00), total P (n = 40, F = 0.00, p = 1.00) or available P (n = 39, F = 0.05, p = 1.00; Table S15). However, farms on previously cultivated agricultural land (n = 22 farms) had soil containing 28% more total N (t = -2.86, p = 0.005, adjusted R-squared = 0.14) and 139% more total P (t = -4.83, p <0.001, adjusted R-squared = 0.491) and 21% more organic C (t = -2.30, p = 0.03, adjusted R-squared = 0.05) compared with farms on sites that had previously been forest (n = 18 farms), implying that previous land-use contributes substantially to current soil characteristics.

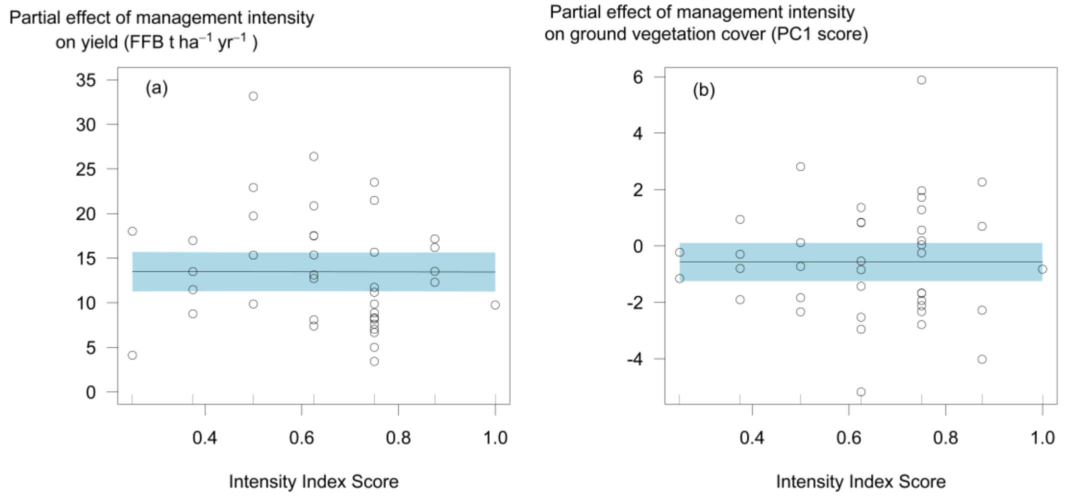

**Figure 3** Partial effect plots of the generalised additive mixed effects models, showing (**a**) the component effect of the smoothed term (fitted with a penalised cubic regression spline as the smooth basis function) for management intensity on smallholder oil palm fresh fruit bunch yield (FFB t $ha^{-1}$ $yr^{-1}$; p = 0.41; n = 38) and (**b**) the component effect of the smoothed term (fitted with a penalised cubic regression spline as the smooth basis function) for management intensity on understorey vegetation cover (PC1 score; F = 0.00, p = 1.00; n = 40). The points show the partial residuals, which are the difference between the partial effect and the data after all partial effects in the model have been accounted for. Management intensity was a non-influential explanatory variable in both models, and so the smoother parameter for has been penalised towards a straight line and shrunk the line towards zero. The blue shaded areas denote the uncertainty within the model, measured as the standard errors of the partial effect term combined with the standard errors of the model intercept. Explanatory variables were scaled prior to fitting the model.

## 2.5 DISCUSSION

### Wide variation in reported yields across smallholder farms

Oil palm yields varied widely across the smallholder farms in our study, ranging from 6.9 to 37.4 FFB t $ha^{-1}$ $yr^{-1}$ (equivalent to 50-275 kg $tree^{-1}$ $yr^{-1}$), with an average farm yield of 15.6 t $ha^{-1}$ $yr^{-1}$ (117 kg $tree^{-1}$ $yr^{-1}$). Thus, 35% of smallholders in our study exceeded the average smallholder production reported by the RSPO (18 t $ha^{-1}$ $yr^{-1}$) (RSPO 2020) and 20% exceeded the production of larger-scale industrial companies (23 t $ha^{-1}$ $yr^{-1}$; Fairhurst and Griffiths 2014). Whilst atypical, such high yields have been reported previously (Jelsma et al. 2009), and a few of our study farms had reported yields similar to the estimated potential yields of large-scale plantations (35-40 t $ha^{-1}$ $yr^{-1}$; (Hoffmann et al. 2015).

However, despite these large variations in reported yields, our results show that management intensity did not influence yield across farms. Increasing the intensity of management practices such as cropping density, fertilisation and harvesting frequency can directly increase oil palm yields (Rhebergen et al. 2020; Woittiez et al. 2017; Lee et al. 2014; Marcelino and Diaz 2016; Euler et al. 2016), but reported yields may not necessarily increase with management intensity. For example, increasing cropping density may result in trees being planted too closely, which can reduce yields as trees start to compete for soil nutrients and light, although most (11 out 40) farms in our study had planting densities within recommended values of 130 – 145 (Corley and Tinker 2016; Rafii et al. 2013), because of advice from WildAsia. Our findings support those of Darras et al. (2019) and Tao et al. (2018) who also found no effect of herbicide and fertiliser intensification on palm plantation yields or nutrient-use efficiency by palms. Thus, increased use of chemical inputs may not be necessary for closing yield gaps on smallholder farms (Soliman et al. 2016).

Our study analysed data on yields and management practices from questionnaires and interviews, which can have potential biases. For example, respondents may be wary when providing responses to questions that involve sensitive information (Hilborn et al. 2005), such as yield or use of herbicides and pesticides, given the negative perception of chemical products on the environment (Lazaroiu et al. 2019; Obiri et al. 2021). Moreover, social desirability bias can occur when respondents may want to 'project a favourable image of themselves and so may provide a more socially desirable response' (Krumpal 2013). Whilst these issues are difficult to eliminate, we mitigated these potential biases by conducting the interviews with WildAsia staff who have a well-established working rapport with the respondents and regularly share this kind of information (Bergen and Labonté 2020).

### Additional drivers of variation in oil palm yield

We found no associations between yield and management practices. There could be time lags between implementing a particular management practice and observing its effects on yield (Rhebergen et al. 2020), but it is unlikely that lags would result in the large yield differences between the farms that we observed (6.9 to 37.4 FFB t $ha^{-1}$ $yr^{-1}$). Yields differed greatly among farms within the same governance area (<10km apart), thus geographic factors that may affect nutrient uptake by the palm trees are also unlikely to be the main causes of yield variation. We also found no effect of climatic factors on yield. It is likely that rainfall was not an important factor in our analysis as the mean monthly rainfall in our study regions, which ranged between 228-289 (mm $month^{-1}$), met the rainfall requirements for optimum FFB production (above 167 mm month$^{-1}$; Oettli, Behera, and Yamagata 2018). We did not include temperature in our analyses because it co-varied with rainfall (see SI7), but the minimum (21.1-23.4°C) and maximum (28.9-31.3°C) temperatures at our study regions fall within the suitable temperature ranges for high FFB yields (22-24°C and 29-33°C respectively) (Corley and Tinker 2016; Oettli et al. 2018). However, site-specific factors may nonetheless cause yield variation, such as topography which can influence water availability and drainage (although topography was fairly similar across our study farms) (Balasundram et al. 2006), as well as local disease and pest outbreaks (Corley and Tinker 2016).

Farms within the same governance regions were sometimes on different soil types (see SI6), which can influence nutrient loss and retention (Fujii et al. 2018), although we found only a weak non-significant effect of soil type on yield. Nutrient deficiencies are known to limit yields (Woittiez et al. 2018), but despite some farms having high total N, available P and total P soil concentrations (the latter of which increased with smallholder management intensity), we found no relationship between soil nutrients and yield. Seed planting material influences yield (Woittiez et al. 2017; Barcelos et al. 2015), with *tenera* being the most productive, followed by *dura* and *psifera* (Corley and Lee et al. 1992). There were insufficient data to include type of planting material in our analyses of yield, but farmers differed in their sourcing of planting materials and seed varieties (e.g. wild harvesting, supply by government agricultural sectors or company nurseries). Different suppliers will provide different types of seeds, which will affect yield (Durand-Gasselin and Cochard 2005; De Vos et al. 2021), and planting material likely contributes to the variation in yields that we observed in our study. Using improved seed materials could help farmers increase productivity without increasing intensity of other management practices, and should be an area of future research as planting material will be of crucial importance for farmers when re-planting crops. Another important factor driving oil palm yield is pruning intensity, as the maintenance of an optimum number of palm fronds affects oil palm fruit production (Marcelino and Diaz 2016). These factors deserve more study to further develop best practices for smallholders, alongside investigating associations with soil arbuscular mycorrhizal fungal (AMF) (Auliana and Kaonongbua 2018) as they have been illustrated to improve yields in other types of crops (Kobae 2019; Gao et al. 2020).

### Causes and consequences of varying management intensity

Smallholders varied considerably in how they managed their farms, even within the same governance area (e.g. intensity score 0.25 - 1.00, and 0 to 3 BMPs in Site 2, Reka Halus). Thus, local village governance is not the only factor affecting management decisions of smallholder farmers, which may be influenced by available capital (Jelsma et al. 2019; Lee et al. 2014; Krishna et al. 2015), farmer experience (Pandey and Diwan 2020), their desire to make environmentally conscious management choices (such as uptake of BMPs; Romero et al. 2019), or wishing to make risk-averse decisions (Chen et al. 2018; Martey and Kuwornu 2021).

Farmers are encouraged to take-up BMPs as a way to improve environmental sustainability on farms, but our results indicate no relationship between the application of BMPs and yield, or with soil chemical properties (SOC, total N, total P and available P). Low total C and SOC levels (<2%) were observed across the majority of the study farms (see SI6), and we found no evidence that BMPs improved soil fertility or soil nutrient content, in contrast to other studies (Tao et al. 2017; Che Ku Hafeez et al. 2020). The implementing of BMPs generally requires more labour inputs (Rhebergen et al. 2020), therefore a better understanding of the sustainability benefits of BMPs, alongside the improved profitability for smallholders is required if farmers are to benefit from their wider take-up. In addition, clear standardised guidance for employing BMPs are needed if BMPs are to improve yields and soil fertility, and farmer incomes.

### Implications of no trade-offs for smallholder farmers

We found little evidence for any strong inter-relationship between yield, vegetation cover and management intensity. Trade-offs have been shown to occur between smallholder profitability, biodiversity and ecosystem processes within tropical agricultural systems (Clough et al. 2016; Grass et al. 2020), but those studies spanned a much greater range of land-use intensities than in our study. We find little evidence that maintaining greater vegetation cover on farms resulted in any reduction in FFB yields, or that increasing intensity of management resulted in higher oil palm yields. By contrast, we found that high yields occurred on some farms with low intensity management. This finding has potentially important implications for smallholder profitability because any reduction in the reliance on expensive agricultural inputs could result in savings in labour costs and chemicals, such as fertilisers and herbicides (Darras et al. 2019). Secondly, high yields from low intensity management is a potential positive inducement for farmers to enhance the environmental sustainability of their smallholdings, given the benefits of retaining vegetation cover with oil palm plantations for promoting biodiversity and ecosystem functions (Ashton-Butt et al. 2018; Darras et al. 2019; Luke et al. 2019).

Most smallholders that we sampled were part of a Smallholder Group Scheme organised by a local social enterprise (WildAsia), who provide support to farmers for the uptake of sustainable agricultural practices, as well as the uptake of RSPO and MSPO certification. Although we found none, trade-offs with yield could occur at much lower or higher intensity management than was observed in our study e.g. non-certified smallholders have differing management practices and lower oil palm yields compared to sustainably certified farmers (De Vos et al. 2021). Smallholders in other regions may have different management strategies, and this should be considered when assessing the generality of our findings, and further studies examining the consequences of different management strategies across a wide range of smallholder landscapes will be important for understanding the ubiquity of our findings.

## 2.6 CONCLUSION

The results of our study showed that applying sustainable management practices does not reduce yields, and we found no evidence for inter-relationships between yield and management practices among oil palm smallholdings. Yields varied about five-fold across farms, but smallholder management, understorey vegetation cover, soil chemical properties, rainfall, and farming system explained only a small amount of this variation, and farms with high understorey vegetation cover did not have reduced yield. These findings have important implications for smallholder livelihoods if farmers can minimise their reliance on chemical inputs, which may also help the conservation of biodiversity and the environmental sustainability of oil palm farms. Better understanding of how some farmers achieve yields as high as those on industrial plantations could be shared among farmer groups to help reduce yield variation across smallholder farms, and improve farmer incomes.

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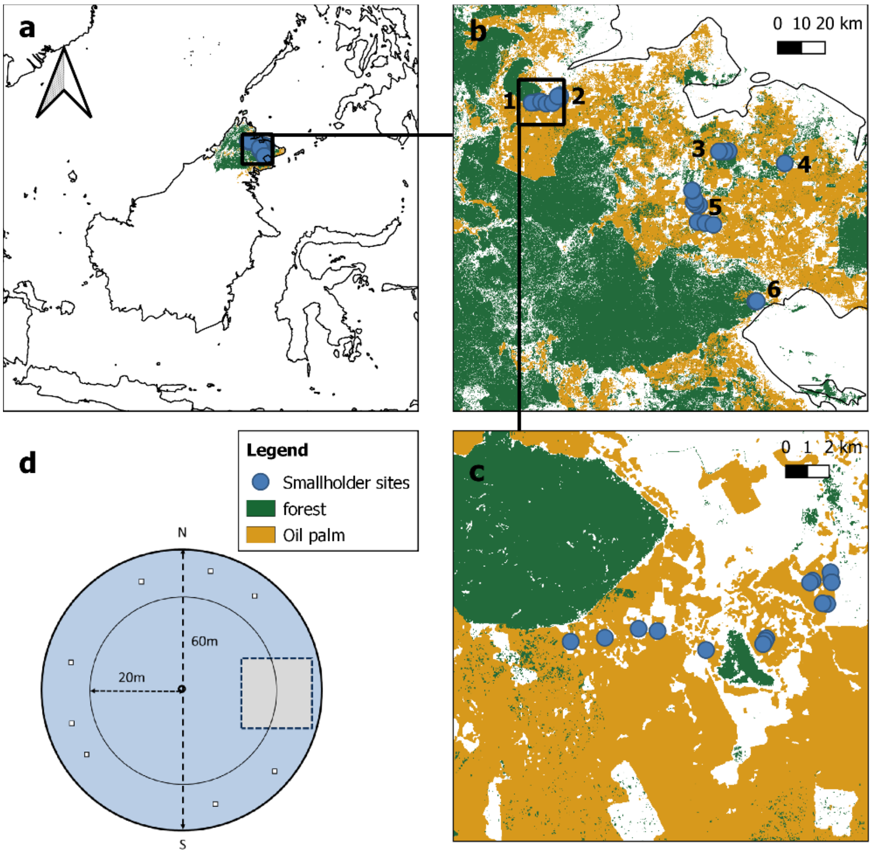
# CHAPTER 2 APPENDIX

# Sustainable management practices do not reduce oil palm yields on smallholder farms on Borneo

## Section 1: Study site and sampling design

**Figure S1**. Smallholder oil palm farms in Sabah vary considerably in management and vegetation cover within farms, ranging from extensive vegetation cover (top picture) to mainly bare ground (middle picture). A mixed agriculture farm (bottom picture), with durian (Durio species), jackfruit (Artocarpus heterophyllus) and langsat (Lansium parasiticum) trees cultivated amongst oil palm trees (photographs by the authors).

**Figure S2** (**a**)-(**c**). Map of smallholder study sites farms (n = 40) located across six governance areas in Sabah, Malaysian Borneo: site 1 (Ulu Sapi; n = 6 farms), site 2 (Reka Halus; n = 12 farms), site 3 (Gomantong; n = 4 farms), site 4 (Sukau; n = 2 farms), site 5 (Paris-Batu Puteh; n = 11 farms), and site 6 (Tampenau; n = 5 farms). (**d**) Sampling design on each farm, comprised one 30m radius (0.28 ha) plot per farm. Within each plot we recorded the number of standing deadwood and live trees in two size classes: (1) 10cm - 25cm diameter at breast height (DBH), (2) > 25cm DBH. Within 20m of the plot centre, we recorded the number of live saplings <10cm DBH. Along a 60m transect running from N to S through the centre of each plot, we recorded epiphyte % cover on palm stems and vegetation % cover within a 2m radius of each oil palm tree stem. We recorded understorey and vegetation height, as well as % cover of various measures of vegetation, deadwood and bare ground in eight 1x1m quadrats placed on random bearings, 25m from the plot centre. We collected soil samples within the area marked by the grey square. The landcover category 'forest' maps above ground carbon density greater than 40 ACD mg C ha$^{-1}$ at 30m special resolution (sourced from Asner et al. 2021), and the category 'oil palm' shows the extent of plantations and smallholder farms at 10m resolution (using Sentinel-1 and Sentinel-2 data; sourced from Descals et al. 2020).



## Section 2: Summary of climatic, understorey vegetation (principal component PC1, PC2), soil and management variability across smallholder oil palm farms

**Table S1.** Summary data (median and range) for farms (n = 40) included in this study collected from interviews and field surveys with smallholder farmers. Monthly mean, minimum and maximum temperature (Tmean, Tmin and Tmax), and monthly mean, minimum and maximum rainfall obtained from the CRU VS 4.05 dataset (Harris et al. 2020), averaged over 36 months prior to harvesting. Soil types correspond to: 1) alluvium, 2) mudstone, sandstone and miscellaneous rocks, and 3) mudstone and alluvium (see Methods and SI6).

| **Governance region** | **1** | **2** | **3** | **4** | **5** | **6** |
|---|---|---|---|---|---|---|
| **Location** | Sapi | Reka Halus | Gomantong | Sukau | Batu Puteh-Paris | Tampenau |
| **Number of farms** | 6 | 12 | 4 | 2 | 11 | 5 |
| **Previous land-use** | forest | forest | agriculture | agriculture | agriculture | agriculture |
| **Soil type** | 1; 2 | 1; 2 | 2 | 1 | 2; 3 | 2 |
| **Tmean (°C)** | 25.0 | 25.0 | 27.4 | 27.4 | 25.8 | 26.8 |
| **Tmin (°C)** | 21.1 | 21.1 | 23.4 | 23.4 | 21.9 | 23.0 |
| **Tmax (°C)** | 28.9 | 28.9 | 31.3 | 31.3 | 29.6 | 30.6 |
| **Rainfall mean (mm)** | 256.6 | 256.6 | 289.1 | 289.1 | 250.8 | 228 |
| **Rainfall min (mm)** | 48.2 | 48.2 | 71.9 | 71.9 | 52.7 | 53.1 |
| **Rainfall max (mm)** | 607.4 | 607.4 | 832.4 | 832.4 | 601.4 | 501.9 |
| **Crop age (years)** | 16 (8-27) | 18.5 (8-26) | 20.5 (15-24) | 15 (14-16) | 17 (10-22) | 19 (19-20) |
| **Farm size (ha)** | 5.64 (3.69-6.07) | 4.47 (2.72-7.73) | 1.21 (1.21-2.00) | 1.21 (1.21-1.22) | 5.66 (0.81-6.07) | 3.64 (2.02-4.86) |
| **Farm area with productive oil palm (ha)** | 5.05 (1.21-6.03) | 4.41 (2.60-7.73) | 1.2 (0.81-1.21) | 1.10 (1.00-1.21) | 5.26 (0.81-5.89) | 3.64 (2.02-4.05) |
| **Fresh fruit bunch yield (FFB t ha$^{-1}$ yr$^{-1}$)** | 20.9 (6.9-36.5) | 13.2 (8.0-37.4) | 18 (14.8-23.7) | 16.5 (14.9-18) | 18.8 (11.2-31.8) | 14.8 (11.9-19.8) |
| **Soil organic carbon (SOC) (%)** | 1.11 (0.65-1.53) | 0.85 (0.68-2.01) | 0.99 (0.78-1.25) | 1.34 (1.10-1.58) | 1.10 (0.65-1.58) | 1.36 (0.87-2.21) |
| **Soil total nitrogen (%)** | 0.115 (0.127-0.21) | 0.139 (0.104-0.252) | 0.157 (0.125-0.201) | 0.211 (0.195-0.227) | 0.163 (0.131-0.249) | 0.187 (0.150-0.26) |
| **Soil total phosphorus (mg/kg)** | 141 (88-182) | 110 (48-519) | 332 (227-451) | 370 (337-403) | 290 (179-650) | 267 (249-365) |
| **Soil available phosphorus (mg/kg)** | 2.09 (0.89-5.44) | 3.44 (1.73-37.27) | 3.02 (1.26-8.74) | 3.45 (2.92-3.97) | 2.56 (1.46-8.32) | 3.09 (1.76-4.41) |

| | | | | | | |
|---|---|---|---|---|---|---|
| **Management intensity index score** | 0.75 (0.25-0.88) | 0.75 (0.25-1.00) | 0.63 (0.63-0.88) | 0.44 (0.38-0.50) | 0.63 (0.38-0.88) | 0.63 (0.38-0.88) |
| **Ground vegetation cover (PC1 score)** | 1.09 (-1.63-6.87) | -0.26 (-3.50-2.95) | -2.27 (-3.24--1.25) | 2.12 (1.44-2.80) | 0.94 (-2.05-3.16) | -2.14 (-4.72-0.15) |
| **Non-palm tree composition and leaf-litter (PC2 score)** | -0.64 (-1.55-2.98) | -0.54 (-2.22-0.97) | 0.69 (-1.54-5.17) | 0.55 (-0.20-1.29) | 0.02 (-3.01-2.74) | -0.24 (-1.66-3.37) |

## **Section 3: Smallholder questionnaires**

Interviews were conducted with smallholder oil palm farmers across six governance areas in Sabah, Malaysian Borneo. We conducted face-to-face interviews with farmers following a questionnaire of standardised close-ended questions to collect data relating to yield and management of farms. This assessment of yield and farmer activities was chosen as opposed to direct fresh fruit bunch weight measurements or self-led questionnaires, as it allowed us to meet the farmers, establishing trust, and gave them the opportunity to ask any questions relating to the project. Interviews were conducted in Bahasa Malay with SGA, ABS and a WildAsia staff to act as translator and liaison. Verbatim transcription was done by either SGA or ABS whilst we conducted the interview. Interviews lasted between 15-60 minutes. The sampling strategy of participants was as follows: smallholder farmers (except in Tampenau) were part of WAGS (WildAsia Group Scheme for smallholder producers) and were asked if they would like to participate in the study by a WildAsia staff. When recruiting participants in Tampenau, we first obtained permission from the head of the local village to approach smallholder members, which we did together with staff from the Southeast Asia Rainforest Research Partnership (SEARRP), who was also a member of the village. For all study participants, we provided information about the purpose of the study and what the collected data would be used for, and then obtained verbal and written consent for conducting interviews and ecological surveys on their farms. Our protocols followed best practice, and ethical permission was granted by the Biology Ethics Committee, University of York (Ref. SGA201906). Participants could leave the study at any time.

## <u>Information leaflet that was presented to farmers before receive verbal and written consent to participate in this study</u>

### Impacts of Agricultural Management Practices within Oil Palm Smallholder Plantations

Funded by UK Research and Innovation (UKRI) through a Natural Environment Research Council Industrial CASE studentship (project number NE/R007624/1).

We are conducting an investigation for a research project, which aims to identify management practices that can increase the sustainability of smallholder oil palm production. Data from this investigation will help smallholder farmers to support certification with the Round Table for Sustainable Palm Oil by identifying agricultural management practices that can boost yields, whilst minimising environmental damage. This investigation is part of a project which is determining whether landscapes that support high levels of wildlife and ecosystem functioning can also maintain high oil palm crop yields and support local livelihoods.

Agricultural management practices employed by smallholder farmers can vary considerably, resulting in variable yields and incomes, and potentially differing impacts on wildlife and the environment. There is potential to boost yields within smallholder farms by employing better management practices. For this, more information is required about current oil palm production and management practices, particularly, examining the relationships between yield, wildlife and management intensity.

We are surveying smallholders to assess how their crops are managed and to quantify the relationship between oil palm crop management and yields. We will survey wildlife (particularly ants) on selected smallholdings differing in their management practices, to assess the impacts of management on wildlife and yield. In this way, we aim to improve the scientific understanding of crop management for oil-palm smallholders, improving crop yields and increasing household incomes without negatively affecting wildlife.

**Biodiversity surveys:**

On each selected smallholding, we will survey wildlife associated with oil palms in the following ways:

- Ants – These will be collected in 10 small plastic tubes, each half-filled with water, alcohol and washing-up liquid, and buried flush with the soil surface for a total period of 6 days. We will leave different types of bait within meshed cages for a period of 24 hours to measure bait removal by ants.
- Decomposition – We will leave 10 small nylon mesh bags filled with leaves and palm fronds for a period of 30 days to measure decomposition of organic material.
- Resource removal – We will leave 8 metal mesh cages over a period of 2 days to measure the removal of fish and seed bait by ants and other invertebrates. We will also place bait on a card with an insect-trapping glue barrier to measure bait removal by non-invertebrates.

- Habitat assessment – We will assess vegetation structure and impacts of management within a 30 m circular plot placed within each farm. These measures will include assessment of ground cover, canopy cover from trees, air temperature, soil characteristics, and presence of empty FFBs and frond piles. To assess this, we will leave a data-logger to record temperature, and we will collect soil samples for further analysis.

**Some questions you may have:**

- If I say yes to participating, what will this involve? You will be asked to complete a questionnaire with myself and the help of one my research assistants. This should take about 10-15 minutes. You will not be asked for anything else other than permission for us to survey your smallholding as described above.
- Where and when will we complete the questionnaire? It could be your house or any other place where you usually spend your time, wherever you feel most comfortable. You can also choose a good time to meet. Ø
- What happens if I change my mind? If you have not completed the questionnaire, your name will be removed from our list of participants. If you have completed it, the paper copy of the form will be destroyed at the end of the project. However, the anonymised data (with your name replaced by a three-digit code) will be retained in electronic format for use in the project. Project partners: University of York, UK; Proforest, UK; Wild Asia, Malaysia; Universiti Malaysia Sabah, Malaysia

## Written consent form that was presented to smallholder farmers that participated in this study

| **Consent to take part in a research project on the Impacts of Agricultural Management Practices within Smallholder Oil Palm Plantations** | **Add your initials next to the statement if you agree** |
|---|---|
| I confirm that I have read and understand the information sheet explaining the research project and I have had the opportunity to ask questions about the project. | |
| I understand that my participation is voluntary and that I am free to withdraw at any time without giving any reason and without there being any negative consequences. In addition, should I not wish to answer any particular question or questions, I am free to decline. I can indicate a wish to withdraw by informing Wild Asia. All questionnaire sheets completed by me will be destroyed at the end of the project. However, anonymised questionnaire data and biodiversity data will be retained in an electronic format for future use by the project. | |
| I give permission for members of the research team to have access to my anonymised responses. I understand that my name will not be linked with the research materials, and I will not be identified or identifiable in the report or reports that result from the research. I understand that my responses will be kept strictly confidential. | |
| I give permission for members of the research team to carry out wildlife and habitat surveys on my smallholding as described in the project information leaflet. | |
| I agree for the data collected from me to be stored and used in relevant future research in an anonymised form. | |
| I understand that relevant sections of the data collected during the study may be looked at in anonymised format by individuals from the University of York or from project partners where it is relevant to my taking part in this research. I give permission for these individuals to have access to my anonymised records. | |
| I agree to take part in the above research project and will inform Wild Asia staff should my contact details change. | |

| | |
|---|---|
| Name of participant | |
| Participant’s signature | |
| Name of Wild Asia staff | |
| Signature | |
| Date* | |

*To be signed and dated in the presence of the participant. Once this has been signed by all parties the participant should receive a copy of the signed and dated participant consent form and the project information sheet. A copy of the signed and dated consent form should be kept with the completed questionnaire form, which must be kept in a secure location.

**Table S2.** Questionnaire used for interviews with smallholder oil palm farmers to collect information relating to farm history and environmental characteristics, palm fruit yield and management inputs. Questions that we had sufficient responses for from farmers (>70% of responses for that question; see SI 2) were considered for developing the management intensity index. Responses to questions that were used in the index are highlighted in bold, and all other responses were used for analyses of Best Management Practices (BMPs; indicated by *), as explanatory variables in statistical models, or for the general understanding of smallholder farm management across study sites.

| | **Sufficient responses (>70% complete)** |
|---|---|
| **(A) Questions about the farm** | |
| Do you own or rent the farm | Yes |
| For how many years have you farmed here? | Yes |
| How big is your farm? | Yes |
| What is the size of the area planted with oil palm trees within your farm? | Yes |
| Do you have land on your farm that isn't planted with oil palm? If so, what is the land used for and what size does the area cover? | Yes |
| How old is the oil palm crop on your farm? | Yes |
| Have you replanted more than one crop cycle on your farm? | Yes |
| What was on your land before you planted oil palms here? | Yes |
| **(B) Questions about oil palm fruit yield** | |
| How many oil palm trees are growing within your farm? | Yes |
| How many productive/fruiting oil palm trees are growing within your farm? | Yes |
| How often is FFB harvested on your farm? | Yes |
| What weight of FFB do you obtain per harvest on average from your farm? | Yes |
| What income do you obtain per tonne of FFB on average from your smallholding? | Yes |
| Do you measure FFB yourself or by a trader or mill, and how do you measure the weight of each bunch (weighing scale, estimate or not measured)? | Yes |
| What seed type do you plant (tenera, dura, psifera or unsure)? | No |
| **(C) Questions about farm management** | |
| Do you plant any other crops beneath your palms? | Yes |
| How often do you weed your crops? | Yes |
| What method do you use for weeding? | Yes |
| When was the last time you weeded on your farm? | No |
| *Do you clear a circle without vegetation around the base of each palm trunk? | Yes |
| Do you contour around each palm trunk to help prevent rainfall, nutrients or fertilisers flowing away? | Yes |
| *Do you apply empty fruit bunches to your farm, and if so how often? | Yes |
| How often do you prune? | Yes |
| What do you do with the cut fronds? | Yes |
| Do you remove ferns and other vegetation from the trunks of the palms? | Yes |

| | |
|---|---|
| Do you change the way you manage your crop depending on tree age? For example, do you apply more chemical nutrients, or shorten the harvesting interval, as your oil palm trees get old? | No |
| **(D) Questions about agricultural inputs** | |
| *Do you apply chemical herbicides?<br>(i) If so, how much, how often and what type?<br>(ii) If not, why not?<br>(iii) If you used to but have now stopped, how long ago did you stop applying? | Yes<br>Yes<br>No<br>No |
| Do you apply pesticides?<br>(i) If so, how much, how often and what type?<br>(ii) If not, why not?<br>(iii) If you used to but have now stopped, how long ago did you stop applying? | Yes<br>No<br>No<br>No |
| Do you apply chemical or organic fertilizers?<br>(i) If so, how much, how often and what type?<br>(ii) If not, why not?<br>(iii) If you use to but have now stopped, how long ago did you stop applying? | Yes<br>Yes<br>No<br>No |

## Section 4: Multiple imputation to handle missing data

When considering the inclusion of questionnaire responses to develop our management intensity index and Best Management Practices (BMPs), we set a cut-off point at a 70% response rate for a question (i.e. <30% missing cases). This is because the rates of type-I errors and bias in the regression coefficients become significantly high when imputing small datasets with 50 or fewer data points and a 30% or higher missingness rate (when using fully conditional specification multiple imputation; McNeish 2017). As is the case with our study (40 smallholder sampling points). We had a small number of missing data in the questionnaire responses relating to the management practices used in our intensity index and Best Management Practices (10/600 responses). For these missing values we applied multiple imputation methods The percentage of missing values across the 15 management variables obtained from questionnaires ranged from 0 and 10%. Information was missing for ten observations from four variables: (i) herbicide L ha$^{-1}$ (n = 4), (ii) herbicide frequency yr$^{-1}$ (n = 1), (iii) fertilizer Kg ha$^{-1}$(n = 4) and (iiv) fertilizer frequency yr$^{-1}$(n = 1). Data were missing from nine smallholder questionnaires from three governance area (six from Reka Halus, one from Tampenau and two from Batu Puteh). In these cases, we used multiple imputation to provide data.

We detected no pattern between missing data with other variables. Thus, we conclude the reason for missing data likely arises randomly across farmers within a governance area, and so we assume that the response can be considered as Missing at Random (MAR; Rubin 1976).This technique was preferred as it provides a more statistically powerful estimation of incomplete values compared to other methods for handling missing data (e.g. pair-wise deletion, mean imputation or regression imputation). Incomplete variables were imputed by using fully conditional specification multiple imputation to create and analyse 100 multiply imputed datasets using the mice package in the R statistical software; we set the number of iterations and multiple imputations to 100 (van Buuren and Groothuis-Oudshoorn 2011; R Core Team 2019) . Within the model, we specified the use of predictor variables that had a correlation greater than 0.3 with the target variable to reduce uncertainty in the imputation, resulting in nine variables used as predictors for the imputation of the missing data. For comparison, we also performed the same statistical analysis on the original dataset with missing variables as well as the multiply imputed dataset, which confirmed little difference in the residual standard error, F-statistic and adjusted R-squared between the two models (see Table S3 a and b).

**Table S3.** Results comparing two linear models fitted with herbicide ha$^{-1}$, herbicide frequency yr$^{-1}$, fertiliser ha$^{-1}$ and fertiliser frequency ha$^{-1}$ as explanatory variables to productive palm trees ha$^{-1}$ as a response variable using (a) the original dataset with missing values, and (b) the multiply imputed dataset.

**(a) lm(formula = productive_perha ~ herb.ha + fert.freq + herb.freq + fert.freq)**

Residual standard error 13.59 on 29 degrees of freedom; adjusted R-squared = -0.139; F-statistic = 0.09; 9 observations deleted due to missingness.

| | Estimate | Std. Error | t value | Pr(>\|t\|) |
|---|---|---|---|---|
| **(Intercept)** | 131.16 | 5.71 | 22.95 | **<0.001***** |
| **herb.ha** | -0.22 | 1.52 | -0.16 | 0.88 |
| **fert.ha** | 0.01 | 0.02 | 0.24 | 0.81 |
| **herb.freq** | 0.45 | 1.26 | 0.35 | 0.73 |
| **fert.freq** | 0.28 | 2.51 | 0.11 | 0.91 |

**(b) lm(formula = productive_perha ~ herb.ha + fert.freq + herb.freq + fert.freq)**

Residual standard error 12.79 on 35 degrees of freedom; adjusted R-squared = -0.0933; F-statistic = 0.09.

| | Estimate | Std. Error | t value | Pr(>\|t\|) |
|---|---|---|---|---|
| **(Intercept)** | 130.00 | 5.31 | 24.45 | **<0.001***** |
| **herb.ha** | 0.09 | 1.25 | 0.08 | 0.94 |
| **fert.ha** | 0.00 | 0.02 | 0.01 | 0.99 |
| **herb.freq** | 0.69 | 1.13 | 0.61 | 0.54 |
| **fert.freq** | 0.47 | 1.93 | 0.25 | 0.81 |

## Section 5: Applying Principal Component Analysis (PCA) to vegetation structure parameters

Within each plot (Fig. S2d) we recorded five variables: understorey density (the number of obscured sections on a 2.5m pole measured at 15m distance from the centre of the plot in 4 directions: N, E, S & W; Barlow et al. 2007), number of standing deadwood stems (>20cm height), and the number of non-palm trees according to three size classes; <10cm, between 20-25cm, and > 25cm diameter at breast height (DBH) (Figure S2). We placed eight 1m$^2$ quadrats at random bearings and 25m from the centre of the plot, and recorded 11 variables: understorey height (cm), vegetation height (cm), leaf litter depth (cm), canopy openness (using a densiometer, Russavage et al. 2020) and percentage cover of leaf litter, moss, bare ground, standing deadwood, fallen deadwood, ground vegetation <10cm height and ground vegetation >10cm height. We ran a 60m transect through the centre of each plot (orientated north-south), and for each oil palm tree within 5m of the transect line, we recorded the percentage cover of epiphytes on the trunk and percentage cover of vegetation within a 2m radius around the palm base.

**Table S4.** Principal component summary statistics. Eigenvalues of principal components and percentage of variance associated with each (obtained by applying principal components analysis to the 18 vegetation structure parameters collected from smallholder farm surveys). PC1 and PC2 scores were used in analyses, as measures of understorey vegetation cover.

| | Eigenvalue | Proportion of variance explained | Cumulative variance |
|---|---|---|---|
| **PC1** | 4.55 | 0.25 | 0.25 |
| **PC2** | 2.78 | 0.15 | 0.41 |
| **PC3** | 2.03 | 0.11 | 0.52 |
| **PC4** | 1.63 | 0.09 | 0.61 |
| **PC5** | 1.40 | 0.08 | 0.69 |
| **PC6** | 1.06 | 0.06 | 0.75 |
| **PC7** | 0.94 | 0.05 | 0.80 |
| **PC8** | 0.69 | 0.04 | 0.84 |
| **PC9** | 0.64 | 0.04 | 0.87 |
| **PC10** | 0.62 | 0.03 | 0.91 |
| **PC11** | 0.52 | 0.03 | 0.94 |
| **PC12** | 0.34 | 0.02 | 0.96 |
| **PC13** | 0.25 | 0.01 | 0.98 |
| **PC14** | 0.16 | 0.01 | 0.99 |
| **PC15** | 0.14 | 0.01 | 0.98 |
| **PC16** | 0.12 | 0.01 | 0.99 |
| **PC17** | 0.07 | 0.00 | 1.00 |
| **PC18** | 0.07 | 0.00 | 1.00 |

**Table S5.** Weighting factor of the first six principal components from the 18 vegetation structure parameters collected from smallholder farm surveys. A positive value indicates that the parameter correlates positively with the principal component, whilst a negative value indicates a negative correlation). PC1 and PC2 scores were used in analyses, as measures of understorey vegetation cover.

| **Vegetation Structure Parameters** | **PC1** | **PC2** | **PC3** | **PC4** | **PC5** | **PC6** |
|---|---|---|---|---|---|---|
| Large tree count (>25cm DBH) | -0.15 | 0.40 | -0.10 | 0.01 | 0.24 | -0.02 |
| Small tree count (>10cm and <25cm DBH) | -0.20 | 0.26 | 0.01 | -0.16 | -0.27 | -0.24 |
| Sapling count (<10cm DBH) | 0.11 | 0.33 | 0.03 | -0.53 | -0.14 | 0.07 |
| Standing deadwood count | -0.09 | -0.10 | 0.32 | 0.02 | -0.16 | -0.69 |
| Understory density (0-10) | 0.14 | -0.05 | 0.19 | -0.40 | 0.40 | 0.24 |
| Canopy openness (%) | 0.07 | 0.03 | 0.53 | 0.12 | -0.15 | 0.33 |
| Palm contour vegetation cover (%) | 0.36 | 0.00 | 0.10 | -0.07 | 0.24 | -0.07 |
| Epiphyte cover (%) | -0.15 | -0.17 | 0.36 | -0.17 | 0.40 | -0.19 |
| Understory height (m) | 0.14 | 0.22 | -0.03 | 0.26 | 0.23 | -0.06 |
| Vegetation height (cm) | 0.32 | 0.20 | -0.20 | -0.20 | -0.22 | 0.04 |
| Leaf litter depth (cm) | -0.30 | 0.39 | 0.05 | 0.04 | 0.00 | -0.05 |
| Leaf litter cover (%) | -0.29 | 0.42 | 0.02 | 0.00 | 0.13 | -0.07 |
| Ground vegetation cover (<10cm height) | 0.36 | 0.03 | 0.02 | 0.00 | 0.13 | -0.07 |
| Vegetation cover (>10cm height) | 0.37 | 0.24 | 0.01 | 0.05 | -0.02 | -0.03 |
| Moss cover (%) | -0.16 | -0.15 | -0.19 | -0.56 | 0.08 | -0.14 |
| Bare ground cover (%) | -0.29 | -0.33 | -0.20 | -0.11 | -0.04 | 0.14 |
| Fallen deadwood cover (%) | -0.23 | 0.12 | 0.00 | 0.15 | 0.44 | 0.13 |
| Standing deadwood cover (%) | -0.09 | 0.08 | 0.55 | -0.14 | -0.23 | 0.17 |

## Section 6: Soil chemical properties and soil type

We obtained information about the soil parent materials that farms were established on from 'The Soils of Sabah' soil survey map. The base map ('Sandakan NB 50-11) was developed from field investigation and related air photo interpretation and was published by the British Government's Overseas Development Administration (Land Resources Division), United Kingdom, 1974, for the Sabah Government. The map is available online from the European digital archive on soil maps (EuDASM; Panagos et al. 2011) of the European Soil Data Centre (ESDAC).

In each 0.28 ha plot, we also collected soil samples (20 cm depth) from four locations to account for spatial heterogeneity in soil carbon and nutrients within plantations (Guillaume et al. 2016): within 2m of a palm, under stacked frond piles, on the path between two palm trees, and between two palms along the planting row (Figure S2). We combined the four soil samples together to obtain one sample per farm. Soil samples were air-dried at 40°C for 7 d and then ground to pass 2 mm and 45 micron sieves, and were analysed for pH, total organic C (SOC), total C, N and P, and available P. Percentage moisture content was determined by drying a subsample of the soil sample to a constant weight at 105°C. The results for SOC, total C and N, available P, and total P were corrected to an oven-dry basis. Soil samples were analysed by the Sabah Forest Research Centre for organic carbon (%) using the rapid dichromate oxidation method (Nelson and Sommers 1982), total carbon (%) and total nitrogen (%) measured simultaneously using the dry combustion method, available P followed the Bray and Kurtz (1945) method, extractable P was determined using colorimetry (Anderson and Ingram 1990), and total phosphorus (mg/kg) using the sulphuric acid-hydrogen peroxide method (Allen 1989) and colorimetry. To avoid redundancy of variables in the soil analysis, we omitted variables that were highly correlated (Pearson's $r > 0.9$; see SI 4; Table S6), and soil organic carbon (%; SOC), total nitrogen and total phosphorus and available phosphorus were used in subsequent statistical analyses. These soil variables are linked to soil fertility and contribute to the development, growth and yield of oil palm trees (Webb et al. 2013; Corley and Tinker 2016; Guillaume, Holtkamp, et al. 2016).

Total C content in the top 20cm of soil varied across farms (median = 1.43%, sd = 0.45; see Table S7), but did not exceed 2.92% with the exception of three farms, indicating relatively low C content (<2%; Guillaume et al. 2016) across the majority of study farms. The maximum soil organic content (SOC) reached 2.21% (median = 1.43%, sd = 0.45; Table S1), classifying farms as having mineral soils (<20% SOC; IUSS Working Group WRB 2014). Farms varied widely in soil nutrient content, with total N content varying from <0.12 to >0.25%, total P from <120 to >400 mg/kg, and available P from <8 to >25 mg/kg across farms (i.e. spanning nutrient values from 'very low' to 'very high' according to Paramanthan 2013). We also found that total P varied across governance areas, with some areas (region 4, Sukau) containing more than double that of other areas (region 2, Reka Halus; 110-370 mg/kg; Table S1).

**Table S6.** Pearson's correlation values of chemical properties of soil samples collected from smallholder farms. Very highly correlated values (r > 0.9) are given in italics. Total C was omitted from subsequent statistical analyses due to its high correlation with SOC (r = 0.98).

| | **Total C** | **Organic C (SOC)** | **Total N** | **Available P** | **Total P** |
|---|---|---|---|---|---|
| **Total C** | 1.00 | - | - | - | - |
| **Organic C (SOC)** | *0.98* | 1.00 | - | - | - |
| **Total N** | 0.83 | 0.81 | 1.00 | - | - |
| **Available P** | -0.07 | -0.07 | -0.13 | 1.00 | - |
| **Total P** | 0.45 | 0.44 | 0.67 | 0.29 | 1.00 |

## Section 7: Obtaining information on climatic conditions, and inter-relatedness with other explanatory covariates

Local climatic conditions such as water availability and temperature have been identified as important factors influencing FFB yields (Corley and Tinker 2016). Drought can limit FFB yields by increasing the risk of inflorescence abortion (~9-10 months prior to harvesting) and reducing inflorescence development (~ 12-19 months prior to harvesting) (Dufour et al. 1998). High temperatures can limit inflorescence development (12-19 months before harvest; Shanmuganathan and Narayanan 2012), but increase fruit ripening stage (0-5 months before harvest; Wen and Sidik 2011). To examine possible inter-relatedness between our rainfall and temperature predictor variables and soil type, we performed an analysis of variance with yield as a response variable and included soil type, minimum rainfall (mm month$^{-1}$) and an interaction between soil type and rainfall as predictor variables. To avoid redundancy, we omitted climate variables from our analyses that were highly correlated (Pearson's r > 0.9; Table S7). We repeated this analysis with maximum temperature ($^{o}$C) instead of minimum rainfall as a predictor variable. These analyses revealed that neither soil type, minimum rainfall or maximum temperature were related to yield. Yield was slightly higher on farms established on alluvium soils (soil type 1, median =18.8 FFB t $ha^{-1}$ $yr^{-1}$) compared to soil type 2 (mudstone, sandstone and miscellaneous rocks; median = 14.9 FFB t $ha^{-1}$ $yr^{-1}$) and soil type 3 (mudstone and alluvium; median = 14.9 FFB t $ha^{-1}$ $yr^{-1}$), but was not significantly different to the other soil types (Kruskal-wallis chi-squared = 3.37, df = 2, p = 0.19). Rainfall was significantly higher on farms established on alluvium soil (Kruskal-wallis chi-squared = 11.13, df = 2, p = 0.004), probably because differences in topography and coastal proximity (Ng et al. 2019), but this did not affect yield (Kruskal-wallis chi-squared = 3.37, df = 2, p = 0.19).

**Table S7.** Pearson's correlation values among climatic variables on smallholder farms (CRU VS4.05 dataset), averaged across 36 months prior to study (November 2016 to December 2019): . monthly mean, minimum and maximum values for temperature are denoted as Tmean, Tmin and Tmax respectively, and rainfall mean, min and max. Very highly correlated values (r > 0.9) are in italics. Monthly mean, minimum and maximum temperature (Tmean, Tmin and Tmax), as well as monthly mean, minimum and maximum rainfall were omitted from subsequent statistical analyses due to their high correlations (r = 0.98).

| | **Tmean (°C)** | **Tmin (°C)** | **Tmax (°C)** | **Rainfall mean (mm)** | **Rainfall min (mm)** | **Rainfall max (mm)** |
|---|---|---|---|---|---|---|
| **Tmean (°C)** | 1.00 | - | - | - | - | |
| **Tmin (°C)** | *1.00* | 1.00 | - | - | - | |
| **Tmax (°C)** | *1.00* | *1.00* | 1.00 | - | - | |
| **Rainfall mean (mm)** | -0.13 | -0.13 | -0.13 | 1.00 | - | |
| **Rainfall min (mm)** | -0.13 | -0.13 | -0.13 | *1.00* | 1.00 | |
| **Rainfall max (mm)** | -0.13 | -0.13 | -0.13 | *1.00* | *1.00* | 1.00 |

## Section 8: Summary of management variability across smallholder oil palm farms

**Table S9.** Summary of data of range (median; standard deviation) for management practices carried out by smallholder farmers that are included in the management intensity index and Best Management Practices (BMPs). Information was collected from interviews with smallholder farmers (see Methods and S3).

| Management practice | Summary of data |
|---|---|
| **Agriculture type** | Number of farms: Monoculture (n = 21); mixed crop (n=19) |
| **Planting density** | 86-165 productive palms ha$^{-1}$ (median = 136; standard deviation = 12.4) |
| **Pruning frequency** | 1-2 month$^{-1}$ (median = 2; standard deviation = 0.42) |
| **Harvest frequency** | 1-2 month$^{-1}$ (median = 2; standard deviation = 0.3) |
| **Weeding frequency** | 1-4 yr$^{-1}$ (median = 2; standard deviation = 1.85) |
| **Weeding method** | Number of farms: Solely hand-weeding (n = 3); herbicide or combination (n = 37) |
| **Herbicide quantity** | 0-40 litres ha$^{-1}$ yr$^{-1}$ (median = 4.8; standard deviation = 7.9) |
| **Fertiliser use** | Number of farms: Yes (n = 5); no (n = 35) |
| **Fertiliser quantity** | 0-1456 kg ha$^{-1}$ yr$^{-1}$ (median = 544; standard deviation = 409) |
| **Pesticide use** | Number of farms: Yes (n = 34); no (n = 6) |
| **EFB application** | Number of farms: Yes (n = 12); no (n = 28) |
| **Contour removal** | Number of farms: Yes (n = 23); no (n = 17) |

**Table S10.** Summary data (median and range) for farms (n = 40) according to the number of BMPs (Best Management Practices) employed by the farmer. Information was collected from interviews with smallholder farmers (see Methods and S3).

| **Number of BMPs** | **0** | **1** | **2** | **3** |
|---|---|---|---|---|
| **Number of farms** | 2 | 9 | 24 | 5 |
| **Crop age (years)** | 15.5 (15-16) | 15.8 (8-19) | 18.4 (9-27) | 18.8 (8-26) |
| **Fresh fruit bunch yield (FFB t ha$^{-1}$ yr$^{-1}$)** | 18 (12.4-23.7) | 21.9 (11.9-37.4) | 17.0 (6.9-36.5) | 14.1 (8-21.9) |
| **Soil organic carbon (SOC) (%)** | 0.74 (0.65-0.82) | 1.23 (0.78-1.56) | 1.11 (0.68-2.21) | 1.12 (0.73-1.53) |
| **Soil total nitrogen (%)** | 0.14 (0.13-0.15) | 0.17 (0.10-0.25) | 0.17 (0.11-0.26) | 0.18 (0.12-0.21) |
| **Soil total phosphorus (mg/kg)** | 142 (52-231) | 288 (59-650) | 264 (48-519) | 175 (69-337) |
| **Soil available phosphorus (mg/kg)** | 4.17 (3.54-4.8) | 7.86 (1.98-37.3) | 3.34 (0.89-10.4) | 2.69 (1.07-4.19) |

## Section 9: Application of GAMMs to identify predictors of smallholder yield

To assess the relationship between yield and predictor variables (management intensity, understorey vegetation cover, soil properties, soil type, farming system, and climate), we fitted Generalized Additive Mixed Affects Models (GAMMs) to the full data set (Fig. S3) and a reduced dataset (Fig. 3a), where we omitted two outlier data points (a farm with a PC1 score > 6 and one farm with available P > 36 mg kg$^{-1}$) from the analysis to assess their effects on the significance of the relationship between yield and our explanatory variables. We applied penalised cubic regression splines as the smoothing basis function, to remove non-influential explanatory variables from the model (Marra and Wood 2011). High covariate dependence (i.e. concurvity > 0.5) leads to unstable parameter estimates of the fitted GAMM, thereby increasing the risk of falsely assuming statistically significant effects of explanatory variables (Amodio, Aria, and D'Ambrosio 2014). There was strong variable dependence between total N and organic C (estimated concurvity = 0.52), as well as between maximum temperature and minimum rainfall (estimated concurvity = 1.00) (Table S11). We fitted the GAMM excluding total N and monthly maximum temperature (as water stress is a more important predictor of yield that solar radiation at a monthly time scale; Oettli, Behera, and Yamagata 2018). The model fitted to the full dataset (n = 40 farms) showed a significant positive effect of ground cover vegetation (PC1) on yield (n = 40, F = 0.41, p = 0.04; Table S12). However, the relationship was strongly driven by two farms with high PC1 values (Fig. S3), and the effect of PC1 was non-significant when excluding these farms from the analysis (n = 38, F = 0.00, p = 1.00). We conclude that predictor variables remained non-significant when excluding these outliers (Table S12) and include only the analyses without outliers in the main text.

To account for the effects of variations in oil palm planting densities across farms, we also fitted GAMMs to identify drivers of yield in kilograms per tree per year (kg tree$^{-1}$ ha$^{-1}$) to the full (N = 40) and reduced dataset (n = 38). The full model also showed a significant positive effect of ground cover vegetation (PC1) on yield (n = 40, F = 0.35, p = 0.05; Table S13), but after removal of outliers, the relationship was not significant (n = 38, F = 0.00, p = 1.00). As such, we conclude that PC1 has little effect on yield in kilograms per tree per year (kg tree$^{-1}$ yr$^{-1}$), similarly to findings for yield in tonnes per hectare per year (t ha$^{-1}$ yr$^{-1}$; see results in main text).

**Table S11.** Concurvity of explanatory variables fitted in the GAMM assessing the drivers of variation of reported fresh fruit bunch yield (FFB t $ha^{-1}$ $yr^{-1}$) using the reduced dataset excluding two outlier farms for available P and PC1 (n = 38 farms). We used penalised cubic regression splines as smoothing basis functions to smooth terms, and scaled variables for model computation. Covariates with high concurvity (> 0.5) are highlighted in bold and italics.

| | **Categorical variables** | **Index score** | **Crop age** | **Productive area** | **PC1** | **PC2** | **Organic C** | **Total N** | **Total P** | **Available P** | **Rainfall min** | **Tmax** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Categorical variables** | 1.00 | | | | | | | | | | | |
| **Index score** | 0.00 | 1.00 | | | | | | | | | | |
| **Crop age** | 0.00 | 0.05 | 1.00 | | | | | | | | | |
| **Productive area** | 0.00 | 0.16 | 0.03 | 1.00 | | | | | | | | |
| **PC1** | 0.00 | 0.07 | 0.11 | 0.06 | 1.00 | | | | | | | |
| **PC2** | 0.00 | 0.05 | 0.10 | 0.04 | 0.07 | 1.00 | | | | | | |
| **Organic C** | 0.00 | 0.01 | 0.02 | 0.03 | 0.15 | 0.08 | 1.00 | | | | | |
| **Total N** | 0.00 | 0.04 | 0.05 | 0.05 | 0.07 | 0.02 | ***0.52*** | 1.00 | | | | |
| **Total P** | 0.00 | 0.11 | 0.04 | 0.14 | 0.07 | 0.07 | 0.20 | 0.36 | 1.00 | | | |
| **Available P** | 0.00 | 0.05 | 0.06 | 0.09 | 0.04 | 0.05 | 0.06 | 0.05 | 0.15 | 1.00 | | |
| **Rainfall** | 0.00 | 0.08 | 0.11 | 0.27 | 0.11 | 0.04 | 0.09 | 0.10 | 0.39 | 0.01 | 1.00 | |
| **Tmax** | 0.00 | 0.08 | 0.11 | 0.27 | 0.11 | 0.04 | 0.09 | 0.10 | 0.39 | 0.01 | ***1.00*** | 1.00 |

**Figure S3.** GAMM model outputs showing the component effects of explanatory variables on smallholder oil palm yield (FFB t ha$^{-1}$ yr$^{-1}$; n = 40). Partial effect plots of the generalised additive mixed effects models, showing the component effect of the smoothed term on smallholder oil palm yield (FFB t ha$^{-1}$ yr$^{-1}$; p = 0.41) for (a) management intensity, (b) crop age (years), (c) farm area with planted with productive trees (ha), (d-e) understorey vegetation cover (PC1 and PC2 score), (f) SOC %, (g) total N %, (h) total P mg/kg, and (i) available P mg/kg, (j) monthly minimum rainfall (mm), and (k) monthly maximum temperature (°C). We used penalised cubic regression splines as smoothing basis functions to smooth terms, and scaled variables for model computation. The points show the partial residuals, which are the difference between the partial effect and the data after all partial effects in the model have been accounted for. The blue shaded areas denote the uncertainty within the model, measured as the standard errors of the partial effect term combined with the standard errors of the model intercept. Non-influential explanatory variable in models, are penalised by the smoothing parameter towards a line and zero.

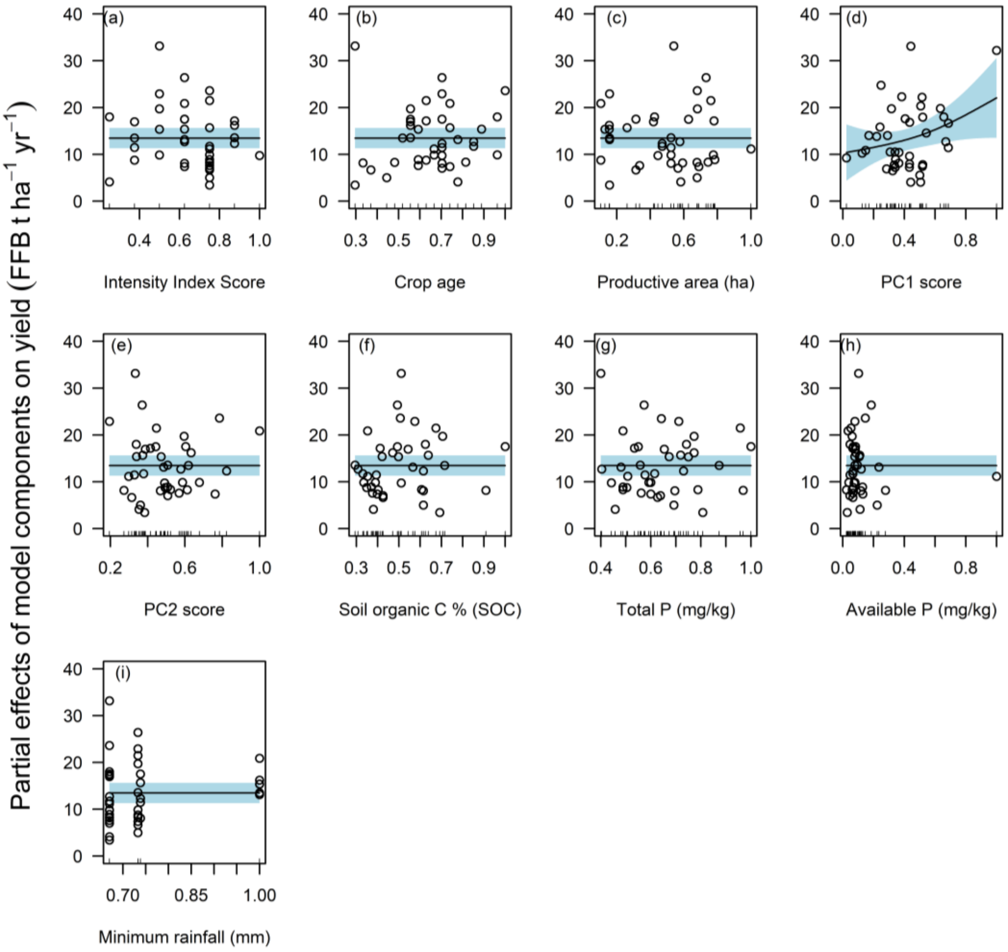


**Table S12.** Results of GAMMs of drivers of variation of reported fresh fruit bunch yield (FFB t ha$^{-1}$ yr$^{-1}$) using the (a) full dataset (n = 40 farms, adjusted R$^2$ = 0.123) and (b) reduced dataset excluding two outlier farms for available P and PC1 (n = 38 farms, adjusted R$^2$ = 0.035). We used penalised cubic regression splines as smoothing basis functions to smooth terms, and scaled variables for model computation. Monthly mean, minimum and maximum temperature (°C; Tmean, Tmin and Tmax), and monthly mean, minimum and maximum rainfall (mm) obtained from the CRU VS 4.05 dataset (Harris et al. 2020), averaged over 36 months prior to harvesting. Soil types correspond to: 1) alluvium, 2) mudstone, sandstone and miscellaneous rocks, and 3) mudstone and alluvium (see Methods and SI4). Significant effects are highlighted in bold: * p <0.05; ** p <0.01; *** p <0.001. Effective degrees of freedom given as e.d.f.

***(a) Full model (n = 40 farms)***

| **Parametric coefficient** | **Estimate** | **Standard error** | ***t*-value** | ***Pr(>\|t\|)*** |
|---|---|---|---|---|
| (intercept) | 13.47 | 3.19 | 4.22 | **<0.001*** ** |
| Soil type: 2 | 3.96 | 3.38 | 1.17 | 0.25 |
| Soil type: 3 | 7.04 | 3.83 | 1.84 | 0.07 |
| Farm system: monoculture | 0.33 | 2.22 | 0.15 | 0.88 |
| **Smooth terms** | **Estimated e.d.f.** | **Reference e.d.f.** | ***F*** | ***Pr(>\|t\|)*** |
| Index score | <0.01 | 3 | 0.00 | 0.32 |
| Crop age | <0.01 | 3 | 0.00 | 1.00 |
| Productive area | <0.01 | 3 | 0.00 | 1.00 |
| Vegetation PC1 | 1.74 | 3 | 0.41 | **0.04*** |
| Vegetation PC2 | <0.01 | 3 | 0.00 | 0.75 |
| Organic C | <0.01 | 3 | 0.00 | 0.39 |
| Total N | <0.01 | 3 | 0.00 | 0.91 |
| Total P | <0.01 | 3 | 0.00 | 0.94 |
| Available P | <0.01 | 3 | 0.00 | 1.00 |
| Rainfall min | <0.01 | 3 | 0.00 | 0.32 |
| Tmax | <0.01 | 3 | 0.00 | 1.00 |

***(b) Reduced model (n = 38 farms)***

| **Parametric coefficient** | **Estimate** | **Standard error** | ***t*-value** | **Pr(>\|t\|)** |
|---|---|---|---|---|
| (intercept) | 13.94 | 3.12 | 4.47 | **<0.001*** ** |
| Soil type: 2 | 2.62 | 3.29 | 0.80 | 0.43 |
| Soil type: 3 | 7.05 | 3.73 | 1.89 | 0.07 |
| Farm system: monoculture | 0.2446 | 2.18 | 0.11 | 0.91 |
| **Smooth terms** | **Estimated d.f.** | **Reference d.f.** | **F** | **Pr(>\|t\|)** |
| Index score | <0.01 | 3 | 0.00 | 0.32 |
| Crop age | <0.01 | 3 | 0.00 | 1.00 |
| Productive area | <0.01 | 3 | 0.00 | 1.00 |

| | | | | |
|---|---|---|---|---|
| Vegetation PC1 | 1.17 | 3 | 0.00 | 0.56 |
| Vegetation PC2 | <0.01 | 3 | 0.00 | 1.00 |
| Organic C | <0.01 | 3 | 0.00 | 1.00 |
| Total N | <0.01 | 3 | 0.00 | 1.00 |
| Total P | <0.01 | 3 | 0.00 | 1.00 |
| Available P | <0.01 | 3 | 0.00 | 1.00 |
| Rainfall min | <0.01 | 3 | 0.00 | 1.00 |
| Tmax | <0.01 | 3 | 0.00 | 1.00 |

**Table S13.** Results of GAMMs of drivers of variation of reported fresh fruit bunch yield (FFB t tree$^{-1}$ yr$^{-1}$) using the (a) full dataset (n = 40, adjusted R$^2$ = 0.117) and (b) reduced dataset excluding an available P and PC1 outlier (n = 38, adjusted R$^2$ = 0.034). We used penalised cubic regression splines as smoothing basis functions to smooth terms, and scaled variables for model computation. Monthly mean, minimum and maximum temperature (°C; Tmean, Tmin and Tmax), and monthly mean, minimum and maximum rainfall (mm) obtained from the CRU VS 4.05 dataset (Harris et al. 2020), averaged over 36 months prior to harvesting. Soil types correspond to: 1) alluvium, 2) mudstone, sandstone and miscellaneous rocks, and 3) mudstone and alluvium (see Methods and SI4). Significant effects are highlighted in bold: * p <0.05; ** p <0.01; *** p <0.001. Effective degrees of freedom given as e.d.f.

***(a) Full model (n = 40)***

| **Parametric coefficient** | **Estimate** | **Standard error** | ***t*-value** | ***Pr(>\|t\|)*** |
|---|---|---|---|---|
| (intercept) | 13.46 | 3.19 | 4.22 | **<0.001*****
| Soil type: 2 | 3.97 | 3.38 | 1.18 | 0.25 |
| Soil type: 3 | 7.05 | 3.83 | 1.84 | 0.07 |
| Farm system: monoculture | 0.33 | 2.22 | 0.15 | 0.88 |
| **Smooth terms** | **Estimated e.d.f.** | **Reference e.d.f.** | ***F*** | ***Pr(>\|t\|)*** |
| Index score | <0.01 | 3 | 0.003 | 0.32 |
| Crop age | <0.01 | 3 | 0.00 | 1.00 |
| Productive area | <0.01 | 3 | 0.00 | 1.00 |
| Vegetation PC1 | 1.74 | 3 | 0.41 | **0.04*** |
| Vegetation PC2 | <0.01 | 3 | 0.00 | 0.75 |
| Organic C | <0.01 | 3 | 0.00 | 0.39 |
| Total N | <0.01 | 3 | 0.00 | 0.91 |
| Total P | <0.01 | 3 | 0.00 | 0.94 |
| Available P | <0.01 | 3 | 0.00 | 1.00 |
| Minimum rainfall (mm month$^{-1}$) | <0.01 | 3 | 0.002 | 0.32 |
| Monthly aximum temperature (°C) | <0.01 | 3 | 0.00 | 1.00 |

***(b) Reduced model (n = 38)***

| **Parametric coefficient** | **Estimate** | **Standard error** | ***t*-value** | **Pr(>\|t\|)** |
|---|---|---|---|---|
| (intercept) | 13.94 | 3.12 | 4.47 | **<0.001***** |
| Soil type: 2 | 2.62 | 3.29 | 080 | 0.43 |
| Soil type: 3 | 7.05 | 3.73 | 1.89 | 0.07 |
| Farm system: monoculture | 0.2446 | 2.18 | 0.11 | 0.91 |
| **Smooth terms** | **Estimated d.f.** | **Reference d.f.** | **F** | **Pr(>\|t\|)** |
| Index score | <0.01 | 3 | 0 | 0.32 |
| Crop age | <0.01 | 3 | 0 | 1.00 |
| Productive area | <0.01 | 3 | 0 | 1.00 |
| Vegetation PC1 | 1.17 | 3 | 0 | 1.00 |
| Vegetation PC2 | <0.01 | 3 | 0 | 1.00 |
| Organic C | <0.01 | 3 | 0 | 1.00 |
| Total N | <0.01 | 3 | 0 | 1.00 |
| Total P | <0.01 | 3 | 0 | 1.00 |
| Available P | <0.01 | 3 | 0 | 1.00 |
| Minimum rainfall (mm month$^{-1}$) | <0.01 | 3 | 0 | 1.00 |
| Monthly aximum temperature (°C) | <0.01 | 3 | 0 | 1.00 |

***(c) Full model (n = 40 farms)***

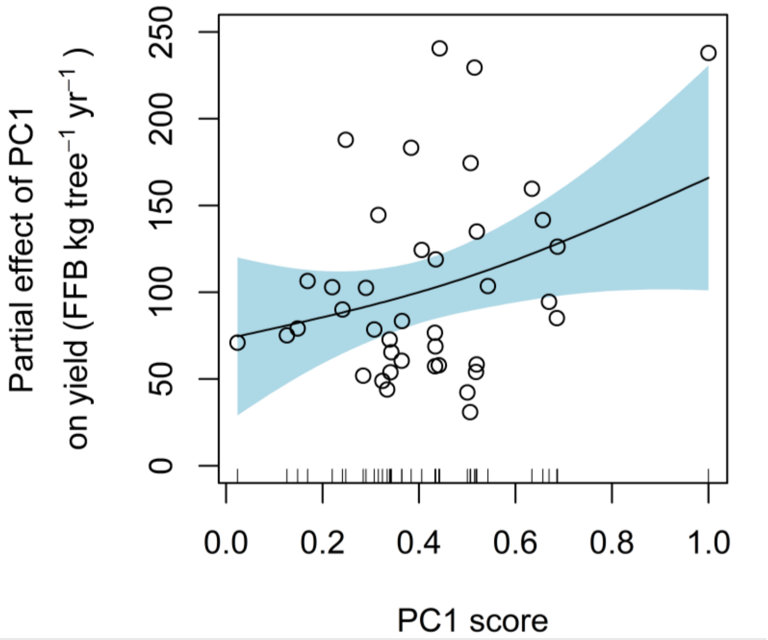
| **Parametric coefficient** | **Estimate** | **Standard error** | ***t*-value** | ***Pr(>\|t\|)*** |
|---|---|---|---|---|
| (intercept) | 103.02 | 25.41 | 4.05 | **<0.001***** |
| Soil type: 2 | 29.55 | 26.92 | 1.10 | 0.28 |
| Soil type: 3 | 51.78 | 30.44 | 1.70 | 0.10 |
| Farm system: monoculture | 2.60 | 17.61 | 0.15 | 0.88 |
| **Smooth terms** | **Estimated e.d.f.** | **Reference e.d.f.** | ***F*** | ***Pr(>\|t\|)*** |
| Index score | <0.01 | 3 | 0.09 | 0.25 |
| Crop age | <0.01 | 3 | 0.00 | 1.00 |
| Productive area | <0.01 | 3 | 0.00 | 0.85 |
| Vegetation PC1 | 1.05 | 3 | 0.35 | **0.05*** |
| Vegetation PC2 | <0.01 | 3 | 0.00 | 0.74 |
| Organic C | <0.01 | 3 | 0.00 | 0.43 |
| Total N | <0.01 | 3 | 0.00 | 0.72 |
| Total P | <0.01 | 3 | 0.00 | 1.00 |
| Available P | <0.01 | 3 | 0.00 | 1.00 |
| Rainfall min | <0.01 | 3 | 0.00 | 1.00 |
| Tmax | <0.01 | 3 | 0.00 | 1.00 |

***(d) Reduced model (n = 38 farms)***

| **Parametric coefficient** | **Estimate** | **Standard error** | ***t*-value** | **Pr(>\|t\|)** |
|---|---|---|---|---|
| (intercept) | 106.36 | 25.33 | 4.20 | **<0.001***** |
| Soil type: 2 | 19.29 | 26.79 | 0.72 | 0.48 |
| Soil type: 3 | 52.43 | 30.29 | 1.73 | 0.09 |
| Farm system: monoculture | 2.67 | 17.71 | 0.15 | 0.88 |
| **Smooth terms** | **Estimated d.f.** | **Reference d.f.** | **F** | **Pr(>\|t\|)** |
| Index score | <0.01 | 3 | 0.00 | 0.25 |

| | | | | |
|---|---|---|---|---|
| Crop age | <0.01 | 3 | 0.00 | 1.00 |
| Productive area | <0.01 | 3 | 0.00 | 1.00 |
| Vegetation PC1 | 1.17 | 3 | 0.00 | 0.34 |
| Vegetation PC2 | <0.01 | 3 | 0.00 | 0.50 |
| Organic C | <0.01 | 3 | 0.00 | 0.34 |
| Total N | <0.01 | 3 | 0.00 | 1.00 |
| Total P | <0.01 | 3 | 0.00 | 0.57 |
| Available P | <0.01 | 3 | 0.00 | 0.59 |
| Rainfall min (mm) | <0.01 | 3 | 0.00 | 1.00 |
| Tmax (ºC) | <0.01 | 3 | 0.00 | 0.68 |

**Figure S4.** Partial effect plots from the GAMM, showing the component effects of ground vegetation cover (PC1 score) on oil palm yield per tree (FFB kg tree$^{-1}$ yr$^{-1}$; n = 38). The points show the partial residuals, which are the difference between the partial effect and the data after all partial effects in the model have been accounted for. The blue shaded areas denote the uncertainty within the model, measured as the standard errors of the partial effect term combined with the standard errors of the model intercept. Explanatory variables were scaled, and governance area was defined as a random effect in the model.



## **Section 10: Examining the effects of Best Management Practices (BMPs) on soil chemical properties**

To assess whether the use of BMPs influences soil chemical properties (SOC, total C, N, and P and available P) on farms, we examined differences across the four groups of farms, split by BMP use (i.e. 0, 1, 2 or 3 BMPs employed by a farmer). For this analysis, we fitted GAMMs with smoothing parameter fitted with a penalised cubic regression spline smoothing basis functions (similar to the GAMMs in SI6) to SOC, total N, total C, total P and available P as dependent variables, and the number of BMPs employed, crop age (years since planting, to control for possible variations in yield as a consequence of palm tree age), extent of farm area with productive trees (ha; to control for differences in yield as a result of farm size), monthly minimum rainfall (mm; to control for potential effects of drought and water stress on yield), previous land-use (forest or agriculture), farm system (monoculture or mixed agriculture) and soil type (to control for potential differences in soil structure and nutrient retention) as explanatory variables. To obtain homoscedasticity and normality of residuals, total P and available P data were modelled with Gaussian identity, total N and SOC data with a Gaussian log link function. We observed no significant relationship between the number of BMPs employed by a farmer with SOC, total N, total P, or available P (Table S14).

**Table S14.** Generalized additive mixed effects modelling (GAMM) the effect of the number of Best Management Practices (BMPs) on: (A) Reported fresh fruit bunch yields (FFB t $ha^{-1}$ $yr^{-1}$), (B) organic Carbon (%), (C) total N (%), (D) total P (mg/kg), (E) available P (mg/kg; n = 39). Variables were scaled for model computation (see main Methods). We used penalised cubic regression splines as smoothing basis functions to smooth terms, and scaled variables for model computation. Monthly mean, minimum and maximum temperature (Tmean, Tmin and Tmax), and monthly mean, minimum and maximum rainfall obtained from the CRU VS 4.05 dataset (Harris et al. 2020), averaged over 36 months prior to harvesting. Soil types correspond to: 1) alluvium, 2) mudstone, sandstone and miscellaneous rocks, and 3) mudstone and alluvium (see Methods and SI4). Significant effects are highlighted in bold: * p <0.05; ** p <0.01; *** p <0.001. Effective degrees of freedom given as e.d.f.

| | **(A) FFB yield** | **(B) Organic C** | **(C) Total N** | **(D) Total P** | **(E) Available P** |
|---|---|---|---|---|---|
| **s(crop age)** | | | | | |
| Edf (Ref.df) | <0.01 (3) | <0.01 (3) | 0.72 (3) | 0.98 (2) | <0.01 (2) |
| F | 0.09 | 6.50 | 498.54 | 0.30 | 0.00 |
| p | 0.26 | 0.06 | 0.05 | 0.06 | 1.00 |
| k | 4 | 4 | 4 | 2 | 4 |
| **s(productive area)** | | | | | |
| Edf (Ref.df) | <0.01 (3) | <0.01 (3) | 0.07 (3) | 1.80 (5) | <0.01 (3) |
| F | 0.00 | 0.00 | 1.55 | 0.36 | 0.00 |
| p | 0.77 | 1.00 | 0.30 | **0.03*** | 1.00 |
| k | 4 | 4 | 4 | 5 | 4 |
| **S(rainfall min)** | | | | | |
| Estimate (std.error) | <0.01 (3) | - | - | - | - |
| F | 0.00 | - | - | - | - |
| p | 1.00 | - | - | - | - |
| k | 4 | - | - | - | - |
| **Parametric coefficients** (intercept) | | | | | |
| Estimate (std.error) | 18.50 (5.30) | 0.81 (0.32) | -1.95 (0.21) | 188.32 (97.11) | 1.29 (0.53) |
| t | 3.49 | 2.52 | -9.30 | 1.94 | 2.44 |
| p | **0.001**** | **0.02*** | **<0.001***** | 0.06 | **0.02*** |
| **BMP: 1** | | | | | |
| Estimate (std.error) | 3.78 (5.63) | 0.45 (0.27) | 0.17 (0.18) | 119.54 (80.31) | 0.01 (0.38) |
| t | 0.67 | 1.68 | 0.89 | 1.50 | 0.04 |
| p | 0.51 | 0.10 | 0.38 | 0.15 | 0.97 |
| **BMP: 2** | | | | | |
| Estimate (std.error) | -1.61 (5.32) | 0.35 (0.26) | 0.19 (0.18) | 128.17 (80.12) | -0.18 (0.38) |
| t | -0.30 | 1.34 | 1.03 | 1.60 | -0.48 |

|  |  |  |  |  |  |
|---|---|---|---|---|---|
| p | 0.76 | 0.19 | 0.31 | 0.12 | 0.63 |
| **BMP: 3** |  |  |  |  |  |
| Estimate (std.error) | -3.21 (6.11) | 0.42 (0.30) | 0.35 (0.20) | 163.60 (95.24) | -0.43 (0.50) |
| t | -0.53 | 1.39 | 1.72 | -0.74 | -0.87 |
| p | 0.60 | 0.17 | 0.09 | 0.47 | 0.39 |
| **Farming system: monoculture** |  |  |  |  |  |
| Estimate (std.error) | 2.01 (2.48) | 0.03 (0.12) | 0.10 (0.07) | 78.78 (36.60) | -0.13 (0.21) |
| t | 0.81 | 0.24 | 1.44 | 2.15 | -0.64 |
| p | 0.42 | 0.81 | 0.16 | **0.04*** | 0.53 |
| **Soil type: 2** |  |  |  |  |  |
| Estimate (std.error) | - | 0.10 (0.17) | 0.09 (0.10) | 49.44 (52.63) | 0.16 (0.34) |
| t | - | 0.58 | 0.83 | 0.94 | 0.48 |
| p | - | 0.57 | 0.41 | 0.36 | 0.64 |
| **Soil type: 3** |  |  |  |  |  |
| Estimate (std.error) | - | -0.11 (0.22) | -0.06 (0.12) | -48.96 (66.37) | 0.18 (0.42) |
| t | - | -0.51 | -0.49 | -0.74 | 0.42 |
| p | - | 0.62 | 0.63 | 0.47 | 0.68 |
| **Previous land-use: forest** |  |  |  |  |  |
| Estimate (std.error) | -2.56 (2.58) | -0.24 (0.14) | -0.29 (0.08) | -265.17 (48.25) | 0.04 (0.25) |
| t | -0.99 | -1.67 | -3.44 | -5.50 | 0.15 |
| p | 0.33 | 0.11 | **0.002**** | **<0.001***** | 0.89 |
| **$R^2$ (adjusted)** | 0.028 | 0.056 | 0.119 | 0.505 | -0.144 |

## Section 11: Supplementary material for analysis of the drivers of variation in yield, understory vegetation and soil chemical properties across smallholder oil palm farms

**Figure S5.** We found no relationships between management intensity and PC2 score (non-palm tree density) on smallholder farms (n = 40). Partial effect plots of the generalised additive mixed effects models, showing the component effect of the smoothed term for management intensity on non-palm tree density (PC2 score; p = 0.13). We used penalised cubic regression splines as smoothing basis functions to smooth terms and scaled explanatory variables for model computation. The points show the partial residuals, which are the difference between the partial effect and the data after all partial effects in the model have been accounted for. The blue shaded areas denote the uncertainty within the model, measured as the standard errors of the partial effect term combined with the standard errors of the model intercept.

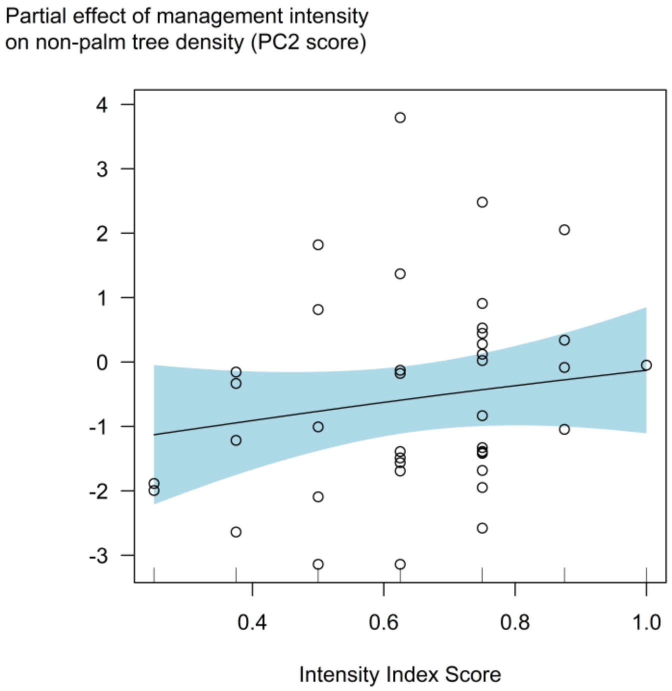


**Table S15.** Generalized additive mixed effects modelling (GAMM) the effect of smallholder management intensity (our intensity index) on: (A) organic carbon (%), (B) total N (%), (C) total P (mg/kg), (D) available P (mg/kg), (E) understorey vegetation cover (PC1 and PC2 score). Variables were scaled for model computation (see main Methods). Significant effects are highlighted in bold: * p <0.05; ** p <0.01; *** p <0.001. Effective degrees of freedom given as e.d.f.

| | **(A) Organic C** | **(B) Total N** | **(C) Total P** | **(D) Available P** | **(E) PC1** | **(F) PC2** |
|---|---|---|---|---|---|---|
| **Fixed effects s(index score)** | | | | | | |
| Edf (Ref.df) | <0.01 (3) | <0.01 (3) | <0.01 (3) | <0.01 (3) | <0.01 (3) | <0.01 (3) |
| F | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.32 |
| p | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 0.13 |
| k | 4 | 4 | 4 | 4 | 4 | 4 |
| **s(crop age)** | | | | | | |
| Edf (Ref.df) | <0.01 (3) | <0.01 (3) | <0.01 (3) | <0.01 (3) | <0.01 (4) | <0.01 (3) |
| F | 14.00 | 176.20 | 0.30 | 0.00 | 0.00 | 0.37 |
| p | **0.04*** | 0.13 | 0.06 | 1.00 | 1.00 | 0.11 |
| k | 4 | 4 | 4 | 4 | 4 | 4 |
| **s(PC1)** | | | | | | |
| Edf (Ref.df) | <0.01 (3) | <0.01 (3) | <0.01 (3) | <0.01 (3) | - | - |
| F | 0.36 | 91.18 | 0.00 | 0.00 | - | - |
| p | 0.31 | 0.16 | 1.00 | 1.00 | - | - |
| k | 4 | 4 | 4 | 4 | - | - |
| **s(productive area)** | | | | | | |
| Edf (Ref.df) | <0.01 (3) | <0.01 (3) | <0.01 (3) | <0.01 (3) | <0.01 (3) | <0.01 (2) |
| F | 0.00 | 0.00 | 0.52 | 0.02 | 0.002 | 0.00 |
| p | 0.91 | 1.00 | **0.03*** | 0.32 | 0.32 | 0.77 |
| k | 4 | 4 | 4 | 4 | 4 | 4 |
| **Rainfall min** | | | | | | |
| Estimate (std.error) | - | - | - | - | <0.01 (2) | <0.01 (2) |
| t | - | - | - | - | 0.00 | 0.00 |
| p | - | - | - | - | 1.00 | 1.00 |
| k | - | - | - | - | 4 | 4 |
| **Tmax** | | | | | | |
| Estimate (std.error) | - | - | - | - | <0.01 (2) | <0.01 (2) |
| t | - | - | - | - | 0.00 | 0.00 |
| p | - | - | - | - | 0.62 | 0.91 |
| k | - | - | - | - | 4 | 4 |
| **Parametric coefficients** | | | | | | |

|  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|
| (intercept) |  |  |  |  |  |  |
| Estimate (std.error) | 0.14 (0.14) | 0.18 (0.02) | 317.91 (57.10) | 3.11 (1.10) | -0.58 (1.07) | 1.42 (0.82) |
| t | 1.06 | 9.73 | 5.57 | 2.84 | 1.07 | 1.74 |
| p | 0.30 | **<0.001*** ** | **<0.001*** ** | **0.008*** | 0.59 | 0.09 |
| **Farming system: monoculture** |  |  |  |  |  |  |
| Estimate (std.error) | 0.01 (0.09) | 0.01 (0.01) | 76.60 (35.97) | -0.42 (0.75) | 0.52 (0.74) | -0.34 (0.56) |
| t | 0.16 | 1.00 | 2.13 | -0.55 | 0.70 | -0.61 |
| p | 0.88 | 0.33 | **0.04*** | 0.58 | 0.49 | 0.55 |
| **Soil type: 2** |  |  |  |  |  |  |
| Estimate (std.error) | 0.13 (0.13) | 0.01 (0.02) | 44.76 (51.62) | 0.60 (1.07) | -0.69 (1.05) | -0.75 (0.80) |
| t | 1.04 | 0.55 | 0.87 | 0.56 | -0.66 | -0.93 |
| p | 0.31 | 0.59 | 0.39 | 0.58 | 0.51 | 0.36 |
| **Soil type: 3** |  |  |  |  |  |  |
| Estimate (std.error) | -0.09 (0.17) | -0.02 (0.02) | -69.16 (69.62) | 0.70 (1.33) | 0.90 (1.30) | -1.60 (0.98) |
| t | -0.54 | -0.84 | -0.99 | 0.53 | 0.69 | -1.62 |
| p | 0.59 | 0.41 | 0.33 | 0.60 | 0.50 | 0.11 |
| **Previous land-use: forest** |  |  |  |  |  |  |
| Estimate (std.error) | -0.26 (0.11) | -0.04 (0.01) | -259.98 (55.48) | 0.02 (0.87) | 1.17 (0.84) | -0.93 (0.64) |
| t | -2.30 | 13.91 | -4.69 | 0.02 | 1.38 | -1.45 |
| p | **0.03*** | **0.005**** | **<0.001*** ** | 0.98 | 0.18 | 0.15 |
| **$R^2$ (adjusted)** | 0.050 | 0.14 | 0.491 | -0.094 | 0.03 | 0.093 |

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# CHAPTER 3

# Non-native ant species do not reduce functional diversity or ecosystem functioning on oil palm smallholdings

A view down the microscope, *Oecophylla smaragdina*

## 3.1 ABSTRACT

1. Conversion of natural habitats to agriculture generally reduces species diversity and alters community composition, with more non-native species. Non-native species can have highly detrimental ecological impacts, and we focus on highly-diverse tropical landscapes dominated by oil palm to examine the impacts of non-native ant species on functional diversity and ecosystem processes.

2. We surveyed ground-dwelling ants on 41 smallholder oil palm farms and at 15 sites in adjacent old-growth protected forest in Sabah, Malaysian Borneo (one 0.28 ha plot per farm/site). Focusing on smallholdings, we examine how the occurrence of non-native ants predicts ant species richness, functional diversity (morphological measures of functional richness, FRich, and dispersion, FDisp), and ecosystem functions (leaf litter decomposition and resource scavenging rates) on farms.

3. Smallholder farms support about two thirds (70%; rarefied species richness = 112) that of old-growth forest (total species richness = 161), with few species in common (7% of species occur in both habitat types), and a much higher proportion of non-native species (17% per farm compared to 5% forest site).

4. The proportion of non-native species on farms increased with increasing native richness, resulting in considerable variation in total ant species richness among farms (5-30 species per farm). Non-native species exhibited morphological traits associated with dietary generalism and local resource exploitation (shorter legs, smaller mandibles, narrower heads), occupying a subset of the functional trait space of native species. However, we found no effect of non-native ants on functional diversity (FRich and FDisp), or on rates of leaf litter decomposition or resource scavenging on farms.

5. Our study shows that oil palm smallholdings are highly susceptible to invasion by non-native species, but we found no evidence for any detrimental impacts on either native ant species or ecosystem functioning. Native ant species that persist in these heavily-modified agricultural habitats may be more resilient to competition, which may explain why we find no detrimental impacts of non-native species in our study. Future studies investigating abiotic and biotic factors and the relative importance of environmental filtering versus interspecific competition will be important for determining the resilience of tropical agricultural landscapes to non-native species.

## 3.2 INTRODUCTION

Increasing globalisation and expansion of trade-routes are contributing to the spread of non-native species around the world (Meyerson & Mooney, 2007). As a result, it has cost economies billions of pounds to mitigate the economic and environmental impacts of non-native introductions (Diagne et al., 2021; Manchester & Bullock, 2000). A growing number of studies report the detrimental consequences of non-native species through outcompeting native species (Rowles & O'Dowd, 2007), predation (Sin et al., 2008), hybridisation (Biedrzycka et al., 2012), and by altering the environment to an extent that native flora and fauna are no longer well-adapted to it (Asner et al., 2008; Sin et al., 2008). By contrast, some studies, particularly in human-modified landscapes, have highlighted how non-native species contribute to important ecosystem functions and services (Castro-Díez et al., 2019; Cusack & McCleery, 2014; Jain et al., 2021). Thus, the impacts of non-native species are highly context dependent, varying across locations and over time (Castro-Díez et al., 2019; Sapsford et al., 2020), and so it is important to explore the impacts of non-native species in novel human-modified landscapes.

Tropical landscapes are being heavily modified by oil palm (*Elaeis guineensis*), which is a rapidly expanding tropical agricultural crop (Sayer et al., 2012). In Southeast Asia, as well as in South America (Castellanos-Navarrete et al., 2021; Pacheco, 2012) and sub-Saharan Africa (Ordway et al., 2019), oil palm is replacing naturally occurring habitats, particularly rainforest biomes (Quezada et al., 2019), creating a novel human-modified habitat within these tropical landscapes. Oil palm plantations support ~20% fewer species than tropical forests (Clough et al., 2016) and more non-native species (Fayle et al., 2010). Despite this, research assessing the impacts of non-native species in oil palm landscapes is limited (e.g., Fayle et al., 2013; Waddell et al., 2020), and no studies to date have assessed how the presence of non-native species affects ecosystem functions in oil palm habitats. Only a small proportion of non-native species end up causing significant negative economic or environmental impact (i.e., ~5-20% become invasive, but this can vary widely across taxa; (Jeschke, 2014), and it can be difficult to predict whether species will become invasive as impacts can be highly context-dependent (Griffen et al., 2021; Paterson et al., 2015). Hence, understanding the ecological impacts of non-native species on oil palm farms will help to further our understand of the factors contributing to biodiversity loss within oil palm landscapes, which can be used to inform the development of more environmentally sustainable oil palm production. Smallholder oil palm farms contribute ~40% of oil palm production and are often located close to built-up areas and roads (Zhao et al., 2022), which may make them particularly susceptible to invasion by non-native species. Given the importance of smallholdings to local livelihoods (Rist et al., 2010), it is important to assess the occurrence and ecological impacts of non-native species on smallholdings.

Functional diversity metrics (i.e., functional richness, dispersion and redundancy) are particularly useful for examining the impacts of non-native species because they examine how changes in functional community structure relate to the provisioning of ecosystem functions and hence the resilience of ecosystems to environmental changes (Mammola et al., 2021; Oliver et al., 2015; Petchey & Gaston, 2006). Functional diversity metrics involve the measurement of species functional traits, which are morphological, physiological or phenological characteristics that relate to the functional role that a species plays within a community (Petchey & Gaston, 2006).

Species' functional traits are affected by two key abiotic and biotic drivers (Boet et al., 2020). Environmental filtering reflects the responses of organisms to environmental conditions (e.g. variation in body size related to thermal tolerance of species; Peralta-Maraver & Rezende, 2021) and interspecific competition can lead to fewer species sharing similar traits (Wong et al., 2022), affecting the distribution of functional traits within a community, and resulting in lower functional redundancy. These two drivers can affect the relationship between species richness and functional diversity (Barabás et al., 2022). However, it is unclear how the conversion of forest to oil palm and associated increases in non-native species might affect environmental filtering and/or inter-specific competition, and the consequences for functional diversity of communities within these human-modified landscapes.

Ants are one of the most successful invaders of novel habitats (Bertelsmeier, 2021; Holway et al., 2002), such as oil palm, where more non-native ant species have been recorded compared to forested areas (Fayle et al., 2010), which might be expected to affect ecosystem functioning in these agricultural areas. Non-native ant species generally share a large number of traits, such as small body size and dietary generalism, and are often more aggressive (e.g. ,Drescher et al., 2011; McGlynn, 1999), which may result in increased competition with native species and cause species to diverge in trait space, resulting in higher functional dispersion at invaded sites. Changes to functional traits within ant assemblages would be expected to translate into differences in rates of ecosystem functions, for example, shorter legs and smaller body size would affect movement and speed of resource discovery and scavenging rates (Gibb & Parr, 2010). Ant mandible size reflects diet and trophic position (i.e., omnivore, herbivore, carnivore, generalist or specialist; (Parr et al., 2017), related to predation and decomposition functions (top-down effects, Nooten et al., 2022). Thus, non-native species are expected to affect the functional diversity of local communities and the provisioning of ecosystem functions.

In this study, we examine the occurrence of non-native ground-dwelling ants on smallholder oil palm farms, and assess how non-native species affect functional diversity and the provisioning of two important ecosystem processes provided by ants: scavenging and leaf-litter decomposition. We measure seven ant morphological variables to compute six functional shape variables, which we then use to calculate two widely used functional diversity metrics (functional richness FRich and dispersion FDisp), and we test the following hypotheses: (1) farms have more non-native species than rainforest sites, and overall species richness on farms decreases as the proportion of non-native species increases, (2) non-native species differ in functional trait composition compared to native species, (3) farm-scale functional richness decreases and functional dispersion increases as the proportion of non-native species increases, resulting in reduced scavenging and decomposition rates.

## 3.3 MATERIALS AND METHODS

### 3.3.1 Study sites

We surveyed ground-dwelling ants on 41 smallholder oil palm farms (defined as farms < 50 ha; 1 site per farm; Fig.1a) across six governance areas in Sabah, Malaysian Borneo, between August to October 2019. Farms had been established between 8-27 years ago, ranged in size from 0.81 to 7.73 ha, and had either been established after conversion from selectively logged forest or from previous agricultural systems other than palm oil (such as rice, vegetable or fruit crops). The smallholder farms are located within a heterogeneous landscape of mixed land-use types (e.g., other farms, housing, remnant forests), which is typical of smallholder landscapes in Sabah. We also sampled 15 sites in undisturbed protected rainforest within the Danum Valley Conservation Area (Fig. 1; total = 56 study farms/sites). Farm plots and rainforest sites were at least 150 metres apart from each other to reduce the effects of spatial replication.

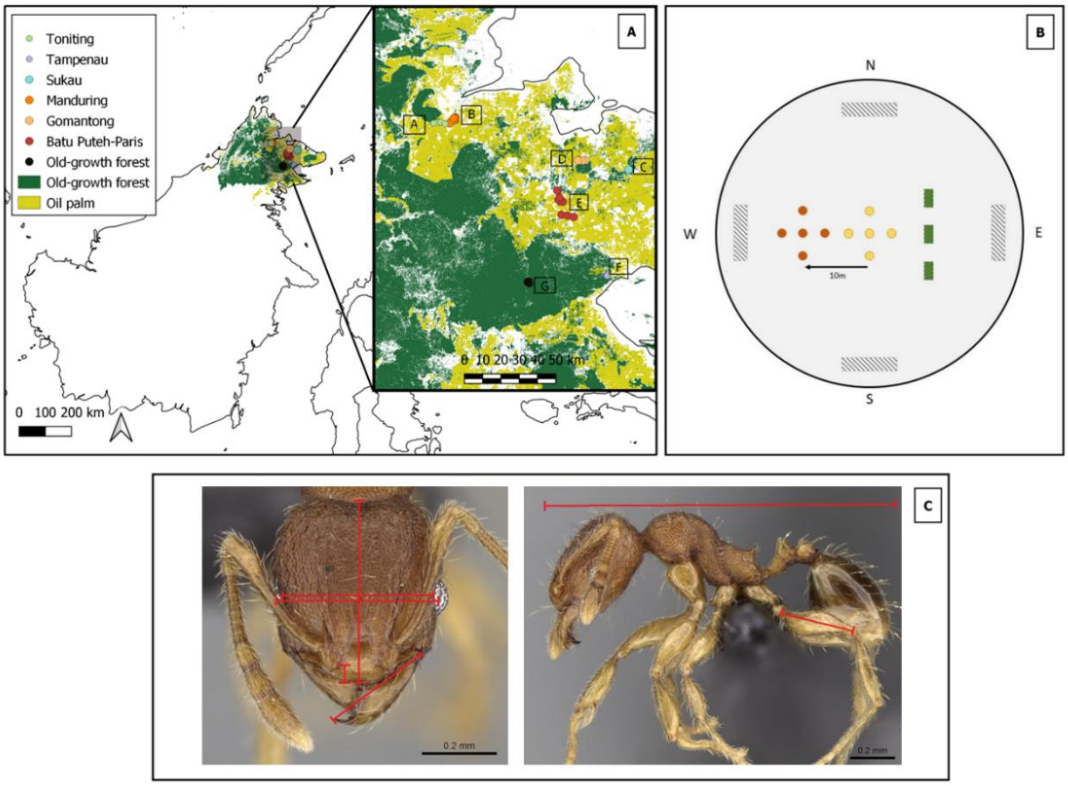

**Figure 1**. **A:** Map of smallholder oil palm farms (n = 40) located across six governance areas in Sabah, Malaysian Borneo: site A (Ulu Sapi; n = 6 farms), site B (Reka Halus; n = 12 farms), site C (Gomantong; n = 4 farms), site D (Sukau; n = 2 farms), site E(Paris-Batu Puteh; n = 11 farms), and site F (Tampenau; n = 5 farms). The landcover category 'forest' maps above ground carbon density (ACD) greater than 40 Mg C ha$^{-1}$ at 30m spatial grid resolution (sourced from (Asner, Broderick, and Heckler 2021), and the category 'oil palm' shows the extent of plantations and smallholder farms at 10m resolution (using Sentinel-1 and Sentinel-2 data; sourced from (Descals et al. 2020). **B:** Sampling design on each farm, comprised one 30m radius (0.28 ha) plot per farm. Ground-dwelling ants were sampled using unbaited pitfall traps (yellow circles) over a period of six days; we placed five traps at the centre of the sites over three days, and then traps were moved and placed 10m from the initial traps and left for a further three days (red circles). Three leaf-litter bags were left at the centre of the plot over six weeks (green box). Bait experiments were performed at 25m from the centre of the plot (hashed rectangle). **C:** Diagrams showing the seven morphological characteristics measured from ant specimens: head length, head width, clypeus length, interocular distance, mandible length, hind femur length and body size. Figure of *Pheidole parva* obtained from Antwiki (Estella Ortega / © AntWeb.org / CC-BY-SA-3.0)

### 3.3.2 Sampling ground-dwelling ants and occurrence of non-native species

At each of the 56 farms/sites, we sampled ground-dwelling ants within a 0.28 ha circular plot (i.e., 30 m radius), which on farms were placed at least 50m from the farm boundary to reduce potential edge effects. Pitfall trapping method was preferred over Winkler extraction for sampling diurnal and nocturnal ground-foraging ants due to low leaf litter availability on farms. We deployed samples over a six-day period, which has been recognised as an optimal sampling period for larger catch rates with pitfall trapping (Sheikh et al., 2018). We placed five unbaited pitfall traps (50ml falcon tubes, 30cm diameter) at the centre of each plot and left for three days: four traps placed 10m to the N, S, E and W of the plot centre and a fifth central trap (Fig. 1.b). To obtain greater spatial coverage and to prevent decomposition and loss of specimens, we replaced these traps with five new pitfalls, placed 5m away from the original traps and left for a further three days (following Lucey & Hill, 2012) as the foraging range of most ground-dwelling ant species is < 3 m (Brühl et al., 2003; Kaspari, 1993). Pitfalls contained 70% ethanol and were lined with fluon (BioQuip) to reduce the surface traction of the pitfall walls, and covered with a rain cover (figure S1). Ant specimens were preserved in 70% ethanol and non-reproductive individuals were identified to species where possible, or morphospecies using the key produced by Fayle et al. (2014) and online resources (AntWeb, 2022; Antwiki, 2022). We classified ant species as native or non-native using information from online databases (www.antwiki.org and www.antmaps.org), following the definition of non-native species by Pfeiffer et al. (2008): “transferred, introduced, alien or exotic individuals collected in habitats not native to the species". For morphospecies, we assigned a native or non-native status according to the geographic distribution of the species for that genus. For example, Borneo has the highest number of native species of *Strumigenys*, so we assigned a native status for morphospecies of this genus as we assumed that this was a more likely outcome. Conversely, there are no known native species of *Solenopsis* in Borneo, so we assigned a non-native status for *Solenopsis* morphospecies.

### 3.3.3 Measuring ant functional traits

We measured seven morphological characteristics from up to 10 individuals per species to the nearest 0.01 mm using an ocular micrometre attached to a stereo microscope: head length (a proxy for overall size), head width, interocular distance, mandible length, clypeus length, hind femur length and body size (following Bishop et al., 2015; figure 1 d-e). These measurements were used to calculate six functional shape traits: body size, head elongation, relative mandible length, relative clypeus length, relative leg length, and eye position selected because of their relevance to the diet and foraging strategy of ants, and these traits are highlighted as priority measurements in ant trait-based studies (see Table 1 for descriptions; Parr et al., 2017). Following recommendations by (Parr et al., 2017), six non-reproductive individuals of each monomorphic species and ten individuals for polymorphic species were measured where possible, resulting in an average of 2.86 individuals measured per species.

**Table 1 –** Six functional shape traits were computed, based on seven morphological characteristics, with information on their functional relevance, and hypothesised links to native and non-native species, and ecosystem functioning (scavenging and decomposition processes).

| **Functional shape trait** | **Calculation** | **Hypothesised link to native and non-native species and ecosystem functioning** | **Reference** |
|---|---|---|---|
| Body size | Length from the tip of mandibles to the tip of gaster, with the ant in an extended position | Thermal tolerance can affect foraging activities (e.g., foraging speed). Non-native species tend to have a smaller body size, and so farms with a higher proportion of non-native species may affect scavenging rates due to differences in thermal tolerance of the ant community. | (Boyle et al., 2021; Holway & Cameron, 2021) |
| Head elongation | Head length divided by head width across eyes | Invasive and non-native species tend to have a more generalist and omnivorous diet, which typically corresponds to ants with a longer head shape. Thus, the proportion of non-native species on farms may influence carbohydrate and protein scavenging rates. | (Holway et al., 2002; Parr et al., 2017) |
| Relative Mandible Length | Mandible length divided by head length | Longer mandibles correspond to a more predacious/specialist diet, whereas shorter mandibles correspond to a more herbivorous/generalist diet. Invasive and non-native species tend to be dietary generalists, which may influence scavenging and decomposition processes through trophic interactions with the decomposer community. | (Holway et al., 2002; Parr et al., 2017) |
| Relative Clypeus length | Clypeus length divided by head length | Clypeus is related to liquid-feeding ability. Dominance of invasive and non-native ants with such traits may occur with access to carbohydrate-rich resources, typically from the tending of honeydew-producing hemiptera, which may | (Davidson et al., 2004; Grover et al., 2007; Holway & Cameron, 2021) |

| | | | |
|---|---|---|---|
| | | negatively impact native ant species occurrences (e.g., via spatial dominance). | |
| Relative leg length | Hind femur length divided by head length | Leg length is related to foraging speed, which varies with habitat complexity. Larger ants with longer legs are faster at resource discovery in lower complexity habitats (e.g., oil palm farms), whereas ants with shorter femurs are slower but will typically monopolise resources. Invasive and non-native ants tend to be resource monopolisers, which may influence scavenging processes and native occurrence (e.g., via competitive exclusion at food resources). | (Gibbs and Parr 2013) |
| Eye position | Interocular width divided by head width; Species without eyes are assigned a value of zero | Distance and positioning of eyes reflects foraging strategy, with eyes positioned towards the sides of the head typically corresponding to slower resource discovery and movement in less complex habitats (e.g., oil palm farms). Speed of resource discovery and movement could influence scavenging processes. | (Gibbs and Parr 2013) |

### 3.3.3 Quantifying functional diversity on farms

We used morphological information from six functional shape trait variables (Table 1) to assess functional diversity (FD) of ant assemblages on smallholdings (Villéger et al., 2008), quantifying functional richness (FRich; the size of the functional trait space), and functional dispersion (FDisp; the dispersion of species within the trait space, following Mammola & Cardoso (2020). We constructed two-dimensional hypervolumes for each smallholder farm by scaling and centering the six functional shape traits, and then applying principal component analysis (PCA) to transform the functional shape trait matrix to a spatial representation of the functional distance between ant species. The first principal component from the PCA (PC1) accounted for 33.4% of the total variance, and was positively associated with relative clypeus length, relative leg length and body size (Table 2). The second principal component (PC2) accounted for a further 26% of the total variance, and was positively associated with mandible length and negatively associated with head elongation and distance between the eyes. We used values for PC1 and PC2 (explaining 59.1% of the total variation) and species occurrence data to construct hypervolumes for each farm using the *kernel.build* function of the *'BAT'* package (Cardoso et al., 2022). We then calculated the FRich and Disp from each farm hypervolume with the *kernel.alpha* and *kernel.dispersion* functions. To avoid redundancy and issues with high dimensionality from using too many variables in the construction of the hypervolume, we checked whether morphological trait variables were highly correlated prior to applying PCA to the trait matrix (Pearson's $r > 0.8$; see SI2).

| | PC1 | PC2 | PC3 | PC4 | PC5 | PC6 |
|---|---|---|---|---|---|---|
| **Eigenvalue** | 1.41 | 1.25 | 1.04 | 0.77 | 0.69 | 0.53 |
| **Functional shape trait** | | | | | | |
| Head elongation | 0.05 | -0.66 | 0.26 | -0.17 | -0.62 | 0.25 |
| Relative mandible | 0.01 | 0.51 | 0.68 | -0.03 | -0.04 | 0.51 |
| Relative clypeus | 0.57 | -0.22 | -0.26 | -0.06 | 0.44 | 0.59 |
| Relative leg length | 0.56 | 0.09 | 0.26 | -0.61 | 0.03 | -0.49 |
| Relative ocular distance | -0.27 | -0.48 | 0.52 | 0.06 | 0.62 | -0.15 |
| Body size | 0.53 | -0.03 | 0.23 | 0.76 | -0.12 | -0.24 |

**Table 2** – Eigenvalues of the principal components and weighting factor of the six functional shape traits. A positive value indicates a positive correlation of the functional shape trait with the principal component, whilst a negative value indicates a negative correlation. PC1 and PC2 scores were used in analyses, as measures of foraging strategy and diet.

### 3.3.4 Measuring ecosystem processes: leaf litter decomposition and scavenging

Within the survey plots on a sub-set of farms (n = 26 farms), we assessed the effects of non-native species on resource scavenging functions, using fish (tuna tinned in freshwater) and seed (sunflower seeds) baits as proxy measures for carnivorous and generalist scavenging activities, respectively (Griffiths et al., 2018). To conduct scavenging assays, we placed fish and seed baits on bait cards for 24 hours within metal cages (20cm x 20cm) with a mesh size (3 x 3cm) large enough to allow access to most invertebrate species, but excluding larger vertebrates (Figure 1c). Fish and seed baits were oven-dried before and after the scavenging assays (40$^{o}$C for 48 hours or until a stable dry mass was reached) to calculate the dry-mass loss of baits. At each of the 26 farms, we carried out two replicates for each bait type, repeated over two days, resulting in a total of eight bait cards per farm (2 bait types x 2 replicates x 2 days).

We also assessed the effects of non-native ants on leaf litter decomposition rates, using standardised litterbags of 1mm mesh size, with five 1cm holes punched into each bag to allow access to ants and other small invertebrates. At each of the 26 farms, three litterbags were pinned to the ground with pegs and left in place for six weeks (Figure 1D). Litterbag contents were standardised across sites by collecting leaves from oil palm fronds from the Beluran region, and from three Dipterocarpaceae tree species with varying light characteristics, from within the Danum Valley Conservation Area: *Dryobalanops lanceolata* (intermediate), *Hopea nervosa* (shade tolerant) and *Parashorea malaanonan* (light demanding; following protocols by Yeong et al. 2016, Bradford et al. 2002). Each bag contained one leaf of each of the four species, except for *H. nervosa* and *E. guineensis* which used two leaves and two frond leaflets respectively to standardise leaf surface area. Leaves were dried at 40°C over ten days before and after treatment to calculate the dry-mass loss of leaf-litter.

### 3.3.5 Data analysis

We refer to species occurrence as an individual of a species being present in at least one pitfall trap within the plot or site. All analyses were performed in R v.4.1.1. (R Core Team, 2021).

We assessed whether smallholder farms support fewer species than old-growth rainforest, and the total estimated species richness in each habitat type, by pooling all species occurrences into one of two habitat types: farm or forest. To account for differences in sampling effort between habitats, we computed the rarefied species richness of oil palm habitats to match the sampling effort of forest sites (Colwell et al. 2004; n = 41 smallholder sites, n = 15 forest sites). We also computed the proportion of non-native species in each habitat, using raw data for species richness.

We first assessed whether non-native species negatively affect ant species on farms by fitting two Generalised Additive Mixed Effects Model (GAMM). To test whether non-native species reduce native species richness, we fitted a GAMM with the proportion of non-native species as an explanatory variable and total species richness as a response variable. To test whether non-natives negatively impact overall species richness, we fitted a second GAMM with non-native species richness as an explanatory variable and native species richness as a response variable. Both models included the total number of trapping days at a site as an explanatory variable to control for potential differences in species richness due to differing sampling efforts (a small number of pitfall traps were lost at sites due to e.g., flooding and interference from wildlife). To account for potential spatial effects, we also fitted models including a smooth term with longitude and latitude and employed an exponential correlation structure and included governance area as a random effect. To test assess whether there was spatial autocorrelation in the residuals of the GAMM models, we calculated Moran's I statistic on the models residuals (see SI for model outputs).

To test whether non-native species form a distinct cluster within the trait space, we applied Partitioning Around Mediums (PAM) clustering analysis on the first two principal components derived from the PCA of morphological functional shape traits (Table 2). We first determined the optimal number of clusters across twenty-six methods (e.g., elbow and silhouette) using the *NbClust* package, with an equal number of methods recommending between two to five clusters (see SI4). We then performed PAM clustering analysis using the *cluster* package with the *k* parameter set to 2, 3, 4 and 5. Alongside the PAM, we also performed a t-test to assess whether PC1 and PC2 values differed significantly between native and non-native species groups.

We fitted two more GAMMs to assess whether non-native species affect functional diversity on farms (measures of FRich and FDisp), using the same modelling framework of the previous GAMMs. The first model included the proportion of non-native species per farm as the explanatory variable and FRich as a response variable (model 1), and the second model included FDisp as a response variable (model 2).

To assess the effect of non-native species on ecosystem functioning on farms we fitted three GAMMs following the same modelling framework, with the proportion of non-native species as the explanatory variable, and one model with the percentage of fish bait removed as a response variable, a second model with the percentage of seed bait removed as a response variable, and a third model with leaf litter loss as a response variable.

## 3.4 RESULTS

### 3.4.1 Species richness and differences between farm and forest habitats

We recorded a total of 301 ant species during the study. Rarefied species richness of smallholder farms was significantly lower than old-growth forest ($X^2$ = 8.7949, df = 1, $p$ = 0.003), supporting about two thirds (70%) of old-growth forest species richness, and with few shared species between habitats (only 7% of species occurred in both habitats).

However, smallholder farms supported a much larger proportion of non-native species (17%; 24 out of 128 species) compared to rainforest habitats (5%; 8 of 153 species). The five most commonly-occurring species on farms were either non-native species (*Anoplolepis gracilipes* and *Solenopsis molesta*), or native species considered invasive in other biogeographic regions (*Monomorium floricola, Pheidole parva* and *Tapinoma melanocephalum*).

There was considerable variation in ant species richness among our 41 study farms (5 to 30 species per farm), and in the proportion of these species that were non-native (0 to 40%; mean per farm = 21%, sd = 0.08). However, farm species richness was not significantly affected by the proportion of non-native species (GAMM: $F = 0.42$, $p = 0.52$, $R^2 = 0.19$; Figure 2b), and in fact the number of native species increased with increasing number of non-native species (GAMM: $F = 6.73$, $p = 0.02$, $R^2 = 0.36$; Figure 2a). Hence, this implies that non-native species can contribute to overall species richness on farms. There was no significant autocorrelation of spatial pattern of the residual values of the GAMMs, and so data from separate smallholder farms could be considered independent.

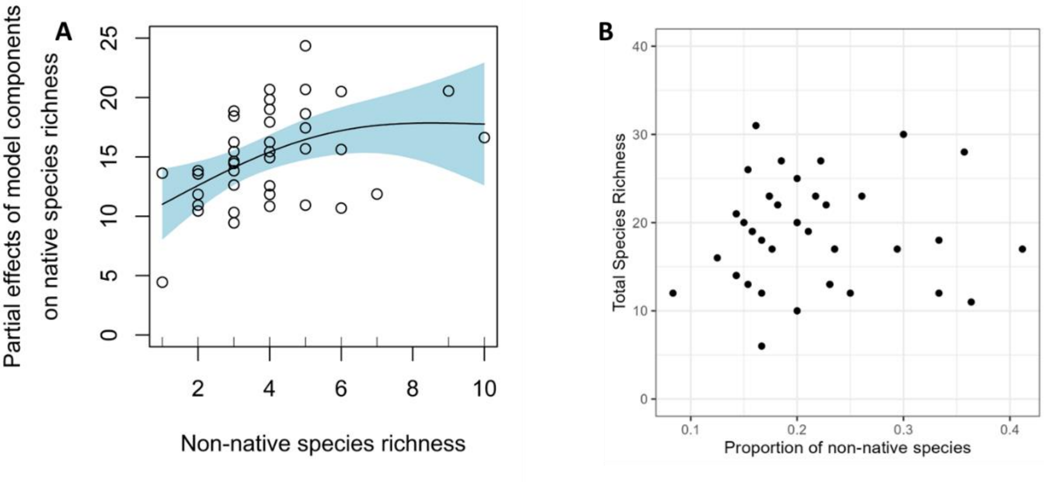

**Figure 2.** (**A**) Partial effect of non-native species richness on native richness (GAMM: $F = 6.73$, $p = 0.02$, $R^2 = 0.36$; Figure 2a), and (**B**) relationship between the proportion of non-native species and total species richness (GAMM: $F = 0.43$, $p = 0.52$, $R^2 = 0.19$).

### 3.4.2 Functional trait differences between native and non-native species

The PCA of ant functional shape traits (Table 2) indicate that non-native species form a cluster within the functional trait space of all farm ant species. Non-native ants generally had a smaller body size, shorter legs, eyes positioned towards the side of the head (lower

PC1 values), and shorter clypeus, shorter mandibles and a narrower head (lower PC2 values). These traits typically correspond to species that are not dietary specialists, are omnivorous or herbivorous, and are competitively dominant at food resources i.e., resource monopolisers (e.g., the non-native *Solenopsis geminata*). Findings from the PAM analysis indicate that most non-native species tend to fall within a particular cluster within the functional trait space (when *k* = 3, 4 and 5), with the cluster corresponding to species with lower PC1 and PC2 values (see SI4). Moreover, non-native species have significantly lower PC1 scores (Wilcox t-test: p < 0.001) and PC2 scores (Wilcox-test results: p = 0.01) compared to native ants on smallholder farms. Together, these findings suggest that non-native ant species form a cluster within the functional trait space of smallholder farms, and overall have significantly different traits from most native ant species. However, non-native ants do not appear to fill a novel niche space within oil palm habitats as there is some overlap between native and non-native species within the functional trait space occupied by ants with more generalist and omnivorous morphological traits.

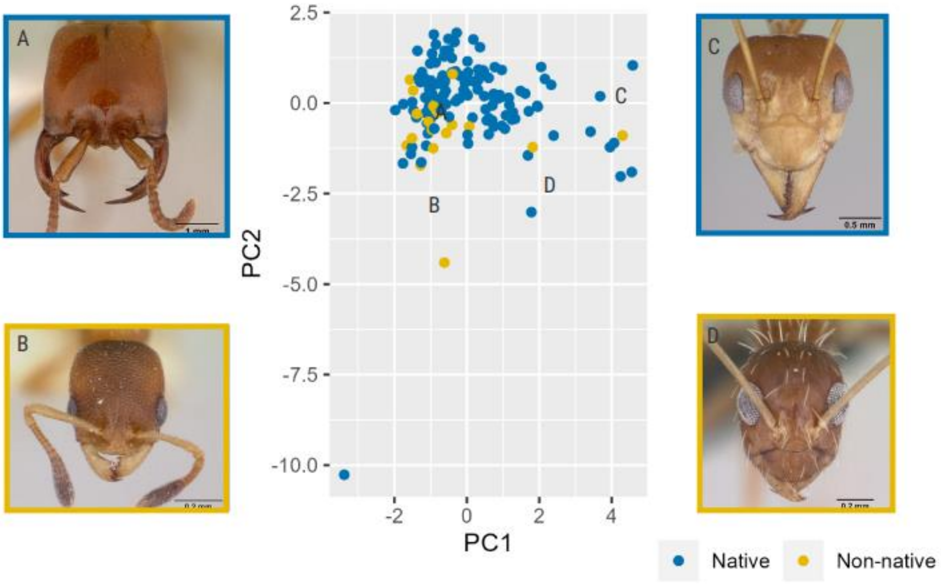

**Figure 3.** The first two principal components derived from the principal component analysis (PCA) of functional trait composition of native and non-native ant species in smallholder oil palm farms, based on six morphological functional shape traits. The first principal component (PC1) accounted for 33.4% of the total variance, which increased with relative clypeus length, relative leg length and body size. The second principal component (PC2) accounted for a further 26% of the total variance, and increased with mandible length but decreased with head elongation and distance between the eyes (Table 2). Non-native species had lower PC1 scores and lower PC2 scores. The outlier point (PC1 = -3.4 and PC2 = -10.3) corresponds to *Strumigenys liophila*, which has particularly short mandibles relative to its head elongation. Example images obtained from Antwiki for native species

*Technomyrmex schimmeri* (A) and *Camponotus variegatus* (C), and non-native species *Cardiocondyla emeryi* (B) and *Solenopsis geminata* (D). Pictures of ants obtained from Antwiki (Estella Ortega / © AntWeb.org / CC-BY-SA-3.0).

### 3.4.3 Non-native impacts on functional diversity (FRich and FDisp) and ecosystem functioning

We found considerable variation in functional richness among the 41 farms (FRich; range 4.6 to 26.3 among farms; mean per farm = 12.8, sd = 4.8), and functional dispersion (FDisp; range 0.90 to 2.30; mean = 1.71, sd = 0.32), but functional diversity was not affected by the proportion of non-native species (FRich GAMM: $F = 0.28$, $p = 0.60$, $R^2 = 0.06$; FDisp GAMM proportion of non-natives: $F = 1.02$, $p = 0.23$, $R^2 = 0.01$; Figure 4a and 4b).

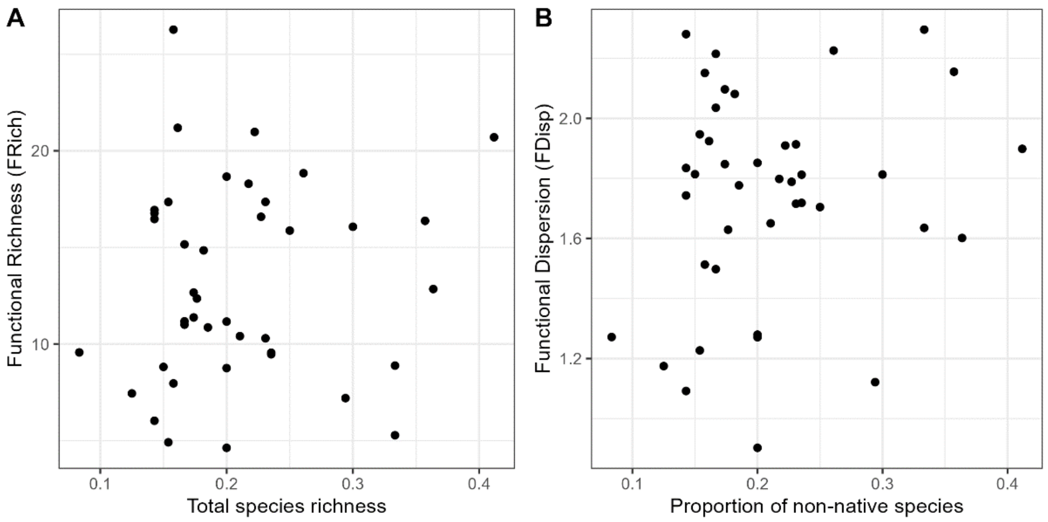

**Figure 4.** Relationship between proportion of non-native species on a farm and (a) functional richness (FRich) and (b) functional dispersion (FDisp) (n = 41).

We also found variation in ecosystem functioning among farms with resource scavenging rates ranging from 3% to 75% of seed baits removed (median = 26% per farm, sd = 20.2, n = 25 farms) and 6% to 100% of fish baits removed across farms (median = 61%, sd = 24), and leaf litter decomposition rates ranged from 53.1% to 96.1% loss of dried leaf weight (median = 74.2, sd = 6.7). However, the proportion of non-native species on farms had no effect on these ecosystem functions (GAMM seed: F = 0.08, p = 0.78, $R^2 = 0.04$; fish: F = 1.10, p = 0.31, $R^2 = 0.01$; decomposition: F = 1.22, p = 0.28, $R^2 < 0.01$). Thus, non-native species impacts on scavenging and leaf litter decomposition are not distinguishable from those of native species.

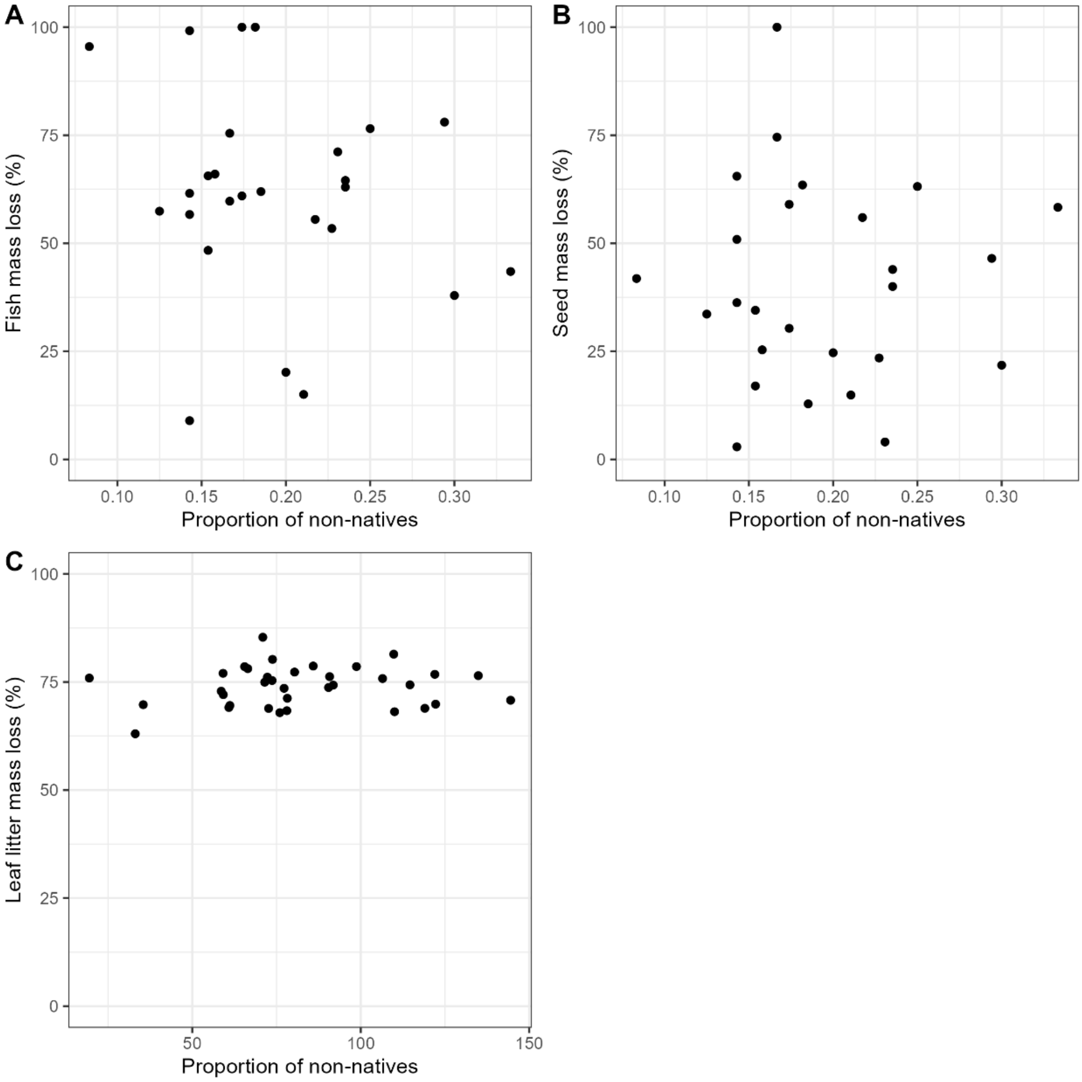

**Figure 4.** Relationship between proportion of non-natives and ecosystem function rates measured as percentage of bait mass removed over 24 hours for (**A**) fish scavenging and (**B**) seed scavenging rates, and over six weeks for (**C**) leaf-litter decomposition.

## 3.5 DISCUSSION

Our study shows for the first time that non-native ant species do not reduce functional diversity or ecosystem functioning within oil palm habitats. Compared with forest, oil palm smallholder farms supported fewer ant species overall, with very few species in common, but having a higher proportion of non-native species. Despite non-native species sharing similar functional traits associated with dietary generalism and local resource monopolisation (shorter legs, smaller mandibles, narrower heads), they did not provide a new functional role within oil palm ant communities as they still occupied a subset of the functional trait space as native species. Overall, we found that non-native ant species did not reduce native species richness, functional diversity or ecosystem functioning on smallholder oil palm farms. This suggests that non-native species do not place strong competitive pressures on the native community (Fayle et al., 2013), and that non-native species may be co-opting native roles thereby maintaining ecosystem functioning. This contrasts with other studies on non-native ant species which often show detrimental impacts for native ant species in forested habitats within Borneo (Drescher et al., 2011; Lessard et al., 2009) and other tropical regions (Rajesh et al., 2022; Walker, 2006). The lack of impacts of non-native species in our study may be because native ant species that persist in these modified habitats are resilient to exclusion by non-natives, meaning other biotic and abiotic factors (e.g. environmental filtering) could be greater drivers of biodiversity and functioning on oil palm farms (Gámez-Virués et al., 2015).

### ***Positive association between non-native and native ant species richness on farms***

Contrary to our expectations, we observed a positive relationship between non-native and native species occurrence, and no relationship between the proportion of non-native species on farms and total species richness. Our findings differ markedly from other studies on non-native ants showing negative associations between non-native and native ant species occurrence in tropical forests (e.g., Drescher et al., 2011; Rajesh et al., 2022; Walker, 2006) and other natural habitats (Holway, 1999), likely due to the competitive exclusion of native species at resource sites due to the aggression and numerical dominance of non-native ants (e.g., *Linepithema humile*; Holway, 1999) Our findings may differ from these studies for several reasons. Firstly, most studies (e.g., Achury et al., 2021; Human & Gordon, 1996; Porter & Savignano, 1990; Wong et al., 2020) have focused on impacts of particularly aggressive invasive species (e.g., *Solenopsis invicta* and *Linepithema humile;* Bertelsmeier et al., 2015), which we did not detect at our farm sites (with the exception of *Anoplolepis gracilipes)*. Secondly, oil palm farms are heavily modified habitats, with a distinct ant community, comprised of fewer forest-dependent species, and a more disturbed, warmer environment compared to lesser modified habitats (Boyle et al., 2021; Fayle et al., 2010; Luke et al., 2014). Abiotic and biotic conditions (e.g., resource availability, habitat structure and temperature) associated with more disturbed habitats can affect the underlying mechanisms governing ant species co-occurrence (Gray et al., 2018) by influencing the degree of niche overlap and competition between non-native and resident species (Grover et al., 2007; Thomas & Holway, 2005; Wittman et al., 2018), potentially influencing the interactions between ant species in oil palm habitats. Moreover, resident native communities in oil palm habitats could be more resistant to competitive exclusion by non-native species (Cordonnier et al., 2020; Devenish et al., 2021) if the competitive abilities of non-native and native species are more equal (Wong et al., 2022). This might be the case in our study as we observed an overlap between native and non-native species in the functional trait space occupied by generalist, omnivorous and resource monopolising ant species (i.e., shorter relative leg and mandible length). Generalist and resource monopolising native species (e.g., *Tapinoma melanocephalum*, a highly abundant and widely spread species) that share the same area of the trait space as non-natives may be competing for similar food resources and have similar competitive abilities in these novel habitats created by oil palm farms, consequently preventing the dominance of non-native species on farms. Our results are important if they imply that in certain highly modified habitats, such as oil palm, non-native species can contribute to species richness rather than suppressing it.

### ***Non-native species traits are a subset of native species functional trait space***

Non-natives species have evolved functional traits as a response to the environmental conditions of their biogeographic origins, which likely differ from those in the introduced habitat. Hence, we expected functional traits of non-native ants to differ from native species. Our findings confirm that non-native ants differ in their morphological traits related to diet and foraging from most native ant species occurring on oil palm farms, forming a distinct cluster within the functional trait space occupied by  native species. Consistent with previous findings (Holway et al., 2002), we observed that non-native species tended to have shorter legs, smaller bodies, elongated heads, and shorter mandibles, which are consistent with dietary generalism and local resource monopolisation (da Silva Camargo et al., 2015; Klunk et al., 2021; Parr et al., 2017). Non-natives also tended to have a shorter clypeus (i.e., not specialised for liquid feeding), which is unexpected as the ability to harvest hemipteran honeydew has been attributed to the invasive success of some non-native species (e.g., super-colonies of *Anoplolepis gracilipes*, Wittman et al., 2018).

The tendency for these types of non-native traits to be present could be explained by a two-stage trait filtering process acting on non-native species: firstly, selection for traits that facilitate survival during dispersal from their biogeographic range (e.g., central Africa and

South America), and secondly, traits that enable survival in oil palm habitats (e.g., smaller bodies in hotter climates). Alternatively, non-native species may have morphological traits that differ from other native species on farms because of limiting trait-similarity, (Macarthur & Levins, 1967), whereby non-native species establish more successfully in novel habitats that have native species with more dissimilar traits (i.e., non-natives fill an empty niche space; Wong et al., 2022). However, our results show that non-native ants do not occupy a novel niche space on oil palm farms because we found that some native species share morphological traits with non-natives, resulting in a portion of overlap within the functional trait space. Moreover, native species with similar traits may be preventing ecological release of non-natives via interspecific competition, preventing them from becoming overly dominant in oil palm farms (Divíšek et al., 2018). Our results suggest that there could be some competition between native and non-native species in this overlapping area of the functional trait space, and so a loss of native species could allow for more non-native species to establish on farms. Alternatively, if environmental filtering during dispersal limits the type of non-native traits on smallholder farms, any further loss of native species could result in the loss of some functional groups not occupied by non-native species. Further research is required to discern which is the driving mechanism, as this could have differing implications for the provisioning and resilience of ecosystem functions on oil palm farms.

### ***No effect of non-native species on functional richness and dispersion or ecosystem functioning***

Our results suggest that non-native species are not displacing native ground-dwelling ants, as functional dispersion (FDisp) did not increase with the proportion of non-native species on farms. We also find that non-native species are not resulting in the homogenisation of functional traits or reducing the size of the functional trait space, as we did not observe a decrease in functional richness (FRich) with the increase in proportion of non-native species on farms. These findings deviate from our expectations that the territorial dominance (Cerdá et al., 2013) of non-natives would result in greater interspecific competition and exclusion of native species, resulting in lower functional richness, higher functional dispersion, and therefore lower functional redundancy on farms. Our results imply that non-native ants may co-exist with the native community in these highly-modified agricultural landscapes, contributing to local species richness. These findings are similar to those of Fayle et al. (2013), that non-native species may facilitate ant species co-existence by reducing the degree of community segregation and negative species co-occurrence in oil palm plantations.

Non-native ants appear to maintain scavenging and decomposition functions on farms, as we observed no effect of the proportion of non-native species on bait removal or leaf litter decomposition rates. Thus, we reject our hypothesis that scavenging and decomposition functions would be affected by the proportion of non-native species due to an effect of non-native species in altering farm-scale functional richness and dispersion. However, we observed no effect of non-native species on functional richness or dispersion, nor on total species richness, so it is not surprising that we also found no effect of non-natives on ecosystem functioning. It is possible that some native and non-native species share similar functional traits related to diet and foraging (e.g., head elongation, mandible size and leg length), meaning that non-natives are likely performing similar scavenging functional roles to native species on farms (Angulo et al., 2011). Similarly, decomposition functions may not be disrupted by non-native species if they fill similar trophic positions (e.g., generalist scavenger) as other native species, and hence do not alter the decomposer fauna (e.g., via predation; Milligan et al., 2016). Differences in ecosystem functioning across farms may instead be driven by other local factors, such as habitat complexity or temperature, affecting ant foraging activities and speed of bait discovery (Boyle et al., 2021; Gibb & Parr, 2010; Thomas & Holway, 2005). For example, scavenging rates in oil palm habitats are strongly influenced by the amount of bait that an individual ant carries rather than species richness or abundance (Gray et al., 2015). Another possibility is that differences in scavenging rates could reflect a shift in dietary requirements to satisfy the nutritional demands of ant colonies at the time of sampling, resulting in more scavenging from baits with the required nutrients (Abbott, 2005; Cornelius & Grace, 1997; Stein et al., 1990). Further research is required to assess whether our findings extend to other ecosystem functions (Devenish et al., 2019) on farms (e.g., predation), and to discern whether environmental conditions or other ant-related factors, such as dominance of generalist scavengers, are the main factors explaining variations in ecosystem functioning on oil palm smallholdings.

## 3.6 CONCLUSIONS

Oil palm habitats are highly susceptible to invasion by non-native species, but our study shows that non-native ants have no detrimental impacts on ground-dwelling ant communities, and that functional diversity and ecosystem functioning are maintained in these highly-modified habitats. Our findings have implications for invasive species management as they suggest that resident native ant communities and environmental conditions on oil palm farms may prevent the dominance and negative impacts of non-native species on native communities. Thus, our findings improve our understanding of which factors may contribute to the invasion success of non-native ants in introduced habitats and highlight the importance of considering the context-dependence of non-native impacts. We recommend that invasive management efforts to be prioritised on minimising the spread of non-native species within forested areas, where negative impacts on local communities have been observed, and to understand whether oil palm habitats harbouring non-native species become hotspots for their spread to forested areas. Finally, we recommend future research to focus on assessing why certain farms support greater species and functional diversity, which factors contribute to higher native and non-native species richness, and the impacts this has on smallholder agricultural productivity.

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# CHAPTER 3 APPENDIX

# Non-native ant species do not reduce functional diversity or ecosystem functioning on oil palm smallholdings

## Section S1: Sampling ground-dwelling ants in oil palm and forest habitats

**Figure S1.** Sampling method used to survey ground-dwelling ants in oil palm farms and tropical forest habitats. Unbaited pitfall traps (50ml falcon tubes, 30cm diameter) were filled with 70% ethanol, lined with fluon (BioQuip), and covered with a plastic rain cover.

## Section S2: Functional shape traits of ground-dwelling ants

| | Head elongation | Mandible length | Clypeus length | Leg length | Interocular distance | Body size |
|---|---|---|---|---|---|---|
| Head elongation | - | | | | | |
| Mandible length | -0.42 | - | | | | |
| Clypeus length | 0.19 | -0.27 | - | | | |
| Leg length | -0.11 | 0.46 | 0.27 | - | | |
| Interocular distance | 0.00 | -0.01 | 0.05 | 0.04 | - | |
| Body size | 0.09 | 0.09 | 0.37 | 0.33 | 0.04 | - |

**Table S1.** Correlation of functional traits of ground-dwelling ants on smallholder oil palm farms. All variables were weakly correlated (Pearson's $r > 0.8$), and so all functional traits were used in the functional diversity analyses.

**Table S2.** Ground-dwelling ant species occurrence within smallholder oil palm farms (n = 40) in Sabah, Malaysian Borneo. Summary of six functional shape traits for each species occurring in oil palm farms (measured in mm). Head elongation, mandible length, clypeus length, and femur length measurements are relative to body size. Species are classified as native or non-native to Borneo, and whether they were found to only occur in oil palm habitats or within both oil palm farms and within protected forest habitat (Danum Valley Forest Reserve).

| Subfamily | Genus | Species | Morphospecies | Head elongation | Mandible length | Clypeus length | Femur length | Interocular distance | Body size | Native status | Habitat occurrence |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Amblyoponinae | *Prionopelta* | *kraepelini* | | 1.39 | 0.43 | 0.13 | 0.54 | 0.94 | 1.96 | native | oil palm |
| Dolychoderinae | *Bothriomyrmex* | | sp1 | 1.07 | 0.46 | 0.15 | 0.75 | 0.76 | 2.14 | non-native | oil palm |
| Dolychoderinae | *Bothriomyrmex* | | sp2 | 1.21 | 0.43 | 0.17 | 0.77 | 0.76 | 1.44 | non-native | oil palm |
| Dolychoderinae | *Iridomyrmex* | *anceps* | | 1.06 | 0.46 | 0.21 | 1.40 | 0.57 | 3.4 | native | oil palm |
| Dolychoderinae | *Ochetellus* | *glaber* | | 1.13 | 0.43 | 0.19 | 1.14 | 0.65 | 5.1 | native | oil palm |
| Dolychoderinae | *Philidris* | *cordata* | | 1.07 | 0.52 | 0.17 | 1.01 | 0.58 | 2.4 | native | oil palm |
| Dolychoderinae | *Tapinoma* | *indicum* | | 1.25 | 0.47 | 0.14 | 0.95 | 0.63 | 1.42 | native | oil palm |
| Dolychoderinae | *Tapinoma* | *melanocephalum* | | 1.10 | 0.51 | 0.12 | 0.93 | 0.62 | 1.5 | native | oil palm |
| Dolychoderinae | *Tapinoma* | | sp3 | 1.18 | 0.51 | 0.13 | 0.87 | 0.76 | 1.48 | native | oil palm |
| Dolychoderinae | *Technomyrmex* | *kraepelini* | | 1.08 | 0.47 | 0.21 | 1.12 | 0.58 | 2.68 | native | oil palm |
| Dolychoderinae | *Technomyrmex* | *gaudens* | | 1.27 | 0.42 | 0.17 | 0.94 | 0.63 | 2.2 | native | oil palm |
| Dolychoderinae | *Technomyrmex* | | sga1 | 1.03 | 0.49 | 0.17 | 0.98 | 0.56 | 1.84 | native | oil palm |
| Dolychoderinae | *Technomyrmex* | | sga2 | 1.19 | 0.46 | 0.21 | 1.03 | 0.63 | 2.5 | native | oil palm |
| Dolychoderinae | *Technomyrmex* | near sp1 | | 1.11 | 0.46 | 0.20 | 1.06 | 0.57 | 2.88 | native | oil palm |
| Dolychoderinae | *Technomyrmex* | near *obscurior* | sp10 | 1.16 | 0.36 | 0.19 | 1.01 | 0.59 | 3 | native | oil palm |
| Dolychoderinae | *Technomyrmex* | | sp4 | 1.14 | 0.52 | 0.20 | 1.15 | 0.63 | 3 | native | oil palm |
| Dolychoderinae | *Technomyrmex* | | sp6 | 1.14 | 0.41 | 0.18 | 1.07 | 0.61 | 3.28 | native | oil palm |
| Dolychoderinae | *Technomyrmex* | | sp7 | 1.08 | 0.48 | 0.18 | 1.17 | 0.61 | 3.02 | native | oil palm |
| Dolychoderinae | *Technomyrmex* | | sp8 | 1.11 | 0.38 | 0.23 | 1.07 | 0.58 | 2.9 | native | both |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Dorylinae | *Aenictus* | near *javanus* | sp1 | 0.98 | 0.62 | 0.02 | 1.34 | 0.96 | 2.70 | native | oil palm |
| Dorylinae | *Aenictus* | | sp2 | 1.20 | 0.47 | 0.03 | 0.83 | 1.00 | 1.64 | native | oil palm |
| Dorylinae | *Dorylus* | *laevitagus* | | 1.00 | 0.56 | 0.06 | 0.81 | 0.97 | 4.30 | native | oil palm |
| Dorylinae | *Dorylus* | *orientalis* | | 1.18 | 0.58 | 0.06 | 0.71 | 0.91 | 5.05 | native | oil palm |
| Ectatomminae | *Gnamptogenys* | | sga17-a | 1.13 | 0.54 | 0.15 | 1.01 | 0.90 | 4.69 | native | oil palm |
| Ectatomminae | *Gnamptogenys* | | sga17-b | 1.20 | 0.47 | 0.15 | 1.02 | 0.90 | 4.80 | native | oil palm |
| Ectatomminae | *Gnamptogenys* | | sga18 | 1.11 | 0.55 | 0.15 | 0.96 | 0.88 | 4.50 | native | oil palm |
| Ectatomminae | *Gnamptogenys* | | sga19 | 1.08 | 0.54 | 0.21 | 1.30 | 0.87 | 4.40 | native | oil palm |
| Ectatomminae | *Gnamptogenys* | | sga19-b | 1.17 | 0.57 | 0.18 | 0.97 | 0.89 | 4.98 | native | oil palm |
| Ectatomminae | *Gnamptogenys* | | sga20 | 1.20 | 0.53 | 0.17 | 1.00 | 0.90 | 4.31 | native | both |
| Ectatomminae | *Gnamptogenys* | | sga20-b | 1.22 | 0.54 | 0.23 | 0.97 | 0.91 | 4.75 | native | oil palm |
| Formicinae | *Acropyga* | *oceanica* | | 0.94 | 0.65 | 0.17 | 0.74 | 0.92 | 2.80 | native | oil palm |
| Formicinae | *Acropyga* | | sp1 | 0.95 | 0.74 | 0.19 | 0.83 | 0.91 | 2.20 | native | oil palm |
| Formicinae | *Acropyga* | | sp2 | 0.96 | 0.48 | 0.17 | 0.74 | 0.88 | 2.46 | native | oil palm |
| Formicinae | *Anoplolepis* | *Gracilipes* | | 1.39 | 0.51 | 0.31 | 2.23 | 0.71 | 3.61 | non-native | both |
| Formicinae | *Camponotus* | | sp1 | 1.17 | 0.39 | 0.31 | 1.26 | 0.63 | 9.69 | native | oil palm |
| Formicinae | *Camponotus* | | sp2 | 1.47 | 0.42 | 0.32 | 1.59 | 0.66 | 7.34 | native | both |
| Formicinae | *Camponotus* | *variegatus* | | 1.48 | 0.45 | 0.33 | 1.63 | 0.68 | 7.77 | native | oil palm |
| Formicinae | *Nylanderia* | *kraepelini* | | 1.23 | 0.46 | 0.22 | 1.16 | 0.62 | 2.10 | native | both |
| Formicinae | *Nylanderia* | | sga40 | 1.35 | 0.53 | 0.21 | 1.17 | 0.72 | 1.65 | native | oil palm |
| Formicinae | *Nylanderia* | | sga41 | 1.17 | 0.51 | 0.27 | 1.24 | 0.62 | 2.60 | native | oil palm |
| Formicinae | *Nylanderia* | | sp6 | 1.17 | 0.50 | 0.21 | 1.29 | 0.65 | 2.54 | native | oil palm |
| Formicinae | *Nylanderia* | | sp7 | 1.22 | 0.50 | 0.26 | 1.18 | 0.64 | 1.96 | native | oil palm |
| Formicinae | *Nylanderia* | | sp8 | 1.68 | 0.38 | 0.27 | 1.21 | 0.65 | 2.20 | native | oil palm |
| Formicinae | *Nylanderia* | | sp9 | 1.20 | 0.46 | 0.17 | 1.04 | 0.70 | 2.08 | native | oil palm |
| Formicinae | *Nylanderia* | | sp13 | 1.17 | 0.46 | 0.21 | 1.41 | 0.70 | 1.45 | native | oil palm |
| Formicinae | *Oecophylla* | *smaragdina* | | 1.11 | 0.65 | 0.29 | 1.85 | 0.72 | 8.57 | native | oil palm |
| Formicinae | *Paraparatrechina* | *butteli* | | 1.26 | 0.42 | 0.20 | 0.93 | 0.71 | 1.35 | native | both |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Formicinae | *Paratrechina* | *longicornis* | | 1.35 | 0.40 | 0.21 | 1.66 | 0.63 | 2.24 | non-native | oil palm |
| Formicinae | *Plagiolepis* | *allaudi* | | 1.13 | 0.43 | 0.20 | 0.74 | 0.71 | 1.20 | non-native | oil palm |
| Formicinae | *Plagiolepis* | | sp2 | 1.21 | 0.46 | 0.20 | 0.97 | 0.72 | 1.24 | non-native | oil palm |
| Myrmicinae | *Cardiocondyla* | near *tjibodana* | sga12-a | 1.23 | 0.43 | 0.14 | 0.70 | 0.80 | 1.40 | native | oil palm |
| Myrmicinae | *Cardiocondyla* | near *tjibodana* | sga12-b | 1.39 | 0.41 | 0.10 | 0.49 | 0.89 | 1.40 | native | oil palm |
| Myrmicinae | *Cardiocondyla* | | sga13-a | 1.41 | 0.41 | 0.12 | 0.62 | 0.88 | 1.48 | non-native | oil palm |
| Myrmicinae | *Cardiocondyla* | | sga13-b | 1.17 | 0.54 | 0.14 | 0.69 | 0.83 | 1.50 | non-native | oil palm |
| Myrmicinae | *Cardiocondyla* | near *wroughtonii* | sga16 | 1.17 | 0.46 | 0.14 | 0.71 | 0.90 | 1.30 | native | oil palm |
| Myrmicinae | *Carebara* | *affinis* | | 1.11 | 0.56 | 0.12 | 1.04 | 0.96 | 1.90 | native | both |
| Myrmicinae | *Carebara* | *pygmaea* | | 1.18 | 0.50 | 0.09 | 0.95 | 0.98 | 2.10 | native | both |
| Myrmicinae | *Carebara* | | sp2 | 1.18 | 0.50 | 0.09 | 0.95 | 0.98 | 2.10 | native | oil palm |
| Myrmicinae | *Crematogaster* | near *egidyi* | sga48 | 1.04 | 0.57 | 0.18 | 1.07 | 0.83 | 2.90 | native | oil palm |
| Myrmicinae | *Crematogaster* | near *linsenmairi* | sga49 | 1.06 | 0.56 | 0.17 | 1.15 | 0.86 | 2.70 | native | oil palm |
| Myrmicinae | *Crematogaster* | | sga50 | 1.03 | 0.61 | 0.15 | 1.08 | 0.83 | 2.80 | native | oil palm |
| Myrmicinae | *Crematogaster* | | sga52 | 0.99 | 0.51 | 0.14 | 1.09 | 0.91 | 3.40 | native | oil palm |
| Myrmicinae | *Crematogaster* | | sga53 | 1.05 | 0.49 | 0.12 | 0.84 | 0.88 | 1.93 | native | oil palm |
| Myrmicinae | *Crematogaster* | | sga54 | 1.08 | 0.51 | 0.16 | 0.87 | 0.88 | 2.86 | native | oil palm |
| Myrmicinae | *Lophomyrmex* | *bedoti* | | 1.08 | 0.49 | 0.13 | 0.91 | 0.93 | 2.35 | native | both |
| Myrmicinae | *Mayriella* | | sp2 | 1.00 | 0.67 | 0.11 | 1.22 | 0.89 | 1.42 | native | both |
| Myrmicinae | *Mayriella* | *transfuga* | | 1.05 | 0.43 | 0.13 | 0.61 | 0.82 | 1.35 | native | oil palm |
| Myrmicinae | *Monomorium* | *floricola* | | 1.33 | 0.42 | 0.11 | 0.61 | 0.93 | 1.26 | native | both |
| Myrmicinae | *Monomorium* | near *liliuokalanii* | sga33 | 1.23 | 0.46 | 0.14 | 0.74 | 0.88 | 1.35 | non-native | oil palm |
| Myrmicinae | *Monomorium* | | sga34-a | 1.29 | 0.45 | 0.16 | 0.58 | 0.88 | 1.14 | native | oil palm |
| Myrmicinae | *Monomorium* | near *pharaoensis* | sga38 | 1.32 | 0.43 | 0.13 | 0.82 | 0.91 | 1.55 | non-native | both |
| Myrmicinae | *Monomorium* | | sp8 | 1.00 | 0.59 | 0.11 | 1.14 | 0.89 | 1.70 | native | oil palm |

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|---|---|---|---|---|---|---|---|---|---|---|---|
| Myrmicinae | *Syllophopsis* | | sga35 | 1.23 | 0.51 | 0.11 | 0.76 | 0.97 | 1.30 | non-native | oil palm |
| Myrmicinae | *Syllophopsis* | | sga36 | 1.25 | 0.40 | 0.11 | 0.66 | 0.96 | 1.20 | native | oil palm |
| Myrmicinae | *Syllophopsis* | | sga37 | 1.28 | 0.57 | 0.08 | 0.62 | 0.86 | 1.46 | native | oil palm |
| Myrmicinae | *Pheidole* | *clypeocornis* | | 1.10 | 0.57 | 0.13 | 0.86 | 0.91 | 1.25 | native | oil palm |
| Myrmicinae | *Pheidole* | between *carniceps* and *plagiaria* | | 1.16 | 0.65 | 0.14 | 1.45 | 0.91 | 3.30 | native | oil palm |
| Myrmicinae | *Pheidole* | near *jacobsoni* | | 1.33 | 0.61 | 0.10 | 1.35 | 0.87 | 2.10 | native | both |
| Myrmicinae | *Pheidole* | *montana* | | 1.36 | 0.53 | 0.12 | 2.03 | 0.83 | 3.80 | native | both |
| Myrmicinae | *Pheidole* | *parva* | | 1.11 | 0.58 | 0.11 | 0.84 | 0.89 | 1.40 | native | both |
| Myrmicinae | *Pheidole* | *submonticola* | | 1.29 | 0.58 | 0.14 | 1.63 | 0.89 | 2.92 | native | oil palm |
| Myrmicinae | *Pheidole* | | sga55 | 1.24 | 0.67 | 0.12 | 1.16 | 0.91 | 2.14 | native | both |
| Myrmicinae | *Pheidole* | near *plagiaria* | sp2 | 1.20 | 0.64 | 0.13 | 1.36 | 0.91 | 2.70 | native | oil palm |
| Myrmicinae | *Pheidole* | near *plinii* | sp4 | 1.15 | 0.63 | 0.14 | 1.35 | 0.90 | 2.30 | native | oil palm |
| Myrmicinae | *Pheidole* | near *jacobsoni* | sp5 | 1.33 | 0.61 | 0.10 | 1.35 | 0.87 | 2.10 | native | both |
| Myrmicinae | *Pheidole* | near *plagiaria* | sp6 | 1.21 | 0.66 | 0.12 | 1.28 | 0.92 | 2.30 | native | oil palm |
| Myrmicinae | *Pheidole* | between *parva* and *rabo* | sp14 | 1.10 | 0.56 | 0.09 | 0.88 | 0.92 | 1.46 | native | oil palm |
| Myrmicinae | *Pheidole* | | sp15 | 1.10 | 0.68 | 0.12 | 1.44 | 0.88 | 2.68 | native | oil palm |
| Myrmicinae | *Pheidole* | near *havilandi* | sp16 | 1.15 | 0.62 | 0.11 | 1.04 | 0.95 | 1.88 | native | oil palm |
| Myrmicinae | *Pheidole* | near *tawaunensis* | sp18 | 1.15 | 0.64 | 0.13 | 1.15 | 0.94 | 1.82 | native | both |
| Myrmicinae | *Pheidole* | near *parva* | sp20 | 1.03 | 0.55 | 0.10 | 0.90 | 0.87 | 1.30 | native | oil palm |
| Myrmicinae | *Pheidole* | between *hortensis* and *deltea* | sp26 | 1.11 | 0.59 | 0.10 | 0.88 | 0.95 | 1.60 | native | oil palm |
| Myrmicinae | *Pheidole* | near *parva* | sp28 | 1.11 | 0.59 | 0.13 | 0.85 | 0.89 | 1.36 | native | oil palm |
| Myrmicinae | *Pheidole* | near *parva* | sp30 | 1.13 | 0.59 | 0.10 | 0.81 | 0.94 | 1.52 | native | oil palm |
| Myrmicinae | *Pheidole* | | sp32 | 1.08 | 0.56 | 0.10 | 0.90 | 0.89 | 1.36 | native | both |
| Myrmicinae | *Pheidole* | | sp33 | 1.19 | 0.61 | 0.13 | 1.25 | 0.91 | 2.35 | native | both |
| Myrmicinae | *Pheidole* | | sp34 | 1.22 | 0.66 | 0.14 | 1.68 | 0.93 | 2.24 | native | both |

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|---|---|---|---|---|---|---|---|---|---|---|---|
| Myrmicinae | *Pheidole* | | sp62 | 1.11 | 0.59 | 0.13 | 0.79 | 0.91 | 1.34 | native | oil palm |
| Myrmicinae | *Pheidole* | | sp63 | 1.18 | 0.49 | 0.11 | 0.82 | 0.92 | 1.60 | native | oil palm |
| Myrmicinae | *Pheidole* | | sp64 | 1.16 | 0.63 | 0.13 | 1.37 | 0.91 | 2.86 | native | oil palm |
| Myrmicinae | *Pheidole* | | sp65 | 1.18 | 0.77 | 0.12 | 1.32 | 0.90 | 2.41 | native | oil palm |
| Myrmicinae | *Pristomyrmex* | *punctatus* | | 1.00 | 0.56 | 0.09 | 1.01 | 0.87 | 2.38 | native | oil palm |
| Myrmicinae | *Pristomyrmex* | *pulcher* | | 1.02 | 0.49 | 0.11 | 1.02 | 0.84 | 2.50 | native | oil palm |
| Myrmicinae | *Recurvidris* | *williami* | | 0.99 | 0.64 | 0.09 | 1.00 | 0.87 | 2.30 | native | oil palm |
| Myrmicinae | *Recurvidris* | | sga46 | 1.02 | 0.66 | 0.14 | 0.91 | 0.86 | 2.16 | native | oil palm |
| Myrmicinae | *Solenopsis* | *geminata* | | 1.09 | 0.54 | 0.11 | 0.71 | 0.95 | 1.35 | non-native | both |
| Myrmicinae | *Solenopsis* | *molesta* | | 1.26 | 0.41 | 0.12 | 0.53 | 0.89 | 1.20 | non-native | both |
| Myrmicinae | *Solenopsis* | | sp1 | 1.09 | 0.43 | 0.14 | 0.74 | 0.97 | 1.54 | non-native | oil palm |
| Myrmicinae | *Solenopsis* | | sp2 | 1.06 | 0.58 | 0.13 | 0.64 | 0.94 | 0.95 | non-native | both |
| Myrmicinae | *Strumigenys* | *rogeri* | | 2.31 | 0.53 | 0.11 | 0.72 | 0.91 | 1.94 | non-native | oil palm |
| Myrmicinae | *Strumigenys* | *liophila* | | 2.10 | 0.36 | 0.16 | 0.59 | 5.92 | 1.78 | native | oil palm |
| Myrmicinae | *Tetramorium* | *indicum* | | 1.12 | 0.51 | 0.15 | 0.88 | 0.89 | 2.86 | native | oil palm |
| Myrmicinae | *Tetramorium* | *insolens* | | 1.19 | 0.49 | 0.10 | 0.83 | 0.94 | 3.22 | non-native | oil palm |
| Myrmicinae | *Tetramorium* | *kheperra* | | 1.10 | 0.50 | 0.11 | 0.77 | 0.90 | 2.20 | native | both |
| Myrmicinae | *Tetramorium* | *lanuginosum* | | 1.10 | 0.47 | 0.13 | 0.77 | 0.87 | 2.22 | non-native | both |
| Myrmicinae | *Tetramorium* | *pacificum* | | 1.18 | 0.51 | 0.10 | 0.86 | 0.88 | 3.66 | native | oil palm |
| Myrmicinae | *Tetramorium* | *palaense* | | 1.08 | 0.56 | 0.10 | 0.94 | 0.92 | 2.90 | native | oil palm |
| Myrmicinae | *Tetramorium* | *simillimum* | | 1.20 | 0.49 | 0.10 | 0.71 | 0.90 | 1.70 | native | oil palm |
| Myrmicinae | *Tetramorium* | *smithi* | | 1.13 | 0.56 | 0.11 | 0.78 | 0.90 | 2.33 | native | oil palm |
| Myrmicinae | *Tetramorium* | *tonganum* | | 1.18 | 0.52 | 0.14 | 0.79 | 0.92 | 2.34 | native | both |
| Myrmicinae | *Tetramorium* | Between *tonganum* and *obtusidens* | | 1.13 | 0.54 | 0.13 | 0.87 | 0.90 | 2.46 | native | oil palm |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Myrmicinae | *Tetramorium* | | sp2 | 1.18 | 0.44 | 0.14 | 0.73 | 0.90 | 1.83 | native | oil palm |
| Myrmicinae | *Tetramorium* | | sp3 | 1.13 | 0.52 | 0.11 | 0.75 | 0.89 | 2.52 | native | oil palm |
| Myrmicinae | *Tetramorium* | | sp3-b | 1.00 | 0.65 | 0.17 | 0.89 | 0.91 | 1.84 | native | oil palm |
| Myrmicinae | *Tetramorium* | | sp9 | 1.04 | 0.55 | 0.11 | 0.72 | 0.89 | 1.94 | native | oil palm |
| Myrmicinae | *Vollenhovia* | *emeryi* | | 1.19 | 0.40 | 0.12 | 0.56 | 0.86 | 1.70 | non-native | oil palm |
| Myrmicinae | *Vollenhovia* | *fridae* | | - | - | - | - | - | - | native | oil palm |
| Ponerinae | *Anochetus* | near *graeffi* | sp1 | 1.13 | 0.64 | 0.06 | 0.80 | 0.74 | 4.10 | native | oil palm |
| Ponerinae | *Brachyponera* | near *luteipes* | sga10-a | 1.19 | 0.52 | 0.11 | 1.00 | 0.81 | 3.50 | native | oil palm |
| Ponerinae | *Brachyponera* | | sp2 | 1.20 | 0.56 | 0.12 | 1.05 | 0.80 | 3.40 | native | oil palm |
| Ponerinae | *Diacamma* | *rugosum* | | 1.39 | 0.54 | 0.25 | 1.27 | 0.69 | 9.23 | native | both |
| Ponerinae | *Diacamma* | *intricatum* | | 1.39 | 0.50 | 0.28 | 1.27 | 0.71 | 9.90 | native | oil palm |
| Ponerinae | *Diacamma* | | sga43 | 1.19 | 0.57 | 0.25 | 1.33 | 0.73 | 10.35 | native | oil palm |
| Ponerinae | *Ectomomyrmex* | | sga26 | 1.25 | 0.51 | 0.09 | 0.70 | 0.98 | 3.50 | native | oil palm |
| Ponerinae | *Euponera* | *sharpi* | | 1.20 | 0.62 | 0.17 | 0.88 | 0.99 | 3.10 | native | oil palm |
| Ponerinae | *Euponera* | | sp1 | 1.23 | 0.64 | 0.07 | 0.85 | 0.96 | 4.80 | native | oil palm |
| Ponerinae | *Leptogenys* | *parvula* | | 1.49 | 0.48 | 0.18 | 1.17 | 0.73 | 5.80 | native | both |
| Ponerinae | *Leptogenys* | *mutabilis* | | 1.19 | 0.63 | 0.20 | 1.15 | 0.68 | 7.50 | native | oil palm |
| Ponerinae | *Leptogenys* | *kitteli* | | 1.40 | 0.53 | 0.24 | 1.34 | 0.70 | 5.10 | native | both |
| Ponerinae | *Leptogenys* | *birmana* | | 1.16 | 0.66 | 0.20 | 1.16 | 0.67 | 7.20 | native | oil palm |
| Ponerinae | *Odontomachus* | *simillimus* | | 1.20 | 0.57 | 0.06 | 1.01 | 0.75 | 8.07 | native | oil palm |
| Ponerinae | *Odontoponera* | *transversa* | | - | - | - | - | - | - | native | both |
| Ponerinae | *Odontoponera* | *denticulata* | | 1.11 | 0.58 | 0.20 | 1.00 | 0.79 | 9.45 | native | both |
| Ponerinae | *Ponera* | *selenophora* | | 1.20 | 0.60 | 0.15 | 0.85 | 0.96 | 4.30 | native | oil palm |
| Ponerinae | *Ponera* | | sga26 | 1.19 | 0.80 | 0.10 | 0.91 | 0.99 | 4.30 | native | oil palm |
| Ponerinae | *Pesudoponera* | | sga7 | 1.10 | 0.62 | 0.11 | 0.79 | 1.00 | 4.70 | non-native | both |

## Section S3: Comparison in species richness and composition between land-use types

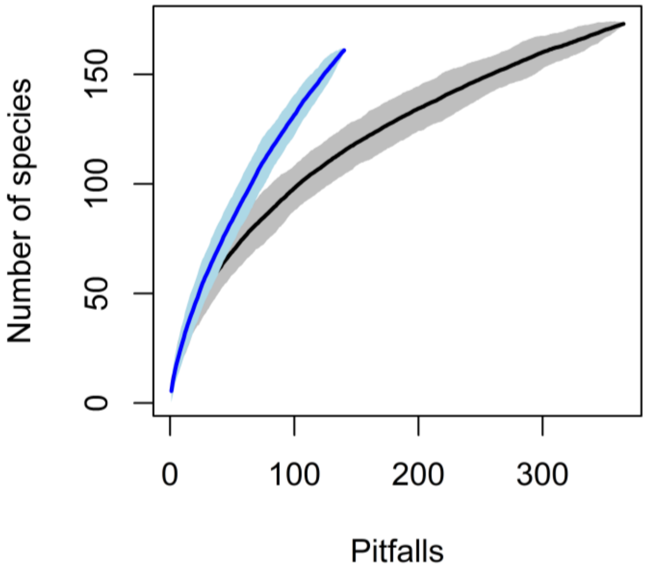

**Figure S3.** Species accumulation curves for ground-dwelling ants occurring in oil palm smallholder farms (n = 40; black line) and old-growth rainforest (n = 15; blue line) over 365 pitfall sampling points (i.e., number of pitfalls) from all oil palm farm sites and 140 pitfall sampling points from all old-growth rainforest sites. Thicker lines denote mean species richness, while shaded areas denote 95% confidence intervals.

| **Habitat** | **Sample effort** | **Ant Occurrences** | **Observed species richness** | **Average species richness** | **Rarefied richness** | **Proportion of non-native species** |
|---|---|---|---|---|---|---|
| **Old-growth rainforest** | 140 | 3,841 | 161 | 9 - 39 species (mean = 25) | 161 | 0 - 0.13 (mean = 0.05) |
| **Smallholdings** | 349 | 11,885 | 161 | 5 - 30 species (mean = 18.1) | 107 | 0.00 - 0.4 (mean = 0.21) |

**Table S3.** Differences in ground-dwelling ant communities between old-growth rainforest sites (n = 15) and smallholder oil palm farm sites (n = 40): sampling effort as the total number of pitfalls within a habitat, total number of ant individual occurrences, total observed species richness, observed species richness at a sites (mean and range), habitat-level rarefied species richness to match sampling effort, and proportion of non-native ants at a site (mean and range).

## Section S4: Clustering analysis using Partitioning Around Medoids (PAM)

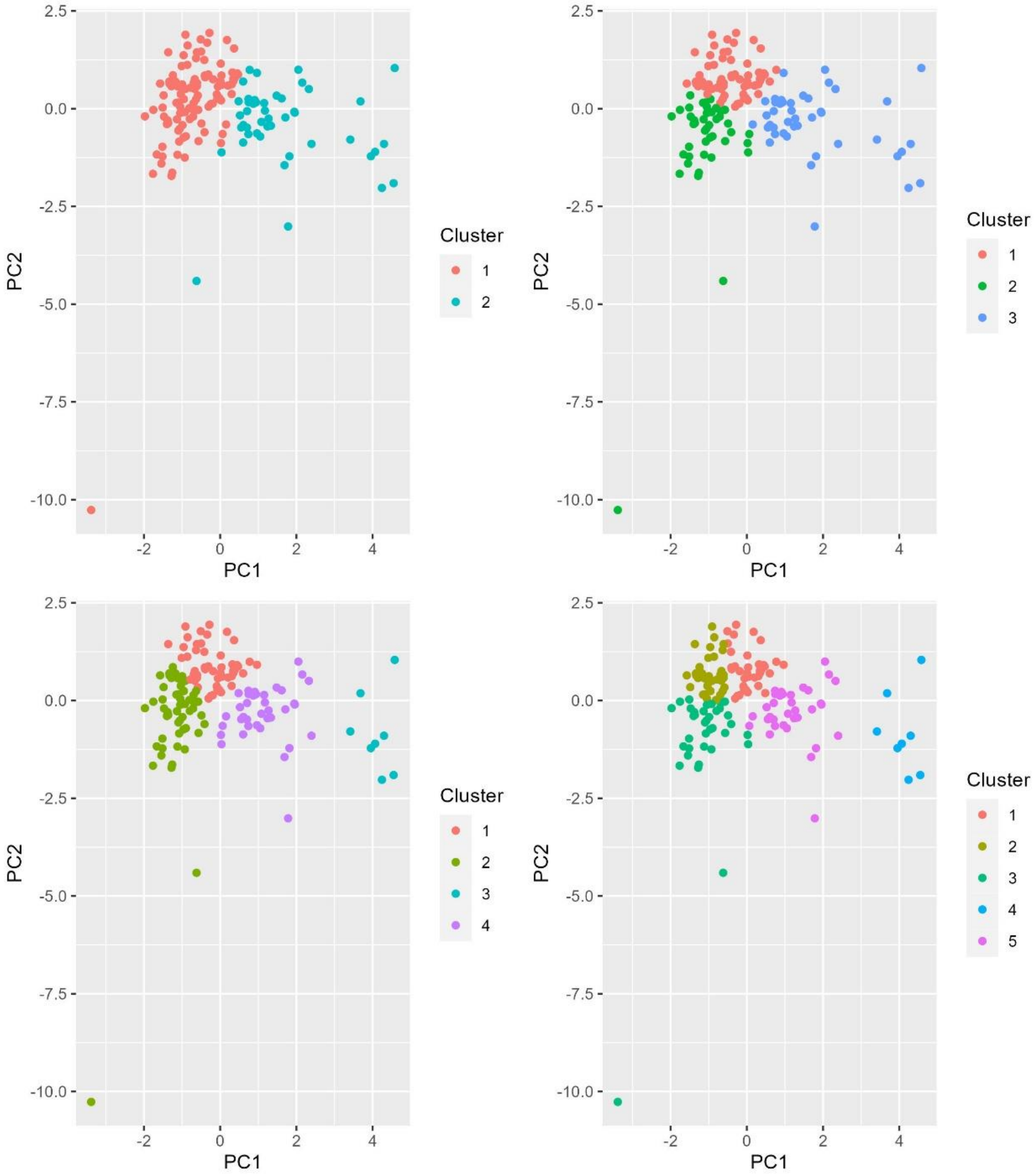

**Figure S4**: Outputs from the PAM clustering analysis performed on the first two components derived from the Principal Component Analysis (PCA) of ant functional shape traits in smallholder oil palm farms. Species colour coded according to PAM clustering with k = 2, 3, 4, and 5.

## Section S5: GAMM diagnostic outputs

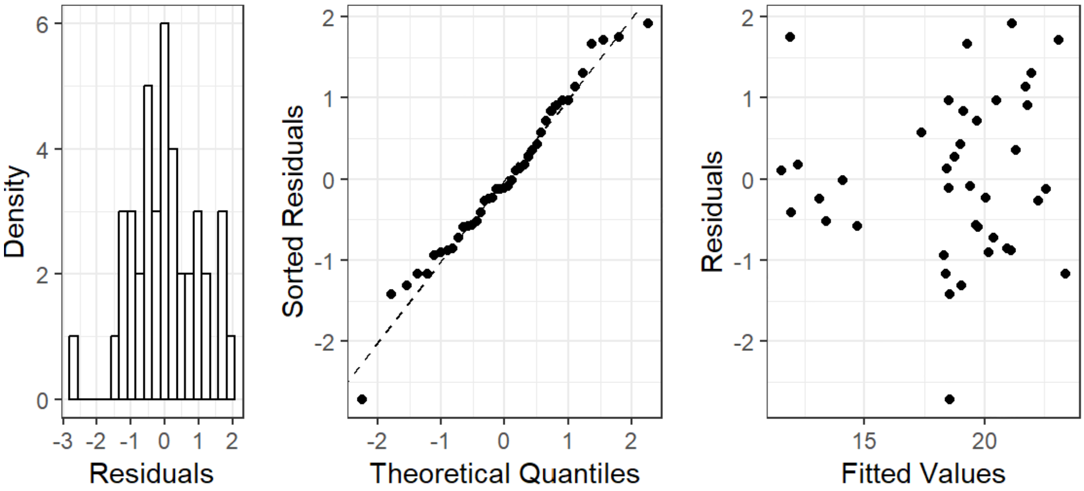

**Figure S5**. Diagnostic plots for checking that error distribution meets model assumptions (of homogeneity of variance, and approximate Normality), for model of proportion of non-native species and total species richness. (a) Histogram of final model residuals; (b) scatterplot of quantiles of the residuals compared to a theoretical Normal distribution; (c) scatterplot of final model residuals and fitted values.

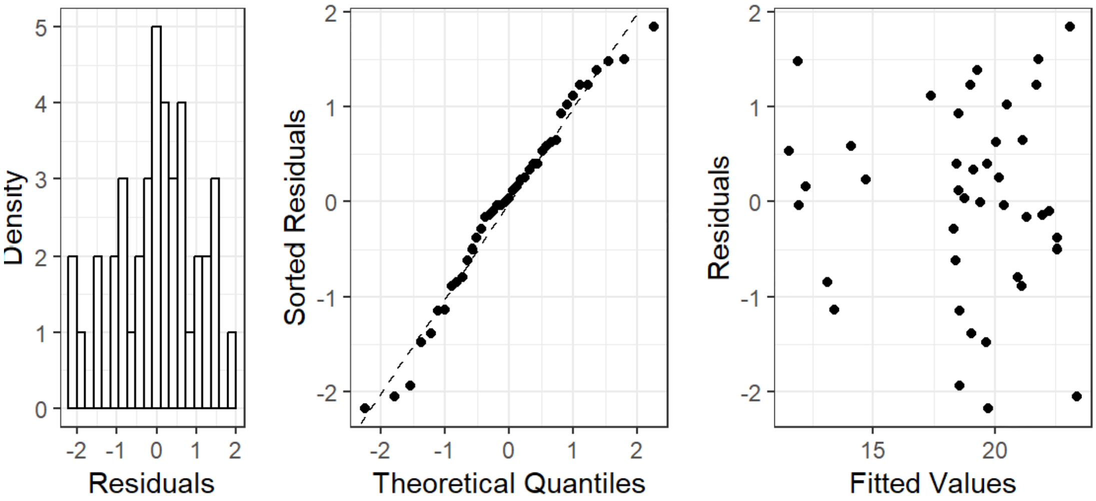

**Figure S6.** Diagnostic plots for checking that error distribution meets model assumptions (of homogeneity of variance, and approximate Normality), for model of proportion of non-native species and total species richness. (a) Histogram of final model residuals; (b) scatterplot of quantiles of the residuals compared to a theoretical Normal distribution; (c) scatterplot of final model residuals and fitted values.

## Section S6: Outputs from GAMM models

| **(a) Without spatial autocorrelation** | | | | | | |
|---|---|---|---|---|---|---|
| **Predictor** | **F** | **p-value** | **ES** | **Error** | **t-value** | **p-value** |
| s(prop NN) | 0.42 | 0.52 | | | | |
| s(trap days) | 8.96 | <0.01*** | | | | |
| (intercept) | | | 19.2 | 1.16 | 16.58 | <0.01*** |
| **(b) Moran's I** | | | | | | |
| **Observed** | **Expected** | **Sd** | **p-value** | | | |
| -0.10 | -0.03 | 0.11 | 0.47 | | | |
| **(c) With lon and lat** | | | | | | |
| **Predictor** | **F** | **p-value** | **ES** | **Error** | **t-value** | **p-value** |
| s(prop NN) | 0.47 | 0.69 | | | | |
| s(trap days) | 10.93 | <0.01*** | | | | |
| s(lon,lat) | 0.731 | 0.02** | | | | |
| (intercept) | | | 18.7 | 0.69 | 27.31 | <0.01*** |

**Table S4.** Effect of proportion of non-natives on total species richness. Outputs of (a) GAMM model fitted without spatial autocorrelation terms, (b) Moran's I test for spatial autocorrelation, (c) GAMM model fitted with spatial autocorrelation term and exponential correlation structure.

| **(a) Without spatial autocorrelation** | | | | | | |
|---|---|---|---|---|---|---|
| **Predictor** | **F** | **p-value** | **ES** | **Error** | **t-value** | **p-value** |
| s(NN Rich) | 6.73 | 0.02 | | | | |
| s(trap days) | 8.35 | <0.01** | | | | |
| (intercept) | | | 14.92 | 0.66 | 22.54 | <0.001*** |
| **(b) Moran's I** | | | | | | |
| **Observed** | **Expected** | **Sd** | **p-value** | | | |
| -0.08 | -0.03 | 0.11 | 0.61 | | | |
| **(c) With lon and lat** | | | | | | |
| **Predictor** | **F** | **p-value** | **ES** | **Error** | **t-value** | **p-value** |
| s(NN Rich) | 7.41 | 0.01 | | | | |
| s(trap days) | 8.97 | <0.01** | | | | |
| s(lon,lat) | 0.13 | 0.12 | | | | |
| (intercept) | | | 18.7 | 0.69 | 27.31 | <0.001*** |

**Table S5.** Effect of non-native species richness on native species richness. Outputs of (a) GAMM model fitted without spatial autocorrelation terms, (b) Moran's I test for spatial autocorrelation, (c) GAMM model fitted with spatial autocorrelation term and exponential correlation structure.

| **(a) Without spatial autocorrelation** | | | | | | |
|---|---|---|---|---|---|---|
| **Predictor** | **F** | **p-value** | **ES** | **Error** | **t-value** | **p-value** |
| s(prop NN) | 6.73 | 0.02 | | | | |
| s(trap days) | 8.35 | <0.01** | | | | |
| (intercept) | | | 14.92 | 0.66 | 22.54 | <0.001*** |
| **(b) Moran's I** | | | | | | |
| **Observed** | **Expected** | **Sd** | **p-value** | | | |
| 0.02 | -0.03 | 0.11 | 0.68 | | | |
| **(c) With lon and lat** | | | | | | |
| **Predictor** | **F** | **p-value** | **ES** | **Error** | **t-value** | **p-value** |
| s(prop NN) | 0.28 | 0.60 | | | | |
| s(trap days) | 4.88 | 0.03* | | | | |
| s(lon,lat) | 0.94 | 0.01* | | | | |
| (intercept) | | | 13.11 | 0.63 | 20.84 | <0.001*** |

**Table S6.** Effect of proportion of non-native on functional richness. Outputs of (a) GAMM model fitted without spatial autocorrelation terms, (b) Moran's I test for spatial autocorrelation, (c) GAMM model fitted with spatial autocorrelation term.

| **(a) Without spatial autocorrelation** | | | | | | |
|---|---|---|---|---|---|---|
| **Predictor** | **F** | **p-value** | **ES** | **Error** | **t-value** | **p-value** |
| s(prop NN) | 1.60 | 0.21 | | | | |
| s(trap days) | 0.35 | 0.56 | | | | |
| (intercept) | | | 1.74 | 0.05 | 32.63 | <0.001*** |
| **(b) Moran's I** | | | | | | |
| **Observed** | **Expected** | **Sd** | **p-value** | | | |
| 0.05 | -0.03 | 0.11 | 0.50 | | | |
| **(c) With lon and lat** | | | | | | |
| **Predictor** | **F** | **p-value** | **ES** | **Error** | **t-value** | **p-value** |
| s(prop NN) | 1.02 | 0.23 | | | | |
| s(trap days) | 0.29 | 0.60 | | | | |
| s(lon,lat) | 0.00 | 0.61 | | | | |
| (intercept) | | | 1.74 | 0.07 | 23.5 | <0.001*** |

**Table S7.** Effect of proportion of non-native on functional dispersion. Outputs of (a) GAMM model fitted without spatial autocorrelation terms, (b) Moran's I test for spatial autocorrelation, (c) GAMM model fitted with spatial autocorrelation term.

| **(a) Without spatial autocorrelation** | | | | | | |
|---|---|---|---|---|---|---|
| **Predictor** | **F** | **p-value** | **ES** | **Error** | **t-value** | **p-value** |
| s(prop NN) | 1.60 | 0.21 | | | | |
| s(trap days) | 0.35 | 0.56 | | | | |
| (intercept) | | | 1.74 | 0.05 | 32.63 | <0.001*** |
| **(b) Moran's I** | | | | | | |
| **Observed** | **Expected** | **Sd** | **p-value** | | | |
| -0.06 | -0.04 | 0.14 | 0.90 | | | |
| **(c) With lon and lat** | | | | | | |
| **Predictor** | **F** | **p-value** | **ES** | **Error** | **t-value** | **p-value** |
| s(prop NN) | 1.10 | 0.31 | | | | |
| s(lon,lat) | 0.00 | 0.77 | | | | |
| (intercept) | | | 63.05 | 4.96 | 12.72 | <0.001*** |

**Table S8.** Effect of proportion of non-native species on fish scavenging rates on oil palm farms (n = 26). Outputs of (a) GAMM model fitted without spatial autocorrelation terms, (b) Moran's I test for spatial autocorrelation, (c) GAMM model fitted with spatial autocorrelation term.

| | | | | | | |
|---|---|---|---|---|---|---|
| **(a) Without spatial autocorrelation** | | | | | | |
| **Predictor** | **F** | **p-value** | **ES** | **Error** | **t-value** | **p-value** |
| s(prop NN) | 0 | 1.00 | | | | |
| (intercept) | | | 40.19 | 4.65 | 8.65 | <0.001*** |
| **(b) Moran's I** | | | | | | |
| **Observed** | **Expected** | **Sd** | **p-value** | | | |
| -0.08 | -0.04 | 0.14 | 0.78 | | | |
| **(c) With lon and lat** | | | | | | |
| **Predictor** | **F** | **p-value** | **ES** | **Error** | **t-value** | **p-value** |
| s(prop NN) | 0.08 | 0.78 | | | | |
| s(lon,lat) | 0.00 | 0.70 | | | | |
| (intercept) | | | 42.14 | 5.01 | 8.41 | <0.001*** |

**Table S9.** Effect of proportion of non-native on seed scavenging rates on oil palm farms (n = 26). Outputs of (a) GAMM model fitted without spatial autocorrelation terms, (b) Moran's I test for spatial autocorrelation, (c) GAMM model fitted with spatial autocorrelation term.

| | | | | | | |
|---|---|---|---|---|---|---|
| **(a) Without spatial autocorrelation** | | | | | | |
| **Predictor** | **F** | **p-value** | **ES** | **Error** | **t-value** | **p-value** |
| s(prop NN) | 1.33 | 0.26 | | | | |
| (intercept) | | | 73.97 | 0.78 | 94.61 | <0.001*** |
| **(b) Moran's I** | | | | | | |
| **Observed** | **Expected** | **Sd** | **p-value** | | | |
| -0.08 | -0.04 | 0.14 | 0.78 | | | |
| **(c) With lon and lat** | | | | | | |
| **Predictor** | **F** | **p-value** | **ES** | **Error** | **t-value** | **p-value** |
| s(prop NN) | 1.22 | 0.28 | | | | |
| s(lon,lat) | 0.03 | 0.28 | | | | |
| (intercept) | | | 73.97 | 0.77 | 96.34 | <0.001*** |

**Table S10.** Effect of proportion of non-native on leaflitter decomposition rates on oil palm farms (n = 35). Outputs of (a) GAMM model fitted without spatial autocorrelation terms, (b) Moran's I test for spatial autocorrelation, (c) GAMM model fitted with spatial autocorrelation term.

# CHAPTER 4

# Landscape-scale and local factors influence the ecological resilience of oil palm smallholdings

Smallholder oil palm farms with a forest fragment in the background

Sabah, Malaysian Borneo

## 4.1 ABSTRACT

1. Employing more sustainable farm management practices could enhance the ecological resilience of tropical smallholdings. However, farm management and factors affecting local biodiversity and crop yields are likely to be inter-linked, and there may also be landscape-level factors that contribute to the ecological resilience of farms.

2. We used Structural Equation Modelling to examine direct and indirect factors affecting the ecological resilience of ground-dwelling ant communities on 39 smallholder oil palm farms in Sabah, Malaysian Borneo. We sampled farms spanning a gradient of farm management intensities and investigated their ecological resilience by quantifying ant species richness (both native and non-native species), and functional richness and dispersion (based on ant morphological measurements).

3. We find that both local and landscape factors influence the ecological resilience of ant communities on farms, but that different factors influence native versus non-native ant species. For example, cooler farms supported more native species, whereas non-native richness was higher on farms with less understory vegetation, and less forest in the surrounding landscape. Proximity of farms to roads increased overall richness of both native and non-native species richness. However, native species contributed most to higher functional richness and dispersion on farms. We also found that farms with higher native species richness had higher crop yields, which may imply a role for ants in crop pest control.

4. Native species contributed most to the ecological resilience of farms in terms of functional richness and dispersion, and were influenced most by local farm temperature, rather than smallholder management practices. Proximity of farms to roads may enhance local ant species richness by assisting dispersal. We conclude that anthropogenic climate warming may reduce the ecological resilience of oil palm farms via its detrimental effects on native species, which may also impact crop yields. More research is needed to understand why farm management practices apparently had little impact on ecological resilience in our study.

## 4.2 INTRODUCTION

Oil palm agriculture has been a major driver of land-use change and deforestation in tropical landscapes over the last few decades (Gaveau et al., 2016, 2018; Pacheco, 2012; Wicke et al., 2011), contributing to fragmentation of natural habitats, biodiversity loss and altered ecological communities (Edwards et al., 2014; Lee-Cruz et al., 2013; Vijay et al., 2016). Intensification of oil palm management aims to close yield gaps, improve livelihoods and meet global demands for palm oil (Mueller et al., 2012; Phalan et al., 2014), but this could have continued detrimental impacts on biodiversity and ecosystem functioning if implemented inappropriately (e.g., leading to soil degradation; Guillaume et al., 2016). These intensive farm management practices may also have negative consequences for the provisioning of ecosystem services (Dislich et al., 2017), which would not only be detrimental for food security (Bullock et al., 2017), but also reduce livelihoods of smallholder producers and communities farming these landscapes (Rist et al., 2010).

To ensure sustainable food production, there has been increased interest in the uptake of agricultural management practices that minimise the social, environmental, and ecological impacts locally as well as within the surrounding landscapes (Brooker et al., 2021; Khasanah et al., 2020; Kremen et al., 2012; Phalan et al., 2011; Rahman et al., 2016; Tanguay & Bernard, 2020). In oil palm landscapes, conservation forest set asides help protect carbon stocks and biodiversity in the wider landscape (Austin et al., 2017; Fleiss et al., 2020; Gray et al., 2016; Senior et al., 2015), while local farm management helps to improve soil quality and enrich vegetation structure on farms (Fairhurst & Griffiths, 2014; Gérard et al., 2017; Teuscher et al., 2016). While these more sustainable management practices can sometimes promote higher biodiversity on farms (Ashton-Butt et al., 2018; Luke et al., 2019), the results are not always consistent (Edwards et al., 2010; Hood et al., 2020). Moreover, we still do not have a good understanding of how sustainable practices influence the ecological resilience of biodiversity within oil palm landscapes. With projected global warming of 1.5°C (IPCC, 2018) and further expansion of tropical agricultural landscapes Williams et al., (2020), the ability of ecological communities to resist and recover from environmental change and disturbances (i.e., resilience) will be critical for sustainable agricultural production (Maleksaeidi & Karami, 2013; Rockström et al., 2017).

Oil palm plantations support fewer species and reduced functional roles compared to natural forested habitats (e.g., fewer specialist species; Barnes et al., 2014), with few little overlap in species composition between land-use types (Edwards et al., 2014; Fayle et al., 2010; see Chapter 3). Species that occur in oil palm tend to share particular traits (e.g., smaller body size and lower trophic position; Boyle et al., 2021; Edwards et al., 2014; Senior et al., 2013), which is likely due to environmental filtering of traits that facilitate survival in these warmer and more simplified environments (Boyle et al., 2021). Reduced species richness and lower trait diversity may leave ecological communities more vulnerable and less adaptable to environmental changes, especially if the species that persist in oil palm show high sensitivity to disturbance and environmental change (Huey et al., 2012; McLean et al., 2019; Oliver et al., 2015). However, given that oil palm habitats support a higher occurrence of non-native species with traits that facilitate dispersal and invasion of novel and more disturbed habitats (Waddell et al., 2020; see Chapter 3), ant communities on oil palm farms may show higher resistance to environmental changes and disturbance, despite supporting lower species richness and functional diversity.

Local farm management and environmental conditions could ameliorate impacts on biodiversity on oil palm farms, while the surrounding landscape may provide source populations to help community recovery on oil palm farms (Oliver et al., 2015). Landscape composition and connectivity can mediate dispersal and contribute to local species richness by providing forest areas as colonising sources and facilitating the introduction of novel species. For example, road networks are a well-known pathway for human-mediated dispersal of species and may contribute to higher colonisation of non-native species on farms (Bullock et al., 2018). Conversely, forest fragments within oil palm landscapes may provide sources of more forest-dependent species, contributing to higher native richness on farms (Hamer et al., 2021; Lucey et al., 2014). At a local farm scale, more intensive farm management (e.g., frequency of weeding and fertiliser applications) could introduce disturbance and influence understory vegetation and abiotic conditions on farms (Luke et al., 2019). This local disturbance may result in the loss of more disturbance-sensitive species (e.g., more carnivorous and larger bodied species), resulting in altered community structure and functioning on oil palm farms.

Ants are important contributors to key ecosystem processes, such as nutrient re-distribution, seed dispersal and predation (Folgarait, 1998). Oil palm farms support a higher number of non-native ants compared to forest habitats (Fayle et al., 2010), which could influence the response of ground-dwelling ant communities to environmental change, and their ecological resilience. Non-native ants differ in traits relating to thermal tolerance, diet and foraging strategy compared with native species (see Chapter 3), and as a result, may show different responses to local farm management and wider landscape changes. For example, non-native ants typically have smaller body sizes, which is related to higher thermal tolerance (Boyle et al., 2021) and traits corresponding to a more generalist diet and monopolisation of food resources (e.g., wider head and shorter mandibles; see Chapter 3). Non-native species are generally less sensitive to disturbances, which may buffer community structure and functioning from species loss on farms, although non-native species may not provide the same range of ecosystem functions as native ant species (Devenish et al., 2019). Hence, investigating which local farm and wider landscape factors contribute to native ant richness is especially important for understanding how to maintain more ecologically resilient tropical agricultural landscapes.

In this study, we examine how local farm factors and landscape-level environmental changes affect native and non-native ground-dwelling ant communities on smallholder oil palm farms in Sabah, Malaysian Borneo. We examine two mechanisms affecting the ecological resilience of oil palm farms: the sensitivity of species to environmental changes, and functional redundancy. Higher functional redundancy corresponds to higher species richness that is distributed more evenly across the functional trait space. We quantify these two mechanisms by measuring three metrics of ecological resilience: (1) species richness of native and non-native ants; and two metrics of functional diversity, (2) functional richness, and (3) functional dispersion (see Fig. 1). We use Structural Equation Models (SEMs) to assess how local farm management variables (e.g., management intensity and understorey vegetation) and wider landscape variables (e.g., forest extent and proximity to roads) influence native and non-native species richness and functional diversity on farms. We hypothesized that native species will be more sensitive to local and wider landscape changes, and so any factors that represent higher levels of disturbance (e.g., more intensively managed farms, landscapes with low forest cover and/or more roads) will have lower ant species richness, lower functional richness and less functional redundancy.

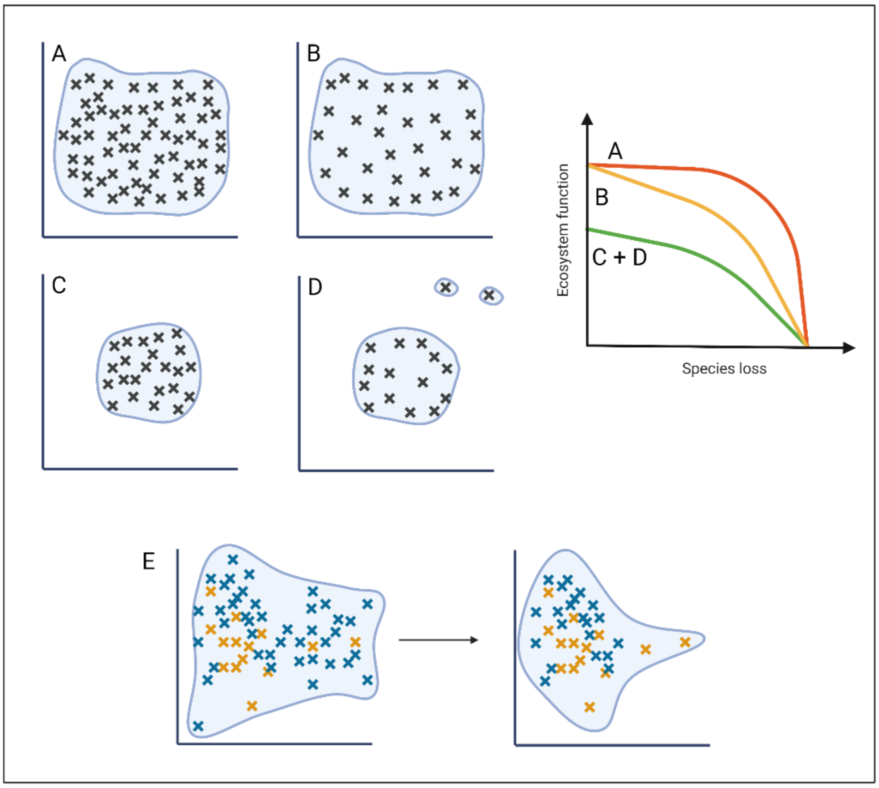

**Figure 1**. **(A-D)** Figure illustrates how variation in species richness and functional diversity might impact ecological resilience. The plots represent variation in functional richness (FRich) and functional dispersion (FDisp); figure adapted from Oliver et al., (2015). Communities with higher ecological resilience are able to maintain ecosystem functioning for longer following species loss. Higher redundancy of species with similar traits (**A;** i.e. functional redundancy) helps to buffer community functioning from the loss of species ('insurance effect'), whereas communities with lower functional redundancy **(B)** change community structure more quickly with continued species loss. Higher FDisp within a community (**D**) indicates higher trait dissimilarity among species within a community. Communities could have similar FRich (**C &D**) but have different FDisp. (**E**)**:** The two panels represent species sensitivity to disturbance. Environmental change may disproportionately affect species with particular traits that make them more vulnerable to that environmental pressure. For example, native species (blue crosses) may be more vulnerable to particular types of environmental pressures than non-native species (yellow crosses), resulting in a greater loss of native species and a loss of functional groups.

## 4.3 METHODS

### 4.3.1. Study area and site selection

We surveyed 39 smallholder oil palm farms (defined as farms < 50 ha; 1 survey site per farm; Fig. 1) across six governance areas in Sabah, Malaysian Borneo, between August to October 2019. Farms were located in heterogenous landscapes with mixed land-use types and histories (i.e., were previously secondary forest or agricultural land other than oil palm), and varying amounts of forest cover and landscape composition. The majority of the smallholders that participated in our study were part of a Smallholder Group Scheme organised by a local social NGO (WildAsia) (n = 34), and the remaining were independent smallholders (n = 5). Contact was made with smallholder farmers through on-going connections with WildAsia and the South East Asia Rainforest Research Partnership (SEARRP). We sampled farmers from various governance areas across Sabah (n = 6) to capture variations in smallholder farm management practices and oil palm yields. In our analyses, we allocated smallholders to governance areas according to the village community the smallholder belonged to, on the assumption that smallholders within the same governance area would manage their farms in a similar way by following the guidance of the local community leader and WildAsia staff. Governance areas varied slightly in climate (rainfall and temperature), soil type and elevation (see Chapter 2; Gutierrez Al-Khudhairy et al., 2023, and SI for further details). Farms were selected for inclusion in our study based on (1) farm size greater than 0.5 ha (i.e., large enough to conduct our ecological surveys) and (2) palms at least eight years since planting to reduce variation in yield due to crop age Hoffmann et al., 2017). At each farm site, we had one survey plot per farm as most farms were too small to fit more than one survey plot. We positioned survey plots randomly within the farm, and at least 50m from the farm boundary to minimise potential edge effects on vegetation structure and ant communities. All survey sites were at least 150m apart to minimise issues of spatial autocorrelation and pseudoreplication in our analyses (see Chapter 3; Lucey & Hill, 2012).

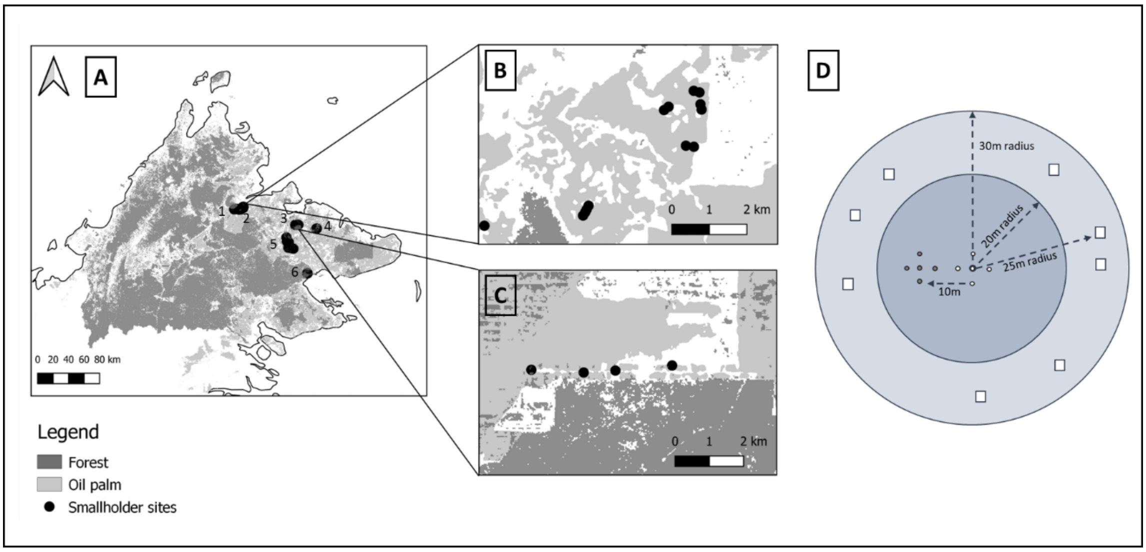

**Figure 2.** (**A-C**) Map of smallholder oil palm farms (n = 39) located across six governance areas in Sabah, Malaysian Borneo: site 1 (Ulu Sapi; n = 6 farms), site 2 (Reka Halus; n = 11 farms), site 3 (Gomantong; n = 4 farms), site 4 (Sukau; n = 2 farms), site 5 (Paris-Batu Puteh; n = 11 farms), and site 6 (Tampenau, independent smallholders; n = 5 farms). The landcover category 'forest' maps above ground carbon density (ACD) greater than 40 Mg C ha$^{-1}$ at 30m spatial grid resolution (sourced from (Asner, Broderick, and Heckler 2021), and the category 'oil palm' shows the extent of plantations and smallholder farms at 10m resolution (using Sentinel-1 and Sentinel-2 data; sourced from (Descals et al. 2020). (**D**) Sampling design on each farm, comprised of one 30m radius (0.28 ha) plot per farm, placed at least 50m from the farm boundary to reduce potential edge effects. Within each plot we recorded the number of standing deadwood and live trees in two size classes: (1) 10cm - 25cm diameter at breast height (DBH), (2) > 25cm DBH. Within 20m of the plot centre, we recorded the number of live saplings <10cm DBH. Along a 60m transect running from N to S through the centre of each plot, we recorded epiphyte % cover on palm stems and vegetation % cover within a 2m radius of each oil palm tree stem. We recorded understory and vegetation height, as well as % cover of various measures of vegetation, deadwood and bare ground in eight 1x1m quadrats placed on random bearings, 25m from the plot centre (white squares). Ground-dwelling ants were sampled using unbaited pitfall traps (white circles) over a period of six days; we placed five traps at the centre of the sites over three days, and then traps were moved and placed 10m from the initial traps and left for a further three days.

### 4.3.2. Characterising local farm management and temperature conditions

To assess farm management practices, we conducted interviews with smallholder farmers to collect information about farm characteristics, management practices (e.g., fertiliser application, herbicide application and harvesting) and fresh fruit bunch (FFB) yield (see SI section S1-3). We calculated yield as FFB ha$^{-1}$ yr$^{-1}$ from the average reported yield per harvest. We created an index of overall farm management intensity by synthesising the information we collected from interviews on nine management practices. Practices were assigned a value of 1 if they were more intensive (i.e., above average for our study farms) or a value of 0 if they were less intensive (i.e., below average). The farm management intensity index (ranging from 0 to 1) was calculated as the total values divided by the total number of management practices (for a detailed description of methods, see Chapter 2; Gutierrez Al-Khudhairy et al., 2023).

To characterise the understory vegetation on farms, we measured 18 vegetation parameters within a 0.28 ha circular plot (i.e., 30 m radius plot; Fig. 2) within each smallholding, using a combination of quadrats, transects and circular plot sampling (see Fig. 1 for further details). Circular plots were used to sample tree and sapling stand within oil palm habitats as this method produces less biased estimates compared to square plots (Paul et al., 2019). We then applied a principal component analysis (PCA) to the understory vegetation data to reduce the number of variables and potential collinearity in subsequent analyses. As outlined in Chapter 2, the first principal component (PC1) accounted for 25% of the total variance, which was positively associated with vegetation height and cover (>10 cm height) and palm contour vegetation cover, and was negatively related to leaf litter depth (Table S2). The second principal component (PC2) accounted for a further 15% of the total variance, and was positively associated with the occurrence of non-palm large trees and saplings, leaf-litter depth, and cover, and was negatively associated with bare ground cover (Table S3). We included PC1 and PC2 in our analyses as measures of understory vegetation cover and structure.

We recorded the daily mean, minimum and maximum temperatures (°C) on farms by averaging measurements from paired sensors (Hobo® loggers), placed at the centre of each farm plot. Loggers were positioned 1.5m above the ground and avoided direct sunlight. Readings of air temperature were taken at 10-minute intervals over the entire period of pitfall sampling (six days). There was high correlation between the temperature variables ($r > 0.8$; Table S4), so we used Principal Component Analysis (PCA) to reduce the number of temperature variables (see Table S5). The first principal component (PC1) accounted for a large proportion of the total variance (75%), and was positively associated with mean daily temperature, maximum daily temperature and diurnal variation (i.e., difference between daily min. and max. temperature) (Table S6). We subsequently refer to the principal component derived from the PCA as ‘local farm temperature’.

### 4.3.3 Characterising the landscape surrounding oil palm smallholdings (distance from road and forest extent)

We used Geographic Information Systems software (QGIS) to characterise the landscape surrounding oil palm smallholdings. To calculate the proximity of farms to main roads, we measured the straight line Euclidean distance from the centre of each farm to the closest road or motorway, as a proxy for human disturbance (e.g., light, noise, temperature and vegetation; Phillips et al., 2021) and as a pathway of human-mediated ant dispersal (Bullock et al., 2018; Gippet et al., 2019), using the HOTOSM Malaysia Roads layer available on OpenStreetMap. We characterised the percentage of forest cover surrounding smallholder farms at two scales (concentric circles of 0.5 and 1km diameter around the centre of the smallholder plots) using the Asner et al., (2021) Sabah map of forest carbon stocks (30m spatial resolution) with a threshold of above ground carbon density greater than 40 Mg C ha$^{-1}$. We selected these scales based on previous study findings of forest fragments influencing ant communities within oil palm habitats in Borneo (Lucey et al., 2014; Rizali et al., 2021). Small forest fragments of poor quality (<~200ha) have been shown to contribute weakly to ant diversity within plantations (Lucey et al., 2014), so we also assessed the influence that proximity to PAs has on within-farm ant communities by calculating the distance of smallholder farms to the nearest edge of a protected forest Area (PA) using maps sourced from Protected Planet (UNEP-WCMC, 2023). All PAs within the landscape were > 1km distance from our smallholder study sites, so we were not able to assess the effect that percentage of PA cover within a 1km boundary around smallholder farms has on within-farm ant communities.

### 4.3.4 Sampling ground-dwelling ant communities on oil palm smallholdings

We sampled ground-dwelling ants at each farm plot using pitfall trapping over six days (see figure 2). This method was preferred over Winkler extraction for sampling ground-foraging ants due to the low amount of leaflitter available on farms, and this method allowed us to sample both diurnal and nocturnal species. Pitfalls containing 70% ethanol were covered with a rain cover and lined with fluon (BioQuip) to reduce the surface traction of the pitfall walls. Non-reproductive individuals were identified to morphospecies or species where possible, following published identification keys (Fayle et al., 2014) and online resources (antwiki.org). Species were then classified as native or non-native to Borneo according to their status from online resources (antwiki.org). Morphospecies were assigned a native or non-native status according to the geographic distribution of the genus of that morphospecies. For example, if the majority of species from that genus are native to Borneo, we assumed the morphospecies to be native.

### 4.3.5 Data analysis

All statistical analyses were conducted in R version 4.2.2 (R Core Team, 2022).

#### 4.3.5.1 Quantifying ant species richness and functional diversity metrics

We examined the ecological resilience of ant communities on each farm in terms of species sensitivity to environmental change and the redundancy of functional traits within the total community (i.e., functional redundancy). More specifically, we use measures of native and non-native species richness (raw taxonomic richness) and two metrics of functional trait diversity: functional richness (FRich) and functional dispersion (FDisp). With these three metrics, we make inferences about the size of the functional trait space, how species are distributed within the trait space, and how much redundancy there is within trait space. To calculate our functional diversity metrics, we measured ants to collect information on six morphological ant traits related to diet and foraging strategy (Parr et al., 2017): body size, head elongation, relative mandible length, relative clypeus length, relative leg length, and eye position (on average 3 individuals measured for each species; see Chapter 3 for more specific details). We transformed the trait matrix using a Principal Components Analysis, from which we obtained two principal components (PCs), which we used together with the species occurrence matrix to construct 2-dimensional hypervolumes for each farm using kernel density estimation (KDE). Hypervolumes are a useful and commonly used tool for addressing trait-based ecological questions (Blonder, 2018), and kernel density estimation were preferred over other methods such as convex hulls as they place less emphasis on outlier datapoints (Mammola et al., 2021; Mammola & Cardoso, 2020). Hypervolumes were constructed using the *kernel.build* function in the *BAT* package in R (Cardoso et al., 2022), using the Support Vector Machine (SVM) algorithm as we found that it produced more reliable outputs at farms with fewer species compared to the default gaussian algorithm (see SI for further information comparing performance).

#### 4.3.5.2 Structural equation modelling

We used piecewise Structural Equation Modelling (SEM) (Lefcheck, 2016) to test for direct and indirect effects of local farm management (management intensity index, FFB yield, ground-vegetation cover, and non-palm tree abundance) and surrounding landscape factors (forest extent, proximity to roads) on ant species richness and metrics of functional diversity (Frich and Fdisp). SEMs are a useful tool to understand the direct and indirect interactions within multivariate systems as they combine multiple models within one framework, eliminating the need to develop single individual models to make inferences about non-linear interactions within complex ecological systems (Fan et al., 2016). PiecewiseSEMs are particularly useful as they can model non-linear relationships and incorporating random or nested effects within model structures, and are becoming increasingly used in the published literature to address multi-parameter relationships within complex ecological systems (Lázaro et al., 2020; Lefcheck, 2016; Prommer et al., 2020; Zemp et al., 2023). We use piecewise SEMs to make inferences about two mechanisms hypothesised to influence ecological resilience: Firstly, species sensitivity to environmental change and functional redundancy. Specifically, we test whether native species show higher sensitivity to environmental change compared to non-native species by assessing the effects of local farm management and landscape factors on the native and non-native species richness within a farm. Secondly, we test whether local farm management and the surrounding landscape influence the functional redundancy of ground-dwelling ant communities by assessing the effect of local farm management and landscape factors on species richness (both native and non-native), functional richness (Frich) and functional dispersion (Fdisp).

We constructed two piecewise SEMs, one modelling the effects of local farm management and surrounding forest factors with Frich as the final response variable and another with Fdisp. Full causal path models were constructed *a priori* by using published literature relating to the influence of local farm management and surrounding landscape factors on ant communities in agricultural landscapes to inform the hypothesised causal relationships (see Figure S1 and Table S9). Prior to fitting the piecewiseSEM to the component models, we first tested the individual component model fits using LMMs following Zuur (2010) and Whytock et al. (2017) and identified predictor variables with high collinearity (using the Variation Inflation Factor, VIF) to be removed from the model as these could result in unstable model outputs and potentially incorrect interpretation of the results. We constructed the two full causal networks (one causal network for modelling Frich and another for Fdisp) using the individual LMM component models with the *piecewiseSEM* and *nlme* packages in R. All component models were fitted with governance area as a random effect in models to control for potential effects of variations in elevation, soil and climate across sites. We updated the models by serially excluded non-significant pathways ($p < .05$) using the Akaike Information Criterion (AIC) score to check improvements in the model fit, and assessed for any missing or incomplete pathways ($p < .05$) that piecewiseSEM model output informs on. We evaluated the final SEMs goodness-of-fit using Shipley's test of directed separation following Lefcheck (2016), which tests the assumption that there are no missing relationships among unconnected variables (Shipley, 2000). We the re-fitted separate piecewise SEMs with the omitted variables causing collinearity to test our hypothetical relationships (see Table S11 for all model outputs that we tested; six additional models were fitted).

## 4.4 RESULTS

We recorded 136 ground-foraging ant species from 45 genera, of which 111 were native species and 25 were non-native (i.e., 18% of species occurring within oil palm farms were non-native). Positive associations between native and non-native species occurrence on farms (see Table S11), suggest there are no negative effects of non-natives on native species richness, and both native and non-native species contribute to higher total species richness on farms. Total ant species richness on farms varied considerably, from 6 to 31 species (mean = 18.6, sd = 5.9), with native species richness ranging from 5 to 26 species (mean = 14.6, sd = 4.7) and non-native species richness ranging from 1 to 10 species per farm (mean = 4.0, sd = 1.9). The most frequently occurring non-native species included *Anoplolepis gracilipes* (on 85% of farms), *Solenopsis molesta* (on 62% of farms) and *Tetramorium lanuginosum* (on 51% of farms).

The final SEM models (Figure 3) explained 20% of the variation in functional dispersion, 32% of variation in functional richness, 43% of non-native species richness and 28% of native species richness. There were good fits for the final piecewise SEMs based on the Fisher C-score for functional richness (Fisher's C = 48.09, p-value = 0.34, 46 degrees of freedom) and functional dispersion models (Fisher's C = 44.85, p-value = 0.52, 46 degrees of freedom) (see Tables S10 and S11 for full details on model evaluation). We observed wide variation in air temperature across farms, for daily mean (ranging from 25.6-30.0°C, mean = 23.4°C) and maximum temperatures (32.7-44.7 °C, mean = 35.3°C), but these were only weakly explained by our landscape and local farm management variables ($p > 0.05$, see Table S10 and S11), with the random effect (i.e., governance area) explaining up to 44% of the variation in temperature (marginal $R^2 = 0.04$ and conditional $R^2 = 0.48$). We conclude that temperature variables relate to the location of farms, e.g., local elevation and topography.

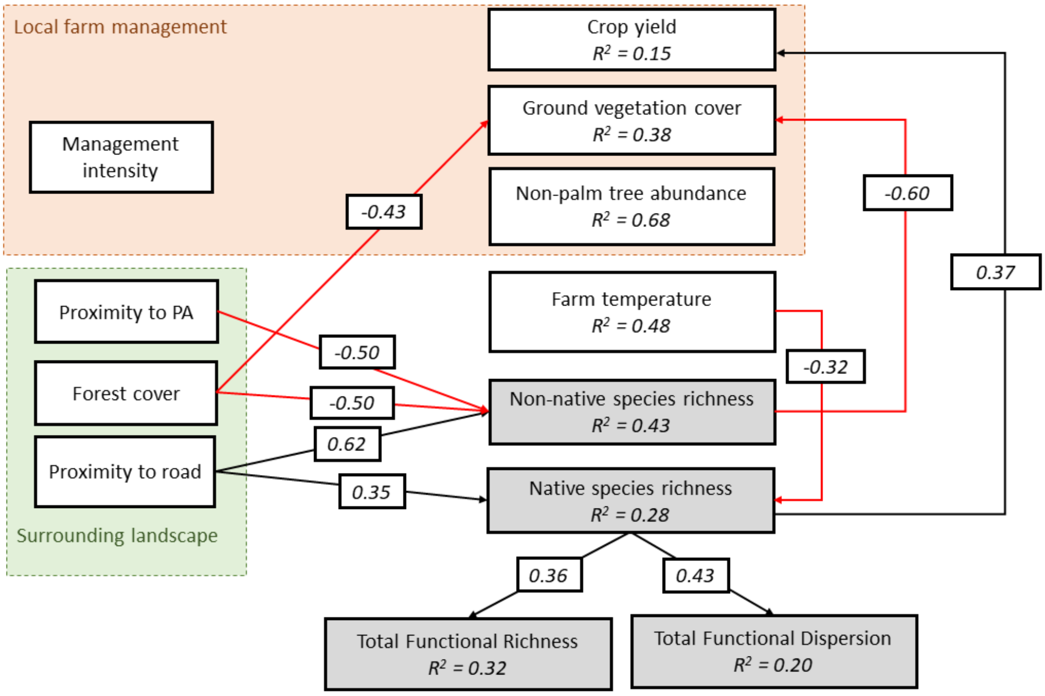

**Figure 3.** Combined outputs from the piecewise SEM models, with governance area fitted as a random effect. Measured variables are given in the white boxes, with grey shaded boxes indicating derived variables that we used as metrics of the ecological resilience of ant communities on oil palm farms. Arrows are given for significant paths ($P \geq 0{\cdot}05$), with red and black lines representing negative and positive relationships, respectively, and the direction of the arrow reflecting the direction of the relationship that was tested in the model (e.g., proximity to road as a predictor of higher native species richness). The standardized regression coefficients for each relationship are given in the small boxes. The conditional $R^2$ (i.e., the variance of both the fixed and random effects) for the component models are reported in the boxes of response variables. Individual piecewiseSEM model outputs are given in the supplementary information (see Tables S10 and S11).

### 4.4.1 Influence of local management and temperature factors on the ecological resilience of ground-dwelling ants

We observed an influence of local farm management variables on the species richness of ground-dwelling ants, but no direct or indirect relationships to farm functional richness (Frich) or functional dispersion (Fdisp) (Figure 3). Understory vegetation cover on farms had a strong negative association with non-native species richness ($p < 0.01$), but no effect on native species richness, suggesting a greater sensitivity of non-native species to understorey vegetation management, and preference for bare ground. However, we observed a positive direct association between native species richness and oil palm farm yields ($p = 0.03$), suggesting that there may be a beneficial interaction provided by native species, potentially from more predatory species controlling crop pests. Native species contributed positively to increased farm Frich ($p = 0.02$) and Fdisp ($p < 0.01$), whereas we detected no contribution of non-native species on these metrics of resilience, suggesting that native species maintain a much wider variety of functional roles on oil palm farms than non-natives. Lastly, we observed no direct or indirect relationships between farm management intensity and non-palm tree abundance with ant species richness or functional diversity (Frich and Fdisp).

Local air temperature had a significant but weak direct effect on native species richness on farms ($p = 0.04$), with the warmest farm supporting 56% fewer native species compared to the coolest (n = 13 and n = 23 respectively) (Figure 3). However, there was no direct influence of temperature on Frich or Fdisp. These results suggests that native species are sensitive to increasing local farm temperatures, without necessarily resulting in a loss of functional diversity (Frich nor Fdisp) (see Fig. 4B.1-B3 for a graphical representation of how local warming can reduce native richness without significantly affecting the functional richness and dispersion of the whole community).

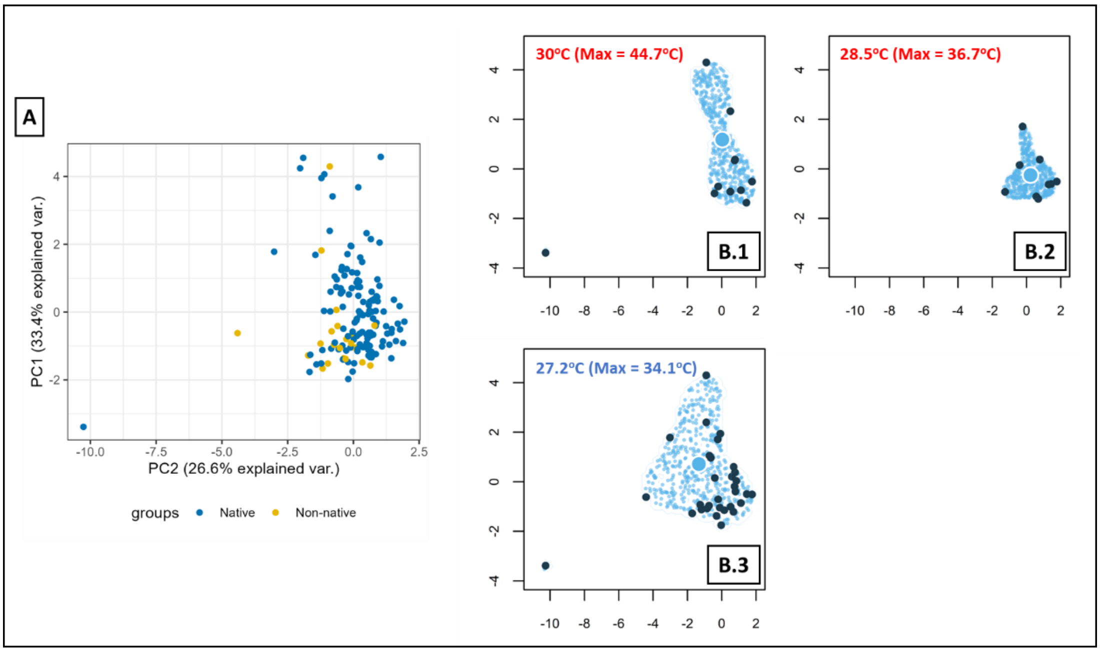

**Figure 4. A.** Representation of the functional trait space of ground-dwelling ant communities on oil palm farms, constructed based on six ant morphological functional shape traits. The first principal component (PC1) accounted for 33.4% of the total variance, which increased with relative clypeus length, relative leg length and body size (Tables S2 and S3). The second principal component (PC2) accounted for a further 26% of the total variance, and increased with mandible length but decreased with head elongation and distance between the eyes (Tables S2 and S3). The outlier point (PC1 = -3.4 and PC2 = -10.3) corresponds to *Strumigenys liophila*, which has particularly short mandibles relative to its head elongation. **B.1-B3.** Hypervolumes representing the functional trait space of ant communities within oil palm smallholdings with (a-b) above and I below average mean and maximum temperatures across our study sites (27.6°C and 35.2°C respectively). (a) Farm with a functionally rich and diverse ground-dwelling ant community but low functional redundancy (total species richness = 13, native richness = 10, non-native richness = 3, Frich = 10.3, Fdiv = 1.9). (b) Farm with a functionally poor ant community and low functional redundancy (total species richness = 10, native richness = 8, non-native richness = 2, Frich = 4.6, Fdiv = 0.9). (c) Farm with a functionally rich ant community and higher functional redundancy (total species richness = 31, native richness = 26, non-native richness = 5, Frich = 21.2, Fdiv = 1.9). Blue dots represent the probabilistic hypervolume trait space determined by the kernel.build function in R with boundary using the SVM method, which were used to calculate our functional diversity metrics (Frich and Fdiv).

### 4.4.2 Influence of landscape factors on the ecological resilience of ground-dwelling ants

We observed both direct and indirect effects of landscape factors on ground-dwelling ant species richness, but no direct influence of landscape factors on the functional diversity

(Frich and Fdisp) of ant communities on oil palm farms (Figure 3). Proximity to main roads had a significant positive effect on the occurrence of both native ($p < 0.01$) and non-native species on farms ($p < 0.01$), but this effect was stronger for non-native species (non-native $R^2 = 0.62$ and native $R^2 = 0.35$). Percentage forest cover also had a significant effect on ground-dwelling ants but only for non-native species, with a direct negative effect of forest extent on non-native species richness ($p = 0.03$). We also observed an indirect effect of forest cover on non-native species richness via its influence on farm ground-vegetation cover ($p =0.04$), and the influence this had on non-native species richness ($p < 0.01$). However, our SEM models show no influence of proximity to protected area or forest cover on native species richness on farms, suggesting no, or very weak, spill-over effects of farm ants from adjacent forest habitats.

## 4.5 DISCUSSION

Using functional trait information of native and non-native ground-dwelling ants, we were able to examine the influence of both local farm and wider landscape factors on the mechanisms that influence the ecological resilience (i.e., ability to resist and recover from environmental change) of ant communities on smallholder oil palm farms. We explore two species-level and community-level mechanisms hypothesised to influence ecological resilience: (a) species sensitivity to environmental change (measured using native and non-native species richness) and (b) functional trait redundancy (i.e., multiple species with similar functional traits; measured using species richness, functional richness and functional dispersion). Our findings from piecewiseSEM models suggest that while native and non-native species richness were positively associated, they showed different responses to local farm and wider landscape changes and so contribute differently to overall ant community resilience on oil palm farms. More specifically, non-native species are more negatively influenced by increased farm vegetation cover and extent of forest in the surrounding landscape, whereas native species show negative associations with farms with higher temperatures. This could have negative implications for oil palm yields as we observed a positive association between native species richness and farm yields. Native species also contributed more to increasing the diversity of functional traits within oil palm farms. Our findings suggest that roads facilitate human-mediated dispersal of ants within smallholder landscapes, because we observed positive associations of proximity to roads for both native and non-native ant species richness.

### 4.5.1 Effects of local farm management on ground-dwelling ant communities

We found some limited evidence that local farm management influenced ground-dwelling ant communities on oil palm farms, but we only observed a negative association between farm vegetation cover and non-native species richness, and no effects on native species richness or farm functional diversity (Frich and Fdisp). There were no effects of management intensity on resilience. These results imply higher sensitivity of non-native species to changes in understory vegetation on farms, which is likely due the preference of non-native ants for open and anthropogenically-disturbed open habitats (Lee et al., 2021). For example, *Tetramorium simillimum*, a non-native ant observed at our study sites, shows a preference for nesting in open habitats and urban areas (Deyrup et al., 2000). Native species that persist on farms after land-use change may not be sensitive to understory vegetation if their persistence on farms indicates a high threshold to resist environmental disturbances. In fact, there is little shared overlap (7% of species) in ground-dwelling ant composition between smallholder oil palm farms and rainforest habitats (see Chapter 3), which suggests that few forest-dependent ant species persist after land-use change and so do not occur on oil palm farms.

Our results indicate a positive association between native species richness and oil palm yields of farms, but not with non-native richness. This may occur for various reasons. Firstly, ants can contribute to pest control and improve crop yields (Anjos et al., 2022). As native species on farms tend to fill more predatory functional roles on farms (see Chapter 3), a higher richness of native species on farms may result in the suppression of invertebrate pests that limit oil palm yields (Kamarudin et al., 2019). Alternatively, the correlation between oil palm yields and native species richness may reflect an influence of a third factor that was not measured in our study. For example, an increase in native ant species could be associated with soil microbial or fungal communities (Huang et al., 2020) which can vary widely across oil palm plantations (Kirkman et al., 2022), and could in turn affect crop health and yields (Lankau et al., 2022). Hence, we recommend future studies to further explore the contribution of native ant species to biological pest control, because this biodiversity benefit could have significant implications for smallholder farmers.

### 4.5.2 Effects of local farm temperature on ground-dwelling ant communities

We found an effect of local farm temperatures on native species richness, with the warmest farm supporting 80% fewer native species relative to the coolest farm. These findings are consistent with previous findings that native ants exhibit sensitivity to thermal gradients and climatic changes (Boyle et al., 2021; Guo et al., 2020). There are several mechanisms that could be driving these results. Firstly, native species occurring on oil palm farms tend to have larger body sizes and more predatory diets (e.g., larger mandibles; see Chapter 3), which are traits typically associated with sensitivity to disturbance and climatic warming (Boyle et al., 2021; Senior et al., 2013). Native species may also have other traits that make them more sensitive to disturbances, such as smaller colony sizes and social structures (Ingram, 2002; Tsutsui & Suarez, 2003), which would also increase their vulnerability to environmental changes such as climatic warming. Lastly, changes in farm temperature may indirectly affect ant species on farms by altering local resource availability (Parr & Bishop, 2022).

We expected to observe a negative effect of climatic warming on the functional diversity (richness and dispersion) of ground-dwelling ant communities due to a disproportionate loss of more predatory and larger-bodied species (Boyle et al., 2021; Senior et al., 2013). However, contrary to our expectations, we observed no reductions in our functional diversity metrics (functional richness and functional dispersion) on warmer farms, suggesting that increased temperatures only reduced the native species richness (i.e., loss of functional redundancy within the trait space occupied by native species) within farms without necessarily affecting functional diversity. The lack of any loss of functional diversity may be due ants being able to exhibit a high degree of morphological, behavioural, and phenotypic plasticity, such as altering foraging times during cooler times of day and switching diets to other available resources (Balzani et al., 2021; Ingram, 2002; Putri et al., 2021), meaning that larger bodied or predatory species can still occur on farms with temperatures that exceed their thermal limits (Boyle et al., 2021). If this is the case, our results suggest that some ant species on farms may show some capacity to adapt to increasing local temperatures, which could have positive implications for the ecosystems functions that they contribute to, and so should be explored further (Parr & Bishop, 2022).

### 4.5.3 Effect of wider landscape factors on ground-dwelling ant communities

Surrounding landscape factors can influence local species richness and diversity by mediating species dispersal and by providing population source for colonising ants within the landscape (Brudvig et al., 2009; Oliver et al., 2015). As such, we expected to observe a positive effect of surrounding forest extent on local farm richness and functional diversity. However, contrary to expectations and previous findings in other taxa (e.g., birds; Hamer et al., 2021), our results suggest that the extent of forest habitat in the landscape decreased non-native ant species richness. Moreover, there is little overlap in species community similarity between forest habitats and farms (see Chapter 3), implying that farms contain few forest-dependent native ant species. Other studies have found evidence of spill-over effects from forest remnants to oil palm habitats, but findings are variable (Gray et al., 2016; Lucey et al., 2014; Lucey & Hill, 2012). Spillover is typically observed when plantations are positioned directly adjacent to forest habitats, and spillover is higher from large, high quality forest sites (Lucey et al., 2014). Our results may be due to the fact that only a small proportion of farms in our study were relatively near to large, protected forest remnants (e.g., Gomantong protection forest reserve). If the intervening habitat matrix between forest remnants and oil palm smallholdings are unfavourable for the movement and survival of more forest-dependent species (avoidance of unfavourable matrix; Bullock et al., 2018), then surrounding forests within smallholder landscapes are unlikely to contribute to the local ant richness and diversity on farms. However, we emphasize that it is still important to conserve forest habitats within oil palm landscapes because these forest areas benefit other taxa (e.g., birds; Hamer et al., 2021) and important ecosystem functions (e.g., pollination; Power et al., 2022).

Our findings that increasing forest extent reduces non-native species richness on farms support previous findings that isolation from forest fragments increases the abundance of invasive ant species on oil palm plantations (Rizali et al., 2021). This finding may be explained by the effect of forest remnants on the ground-vegetation cover on our farms, as increased forest fragmentation can contribute to higher occurrence of invasive plant species and fewer native tree saplings on oil palm plantations (Waddell et al., 2020). Ants can exhibit associations or preferences with certain plants (e.g., myrmecophiles; Lach et al., 2010; Savage et al., 2009), and so farms with more surrounding forest may support a higher dominance of plant species that are less favourable to non-native ants. Alternatively, non-native species exhibit a preference for more disturbed land-use types (Liu et al., 2023), and so a higher forest extent around farm may reflect a decreased availability of disturbed habitats within the landscape, and so contribute to reduced local non-native species richness on farms.

Transport links have been shown to be important pathways for human-mediated dispersal of ants and other invertebrates via the movement of vehicles and trade of goods (Bullock et al., 2018; Gippet et al., 2019), which may explain why we observed a positive effect of proximity to main roads on ant species richness. Our study area is characterised by linear settlements along main roads with high human-related activity (e.g., food markets, residential housing, restaurants). As such, farms positioned closer to main roads may receive higher propagule pressures from ants (Meyer et al., 2021), contributing to higher ant species richness (Chen & Adams, 2018). Human-mediated dispersal is usually associated with the spread of invasive species (Suarez et al., 2001), however, we observed a positive effect of proximity to roads for both native and non-native species. This suggests that native species that persist within oil palm landscapes may also benefit from human-mediated dispersal along transport routes, which is supported by the fact that some native species occurring at our farms are widely spread and invasive species in other geographic regions (e.g., *Tapinoma melanocephalum;* Zima et al., 2016), and also share traits with non-natives that facilitate human-mediated dispersal (e.g., small body size, dietary generalism and opportunistic nesting; Holway et al., 2002).

These results have important implications for the ecological resilience of oil palm farms as they suggest that roads may provide some connectivity to smallholder oil palm farms within these highly modified agricultural landscapes via human-mediated dispersal. Landscape connectivity has been recognised as an important factor contributing to greater resistance and improving recovery rates of ecological communities (Shackelford et al., 2018) but is rarely consider in the context of roads. Hence, findings ways to improve connectivity to more isolated oil palm farms, whether by roads or the retention of habitat corridors (Gray et al., 2017), may be important for maintaining the ecological resilience on oil palm farms to facilitate community recovery from species loss following environmental changes.

### 4.5.6 Implications of native and non-native responses for ecological resilience of oil palm farms

We used species richness, functional richness and functional dispersion as metrics of ecological resilience of oil palm farms, with farms supporting higher species richness and a more even distribution of species within the ant functional trait space contributing to higher ecological resilience. Our findings suggest that native and non-native species exhibit sensitivity to changes at the local farm and wider landscape scale, but to different factors. For example, farms support higher non-native species richness in landscapes that have less forest cover, whereas higher native species richness is observed on cooler farms. However, we observed no direct effect of local farm and wider landscape factors on our functional diversity metrics (FRich and FDiv), indicating that local and landscape-scale changes contribute to a loss of redundancy of species which have similar traits (i.e., functional redundancy) rather than a loss in the variety of functional roles performed by ant communities on oil palm farms.

However, loss of functional redundancy may not be equal throughout the trait space. Native species occupy a wider area of the functional trait space, whereas non-natives only occupy a subset of the functional trait space of natives. Hence, increased farm vegetation cover or forest extent only results in a loss of functional redundancy within the subset of trait space occupied by non-native species. In comparison, increases in local farm temperature may result in a loss of functional redundancy throughout the entire trait space. This implies that loss of native species could have more severe implications for the ecological resilience and functioning of ground-dwelling ants, especially under future climatic warming. The daily maximum temperatures at some of our sites reached 44.7°C, exceeding the thermal limits of most ant species occurring within oil palm landscapes (Boyle et al., 2021). With a predicted 1.5°C global warming (IPCC), this may have serious consequences for native species if they are less adaptable, resulting in less redundant farm communities that are more vulnerable to further species loss and provisioning of ecosystem functions (Folgarait, 1998; Oliver et al., 2015). However, findings from other studies show that ecosystem functions are resilient to disturbances if other species within the community can replace the functional role of the species that are lost (Ewers et al., 2015; García et al., 2018). In fact, generalist functions such as scavenging and decomposition were still maintained on oil palm farms with a higher proportion of non-native species (see Chapter 3), as well as showing resilience to drought events in oil palm agroforests (Eycott et al., 2019). We recommend that future research investigates the relationships between response-effect traits on specialist ecosystem functions (e.g., pest predation or pollination) under future warming scenarios, and the implications that native species loss could have for oil palm farm yields.

### 4.5.7 Oil palm management and general implications

Oil palm landscapes in Sabah may expand, even under compliance with RSPO zero-deforestation commitments, and experience further development and land-use change with the construction of the Pan Borneo Highways, which will run from the East to the West coast of the region (Abram et al., 2022). Moreover, maximum temperatures on Borneo are projected to increase by 3.0-4.6°C by the end of this century, alongside changes in rainfall patterns (Sa'adi et al., 2020). Our finds show a 57% decrease in species richness between the warmest and coolest farms (12°C difference in maximum temperature). A further increase in 3°C may have serious consequences for the resilience and functioning of ecological communities, potentially affecting agricultural production within these landscapes. However, it appears that factors affecting the resilience of oil palm farms that were identified in this study (e.g., proximity to roads and climatic warming) are out of the control of smallholder farmers, and there were no noticeable benefits of farmers carrying out more sustainable management practices on their farms for benefitting native ant species richness. Nonetheless, we still recommend that farmers continue to carry out sustainable management of their farms as this is likely to have other benefits for smallholder farmers, such as improved soil fertility, reduced chemical inputs, and improved financial cost-benefits. Finally, we recommend that stakeholders involved with the development of sustainable oil palm agriculture should consider both local farm management and the surrounding landscapes for building more resilient oil palm landscapes. Improving connectivity and facilitating species recovery in these highly modified landscapes will be important for boosting biodiversity and increasing ecological community recovery from environmental disturbances. Protecting biodiversity and ecosystem functioning requires careful landscape planning because roads may facilitate dispersal of ant species, but they will limit the dispersal of others (Laurance et al., 2009), and not all taxa may show as much adaptability to environmental changes and disturbance as ants. Involvement and collaboration between stakeholders, NGOs (e.g., Wildasia) and landscape initiatives to protect biodiversity (e.g., through RSPO and HCVRN) will be especially important for address these complex and multi-faceted problems affecting the resilience tropical agricultural landscapes.

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# CHAPTER 4 APPENDIX

# Landscape-scale and local factors influence the ecological resilience of oil palm smallholdings: Supplementary Information

## <u>Section S1 – Information leaflet that was presented to farmers before receive verbal and written consent to participate in this study</u>

### Impacts of Agricultural Management Practices within Oil Palm Smallholder Plantations

Funded by UK Research and Innovation (UKRI) through a Natural Environment Research Council Industrial CASE studentship (project number NE/R007624/1).

We are conducting an investigation for a research project, which aims to identify management practices that can increase the sustainability of smallholder oil palm production. Data from this investigation will help smallholder farmers to support certification with the Round Table for Sustainable Palm Oil by identifying agricultural management practices that can boost yields, whilst minimising environmental damage. This investigation is part of a project which is determining whether landscapes that support high levels of wildlife and ecosystem functioning can also maintain high oil palm crop yields and support local livelihoods.

Agricultural management practices employed by smallholder farmers can vary considerably, resulting in variable yields and incomes, and potentially differing impacts on wildlife and the environment. There is potential to boost yields within smallholder farms by employing better management practices. For this, more information is required about current oil palm production and management practices, particularly, examining the relationships between yield, wildlife and management intensity.

We are surveying smallholders to assess how their crops are managed and to quantify the relationship between oil palm crop management and yields. We will survey wildlife (particularly ants) on selected smallholdings differing in their management practices, to assess the impacts of management on wildlife and yield. In this way, we aim to improve the scientific understanding of crop management for oil-palm smallholders, improving crop yields and increasing household incomes without negatively affecting wildlife.

**Biodiversity surveys:**

On each selected smallholding, we will survey wildlife associated with oil palms in the following ways:

- Ants – These will be collected in 10 small plastic tubes, each half-filled with water, alcohol and washing-up liquid, and buried flush with the soil surface for a total period of 6 days. We will leave different types of bait within meshed cages for a period of 24 hours to measure bait removal by ants.

- Decomposition – We will leave 10 small nylon mesh bags filled with leaves and palm fronds for a period of 30 days to measure decomposition of organic material.
- Resource removal – We will leave 8 metal mesh cages over a period of 2 days to measure the removal of fish and seed bait by ants and other invertebrates. We will also place bait on a card with an insect-trapping glue barrier to measure bait removal by non-invertebrates.
- Habitat assessment – We will assess vegetation structure and impacts of management within a 30 m circular plot placed within each farm. These measures will include assessment of ground cover, canopy cover from trees, air temperature, soil characteristics, and presence of empty FFBs and frond piles. To assess this, we will leave a data-logger to record temperature, and we will collect soil samples for further analysis.

**Some questions you may have:**

- If I say yes to participating, what will this involve? You will be asked to complete a questionnaire with myself and the help of one my research assistants. This should take about 10-15 minutes. You will not be asked for anything else other than permission for us to survey your smallholding as described above.
- Where and when will we complete the questionnaire? It could be your house or any other place where you usually spend your time, wherever you feel most comfortable. You can also choose a good time to meet.
- What happens if I change my mind? If you have not completed the questionnaire, your name will be removed from our list of participants. If you have completed it, the paper copy of the form will be destroyed at the end of the project. However, the anonymised data (with your name replaced by a three-digit code) will be retained in electronic format for use in the project. Project partners: University of York, UK; Proforest, UK; Wild Asia, Malaysia; Universiti Malaysia Sabah, Malaysia

## Section S2 – Written consent form that was presented to smallholder farmers that participated in this study

| **Consent to take part in a research project on the Impacts of Agricultural Management Practices within Smallholder Oil Palm Plantations** | **Add your initials next to the statement if you agree** |
|---|---|
| I confirm that I have read and understand the information sheet explaining the research project and I have had the opportunity to ask questions about the project. | |
| I understand that my participation is voluntary and that I am free to withdraw at any time without giving any reason and without there being any negative consequences. In addition, should I not wish to answer any particular question or questions, I am free to decline. I can indicate a wish to withdraw by informing Wild Asia. All questionnaire sheets completed by me will be destroyed at the end of the project. However, anonymised questionnaire data and biodiversity data will be retained in an electronic format for future use by the project. | |
| I give permission for members of the research team to have access to my anonymised responses. I understand that my name will not be linked with the research materials, and I will not be identified or identifiable in the report or reports that result from the research. I understand that my responses will be kept strictly confidential. | |
| I give permission for members of the research team to carry out wildlife and habitat surveys on my smallholding as described in the project information leaflet. | |
| I agree for the data collected from me to be stored and used in relevant future research in an anonymised form. | |
| I understand that relevant sections of the data collected during the study may be looked at in anonymised format by individuals from the University of York or from project partners where it is relevant to my taking part in this research. I give permission for these individuals to have access to my anonymised records. | |
| I agree to take part in the above research project and will inform Wild Asia staff should my contact details change. | |

| | |
|---|---|
| Name of participant | |
| Participant's signature | |
| Name of Wild Asia staff | |
| Signature | |
| Date* | |

*To be signed and dated in the presence of the participant. Once this has been signed by all parties the participant should receive a copy of the signed and dated participant consent form and the project information sheet. A copy of the signed and dated consent form should be kept with the completed questionnaire form, which must be kept in a secure location.

**Section S3 – Written consent form that was presented to smallholder farmers that participated in this study**

| | **Sufficient responses (>70% complete)** |
|---|---|
| **(A) Questions about the farm** | |
| Do you own or rent the farm | Yes |
| For how many years have you farmed here? | Yes |
| How big is your farm? | Yes |
| What is the size of the area planted with oil palm trees within your farm? | Yes |
| Do you have land on your farm that isn’t planted with oil palm? If so, what is the land used for and what size does the area cover? | Yes |
| How old is the oil palm crop on your farm? | Yes |
| Have you replanted more than one crop cycle on your farm? | Yes |
| What was on your land before you planted oil palms here? | Yes |
| **(B) Questions about oil palm fruit yield** | |
| How many oil palm trees are growing within your farm? | Yes |
| How many productive/fruiting oil palm trees are growing within your farm? | Yes |
| How often is FFB harvested on your farm? | Yes |
| What weight of FFB do you obtain per harvest on average from your farm? | Yes |
| What income do you obtain per tonne of FFB on average from your smallholding? | Yes |
| Do you measure FFB yourself or by a trader or mill, and how do you measure the weight of each bunch (weighing scale, estimate or not measured)? | Yes |
| What seed type do you plant (tenera, dura, psifera or unsure)? | No |
| **(C) Questions about farm management** | |
| Do you plant any other crops beneath your palms? | Yes |
| How often do you weed your crops? | Yes |
| What method do you use for weeding? | Yes |
| When was the last time you weeded on your farm? | No |
| *Do you clear a circle without vegetation around the base of each palm trunk? | Yes |
| Do you contour around each palm trunk to help prevent rainfall, nutrients or fertilisers flowing away? | Yes |
| *Do you apply empty fruit bunches to your farm, and if so how often? | Yes |
| How often do you prune? | Yes |
| What do you do with the cut fronds? | Yes |
| Do you remove ferns and other vegetation from the trunks of the palms? | Yes |
| Do you change the way you manage your crop depending on tree age? For example, do you apply more chemical nutrients, or shorten the harvesting interval, as your oil palm trees get old? | No |
| **(D) Questions about agricultural inputs** | |

| | |
|---|---|
| *Do you apply chemical herbicides?<br>(iv) If so, how much, how often and what type?<br>(v) If not, why not?<br>(vi) If you used to but have now stopped, how long ago did you stop applying? | Yes<br>Yes<br>No<br>No |
| Do you apply pesticides?<br>(iv) If so, how much, how often and what type?<br>(v) If not, why not?<br>(vi) If you used to but have now stopped, how long ago did you stop applying? | Yes<br>No<br>No<br>No |
| Do you apply chemical or organic fertilizers?<br>(iv) If so, how much, how often and what type?<br>(v) If not, why not?<br>(vi) If you use to but have now stopped, how long ago did you stop applying? | Yes<br>Yes<br>No<br>No |

**Table S1.** Questionnaire used for interviews with smallholder oil palm farmers to collect information relating to farm history and environmental characteristics, palm fruit yield and management inputs. Questions that we had sufficient responses for from farmers (>70% of responses for that question; see SI 2) were considered for developing the management intensity index. Responses to questions that were used in the index are highlighted in bold, and all other responses were used for analyses of Best Management Practices (BMPs; indicated by *), as explanatory variables in statistical models, or for the general understanding of smallholder farm management across study sites.

## Section S4 – Outputs from principal component analysis on farm vegetation parameters

| | Eigenvalue | Proportion of variance explained | Cumulative variance |
|---|---|---|---|
| **PC1** | 4.55 | 0.25 | 0.25 |
| **PC2** | 2.78 | 0.15 | 0.41 |
| **PC3** | 2.03 | 0.11 | 0.52 |
| **PC4** | 1.63 | 0.09 | 0.61 |
| **PC5** | 1.40 | 0.08 | 0.69 |
| **PC6** | 1.06 | 0.06 | 0.75 |
| **PC7** | 0.94 | 0.05 | 0.80 |
| **PC8** | 0.69 | 0.04 | 0.84 |
| **PC9** | 0.64 | 0.04 | 0.87 |
| **PC10** | 0.62 | 0.03 | 0.91 |
| **PC11** | 0.52 | 0.03 | 0.94 |
| **PC12** | 0.34 | 0.02 | 0.96 |
| **PC13** | 0.25 | 0.01 | 0.98 |
| **PC14** | 0.16 | 0.01 | 0.99 |
| **PC15** | 0.14 | 0.01 | 0.98 |
| **PC16** | 0.12 | 0.01 | 0.99 |
| **PC17** | 0.07 | 0.00 | 1.00 |
| **PC18** | 0.07 | 0.00 | 1.00 |

**Table S2.** Principal component summary statistics. Eigenvalues of principal components and percentage of variance associated with each (obtained by applying principal components analysis to the 18 vegetation structure parameters collected from smallholder farm surveys). PC1 and PC2 scores were used in analyses, as measures of understorey vegetation cover.

| **Vegetation Structure Parameters** | **PC1** | **PC2** | **PC3** | **PC4** | **PC5** | **PC6** |
|---|---|---|---|---|---|---|
| Large tree count (>25cm DBH) | -0.15 | 0.40 | -0.10 | 0.01 | 0.24 | -0.02 |
| Small tree count (>10cm and <25cm DBH) | -0.20 | 0.26 | 0.01 | -0.16 | -0.27 | -0.24 |
| Sapling count (<10cm DBH) | 0.11 | 0.33 | 0.03 | -0.53 | -0.14 | 0.07 |
| Standing deadwood count | -0.09 | -0.10 | 0.32 | 0.02 | -0.16 | -0.69 |
| Understory density (0-10) | 0.14 | -0.05 | 0.19 | -0.40 | 0.40 | 0.24 |
| Canopy openness (%) | 0.07 | 0.03 | 0.53 | 0.12 | -0.15 | 0.33 |
| Palm contour vegetation cover (%) | 0.36 | 0.00 | 0.10 | -0.07 | 0.24 | -0.07 |
| Epiphyte cover (%) | -0.15 | -0.17 | 0.36 | -0.17 | 0.40 | -0.19 |
| Understory height (m) | 0.14 | 0.22 | -0.03 | 0.26 | 0.23 | -0.06 |
| Vegetation height (cm) | 0.32 | 0.20 | -0.20 | -0.20 | -0.22 | 0.04 |
| Leaf litter depth (cm) | -0.30 | 0.39 | 0.05 | 0.04 | 0.00 | -0.05 |
| Leaf litter cover (%) | -0.29 | 0.42 | 0.02 | 0.00 | 0.13 | -0.07 |
| Ground vegetation cover (<10cm height) | 0.36 | 0.03 | 0.02 | 0.00 | 0.13 | -0.07 |
| Vegetation cover (>10cm height) | 0.37 | 0.24 | 0.01 | 0.05 | -0.02 | -0.03 |
| Moss cover (%) | -0.16 | -0.15 | -0.19 | -0.56 | 0.08 | -0.14 |
| Bare ground cover (%) | -0.29 | -0.33 | -0.20 | -0.11 | -0.04 | 0.14 |
| Fallen deadwood cover (%) | -0.23 | 0.12 | 0.00 | 0.15 | 0.44 | 0.13 |
| Standing deadwood cover (%) | -0.09 | 0.08 | 0.55 | -0.14 | -0.23 | 0.17 |

**Table S3.** Weighting factor of the first six principal components from the 18 vegetation structure parameters collected from smallholder farm surveys. A positive value indicates that the parameter correlates positively with the principal component, whilst a negative value indicates a negative correlation). PC1 and PC2 scores were used in analyses, as measures of understorey vegetation cover.

## Section S5 – Outputs from principal component analysis on local farm temperature variables

| | **Mean Temp** | **Min Temp** | **Max Temp** | **Var Temp** |
|---|---|---|---|---|
| **Mean Temp** | 1.00 | - | - | - |
| **Min Temp** | 0.70 | 1.00 | - | - |
| **Max Temp** | 0.80 | 0.31 | 1.00 | - |
| **Var Temp** | 0.66 | 0.12 | *0.94* | 1.00 |

**Table S4.** Pearson’s correlation values of local farm daily temperature variables recorded from smallholder farms (n = 39), averaged over a six day period. Very highly correlated values (r > 0.8) are given in italics.

| | **Eigenvalue** | **Proportion of variance explained** | **Cumulative variance** |
|---|---|---|---|
| **PC1** | 1.69 | 1.01 | 0.71 |
| **PC2** | 1.01 | 0.25 | 0.96 |
| **PC3** | 0.31 | 0.02 | 0.99 |
| **0.19** | 0.19 | 0.01 | 1.00 |

**Table S5.** Principal component summary statistics. Eigenvalues of principal components and percentage of variance associated with each (obtained by applying principal components analysis to the four daily temperature variables structure parameters collected from smallholder farm surveys. PC1 scores were used in analyses, as measures of local farm temperature.

| **Vegetation Structure Parameters** | **PC1** | **PC2** | **PC3** | **PC4** |
|---|---|---|---|---|
| Mean Temp | -0.56 | 0.24 | -0.77 | 0.21 |
| Min Temp | -0.34 | 0.79 | 0.50 | 0.02 |
| Max Temp | -0.56 | -0.29 | 0.10 | -0.77 |
| Var Temp | -0.51 | -0.48 | 0.39 | 0.60 |

**Table S6.** Weighting factor of the principal components from the four vegetation structure parameters collected from smallholder farm surveys. A positive value indicates that the parameter correlates positively with the principal component, whilst a negative value indicates a negative correlation). PC1 scores were used in analyses as a measure of local farm temperature.

## Section S6 – Correlation between landscape variables

| **Landscape parameters** | Forest 1km | Distance PA (km) | Distance road (m) |
|---|---|---|---|
| Forest 1km | - | | |
| Distance PA (km) | -0.26 | - | |
| Distance road (m) | -0.30 | 0.29 | - |

**Table S8.** Pearson’s correlation values of surrounding landscape variables. Highly correlated values (r > 0.8) are given in italics.

## Section S7 – Structural Equation Modelling

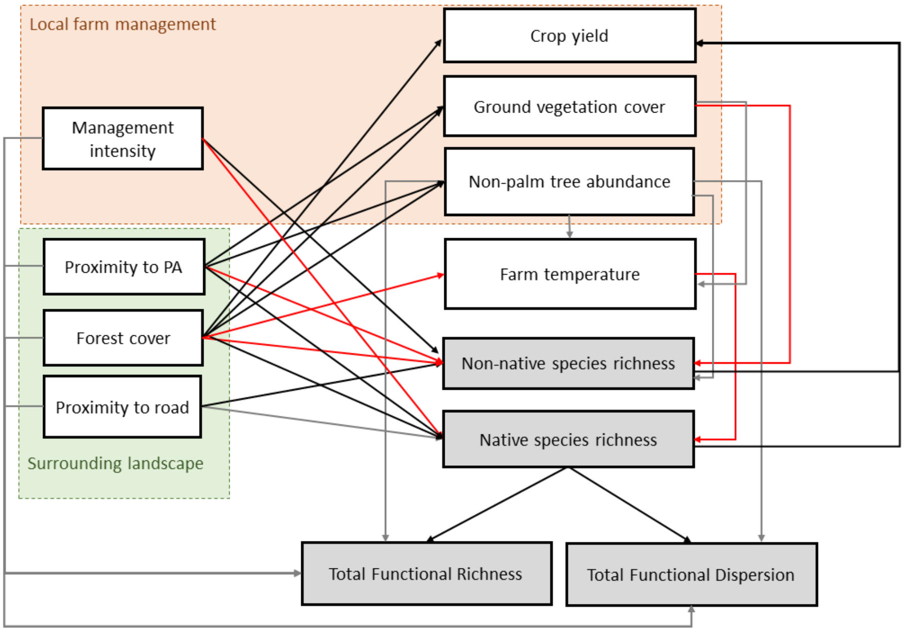

**Figure S1. Our *a priori* causal path model for the Structural Equation Model (SEM) based on our current knowledge.** Measured variables are given in the white boxes, with grey shaded boxes indicating derived variables that we used as metrics of the ecological resilience of ant communities on oil palm farms. Red and black arrows are given for significant paths ($P \geq 0{\cdot}05$), with red and black lines printing negative and positive relationships, respectively, and the direction of the arrow reflecting the direction of the relationship that was tested in the model (e.g., proximity to road as a predictor of higher native species richness). Grey arrows are given for paths given for non-significant paths ($P < 0{\cdot}05$) that were tested within the models.

**Table S9.** Summary of hypothesised relationships used to construct the causal pathways in the Structural Equation Models.

| **Response variable** | **Predictor variable** | **Hypothesised link between response and predictor variable** | **References** |
|---|---|---|---|
| **Crop yield** | Percentage forest cover | Landscape factors can influence crop yields through effects on local biodiversity that is beneficial to crop productivity. | (González et al., 2020) |
| | Non-native species richness | Ants can influence crop yields through predation of crop pests and effects on pollinating insects. | (Anjos et al., 2022; Denmead et al., 2017; Martínez-Núñez et al., 2021; Offenberg, 2015) |
| | Native species richness | Ants can influence crop yields through predation of crop pests and effects on pollinating insects. | (Anjos et al., 2022; Denmead et al., 2017; Martínez-Núñez et al., 2021; Offenberg, 2015) |
| **Ground vegetation cover** | Percentage forest cover | Forest fragments can influence plant propagule pressure within oil palm habitats. | (Waddell et al., 2020) |
| | Proximity to PA | Proximity to forest fragments can influence plant propagule pressure within oil palm habitats. | (Waddell et al., 2020) |
| **Non-palm tree abundance** | Percentage forest cover | Proximity to forest fragments can influence plant propagule pressure within oil palm habitats. | (Waddell et al., 2020) |
| | Proximity to PA | Proximity to forest fragments can influence plant propagule pressure within oil palm habitats. | (Waddell et al., 2020) |
| **Farm temperature** | Ground vegetation cover | Within-farm vegetation cover and complexity can influence local temperature conditions. | (Donfack et al., 2021; Luskin & Potts, 2011) |
| | Non-palm tree abundance | Within-farm vegetation cover and complexity can influence local temperature conditions. | (Donfack et al., 2021; Luskin & Potts, 2011) |
| | Percentage forest cover | Surrounding forest cover can influence local temperatures. | (Cohn et al., 2019) |
| **Non-native species richness** | Percentage forest cover | Forest habitats can provide a species pool for more forest-dependent species or limit occurrence of non-natives. | (Hamer et al., 2021; Lucey et al., 2014) |
| | Proximity to PA | Forest habitats can provide a species pool for more forest-dependent species or limit occurrence of non-natives. | (Hamer et al., 2021; Lucey et al., 2014) |
| | Proximity to road | Pathway for human-mediated dispersal of species and may contribute to higher colonisation of non-native species on farms. | (Bullock et al., 2018) |
| | Management Intensity | Farm management can introduce disturbance and influence biotic and abiotic conditions on farms. | (Ashton-Butt et al., 2018; Luke et al., 2019) |
| | Farm temperature | Local temperatures can limit ant species occurrence due to thermal limitations. | (Boyle et al., 2021) |

| | | | |
|---|---|---|---|
| | Non-palm tree abundance | Vegetation abundance and plant diversity influences invertebrate communities in oil palm habitats. | (Ashton-Butt et al., 2018; Luke et al., 2019) |
| | Ground vegetation cover | Vegetation abundance and plant diversity influences invertebrate communities in oil palm habitats. | (Ashton-Butt et al., 2018; Luke et al., 2019) |
| **Native species richness** | Management intensity | Farm management can introduce disturbance and influence biotic and abiotic conditions on farms. | (Ashton-Butt et al., 2018; Luke et al., 2019) |
| | Percentage forest cover | Forest habitats can provide a species pool for more forest-dependent species or limit occurrence of non-natives. | (Hamer et al., 2021; Lucey et al., 2014) |
| | Distance to PA | Forest habitats can provide a species pool for more forest-dependent species or limit occurrence of non-natives. | (Hamer et al., 2021; Lucey et al., 2014) |
| | Proximity to road | Pathway for human-mediated dispersal of species. May contribute to higher colonisation of non-native ants on farms. | (Bullock et al., 2018) |
| | Farm temperature | Local temperatures can limit ant species occurrence due to thermal limitations. | (Boyle et al., 2021) |
| | Non-palm tree abundance | Vegetation abundance and plant diversity influences invertebrate communities in oil palm habitats. | (Ashton-Butt et al., 2018; Luke et al., 2019) |
| | Ground vegetation cover | Vegetation abundance and plant diversity influences invertebrate communities in oil palm habitats. | (Ashton-Butt et al., 2018; Luke et al., 2019) |
| **Functional richness** | Management intensity | Environmental filtering of species with sensitivity to disturbance of more intensive farming activities. | No evidence from previous studies |
| | Non-native species richness | Non-native species may influence functional richness if they tend to have more similar traits (e.g., similar body size and head shape). | (Chapter 3) |
| | Native species richness | Native species may influence functional richness by introducing a wider variety of functional traits. | (Chapter 3) |
| | Percentage forest cover | May influence the occurrence of forest-dependent native species, introducing a wider variety of functional traits. | No evidence from previous studies |
| | Proximity to road | May influence the influx of non-native species, thereby influencing the variety of functional traits. | No evidence from previous studies |
| | Ground vegetation cover | May affect the richness of native and non-native species, influencing the variety of functional traits within farms. | No evidence from previous studies |
| | Non-palm tree abundance | May affect the richness of native and non-native species, influencing the variety of functional traits within farms. | No evidence from previous studies |
| | Farm temperature | May affect the richness of native and non-native species, influencing the variety of functional traits within farms. | (Boyle et al., 2021) |

| | | | |
|---|---|---|---|
| **Functional dispersion** | Non-native species richness | Non-native species may influence functional trait diversity if they tend to have more similar traits. | (Chapter 3) |
| | Native species richness | Non-native species may influence functional trait diversity if they have a wider variety of traits. | (Chapter 3) |
| | Management intensity | Environmental filtering of species with sensitivity to disturbance of more intensive farming activities. | No evidence from previous studies |
| | Percentage forest cover | May influence the occurrence of native species, affecting functional trait composition on farms. | No evidence from previous studies |
| | Non-palm tree abundance | May affect the richness of native and non-native species, thereby influencing the variety of functional traits within farms. | No evidence from previous studies |
| | Ground vegetation cover | May affect the richness of native and non-native species, affecting functional trait composition on farms. | No evidence from previous studies |
| | Proximity to roads | May influence the influx of non-native species, affecting functional trait composition on farms. | No evidence from previous studies |
| | Temperature | May affect the richness of native and non-native species, thereby influencing the variety of functional traits within farms. | (Boyle et al., 2021) |

|  | Estimate | Std. Error | DF | Crit. Value | P value | Std. Estimate | Marginal | Conditional |
|---|---|---|---|---|---|---|---|---|
| Tree ← Forest | -0.00 | 0.00 | 28 | -1.41 | 0.17 | -0.33 | 0.22 | 0.68 |
| Tree ← PAdist. | 0.04 | 0.03 | 28 | 1.27 | 0.21 | 0.47 |  |  |
| Tree ← Road | 0.00 | 0.00 | 28 | 0.47 | 0.64 | 0.13 |  |  |
| Veg. ← Forest | -0.00 | 0.00 | 28 | -2.16 | **0.04** | -0.43 | 0.19 | 0.38 |
| Veg. ← PAdist. | -0.03 | 0.02 | 28 | -1.42 | 0.17 | -0.32 |  |  |
| Veg. ← Road | 0.00 | 0.00 | 28 | 1.09 | 0.29 | 0.24 |  |  |
| Temp. ← Veg. | -0.18 | 0.13 | 29 | -1.42 | 0.16 | -0.20 | 0.04 | 0.48 |
| Temp. ← Tree | 0.02 | 0.13 | 29 | 0.15 | 0.88 | 0.02 |  |  |
| Yield ← Native | 0.54 | 0.23 | 29 | 2.32 | **0.03** | 0.37 | 0.13 | 0.15 |
| Yield ← Forest | -0.00 | 0.00 | 29 | -0.31 | 0.76 | -0.05 |  |  |
| NonN. ← Veg. | -0.60 | 0.15 | 27 | -4.01 | **<0.01** | -0.60 | 0.43 | 0.43 |
| NonN ← Tree | -0.32 | 0.15 | 27 | -2.03 | 0.05 | -0.28 |  |  |
| NonN. ← Road | -0.00 | 0.00 | 27 | 4.20 | **< 0.01** | 0.62 |  |  |
| NonN. ← Forest | -0.00 | 0.00 | 29 | -2.29 | **0.03** | -0.35 |  |  |
| Native ← Road | 0.00 | 9.99 | 29 | 2.28 | **<0.01** | 0.47 | 0.28 | 0.28 |
| Native ← Temp | 0.88 | 0.42 | 29 | 2.08 | **0.04** | 0.31 |  |  |
| FRich. ← PADist. | 0.06 | 0.05 | 28 | 1.13 | 0.27 | 0.21 | 0.21 | 0.32 |
| FRich. ← N | -0.85 | 0.46 | 28 | 2.37 | **0.02** | 0.36 |  |  |
| FRich. ←Tree | -0.86 | 0.47 | 28 | -1.85 | 0.07 | -0.27 |  |  |
| FDisp. ← PADist. | 0.00 | 0.00 | **28** | 1.04 | 0.31 | 0.16 | 0.20 | 0.20 |
| FDisp ← Native | 0.03 | 0.01 | 28 | 2.80 | **< 0.01** | 0.43 |  |  |
| FDisp. ← Tree | -0.02 | 0.03 | 28 | -0.86 | 0.40 | -0.13 |  |  |

**Table S10.** Final model output of piecewiseSEM model. The variance for the fixed effects for the predictor latent variable are given with the marginal (i.e., variance of the fixed effects) and conditional $R^2$ (i.e., the variance of both the fixed and random effects) for the component models. Abbreviations: Tree = non-palm tree abundance, Temp. = local farm temperature, Veg. = ground vegetation cover, Forest = forest extent surrounding smallholder farms, Road = proximity to road, Yield = oil palm fresh fruit bunch yield, Intens. management intensity index, NonN = non-native species richness, Native = native species richness, FRich. = functional richness, FDisp = functional dispersion. Statistically significant relationships ($p < 0.05$) are highlighted in bold.

|  | **Estimate** | **Std. Error** | **DF** | **Crit. Value** | **P value** | **Std. Estimate** | **Marginal** | **Conditional** |
|---|---|---|---|---|---|---|---|---|
| *Yield ← NonN.* | *0.97* | *0.58* | *29* | *1.65* | *0.11* | *0.27* | *0.09* | *0.10* |
| Yield ← Intens. | -10.35 | 7.06 | 29 | -1.47 | 0.15 | -0.23 |  |  |
| Native ← Temp. | 0.88 | 0.42 | 29 | 2.08 | **0.05** |  | 0.33 | 0.33 |
| *Native ← NonN* | *1.00* | *0.35* | *29* | *2.87* | ***0.01*** | *0.41* |  |  |
| *FRich. ← NonN.* | *0.72* | *0.42* | *28* | *1.72* | *0.10* | *0.27* | *0.13* | *0.31* |
| FRich. ← Intens. | -0.56 | 4.98 | 28 | -0.11 | 0.91 | -0.02 |  |  |
| FRich. ← Tree | -0.76 | 0.47 | 28 | -1.63 | 0.12 | -0.24 |  |  |
| FRich. ← Road | 0.00 | 0.00 | 27 | -0.76 | 0.46 | -0.19 | *0.11* | *0.44* |
| *FRich. ← Forest* | *0.01* | *0.01* | *27* | *1.01* | *0.32* | *0.21* |  |  |
| *FRich. ← Intens.* | *-0.56* | *4.98* | *28* | *-0.11* | *0.91* | *-0.02* |  |  |
| FRich. ← Tree | -0.76 | 0.47 | 28 | -1.63 | 0.12 | -0.24 |  |  |
| FDisp. ← Intens. | -0.56 | 0.35 | 28 | -1.59 | 0.12 | -0.24 | 0.13 | 0.13 |
| *FDisp ← NoNn.* | *0.06* | *0.03* | *28* | *2.10* | ***0.05*** | *0.34* |  |  |
| FDisp. ← Tree | -0.01 | 0.03 | 28 | -0.42 | 0.67 | -0.07 |  |  |
| FDisp. ← Intens. | -0.39 | 0.38 | 27 | -1.04 | 0.31 | -0.17 | 0.12 | 0.12 |
| *FDisp ← Forest* | *0.00* | *0.00* | *27* | *-0.99* | *0.33* | *-0.17* |  |  |
| *FDisp. ← Road* | *0.00* | *0.00* | *27* | *-1.96* | *0.06* | *-0.34* |  |  |
| FDisp. ← Tree | -0.02 | 0.03 | 27 | -0.55 | 0.59 | -0.09 |  |  |

**Table S11.** All additional model output of piecewiseSEM models fitted with the collinear variables (text for additional models are given in italics). The variance for the fixed effects for the predictor latent variable are given with the marginal (i.e., variance of the fixed effects) and conditional $R^2$ (i.e., the variance of both the fixed and random effects) for the component models. Abbreviations: Tree = non-palm tree abundance, Temp. = local farm temperature, Veg. = ground vegetation cover, Forest = forest extent surrounding smallholder farms, Road = proximity to road, Yield = oil palm fresh fruit bunch yield, Intens. management intensity index, NonN = non-native species richness, Native = native species richness, FRich. = functional richness, FDisp = functional dispersion. Statistically significant relationships ($p < 0.05$) are highlighted in bold.

# CHAPTER 5

# General Discussion

Smallholder farm mid harvest

Sabah, Malaysian Borneo

## 5.1 ABSTRACT

In this general discussion, I summarise my findings from the overall aim of my thesis to understand which factors contribute to ecologically resilient tropical agricultural landscapes. I synthesize the findings from the three data chapters and discuss whether sustainable management practices can improve the biodiversity and ecosystem functions of oil palm farms. I conclude that the application of more sustainable farming practices (e.g., BMPs and less intensive practices) does not result in smallholder yield losses, but may not be sufficient to contribute to more resilient ground-dwelling ant communities within farms (i.e., weak influences on ant species richness and functional diversity). However, findings that ant richness increase with proximity to roads suggest that identifying movement corridors that aid ant dispersal within the wider landscape may help maintain higher functional diversity, which is a key mechanism contributing to greater ecological resilience to environmental change. I discuss the implications of the apparent lack of trade-offs between sustainable farming practices and yield, which imply that farmers can carry out Best Management Practices (BMPs) to improve the environmental sustainability of their farms without reducing crop yields. Understanding any barriers to the uptake of BMPs by farmers, and providing more standardised guidance on the application of BMPs will be key to improving oil palm sustainability. I discuss the importance of maintaining local biodiversity on smallholder farms, and how local farm factors and wider landscape management interact to influence the ecological resilience of oil palm landscapes. I conclude that improved coordination of management practices among local smallholder farmers, as well as wider landscape management, will be required to improve the long-term sustainability of palm oil production.

## 5.2 Summary of thesis findings

In this thesis, I examined the inter-relationships between local farm management, local farm biodiversity, and oil palm farm yields in order to understand whether sustainable management of oil palm farms can contribute to more ecologically resilient oil palm landscapes whilst still maintaining smallholder livelihoods.

Chapter 2 quantifies variation in management practices and oil palm yields among smallholdings in Sabah. I conducted questionnaire-led interviews with smallholders to collect information on the uptake of RSPO Best Management Practices (BMPs) and other management practices known to influence oil palm yields. I created two metrics to assess the impacts of sustainable farming practices: (1) the number of BMPs employed by farmers, and (2) an index quantifying the overall farm management intensity that was synthesised from nine farming practices. In this chapter, I examined whether applying less intensive management practices and a higher number of BMPs increased the environmental sustainability of farms (measured by understory vegetation, non-palm tree abundance and soil organic carbon), and whether lower management intensity was related to lower oil palm yields. Contrary to expectation, I found no evidence for trade-offs between the application of more sustainable farming practices and oil palm yields, but also no evidence that these farming practices improved the environmental sustainability of farms. I concluded that the wide variation in yields that I observed across smallholder farms (6.9-37.4 t $ha^{-1}$ $yr^{-1}$) are most likely due to differences in site-specific factors, such as planting material, and pest and disease prevalence. I also conclude that the lack of consistency in take-up of BMPs among farmers may contribute to the weak relationship I observed between BMPs and my measures of environmental sustainability. Overall, I conclude that sustainable management practices can be applied without reductions in oil palm yields. This finding has important implications for smallholder livelihoods and environmental sustainability, if farmers can minimize their reliance on agrochemical inputs.

In chapter 3, I surveyed ground-dwelling ant communities and ant-mediated ecosystem functions (scavenging and leaf-litter decomposition) on oil palm farms. I quantified the local functional diversity (functional richness and functional dispersion) on farms by measuring ant morphological traits related to diet and foraging strategy of native and non-native species. I examined whether farms with more non-native species supported lower species richness, lower functional diversity and reduced ecosystem functions. I found that non-native species tend to have different functional traits to native ant species, but still occupy a subset of the functional trait space of native species. Moreover, non-native and native species richness on farms were positively associated, and neither functional diversity nor ecosystem functions were affected by the number of non-native species. This finding suggests that non-native species do not suppress species richness or functional diversity of ground-dwelling ant communities.  I conclude that native species occurring on farms show high resistance to the impacts of non-native species, and that non-native species contribute to scavenging and leaf-litter functions on farms.

In chapter 4, I use the information collected in my previous two chapters to assess the inter-relationships between local farm management and wider landscape factors, and how these interact to influence the ecological resilience of ant communities on oil palm farms. I use three biodiversity metrics to explore the mechanisms influencing ecological resilience: (1) species richness, (2) functional richness, and (3) functional dispersion. I use these metrics to make inferences about the sensitivity of species to environmental change and the functional redundancy of ant communities. I examine whether native and non-native ants are affected by similar local farm and landscape factors, and whether any differences affect the mechanisms influencing the ecological resilience of farms. I found that non-native species preferred farms with less understory vegetation cover and less forest in the surrounding landscape. By contrast, native species preferred farms that were cooler, suggesting they may be more vulnerable than non-native species to future climate changes. However, farms that were in close proximity to roads supported higher richness of both native and non-native species, suggesting that human-mediated dispersal facilitates the movement of both native and non-native ant species within oil palm landscapes. Moreover, native species positively influenced functional richness and functional dispersion, suggesting that they play a more important role than non-native species for contributing to functional trait diversity of ground-dwelling ant communities on oil palm farms. Overall, I conclude that climatic warming is likely to reduce the ecological resilience of oil palm farms by negatively impacting native species that contribute to greater functional diversity within-farms, leaving communities more vulnerable to further environmental changes. Increasing habitat connectivity to aid species dispersal between farms may be important for improving the ecological resilience within farms by facilitating community recovery following species loss from environmental change.

### 5.3 Implications of no trade-offs between sustainable management practices and farm yields

Implementing more sustainable farm management is needed to reduce the environmental impacts of oil palm production, but it is important to maintain smallholder livelihoods and oil palm yields. My findings from chapter 2 indicate that smallholder farmers may be able to opt for more sustainable farming practices without having to compromise oil palm yields. My thesis findings are consistent with previous study findings of no trade-offs between yields and the uptake more sustainable farming practices in Southeast Asia (e.g., Warren-Thomas et al., 2020). The uptake of Best Management Practices (BMPs) includes recommended guidance for herbicide applications of between 0.5 – 2 L $ha^{-1}$ along harvesting paths, or on target areas with high abundance of 'weeds' (Woittiez et al., 2023). However, I observed some farmers applying up to five times more than the recommended quantity (40 L $ha^{-1}$ $yr^{-1}$, averaging at 10L per application), and around a third of farmers applied herbicides throughout their farm (i.e., "blanket spraying"), resulting in considerable changes in understory vegetation cover before and after applications. This indiscriminate use of herbicides is not recommended by the RSPO (RSPO P&C, 2018) as it can expose bare soils, contributing to nutrient leaching (Formaglio et al., 2020). However, while previous studies show that intensive herbicide treatments can reduce understorey vegetation complexity and floral diversity in experimental plots in Indonesia (Luke et al., 2019), my findings show weak associations between management intensity and understorey vegetation cover within smallholder farms (see Chapter 2). Differences between my thesis findings and those of previous studies could arise due to differences in the habitat cover surrounding study sites, as findings from Chapter 4 suggest that the amount of forest cover surrounding farms can significantly influence within-farm vegetation. Moreover, as previously mentioned, the applications of herbicides can dramatically alter the understorey vegetation within farms, especially when farmers "blanket sprayed", which could contribute to weaker associations between within-farm management intensity and understorey vegetation depending on the time of sampling. Thus, we recommend for future studies investigating the impacts of farm management practices on understorey vegetation to also consider the influence of surrounding habitat cover, as well as controlling for variations in understory vegetation caused by herbicides and weeding activities.

My study found no evidence that understory vegetation or occurrence of non-palm trees resulted in any loss of oil palm yields, and so farmers could reduce their use of agrochemicals, by confining their applications to paths and targeted areas (Luke et al., 2019). Alternatively, intercropping with ground-cover crops could be a method to suppress weed growth (Nchanji et al., 2016). Although I found no effect of understory vegetation on ant species richness or ecosystem functioning in my study, increased understory vegetation cover can increase the abundance and diversity of invertebrates that contribute to soil functioning (Ashton-Butt et al., 2018; Hood et al., 2020). Reductions in agrochemicals and intercropping would not only help to achieve environmental sustainability goals by reducing chemical pollution and increasing within-farm biodiversity, but could also improve smallholder livelihoods by reducing agricultural costs and providing alternative income sources.

Best Management Practices (BMPs) are recommended as a way to sustainably intensify smallholder oil palm yields (Rhebergen et al., 2020), with the aim of improving soil fertility and reducing environmental impacts (RSPO P&C, 2018). Whilst I observed no trade-offs between yields and the adoption of BMPs by smallholder farmers, my findings only showed a weak association between the application of BMPs and soil fertility metrics (e.g., soil organic carbon; Guillaume et al., 2016). Moreover, I observed variation in the application of BMPs across my study farms in terms of number and type of BMPs applied. For example, application of mulching materials such as empty fruit bunches (EFB) was only carried out by about a third of farmers, and varied from once a month to once every three years among farms. This means that some farmers are applying much lower EFB quantities compared to those tested by Tao et al., (2018) in their low EFB treatment plots (210 kg tree$^{-1}$ yr$^{-1}$ or 30 t ha$^{-1}$ yr$^{-1}$). Identifying the factors that contribute to the wide variation in take-up of BMPs and their applications will be crucial for understanding the barriers to implementing sustainable farming practices by smallholders. Previous studies have reported the difficulties that smallholder farmers have in accessing mulching materials such as EFB and palm oil mill effluents (POME) from mills (Jelsma et al., 2019). Also, farmers may not have sufficient capital to invest in sustainable practices, which can be perceived as higher cost (e.g., from increased labour inputs; Rhebergen et al., 2020), or more risky (Liu et al., 2018). There is often insufficient guidance on implementing BMPs and how they can lead to lower costs for farmers (Jelsma et al., 2019).

Whilst crop yield is a useful and widely used indicator to assess trade-offs between farmer livelihoods and environmental sustainability (e.g., Clough et al., 2016; Gérard et al., 2017; Grass et al., 2020; Hamer et al., 2021), I would like to highlight the importance of considering other socio-economic and -environmental indicators when assessing the impacts of sustainable farming practices on smallholder livelihoods. Especially when considering the barriers to the uptake of these practices and the long-term viability of employing these. For instance, findings by Dompreh et al., (2021) show that achieving sustainability certifications can improve livelihoods and yields among cocoa and oil palm smallholder farmers in Ghana, but farmers still remained vulnerable to food insecurity despite certification (measured by the Food Consumption Score). Similarly, Santika et al., (2021) provide a good example of how socioeconomic and socioenvironmental indicators (e.g., child malnutrition and water pollution) can be used to gain a deeper understanding of the impacts of sustainability certification amongst oil palm communities in Southeast Asia. The use of these metrics still remain relatively unexplored when assessing the trade-offs between the uptake of sustainable management practices and farmer livelihoods within oil palm, and so I recommend future studies use a wider variety of metrics take to gain a more holistic understanding of the services and disservices that sustainable farming practices have for smallholder oil palm farmers.

To conclude, it is important that RSPO and NGOs provide more resources and standardised guidance, especially for independent smallholder farmers, who are not supported by smallholder schemes (e.g., plasma farmers in Indonesia who are partnered with local companies). More uptake of BMPs could be an important way to sustainably increase oil palm crop yields. Thus, I recommend that future research should investigate the minimum number of BMP practices that farmers should apply to be effective, as well as the affordability of these practices, so that even low income farmers can be confident that switching to sustainable farming practices will not incur additional costs and losses in yield. Addressing these gaps will not only by valuable to improving livelihoods of smallholder oil palm farmers, but will likely have wider applications to other smallholder crops within tropical agricultural landscapes.

### 5.4 Maintaining biodiversity on smallholder farms

The land sparing/sharing debate addresses the best ways to maintain species in agricultural landscapes (Green et al., 2005). Land-sparing involves intensifying management on existing plantations (Yue et al., 2015) and focusing on the protection of contiguous areas of forest

(Edwards et al., 2010), and is often the optimal way to conserve biodiversity within oil palm landscapes (Edwards et al., 2010, 2012). However, this approach has been met with debate about the benefits of land sparing versus sharing (i.e., 'wildlife friendly' farming; Tscharntke et al., 2012). The intensification of agricultural land may protect forests, but it does not necessarily prevent subsequent forest encroachment, and can contribute to further agricultural expansion and deforestation (Phelps et al., 2013). Alternatively, wildlife friendly land-sharing recognises the benefits of increasing habitat heterogeneity, and the protection of biodiversity through agri-environment schemes, such as conservation set-asides. In oil palm landscapes, forest biodiversity is protected through the High Conservation Values (HCV) and High Carbon Stocks (HCS) approach (Fleiss et al., 2020). I suggest that in addition to focusing on protecting forest biodiversity in HCVs and HCS sites, more attention should be given to supporting biodiversity on farms. In the following section, I will explain my reasoning for this argument.

In chapter 3, I show that although farms have fewer species than forest sites, they support many native ant species, which accounted for 60-100% of species occurrences on smallholder farms, and contributed to a wide variety of functional roles. These findings are consistent with previous research showing that oil palm plantations can support a diverse range of native species (Luke et al., 2019), highlighting the potential for managing and conserving native species within oil palm planted areas. In addition, the findings from chapter 4 show a positive association between native ant species richness and farm yields. This association could be due to native species contributing to pest predation (Symondson et al., 2002), which is supported by findings in chapter 3 showing that native ant species tend to occupy more predatory roles. In addition, other studies find that more diverse ant communities provide higher predation rates and contribute more to biological control within tropical farmland systems (Frizzo et al., 2020). Thus, maintaining more diverse native ant communities on oil palm farms could act as a cheaper and more sustainable method of biocontrol within Integrated Pest Management systems (Turner & Hinsch, 2018), and contribute to the prevention of pest outbreaks that suppress oil palm yields (Kamarudin et al., 2016).

My thesis findings show that non-native ants provide important ecosystem functions and contribute to biodiversity within these highly-modified agricultural landscapes. This conclusion contrasts with the general consensus that non-native species can be invasive and environmentally and economically damaging in areas that they colonise (Angulo et al., 2022). In fact, findings in chapter 3 show positive association between native and non-native species richness on farms, and no reductions in functional diversity on farms with a higher proportion of non-native species. Under on-going climate warming, non-native species may become increasingly important to buffer against the loss of less thermally tolerant native species. My findings show that farms with a higher proportion of non-native species still maintain scavenging functions, and so non-native species may support functional value in these highly modified agricultural habitats (Fayle et al., 2015), maintaining generalist functions e.g., contributions to soil health and nutrient cycling, despite the loss of native species. However, it is important to consider that non-native ants may negatively impact other taxonomic groups that we did not consider in this study (e.g., other invertebrates, vertebrates and plants; Siddiqui et al., 2021; Tercel et al., 2023), which could have negative consequences for native biodiversity and related ecosystem functions. To date, there are few studies investigating the associations between non-native ants and other non-native species on biodiversity within oil palm landscapes, and so this may pose an interesting.

Chapter 4 examines the local and landscape-scale factors that affect local biodiversity on farms. A main aim of my thesis was to investigate whether farm management could improve local biodiversity. However, I found that management intensity, understory vegetation cover and non-palm tree abundance had only weak effects on native ant species richness and functional diversity on farms. While my findings reflect those of (Hood et al., 2020), they contrast with other studies showing that increasing vegetation cover on oil palm farms supports more diverse invertebrate communities (Ashton-Butt et al., 2018; Azhar et al., 2022). This lack of consensus suggests that the impacts of local farm management on local farm biodiversity may be context-dependant. In fact, the wider landscape context, such as landscape composition, has been shown to influence local biodiversity (Li et al., 2023). This might be the case in my study as I found that surrounding landscape factors had a stronger influence on ant species richness than did local farm management, with proximity to main roads boosting overall ant species richness on farms. However, there was still a lot of unexplained variation within the structural equation models, suggesting that other factors that I did not study are also important. These factors may include landscape history, which can determine the composition of current species assemblages and functional trait composition (Lecoq et al., 2021), as well as the amount of habitat heterogeneity in the wider landscape (Benton et al., 2003). To conclude, when understanding the impacts of local oil palm farm management, future studies should consider the context of the wider landscape in order to understand how farm management can improve local species richness and functional diversity on farms. This needs to be explored further because it has important implications for understanding the ecological resilience of farms.

There are very few studies directly testing the resilience of ecological communities within oil palm landscapes (e.g., resilience of ecosystem functioning to drought in oil palm agroforests; Eycott et al., 2019), especially when considering the greater number of publications investigating resilience within tropical forest habitats (e.g., Ashton et al., 2019; Bregman et al., 2016; Cole et al., 2014; Verbesselt et al., 2016). Directly testing the ecological resilience of a community or ecosystem function requires the assessment of how communities and functions respond to environmental change or disturbance over time (Oliver et al., 2015). However, this is quite difficult to achieve in real-world landscapes where there are a lot of interacting and confounding factors to control for, and so, investigations such as my thesis can apply space-for-time approaches to make inferences about an ecosystems ecological resilience (e.g., resilience of community interactions and ecosystem functioning to logging in tropical forest habitats; Ewers et al., 2015; Gray et al., 2018). However, in spite of these and my own work, we still require further studies to directly assess the ecological resilience of oil palm systems in response to environmental changes within production landscapes.

## 5.5 Resilience and sustainability within smallholder oil palm landscapes requires a landscape approach

Tropical landscapes are expected to continue to change due to land-use change, climate warming, and infrastructural development (Sa’adi et al., 2020; Sloan et al., 2019), which will impact biodiversity within oil palm landscapes. Mitigating these impacts requires management strategies that are able to maintain ecological resilience within these dynamic landscapes. This will require collaboration between farms and across jurisdictional boundaries, whilst taking into consideration the different perspectives of stakeholders (.see Beller et al., 2019).

Landscape features, such as forest fragments and habitat corridors, may support biodiversity and aid the recovery of populations from environmental disturbances (Oliver et al., 2015). However current understanding of what provides habitat connectivity in oil palm landscapes is not yet understood for a wide range of species. HCV areas for instance can provide connectivity benefits for species movement across oil palm landscapes, such as for birds and mammals (e.g., Hamer et al., 2021; Seaman et al., 2021). However, my findings suggest that this may not be the case for species with smaller dispersal ranges, such as ants (Suni & Gordon, 2010). I observed no benefits of higher forest cover in the wider landscape for improving species richness or functional diversity on farms, which reflects the fact that few native ant species on farms were forest-dependent species (Chapter 3). However, I found that proximity to roads contributed to higher species richness and functional redundancy in ant communities, thereby increasing the ecological resilience of these communities to environmental disturbances. This effect was more pronounced for non-native ant species, indicating that generalist species may benefit more from human-mediated dispersal.

Connectivity of habitats is a key factor for addressing resilience in oil palm landscapes, however it may also create specific challenges, suggesting the need for a deeper understanding of resilience and sustainability at the landscape scale. My findings in Chapter 4 suggest that oil palm landscapes with more road networks and low forest cover may contribute to the spread of non-native species. While we found that non-native ants were not harmful to native ant communities or oil palm yields, these findings could have implications for the spread of more economically damaging invasive species and pests. Roads are a well-known pathway for human-mediated dispersal and spread of non-native insects (Bullock et al., 2018). In addition, Waddell et al., (2020) found that forest fragmentation was associated with higher richness and abundance of non-native plants within oil palm plantations. The role of landscape composition and the spread of non-native species has been less explored but is gaining attention (Bianchi, 2022; Bianchi et al., 2006; Delaune et al., 2021; Haan et al., 2020) and should be considered within the context of oil palm and other tropical agricultural landscapes.

To conclude, future studies should investigate the value of retaining forest fragments such as HCVs and HCSAs for reducing the spread of economically damaging non-native species, which may become increasingly more dominant with further infrastructural development and land-use change in this region (Abram et al., 2022; Van de Vuurst & Escobar, 2020). However, current composition of smallholder landscapes may not be capable of providing habitat connectivity for more specialised or species with a shorter dispersal capacity. Thus, consideration of improving habitat connectivity for a wider range of species (Gray et al., 2022; Scriven et al., 2019) is required to achieve the goals of more resilient oil palm landscapes, particularly when supporting species range shifts under climatic warming.

### 5.6 Future directions for sustainable and ethical oil palm production

There are many ongoing advancements that could transform the oil palm industry, including sustainability commitments and global policies and regulations. However, it is crucial to consider the impact of these changes on smallholders to ensure that sustainability goals are achieved in an inclusive manner.

"Regenerative agriculture" is being increasingly used by stakeholders, including being championed by NGOs, agribusinesses and business-led coalitions. Although the term has been around since the 1980s, it has gained more recent attention due to its potential for helping companies meet net-zero carbon targets. Regenerative agriculture is frequently associated with practices that aim to improve soil fertility and soil conservation (e.g., Schreefel et al., 2020), but now encompasses a broader range of sustainability practices which aim to conserve and rehabilitate socio-agroecological agricultural systems. For example, the One Planet Business for Biodiversity (OP2B) 'Framework for Regenerative Agriculture' covers actions that address sustainability issues related to climate, water, livelihoods, and biodiversity (OP2B, 2021). Thus, regenerative agriculture can cover a wide variety of agricultural practices (Newton et al., 2020) incorporating traditional farming techniques, such as agroforestry, intercropping and subsistence farming.

While regenerative agriculture is not a commonly use term within the oil palm industry compared to other crop sectors (e.g., cocoa), there is existing overlap between regenerative agriculture practices with BMPs and management practices outlined by the RSPOs P&Cs, as well as traditional farming practices employed by agricultural communities. For example, the use of organic mulching materials such as POMEs and EFBs provide alternatives to chemical fertilisers and agrochemicals to increase soil fertility, and so mitigate the environmental impacts on watersheds and people's health (RSPO P&C, 2018). Moreover, practices such as agroforestry and mixed-crop farming, which are highlighted as valuable regenerative agriculture practices to improve soil quality and support farmer livelihoods (Giller et al., 2021; Schreefel et al., 2020), are already being employed by some smallholder oil palm farmers in Africa (Proforest, 2014), where oil palm may have traditionally grown as a subsistence practice or within an agroforestry system as it occurred naturally near secondary forests (Logan & D'Andrea, 2012). There is now growing interest from on-the-ground organisations and NGOs in Southeast Asia (e.g., my project partners WildAsia and Proforest, as well as organisations in Africa and Latin America) to collaborate with smallholder producers to identify sustainable and regenerative farming practices that can reduce production costs for smallholders whilst still improving soil fertility, palm tree health and fruit yields.

Monocultures have been the conventional model of oil palm production since the introduction of the crop to Southeast Asia and Latin America in the 20th century. While intercropping and agroforestry have been widely discouraged by agro-industries due to the belief that this will diminish oil palm fruit yields (Nchanji et al., 2016), there has been a growing interest to assess the beneficial impacts of cultivating palm oil as an agroforestry or polyculture system within a regenerative agriculture framework. Findings show that intercropping with other annual crops (e.g., plantain and banana) during the immature stages of oil palm (first 1-4 years) can have significant positive benefits to smallholder farmer livelihoods in Cameroon by providing an alternative source of food and income (Nchanji et al., 2016). Moreover, a field experiment in India combining oil palm agroforestry with other crops also show increased oil palm and intercrop yields, as well as increased carbon storage (Ahirwal et al., 2022). Thus, these approaches show potential for achieving climate-mitigation and conservation goals (e.g., via carbon-sequestration and by providing more suitable habitats for species), whilst improving smallholder livelihoods (McNeely & Schroth, 2006; Mulatu & Hunde, 2020; Yamoah & Kaba, 2022). These concepts have started trickling up, with industrial companies also starting to invest efforts to scale up the application of regenerative agricultural practices across smallholder farmers (e.g., Musim Mas; Sharma, 2022), such as by providing training in sustainable management practices and providing resources for replacing aging oil palm crops. However, more research is required to assess the direct impacts of oil palm agroforestry and intercropping on biodiversity, soil quality and oil palm yields, and which intercrop species are most suitable to prevent reductions in oil palm yields (Budiadi et al., 2019). The application of agroforestry and intercropping from other tropical perennial crops such as cocoa and rubber has been extensively researched in the published literature (e.g., (Aboah & Setsoafia, 2022; Asare et al., 2014; Hougni et al., 2018; Romyen et al., 2018; Warren-Thomas et al., 2020). Translating findings from other tropical crops and applying these practices to oil palm may aid the development of more sustainable smallholder farming systems. If this approach does improve smallholder livelihoods and income stability, then regenerative agriculture and other forms of sustainable management practices may help reduce environmental challenges including smallholder-related deforestation (Acheampong et al., 2018; Kubitza et al., 2018; Miyamoto, 2020), thereby increasing smallholder access to a wider global supply chain through compliance with certification requirements.

The recent rise in international legislation and company commitments surrounding zero-deforestation may impact smallholder access to global markets. Since 2018, the RSPO has committed to zero-deforestation, through the HCV-HCSA process (RSPO, 2018)**.** Moreover, the EU Deforestation Due Diligence (EU DDD) also aims to protect and restore the world's forests by preventing the import of goods into EU markets that are linked to deforestation (December 2020 cut-off date). The policy initiative aims to minimize the detrimental social and environmental impacts of agricultural production. However, there are concerns that the regulation may exclude small-scale farmers as they may be more likely to be linked to deforestation activities from encroachment into forest areas. There have been mixed responses to the EU DDD regulation, with some recognising it as an important step towards reducing global deforestation rates. For example, some smallholder collectives view the regulation positively as it increases EU market access for certified smallholders (SPKS, 2022). However, to prevent the EU DDD from excluding market access to smallholder farmers, it is important to halt deforestation activities and find ways to support sustainable agricultural practices. Furthermore, it is important to recognize that current zero-deforestation commitments can lead to unintended consequences, and the expansion of oil palm into more open natural habitats, such as dry forests and grassland ecosystems (Fleiss et al., 2023), that also support unique biodiversity. Without careful consideration of the indirect consequences of these legislations, there is a risk of displacing biodiversity loss to other areas, as well as failing to address the social issues surrounding livelihoods and welfare within tropical agricultural landscapes.

## 5.7 Conclusions

In this thesis I examined the impacts of sustainable management practices on smallholder oil palm yields and the ecological resilience of farms. Farmer yields and management practices varied widely across farms, with no evidence that opting for more sustainable farming practices reduced oil palm yields. Addressing the factors limiting smallholder uptake of BMPs and other sustainable farming practices will be an important step to increase the sustainability of farms. Development of standardised guidance for the application of BMPs and regenerative agricultural practices may facilitate the uptake of such practices by smallholders. Ground-dwelling ant communities and ant-mediated ecosystem functioning varied widely across farms, with both native and non-native species contributing to ant community functioning and the ecological resilience of farms. However, climatic warming in tropical regions may reduce the ecological resilience of ant communities on farms, with potentially negative consequences for oil palm farm yields through the loss of native ants. Thus, more research is required to understand what smallholder farmers can do to enhance local biodiversity on farms, and why the impacts of farm management practices on biodiversity are often inconsistent across studies. Wider landscape factors may help mitigate the negative impacts of environmental change on the ecological resilience of farms. However, more collaboration is needed between farmers, NGOs and the scientific community, to better understand how we can optimise the management of farms and the surrounding landscape, to address smallholder and biodiversity conservation goals. Increasing the environmental sustainability of smallholder producers is key to maintaining livelihoods and the ecological resilience of oil palm landscapes.

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