Pollinators and Ecosystem Services in an Oil Palm Transformation Landscape

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Submitted by

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In memory of my grandfather, Mr. Jen-kuen Chen.

謹以此論文紀念我的外公陳貞堃先生,

謝謝他的支持和鼓勵.

This dissertation is also dedicated
to my parents, Liang and Susie; my sister Lauren;

and to Rachel.

Summary

Insect pollination is an economically important ecosystem service that depends heavily on wild pollinators. Landscape transformation caused by conversion to agriculture threatens habitats of wild pollinators, reducing their potential to provide ecosystem services. The landscape in Jambi Province, Sumatra, Indonesia, is an example of a region undergoing landscape transformation, from biodiverse natural forests, to intermediate land uses such as fallow shrubland and jungle rubber, to monospecific oil palm plantations. My dissertation explores how transitions between these land uses impact pollinator biodiversity and ecosystem functions and services. I consider different facets of this interface: spatial spillover of pollination services from forest to oil palm; mechanisms driving ecosystem functions and services following agroforestry enrichment within oil palm; and landscape-scale comparisons quantifying interacting local and landscape effects on a native pollinator species.

My **first chapter** reviews the state of the knowledge of oil palm pollination by insects. I conducted a systematic review of biotic and abiotic drivers of oil palm pollination and pollinator populations. I present the current understanding of the globally introduced West African Weevil (*Elaeidobius kamerunicus*), whose regional population fluctuations have negatively impacted yield and resilience, as well as other potential pollinator species endemic to particular growing regions. Based on my review, I describe specific issues concerning biotic, management, and climate drivers of pollination that should be the focus of future oil palm pollination research.

In my **second chapter**, I examine the role that natural habitat can play as a source of pollination ecosystem services and ecological spillover effects in an oil palm field experiment. I compared treatments controlling visitors and pollination of female oil palm inflorescences over a distance gradient to nearby forest. I found that exclusion of large visitors significantly increased fruit set over open and assisted pollination treatments. Forest proximity had a positive effect on fruit set except with treatments that minimized pollinator contributions, suggesting this effect was not abiotic. My results suggest that nearby forests and ecological processes such as predation may play an important role in driving oil palm pollination, though more experimental work is needed to disentangle these and potential further effects of landscape configuration.

In my **third chapter**, I explored how enriching the oil palm agricultural matrix with up to six tree species plays a role in driving ecosystem function and, consequently, ecosystem services and disservices. Within a plantation-scale, long-term oil palm biodiversity enrichment project, I disentangle the direct and indirect effects of enrichment on services (pollination, biocontrol) and disservices (herbivory) using random partition analysis and structural equation models. These models indicate that light availability, driven by enrichment treatments, played an important role in ecological patterns at multiple levels of interaction. These had effects on herbivorous insects and pollinators, the latter of which had a positive effect on reproduction of phytometer plants (*Capsicum annuum*) placed in the plots. Our results show that even in early stages of ecological restoration of oil palm, ecosystem functions and services are affected, sometimes through indirect pathways; however, these relationships may change as enrichment communities develop.

In my **fourth chapter**, I examine the counterbalancing roles of local land use and amount of landscape habitat in pollinator survival and growth, using the native stingless bee *Tetragonula laeviceps* as a focal species. I established three colonies in 40 plots within Jambi's transformation landscape, selecting from four predominant habitat types (degraded primary forest, shrubland, rubber plantation, and oil palm plantation) and controlling for a gradient of natural habitat (i.e. forest and shrubland) composition in a 500 m radius. I found that hives with higher local flower species richness had more pollen stores, which in turn was associated with increased bee and colony size. Colonies in structurally complex habitats such as forest and rubber plantations had lower mortality and greater gains in hive size than colonies in open habitats such as oil palm and shrubland; however, open habitats had higher flower species richness and abundance. Open habitats, which are increasing with rainforest conversion, reduce suitable nesting habitat but may increase floral resources in the landscape. Considering the key ecosystem function of stingless bees, understanding how this trade-off translates to the landscape and population levels will be critical in light of the continued deforestation crisis in the tropics.

In summary, understanding and protecting the resources supporting pollination are critical to improving the sustainability of oil palm and can support the livelihoods of people living in the landscape. The impact of habitat loss from agriculture conversion can adversely impact wild pollinator populations through the loss of suitable habitats, as I observed with *T. laeviceps*, but also changes the flowering resource landscape. In my review of oil palm pollination, I show that a better understanding of biodiversity and landscape drivers of pollination of oil palm itself is needed. My own oil palm field experiment demonstrates how natural habitat and biodiversity may interact positively with oil palm production, which could lead to yield improvements as well as new incentives for conservation. I show in my experiments within the oil palm biodiversity enrichment project that tree biodiversity enrichment can indirectly influence pollination services and ecosystem functions, even at an early stage. However, the ecosystem services and disservices affected by ecological restoration will continue to change as the ecological community develops. Our task in future research will be to continue to disentangle these relationships with the aim of recovering or preserving biodiversity and ecosystem function while informing sustainable ecological strategies for farmers and land managers.

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Introduction

Enabled by fossil fuels and technology, human activity is impacting the global environment exponentially, bringing about an unprecedented era of anthropogenic global change (Crutzen 2002). If left unaddressed, the consequences of our environmental impacts become sharply apparent, such as in desertification (Kéfi et al. 2007), fisheries collapses (Jackson et al. 2001), insect and pollinator declines (Potts et al. 2010, Hallmann et al. 2017), and the emerging effects of global climate change (IPCC 2014). The drivers leading to these collapses are complex, as they operate on multiple scales and are intertwined with social and economic systems (Akamani et al. 2016). Solutions are therefore difficult to identify, as they require systemic changes that are difficult to implement (Game et al. 2014).

Biodiversity and ecosystem function loss through land conversion to agriculture is one such issue that affects ecosystems worldwide (Newbold et al. 2015). While conservation and agriculture are often presented as opposing forces, they can find a mutually beneficial common ground given an appropriate supporting framework (Fischer et al. 2014). Agroecological research has demonstrated the important role that biodiversity can play in providing ecosystem services to agricultural activities. Wild pollinators contribute a majority of pollination services in global crops (Garibaldi et al. 2013, 2016) and natural enemies can significantly control agricultural pests (Bianchi et al. 2006, Chaplin-Kramer et al. 2011, Maas et al. 2013). However, the provision of these services depends critically on the availability of habitat for pollinator and natural enemy populations (Landis et al. 2000, Langellotto and Denno 2004, Garibaldi et al. 2011). Stable and diverse communities are also important in maintaining robust beneficial populations that provide consistent ecosystem services (Winfree and Kremen 2009, Vandermeer et al. 2010).

Understanding the ecological contexts that foster biodiversity and targeted ecosystem services is therefore a critical link between conservation and sustainable agricultural practices. My thesis focuses on specific contexts that represent interfaces between conditions with high biodiversity (e.g. natural habitat) and intensified, low biodiversity conditions (e.g. agricultural fields). Within the following chapters, these interfaces occur spatially, via spillover from forest into monocultural oil palm; over biodiversity restoration treatment levels; and between spatial scales of interacting local and landscape effects.

Study system and region

I conducted my studies in Jambi Province, Sumatra, Indonesia (Figure 1), a region of landscape-scale ecological transformation. My research was part of the Ecological and Socio-economic Functions of Tropical Lowland Rainforest Transformation Systems (EFForTS) project, a collaboration between German and Indonesian research groups studying the ecological and socio-economic dimensions of the landscape transformation in Jambi. The project is interdisciplinary and aims to assess ecological and socio-economic functions in the landscape; quantify effects of spatial and temporal variability on these ecological and socio-economic functions; identify the scaling of these functions from local to landscape levels; and contribute to more sustainable land use practices (Drescher et al. 2016). My work was part of

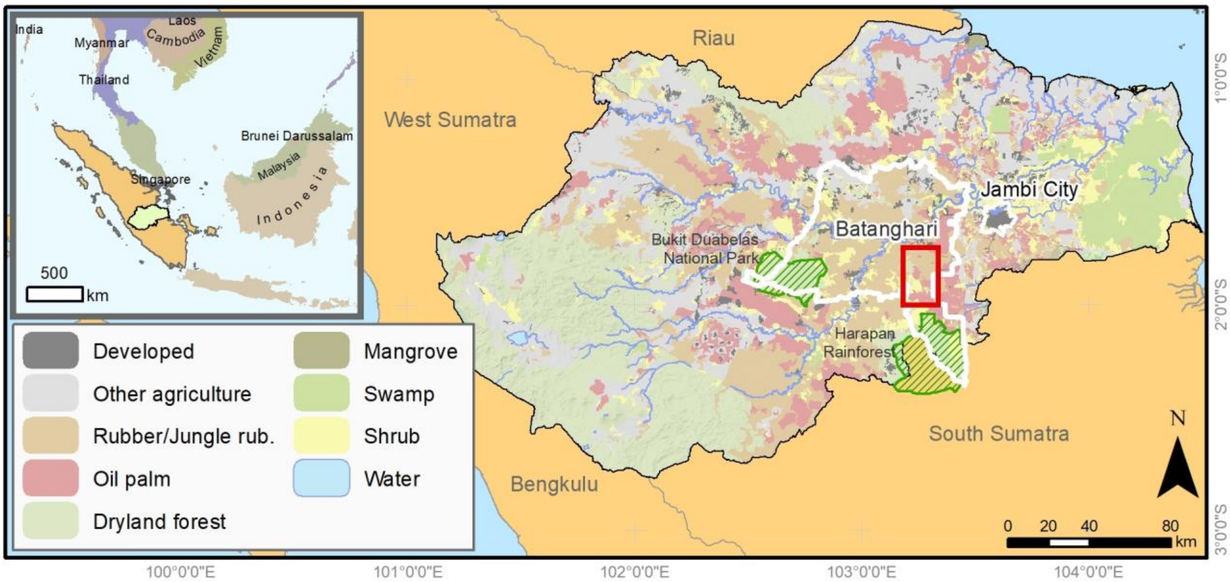

Figure 1. Map of Jambi province and surrounding context. The study region is located within the red rectangle, which corresponds to the extent of the map in **Figure 2a**. General land use categories are based on classified 2013 Landsat data by D. Melati.

the sub-project B09: Aboveground biodiversity patterns and processes across rainforest transformation landscapes.

Jambi, and more generally, Sumatra and surrounding islands, comprise an important biodiversity hotspot that has one of the world's richest endemic assemblages (Mittermeier et al. 2011). Prior to major land conversion, the lowland areas of Jambi Province where my sites are located were dominated by dipterocarp forest (Laumonier et al. 2010). Jambi underwent a 71% reduction in its forest area from nearly 2.5 million ha in 1985 to 715,000 ha in 2007 (Laumonier et al. 2010). This has been in part due to a transmigration program that increased the area's population and resulted in the conversion of land to cash crop production (Drescher et al. 2016). Like many areas in Southeast Asia and the tropics, monocultural oil palm (*Elaeis guineensis*) cultivation has increased drastically, often at the expense of natural forest (Koh and Wilcove 2008, Vijay et al. 2016). By 2013, approximately 55% of Jambi's area had been converted to agriculture, of which more than 590,000 ha was oil palm and more than 650,000 ha was rubber (*Hevea brasiliensis*) plantations (Drescher et al. 2016).

Conversion to the intensified agricultural practices typical of oil palm has severe ecological consequences, through microclimatic and biological effects (Foster et al. 2011). Oil palm changes the abiotic and biotic environment, resulting in dryer, hotter conditions (Meijide et al. 2018), more open canopy, and lower leaf litter and tree biomass carbon than forest (Drescher et al. 2016). Oil palm often also has lower biodiversity than forest (Foster et al. 2011, Drescher et al. 2016), and supports different species communities (Koh 2008, Fayle et al. 2010, Lucey and Hill 2012, Lucey et al. 2014). Overall, ecosystem functions decrease in oil palm compared to natural systems (Dislich et al. 2015, Clough et al. 2016, Grass et al. 2020) and biodiversity loss also has indirect effects on ecosystem functions and services (Barnes et al. 2017). However, much remains to be understood, including the processes by which biodiversity supports ecosystem functions such as pollination and biocontrol, and cross-scale and landscape context effects on biodiversity and ecosystem functions (Foster et al. 2011, Dislich et al. 2015).

However, it is also important to consider the economic significance of these transformations for local communities. Within Jambi, preferences for rubber or oil palm by small holders depend in part on the availability of labor or land resources (Drescher et al. 2016). Conversion from forest to other predominant land use types in Jambi, including oil palm, rubber plantation, or jungle rubber result in trade-offs in ecosystem functions and services for economic production, with oil palm providing the lowest biotic function but highest economic function (Clough et al. 2016). Without incentive structures to protect biodiversity and ecosystem functions, the tropical forest landscape of Jambi risks further conversion to high-profit, low biodiversity land uses such as oil palm (Grass et al. 2020).

Approach and chapter outlook

The unifying theme among the chapters of this dissertation is an examination of how biodiversity and ecosystem functions transition across gradients or interfaces between areas or conditions of high to low intensification. Following a review of the state of oil palm pollinator research in my first chapter, I examine this transition in a spatial gradient at the border between forest and oil palm in my second chapter. In my third chapter, I investigate the interaction between biodiversity and plot size gradients in an oil palm biodiversity restoration and enrichment experiment. In my fourth chapter, I examine the interface between spatial scales in an experimental design that contrasts local and landscape habitat effects on native stingless bee survival and health.

Spatial interface: Pollination spillover from natural habitat

In heterogeneous landscapes, organisms may cross between natural habitats and managed land such as agriculture. When this movement is also accompanied by the transfer of associated ecosystem functions, functional spillover occurs (Blitzer et al. 2012). Spillover from natural habitat is an important mechanism that drives ecosystem service provision in diversified agriculture (Landis et al. 2000, Rand et al. 2006, Garibaldi et al. 2011, Blitzer et al. 2012). In oil palm, natural enemy spillover from neighboring habitat can play a role in controlling pests (Nurdiansyah et al. 2016), but the importance of spillover has not been investigated for pollinators of oil palm. Natural areas may provide habitat for flower visitors, be a source of other competing species, or a source of their natural enemies (Blitzer et al. 2012). Other studies have examined species diversity and abundance gradients of pollinators from natural habitat into oil palm (Mayfield 2005, Lucey and Hill 2012), but the effect of such gradients on pollination services has not been directly investigated.

I first establish the state of knowledge in oil palm pollination in my **first chapter** through a review of the drivers of insect pollination in oil palm. Oil palm pollination has been a major concern in palm oil production historically, and the key role of insects has only been recently understood (Syed 1979). After the discovery of insect pollination, the introduction of the African weevil *Elaeidobius kamerunicus* (Coleoptera) in Indonesia and other oil palm growing regions worldwide has led to the transition from labor-intensive hand pollination methods to reliance on introduced weevil populations. However, despite concerns about the stability and resilience of introduced weevil populations, there appears to be little research on the ecology of the oil palm pollinator community, or on landscape effects on pollination.

My review demonstrated that little is known about the effect of pollinator and natural enemy spillover from nearby natural habitat on oil palm pollination services. This served as the background and motivation for my **second chapter**, which presents the results of a field experiment examining evidence for spillover in a smallholder oil palm farm in Jambi. I used selective exclusion methods to control pollination visitation in blooming oil palm inflorescences over a 100-m gradient from a forest border, either excluding all visitors or excluding larger (>1.7mm) visitors. I compared these treatments with open and assisted pollination treatments. These methods were paired with sticky traps to sample visitor biodiversity. I compared treatment effects on yield (fruit set and fruit bunch weight) and associated insect biodiversity patterns.

Biodiversity and patch size gradients in agroforestry enrichment and restoration

Ecosystem restoration has become a global priority in conservation and sustainable resource use (Suding et al. 2015, Gann et al. 2019). With over 6 million ha already dedicated to oil palm in Indonesia (Meijaard et al. 2018), creating and maintaining connections between existing habitat patches through the existing agricultural matrix is important for the viability of fragmented wildlife populations and improving landscape-wide ecosystem functions and services (Koh et al. 2009).

For habitat restoration to be effective, it must restore ecosystem function and biodiversity (Suding et al. 2015), which are interconnected (Duffy et al. 2017). Therefore, an understanding of how biodiversity can foster improved ecosystem functioning is valuable for restoration planning (Srivastava and Vellend 2005). In theory, the biodiversity of an ecosystem has a connection to the quantity and stability of its ecosystem functions (Hector and Bagchi 2007). In forests, tree diversity can increase microhabitat and resource availability for a wider diversity of organisms, which in turn increase the quantity and stability or ecosystem functions through various mechanisms (Aerts and Honnay 2011, Grossman et al. 2018) and could help mitigate the impacts of biological simplification from oil palm conversion (Foster et al. 2011). Furthermore, the size of restored habitat can play a role, as it is hypothesized that biodiversity increases with habitat patch size (MacArthur and Wilson 1963).

My **third chapter** took place in an ongoing biodiversity enrichment experiment (EFForTS-BEE) that systematically contrasted the effects of increasing species richness and size of restoration plots within oil palm monoculture. I quantified the ecosystem functions and services of insect herbivores, natural enemies, and pollinators using vegetation and insect surveys and phytometer plants. I then investigated how the enrichment experimental treatments affected these variables and further, I disentangled the indirect effects of the treatments on downstream ecosystem functions and services.

Scale interface: Pollinator response to local and landscape drivers

Eusocial bees and other wild pollinator groups are important contributors to pollination (Garibaldi et al. 2013). The amount of natural habitat in the landscape can therefore influence pollination services (Klein 2009, Garibaldi et al. 2011, Livingston et al. 2013). However, while

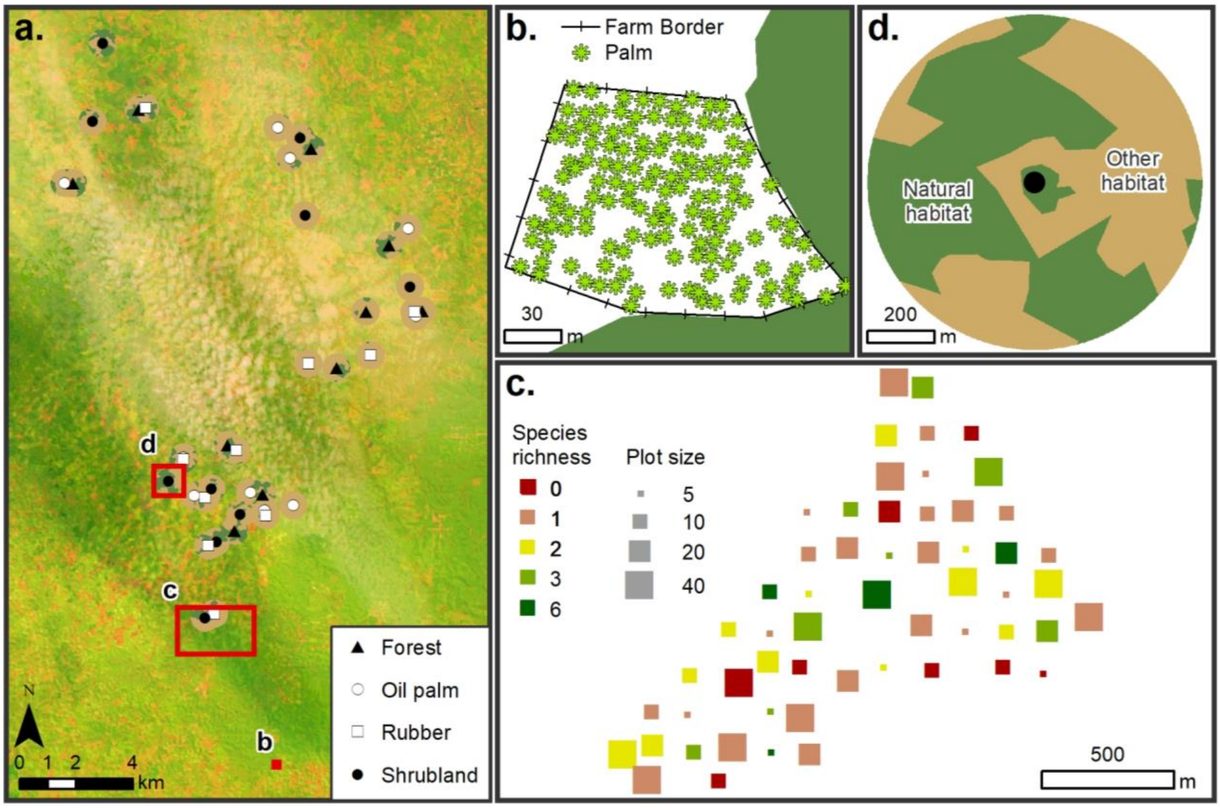

Figure 2. Maps of study areas for (a) landscape hives project in Chapter 4, (b) oil palm pollinators project in Chapter 2, (c) the biodiversity enrichment experiment (EFForTS-BEE) in Chapter 3, and (d) an exemplary map of a hive foraging area from Chapter 4. Background land cover in (a) is from a 2013 Landsat image.

high quality habitats are important, the types of land use in the matrix separating habitat patches also play a significant role in the survival and growth of wider-ranging organisms (Ong et al. 2020). This is true for eusocial bees, which build semi-permanent nests and use the surrounding landscape for resource collection and reproduction (Heard 1999). However, beyond quantifying effects on pollination services, understanding how wild pollinators adapt to trade-offs in habitat quality at local and landscape scales can provide insight into how landscape transformation impacts this ecologically and economically important group and suggest possible conservation measures.

In my **fourth chapter**, I focus on the Southeast Asian native stingless bee species *Tetragonula laeviceps* as a case study for how a eusocial bee adapts to and is impacted by local and landscape habitat qualities. I placed 120 beehives in 40 sites representing four predominant land use types in the landscape: degraded primary forest, shrub, rubber plantation, and oil palm plantation. These sites were selected to have comparable gradients of increasing landscape natural habitat area for each type of land use. I monitored bee foraging activity and hive growth over a four-month period and measured colony size at the end of the study. I examined the effects of local habitat type, floral resources, and landscape habitat area on these hive and colony measures.

Hypotheses

The general hypothesis guiding my approach in my experimental chapters is that biodiversity and ecosystem function will benefit from closer proximity (physical or conceptual) to more "natural" conditions, i.e. conditions more closely resembling the forest that preceded land use conversion. Therefore, in my second chapter, I hypothesized that proximity to forest would affect pollination services to oil palm, though conditionally upon interactions with pollinator antagonists. In my third chapter, I hypothesized that the relationships between vegetation, insect groups, and services and disservices would reflect their ecological relationships. By comparing these relationships across the enrichment gradients, I also implicitly hypothesized that the relationships under greater biodiversity enrichment (more tree species and larger plots) would more closely resemble natural forest conditions. In my fourth chapter, I hypothesized that less intensified land uses at the local and landscape levels would benefit bee survival and growth, and that these effects may be able to compensate for each other across scales.

Field sites and methods

My studies took place in Batang Hari Regency, a region of central Jambi (Figure 2a). This region experiences a tropical humid climate with rainier seasons around March and December and a drier season from July through August. Annual temperatures averaged 26.7±0.2°C and average annual precipitation was 2235±381mm from 1991-2011 (Drescher et al. 2016).

The oil palm pollination experiment in chapter two took place on a smallholder oil palm farm (Figure 2b), with master's student Tien-Yi Fung. At this site we observed a variety of species visiting oil palm inflorescences including, *Elaeidobius kamerunicus,* stingless bees, and *Apis dorsata* bees. However, the latter two appeared to only visit male inflorescences (Figure 3a). We studied oil palms in an approximately 1 ha site (Figure 3b) bordering remnant primary forest (Figure 3c). We applied exclusion treatments and placed sticky traps on receptive female oil palm inflorescences over a 100 m gradient from the forest. The application of our exclusion methods was novel but based on methods used in the industry for isolating breeding material when developing hybrid varieties (Donough et al. 1993). It was also necessary to build cages around the developing fruit to protect against monkeys living in the forest (Figure 3d). We estimated pollination services by counting the proportion of pollinated fruits in a fruit bunch, which we related to the visiting insect community caught in the sticky traps. For half of the inflorescences in all treatment groups, we allowed the fruit bunch to develop to full maturity. We weighed the ripe fruit bunch and took measurements of component fruit bunch parts, which we related to fruit set and tree age.

The insect and vegetation surveys and phytometer experiment in my third chapter took place in the enrichment plots (Figure 3e) of a long-term biodiversity enrichment experiment (EFForTS-BEE) arrayed within an approximately 150 ha area of an oil palm plantation (Figure 2c). Insect surveys, and later, pollinator and phytometer monitoring were conducted within a limited time window to minimize variability due to seasonal or environmental differences (and for phytometer plants, to accomplish sufficient repetitions before blooming ended). This

Figure 3 (next page). Photos field work from the oil palm pollinators experiment (Chapter 2): (a) stingless bee and *Apis dorsata* visiting male inflorescence (credit: T. Fung); (b) overviw of plantation area; (c) nearby remnant forest; (d) exclusion treatment protected against monkeys. Biodiversity enrichment interactions experiment (Chapter 3): (e) comparison of oil palm matrix (left) and enrichment plot (right); (f) raising phytometer chili plants; (g) conducting phytometer flower visitor observations. Landscape hives experiment (Chapter 4): (h) unloading bee hive delivery; (i) conducting a forager observation survey; (j) a plot in the forest destroyed by wildlife.


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required the help of several teams of assistants working simultaneously to cover the many plots in the experiment. Phytometer plants (chili pepper, *Capsicum annuum*) were grown from seed in Jambi city and transferred as seedlings to the field station in Humusindo where they were raised to sexual maturity (Figure 3f), after which they were placed in the plots for pollinator observation (Figure 3g). Chili fruits were harvested from the phytometer plants once they turned red. We related all the variables we collected to the separate effects of tree richness, tree species identity, species interactions, and plot size using the random partition method (Bell et al. 2009). We tested cascading (i.e. linked direct and indirect) relationships between the variables using structural equation models (Grace 2008).

The beehive sites in my fourth chapter were distributed in an approximately 200km^2 area in the Batang Hari Regency (Figure 2a). Colonies of *T. laevicips* were purchased from Bengkulu Province to the southwest of Jambi and delivered overnight (Figure 3h). The colonies were placed in their sites within the day of delivery with the help of multiple teams of assistants. Three hives were placed at each site inside a shelter that had been installed beforehand (Figure 3i). Hives were allowed to acclimate for several weeks before we began foraging behavior surveys (Figure 3i), which were conducted by master's student Sonja Schröck. Foraging survey methods were standardized through training conducted by our project's Indonesian counterpart, Professor Dr. Rika Raffiudin, whose master's students also studied a subset of the hive sites. A challenge in fieldwork was the loss of hives due to damage by wildlife and humans (Figure 3j). Colony foraging surveys were conducted from August to November 2018 by multiple teams to cover all plots once a month. Flowering vegetation surveys were conducted at each plot before and after the foraging survey period. At the end of the four months, the surviving hives were collected, and hive structure and colony size were measured.

Major findings

Chapter 1

In addition to the introduced pollinator *Elaeidobius kamerunicus*, other insect groups are reported to pollinate oil palm, including Thysanoptera, Lepidoptera, and other Coleoptera species. Nevertheless, few studies have examined interactions between these groups for possible complementarity or competition, or effects of landscape context and natural enemies. Significantly, pollination services and *E. kamerunicus* populations have fluctuated since their introduction in growing regions worldwide. Management research also could take pollinator population dynamics into account, by optimizing male and female flower densities. Further, research should also address possible climate change impacts on pollinator populations and services.

Chapter 2

Oil palm pollination increased closer to forest, most strongly when large visitors to flowers were excluded, though also slightly so under open pollination. This distance effect was not significant with treatments minimizing the pollination contributions of flower visitors, suggesting that the effect was not abiotic. Pollination rate was an important driver of yield and explained more difference in yield than the palm age. Insect groups associated with higher fruit set under open pollination were *E. kamerunicus* and possibly Phoridae (Diptera), while under partial exclusion Gelechiidae (Lepidoptera) was associated with fruit set. Insect abundance patterns suggest effects from unexamined interactions, such as predation, may also play a role in oil palm pollination patterns with forest proximity.

Chapter 3

Oil palm biodiversity enrichment treatments had the strongest direct effect on abiotic and vegetation variables in enrichment plots. One fast-growing species strongly affected canopy openness and structural complexity. In turn, canopy openness, as well as understory vegetation variables were important drivers for herbivore and pollinator abundance, while natural enemy abundance may have been driven by herbivore abundance. Pollinator abundance-driven flower visits increased the yield of the phytometer chili plants, while herbivore abundance had no apparent disservice effect on phytometers.

Chapter 4

Colonies of *T. laeviceps* in forest and rubber plantation plots had lower mortality and gained more in size than colonies in shrubland and oil palm plantations, which were more open habitats. However, open habitats had higher floral richness and density. Floral richness was associated with more hive pollen, which in turn drove bee and colony size.

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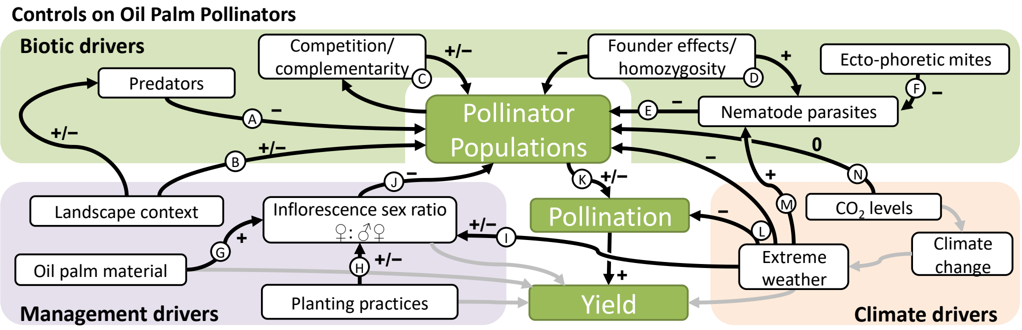
Chapter 1

Critical factors limiting pollination success in oil palm: A systematic review



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Abstract

Oil palm (*Elaeis guineensis* Jacq) is an economically important crop, yet it plays a major role in tropical deforestation and has significant negative impacts on biodiversity. The ecological drivers of oil palm pollination are still poorly understood, despite pollination being a key ecosystem service for the yield of this multi-billion-dollar industry, with potential links to biodiversity conservation. Here we review biotic and abiotic drivers of pollination and known oil palm pollinators, including local insect species endemic to specific growing regions, and an important, globally-introduced West African weevil (*Elaeidobius kamerunicus*) whose fluctuating populations have led to concerns about yield and resilience. Future research should clarify pollinator community dynamics to facilitate pollination complementarity, which may strengthen pollination services in regions beyond the oil palm and weevil's native West African ecosystem. In addition, other interactions such as mutualism, predation, and parasitism are not yet well understood, but could provide further insight into population drivers. Future management research should explore manipulating male palm inflorescence density, a key resource for pollinators, as well as investigate spatial and landscape effects on pollinator populations. Critically, no studies have investigated the effects of climate change on pollination, despite the impacts of rain and temperature on pollination efficiency. A greater understanding of the role of pollinator species and their nonlinear relationships to yield, as well as the complexity of biotic, management, and climate drivers of successful pollination can contribute to a more sustainable oil palm production system that values ecosystem services gained from biodiversity, while also improving producer livelihoods.

Key words: fruit set, land-use management, oil palm, pollinator complementarity, pollen limitation, weevil, yield

1.1. Introduction

Pollination plays an important role in the yield of many major crops (Klein et al. 2007), providing a significant economic service (Fijen et al. 2018). A majority of animal-pollinated crop systems depend on wild insect pollinators; these interactions can be an important link between biodiversity conservation and ecosystem services (Garibaldi et al. 2011, Bommarco et al. 2013). However, major ecological research in wild pollination of crops has focused mainly on the role of bees (Hymenoptera) and the crops they pollinate; research in the roles of other insect groups and pollination systems are comparatively lacking (Rader et al. 2016).

African oil palm (*Elaeis guineensis* Jacq), a monoecious arecale plant that produces the fruit used to make palm oil, is grown in tropical regions of equatorial Africa, South and Central America, and South and Southeast Asia (Sheil et al. 2009). Depending on pollination efficiency, 30%-60% of flowers on a female oil palm inflorescence develop into 500-4000 fruits clustered on a 5-25 kg bunch (e.g. Figure 1-1) (Corley and Tinker 2016). Since the discovery of pollination by insects in its native range in Africa (Syed 1979), oil palm agriculture in non-native regions has come to rely heavily on introduced populations of the African weevil *Elaeidobius kamerunicus* (Coleoptera: Curculionidae) (Corley and Tinker 2016). However, reliance on a single pollinator species for crop production comes with risks (cf. current declines in honeybees; Potts et al., 2010), and indeed, the population and pollination effectiveness of *E. kamerunicus* has seen declines in Southeast Asia (Donough et al. 1996, Rao and Law 1998). Notwithstanding, literature on these trends and the biotic and abiotic forces driving oil palm pollination is scarce.

The expansion of oil palm, a strictly tropical crop, threatens some of the most biodiverse areas of the world (Fitzherbert et al. 2008, Koh and Wilcove 2008). The oil palm industry’s high productivity and low production cost, coupled with broadening demand, has led to an exponential expansion in production since the 1960s, reaching 56 million tons in 2012, far exceeding soya bean (42 million) and rapeseed (25 million) (Corley and Tinker 2016). Conversion is often coupled with deforestation and habitat fragmentation (Koh et al. 2011, Vijay et al. 2016), in addition to increased greenhouse gas emissions and negative consequences for soils, environment, and biodiversity (Fitzherbert et al. 2008, Clough et al. 2016, Drescher et al. 2016). Indonesia and Malaysia, now the leading producers and exporters of palm oil worldwide, account for approximately 85% of total world production (Corley and Tinker 2016), and are on track to lose three-quarters of their forest cover and 13%-42% of their regional species by 2100 (Koh and Wilcove 2008).

Figure 1-1. Well-pollinated (a) and poorly-pollinated (b) oil palm fruit bunches. Photo credit: N. Marbun.

However, as the highest-yielding of all vegetable oil crops per area (Sheil et al. 2009), oil palm could have the potential to limit land under production while maximizing economic gains. Despite constituting 32% of world vegetable oil production, oil palm occupied only 6% of the total land cultivated for vegetable oils in 2012 (Corley and Tinker 2016). While much of the research in reducing the environmental impacts of oil palm has focused on optimizing agronomical practices (Euler et al. 2016, Woittiez et al. 2017), little has focused on conserving and enhancing the ecological mechanisms that affect pollination, a key contributor to yield.

Given the major economic and environmental significance of oil palm and its dependence on insect pollination, oil palm pollination ecology should be factored into any strategy for reducing its ecological impacts and limiting further expansion, while also sustaining local livelihoods and meeting global demand. Here, we present a systematic review of the current scientific literature on the biotic aspects of oil palm pollination, focusing on the drivers of pollination, pollination efficiency, and pollination limitation. We conclude by highlighting gaps in our current understanding of oil palm pollination and how to address these gaps.

1.2. Methods

We conducted a systematic review of peer-reviewed literature on oil palm pollination in April 2018, which we updated for new entries in April 2019. The criterion for inclusion in the review was that the material presented original research investigating drivers governing known or potential oil palm pollinators. Relevance was assessed successively by title, abstract, and manuscript text. In addition, we also included relevant studies cited by original returns.

We first searched the *ISI Web of Science* (WoS) database of peer-reviewed literature, using the search string ‘(“oil palm” OR *Elaeis*) AND (pollinat* OR *Elaeidobius*)’. Grey literature can also be an important and influential information source for research and policymaking in the tropics, especially in Southeast Asia (Corlett 2011). Therefore, we supplemented the WoS search with searches in *CAB Direct* (CAB) and *Google Scholar* (GS) databases for grey literature using the same search string. As a simple and conservative classification, we categorized any material not found in WoS as grey literature.

1.3. Results

We included all results returned by WoS (84) and CAB (100), and the first 100 results (out of more than 11,000) from GS. Extending the GS search to include 200 results did not add any significant results to the original and related searches. Altogether, the searches produced 243 unique results, 72 of which were relevant to our review (Section 1.6, Online Supplementary Material 1).

Within our results, we conservatively classified 44 as grey literature (i.e. not found in WoS), which we have indicated in Section 1.6, Online Supplementary Material 1. Much of this grey literature comes from industry reports and trade journals, or originates from local research institutions, and therefore provides invaluable insights close to decisionmakers in the field. Furthermore, the peer-reviewed literature cited from the grey literature extensively, indicating the latter’s importance in this subject area, and brings attention to the lack of comparable peer-reviewed studies. In our results we mostly reference grey literature that is widely cited, though we note that more obscure literature also support our main results.

We present the synthesis of our results in two sections: in Section 1.3.1, we introduce the known pollinating insects of oil palm (Table 1-1) and their interactions; and in Section 1.3.2, we describe the relationship of insect pollination to yield, including emerging limitations in pollinating efficiency and their controlling factors (Figure 1-2), which we discuss further in the discussion (Section 1.4).

1.3.1. Pollinating insects of oil palm

Coleoptera

In the oil palm's native West African range, several weevil species of genus *Elaeidobius* (Coleoptera: Curculionidae) (Table 1-1) are found in oil palm inflorescences. Adults feed on flower parts and pollen in the male inflorescence while females oviposit in male flower structures, on which the larvae develop and feed as it decomposes (Syed 1982, Mariau et al. 1991).

During male inflorescence anthesis, more than 100,000 flowers open gradually over two to four days, ceasing pollen production after five days (Corley and Tinker 2016). Over the anthesis period, researchers have observed over 8,000 weevils of various species per inflorescence in West Africa (Mariau et al. 1991), and 2,000-3,000 introduced weevils in India (Tandon et al. 2001).

Weevils are attracted to receptive female flowers by an aniseed-like smell similar to that of the male flowers (Adaigbe et al. 2011). Female receptivity lasts 36-48 hours, with a few hundred (in a 3-year old palm) to several thousand (10 year-old palm) flowers per inflorescence (Corley and Tinker 2016). As female inflorescences have no resources, weevils only stay briefly; however, 5,000-12,000 visits can occur during the receptive period (Syed 1979, Chinchilla and Richardson 1991, Mariau et al. 1991).

Elaeidobius species differ in pollen-carrying ability and transported pollen viability (Table 1-1), as well as search capacity (Syed 1982). *Elaeidobius kamerunicus* was introduced to Southeast Asia in the 1980s due to its robustness in long rainy seasons, host-specificity to oil palm, and high pollen-carrying capacity (Syed et al. 1982). This species was also introduced in tropical America, though *E. subvittatus* was already naturalized there accidentally (Chinchilla and Richardson 1991). A few other *Elaeidobius* species (Table 1-1) were introduced within limited areas of tropical America as well (Meléndez and Ponce 2016).

The Nitidulid beetle *Mistrops costaricensis* (Table 1-1) is a native pollinator in regions of tropical America that feeds on oil palm pollen (Syed 1984). Though its presence on female inflorescences is less than 1% of the 27,000-38,000 individuals found on male inflorescences, it carries high (70%) viability pollen and remains active on female inflorescences after its diurnal foraging period, which may improve pollination (Chinchilla and Richardson 1991). Its rain tolerance may allow it to compensate for seasonal *E. kamerunicus* decreases in very wet regions (Syed 1984), though foraging time and rain resistance varies between regional sub-species and it is still affected by heavy rains (Mariau and Genty 1988).

Other coleopteran genera found on African oil palms include *Prosoestus* (Curculionidae), *Atheta* (Staphylinidae), and *Microporum* (Nitidulidae) (Table 1-1). However, the amount of pollen carried by these species is relatively limited and lower in quality (Mariau et al. 1991, Kouakou et al. 2014).

Thysanoptera

In Southeast Asia, the Thysanopteran *Thrips hawaiinensis* (Table 1-1) was seen as the main pollinator before *E. kamerunicus* was introduced (Syed 1979). Syed (1979) found that a male flower spikelet could contain up to 1,000 individuals (with up to 200 spikelets per inflorescence). Many thrips may swarm female inflorescences (up to seven per flower), making continuous, brief visits. On average, thrips may carry four to five pollen grains, with high (76%) viability. However, this species is absent from young plantations, perhaps due to difficulty flying in open and windy areas (Syed 1979). Hand pollination was therefore necessary to improve fruit set before weevil introduction in Southeast Asia (Donough and Law 1987). This species is also reported in South America (Labarca and Narvaez 2009), and *Thysanoptera* species are observed visiting oil palm in the Ivory Coast, but primarily male inflorescences (Hala et al. 2012).

Lepidoptera

The moth *Pyroderces* sp. (Lepidoptera: Cosmopterygidae) is another pollinator endemic to Southeast Asia (Table 1-1). This species oviposits on male inflorescences but also visits female inflorescences, often depositing pollen on them (Syed 1979). It is only active for 2-3 hours around sunset, which may reduce contribution to fruit set (Tan and Basri 1984). Syed (1979) estimated visitors to a female inflorescence in one night did not exceed 500 individuals.

Other visiting groups

Bees (Hymenoptera: Apidae) also visit oil palm inflorescences, including the Indian honeybee *Apis cerana indica* in India (Sambathkumar and Ranjith 2011), and *Apis mellifera* and *Nomia* sp. in the Ivory Coast (Chenon 1982, Hala et al. 2012). In Brazil, Meliponid bees (*Trigona* spp.) made up 13% of male flower visits, second in frequency to *E. kamerunicus* (56%) (Silva et al. 1986). However, as bees mainly visit male flowers for pollen, they likely do not contribute to direct pollination (Meléndez and Ponce 2016). True flies (Diptera) can also be found in oil palm inflorescences, but their role in pollination has not yet been assessed (Mayfield 2005, Hala et al. 2012).

Pollinator complementarity

Contributions from multiple pollinator species could translate to more robust pollination services. Wahid and Kamarudin (1997) observed 60% fruit set in Malaysia, even after weevil populations dropped to levels considered too low for adequate pollination. They attribute this to complementary pollination by *T. hawaiiensis*, which is not as affected by dry seasons. In Columbia, Montes Bazurto et al. (2018) suggest a similar relationship between *E. kamerunicus* and *M. costaricensis*.

Complementary behaviors exist among *E. kamerunicus* and other pollinators (Table 1-1). Most *E. kamerunicus* populations visit female inflorescences in the morning to midday (Sambathkumar and Ranjith 2011, Yue et al. 2015, Auffray et al. 2017). In Brazil, *E. subvittatus* is active simultaneously, but additionally visits female flowers in the late afternoon, while *M. costaricensis* visits in the evening (Moura et al. 2012). In Indonesia, *T. hawaiiensis*

Table 1-1. Commonly reported oil palm pollinators. Regional presence is indicated as native (filled circle) or introduced (empty circle). Also shown are each species' contribution to fruit set (%), transported pollen viability (%), activity on male and female inflorescences, and range of reported average pollen grain load by sex. ND = no data.

		Presence (●:native; ○:introduced)								
Order	Genus species	Africa	S Asia	SE Asia	Latin Amer.	Fruit set (%)	Pollen via. (%)	♂ inflorescence activity	♀inflorescence activity	Range of reported average pollen grain loads (sex)
Coleoptera	*Elaeidobius kamerunicus*	●	○	○	○	68[a], 56[b]	93[b]	Feeds, oviposits on flower structures[g]	Incidental[g]	56[f]-534[j] (♀); 235[g]-1842[k] (♂)
	E. plagiatus	●			○	71[a], 46[b]	77[b]			20[c]-203[g] (♀); 27[g]-236[b] (♂)
	E. singularis	●			○	ND	ND			ND
	E. subvittatus	●			○	32[a], 25[b]	54[b]			9[a]-78.6[j]
	Microporum sp.	●				52[a], 13[b]	27[b]	Adults, larvae feed on pollen[a]	Incidental, <than *Elaeidobius*[a]	6[a]-77[b]
	Atheta sp.	●				17 [a]	ND	Predator[a]	Rare[a]	1[g]-4[a]
	Prosoestus sp.	●				ND	ND	Rare[g]	Feeds on flower structures[a]	4[g]
	Mistrops costaricensis				●	67[c]	70[f]	Adults, larvae feed on pollen[h]	Low, but still active at night[f]	11 (♀); 13 (♂) [f]
Thysanoptera	*Thrips hawaiiensis*			●	○	53[d]	76[g]	Feeds on pollen[i]	Inhabits[i]	5[g]
Lepidoptera	*Pyroderces sp.*			●		31[e]	-	Oviposits[g]	Visits[g]	6[g]

[a] Mariau et al., 1991; [b] Kouakou et al., 2014; [c] Mariau & Genty, 1988; [d] Donough & Law, 1987; [e] Tan & Basri, 1984; [f] Chinchilla-López & Richardson, 1991; [g] R. A. Syed, 1979; [h] Meléndez & Ponce, 2016; [i] Anggraeni et al., 2013; [j] Moura et al., 2012; [k] Dhileepan, 1992

avoids *E. kamerunicus* by visiting in the morning and late afternoon (Anggraeni et al. 2013). Additionally, since *E. kamerunicus* consumes flower parts only, its resource use differs from other species such as *T. hawaiiensis* and *M. costaricensis*, which consume only pollen (Syed et al. 1982, Syed 1984).

Differing reproduction and development also allow complementarity (Table 1-1). In their native range, Syed (1982) observed that *E. kamerunicus* and *E. plagiatus* feed and lay their eggs in different parts of the anther tube of the male flower while *E. subvittatus*, which develops stronger jaws at an earlier larval stage, oviposits and feeds on the tougher upper part of the flower and the anther filaments. In tropical America, *M. costaricensis* larvae pupate outside the inflorescence, reducing competition with *E. kamerunicus* and *E. subvittatus* (Syed 1984). In peninsular Malaysia, Wahid and Kamarudin (1997) attribute the coexistence of three pollinators to their differing pupation habitats: *E. kamerunicus* and *Pyroderces* sp. pupate in male flowers while *T. hawaiinensis* pupates in soil.

Nevertheless, *E. kamerunicus* introduction can still negatively impact the local pollinator community. Where *E. kamerunicus* was introduced in

Central America, *E. subvittatus* and *M. costaricensis* populations decreased with *E. kamerunicus* increase (Chinchilla and Richardson 1991). Moura et al. (2012) reported similar outcomes in Brazil, where *E. subvittatus* very rarely dominated. In Southeast Asia, recent studies have observed coexistence of *T. hawaiiensis* and *Pyroderces* sp. with *E. kamerunicus* (Wahid and Kamarudin 1997, Anggraeni et al. 2013), though following the initial release of the weevil in peninsular Malaysia, Syed (1982) observed a decrease in *T. hawaiiensis* that paralleled *E. kamerunicus* population increase.

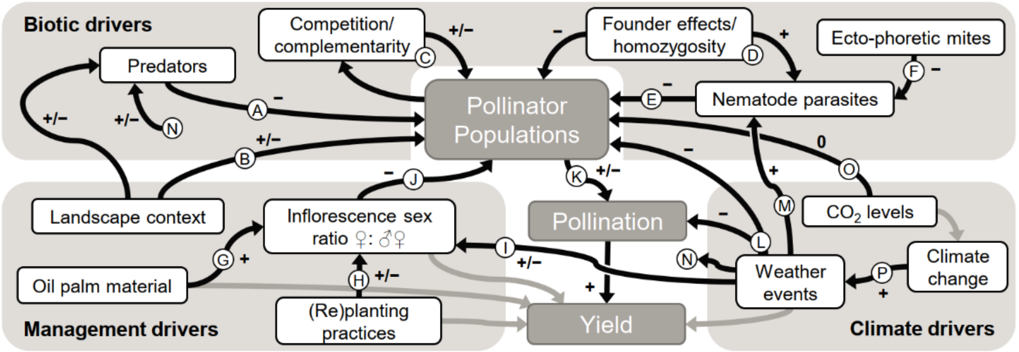
1.3.2. Controls on oil palm pollination

Insect pollination and effects on production

Once *E. kamerunicus* was introduced to Southeast Asia in the early 1980s, insect-pollinated oil palms achieved higher fruit sets than previous hand-pollinated rates (Syed et al. 1982). This could be due to the weevil's ability to penetrate deeper into the inflorescence than hand-applied pollen and to its continuous visitation over the course of the asynchronous blooming period (Harun and Noor 2002). Syed (1984) compared before (1981) and shortly after (1982) *E. kamerunicus* introduction in a Malaysian plantation and found a fruit set increase from 48% to 71%, and increases in fruit to bunch ratio and bunch weight. The total oil produced per bunch increased by 48%, approximately one kg. Donough and Law (1987) continued to observe such improvements in Malaysia five years after introduction. Similar yield increases were also observed in Indonesia (Hutauruk et al. 1984), India (Dhileepan and Nampoothiri 1989), and tropical America (Mariau and Genty 1988, Chinchilla and Richardson 1991, Moura et al. 2012).

Some weevil population parameters for achieving acceptable fruit set levels have been proposed, e.g. a minimum population density of 20,000 ha^{-1} for 55% fruit set (Donough et al. 1996). However, the relationship between pollinator population size, pollination services, and yield are not altogether linear or monotonic. While bunch weight and fruit set generally increased with weevil introduction, bunches produced per year decreased in some cases, though this was still offset by bunch weight (Taniputra and Muluk 1989, Harun and Noor 2002). Though oil content is closely related to fruit set, the ratio of oil to bunch weight only increases with fruit set up to about 75% fruit set and decreases above that (Harun and Noor 2002).

These nonlinear effects require a deeper understanding of the mechanisms controlling pollination and yield. Once introduced, weevil pollination changed aspects of fruit bunch production in Southeast Asia. Individual fruits became more densely packed in the bunch (Syed et al. 1982), causing inner fruits to develop poorly and yield less oil (Harun and Noor 2002), leading to less efficient factory oil extraction (Syed et al. 1982). On the other hand, Genty et al. (1986) observed a compensation phenomenon in some poorly-pollinated bunches in which the fewer fruits grow larger, resulting in oil production comparable to higher pollination levels.



Explanations	
A	Birds, spiders, insects, rats predate on pollinators
B	Nearby forest had no effect on pollinator diversity (in Costa Rica)
C	Native and non-native pollinators compete or complement
D	*Elaeidobius kamerunicus* may be susceptible to nematode parasites in SE Asia due to genetic bottleneck
E	*Elaeolenchus parthenonema* identified as a parasitic nematode important in Southeast Asia
F	Mites feed on nematodes found on African populations
G	More productive oil palm material favors female inflorescences
H	Planting/replanting practices (e.g. pruning, leaving old trees, tree density) affect inflorescence sex ratio
I	Extreme weather can influence inflorescence sex ratio
J	Fewer male inflorescences reduces breeding/feeding sites for *E. kamerunicus*
K	More pollinators improves fruit set
K	Very high pollinator populations may lower fruit set
L	Extreme weather (rain, temperature) affects pollinator activity and fruit set
M	More rain is hypothesized to advantage parasitic nematodes over *E. kamerunicus*
N	Drier weather hypothesized to release *Elaeidobius subvitattus* from a major predator, *Lestodiplosis* sp.
O	No effect of higher CO$_2$ levels observed on *E. kamerunicus*
P	Climate change increases the frequency and severity of extreme weather events (e.g. El Niño)

Figure 1-2. Diagram of major drivers (white boxes) of components of the oil palm pollination process (dark gray boxes). Black arrows represent relationship direction, and positive (+) or negative (–) symbols indicate relationship; both (+/–) are shown for complex or inconclusive results; "0" indicates no relationship was found. Letters correspond to the attached explanations. Gray arrows represent relationships not included in the review. Source literature available in Section 1.6, Online Supplementary Material 2.

Still other nonlinear relationships have yet to be fully understood. Several studies report that, at very high weevil populations, fruit set is no different (Dhileepan 1994) or worse (Dhileepan 1992, Wahid and Kamarudin 1997) than at lower weevil population levels. Wahid and Kamarudin (1997) hypothesize that could be due to greater confusion and competition at higher weevil densities, but direct observations are lacking.

Population fluctuations of E. kamerunicus and consequences for pollination

After a period of yield improvement following weevil introduction, fruit set and oil extraction rates declined in parts of East Malaysia and Sumatra (Indonesia) (Donough et al. 1996, Rao and Law 1998), sometimes necessitating a return to assisted pollination (Prasetyo et al. 2014, Kamarudin et al. 2018). Between 1982 and 1997, kernel oil extraction in a Malaysian estate decreased from 6% to 4% with steep seasonal variations (Rao and Law 1998). This was accompanied by decreases in weevil population, for example falling from 40,000 to 15,000 ha^{-1} between 1994 and 1997 (Rao and Law 1998), and in some cases falling below 10,000 ha^{-1} (Donough et al. 1996). Surveys in 2016-2017 estimate 15% of Malaysia's oil palm cultivation area (88,381 ha surveyed) are affected by low fruit set (Kamarudin et al. 2018). The necessity for assisted pollination due to low pollinator populations has also been reported in South America (Vera 1996, Meléndez and Ponce 2016).

Rao and Law (1998) hypothesize that low pollination rates leading to poor fruit set could be caused by low pollen quantity (while pollen quality appears to be unrelated to fruit set) or reduced pollination by pollinators. Below we report the drivers that may be relevant to understanding pollination fluctuations and decreases, which are summarized in Figure 1-2.

Climate drivers

Elaeidobius kamerunicus populations can vary strongly with climatic factors. In addition to a gradual decline in fruit set, Rao and Law (1998) observed annual mid-year decreases throughout Malaysia, indicating poor pollination in the rainy season five to six months earlier. Though *E. kamerunicus* is not as impacted as other *Elaeidobius* species, its pollination efficiency can still decrease in heavy rains (Syed et al. 1982, Mariau and Genty 1988, Sambathkumar and Ranjith 2015), as rain reduces inflorescence visits, removes pollen from weevil bodies, and decreases pollen viability (Dhileepan 1994, Ponnamma 1999, Kouakou et al. 2018).

A prolonged dry season also negatively impacts *E. kamerunicus*. In Kerala, India, where weevils were introduced in 1985, populations fluctuate widely, with the lowest levels in the dry season (Dhileepan 1994, Sambathkumar and Ranjith 2015). Dry conditions also negatively affect *Elaeidobius* and *Mistrops* species in Venezuela (Labarca and Narvaez 2009), and *E. kamerunicus* in Costa Rica and Columbia (Chinchilla and Richardson 1991, Montes Bazurto et al. 2018). Where *E. kamerunicus* shares its range with *E. subvittatus*, the latter tends to dominate during hot, dry seasons (Moura et al. 2012).

Few studies have investigated the potential effects of global climate change on pollinator activity and distribution. Amanina et al. (2016) found that *E. kamerunicus* was not affected by a high level of CO_2 (800 ppm versus 400 ppm) and concluded increased CO_2 does not significantly affect weevil emergence; though impacts on activity and other life stages remain to be explored. Importantly, global climate change may be linked to stronger and more frequent El Niño-Southern Oscillation (ENSO) events, which impact growing conditions in the tropics by altering drought and rainfall patterns (Rosenzweig et al. 2001). However, we found no studies examining the risk these changes pose to pollinator communities and pollination services of oil palm-growing regions. This is despite the demonstrated impacts of weather patterns on sex ratio and pollination efficiency – for example, excessive rain in Costa Rica in 1994 led to fewer male oil palm inflorescences during an extended dry season two years later, causing a crash in the *E. kamerunicus* population that decreased yield (Bulgarelli-Mora et al. 2002).

Biotic drivers

Weevil-dwelling nematodes may have been inadvertently introduced to Southeast Asia with *E. kamerunicus*. Weevils infected with parasitic nematodes can have shortened lifespans (i.e. fewer reproductive cycles), reduced fecundity and egg production, and fewer and smaller larvae that may not complete development (Rao and Law 1998, Poinar et al. 2002). The internal parasitic nematode, *Elaeolenchus parthenonema* has been found in Papua New Guinea and Indonesia, but is thought to be widespread in oil palm-growing areas in Southeast Asia (Caudwell et al. 2003). It infects all life stages of the weevil (larvae, pupae and adult) and its parasitic burden can inhibit the weevil's ability to fly, likely impacting pollination services (Poinar et al. 2002, Caudwell et al. 2003).

While nematode parasitism seems to be prevalent throughout Malaysia and may substantially decrease the fitness of populations there, the presence and effects of nematodes on weevil populations in West Africa and elsewhere appear limited (Rao and Law 1998, Caudwell et al. 2003, Aisagbonhi et al. 2004). No nematodes were detected in six populations in Costa Rica (Caudwell et al. 2003), and very low rates of infestation were found in Ghana and Nigeria (Caudwell et al. 2003, Aisagbonhi et al. 2004). Of note, ectophoretic mites were often found on weevil samples from West Africa. Such mites have been observed searching for and consuming *E. parthenonema* and phoretic nematodes on the surface of the weevil (Poinar et al. 2002, Caudwell et al. 2003, Krantz and Poinar Jr 2004).

Inbreeding depression or extreme homozygosity, stemming from the founding weevil population in Southeast Asia, could explain the vulnerability of this region's populations (Rao and Law 1998). Indeed, Ghanaian weevil populations are genetically distinct from introduced populations in Papua New Guinea and Costa Rica (Caudwell et al. 2003). However, Caudwell et al. (2003) also found no less genetic diversity in introduced populations, suggesting no genetic bottleneck, though more time may still need to pass for an effect to become detectable. Thus, they attribute decreased pollination efficiency to nematode parasitism, but do not rule out increased susceptibility as a founder effect.

Predation could also play a role in controlling *E. kamerunicus* population levels, as spiders, mites, ants, birds, and rats have all been reported to prey on all weevil life stages (Ponnamma et al. 2006, Prasetyo et al. 2014, Yue et al. 2015). *Pycnonotus goiavier*, a common bird in Malaysian plantations, feeds preferentially on *E. kamerunicus* (Amit et al. 2015). In tropical America, *Lestodiplosis* sp. (Diptera: Cecidomyiidae) is an important predator of *E. subvittatus* (Genty et al. 1986). The impact of predation on pollinators and pollination services has not been directly quantified, though in a bat and bird exclusion experiment in oil palm in Indonesia, Denmead et al. (2017) found a significant (p<0.05) decrease in arthropod predators with increasing insectivorous bird activity (measured by detected vocalizations). This was associated with a concurrent positive (non-significant) trend in *E. kamerunicus*.

Management drivers

Plantation management practices can affect the ratio of female to total oil palm inflorescences, i.e. the sex ratio. An oil palm produces a single male or female inflorescence in each leaf axil, which anthesizes in turn (Corley and Tinker 2016). Young palms and higher-yielding varieties typically favor female inflorescences (Rao and Law 1998, Prasetyo et al. 2014), while water and radiation stress can lead to more male inflorescences (Corley and Tinker 2016). Strong environmental stimuli can also synchronize the production of male and female inflorescences among palms (Rao and Law 1998), e.g. as in Bulgarelli-Mora et al. (2002).

More female inflorescences results in less available pollen and fewer weevil breeding sites, potentially reducing pollination (Rao and Law 1998). Donough et al (1996) suggest restoring assisted pollination where there are insufficient male inflorescences, heavy rains, and a lack of alternative insect pollinators. Assisted pollination is typically done by applying pollen to female inflorescences by hand (Meléndez and Ponce 2016), though novel techniques have been proposed using weevils as a distribution mechanism (Vera 1996, Prasetyo et al. 2014).

Assisted methods can increase weevil population and fruit set, but the problem of insufficient male inflorescences for sustaining weevil populations remains. Oil palm plantations have an approximately 25-year life cycle, with fruit production beginning two to three years after planting and remaining economical until excessive tree height and declining yield necessitates replanting (Corley and Tinker 2016). The replanting stage could provide an opportunity to experiment with planting configuration and other treatments to improve conditions for pollinators. Rao and Law (1998) propose leaving a few old palms when replanting a stand to retain male inflorescences as weevil breeding sites, planting a mixture of palms from different source materials to reduce the likelihood of synchronized sex differentiation, and severely pruning some palms to encourage more male inflorescences. Breure et al. (1990) also propose increasing planting density to increase competition, thus stimulating palms to develop more male inflorescences while fostering darker, moister environments preferred by *E. kamerunicus.* However, our search found no reports of the effectiveness of these methods.

1.4. Discussion and research needs

Insect pollinators play an important role in the global expansion of oil palm, as well as its recent fluctuations and declines. We discuss current and future research in the biotic, management, and climate drivers of pollination, summarized in Table 1-2.

1.4.1. Climate drivers

Critically, the impacts of climate change and the associated intensification of ENSO events are under-examined in the literature (Figure 1-2), as no studies investigated the potential effects of increasing temperature and extreme weather on weevil populations. Future research should examine how these changes could directly affect pollinator populations, e.g. changing the pollinator community through shifting environmental conditions, leading to changes in pollination that necessitate interventions. Indirect impacts on interacting species are also important. For example, wetter weather may advantage parasitic nematodes in Southeast Asia (Rao and Law 1998), while dry weather in tropical America may release *E. subvittatus* from *Lestodiplosis* sp. predation (Genty et al. 1986). Climate change effects, especially more frequent and intense ENSO events, may also impact oil palm sex ratios and subsequently dependent pollinator populations. Further research should investigate and model the ongoing and future impact of these effects on pollination and identify appropriate management solutions.

Table 1-2. Recommendations for future research.

	Future research should address:
Biotic drivers	• The relative role of each pollinator species and effects of competition on pollinator populations and services • Impacts of predation and nematode parasitism on weevil populations and pollination services • Prevalence and effects of homozygosity and inbreeding depression in introduced weevil populations • Potential mutualism between *E. kamerunicus* and nematophagous mites
Management drivers	• Optimizing inflorescence sex ratio between fruit bunch production (female inflorescences) and pollinator resources (male inflorescences) • Effects of inflorescence spatio-temporal sex distribution on pollinators and pollination services • Landscape effects on pollinator populations and pollination services in different growing regions • Risks and benefits of introducing additional pollinator species to regions with insufficient or unstable pollination • Maintaining sustainable multi-pollinator communities
Climate drivers	• Direct and indirect impacts of climate change on pollinator communities and interacting species • Impacts of increasing frequency of severe weather phenomena (e.g. El Niño)

1.4.2. Biotic drivers

Though much has been published on the biology of major pollinator species of oil palm, there is little research on their interactions and feedbacks within the larger agroecosystem (Figure 1-2). Certain ecological processes play important roles in agroecosystems, e.g. community assembly and trait-mediated trophic cascades in coffee (Perfecto et al. 2014); but these remain underexplored in oil palm research.

Further investigation into the effects of competition between pollinators (e.g. *E. kamerunicius* and *T. hawaiiensis* in Southeast Asia or *E. kamerunicus*, *E. subvittatus*, and *M. costaricensis* in tropical America), predation (e.g. identifying major natural enemies of *E. kamerunicus* and other pollinators), and mutualism (e.g. investigating the importance of nematophagous mites) could clarify the significance of ecological interactions in population patterns and pollination. These relationships could be quantified in the field through standardized-effort observation methods using direct observation (Vergara and Badano 2009) or cameras (Lortie et al. 2012); as well as through trapping methods such as sticky traps (Yue et al. 2015). Their effects could be measured with field experiments using exclusion treatments to isolate pollinator contributions to yield (Vergara and Badano 2009) or predation effects (Denmead et al. 2017). Laboratory experiments can also be used to test trophic interactions, e.g. predation (Morris and Perfecto 2016).

Increased parasite infestation in introduced *E. kamerunicus* populations, possibly due to limited genetic diversity, may play a role in yield declines and fluctuations (Rao and Law 1998, Caudwell et al. 2003). Long-term monitoring could determine how these factors are manifested in field populations and their pollination services. Future research could also compare heritable susceptibility and fitness using transplant experiments that expose individuals from regional *E.*

kamerunicus populations to nematode parasites. Caudwell et al. (2003) also recommend developing a microsatellite marker library to quantify rates of integration and spread in existing populations and new introductions. These studies can support a decision-making process for considering additional introductions.

As seen from pollinator declines in Europe and North America, dependence on a single pollinator species could become a liability for some tropical crops, including oil palm (Ghazoul 2005). In West Africa, complementarity within the diverse native pollinator community could explain higher year-round fruit set despite seasonality. Where current pollinator populations do not provide adequate pollination, future research should assess whether complementary pollinators could be introduced. For example, in regions with pronounced dry seasons, Syed (1982) recommends potentially introducing *E. plagiatus* and *E. subvittatus* for, respectively, resilience in dry conditions and better search capability over *E. kamerunicus*. Given the risks of unforeseen ecological impacts, however, careful considerations should be made before any introduction (Ewel et al. 1999).

Understanding drivers of pollination fluctuations is critical, as yield fluctuations can take on major economic importance. In some dry environments, the highest and lowest months can represent 40% and 1% of annual production, respectively (Nouy et al. 1996). More research should be applied towards understanding the conditions and drivers of coexistence among pollinators with complementary behavior and climatic tolerances, e.g. *E. kamerunicus*, *E. subvittatus* and *M. costaricensis* in tropical America (Syed 1984).

1.4.3. Management drivers

Sex ratio represents an important trade-off between supporting pollination with more male inflorescences and increasing fruit bunch production with more female inflorescences (Figure 1-2). Though Rao and Law (1998) and Breure et al. (1990) suggest methods of influencing sex ratio, current management practices do not appear to optimize this tradeoff (Corley and Tinker 2016). Further modeling and field testing could explore optimizing sex ratio for overall yield, incorporating feedback effects with pollinator populations.

Many pollinators differ in their dispersal ability (Syed 1979, 1982), and future work should investigate the effects of male and female inflorescence spatio-temporal distribution on pollinator populations. Though studies have examined the effect of palm density on yield, pollination is often assumed constant (Breure et al. 1990). Future studies should investigate the dynamic and spatially explicit interaction between palm density, inflorescence sex, and pollinator populations and services (Dumont et al. 2018).

Landscape context is also underexplored (Figure 1-2). Although Mayfield (2005) found that oil palm flower visitor diversity did not differ with distance to forest in Costa Rica, studies are needed on other pollinator communities (e.g. in Southeast Asia) and on effects on pollination and yield. Nearby plantations and different land use types could serve as sources or sinks of pollinator metapopulations (Hanski 1999), or as sources of wild pollinators or natural enemies (Mayfield 2005, Garibaldi et al. 2011), driving pollinator population sizes and pollination services. This may become particularly important in Southeast Asia where many plantations are reaching the replanting stage (Corley and Tinker 2016), as a synchronized removal of mature palms and replacement with immature or female-favoring young palms could severely reduce *E. kamerunicus*'s obligate resource.

A better understanding of management drivers could provide guidance to sustainable oil palm certification schemes, such as the Roundtable on Sustainable Palm Oil (RSPO), on how to manage for pollination. Although recommended best practices exist for certain aspects of sustainable oil palm management, e.g. for riparian areas (Barclay et al. 2017), further research is needed to develop specific wildlife-friendly management guidelines for supporting stable, diverse pollinator communities. As our review demonstrates, many basic questions about biotic and management drivers of pollination remain. A deeper understanding of the community ecology and landscape drivers of pollination is needed to identify mutually beneficial scenarios for pollination ecosystem services and conservation that can be used to guide sustainable practice recommendations.

1.5. Conclusions

Oil palm is a globally controversial crop, due to its high commercial value and significant ecological consequences. Further research in optimizing pollination services could play an important role in reducing habitat conversion pressure while meeting global demand and supporting farmer livelihoods, especially given recent yield issues. We recommend that future research focus on pollinator community dynamics by applying theories from agroecology and landscape ecology. Topics include complexities in pollinator interactions with competitors, mutualists, and natural enemies; optimizing management for inflorescence sex ratio; and the role of landscape contexts and climate change. Understanding drivers of pollinator populations and pollination efficiency is an important component to addressing the issues facing this crop and its environmental and economic sustainability. However, improving efficiency alone is not enough to ensure habitat and biodiversity conservation. Policies, economic incentives, and outreach must prioritize local livelihoods and involvement with conservation to prevent further land conversion (Pretty and Smith 2004). Here too, a deeper understanding of the pollinator community, and of biodiversity's role in the oil palm agroecosystem in general, can inform effective and mutually beneficial agri-environmental schemes and best practices.

Authors' contributions

KL wrote the final manuscript and conducted a literature review based on earlier work by BS; IG, TT, and DB provided guidance and feedback. All authors contributed to and approved final publication.

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1.6. Supporting Information

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.agee.2019.05.001.

1.7. References

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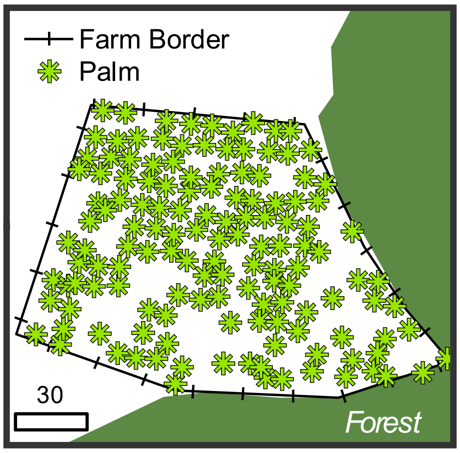
Chapter 2
Oil palm pollinators and fruit set benefit from adjacent forest



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Abstract

1. Oil palm (*Elaeis guineensis*) is a globally important crop whose expansion has been linked to deforestation. Though natural habitat can play a key role in many agroecosystems as a source of pollination ecosystem services and ecological spillover effects, these are largely unquantified for oil palm.

2. In a field experiment in Sumatra, Indonesia, we manipulated visitors to female oil palm inflorescences over a 100m gradient to nearby forest, either excluding all visitors or selectively including small (< 1.4mm diameter) visitors (including introduced pollinator *Elaeidobius kamerunicus*, Coleoptera: Curculionidae). We compared these treatments to open pollination and assisted pollination treatments. We placed sticky traps in front of inflorescences to sample the flower visitor community.

3. We find pollination is an important driver of yield, explaining approximately 50% more variability in ripe bunch weight than palm age. Partial exclusion significantly increased fruit set (mean = 75%) over open (62%) and assisted (61%) pollination treatments. When insect visitors were excluded, fruit set dropped (12%), demonstrating that insects are necessary to maintain minimum acceptable levels (> 40%).

4. Forest proximity had a positive effect on fruit set in partial exclusion and open pollination treatments, though this trend was much clearer with partial exclusion. We found no trends in fruit set under complete exclusion or assisted pollination treatments, suggesting a lack of an abiotic gradient.

5. Two major inflorescence visitors, *E. kamerunicus* (3217 individuals, 87% prevalence) and Gelechiidae (Lepidoptera) (1590 individuals, 90% prevalence) decreased with proximity to forest. Thysanoptera, the most abundant taxon (55,725 individuals, 91% prevalence), did not vary with forest proximity. Higher abundances of *E. kamerunicus*, and possibly Phoridae, were positively associated with fruit set under open pollination, but only Gelechiidae had this relationship under partial exclusion.

6. Synthesis and applications

Nearby forests and ecological processes such as predation may play an important role in driving oil palm pollination, but more experimental work is needed to disentangle these and potential further effects of landscape configuration. As fruit set could be shown to vary greatly with flower visitors, understanding these drivers may lead to yield improvements as well as additional narratives for conservation.

Key words: oil palm, pollination limitation, spillover, pollination, ecosystem service, biodiversity, forest

2.1. Introduction

Oil palm (*Elaeis guineensis*), a tropical arecale crop, accounts for the largest share of total global vegetable oil production and is the most productive oil crop by cultivated area (Corley and Tinker 2016). However, its expansion has been linked to deforestation, fires, and biodiversity loss (Koh and Wilcove 2008, Clough et al. 2016) and its sustainability in terms of greenhouse gas emissions, biodiversity impacts, and socioeconomic impacts has been called into question (Koh and Ghazoul 2008). Conservation landscape planning approaches surrounding oil palm often prescribe to a “land sparing versus land sharing” debate framework (Grass et al. 2019), which focuses on balancing wildlife conservation against production and farmer livelihood (Koh et al. 2009, Edwards et al. 2010). However, within these debates, possible synergistic benefits of biodiversity are often not discussed (Grass et al. 2019), even though ecosystem services such as pollination can play a major role in agricultural production (Klein et al. 2007).

Insect pollinators play a key role in palm oil production, but little is known about the processes that drive variability in pollination rates. Observational evidence positively correlates yield with African weevil (*Elaeidobius kamerunicus*) introductions (Syed et al. 1982) conducted after the discovery of insect pollination (Syed 1979), and with subsequent weevil population fluctuations (Donough et al. 1996, Wahid and Kamarudin 1997). However, experimental evidence to identify the relative importance of insect pollination and other ecological processes in driving yield is lacking (Li et al. 2019).

Among potential drivers of variability, the role of biodiversity in oil palm pollination is not well understood. For many insect-pollinated crop systems, a major line of research has been in identifying the contributions of wild pollinators, whose services have important economic implications (Klein et al. 2007, Garibaldi et al. 2013). Oil palm pollination research since weevil introductions has focused mainly on introduced populations (Li et al. 2019), though recent studies are beginning to consider the wider community of flower visitors (e.g. Rizali et al. 2019b).

Landscape context is a critical factor for pollination success in many insect-pollinated crops, but this is also not well understood for oil palm. The concept of ecological spillover describes how biodiversity and ecosystem function decreases with distance from the source habitat into an agroecological matrix, or vice-versa (Tscharntke et al. 2012). In oil palm systems, reliance on a single species (i.e. *E. kamerunicus*) that lives on male oil palm inflorescences (Syed 1982) has meant that the role of landscape context around the farm is largely unexplored. Nearby natural habitats support wild pollinator populations (Klein et al. 2003) but can also be a source for pollinator antagonists (Klein et al. 2006, Maas et al. 2015). Further work is needed to understand how neighboring natural land cover may provide a habitat for other potential pollinating species (Mayfield 2005).

We present an experimental manipulation of oil palm flower visitors and pollination using three levels of exclusion (none/open, partial, full) and assisted open pollination over a 100m gradient from neighboring forest. We test how restricting visitor composition (i.e. only allowing *E. kamerunicus* and other small arthropods), along with the accompanying effect of excluding pollinator antagonists (e.g. large predatory insects and vertebrates), affects pollination rate (fruit set) and yield over increasing distance to forest.

We hypothesized that change in fruit set would depend on the main pollinator group affected (Figure 2-1a, b). As baselines, we expected complete pollinator exclusion would significantly lower fruit set relative to open pollination, while assisted pollination would increase fruit set. With partial exclusion, we hypothesized that fruit set would be lower if the treatment mainly reduces pollinating visitors (Figure 2-1a), and higher if it mainly reduces antagonist interference (Figure 2-1b).

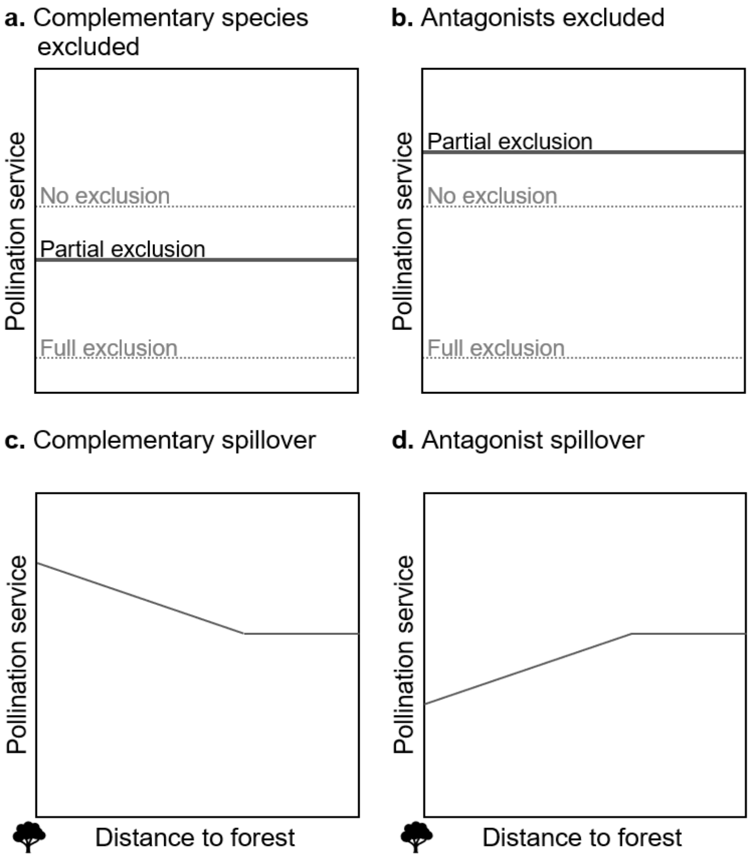

Figure 2-1. Cartoons of the hypothesized outcomes of partial exclusion: (a) if complementary species are excluded or (b) if pollinator antagonists are excluded; and outcomes of ecological spillover if forest is (c) a source of complementary species, or (d) a source of pollinator antagonists.

We hypothesized that spillover effects would influence fruit set over the distance gradient (Figure 2-1c, d). If forest is mainly a source of complementary species for oil palm pollination (e.g. additional pollinators), we expected fruit set to increase closer to forest (Figure 2-1c). If proximity to forest results in increased exposure to pollinator antagonists (e.g. predators or competitively excluding, poor pollinators), we expected fruit set to decrease closer to forest (Figure 2-1d). On the other hand, we expected that fruit set under the full exclusion and assisted pollination treatments would not vary with distance to forest, since these treatments should minimize the influence of flower visitors.

Using a piecewise structural equation model (Lefcheck 2016), we compared the relative effects of fruit set and palm age on yield, with the importance of palm age being well known in young palms (Corley and Tinker 2016). We used sticky traps to survey major arthropod visitors to oil palm inflorescences over the forest distance gradient and examined changes in the arthropod community associated with variability in fruit set in open and partial pollination treatments.

2.2. Methods

2.2.1. Study area

From August 2018 to April 2019, we monitored oil palms within a 1.5-ha area, tracking the progression of female inflorescences from blooming and pollination to harvest. The farm was in Batang Hari Regency of Jambi Province, Sumatra, Indonesia. Jambi Province receives a mean annual rainfall of 2235 ± 385 mm (Teuscher et al. 2016). We recorded a mean temperature of 27.1 (±4.1 S.D.) C and a mean relative humidity of 84.2 (±15.2 S.D.) % on the farm (August-November 2018), using an iButton logger (Fawcett et al. 2019).

The study area borders a 7-ha forest patch to the west and south and large-scale and smallholder plantations to the east and north. The neighboring forest is a remnant of characteristic lowland dipterocarp forests in the region (Laumonier et al. 2010). Palms were planted at a density of approximately 92 palms per hectare and were 3 to 4 years old. Prior to the beginning of the study, undergrowth vegetation was standardized by weeding and herbicide application, which is common management practice.

We mapped palm and forest edge positions using a handheld GPS device (Garmin GPSMap 67) and ArcGIS geoprocessing tools (ESRI 2011) to calculate distance to forest. Although the main environmental gradient we consider in our analysis is distance to forest, we also estimated a 40m elevation difference across the site. However, we do not consider this variable in our analyses because we do not expect this elevation change to drive significant differences in insect abundance or presence. Correlation between elevation and distance to forest was low (Pearson’s $r = 0.43$).

2.2.2. Oil palm inflorescence treatments

We applied one of four experimental treatments to female oil palm inflorescences anticipated to become receptive during the study. We restricted flower access by enclosing a female inflorescence with one of two different sizes of mesh: a “full exclusion” treatment using 0.1mm mesh that essentially isolated the inflorescence from all visitors, and a “partial exclusion” treatment using coarser (1.4 mm opening) mesh that allowed smaller insects access to the inflorescence. We found the coarser mesh was penetrable by small insects such as *E. kamerunicus* and stingless bees (Apidae: *Tetrigona*). We compared exclusion treatments to an “open” pollination treatment that allowed full access, and an “assisted pollination” treatment where we supplemented open pollination with pollen applied by hand (Section 4.6 Appendix B).

We selected at least 20 inflorescences for each treatment, ensuring that their locations covered a gradient of distance from the neighboring forest. We set up exclusion treatments on developing inflorescences approximately one week prior to predicted receptivity. For both types of exclusions, we enclosed the inflorescence with a mesh “exclosure” that was tied securely at the base of the inflorescence (Appendix Figure 2-1a). After the receptive period, we removed exclosures and constructed bamboo or wire netting cages around all study inflorescences to prevent damage; these remained on the inflorescence until harvest.

2.2.3. Fruit bunch metrics and drivers of yield

We assessed each fruit bunch to determine fruit set rate as a representation of pollination rate. We made assessments of the fruit structure for half the fruits from all treatments, including spikelet count, mean individual weights of pollinated and unpollinated fruit types, and bunch weight (Section 2.6 Appendix C, Appendix Figure 2-2). We quantified the relative importance of pollination to yield (bunch weight) by comparing the standardized coefficient sizes of fruit set against palm age in a piecewise structural equation model (SEM) (Lefcheck 2016). We estimated palm age by counting leaf scars (Section 2.6 Appendix C, Appendix Figure 2-2a).

2.2.4. Flower visitor community sampling

We placed sticky traps on treatment inflorescences near mid-day and exposed them for 24 hours on the first and second days of flower receptivity. We constructed traps by applying non-drying glue to the bottom of 100mm petri dishes and hanging them approximately 10 cm above the inflorescence (Appendix Figure 2-1b). We placed the traps outside of any exclosure structures in order to sample all insect visitors regardless of treatment type. We also placed traps opportunistically on anthesizing male inflorescences and non-blooming “control” palms.

We identified arthropods to family using a binocular microscope, consulting general and region-specific guides (Goulet et al. 1993, Johnson and Triplehorn 2004, Bosuang et al. 2017). We organized the flower visitor assemblage by combining arthropod families into functionally and taxonomically related “pollinator groups” (Appendix Table 2-2). Although we denote our groups as pollinator groups, we also included taxa with other potential roles in agroecology, e.g. parasitic wasps and ants.

We modeled family richness, total abundance, and abundance by pollinator groups of female inflorescence visitors using distance from forest, palm age, and flowering day as explanatory variables. In order to identify major gradients in the pollinator group composition on female inflorescences, we performed a principal component analysis (PCA) of Hellinger-transformed community data (Legendre and Gallagher 2001). We then modeled associations between abundances of major pollinator groups identified by the PCA and the fruit set of open pollination and partial exclusion treatment inflorescences, which would have been most affected by visiting insects.

2.2.5. Statistical analyses

We performed statistical analyses using the software R (R Core Team 2016) and R packages for mixed effects modeling (“lme4” and “glmmTMB”) (Bates et al. 2015, Brooks et al. 2017) and multivariate analysis (“vegan”) (Oksanen et al. 2019). Structural equation models were constructed using “piecewiseSEM” (Lefcheck 2016). We used “lmerTest” (Kuznetsova et al. 2016) to conduct significance tests of mixed effects models and “emmeans” (Lenth 2019) to visualize marginal effects. We assessed model fits by simulating residuals with the package “DHARMa” (Hartig 2019). We report the marginal coefficient of determination (R^2_m) for mixed-effects models, which represents the proportion of variance explained by fixed effects (Nakagawa and Schielzeth 2013).

We modeled fruit set using mixed effects beta regression models with a logit link (Ferrari and Cribari-Neto 2004), and abundance with negative binomial generalized linear mixed effects models. These models included palm ID as a random effect to account for exogenous environmental covariates. Independent variables distance to forest and palm age were mean-centered and scaled by standard deviation prior to regression. We modeled treatments as interacting with distance to forest or pollinator abundance in fruit set models so that they could be estimated independently between treatment types.

2.3. Results

We tracked 92 inflorescences from 45 palms, which we split into the four treatment groups: 31 open pollinated treatments, 20 partial exclusion treatments, 20 full exclusion treatments, and 21 assisted pollination treatments. Of these inflorescences, we made additional bunch structure measurements on 14 open pollinated, 10 partial exclusion, 10 full exclusion, and 10 assisted pollination fruit bunches. Inflorescences opened starting from September 2018 and were harvested up to April 2019. Distances to forest of treatment inflorescences ranged from 1m to 101m.

2.3.1. Fruit set and distance to forest

We fit a model of fruit set with exclusion type interacting with distance to forest as explanatory variables, which explained 70% of fruit set variance (marginal R^2). Palm age was not a significant predictor of fruit set and was not included. The model estimated 61% fruit set under assisted pollination ($\beta_0 = 0.47 \pm 0.19$ S.E., $p = 0.016$) at the mean sampling distance from the forest (Figure 2-2a). Estimated at the same distance, full exclusion (Figure 2-2c) significantly lowered the predicted fruit set to 12 % ($\beta = -2.50 \pm 0.34$, $p < 0.001$), while partial exclusion (Figure 2-2d) increased predicted pollination to 75% ($\beta = 0.64 \pm 0.33$, $p = 0.051$). The predicted fruit set for open pollination treatments (62%, Figure 2-2b) was not significantly different from assisted pollination ($\beta = 0.02 \pm 0.15$, $p = 0.92$).

Under assisted pollination, distance from forest did not have a significant effect on fruit set ($\beta = 0.16 \pm 0.20$, $p = 0.42$), and exclusion treatments did not significantly differ from this absence of a trend ($\beta = -0.22 \pm 0.35$, $p = 0.52$). However, partial exclusion did have a significantly greater negative relationship ($\beta = -0.65 \pm 0.31$, $p = 0.04$), i.e. fruit set decreased for inflorescences farther away from the forest. Within 70m from the forest edge, fruit set of partial exclusion inflorescences exceeded 65% in our model, higher than both open and assisted pollination averages. Within 25m of forest, fruit set under partial exclusion was especially high – exceeding 80% in the model and empirically ranging from 79% to 98% ($n = 6$). The difference between the effect of distance on open and assisted pollination treatments was marginally significant ($p = 0.07$), with open pollination being associated with a negative effect of distance to forest ($\beta = -0.30 \pm 0.17$), but under both of these treatments the effect of distance was not significantly different from zero.

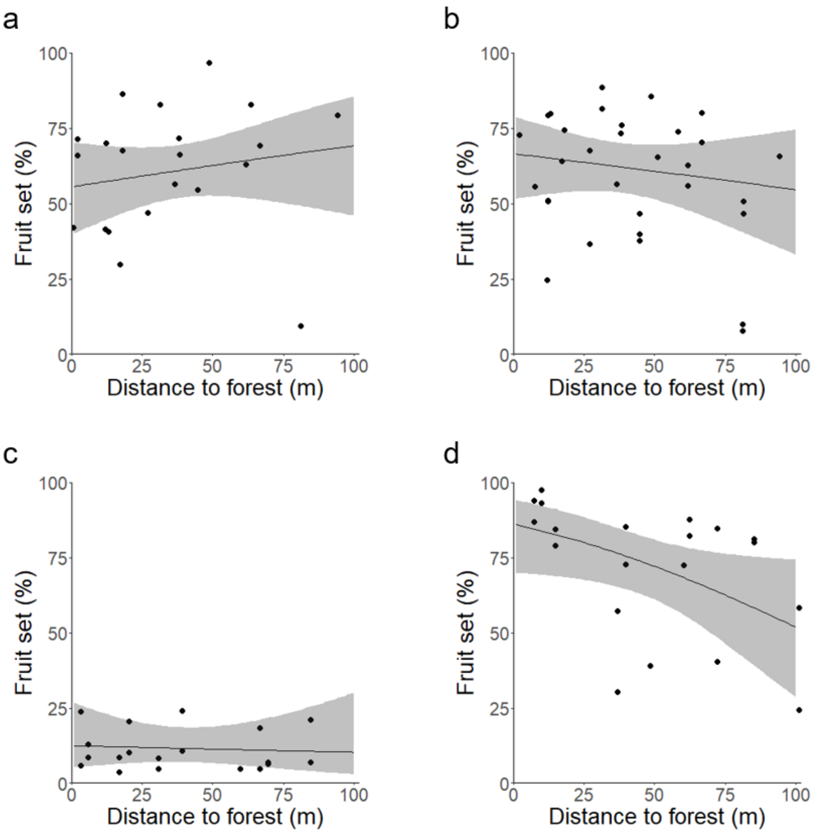

Figure 2-2. Pollination rate results over gradient of distance to forest, under four treatments: (a) assisted pollination, (b) open pollination, (c) pollinator exclusion, and (d) partial exclusion. Line represents model estimate, with 95% confidence interval (gray band).

2.3.2. Fruit set and yield

Mean pollinated fruit size decreased significantly with increasing fruit set by an estimated 0.47g (± 0.15g S.E., $p = 0.005$) for every 10% increase in fruit set. Over the range of observed fruit set, this amounts to a predicted 35% decrease in pollinated fruit weight, from 11.8g at 4% pollination, to 7.7g at 98% pollination. On the other hand, fruit set had no significant effect on the unpollinated fruits (Appendix Table 2-1).

We modeled the effects of fruit set and palm age on bunch weight by linking individual mixed effects models in a hypothesized causal network using piecewise SEM. The final model (Figure 2-3) explained the relationships in the data well (Fisher's $C_{16} = 22.751$, $p = 0.121$) and supported both a significant negative indirect effect of increasing fruit set on bunch weight through decreasing mean pollinated fruit weight, and a significant positive effect on bunch weight through increasing the number of pollinated fruits per spikelet. Of these two paths, the positive effect of increasing pollinated fruits per spikelet had a greater effect on bunch weight than the negative effect of decreasing fruit size, with a cumulative path coefficient (obtained by multiplying component paths) of 0.89 standard deviations for the former, as opposed to -0.18 for the latter. The contribution of pollination had an overall positive effect (0.71) that was greater than that of palm age (0.34), which increased bunch weight through a positive effect on total number of spikelets.

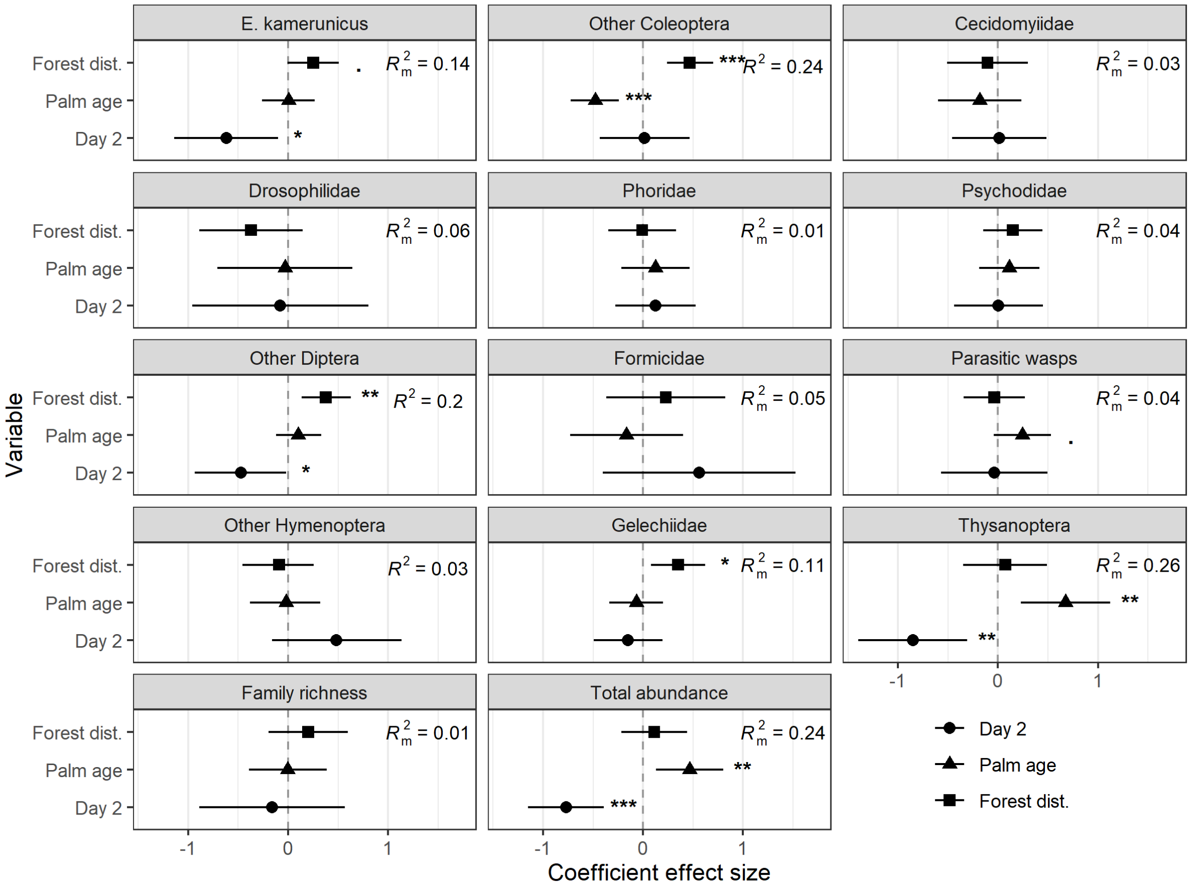

Figure 2-4. Fitted coefficients of taxa group abundance, family richness, and total abundance models, with distance to forest, palm age, and flowering day as explanatory variables. The (marginal) coefficient of determination is given for each model.

2.3.3. Flower visitor results

We set 144 traps on 82 female inflorescences over 44 palms from September to October 2018. Additionally, as an informal comparison, we opportunistically set 7 traps on 5 palms with blooming male inflorescences, as well as 10 “control” traps on palms with neither male nor female inflorescences in bloom. Distance from forest of the additional male and control traps ranged between 2 and 101m, matching the range of the female inflorescence traps.

We collected 63,703 individual arthropods representing 13 orders, which were dominated by Coleoptera (3,496), Diptera (2,366), Lepidoptera (1,591), and Thysanoptera (55,725) (Appendix Table 2-2). Based on potential agroecological importance and major representation in traps, we selected a subset of the taxa for further analysis, which we organized into 12 pollinator groups. We checked that these pollinator groups were notably represented in both male and female inflorescence traps, suggesting the potential for effective pollination.

Our pollinator groups separate the family Curculionidae from Coleoptera. This family is completely composed of the introduced *E. kamerunicus* weevil (3,217 individuals), so we refer to this group by the species name hereafter. Remaining Coleoptera were grouped into “Other Coleoptera”, which represents 279 individuals from 21 families. We separated Dipterans into groups, as some families represented a notable proportion of the samples (Appendix Table 2-2). Dipteran pollinator groups include Cecidomyiidae (294), Drosophilidae (443), Phoridae (696), and Psychodidae (629), which we found in over half of female traps and male traps. We grouped the remaining 304 Dipteran individuals from 17 additional families into an “Other Diptera” pollinator group. We split Hymenoptera into Formicidae (119 individuals), “Parasitic wasps” (257 individuals, 14 families), and “Other Hymenoptera” (43 individuals, 5 families). The order Lepidoptera was made up almost entirely of family Gelechiidae (1590) and one individual of Hesperiidae, so we simply refer to this group as Gelechiidae. We grouped Thysanoptera together because the two families we found (Thripidae and Phlaeothripidae) had high, correlated abundances (r = 0.71), suggesting similar environmental responses. More detailed information about the taxa found is in Appendix Table 2-2.

Wilcoxon rank tests indicated significantly more visitors to female inflorescences than to non-flowering (control) palms (W = 1224.5, $p < 0.001$) but no difference in family richness (W = 800.5, $p = 0.55$). There were no significant differences between female and male inflorescences in overall abundance (W = 336.5, $p = 0.14$) or family richness (W = 440, $p = 0.57$). From our model of total visitor abundances on female inflorescences ($R^2_m = 0.24$, Figure 2-4), we found no effect of forest distance, while abundances decreased significantly on the second day and increased on older palms (Figure 2-4). However, these independent variables had little relationship to family richness ($R^2 = 0.01$).

We fit mixed-effects models for all pollinator groups except “Other Coleoptera”, “Other Diptera” and “Other Hymenoptera”, which fit random effects of nearly zero for palm ID. The GLM models (Figure 2-4) that explained the highest variation were Thysanoptera (26%), Other Coleoptera (24%), Other Diptera (20%), *E. kamerunicus* (14%), and Gelechiidae (11%). Increasing distance to forest had a notable significant effect on the abundance of Other Coleoptera, Other Diptera, and Gelechiidae, and a marginally positively effect on Curculionidae abundance. Older palms were associated with more Thysanoptera but fewer Other Coleoptera. The second day of flowering had a notable negative effect on abundance of *E. kamerunicus*, Other Diptera, and Thysanoptera. Model details can be found in Appendix Table 2-3.

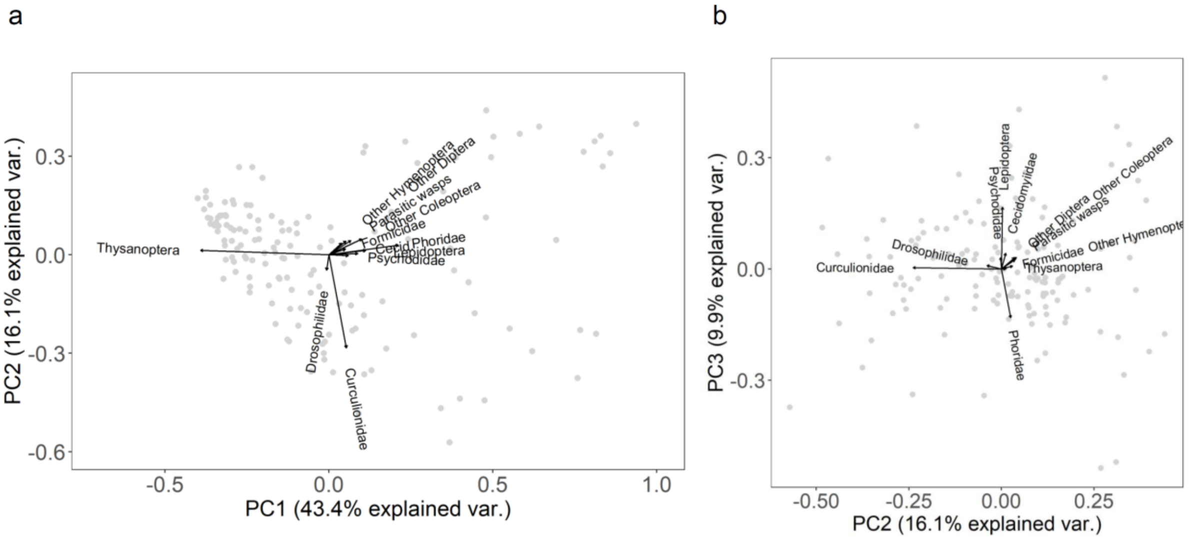

Figure 2-5. Biplots of (a) first and second principle component (PC) axes and (b) second and third PC axes of PC analysis of Hellinger-transformed abundances from traps placed on blooming female inflorescences (first day).

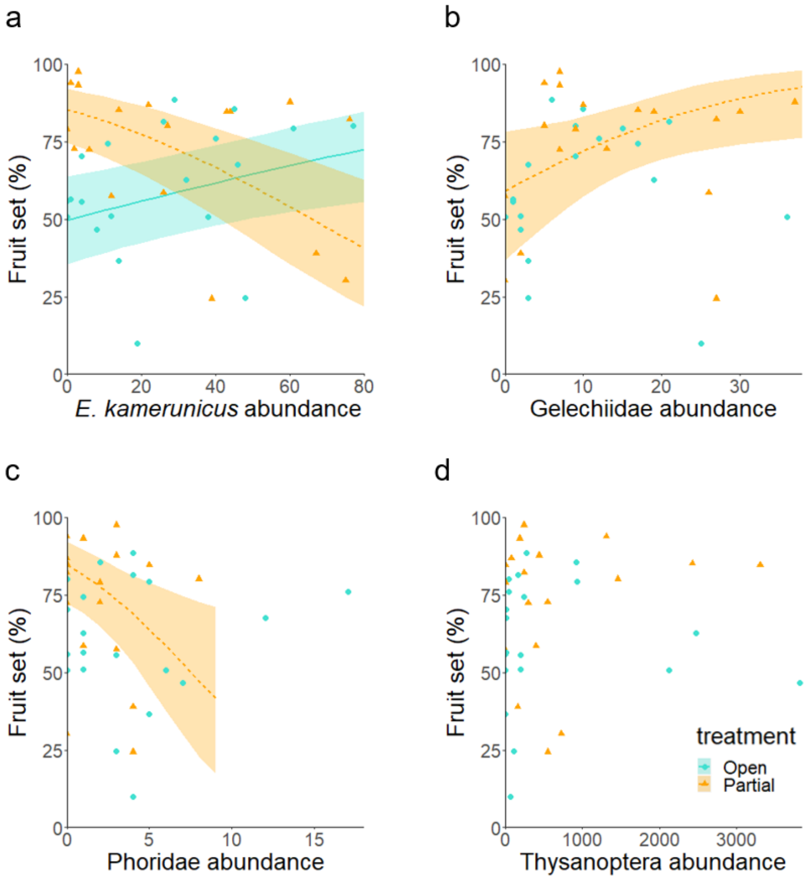

Figure 2-6. Estimated marginal effects of major pollinator groups in open (solid line) and partial exclusion (dashed line) inflorescences on fruit set, including (a) *E. kamerunicus*, (b) Gelechiidae, (c) Phoridae, and (d) Thysanoptera. Only significant (α = 0.05) effects (and 95% confidence interval) are shown, with covariates held at mean values. Points represent actual abundance and fruit set under open pollination (circles) and partial exclusion (triangles).

2.3.4. Major pollinator groups and fruit set

The first three principle component (PC) axes of the PCA of Hellinger-transformed pollinator group abundances accounted for 69.4% of total variance (Figure 2-5). The first axis (43.4% variance explained) mainly described Thysanoptera variation, while the second axis (16.1%) was dominated by *E. kamerunicus*. The third axis (9.9%) mainly represented Gelechiidae and Phoridae variation on opposing ends of its gradient. Based on these results, we focused on how fruit set varied with Thysanoptera, *E. kamerunicus*, Gelechiidae, and Phoridae abundance, under open and partial exclusion conditions.

The dataset we used to model fruit set was based on 38 fruit bunches. We dropped one fruit bunch due to uniquely high *E. kamerunicus* abundance (n = 230, mean abundance = 22.9±28.0 S.D.). All major pollinator groups were significantly associated with fruit set rate in our model ($R^2_m = 0.42$) and significantly mediated by treatment type (open pollination or partial exclusion), except for Thysanoptera (Figure 2-6, a-d). A significant interaction with partial exclusion suggests a positive association between *E. kamerunicus* and fruit set under open pollination ($\beta_{open} = 1.18 \pm 0.45 \times 10^{-2}$, $p = 0.01$) that changed to a negative association under partial exclusion ($\beta_{partial}$ = -2.81±0.56×10^{-2}, $p < 0.001$) (Figure 2-6a). Similarly, Phoridae only had a negative association under partial exclusion ($\beta_{partial}$ = -0.22±0.08, $p = 0.005$). Though there is a marginally significant positive effect under open pollination (β_{open} = 6.87±3.53×10^{-2}, $p = 0.05$), it appears to be driven by two points with abundances higher than 10 (Figure 2-6c). This relationship is possibly less robust, though we had no reason to drop these points as outliers. Gelechiidae abundance was not significantly associated with fruit set under open pollination (β_{open} = -1.87±1.83×10^{-2}, $p = 0.31$), but had a positive association with fruit set ($\beta_{partial}$ = 5.25±2.54×10^{-2}, $p = 0.04$) under partial exclusion. Thysanoptera was not a significant predictor of fruit set under either treatment (β_{open} = 0.66±2.02×10^{-4}, $p = 0.74$; $\beta_{partial}$ = 2.22±1.97×10^{-4}, $p = 0.26$) (Figure 2-6d).

2.4. Discussion

Oil palm is a major crop, but our understanding of the role of insect-mediated pollination is incomplete. Using field experimental exclusion methods, we demonstrate that flower visitors drive a significant share of yield variability. Fruit set appeared to be positively related to forest proximity on our study site, especially when insect visitors were partially excluded. We did not observe this effect when visitors were completely excluded or pollination was supplemented, suggesting it was not due to abiotic gradients. Some major pollinator groups captured on sticky traps varied with distance to forest, but these decreased with forest proximity. Nevertheless, we found positive associations between fruit set and *E. kamerunicus* abundance under open pollination, and with Gelechiidae under partial exclusion.

2.4.1. Effects of exclusion and forest distance

Compared to open pollination, exclusion of flower visitors significantly lowered fruit set by over 80%, i.e. from 62% fruit set to 10% fruit set. This reduction is economically significant, as a fruit set of at least 40% is considered minimally sufficient, and oil production efficiency is thought to peak between 60% and 80% fruit set (Harun and Noor 2002). Further, we find fruit set to be an important positive driver of yield, accounting for two times the variability in bunch weight (0.71 against 0.34 standard deviations) compared to palm age, the latter of which is already known to play a major role in determining yield for younger (<10 years) palms (Corley and Tinker 2016). This was also in spite of a decrease in average pollinated fruit size with higher fruit set, which reflects a tradeoff due to carbohydrate and spatial limitation of developing fruits (Harun and Noor 2002).

We hypothesized that restricting inflorescence access through partial exclusion would change fruit set, reflecting the role of the excluded visitors. We find that partial exclusion apparently reduced pollinator antagonists, as fruit set improved compared to open pollination. We also hypothesized that, if these effects were the result of ecological spillover from the forest, there would be an association between fruit set and forest proximity. We observed a positive relationship with forest under partial exclusion, suggesting a spillover effect favoring effective pollination agents. Open pollination also had a similar, but weaker, trend. On the other hand, forest proximity had no effect when we applied pollen manually or completely excluded flower visitors, suggesting that proximity was not standing in for an abiotic gradient such as nutrient or water supply.

2.4.2. Role of inflorescence visitors

Based on the model of our observational visitor data, higher fruit set was associated with more *E. kamerunicus* and marginally associated with more Phoridae under open pollination. The former result supports the well-established role of *E. kamerunicus* as an important oil palm pollinator. However, under partial exclusion, higher *E. kamerunicus* abundance was negatively associated with fruit set. Authors observing a similar pattern at the farm scale suggest this could be due to intraspecific competition (Wahid and Kamarudin 1997), which in our case could have been triggered by access limited by partial exclusion. Although Phoridae did not exhibit a robust positive relationship with fruit set, it exhibited similar trends to *E. kamerunicus* and was negatively correlated to Gelechiidae. Further work could examine whether these patterns reflect indirect interactions, e.g. through density dependent parasitism (Philpott et al. 2009).

Gelechiidae was significantly associated with fruit set under partial exclusion. This family has not previously been reported as an oil palm pollinator. However, Rizali et al. (2019b) noted its presence on oil palm flowers in Borneo, and another moth species, *Pyroderces* sp., is reported to be an oil palm pollinator (Syed 1979, Wahid and Kamarudin 1997). Gelechiid species are mainly known as crop pests (Picanço et al. 1998), but two species have been noted as pollinators of Phyllanthaceae (Luo et al. 2011).

Previous literature has identified the Thysanopteran *Thrips hawaiiensis* as a potential pollinator (Syed 1979, Anggraeni et al. 2013). This species typically occurs in very high numbers, but their small size prevents them from carrying much pollen (Syed 1979). Though we found no significant association with fruit set, it is notable that very high Thysanoptera abundance (>1000) accompanied higher and less variable fruit set, especially under partial exclusion (Figure 2-6d). However, more data would be needed to identify significant patterns.

The aggregate groups Other Coleoptera and Other Diptera had significant relationships with environmental variables, but these cosmopolitan groups only represented a small proportion of the community, so interpreting their results further, or in relation to fruit set, was outside of the scope of the current study. In future studies, longer distance gradients and additional capture and observation methods could corroborate the patterns observed, while more experimental methods could examine causal mechanisms, including for potentially important groups that we could not include in our study, e.g. *Scaptodrosophila sp* (Rizali et al. 2019b).

2.4.3. Ecological spillover in oil palm

Within 25m of the forest, fruit set for partial exclusion bunches was higher than open and assisted pollination bunches, suggesting that pollination has a relationship with forest and is still limited under open conditions. We found that some pollinator groups responded significantly to distance to forest, though most of these groups increased in abundance away from the forest, including two of the major pollinator groups, *E. kamerunicus* and Gelechiidae. Forest likely does not play a role in the natural history of *E. kamerunicus*, which relies solely on oil palm as a habitat, as a breeding ground, and for food (Syed 1982). Although previous research on Lepidoptera spillover in oil palm has shown that neighboring forest has a positive effect on diversity, responses may vary by individual species (Lucey and Hill 2012). Our own results suggest Gelechiidae do not respond in this way.

On the other hand, forest may be a source of predators or other antagonists that influence pollinator abundance by deterring visitation. High predator activity may reduce herbivore activity, leading to a decrease in herbivore abundance around high risk areas (Laundré et al. 2010). Predator activity may also explain the mediating role that partial exclusion played in predicting fruit set. Pollinators sheltering from predation in an exclosure may spend more time on an inflorescence, which in turn confers higher pollination effectiveness (Ivey et al. 2003). As a trait-mediated interaction that affects an ecosystem service, this effect is of agroecological interest and could potentially be applied to enhance pollination effectiveness and yield. Future studies should directly examine treatment effects on visitation activity.

Natural enemies in oil palm can have an important impact on herbivores (Nurdiansyah et al. 2016) and can vary with neighboring natural habitat (Rizali et al. 2019a). However, the effect of these two factors on pollination needs to be explored further. Denmead et al. (2017) found that increased bird activity decreased arthropod predators while *E. kamerunicus* increased, demonstrating the potential role of trophic cascades. Experimental methods designed to disentangle community interactions on pollinators and pollination services, in conjunction with natural habitat proximity, are needed to assess the importance of these effects on yield.

2.5. Conclusions

The debate on reconciling oil palm's impacts with conservation has given rise to contrasting proposals along the lines of the land sparing versus sharing paradigm (Koh et al. 2009, Edwards et al. 2010); however, our findings demonstrate that a more nuanced approach (e.g. Grass et al., 2019) is warranted. Within our study, we show that a small (7 ha) forest can confer pollination services through higher fruit set. Using exclusion treatments and insect trapping on oil palm inflorescences, we demonstrate apparent biotic contributions to oil palm yield with associations with multiple groups of insects. Although our results are preliminary, they demonstrate that biodiversity and natural habitat can have an important effect on oil palm production and illuminate a potential path connecting conservation and production (c.f. Vandermeer et al., 2019), which merits further investigation.

Authors' contributions

KL, TT, and IG conceived of the study, with DB consulting. KL organized fieldwork, analyzed data, and led writing. TF collected data and RF provided identification expertise. All authors contributed critically and gave final approval for publication.

Acknowledgements

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2.6. Supporting Information

Appendix A

Appendix Figure 2-1. Examples of (a) exclusion treatment setup (partial exclusion), and (b) sticky trap setup in the field. Credit: T. Fung.

Appendix B

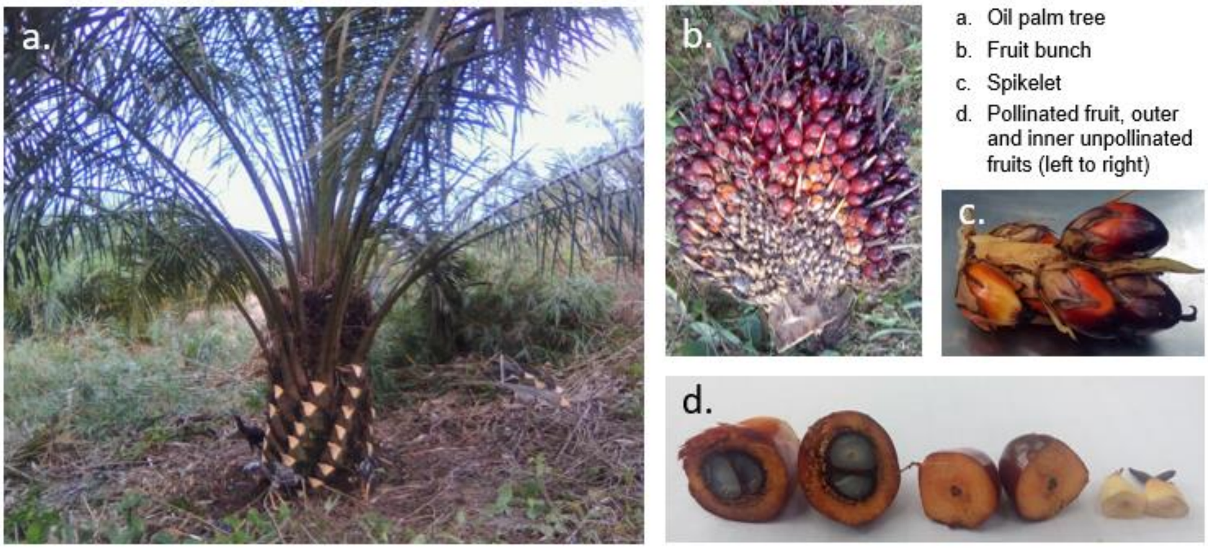
Assisted pollination methods

To conduct the assisted pollination treatment, we collected pollen from a male inflorescence from a neighboring farm and dried it following suggested practices (Donough et al. 1993). We ensured the viability (>75%) of the pollen by germinating samples in a 15% sucrose solution with 1.6mM boric acid for 24 hours and counting the proportion of pollen grains that had developed pollen tubes (Corley and Tinker 2016). Once 70% of the flowers on a female inflorescence in the assisted pollination group became receptive, we applied a mixture of pollen and talcum powder (1:4 pollen to talcum powder) using a clean handheld pump applicator.

Appendix C

Palm and fruit bunch assessment methods

Although oil palm is monoecious, it only produces a single male or female inflorescence at a time, which is accompanied by a leaf (Corley and Tinker 2016). This process results in multiple columns of leaf scars spiraling down the trunk (Appendix Figure 2-2a) (Corley and Tinker 2016). We counted the scars in one of these cycles to make a relative estimate of age through a palm’s flowering history.



Appendix Figure 2-2. Example photos of: (a) a typical young oil palm tree used in this study. Note the triangular leaf scars, which we used to estimate palm age. (b) A ripe fruit bunch after harvest. (c) A spikelet removed from the fruit bunch. (d) Cross sections of (left to right): a pollinated fruit, an outer unpollinated (parthenocarpic) fruit, and an inner unpollinated fruit. Credit: N. Marbun.

Inflorescences develop and are harvested as bunches of several hundred fruits (Appendix Figure 2-2b) that are clustered on branches called spikelets (Appendix Figure 2-2c). Pollinated fruits contain a seed housing the kernel, while unpollinated flowers develop into parthenocarpic fruit without seeds (Appendix Figure 2-2d) (Mathews et al. 2009). To estimate the proportional fruit set in each fruit bunch and fruit structure measures of ripe bunches, we made a stratified random selection of one-third of the spikelets in each fruit bunch for destructive sampling. We did this by separating and sorting spikelets by size and selecting every third spikelet to ensure that the subset selection was representative of the distribution of spikelet sizes. For both the immature and ripe fruit bunches, we counted the number of pollinated and unpollinated fruits on the spikelet subset to estimate fruit set. We calculated fruit set as the number of pollinated fruits divided by the sum of the pollinated and unpollinated fruits.

For half of the fruit bunches in all treatments, we collected additional data to estimate yield and characterize bunch structure. We calculated total ripe fruit bunch weight using a digital hanging scale. For the subset of spikelets we used to estimate fruit set, we also measured the total weights of pollinated and unpollinated fruit types, as well as the mean number of each fruit type per spikelet. For metrics of different fruit types, we further separated unpollinated fruits into “inner” and “outer” fruits (Appendix Figure 2-2d), as these were characteristically different depending on their location within the bunch (Mathews et al. 2009). We calculated the average individual weights of each type from a random sample of 30 fruits. If less than 30 fruits could be found on the spikelet subset, all available fruits were used to calculate the average weight.

Appendix D

Appendix Table 2-1. Linear mixed effects models of pollination rate effects on fruit average individual weight of pollinated fruit, outer unpollinated fruit, and inner unpollinated fruit. Tree ID was included as a random effect. Also presented are the marginal ($R_m{}^2$) and conditional ($R_c{}^2$) coefficients of determination (Nakagawa and Schielzeth 2013), which estimate, respectively, the percent variability explained by the fixed effects only, and both the fixed and random effects.

		Pollination rate				
Model	Intercept	Coefficient	S.E.	*p*	R_m^2	R_c^2
Pollinated fruit (g)	12.0	-4.47	1.51	0.005 *	0.16	0.92
Outer unpollinated fruit (g)	2.14	-0.42	0.41	0.31	0.02	0.95
Inner unpollinated fruit (g)	0.55	0.008	0.14	0.95	0.00	0.84

Appendix E

Appendix Table 2-2. Table of family level summary statistics of collected arthropods

				Female traps (n = 144)		Male traps (n = 7)		Control traps (n = 10)	
Order/Taxon	Pollinator Group	Families	Total	% Traps present	Mean when present (s.d.)	% Traps present	Mean when present (s.d.)	% Traps present	Mean when present (s.d.)
Acari		Acari	16	6	2 (1.8)	0	-	0	-
Araneae		Salticidae	8	6	1 (0)	0	-	0	-
Blattodea		Isoptera	1	1	1 (-)	0	-	0	-
		Termitidae	4	3	1 (0)	0	-	0	-
Coleoptera	*E. kamerunicus*	Curculionidae	3217	87	22.9 (28)	86	53.3 (39)	20	15 (19.8)
	Other Coleoptera	Anthicidae	8	6	1 (0)	0	-	0	-
		Bothrideridae	1	1	1 (-)	0	-	0	-
		Brentidae	2	1	2 (-)	0	-	0	-
		Carabidae	1	1	1 (-)	0	-	0	-
		Chrysomelidae	20	10	1.3 (0.6)	14	1 (-)	0	-
		Cicindelidae	1	1	1 (-)	0	-	0	-
		Coccinellidae	9	6	1 (0)	0	-	0	-
		Elateridae	9	6	1.1 (0.4)	0	-	0	-
		Eucnemidae	2	1	1 (-)	0	-	10	1 (-)
		Geotrupidae	1	0	-	0	-	10	1 (-)
		Languriidae	5	2	1.7 (0.6)	0	-	0	-
		Lophocateridae	2	1	1 (0)	0	-	0	-
		Lyctidae	2	1	1 (0)	0	-	0	-
		Nitidulidae	75	24	2 (1.8)	43	1.7 (1.2)	10	1 (-)
		Phalacridae	1	1	1 (-)	0	-	0	-
		Ptiliidae	75	14	3 (3.1)	14	1 (-)	30	5 (4)
		Scolytidae	7	3	1.2 (0.4)	14	1 (-)	0	-
		Silvanidae	18	5	2.6 (2.3)	0	-	0	-
		Staphylinidae	38	19	1.3 (0.8)	14	1 (-)	20	1.5 (0.7)
		Throscidae	1	1	1 (-)	0	-	0	-
		Unknown Coleoptera	1	1	1 (-)	0	-	0	-

Order/Taxon	Pollinator Group	Families	Total	Female traps (n = 144)		Male traps (n = 7)		Control traps (n = 10)	
				% Traps present	Mean when present (s.d.)	% Traps present	Mean when present (s.d.)	% Traps present	Mean when present (s.d.)
Collembola		Collembola	11	2	3.7 (1.5)	0	-	0	-
Dermaptera		Anisolabididae	1	1	1 (-)	0	-	0	-
		Labiidae	2	1	1 (0)	0	-	0	-
		Pygidicranidae	1	1	1 (-)	0	-	0	-
Diptera	Cecidomyiidae	Cecidomyiidae	294	53	3.2 (3.4)	43	2.7 (2.9)	90	4.2 (1.5)
	Drosophilidae	Drosophilidae	443	38	8 (10.6)	29	5.5 (6.4)	10	1 (-)
	Other Diptera	Anthomyiidae	1	1	1 (-)	0	-	0	-
		Camillidae	2	1	2 (-)	0	-	0	-
		Ceratopogonidae	51	3	1.2 (0.4)	0	-	80	5.6 (3.2)
		Chironomidae	45	11	1.9 (1)	14	2 (-)	60	2 (1.3)
		Chloropidae	20	3	2 (2)	0	-	50	2.4 (0.9)
		Culicidae	31	10	1.9 (1.9)	14	2 (-)	10	3 (-)
		Dolichopodidae	53	13	2.5 (2)	57	2 (1.4)	0	-
		Lauxaniidae	2	1	1 (-)	0	-	10	1 (-)
		Micropezidae	8	6	1 (0)	0	-	0	-
		Muscidae	1	1	1 (-)	0	-	0	-
		Mycetophilidae	4	1	1.5 (0.7)	14	1 (-)	0	-
		Sciaridae	7	3	1.4 (0.9)	0	-	0	-
		Sphaeroceridae	71	15	2.2 (1.6)	43	8 (7.9)	0	-
		Stratiomyidae	2	1	1 (0)	0	-	0	-
		Syrphidae	1	1	1 (-)	0	-	0	-
		Tachinidae	1	1	1 (-)	0	-	0	-
		Tipulidae	2	1	1 (0)	0	-	0	-
	Phoridae	Phoridae	696	76	5.9 (9.9)	71	2.6 (1.8)	100	3.2 (1.9)
	Psychodidae	Psychodidae	629	77	5.5 (6.7)	57	2 (0.8)	30	1.7 (1.2)
Hemiptera		Aleyrodidae	1	1	1 (-)	0	-	0	-
		Alydidae	1	1	1 (-)	0	-	0	-

Order/Taxon	Pollinator Group	Families	Total	Female traps (n = 144)		Male traps (n = 7)		Control traps (n = 10)	
				% Traps present	Mean when present (s.d.)	% Traps present	Mean when present (s.d.)	% Traps present	Mean when present (s.d.)
Hemiptera		Aphididae	11	7	1.1 (0.3)	0	-	0	-
		Cicadellidae	24	10	1.4 (0.6)	0	-	20	2 (0)
		Miridae	14	7	1.3 (0.9)	14	1 (-)	0	-
Hymenoptera	Formicidae	Formicidae	119	26	3 (3.7)	29	1 (0)	40	1 (0)
	Other Hymenoptera	Agaonidae	1	1	1 (-)	0	-	0	-
		Mutilidae	2	1	2 (-)	0	-	0	-
		Mymaridae	36	21	1.1 (0.4)	29	1.5 (0.7)	10	1 (-)
		Mymarommatidae	2	1	1 (-)	0	-	10	1 (-)
		Vespidae	2	1	1 (0)	0	-	0	-
	Parasitic wasps	Aphelinidae	1	1	1 (-)	0	-	0	-
		Braconidae	14	8	1.2 (0.4)	0	-	0	-
		Ceraphronidae	13	3	1.8 (1.5)	0	-	20	3 (1.4)
		Diapriidae	16	10	1.1 (0.4)	0	-	0	-
		Elasmidae	2	1	1 (-)	14	1 (-)	0	-
		Encyrtidae	139	26	2.1 (2.4)	43	19 (20.7)	40	1.3 (0.5)
		Eulophidae	4	1	1.5 (0.7)	14	1 (-)	0	-
		Eupelmidae	1	1	1 (-)	0	-	0	-
		Ichneumonidae	1	1	1 (-)	0	-	0	-
		Platygastridae	8	3	1.5 (1)	0	-	20	1 (0)
		Pteromalidae	5	2	1 (0)	0	-	20	1 (0)
		Scelionidae	10	3	1.2 (0.4)	14	2 (-)	20	1 (0)
		Torymidae	3	2	1 (0)	0	-	0	-
		Trichogrammatidae	40	6	1 (0)	29	15.5 (17.7)	0	-
Lepidoptera	Gelechiidae	Gelechiidae	1590	90	11.9 (13.4)	71	7.6 (1.8)	80	2.8 (2.8)
		Hesperiidae	1	1	1 (-)	0	-	0	-
Orthoptera		Gryllidae	1	1	1 (-)	0	-	0	-
		Orthoptera	1	1	1 (-)	0	-	0	-

				Female traps (n = 144)		Male traps (n = 7)		Control traps (n = 10)	
Order/Taxon	Pollinator Group	Families	Total	% Traps present	Mean when present (s.d.)	% Traps present	Mean when present (s.d.)	% Traps present	Mean when present (s.d.)
Psocoptera		Elipsocidae	2	1	1 (0)	0	-	0	-
		Pachytroctidae	6	3	1.3 (0.5)	0	-	10	1 (-)
		Psocidae	1	0	-	0	-	10	1 (-)
Thysanoptera	Thysanoptera	Phlaeothripidae	34778	91	258 (528.8)	100	129.6 (118.1)	40	18.8 (33.5)
		Thripidae	20947	91	150.3 (273.9)	100	173.9 (127.9)	30	13.7 (21.9)

Appendix F

Appendix Table 2-3. Generalized linear (mixed) models of pollinator group abundance. Predictor variables include distance to forest, palm age, and flowering day. An asterisk (*) indicates a coefficient is significant at α = 0.05 and a dot (·) indicates significance at α = 0.10. For models with mixed effects, marginal (R^2_m) and conditional (R^2_c) coefficients of determination values are presented.

		Distance to forest			Palm age			Flowering day 2					
Model	Intercept	*Estimate*	S.E.	*p-value*	*Estimate*	S.E.	*p-value*	*Estimate*	S.E.	*p-value*	R^2	R^2_m	R^2_c
E. kamerunicus	3.16	0.25	0.13	0.056 ·	0.00	0.14	0.980	-0.62	0.27	0.020 *		0.14	0.18
Other Coleoptera	0.39	0.47	0.12	<0.001 *	-0.48	0.13	<0.001 *	0.02	0.22	0.944	0.24		
Cecidomyiidae	0.16	-0.10	0.21	0.611	-0.18	0.21	0.388	0.01	0.24	0.954		0.03	0.50
Drosophilidae	1.01	-0.37	0.26	0.158	-0.03	0.34	0.926	-0.08	0.45	0.860		0.06	0.23
Phoridae	1.11	-0.01	0.17	0.958	0.12	0.17	0.476	0.13	0.21	0.541		0.01	0.48
Psychodidae	1.32	0.15	0.15	0.326	0.11	0.15	0.463	0.00	0.23	0.987		0.04	0.27
Other Diptera	0.36	0.38	0.12	0.002 *	0.10	0.12	0.380	-0.47	0.23	0.042 *	0.20		
Formicidae	-0.91	0.23	0.30	0.452	-0.17	0.29	0.565	0.56	0.49	0.253		0.05	0.28
Parasitic wasps	-0.03	-0.04	0.16	0.810	0.24	0.15	0.097 ·	-0.04	0.27	0.888		0.04	0.15
Other Hymenoptera	-1.56	-0.09	0.18	0.613	-0.02	0.18	0.918	0.48	0.33	0.142	0.03		
Lepidoptera	2.19	0.35	0.14	0.011 *	-0.07	0.14	0.619	-0.15	0.18	0.392		0.11	0.47
Thysanoptera	5.71	0.07	0.21	0.738	0.68	0.23	0.003 *	-0.85	0.28	0.002 *		0.26	0.58
Abundance	5.91	0.11	0.17	0.505	0.46	0.17	0.007 *	-0.77	0.19	<0.001*		0.24	0.60
Family richness	9.53	0.20	0.20	0.317	0.00	0.20	0.984	-0.16	0.37	0.668		0.01	0.01

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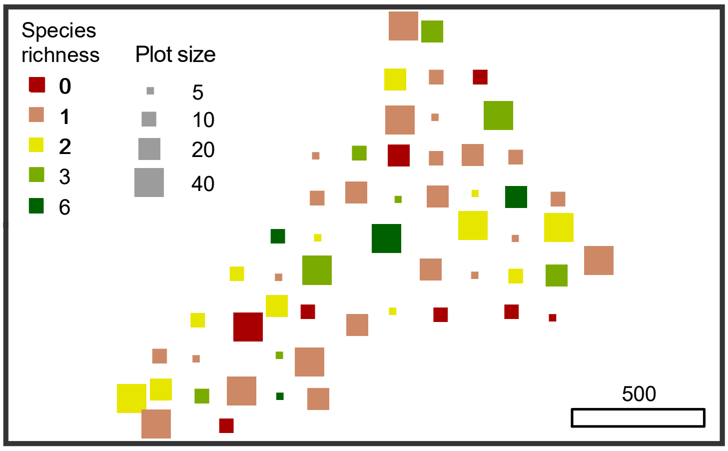
Chapter 3

Trade-offs of ecosystem services and disservices in an oil palm biodiversity enrichment experiment in Sumatra, Indonesia



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Abstract

In recent decades, the extent of oil palm (*Elaeis guineensis*) cultivation has expanded exponentially, often at the expense of natural habitat and with severe consequences to biodiversity and ecosystem services. Enriching the oil palm agricultural matrix with native trees has been proposed as a strategy for recovering landscape biodiversity and ecosystem function. However, how enrichment increases ecosystem functions and translates to trade-offs in services and disservices remains an open question. We examined these mechanisms in the fourth year of a plantation-scale, long-term oil palm biodiversity enrichment project in Jambi, Indonesia. Within 48 plots systematically varying in size (25-1600m^2) and planted tree species richness (1-6 species), we collected data on vegetation structure, sampled herbaceous layer insects, and observed pollinator visitation to phytometer plants (*Capsicum annuum*). We measured phytometer fruit yield and leaf damage to quantify ecosystem services and disservices. Partitioning experimental effects into plot size, tree richness, and identity effects, we found that the experiment explained the most variability for vegetation structure variables (canopy openness, vegetation cover and richness, and flower density). Effects on herbivorous insects and natural enemies in the herbaceous layer were also significant, but few significant direct relationships were found between enrichment treatments and phytometer plant outcomes. Structural equation models reveal a direct negative effect of an individual enrichment species on canopy openness. This in turn mediated the positive effects of canopy openness on understory plant richness and cover, and on herbivore and pollinator abundance. Insect herbivores were the most important driver of the relative abundance of herbivores and natural enemies, and natural enemies were positively correlated with herbivores, suggesting bottom-up control in these environments. Pollinator abundance decreased with increased flower density, suggesting a dilution effect on a limited pollinator pool. More pollinator visits resulted in higher phytometer yield, while impacts by insect herbivory were not apparent. These results show that, even at early stages, ecological restoration affects ecosystem functions, sometimes through indirect pathways. As canopy openness was a significant driver of many functions and services, the trade-offs we observed may change as stands grow more complex and enrichment communities continue to develop.

Key words: biodiversity, restoration, ecosystem functions, ecosystem services, trade-offs, pollinators, natural enemies, herbivores

3.1. Introduction

In oil palm (*Elaeis guineensis*) dominated landscapes, biodiversity is typically lower than in natural forests (Savilaakso et al. 2014, Barnes et al. 2017), which impacts ecosystem functions and services (Foster et al. 2011, Clough et al. 2016, Dislich et al. 2016). With oil palm expanding at the expense of forests (Koh and Wilcove 2008, Vijay et al. 2016), landscape biodiversity and ecosystem functioning is threatened, which has led to calls to halt or reverse these trends (Wilcove and Koh 2010). Globally, the United Nations recently declared 2021-2030 the “Decade on Ecosystem Restoration” aiming to reverse degradation in ecosystems worldwide (Gann et al. 2019). This adds to the increasing number of international initiatives on forest restoration, such as the Bonn Challenge in 2011 and the New York Declaration on Forests in 2014, which aim to restore forest ecosystems for recovering ecological integrity and carbon sequestration (Suding et al. 2015). As oil palm is grown in tropical regions that are among Earth’s richest biodiversity hotspots (Mittermeier et al. 2011, Meijaard et al. 2018), oil palm landscapes are a compelling priority for such initiatives. There is therefore growing interest in methods of improving biodiversity and ecosystem function in these landscapes (Koh et al. 2009, Foster et al. 2011, Darras et al. 2019).

The link between biodiversity and ecosystem function is an important question in ecological research (Cardinale et al. 2006, Benayas et al. 2009), with applications in conservation and agroecology (Manning et al. 2019). Diversified ecosystems can contribute significantly to the provision of important ecosystem services such as pollination and biocontrol (Kremen and Miles 2012), but they can also contribute ecosystem disservices like increased herbivory (Zhang et al. 2007, Wielgoss et al. 2014). Understanding trade-offs of services and disservices from increasing natural habitat is important in restoration and agricultural management, but research in ecosystem services and disservices rarely examine the associated ecological processes and interactions behind these outcomes (Saunders 2020).

In this study, we investigate the effects of experimental enrichment plantings on pollination and biocontrol services and herbivory disservices using an experimental tree biodiversity enrichment framework. Our study makes use of a long-term biodiversity enrichment experiment, EFForTS-BEE (Teuscher et al. 2016), within EFForTS, the Ecological and Socio-economic Functions of Tropical Lowland Rainforest Transformation Systems (Sumatra, Indonesia) collaborative research center (Drescher et al. 2016). In the experiment, planted native tree diversity has been systematically varied in experimental plots of different sizes within an oil palm monoculture following a “random partition” biodiversity experiment design (Bell et al. 2009), allowing us to disentangle the effects of planted tree species richness, identity, and plot size. We quantify the potential and realized ecosystem services and disservices to a phytometer plant that is also an important home garden crop (chili pepper, Solanaceae: *Capsicum annuum*) through herbivore, natural enemy, and flower visitor metrics. Furthermore, to explore the ecological pathways of the observed effects of enrichment, we test for complex relationships and direct and indirect relationships using structural equation models (SEM).

We hypothesize that tree enrichment of oil palm affects ecosystem services and disservices through the indirect effects on different levels of ecosystem functions shown in Figure 3-1. The experimental treatments of increasing plot size and planted tree diversity can directly affect vegetation structure in the plot, such as through limiting canopy openness. Previous research has shown that these treatments significantly affect stand structural complexity (Zemp et al. 2019a). These conditions in turn may lead to second-level effects on the herbaceous vegetation. We focused on conditions that are relevant to services and disservices at higher trophic levels including pollination, biocontrol, and herbivory in relation to flower density, plant (flower) diversity, and vegetation cover. We then modeled the effects on insects, including understory vegetation herbivores and predators, and phytometer flower visitors. Finally, we modeled how potential ecosystem services and disservices, measured from insect activity, affected phytometer yield.

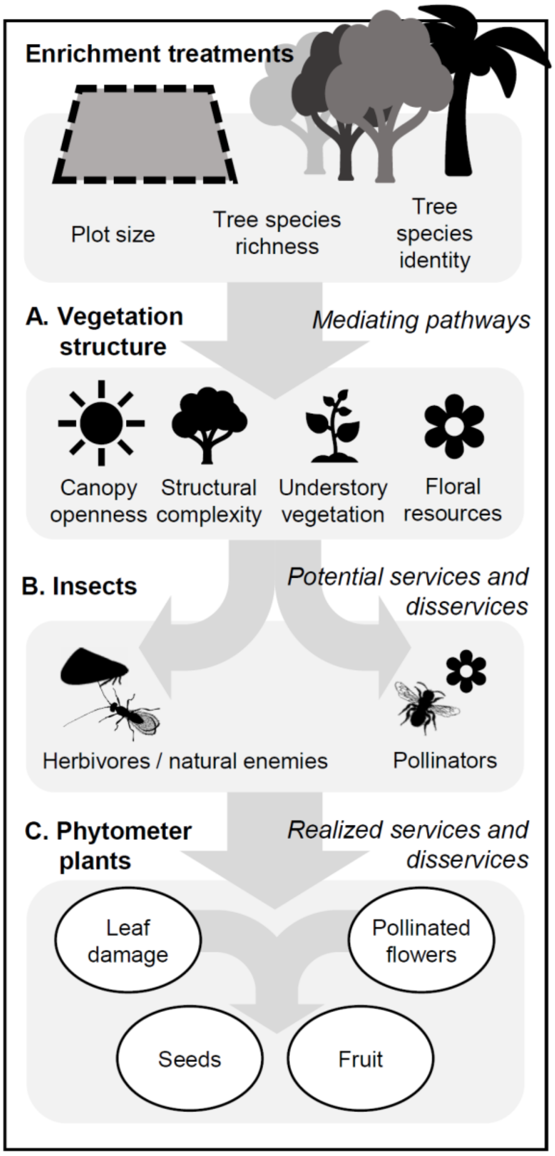

Figure 3-1. Diagram of hypothesized flow of effects from enrichment treatments to levels of endogenous variables: (A) vegetation structure, (B) insects and potential services and disservices, and (C) realized services and disservices in phytometer plants.

3.2. Methods

3.2.1. Study site

We conducted our study in the fourth year of a long-term biodiversity enrichment experiment (EFForTS-BEE) started in December 2013 in Jambi province of the island of Sumatra, Indonesia (Teuscher et al. 2016). The site is located at 103.25° E, and 1.95° S in a region formerly dominated by lowland dipterocarp forest (Laumonier et al. 2010) that receives on average 2235±385mm of annual rainfall (Drescher et al. 2016).

EFForTS-BEE consists of an array of 52 enrichment plots (plus four “business-as-usual” plots) established within a conventional oil palm monoculture to test the effects of native tree planting treatments on biodiversity and ecosystem functioning (exemplary photo in Appendix Figure 3-1) (Teuscher et al. 2016). The square plots are combinations of size and planted tree species richness treatments that are organized into partitions by plot sizes (25, 100, 400, and 1600 m^2), which are further stratified by levels of planted tree species richness (0, 1, 2, 3, 6 species). Planted tree species are *Archidendron pauciflorum* (Fabaceae), *Parkia speciosa*, (Fabaceae), *Peronema canescens* (Lamiaceae), *Durio zibethinus* (Malvaceae), *Dyera polyphylla* (Apocynaceae), and *Shorea leprosula* (Dipterocarpaceae). All species are native to the study region and also serve various uses including fruit, timber, and latex (Teuscher et al. 2016, Zemp et al. 2019b).

Within the random partition framework subset of plots (48 plots, i.e., plots of all sizes with 1-6 species), each enrichment tree species is represented exactly once in every combination of plot size and richness level, in combinations selected randomly without replacement from the species pool. This setup allows us to separate the effects of the plot size, tree species richness, and tree species composition without the need for a full factorial design (Bell et al. 2009).

Enrichment plots were established by thinning oil palms in all plots except 25 m^2 plots and planting enrichment tree species in a 2 m grid. Plots were protected by a fence and managed less intensively than the surrounding oil palm plantation matrix. Fertilizer and pesticide applications were halted after tree planting, and weeding was halted 2.5 years after plot establishment, which therefore allowed 1.5 years of natural vegetation development before the earliest sampling of this study, in November 2017. Further details about enrichment plot establishment can be found in Teuscher et al. (2016).

3.2.2. Plot field data

We obtained data about the plot environment and plot insects using field surveys or from datasets of collaborating researchers working in the biodiversity enrichment experiment. Data was collected or summarized at the plot level for statistical analysis.

Vegetation structure variables

Vegetation structure variables included canopy openness and stand structural complexity index. Canopy openness is an estimate of light availability and was measured using hemispherical photos following recommended practices (Beckschäfer et al. 2013) and processed using the program ImageJ (Schindelin et al. 2012) with the “Hemispherical” plugin (Beckschäfer 2015). The estimated value quantifies the fraction of sky in the photo that was not blocked by vegetation. For larger plots, multiple measurements were taken in a spatial array following Teuscher et al (2016) and averaged to represent light availability over the entire plot.

We estimated percent coverage of vegetation below 1.3 m in 5x5 m subplots established within each enrichment plot for ongoing monitoring (Teuscher et al. 2016). Vegetation coverage estimation was based on consensus by two observers and excluded coarse woody debris, bare ground, senescent plants, leaf litter, or other experimental treatments (e.g. the phytometer plants). Patterns in stand structural complexity with enrichment treatments have already been analyzed and discussed by Zemp et al. (2019a). Here, we build off their results by linking plot stand structural complexity index, an integrative measure of tree and canopy dimensional and distributional patterns in 3D space (Ehbrecht et al. 2017), to higher trophic level functions and ecosystem services.

We conducted 228 flower transect surveys (six transects per plot) from November-December 2017 to estimate floral resource density and plant richness. In three rounds, a pair of surveyors each walked a random 10 m transect within each plot, identifying and counting all flower units (single flowers or inflorescences) within one meter of either side of the transect. We used the average density of flower units per transect area from these three survey rounds to represent floral resource density.

We estimated understory plant richness using flower richness as a proxy, as plant species richness has been shown to increase linearly with flower richness (Ebeling et al. 2008). We supplemented the repeated random transects described above with a spatially stratified quadrat survey of flower richness. In January 2018, we made 216 spatially representative quadrat (5x5 m) surveys of flower richness, placing one quadrat in the 25 m^2 and 100 m^2 plots, three quadrats in the 400 m^2 plots, and 13 quadrats in the 1600 m^2 plots. These surveys amounted to 100%, 25%, 19%, and 20% of the total plot areas, respectively. The quadrats were spatially randomly stratified: one quadrat was always placed in the plot center and additional quadrats were randomly placed within equal divisions of the enrichment plot. We estimated the plot richness from the combined transect and quadrat surveys samples, correcting for sampling bias and undersampling using the Chao asymptotic species richness estimator and small sample bias corrector (Chiu et al. 2014).

Survey of vegetation insects

We estimated abundance of mobile insect herbivores and natural enemies using diversity and abundance data from a sweep net survey of the herbaceous vegetation layer in the enrichment plots conducted from November to December 2017. Within the ground cover vegetation of each plot, a surveyor made five evenly spaced sweeps along a randomly placed 5 m transect using a 32 cm diameter sweep net (BioForm, Nuremburg, Germany). All flying insects (i.e. excluding Formicidae and Araneae) were collected and individually preserved on site in 1.5 ml Eppendorf tubes with 70% ethanol. We later identified samples with a binocular microscope to family, using general and region-specific guides (Goulet et al. 1993, Johnson and Triplehorn 2004, Bosuang et al. 2017). We used family information to classify individuals as herbivores, predators, or other categories, and made herbivore and natural enemy abundance estimates based on the counts from within these classifications. We conservatively excluded families with mixed trophic niches from our counts.

3.2.3. Phytometer plants

We estimated effects on pollination and leaf damage using phytometer (sentinel) plants (Dietrich et al. 2013), which we set in the enrichment plots to measure direct (i.e. pollination and leaf damage) and indirect (i.e. fruit and seed production) effects of ecosystem functions. We selected *Capsicum annuum* (chili pepper) as a phytometer plant species because of its potential shade tolerance (Pouliot et al. 2012), widespread home garden cultivation in this region (Prabowo et al. 2016), and the potential role pollination can play in fruit quality and yield (Roldán Serrano and Guerra-Sanz 2006). We raised 1500 individuals of a locally available variety of *C. annuum* from seed. During the growth period outside the enrichment plots, we applied NPK fertilizer and pesticide (imidacloprid, deltamethrin, mancozeb, and abamectin) following local practices to standardize growing conditions and control pest damage before transfer to field sites. We selected 192 healthy individuals of comparable size to transfer to the 48 enrichment plots (four plants per plot). We halted fertilizer and pesticide application one week prior to placement in the plots and only watered as conditions required thereafter.

Within each plot, we organized the four chili plants as a cluster at approximately the plot center with plant stems 60-100 cm apart. We took microhabitat conditions into consideration by selecting locations that received at least partial sunlight and were free from encroaching vegetation. Prior to placement in the field, any flowers that had already opened were removed to ensure any pollination could be attributed to the plot conditions. Phytometer plants were placed in the field in early February 2018, followed by five weeks of monitoring and three weeks of harvesting. All plants were placed into the field on the same day. We kept the plants in their polyethylene containers to isolate them from local soil conditions.

Monitoring phytometers and insect visitors

We conducted five rounds of flower visitor observation from February to March 2018 while the chili plants bloomed in the field. Once a week for each plot, a pair of observers counted the flower visits by flying insects in a 5-minute period on a non-rainy day between 9:00 and 15:00. We allowed a one-minute acclimatization period before the observation to reduce the effect of disturbance by the observers. We thus accumulated 25 minutes of monitoring for each plot. Monitoring for each plot was rotated among three teams to reduce bias in the aggregated data. After each observation session, we counted the number of chili flowers and estimated the proportion of leaves with damage.

Phytometer yield

Fruit harvesting began after the five weeks of monitoring, i.e. once fruits began to ripen. We checked plants for ripe fruits continuously until all fruits were harvested (approximately three weeks), picking fruits as they began to turn red. For each plant, we counted the number of harvested fruits and selected a random subset of ten fruits to count the number of seeds per fruit. We estimated the total seeds produced by each plant by multiplying the mean fruit seeds by total harvested fruits. Plant means were subsequently averaged over the plot. We calculated the plot fruit-flower ratio, i.e. the number of fruits against the number of flowers, by dividing the mean fruits per plant by the mean total number of flowers observed before harvest.

3.2.4. Analysis

To analyze the biodiversity enrichment experiment effects on the ecological response variables (Table 3-1), we applied the random partition linear modeling procedure (Bell et al. 2009). Then, focusing on the significant effects identified by that analysis, we constructed structural equation models (SEMs) following the hypothesized levels of direct and indirect effects (Figure 3-1 and Table 3-1), from the experimental enrichment treatments to plot vegetation structure (A); to herbivores, natural enemies, and pollinators (B); and then to phytometer plants (C).

Analyses were conducted with R statistical software (R Core Team 2016). We estimated plant richness using the “vegan” package (Oksanen et al. 2019) and made random partition analysis calculations based on code made available by Bell et al. (2009). Structural equation models were constructed with the package “lavaan” (Rosseel 2012).

We applied appropriate transformations (Table 3-1) to the ecological endogenous variables (i.e. SEM dependent variables) to meet assumptions for linear models (i.e. normal distribution of residuals), which is recommended for both the partition analysis and covariance-based SEM (Grace and Bollen 2006, Bell et al. 2009). We checked this assumption by simulating model residuals using the package “DHARMa” (Hartig 2019). Following recommended practices (Gotelli and Ellison 2004, Warton and Hui 2011), we log-transformed count-based data after adding one or an appropriate small value, and logit-transformed transformed proportion data.

Table 3-1. Ecological response (endogenous) variables, with transformation used, interaction level, and hypothesized driver (and relationship direction) in structural equation models. Interaction levels correspond to those presented in **Figure 3-1**. They are: A = Vegetation structure; B = Insects and potential ecosystem services and disservices; C = Phytometer plant realized ecosystem services.

Endogenous variable	Trans-formation	Level	Hypothesized drivers
Canopy openness	Logit	A	Tree species identity (+/-), plot size (+/-)
Structural complexity	None	A	Tree species identity (+/-) (Zemp et al. 2019a)
Vegetation cover	None	A	Canopy openness (+)
Plant (flower) richness	Log	A	Plot size (+), Canopy openness (+/-)
Vegetation flower density	Log	A	Canopy openness (+)
Herbivore abundance	Log	B	Vegetation cover (+), plant richness (+), canopy openness (+), stand structural complexity (+)
Natural enemy abundance	Log	B	Vegetation cover (+), plant richness (+), canopy openness (+), stand structural complexity (+)
Herbivore-natural enemy ratio	Log	B	Herbivore abundance (+), natural enemy abundance (-)
Chili pollinator abundance	Log	B	Plant richness (+/-), vegetation flower density (+/-), canopy openness (+)
Chili flower visits	Log	B	Chili pollinator abundance (+), vegetation flower density (+/-), canopy openness (+)
Chili fruit-flower ratio	Log	C	Chili flower visits (+), chili leaf damage (-)
Chili leaf damage	None	C	Herbivore abundance (+), herbivore-natural enemy ratio (+)
Seeds per chili fruit	None	C	Chili flower visitors (+), chili leaf damage (-)

We then scaled all endogenous variables by zero-centering and scaling by standard deviation, so that effect sizes are presented on a standard scale.

Random partition linear models

The experimental treatments of the enrichment plot were assigned according to the random partition design (Bell et al. 2009, Teuscher et al. 2016), which allowed us to separately quantify linear, nonlinear, and interacting effects of the planted enrichment tree species richness, and the factorial effect of plot size on the ecological response variables. The overall model is specified as:

$$y = \beta_0 + \beta_{LR}x_{LR} + (\Sigma_i^6\beta_i x_i) + \beta_{NLR}x_{NLR} + \beta_P x_P + e \tag{1}$$

where y is the ecological response variable; β_0 is the model intercept; x_{LR} is the planted enrichment tree species richness treated as a continuous variable (“linear richness”); x_i is an indicator of the presence or absence of species i from among the six enrichment tree species originally planted at the outset of the experiment; x_{NLR} is the “non-linear richness”, i.e. the effects of specific richness levels as factors; x_P is the enrichment plot size as a factor; and e is the residual term. The method estimates the β coefficients using sequential models in the order presented in Equation 1, fitting subsequent models to the residuals of the previous model. All variables in Table 3-1 were analyzed as the response variable y in Equation 1. Coefficients for each enrichment tree species i are estimated relative to the “average” species effect.

Conveniently, this does not require the contribution of each species to the response to be directly measurable. The non-linear species richness term β_{NLR} represents species interaction strength, which is orthogonal to species identity effects (β_i).

Structural equation models

We used structural equation models fitted by maximum likelihood estimation in the 'lavaan' package (Rosseel 2012), following a "weight of evidence" approach (Grace 2020) to test the hypothesized levels of direct and indirect effects presented in Table 3-1. Covariance-based structural equation models are a useful statistical framework for disentangling interrelated data by comparing the covariance matrix of observed data to the theoretical covariance of a proposed system of relationships (Grace 2008). Grace (2020) recommends a series of steps for fitting SEM in ecological research, which involves building models based on prior knowledge, making ecologically-sound adjustments based on information from local and global fit metrics of intermediate models, and finally comparing candidate alternative models using fit metrics.

Informed by general knowledge of ecosystem processes, we built four separate structural equation models following the hypothesized flow diagram of enrichment treatment effect (Figure 3-1), which are presented in Table 3-1 as the drivers of each endogenous variable. We compared these models to alternatives that proposed more direct effects, either directly to the significant enrichment treatments indicated in the random partition analysis, or other simpler alternative pathways through fewer intermediate levels. To avoid model overfitting, we only considered significant regression coefficients ($p<0.05$). In "downstream" SEMs flowing from the vegetation structure SEM (i.e. within levels B or C in Figure 3-1), we also fit covariance terms for exogenous variables (variables with no linked independent variables) if we found direct or indirect relationships between these variables in preceding SEMs.

At the vegetation structure level (Level A), we hypothesized that the planted tree species would directly affect canopy openness and stand structural complexity index (Zemp et al. 2019a). We hypothesized that understory vegetation variables (vegetation coverage, richness, and flower density) would be driven by canopy openness. Additionally, we expected plant richness to increase with plot size due to the habitat size-species diversity relationship (MacArthur and Wilson 1963).

We fit two structural equation models at the insect level (Level B): one for herbivores and natural enemies, and a separate model for pollinator activity (Table 3-1). We hypothesized that the abundance of herbivore and natural enemy insects would be positively related to vegetation cover and richness as indicators of habitat availability and heterogeneity, as well as food resources for herbivores (Moreira et al. 2016). We also hypothesized that structural complexity increases microhabitat availability for both groups (Langellotto and Denno 2004). To examine the importance of top-down or bottom-up control, we compared alternative model structures to test whether one of these groups was driving the other, and compared their standardized SEM path contributions to an index of their relative abundance (log of herbivore-natural enemy ratio).

In the pollinator SEM, we hypothesized that pollinator abundance drove chili flower visits, with contributions from vegetation (flower) richness and flower density. These contributions could be positive, by enriching floral resources and attracting more pollinators (Johnson et al.

2003), or negative, by diluting the effectiveness of a limited pollinator pool (Knight et al. 2005, Veddeler et al. 2006, Holzschuh et al. 2011). In both insect SEMs (Level B), we also considered the importance of light access on insect activity (Steffan-Dewenter et al. 2007) by including canopy openness as a potential driver.

We fit an SEM to represent ecological functions on chili phytometer plants (Level C). In our hypothesized model, we linked ecosystem functions to relevant services or disservices, i.e. flower visits to chili fruit-flower ratio, and herbivore-natural enemy ratio or herbivore abundance to leaf damage. We also considered possible direct linkages between insect functions to phytometer outcomes (seeds per fruit and total fruit per plant), as well as the mediating roles of canopy openness (light availability). We fit the effect of seeds per fruit and total fruit per plant on the estimated total seeds produced per plant to compare their relative importance in seed production.

We evaluated our candidate models with the χ^2 exact fit index and three approximate fit indices: root mean square error of approximation (RMSEA), comparative fit index (CFI), and standardized root mean square residual (SRMR), as recommended by Grace (2020). We checked the robustness of these indices at our sample size (n=48) using the Monte-Carlo simulation in the package “simsem” to estimate distributions of the index values from 1000 simulated datasets generated from the fitted SEM parameters (Muthén and Muthén 2002, Pornprasertmanit et al. 2015). We assessed nested and non-nested model differences in distinguishability and fit with Vuong’s variance and likelihood ratio tests, respectively, using the package “nonnest2” (Merkle et al. 2016b). The Vuong likelihood ratio test is similar to the χ^2 likelihood ratio test for model comparison, but does not make the assumption that the “true” model is included in the comparison set and is therefore also suitable for non-nested models (Vuong 1989, Merkle et al. 2016a).

3.3. Results

3.3.1. Plot variable summaries

Across all plots and transects, we found a total of 21 flowering species. The two most abundant flower species were *Clidemia hirta* and *Asystasia gangetica*, which accounted for 57 and 21% of all flower units, respectively. These species are invasive pantropical plants native to other tropical regions (Rembold et al. 2017). Flower density had a mean of 0.71 (±0.41 standard deviation) flower units/m^2. We found a mean vegetation coverage of 70 (±15) % in 5x5m subplots. Plot canopy openness had a mean of 10 (±8.2) %. See Zemp et al. (2019a) for complete analysis of stand structural complexity index.

We collected and identified a total of 934 insects in 48 transects. Of these, 260 samples were from 29 families that were completely herbivorous, and 231 samples were in 35 predatory families. Mean plot herbivore count was 4.8 (±4.5) and mean natural enemy count was 5.4 (±3.6). The herbivore-natural enemy ratio had a mean of 1.0 (±1.2). From the cumulative 25 minutes of phytometer plant monitoring at each plot, we observed 89 pollinators (plot mean = 1.9±2.2) making a total of 327 chili flower visits (plot mean = 6.8±9.5).

The mean fruit-flower ratio was 0.56±0.39 fruits per observed flower. We harvested 3108 fruits from the plants (plant mean = 18.9±23.2). From the fruit harvested, we processed 1287 to count

Table 3-2. Random partition model results for vegetation structure variables (level A in **Figure 3-1** and **Table 3-1**). Variables are transformed according to Table 3-1 and standardized to Z-score.

	Df	*Sum.Sq*	*Mean.Sq*	*F.value*	*p-value*
Canopy openness					
Linear richness	1	1.335	1.335	1.957	0.170
Species identity	5	16.417	3.283	4.813	0.002 **
Non-linear richness	2	0.491	0.246	0.360	0.700
Plot size	3	4.199	1.400	2.052	0.124
Residuals	36	24.558	0.682		
Vegetation cover					
Linear richness	1	0.983	0.983	1.258	0.269
Species identity	5	13.004	2.601	3.330	0.014 *
Non-linear richness	2	1.488	0.744	0.953	0.395
Plot size	3	3.412	1.137	1.456	0.243
Residuals	36	28.114	0.781		
Plant (flower) richness					
Linear richness	1	2.106	2.106	2.492	0.123
Species identity	5	4.042	0.808	0.957	0.457
Non-linear richness	2	0.331	0.166	0.196	0.823
Plot size	3	10.100	3.367	3.984	0.015 *
Residuals	36	30.421	0.845		
Vegetation flower density					
Linear richness	1	4.432	4.432	5.865	0.021 *
Species identity	5	5.270	1.054	1.395	0.249
Non-linear richness	2	3.055	1.527	2.021	0.147
Plot size	3	7.038	2.346	3.104	0.039 *
Residuals	36	27.205	0.756		

seeds and quantify other attributes. At the plant level, mean seeds per fruit was 41.1±12.8 and estimated total seeds produced was 860.5±920.1. We excluded six plants that never produced any flowers from fruit mean calculations, as these outlier plants could not be pollinated.

3.3.2. Effects of enrichment treatments

The number of tree enrichment species as a linear predictor ("linear richness") explained significant variability in flower density (Table 3-2), herbivore abundance, and the herbivore-natural enemy ratio (Table 3-3). In all these cases, linear richness had a negative effect. Among the coefficient estimates of the corresponding random partition component model (Figure 3-2a), flower density (β = -0.21±0.10 standard error) and herbivore-natural enemy ratio (β = -0.21±0.10) were significant (p= 0.03 and p= 0.04, respectively). Herbivore abundance had a marginally significant coefficient estimate (β = -0.20±0.10, p= 0.050).

Planted tree species identity had a significant effect on canopy openness and vegetation cover (Table 3-2). *Peronema canescens* significantly decreased canopy openness when it was included in the planted enrichment composition (β = -1.0±0.25, p< 0.001); on the other hand, the presence of *Shorea leprosula* contributed to significant increase in canopy openness (β = 0.65±0.26, p= 0.02) (Figure 3-2b). This same pattern was mirrored in vegetation cover, though only the negative effect of *P. canescens* was significant (β = -0.95±0.27, p= 0.001); the positive effect of *S. leprosula* was marginally significant (Figure 3-2b).

Significant nonlinear coefficients in our random partition configuration are orthogonal to linear richness effects and indicate effects of species interaction (Bell et al. 2009). Only two-species

Table 3-3. Random partition model results for phytometer plant effects (level C in **Figure 3-1** and **Table 3-1**). Variables are transformed according to Table 3-1 and standardized to Z-score.

	Df	*Sum.Sq*	*Mean.Sq*	*F.value*	*p-value*
Herbivore abundance					
Linear richness	1	3.791	3.791	4.891	0.033 *
Species identity	5	3.483	0.697	0.899	0.493
Non-linear richness	2	6.195	3.097	3.996	0.027 *
Plot size	3	5.624	1.875	2.418	0.082 .
Residuals	36	27.907	0.775		
Natural enemy abundance					
Linear richness	1	0.022	0.022	0.023	0.879
Species identity	5	2.385	0.477	0.518	0.761
Non-linear richness	2	9.225	4.613	5.010	0.012 *
Plot size	3	2.222	0.741	0.805	0.500
Residuals	36	33.146	0.921		
Herbivore-natural enemy ratio					
Linear richness	1	3.986	3.986	4.225	0.047 *
Species identity	5	1.963	0.393	0.416	0.834
Non-linear richness	2	1.616	0.808	0.857	0.433
Plot size	3	5.471	1.824	1.933	0.142
Residuals	36	33.963	0.943		
Chili pollinator abundance					
Linear richness	1	0.285	0.285	0.575	0.453
Species identity	5	2.191	0.438	0.885	0.501
Non-linear richness	2	0.280	0.140	0.282	0.756
Plot size	3	0.751	0.250	0.506	0.681
Residuals	36	17.819	0.495		
Chili flower pollinator visits					
Linear richness	1	0.297	0.297	0.260	0.613
Species identity	5	3.173	0.635	0.554	0.734
Non-linear richness	2	0.951	0.475	0.415	0.663
Plot size	3	1.372	0.457	0.399	0.754
Residuals	36	41.207	1.145		

compositions had positive effects on herbivore and natural enemy insect abundance (Table 3-3). For herbivores, the two-species coefficient was β = 0.62±0.25 (*p*= 0.02); for natural enemies, β = 0.72±0.26 (*p*= 0.008) (Figure 3-2c).

Plot size was significant for flower density, plant richness, and chili plant damage (Tables Table 3-2 and Table 3-4). For all these variables, the smallest plot size, 25 m^2, had a significant negative effect (flower density: β = -0.66±0.23, *p*= 0.006; plant richness: β = -0.66±0.24, *p*= 0.008; and chili plant leaf damage: β = -0.67±0.23, *p*= 0.006) (Figure 3-2d). For flower density and chili plant leaf damage, only this level of plot size had a significant effect. The results for plant richness suggest an increasingly positive effect with larger plots, though our analysis was not set up to test for a linear effect. The effect on plant richness was significant at the largest plot size (β = 0.49±0.24, *p*= 0.047).

Some response variables did not have significant relationships with any enrichment effects. At the insect level, pollinator abundance and number of phytometer flower visits indicated no significant effects (Table 3-3); and at the phytometer level, fruit-flower ratio, fruit per plant, seeds per fruit, and seeds per plant did not show significant effects (Table 3-4).

Table 3-4. Random partition model results for phytometer plant effects (level C in **Figure 3-1** and **Table 3-1**). Variables are transformed according to Table 3-1 and standardized to Z-score.

	Df	*Sum.Sq*	*Mean.Sq*	*F.value*	*p-value*
Mean damaged leaves					
Linear richness	1	0.134	0.134	0.171	0.682
Species identity	5	6.811	1.362	1.733	0.152
Non-linear richness	2	3.957	1.978	2.517	0.095 .
Plot size	3	7.803	2.601	3.309	0.031 *
Residuals	36	28.295	0.786		
Fruit-flower ratio					
Linear richness	1	0.012	0.012	0.012	0.914
Species identity	5	8.359	1.672	1.593	0.187
Non-linear richness	2	0.040	0.020	0.019	0.981
Plot size	3	0.814	0.271	0.258	0.855
Residuals	36	37.775	1.049		
Fruit per plant					
Linear richness	1	0.011	0.011	0.013	0.911
Species identity	5	10.152	2.030	2.424	0.054 .
Non-linear richness	2	0.713	0.357	0.426	0.657
Plot size	3	5.965	1.988	2.373	0.086 .
Residuals	36	30.159	0.838		
Seeds per fruit					
Linear richness	1	3.295	3.295	3.451	0.071 .
Species identity	5	4.601	0.920	0.964	0.453
Non-linear richness	2	1.549	0.775	0.811	0.452
Plot size	3	3.183	1.061	1.111	0.357
Residuals	36	34.373	0.955		
Seeds per plant					
Linear richness	1	0.162	0.162	0.187	0.668
Species identity	5	8.543	1.709	1.965	0.108
Non-linear richness	2	1.684	0.842	0.969	0.389
Plot size	3	5.308	1.769	2.035	0.126
Residuals	36	31.302	0.869		

3.3.3. Structural equation model results

We selected the final models from among the possible relationships presented in Figure 3-1 and Table 3-1. Below we present overviews of major results and χ^2 fit statistics of each model. Full model results and additional fit statistics can be found in Section 3.6 Appendix B.

The final vegetation structure SEM (χ^2= 12.36, p= 0.578) supports our hypothesis that enrichment species identity directly drives canopy openness and structural complexity (Figure 3-3a). We chose to only include enrichment species identity information on *P. canescens* as a dummy variable in our SEMs since this species had the most consistent significant effect across multiple variables in the random partition analysis. We found strong evidence that the positive effect of *P. canescens* on vegetation coverage was mediated through canopy openness, as an SEM with a direct effect of *P. canescens* on vegetation coverage fit significantly worse than the final model (z= -2.60, p < 0.001). We also found that canopy openness and structural complexity contributed significantly to plant richness, but plot size also remained a significant variable. Plot size and tree species richness had significant relationships with flower density, as also shown by the random partition analysis. An alternative model we considered significantly linked canopy openness to flower abundance as the sole explanatory variable. Though this model was indistinguishable from the model presented in Figure 3-3a (ω^2= 0.17,

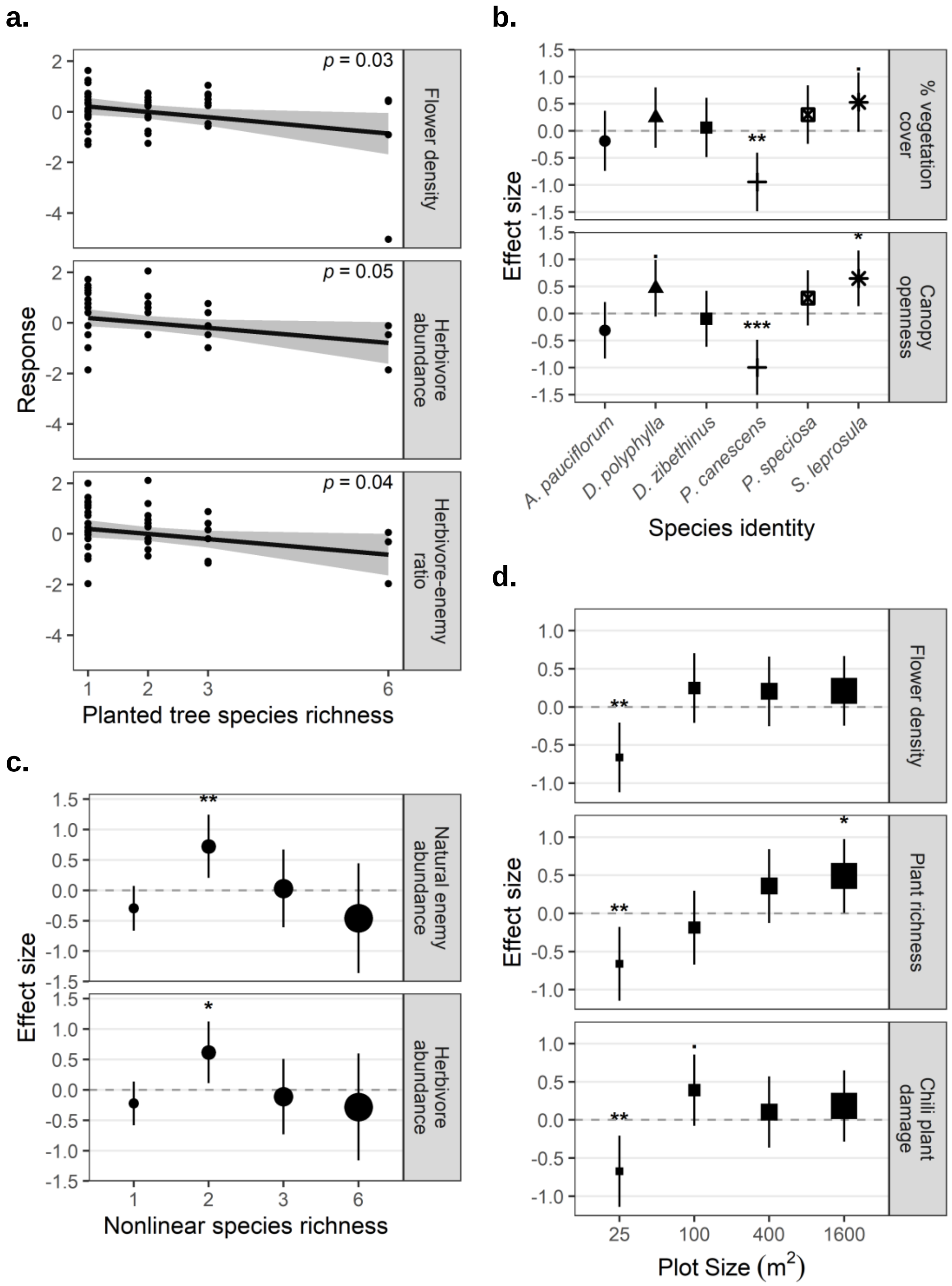

Figure 3-2. Plotted coefficient effect sizes from random partition sequential models. Selection of significant contributors ($\alpha > 0.05$ in Tables 3-2 to 3-4) shown, for (a) linear richness effect, (b) species identity effect, (c) nonlinear richness effect, and (d) plot size effect.

p= 0.24), canopy openness alone explained less variance in flower abundance (R^2= 0.11) than the two enrichment variables (R^2= 0.18).

In our final herbivore and natural enemy SEM (χ^2= 4.84, p= 0.939), we found that stand structural complexity index was a significant positive predictor of herbivore and natural enemy abundance in addition to the enrichment variables indicated by the random partition analysis (Figure 3-3b). Canopy openness was a significant positive predictor of herbivore abundance.

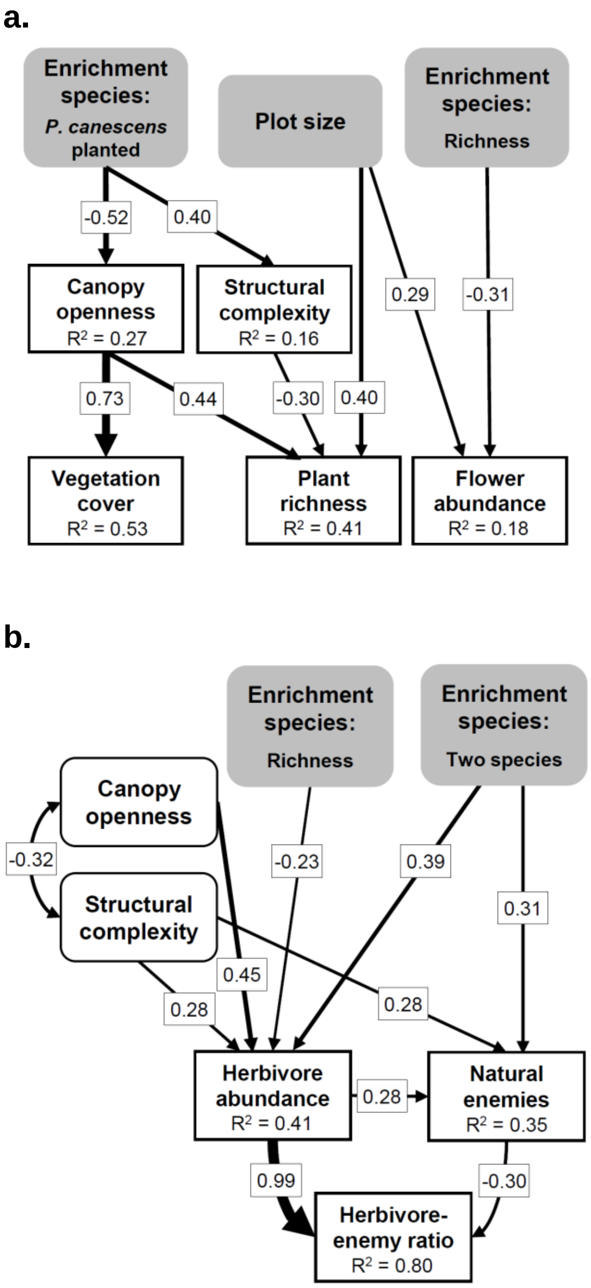

Figure 3-3. Diagrams of structural equation models of (a) vegetation structure and (b) herbivore and natural enemies interactions. Rounded boxes represent exogenous variables in the model, i.e. those without regressions, and those with grey fill represent enrichment treatment variables. Square boxes represent endogenous variables, i.e. dependent variables in regressions. Single-headed arrows represent independent variable relationship with standardized effect size in the associated box. Double-headed arrows represent model-fitted standardized covariance terms. Arrow widths are scaled by effect size.

In alternative models, we found that either canopy openness or herbivore abundance was also a significant positive predictor of natural enemy abundance. The difference in fits of these models was not distinguishable with our dataset (ω^2= 0.096, p= 0.12). We present the significant link between herbivore and natural enemy abundance in Figure 3-3b (see Appendix Table 3-6 for alternative model). Herbivore abundance had more than a threefold positive standardized effect on the log herbivore-enemy ratio compared to natural enemy abundance. We did not find significant relationships with vegetation cover or richness. The model fit a significant negative covariance between the exogenous variables canopy openness and structural complexity, reflecting their relationships in the vegetation structure SEM.

In the final pollinator SEM (χ^2= 1.16, p= 0.76), we found that flower abundance and vegetation cover both had a negative effect on pollinator abundance, while canopy openness had a strong positive effect (Figure 3-3c). Pollinator abundance was the major driver of the number of chili flower visits, accounting for 88% of variability as the only independent variable; the exogenous variables did not play any significant mediating roles. Reflecting relationships in the vegetation structure SEM, the covariance terms between the exogenous variables (canopy openness, flower abundance, and vegetation cover) were significant, except between flower abundance and vegetation cover, which was marginally significant (p= 0.06). We compared the final SEM to an alternative without vegetation cover, which suggested that including vegetation cover significantly improved model fit

(LR= 4.276, *p*= 0.048; ΔAIC= -2.27), though the distinguishability between the models was marginal (ω=0.079, *p*=0.07).

The best phytometer SEM (χ^2= 5.90, *p*= 0.43) supported a significant positive link between pollinator visits to chili flowers and the fruit-flower ratio, which in turn had positive effects on the seeds per fruit and fruits per plant (Figure 3-3d). The variability in seeds per plant was strongly driven by the number of fruits produced compared to the number of seeds per fruit (0.89 against 0.22 standard deviations, respectively). We fit a covariance term between canopy openness and pollinator visits, which was significant, reflecting the finding of the pollinator model. The covariance between seeds per fruit and fruit per plant was marginally significant (*p*= 0.09). Canopy openness had significant positive effects on the fruit-flower ratio and the number of fruits per plant. We compared our final model to an alternative model that did not include canopy openness as a driver of the fruit-flower ratio. Though the difference in model fit was small (ΔAIC= -1.77), the Vuong likelihood ratio test indicated that the improvement to fit was significant (LR = 3.768, *p*= 0.04), suggesting that canopy openness also influenced the fruit-flower ratio directly. We did not find significant meaningful relationships between plant damage, herbivore abundance, or herbivore-enemy ratio with the yield variables.

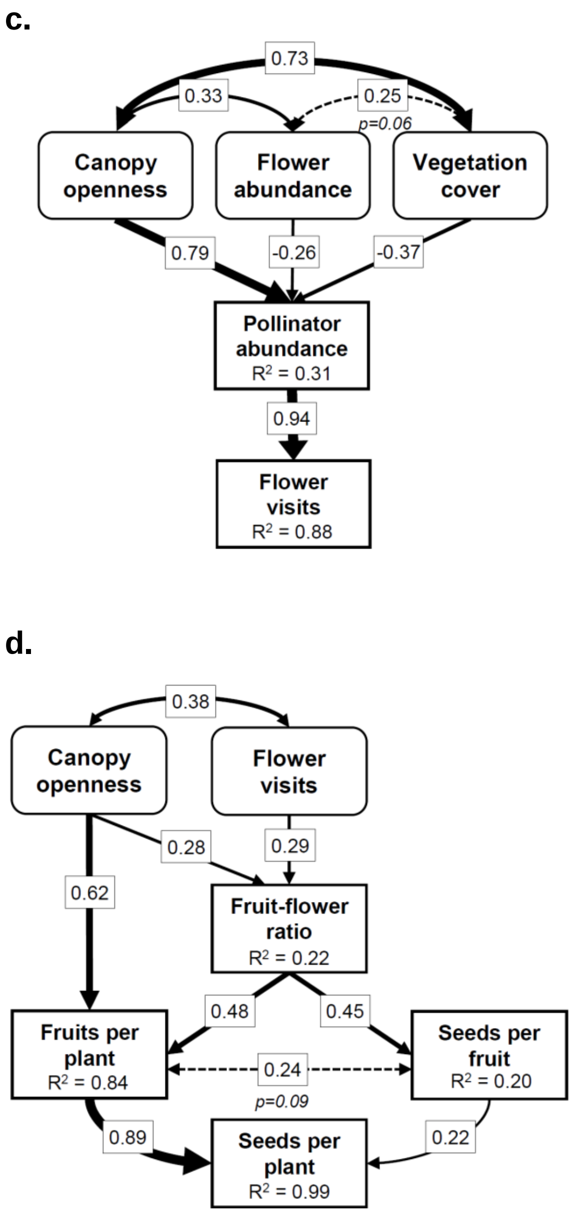

Figure 3-3 (continued). Diagrams of structural equation models of (c) pollinator and (d) phytometer interactions.

3.4. Discussion

Using the random partition analysis approach, we found significant effects of tree enrichment in oil palm on vegetation structure variables within the enrichment plots. These significant effects were mainly limited to the levels of the vegetation structure, or understory vegetation insects, while direct effects on pollinator activity and phytometer yield were not significant. Using structural equation models, we demonstrate that the significant enrichment effects at the vegetation structure level translated to effects at the pollinator and phytometer levels through indirect effects. The identity of the planted tree species played a significant role in determining canopy openness, which in turn was important in driving trends at all levels, and in many cases played a mediating role alongside the drivers to which it also contributed. In this way, canopy openness accounted for variability in vegetation cover that was originally attributed to species identity in the random partition analysis. Canopy cover or stand structural complexity index also explained some variability in plant richness, herbivore abundance, and natural enemy abundance, but in these cases, enrichment treatments still accounted for some variability in SEMs, suggesting effects of other processes from these treatments. Canopy openness and vegetation variables further explained pollinator activity, and subsequently, phytometer yield, demonstrating indirect effects of enrichment that were not apparent through modeling enrichment as a direct effect.

3.4.1. Effects on vegetation structure variables

Importantly, our final vegetation structure SEM results demonstrates that tree species identity, a factor not commonly considered in ecosystem function comparisons across forest cover (e.g. Steffan-Dewenter et al. 2007), can play an influential role in determining downstream effects. The SEM confirms that the presence of *P. canescens* directly affected canopy openness and structural complexity, which in turn played important mediating roles for understory vegetation variables. This species is a fast-growing, early successional species that performed very well in the plots; on the other hand, *S. leprosula*, which we did not include in the SEM, is a primary forest species and had low survival rates (Zemp et al. 2019b). The marginally significant positive effect on canopy openness by this latter species in the random partition analysis results may have therefore been due to gaps caused by tree mortality.

Canopy structure explained varying degrees of variability in the understory vegetation and flower variables in the SEM. Vegetation cover was completely mediated by canopy openness. Plant richness was positively related to plot size, as predicted by ecological theory (MacArthur and Wilson 1963), but was indirectly related to planted tree species as well, through canopy openness and structural complexity. Canopy openness may have also influenced flower abundance, though this did not explain as much variability as the plot size and species richness variables indicated in the random partition analysis. We observed that flower abundance was patchy and heterogeneous; its drivers may be more complex than can be described by the simple relationships we examined in our analyses.

3.4.2. Effects on insect abundance and ecosystem functions

Structural complexity played an important role in driving both herbivore and natural enemy abundance, which is supported in the literature (Langellotto and Denno 2004, Letourneau et al. 2011). We found evidence that canopy openness played a role in insect abundance. For herbivores, it is thought that this effect is mediated through microclimate changes or vegetation cover increase (Basset et al. 2001, Franc and Götmark 2008). However, vegetation cover did not emerge as an important variable for the abundances of either insect groups, despite the significant positive association between vegetation cover and canopy openness. Neither did plant species richness play a role. As our survey methods targeted insects on vegetation, however, these results may not reveal patterns due to the distribution of the vegetation itself.

It was not clear from our data whether herbivore abundance mediated the effect of canopy openness on natural enemies, as we present in Figure 3-3b, or if canopy abundance directly drove natural enemy abundance. Nevertheless, two other aspects of our results support bottom-up control in the insect population. Herbivore and natural enemy abundance were positively correlated, which suggests the lack of a density-dependent effect that might be expected in top-down control. However, this can also depend on other controlling factors of predator and prey populations, such as environmental sensitivity (Levins and Schultz 1996). In addition, herbivore abundance was the predominant driver of the log herbivore-enemy ratio. These results suggest that insect herbivores respond more strongly to environmental changes related to enrichment. This differs from other studies, which tend to find stronger top-down effects (Vidal and Murphy 2018), though not in all cases (Denno et al. 2003). Notably, in a review of tree diversity experiments, Grossman et al. (2018) found that predators tended to be unaffected by tree diversity; however, this may have been related to the young age of the experimental forests examined. Our own results may indicate that herbivores and natural enemies have asymmetrical habitat requirements under enrichment conditions (Levins and Schultz 1996, cf. Denno et al. 2005), though more research is needed.

Two-species enrichment treatments had a significant effect on both groups of vegetation insects, which apparently was not explained through the vegetation structure variables canopy openness and structural complexity. As the nonlinear richness factors of the random partition framework represent species interactions (Bell et al. 2009), this suggests two-species interactions have additional effects not associated with canopy openness or structural complexity. Zemp et al. (2019b) concurrently analyzed planted tree performance within these plots and found that trees in two-species plots experienced higher mortality, and as a consequence, plot basal area was lower compared to higher and lower-diversity plots. This may have contributed to habitat conditions that promoted higher insect populations, which could be investigated in future research.

While the random partition analysis found no direct relationship between enrichment and pollination functions, SEM revealed significant indirect pathways (Figure 3-3c). The negative relationship between pollinator abundance and flower abundance could suggest that co-flowering species in the plot have a diluting effect on phytometer pollinator visits (Knight et al. 2005). A dilution effect could indicate a limited population of effective pollinators, which could be indicative of a depauperate pollination landscape where pollination services are a finite resource, leading to pollination competition (Knight et al. 2005, Veddeler et al. 2006, Holzschuh et al. 2011), though more study would be needed to confirm this. Lower vegetation cover, which our results suggest was positively associated with pollinator visits independently of flower abundance, may reflect additional aspects of habitat complexity in the vegetation layer that are favorable for pollinators, for example availability of nesting sites in bare soil or dead wood (Proctor et al. 2012, Rodríguez and Kouki 2015).

3.4.3. Effects on phytometer ecosystem services and disservices

Our results suggest that the variation in pollination ecosystem service attributed to flower visits in the enrichment plots was not negligible. We found significant effects of flower visits on the fruit-flower ratio, leading to indirect effects on seeds per fruit and total seeds produced by the plant. Our data suggest that pollinator visits did not have a direct effect on the number of seeds per fruit, as some studies have shown (Roldán Serrano and Guerra-Sanz 2006); but rather this effect was related to the fruit-flower ratio. As flower visits were a significant positive driver of successful development from flowers to fruit, we may infer that fruit loss during development was not a major factor for chilis (Bos et al. 2007). This may indicate plants were not under major stress and could explain why leaf damage did not have the expected negative impact on phytometer yield. We also found no relationships between either herbivore abundance or the herbivore-enemy index, which could also suggest that herbivory did not have a significant effect in this case. Plant tolerance of herbivory may depend on many factors, including environmental stress and nutrients (Wise and Abrahamson 2007), though we also note that the resolution of our data does not differentiate the relative amounts of different types of damage and our herbivore metric is based on a limited representative survey.

3.4.4. Enrichment, ecosystem functions, and services

Biodiversity enrichment can play an important role in conservation and restoration. However, the mechanisms of how enrichment changes ecological communities are not always clear or investigated. The study design of the biodiversity enrichment experiment allowed us to disentangle enrichment effects by their component treatments (Bell et al. 2009, Teuscher et al. 2016), which we investigated further by testing structural equation models that have revealed important indirect effects that were not initially evident in the random partition analysis. This demonstrates that the effects of ecological enrichment are not always directly apparent or clearly associated with an enrichment treatment.

We find that most effects of enrichment were mediated through other, more direct effects. Earlier studies within this same system have shown limited effects of enrichment treatments on biodiversity (Gérard et al. 2017). However, our findings demonstrate that effects may be more apparent at different scales and gradients from those defined in the original enrichment treatment. The most important driver in the enrichment plots was canopy openness, which had a significant relationship with individual enrichment species. At the pollinator and phytometer interaction levels, canopy openness, rather than enrichment species or any other enrichment treatment, drove variability.

At four years, the progression of development for this enrichment experiment was still relatively early (Zemp et al. 2019a), and our finding of the importance of canopy openness reflects an early succession forest (Holmes and Matlack 2017). The ecosystem functions implied by herbivore and pollinator insect populations most clearly translated to pollination services in our phytometer plants, with no apparent negative effects by herbivorous insects, suggesting a net gain in pollination ecosystem services for plots with lower canopy cover. Our results therefore indicate a trade-off between beneficial insect activity and forest biomass, the former driven by canopy openness and associated with significant pollination services, and the latter exemplified by the fast-growing species *P. canescens* and associated with canopy closure and greater stand structural complexity. A similar dynamic may be behind an initial increase in oil palm yield within enrichment plots, which Gérard et al. (2017) attributed to light and other resource availability associated with oil palm thinning. However, as structural complexity is indicative of the productivity and diversity characteristic of mature natural forests (Hardiman et al. 2011, Ehbrecht et al. 2017), it is an important metric of forest restoration progression (Lamb et al. 2005, Zemp et al. 2019a). As tree growth continues to close canopy gaps and increase stand structural complexity, plot dynamics may change further. Herbivore abundance, which was strongly driven by canopy openness, may decrease. Understory vegetation cover and richness likewise may also decrease, though decreases in plant richness may be dampened for large plots. On a longer timescale, immigration of shade-adapted plant species through seed dispersal may reverse these trends, though plot size may play a mediating role in this process as well (Arroyo-Rodríguez et al. 2009).

Current relationships may not necessarily reflect future trade-offs either, as plot development may also change the role or importance of enrichment treatments. For example, two-species enrichment treatments had a positive significant effect on the abundances of both groups of vegetation insects, which may be due to habitat environmental changes resulting from higher tree mortality in these plots (Zemp et al. 2019b). However, as the surviving and spontaneously established trees grow to occupy gaps, differences between diversity levels may even out, especially if self-thinning occurs on denser plots. The trade-off between canopy openness and stand structural complexity index may also affect the ratio of herbivores to natural enemies as trees continue to reduce canopy gaps and increase structural complexity, since natural enemies were more positively affected by structural complexity than negatively affected by canopy openness, as compared to herbivores.

3.5. Conclusions

The importance and prevalence of restoration approaches is increasing in oil palm and other ecologically simplified land uses, as demonstrated by the upcoming “Decade on Ecosystem Restoration” declared by the United Nations (Gann et al. 2019). Our findings provide insight into how enrichment may affect ecosystem functions in early stages of restoration in oil palm. We demonstrate that the indirect effects of biodiversity enrichment treatments may be more apparent in patterns of ecosystem functions and services than the direct effects. In addition, enrichment species identity may play an important role, as we found with the fast-growing species *Peronema canescens,* which mediated canopy openness, leading to many secondary effects. We observed a net benefit for phytometer plants through insect-mediated pollination services with no apparent disservices; however, as this was driven by canopy openness, an eventual trade-off with forest stand structural complexity and the emergence of new patterns will likely occur as restoration communities continue to develop.

Authors’ contributions

KL, IG, and TT designed the study. KL, LS, and HL collected data with guidance by DCZ, DH, FN, HK, IG, and TT. KL performed analysis and drafted the manuscript with input from all authors.

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3.6. Supporting Information

Appendix A

Appendix Figure 3-1. Exemplary photo of a plot (left side) within oil palm context. Plot is 20 x 20m and is planted with one enrichment tree species, *Parkia speciosa* (Fabaceae). Photo credit: KL.

Appendix B

The following sections report final structural equation model (SEM) fit metrics (first table of each section). Model outputs are reported in the format of the lavaan R package (Rosseel 2012, R Core Team 2016). The second table in each section reports the calculated p-values of fit indices compared to Monte Carlo simulation data. P-values represent the proportion of 1000 replications that provided poorer fit (e.g., less CFI value or greater RMSEA value) than the fit statistic based on the observed data (Pornprasertmanit et al. 2015). A non-significant p-value indicates that the observed data matches the model-implied data distribution.

Appendix Table 3-1. Model variable codes used in the SEM outputs

Code	Explanation
logitgap	Canopy openness
ssc	Stand structural complexity
sungkai	Tree species *Peronema canescens* planted in the plot
veg.cov	Vegetation cover
logfl.chao	Vegetation richness (Chao estimation)
logfl.d	Flower density
size.ord	Plot size (ordinal variable)
planted.R	Planted tree richness
logher.a	Herbivore abundance
lognen.a	Natural enemy abundance
planted.2	Two tree species planted in the plot
logpoll.a	Pollinator abundance
logflrvis	Total flower visits
fruitseed.mn	Mean seeds per fruit
frflr.mn	Mean fruit to flower ratio
logfruit	Mean total fruit per plant
logplntseed	Mean total seeds per plant

Vegetation structure SEM

Appendix Table 3-2. Final vegetation structure model output

```
lavaan 0.6-5 ended normally after 26 iterations

  Estimator                                         ML
  Optimization method                           NLMINB
  Number of free parameters                         16

  Number of observations                            48

Model Test User Model:

  Test statistic                                12.358
  Degrees of freedom                                14
  P-value (Chi-square)                           0.578

Model Test Baseline Model:

  Test statistic                               110.138
  Degrees of freedom                                25
  P-value                                        0.000

User Model versus Baseline Model:

  Comparative Fit Index (CFI)                    1.000
  Tucker-Lewis Index (TLI)                       1.034

Loglikelihood and Information Criteria:

  Loglikelihood user model (H0)               -238.855
  Loglikelihood unrestricted model (H1)       -232.676

  Akaike (AIC)                                 509.710
  Bayesian (BIC)                               539.650
  Sample-size adjusted Bayesian (BIC)          489.454
```

```
Root Mean Square Error of Approximation:

  RMSEA                                          0.000
  90 Percent confidence interval - lower         0.000
  90 Percent confidence interval - upper         0.125
  P-value RMSEA <= 0.05                          0.685

Standardized Root Mean Square Residual:

  SRMR                                           0.089

Parameter Estimates:

  Information                                 Expected
  Information saturated (h1) model          Structured
  Standard errors                             Standard

Regressions:
                   Estimate  Std.Err  z-value  P(>|z|)
  logitgap2 ~
    sungkai          -1.013    0.243   -4.158    0.000
  ssc ~
    sungkai           0.700    0.233    3.011    0.003
  veg.cov ~
    logitgap2         0.777    0.105    7.399    0.000
  logfl.chao ~
    logitgap2         0.184    0.063    2.941    0.003
    size.ord          0.184    0.051    3.636    0.000
    ssc              -0.188    0.070   -2.692    0.007
  logfl.d ~
    planted.R        -0.184    0.077   -2.402    0.016
    size.ord          0.216    0.097    2.225    0.026

Covariances:
                   Estimate  Std.Err  z-value  P(>|z|)
 .veg.cov ~~
   .logfl.chao       -0.021    0.039   -0.548    0.584
   .logfl.d           0.007    0.073    0.096    0.923
 .logfl.chao ~~
   .logfl.d          -0.013    0.043   -0.315    0.753

Variances:
                   Estimate  Std.Err  z-value  P(>|z|)
   .logitgap2         0.632    0.129    4.899    0.000
   .ssc               0.577    0.118    4.899    0.000
   .veg.cov           0.456    0.093    4.899    0.000
   .logfl.chao        0.155    0.032    4.899    0.000
   .logfl.d           0.564    0.115    4.899    0.000
```

Appendix Table 3-3. Calculated p-values of fit indices compared to Monte Carlo simulation data.

Fit measure	Chi-square	AIC	BIC	RMSEA	CFI	TLI	SRMR
p-value	0.991	0.241	0.254	1.000	1.000	0.913	0.872

Herbivore and natural enemy SEM

Appendix Table 3-4. Final herbivore and natural enemy model output

```
lavaan 0.6-5 ended normally after 34 iterations

  Estimator                                         ML
  Optimization method                           NLMINB
  Number of free parameters                         17

  Number of observations                            48
```

```
Model Test User Model:

  Test statistic                                 4.836
  Degrees of freedom                                11
  P-value (Chi-square)                           0.939

Model Test Baseline Model:

  Test statistic                               133.093
  Degrees of freedom                                21
  P-value                                        0.000

User Model versus Baseline Model:

  Comparative Fit Index (CFI)                    1.000
  Tucker-Lewis Index (TLI)                       1.105

Loglikelihood and Information Criteria:

  Loglikelihood user model (H0)               -339.884
  Loglikelihood unrestricted model (H1)       -337.466

  Akaike (AIC)                                 713.768
  Bayesian (BIC)                               745.578
  Sample-size adjusted Bayesian (BIC)          692.245

Root Mean Square Error of Approximation:

  RMSEA                                          0.000
  90 Percent confidence interval - lower         0.000
  90 Percent confidence interval - upper         0.034
  P-value RMSEA <= 0.05                          0.960

Standardized Root Mean Square Residual:

  SRMR                                           0.053

Parameter Estimates:

  Information                                 Expected
  Information saturated (h1) model          Structured
  Standard errors                             Standard

Regressions:
                   Estimate  Std.Err  z-value  P(>|z|)
  logher.a ~
    planted.R        -0.129    0.061   -2.098    0.036
    planted.2         0.710    0.201    3.537    0.000
    logitgap2         0.382    0.099    3.861    0.000
    ssc               0.267    0.111    2.408    0.016
  lognen.a ~
    planted.2         0.425    0.176    2.422    0.015
    ssc               0.203    0.085    2.384    0.017
    logher.a          0.216    0.098    2.201    0.028
  loghrbenm ~
    logher.a          1.251    0.091   13.693    0.000
    lognen.a         -0.498    0.120   -4.154    0.000

Covariances:
                   Estimate  Std.Err  z-value  P(>|z|)
  logitgap2 ~~
    ssc              -0.245    0.116   -2.106    0.035
  planted.R ~~
    planted.2         0.000

Variances:
                   Estimate  Std.Err  z-value  P(>|z|)
   .logher.a          0.363    0.074    4.899    0.000
```

```
   .lognen.a          0.234    0.048    4.899    0.000
   .loghrbenm         0.198    0.040    4.899    0.000
    planted.R         2.000    0.408    4.899    0.000
    planted.2         0.187    0.038    4.899    0.000
    logitgap2         0.860    0.176    4.899    0.000
    ssc               0.686    0.140    4.899    0.000
```

Appendix Table 3-5. Calculated p-values of fit indices compared to Monte Carlo simulation data.

Fit measure	Chi-square	AIC	BIC	RMSEA	CFI	TLI	SRMR
p-value	0.943	0.188	0.188	1.000	1.000	0.959	0.931

Appendix Table 3-6. Alternative herbivore and natural enemy model output

```
lavaan 0.6-5 ended normally after 30 iterations

  Estimator                                         ML
  Optimization method                           NLMINB
  Number of free parameters                         17

  Number of observations                            48

Model Test User Model:

  Test statistic                                 5.234
  Degrees of freedom                                11
  P-value (Chi-square)                           0.919

Model Test Baseline Model:

  Test statistic                               133.093
  Degrees of freedom                                21
  P-value                                        0.000

User Model versus Baseline Model:

  Comparative Fit Index (CFI)                    1.000
  Tucker-Lewis Index (TLI)                       1.098

Loglikelihood and Information Criteria:

  Loglikelihood user model (H0)               -340.083
  Loglikelihood unrestricted model (H1)       -337.466

  Akaike (AIC)                                 714.166
  Bayesian (BIC)                               745.977
  Sample-size adjusted Bayesian (BIC)          692.644

Root Mean Square Error of Approximation:

  RMSEA                                          0.000
  90 Percent confidence interval - lower         0.000
  90 Percent confidence interval - upper         0.054
  P-value RMSEA <= 0.05                          0.947

Standardized Root Mean Square Residual:

  SRMR                                           0.059

Parameter Estimates:

  Information                                 Expected
  Information saturated (h1) model          Structured
  Standard errors                             Standard
```

```
Regressions:
                   Estimate  Std.Err  z-value  P(>|z|)
  logher.a ~
    planted.R        -0.129    0.061   -2.098    0.036
    planted.2         0.710    0.201    3.537    0.000
    logitgap2         0.382    0.099    3.861    0.000
    ssc               0.267    0.111    2.408    0.016
  lognen.a ~
    planted.2         0.595    0.162    3.674    0.000
    ssc               0.288    0.089    3.223    0.001
    logitgap2         0.171    0.080    2.146    0.032
  loghrbenm ~
    logher.a          1.251    0.086   14.472    0.000
    lognen.a         -0.498    0.113   -4.410    0.000

Covariances:
                   Estimate  Std.Err  z-value  P(>|z|)
  logitgap2 ~~
    ssc              -0.245    0.116   -2.106    0.035
  planted.R ~~
    planted.2         0.000

Variances:
                   Estimate  Std.Err  z-value  P(>|z|)
   .logher.a          0.363    0.074    4.899    0.000
   .lognen.a          0.236    0.048    4.899    0.000
   .loghrbenm         0.198    0.040    4.899    0.000
    planted.R         2.000    0.408    4.899    0.000
    planted.2         0.188    0.038    4.899    0.000
    logitgap2         0.860    0.176    4.899    0.000
    ssc               0.686    0.140    4.899    0.000
```

Pollinator SEM

Appendix Table 3-7. Final pollinator model output

```
lavaan 0.6-5 ended normally after 26 iterations

  Estimator                                         ML
  Optimization method                           NLMINB
  Number of free parameters                         12

  Number of observations                            48

Model Test User Model:

  Test statistic                                 1.159
  Degrees of freedom                                 3
  P-value (Chi-square)                           0.763

Model Test Baseline Model:

  Test statistic                               161.378
  Degrees of freedom                                10
  P-value                                        0.000

User Model versus Baseline Model:

  Comparative Fit Index (CFI)                    1.000
  Tucker-Lewis Index (TLI)                       1.041

Loglikelihood and Information Criteria:

  Loglikelihood user model (H0)               -236.234
  Loglikelihood unrestricted model (H1)       -235.655

  Akaike (AIC)                                 496.468
```

```
  Bayesian (BIC)                                 518.922
  Sample-size adjusted Bayesian (BIC)            481.275

Root Mean Square Error of Approximation:

  RMSEA                                            0.000
  90 Percent confidence interval - lower           0.000
  90 Percent confidence interval - upper           0.165
  P-value RMSEA <= 0.05                            0.794

Standardized Root Mean Square Residual:

  SRMR                                             0.012

Parameter Estimates:

  Information                                   Expected
  Information saturated (h1) model            Structured
  Standard errors                               Standard

Regressions:
                   Estimate  Std.Err  z-value  P(>|z|)
  logpoll.a ~
    logfl.d          -0.208    0.102   -2.041    0.041
    logitgap2         0.564    0.129    4.366    0.000
    veg.cov          -0.250    0.118   -2.115    0.034
  logflrvis ~
    logpoll.a         1.673    0.091   18.430    0.000

Covariances:
                   Estimate  Std.Err  z-value  P(>|z|)
  logitgap2 ~~
    veg.cov           0.671    0.164    4.088    0.000
  logfl.d ~~
    veg.cov           0.205    0.122    1.684    0.092
    logitgap2         0.250    0.117    2.144    0.032

Variances:
                   Estimate  Std.Err  z-value  P(>|z|)
   .logpoll.a         0.306    0.062    4.899    0.000
   .logflrvis         0.176    0.036    4.899    0.000
    logfl.d           0.687    0.140    4.899    0.000
    logitgap2         0.860    0.176    4.899    0.000
    veg.cov           0.979    0.200    4.899    0.000
```

Appendix Table 3-8. Calculated p-values of fit indices compared to Monte Carlo simulation data.

Fit measure	Chi-square	AIC	BIC	RMSEA	CFI	TLI	SRMR
p-value	0.802	0.211	0.211	1.000	1.000	0.823	0.773

Phytometer SEM

Appendix Table 3-9. Final phytometer yield SEM results. Three plots had phytometer plants that did not produce flowers; the data from these plots could not be included in the SEM, so the number of observations was decreased to 45 from 48.

```
lavaan 0.6-5 ended normally after 78 iterations

  Estimator                                         ML
  Optimization method                           NLMINB
  Number of free parameters                         15

  Number of observations                            45
```

```
Model Test User Model:

  Test statistic                                 5.904
  Degrees of freedom                                 6
  P-value (Chi-square)                           0.434

Model Test Baseline Model:

  Test statistic                               339.846
  Degrees of freedom                                15
  P-value                                        0.000

User Model versus Baseline Model:

  Comparative Fit Index (CFI)                    1.000
  Tucker-Lewis Index (TLI)                       1.001

Loglikelihood and Information Criteria:

  Loglikelihood user model (H0)               -148.257
  Loglikelihood unrestricted model (H1)       -145.305

  Akaike (AIC)                                 326.513
  Bayesian (BIC)                               353.613
  Sample-size adjusted Bayesian (BIC)          306.595

Root Mean Square Error of Approximation:

  RMSEA                                          0.000
  90 Percent confidence interval - lower         0.000
  90 Percent confidence interval - upper         0.192
  P-value RMSEA <= 0.05                          0.506

Standardized Root Mean Square Residual:

  SRMR                                           0.053

Parameter Estimates:

  Information                                 Expected
  Information saturated (h1) model          Structured
  Standard errors                             Standard


Regressions:
                   Estimate  Std.Err  z-value  P(>|z|)
  fruitseed.mn ~
    frflr.mn          0.747    0.221    3.379    0.001
  frflr.mn ~
    logflrvis         0.089    0.044    2.007    0.045
    logitgap2         0.118    0.060    1.983    0.047
  logfruit ~
    frflr.mn          1.111    0.151    7.371    0.000
    logitgap2         0.599    0.062    9.712    0.000
  logplntseed ~
    logfruit          1.134    0.017   66.306    0.000
    fruitseed.mn      0.386    0.024   16.137    0.000

Covariances:
                   Estimate  Std.Err  z-value  P(>|z|)
  logflrvis ~~
    logitgap2         0.396    0.168    2.355    0.019
 .fruitseed.mn ~~
   .logfruit          0.045    0.029    1.548    0.122

Variances:
                   Estimate  Std.Err  z-value  P(>|z|)
   .fruitseed.mn      0.304    0.064    4.743    0.000
```

```
   .frflr.mn         0.108    0.023    4.743    0.000
   .logfruit         0.121    0.026    4.743    0.000
   .logplntseed      0.008    0.002    4.743    0.000
    logflrvis        1.417    0.299    4.743    0.000
    logitgap2        0.786    0.166    4.743    0.000
```

Appendix Table 3-10. Calculated p-values of fit indices compared to Monte Carlo simulation data.

Fit measure	Chi-square	AIC	BIC	RMSEA	CFI	TLI	SRMR
p-value	0.507	0.178	0.178	1.000	1.000	0.506	0.305

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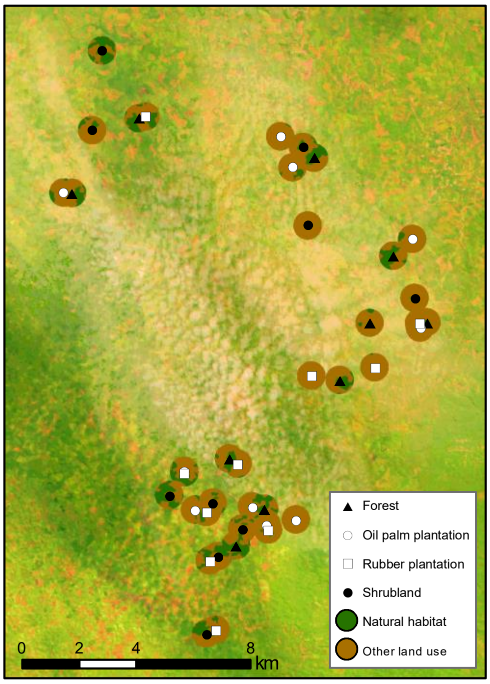
Chapter 4

Rainforest transformation with contrasting effects on bee reproduction at local and landscape scales



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Abstract

Stingless bees are important pollinators in tropical landscapes for wild and cultivated plants. However, our understanding of local and landscape effects of ongoing rainforest conversion on stingless bee behavior and survival remains limited. Focusing on the native Southeast Asian species *Tetragonula laeviceps*, we conducted a landscape-scale field experiment in Jambi Province (Sumatra, Indonesia), contrasting effects of rainforest transformation at two spatial scales on colony activity, survival, and growth. We placed 120 hives in 40 plots divided among four predominant land use types (primary degraded forest, shrubland, and rubber and oil palm plantations) while controlling for a gradient of increasing natural habitat (forest and shrubland) within the bees' foraging range (500 m). Our results suggest trade-offs for *T. laeviceps* in transformation landscapes that influence colony response. Hives in forest and rubber experienced much lower mortality than hives in the more open and hotter shrub and oil palm plots, though the latter supported higher floral richness. Floral richness enhanced pollen weight in the hives, which in turn drove brood size and individual bee weight, finally promoting overall colony weight. For stingless bees, the loss of structurally complex nesting habitats such as forest and rubber plantations to more open shrub and oil palm habitats may be most detrimental, but open habitats increase floral resources. We also observed negative correlations between hive resin and both resin foraging and bee size, while availability of resin resources in the landscape so far plays an unknown role. Considering the key ecosystem function of stingless bees and the continued deforestation crisis in the tropics, understanding the aspects of landscape transformation that impact bee response will be critical. Moving forward, this includes clarifying the impacts of increasing open habitats and how such transformation effects translate to landscape and population levels.

4.1. Introduction

In the tropics, wild bees (Hymenoptera: Apidae) provide critical pollination services (Klein et al. 2007, Garibaldi et al. 2011, 2013) but face an increasingly transformed landscape due to conversion of forests to simplified agricultural environments such as oil palm (*Elaeis guineensis*) (Koh and Wilcove 2008, Vijay et al. 2016). A shift to monoculture reduces the diversity of the bee community and the floral resources on which they rely (Tscharntke et al. 2008, Rembold et al. 2017a), and creates drier, hotter, and more variable microclimates (Foster et al. 2011). On a landscape scale, this intensification increases the distance between pollinator habitats and floral resources, which reduces flower visitation, an effect that appears to be more severe for tropical social bees (Klein et al. 2003b, Ricketts et al. 2008, Winfree et al. 2009). In meta-analyses, the role of local floral resources and landscape forest cover appears to be broadly important in driving wild social bee diversity and abundance (Ricketts et al. 2008, Winfree et al. 2009, Kennedy et al. 2013). However, tropical landscapes remain underrepresented in the literature, despite their importance in terms of biodiversity and food production (Ghazoul 2005, Brosi et al. 2008, Viana et al. 2012, Steward et al. 2014, Garibaldi et al. 2016). A better understanding of these effects at the local and landscape scale is needed to support conservation of wild bee populations and the pollination services they provide, which may be threatened globally (Tscharntke et al. 2008, Winfree et al. 2009, Potts et al. 2010).

Stingless bees (Meliponini) are an important group in tropical pollinator communities, both in terms of abundance and pollinating function (Brosi et al. 2007, Ramírez et al. 2013). As generalist eusocial pollinators, stingless bees along with honey bees (*Apis* spp.) can adapt to new flowering species and conduct organized foraging behaviors from long-lived nests, all of which increases the effectiveness of their pollination services (Heard 1999). Stingless bees are widely distributed and endemic in both the paleo- and neo- tropics and subtropics, including regions where honey bees are not native (Heard 1999). Throughout their geographic range, local stingless bee communities are often diverse (Liow et al. 2001, Siqueira et al. 2012, Rasmussen 2013, Brown and de Oliveira 2014), and their nests can number up to 1500 per km^2 in natural vegetation (Roubik 2006). They also represent a wide range of foraging behaviors and body sizes, which increases their overall pollination efficiency for a broader range of cultivated and wild plants (Kato 1996, Brosi et al. 2007). They have been shown to successfully contribute to pollination for over 60 crops, and in some cases are more effective than other major pollinator groups (Heard 1999, Slaa et al. 2006).

Though stingless bees can forage in open areas, they appear to prefer nesting in forest and are found foraging in greater abundance and richness closer to forests (Brown and Albrecht 2001, Klein et al. 2003a, Brosi et al. 2007, 2008). Forests provide nesting sites in tree cavities or dead wood (Wille 1983, Eltz et al. 2003), as well as access to plant resins, which they use for nest construction and defense (Roubik 2006, Leonhardt and Blüthgen 2009). Nevertheless, variability exists within Meliponine responses to landscape change. Isolation from forest appears to increase spatiotemporal variability in community composition (Klein 2009) and is negatively associated with specific traits, such as smaller body size (Brosi 2009, Gutiérrez-Chacón et al. 2018, Mayes et al. 2019) or wider diet breadth (Lichtenberg et al. 2018). Still, many species appear to be flexible in selecting nesting sites, as suitable sites do not appear to be the most limiting resource within forest habitat (Hubbell and Johnson 1977, Eltz et al. 2002, Silva et al. 2013) and nests have also been observed in disturbed and urban areas (Brosi et al. 2007, Aidar et al. 2013).

Flowering resources in the landscape also play an important role in bee health, as bees collect pollen and nectar to feed adults and larvae (Nicolson 2011). Flower species diversity may be critical to obtaining specific nutrients while diluting the toxicity of certain resources (Eckhardt et al. 2014, Moerman et al. 2017). Different habitat types can be associated with characteristic levels of flowering plant diversity important to bees (Williams and Kremen 2007). Kaluza et al. (2016) found that landscape type (macademia plantation, urban garden, or forest) affected colony foraging behavior of the Australian species *Tetragonula carbonaria*; subsequent research indicated that bees responded to floral and plant resource diversity by increasing the diversity, abundance, and quality of resources collected (Kaluza et al. 2017, Trinkl et al. 2020), which resulted in higher colony fitness and reproduction (Kaluza et al. 2018).

As tropical landscapes continue to transform due to conversion pressures, there is an urgent need to expand our understanding of stingless bee biology (Roubik 2006), both for their conservation and the conservation of their ecosystem function. A critical frontier in this regard is how stingless bees adapt to intensification, both at the local and landscape scale (Viana et al. 2012). Much of the evidence we have for the impacts of intensification has been inferred indirectly through observations of forager or nest presence within different environments (Gutiérrez-Chacón et al. 2018, Lichtenberg et al. 2018, Mayes et al. 2019). Little experimental research has been conducted on how local and landscape factors translate to stingless bee colony survival and health (Viana et al. 2012, but see Kaluza et al. 2016), though such behavioral responses form a critical link between landscape patterns and processes (Bélisle 2005). No study so far has systematically examined how increasing levels of natural habitat loss in the landscape or intensification of nest habitats (i.e. non-forest habitats) jointly affect stingless bee colonies, though such scenarios will only increase with continued landscape transformation.

In the rainforest transformation landscape of Jambi Province, Sumatra, Indonesia, we conducted a landscape-scale experiment examining the interacting effects of local (plot-level) nesting habitat, land use, and amount of landscape-level natural habitat on colonies of a common Southeast Asian stingless bee species, *Tetragonula laeviceps* SMITH, 1857. Following an *a priori* experimental design, we placed 120 hives within 40 sites of four predominant land uses: degraded primary forest, shrubland, rubber plantation, and oil palm plantation. These land use categories, in this order, represent an increasing gradient of agricultural intensification, i.e. progressively greater harvested biomass but fewer ecosystem functions (Clough et al. 2016, Grass et al. 2020). As part of the experimental design, we selected the locations of the plots in each land use group to cover a maximal gradient of surrounding natural habitat (i.e. "landscape habitat"), which we defined as the proportion of forest and shrub land cover within the estimated foraging range of *T. laeviceps* (500 m). In addition to these two main treatments, we considered the effects of floral abundance and floral richness at the plot level. We also considered monthly changes in foraging activity and hive growth, as well as the role of temperature in hive survival.

We monitored hive foraging activity, survival, and development from August to November 2018 and measured hive and colony size at the end of the study period. We hypothesized that increasing intensification at the plot level (from forest to oil palm land uses) and at the landscape level (decreasing landscape habitat) would negatively affect the hive and colony response variables, i.e. decrease foraging activity, hive development, colony survival, and final hive and colony size. We also hypothesized that the role of habitat in the landscape could differ between land uses, so that landscape habitat would have a larger positive role in more intensified land use types, as it would compensate for local conditions. We inferred this relationship from the interaction effect size between plot land use and landscape-level treatments. We also expected less intensified habitat and more diverse and abundant floral resources to have positive interrelated effects on hive and colony development, which we defined and tested using structural equation modeling (SEM). We compared alternative hypothesized relationships that tested whether exogenous variables (i.e. the habitat treatments and floral resources) directly drove reproductive capacity (brood) and stored pollen, or whether the exogenous effects were mediated through stored pollen. Our SEM also proposed that larger hive structures would in turn be positively related to total colony weight through the number of workers and the average bee weight.

4.2. Methods

4.2.1. Study region and sites

The study was conducted in the Batang Hari regency of Jambi Province of Sumatra, Indonesia (Figure 4-1). Forest cover in Jambi decreased by over 70% from 1985 to 2007 (Laumonier et al. 2010), which has primarily been replaced with rubber (*Hevea brasiliensis*) and oil palm plantations (Grass et al. 2020). This region has a tropical humid climate and typically two rainy seasons around March and December and a dry period from July through August. From 1991 to 2011, mean annual temperature in this region was 26.7 ± 0.2° C and mean annual precipitation was 2235 ± 381 mm (Drescher et al. 2016)

4.2.2. Study species

Tetragonula laeviceps SMITH, 1857 is one of the most common stingless bee species (or species complex) in Southeast Asia (Rasmussen and Michener 2010). As is the case for most Meliponinae, *T. laeviceps* is a generalist, and has been found to feed on pollen from Fabaceae, Palmae, and Poaceae families (Nurasiqin 2016, Pangestika et al. 2017). In their natural forest habitat, they build nests in cavities at the base or in higher parts of trees. However, hives are also found in suburban areas and in pillars and eaves of wooden houses (Sakagami et al. 1983). This opportunistic nesting also makes the species suitable for beekeeping, which is common in parts of Southeast Asia (Chuttong and Burgett 2017).

The inner nest architecture of *T. laeviceps* is clustered and disorganized, which may allow it to adapt to human constructs (Sakagami et al. 1983). Storage pots for honey and pollen are clustered together and usually attached to the cavity walls or to pillars. Brood cells are built separately from storage pots and may be found in more than one cluster (Sakagami et al. 1983). Resin is distributed in unoccupied areas of the cavity and stored either on the walls in thick layers or in a very thin layer along the ceiling (Schröck, personal observation).

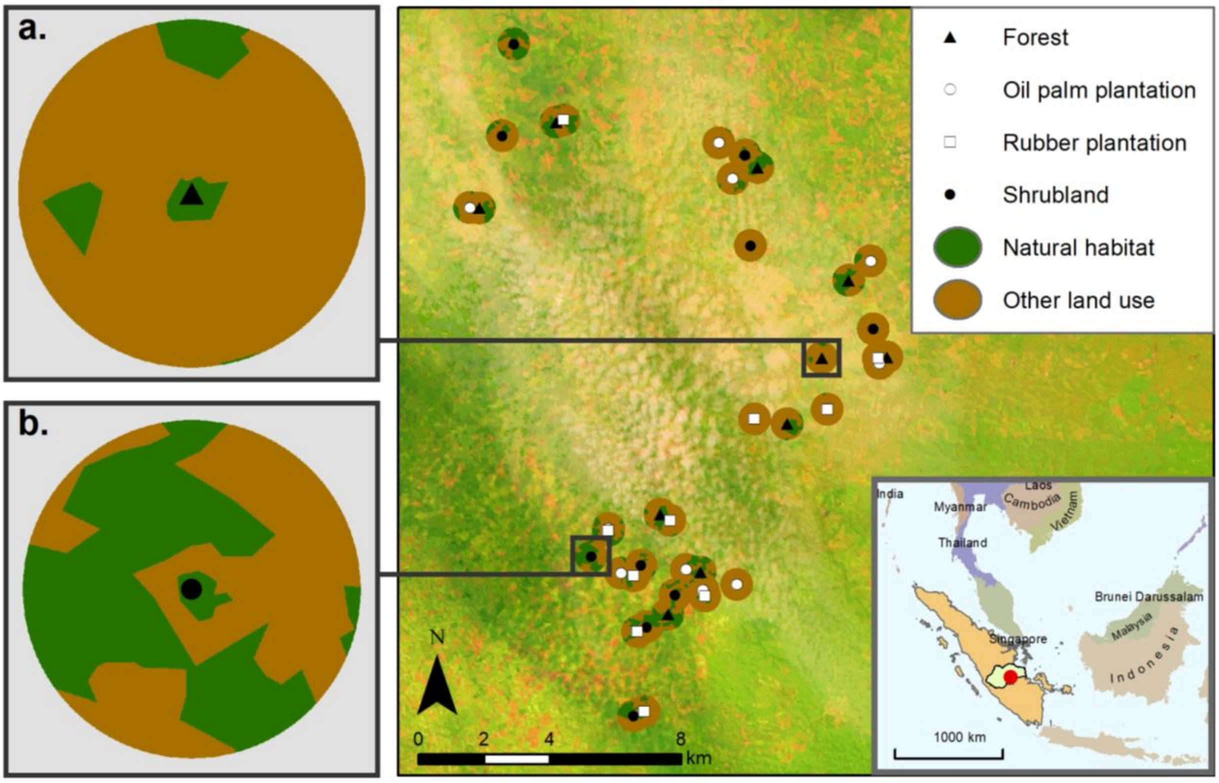

Figure 4-1. Map of study region in Batang Hari Regency, which is in Jambi Province, Sumatra, Indonesia (inset map). Call-outs show examples of (a) a forest plot with low surrounding natural habitat in the landscape and (b) a shrub plot with high surrounding natural habitat. Buffers are 500 m radius. Background imagery from Landsat 8.

4.2.3. Experimental design

Using a crossed experimental design, we contrasted the effects of two main treatment variables on *T. laeviceps* colony behavior, survival, and hive growth: 1) land use type and 2) the proportion of natural habitat in the landscape (“landscape habitat”). We selected 40 plots in the region between the Harapan Rainforest and Jambi City (Figure 4-1), taking care that the proportion of natural habitat around each plot (within 500 m) would cover an increasing gradient for all land use types. In addition to the plot land use and landscape treatments, we collected covariate data on the floral resources and mean midday temperature of each plot at the local scale.

We placed three hives at each plot in a shelter consisting of a platform elevating the hives 1 m from the ground and a roof to provide some protection from direct sun and rain (Appendix Figure 4-1). We sourced the 120 colonies of *T. laeviceps* from an apiary on a coffee plantation in Bengkulu Province, Indonesia. The colonies were established in 30x20x16 cm wooden boxes with removable lids. A transparent plastic window was attached to the box opening underneath the lid to allow direct visual inspection of the hive without physically disturbing nest structures (Appendix Figure 4-2). Hives were temporarily sealed and transported from their rearing location overnight to the study region and placed in study sites within 24 hours. Hives and shelters were oriented to face east where site conditions allowed to standardize sun exposure. We cleared the surrounding area of encroaching vegetation and applied oil on shelter supports to deter ants.

Plot land use

The 40 plots were comprised of four land uses (represented by ten sites each): secondary forest, shrubland, rubber plantation, and oil palm plantation, which represent the predominant land covers in the region (Grass et al. 2020). Forest land cover predominantly consisted of Dipterocarpaceae, Burseraceae, and Lauraceae families, as well as other native species (Rembold et al. 2017a). Shrubland was regrown cleared land that was dominated by shrubby vegetation but could have also been mixed with young oil palm or rubber trees in preparation for agricultural use (Drescher et al. 2016). Rubber and oil palm plots were monoculture plantations mostly owned by smallholder farmers. Their plant communities were characterized by alien species; common families include Melastomataceae and Poaceae (Rembold et al. 2017a). Biodiversity and ecosystem function decrease from forest to monoculture rubber and oil palm plantations (Clough et al. 2016). Forests have higher tree biomass and air humidity while monocultures have higher air temperature, and canopy openness (Drescher et al. 2016). These plots were a subset of 112 plots originally established for a bird landscape survey (Darras, in prep).

Landscape habitat

We assumed forest and shrub cover to be high-value land covers for resource collection and maximized the range of shrub and forest coverage within each land use group based on our understanding of the species and stingless bee biology (Sakagami et al. 1983, Roubik 2006). We used a 500 m radius for calculating natural habitat in the landscape based on the results of translocation experiments by Smith et al. (2017), who found that the number of returning foragers of a similarly-sized congener species (*Tetragonula carbonaria*) decreased significantly between 400 and 500 m. As body size is a significant predictor of bee foraging distance (Gathmann and Tscharntke 2002, Greenleaf et al. 2007), and these species differed in length by only 0.5 mm (Rasmussen and Michener 2010, Smith et al. 2017), we assumed *T. laeviceps* to have a similar foraging range.

We quantified the natural habitat surrounding the hives based on manually classified 1.5 m resolution SPOT satellite imagery from 2016. Land cover was identified at 1:5000 scale in the program QGIS (QGIS Development Team 2019) and verified by comparing to supporting imagery in Google Maps as well as informal field checks and local expert knowledge (Darras et al. in prep.). We used the package “landscapemetrics” (Hesselbarth et al. 2019) in the statistical software R (R Core Team 2016) to calculate the total proportion of forest and shrub cover within a 500 m radius of each hive.

Plot-level floral resources and temperature

We conducted surveys of flowering vegetation before and after the study period, in August-September 2018 and January 2019. In four 25 m^2 quadrats placed 10 m from the hives in the cardinal directions, we counted abundance and species richness of flower units within 5 m above the ground. We defined flower units as a cluster of flowers within ca. 5 cm, i.e. the distance a bee could easily walk. We identified flowering plants based on a field guide (Rembold et al. 2017b) and expert identification (Fabian Brambach, personal communication).

After initial vegetation sampling in August 2018, we conducted additional surveys in September for some plots to ensure sufficient sampling of species richness based on preliminary accumulation curves. We placed quadrats in the northeast, southeast, southwest and northwest positions around these plots. We also added six forest survey sites near some forest plots for additional sampling. Because our study period spanned both the dry and rainy season, we conducted a second round of surveys of all plots to characterize the flowering community over the entire period. To adjust for uneven sampling effort, we used the estimated asymptotic richness (Chao 1987), which we included as a covariate in our analyses along with mean floral density. To test whether floral resources in the plots differed before and after the study, we also conducted a non-parametric bootstrap (10,000 resamplings) of plot-level differences in floral density and richness between the August and January surveys.

We collected temperature data at each plot with iButton temperature loggers (Maxim Integrated, San Jose, USA) fixed underneath the shelter roof about 10 cm above the center of the three hives. We used the mean daily midday (12:00 PM) temperature over the preceding month as a covariate in our survival analysis.

4.2.4. Colony and hive data collection

We placed hives in the field in mid-July 2018. Beginning in August, we visited each plot monthly until the end of November, i.e. four times for each plot, except in 12 plots where all hives were lost. In each visit, we observed forager activity and made measurements of the hive (Section 2.4.1). In December, we collected the hives to make further measurements of the colony and hive structures (Section 2.4.2).

Forager activity survey

We conducted forager observations on rain-free days between 9 am and 11 am, when the bees are typically most active (Nurasiqin 2016). In each survey, two observers alternately monitored each of the hives at a plot in turn for five minutes, during which the number of bees leaving the hive ("outgoing foragers"), returning with pollen ("pollen foragers"), and returning with resin ("resin foragers") were counted. Bees carrying pollen and resin were easily distinguishable because pollen and resin loads were visible on their corbiculae. Bees returning with no visible loads could have had nectar in their crops or were unsuccessful; however, we could not make this distinction without disrupting foraging.

Hive measurement

After each foraging activity survey, we recorded the hive structure by visually inspecting the hive through the plastic window built into the top of the hive box (Appendix Figure 4-2). We placed a 2x2 cm grid over the top of the window to estimate the volumes of four main types of structures in the hive (resin, brood cells, pollen pots, and honey pots), which we drew on a gridded datasheet. The volumes of the overall hive structure, brood cells, pollen + honey pots, and resin were estimated in "hive volume units" (hereafter, "hvu"), defined as a grid cell (2x2 cm) multiplied by a height unit equivalent to 1/3 of the depth of the hive box (approximately 5 cm), or approximately 20 cm^3. We counted pollen and honey pots together as they were difficult to distinguish without disturbing the hive. This method facilitated volume estimation in the field and allowed relative quantification of hive structure development.

At the end of the study period (December 2018), all the remaining beehives (n=61) were placed into a freezer for at least 12 hours to kill the bees. The colony size was determined by counting the bees in each hive and weighing the entire colony, as well as the individual weights of 10 workers from each hive. We then separated and weighed the component hive structures (pollen, honey, resin, and brood).

4.2.5. Analytical Methods

Our analyses focused on the interacting effects of the two main experimental treatments, i.e. the plot land use (“land use”) and the proportion of natural habitat within 500m (“landscape habitat”), while also accounting for covariate effects including local flower resources (represented by the floral richness and floral density) and other model-specific covariates described in the sections below. Using the likelihood ratio test (LRT) (Johnson and Omland 2004), we tested the inclusion of an interaction between the land use and landscape habitat treatments, as well as interactions between these two treatments and the month factors in the multi-month forager activity and hive change datasets. We present the most parsimonious model (i.e. containing the fewest interactions) that the LRT indicated could not be significantly improved by additional interaction terms. Full comparisons are presented in Section 4.6 Appendix E.

We performed all statistical analyses with R (R Core Team 2016). The R packages “lme4” (Bates et al. 2015) and “lmerTest” (Kuznetsova et al. 2016) were used to create and test linear mixed effects models; “glmmTMB” (Brooks et al. 2017) was used to create generalized linear mixed effect models (GLMMs); and the packages “DHARMa” (Hartig 2019) and “performance” (Lüdecke et al. 2020) were used to assess model performance; and “emmeans” (Lenth 2019) was used to conduct post-hoc tests and multiple testing corrections. We used “iNEXT” (Hsieh et al. 2016) to evaluate vegetation richness using rarefaction and extrapolation methods (Chao and Jost 2012).

Monthly activity, growth, and survival

We modeled the monthly counts of outgoing foragers, returning pollen foragers, and returning resin foragers in separate generalized linear mixed models (GLMM) with a negative binomial link. In these analyses, we controlled for temporal effects (e.g. changing season or colony adaptation to the site) by including month factors in each model. In addition to treatment and flower resources variables, we also included hive size (total estimated volume) as a covariate to account for colony size, as larger colonies may have more foragers. For returning pollen forager and resin forager models, we included the proportion of total hive volume occupied by pollen + honey pots and by resin, respectively. Each model had a random effect for hive identity to account for pseudoreplication due to repeated measures taken in the monthly surveys, which was nested within a plot random effect to account for the spatial autocorrelation of the hives’ shared location. As we found that light intensity, temperature, and humidity were correlated and varied with time, we accounted for these interrelated effects with a time random effect of five half-hour levels from 09:00 to 11:00.

We ran a complementary log-log survival model (Gompertz model) of colony mortality with random effects for hive nested within plot. Incidences where hives were lost due to vandalism or wildlife predation were not counted as mortalities, though their survival prior to the event was still included in the model (i.e. their data were “right censored”). The model predictors included land use, landscape habitat, flowering resources covariates, mean midday plot temperature, and the number of timesteps (i.e. months) since the beginning of the experiment. We considered the last month a half timestep because we collected all the hives simultaneously instead of checking on them throughout the month, as we had done in other months. The temperature data from six of the plots could not be recovered, so our model covered 90 colonies in 31 plots.

We modeled hive volume change from the start of the project in August with a linear mixed effects model. As with the forager and survival models, we nested random effects for hive identity within plot random effects. Predictors included the plot land use and landscape habitat treatments, the two floral resource covariates, and factors for month (September-November).

Final hive and colony size

We modeled the final weight of the four component hive structures (pollen, brood, honey, and resin), which we were able to measure after collecting the hives at the end of November. We fit linear mixed effects models with land use, landscape habitat, and floral covariates as fixed effect predictors. We included plot identity as a random effect, except for the model of honey weight, which was estimated to have a random effect variance close to zero and so was fit with only fixed effects.

We expected the colony size and hive structure sizes to be interrelated, reflecting the biological mechanisms of the hive and bee development (Maia-Silva et al. 2016). We therefore fit hive and colony data to structural equation models (SEMs) to test whether relationships in the data reflect a hypothesized structure based on our biological understanding and whether this in turn implied other indirect effects by the experimental treatments. We took a piecewise approach, using the package “piecewiseSEM”, as this method can handle the nested data structure, small sample size, and nonlinear effects found in our dataset (Lefcheck 2016). We hypothesized that worker number and bee weight drove total colony weight. In preliminary analyses, we confirmed that brood weight was associated with worker numbers, and pollen and resin weight was associated with average bee weight and included these relationships as links in the candidate models. We also added an indicator variable for oil palm plot, as the results from the pollen weight model suggested it had a significant negative effect. We did not model resin in the SEM, as prior biological knowledge does not suggest a relationship with flower resources, which our hive resin analysis confirmed. We tested alternative relationships between brood, pollen, and flower resource variables (Figure 4-6a) and used LRT to compare these candidate models.

4.3. Results

We placed hives in plots in mid-July 2018 and began hive monitoring in August. Three plots (forest, oil palm, and shrub) were lost before the study started due to theft or wildlife damage. Of the remaining 37 plots (111 hives), 25 finished the study with hives. One forest plot, five shrub plots, two rubber plots, and four oil palm plots lost all hives. Sixty-three hives survived to the last forager and hive survey in November, though 61 were collected at the end of the month due to further mortalities.

4.3.1. Landscape and plot conditions

Landscape habitat

The proportion of natural habitat in the landscape (Section 4.6 Appendix B1. Landscape habitat, Appendix Figure 4-3) ranged from 6.3 to 52.2% around forest plots; from 0.6 to 62.0% around shrub plots; from 0.1 to 36.0% around rubber plots; and from 0 to 33.2% around oil palm plots. Only the mean landscape habitat around forest plots (29.8 ± 14.3% standard deviation) differed significantly from the mean surrounding oil palm plots (11.7 ± 10.3%) ($p = 0.049$). Mean landscape habitat around rubber plots (15.6 ± 13.1%) and shrub plots (24.8 ± 20.2%) did not differ significantly from any other plot land use types.

Although the mean landscape habitat did not differ significantly between plots at the end of the study ($p > 0.05$, Section 4.6 Appendix B1. Landscape habitat), the range represented in each land use group changed, as some plots lost all hives (Section 4.6 Appendix B1. Landscape habitat, Appendix Figure 4-3). This was most notable in oil palm plots, which had a lower maximum landscape habitat percentage (16.4%) compared to forest (42.2%), shrub (29.8%), and rubber (30.1%). We take this into account when plotting contrasting effects of low and high landscape habitat in Figure 4-3. Minimum landscape amount remained close to zero for all plots.

Plot floral resources

We identified 48 species and morphospecies of flowering plants (species list in Section 4.6 Appendix C). We found a total of 16 species in forest, 21 species in shrubland, 14 species in rubber plantations, and 19 species in oil palm plantations. The most prevalent species was *Clidemia hirta*, which was found in all land use types. *Asystasia gangetica*, *Hyptis capitata*, *Ageratum conyzoides*, *Clibadium surinamense*, and *Melastoma malabathricum* were also found in 20-90% of shrub, rubber, and oil palm plots. All these prevalent species except *M. malabathricum* are non-native to the region (Rembold et al. 2017a).

Comparing between land use types (Section 4.6 Appendix B2. Comparison of plot floral richness), our results indicated a similar estimated flowering species richness in forest (4.7 ± 4.8 standard deviation) and rubber (4.6 ± 4.1) plots. These plots did not differ significantly from shrub plots (6.9 ± 3.2). Oil palm plots (12.3 ± 5.7) had significantly more species than forest plots ($p = 0.006$) and rubber plots ($p = 0.004$) but also did not differ significantly from shrub plots.

We compared the mean plot flower density by land use, using a generalized linear model (GLM) with a gamma link (Section 4.6 Appendix B3. Comparison of plot floral density). Forest (0.79 ± 1.25 flower units/m^2), rubber (0.62 ± 0.63), and oil palm (1.00 ± 0.73) plots had similar estimated mean flower densities. Shrub plots (4.4 ± 5.7) had a significantly higher density than all other plot types ($p<0.05$).

We used the aggregated species incidences in the quadrats from both survey rounds to estimate species richness of each land cover, standardized by sampling coverage (Chao and Jost 2012). Although we conducted the most surveys in forest (n = 140), we achieved the lowest estimated sampling coverage in this land use (80%). When comparing at this level of coverage-standardized estimated richness, forest had the highest floral richness with 16.0 species (confidence intervals in Section 4.6 Appendix B4. Sampling coverage-based richness), followed by shrub (11.3 species) and oil palm (9.6 species). At this coverage, rubber had significantly fewer species than all other land covers (6.1 species). However, when comparing the effective number of species (exponentiated Shannon index), shrub had the most species (9.1 species), followed by forest (8.0 species), and oil palm (7.6 species). Rubber still had the fewest species (4.2).

Between the August and January surveys, floral density, but not richness, tended to increase in shrub (p=0.037) and oil palm (p=0.085) plots between these survey times. Forest and rubber plots did not experience meaningful changes in floral density or richness; although the difference in forest richness was significant (p=0.049), the estimated change amounted to an average decrease of less than one species (Section 4.6 Appendix B5. Seasonal floral resource differences).

Plot temperature

The mean daily midday temperature of forest plots (30.2 ± 2.6°C) was significantly lower than that in all other plots (p <0.001). Oil palm (32.4 ± 2.6°C) and rubber (32.7 ± 3.0°C) temperatures did not differ significantly. Shrub plots had the highest mean midday temperature (33.2 ± 4.3°C), which was significantly higher (p<0.05) than any other land use type (Section 4.6 Appendix B6. Temperature).

4.3.2. Forager activity

Two observers collected 652 survey records of forager activity for each month, from August to November. The best-supported model for all three types of forager activities included a three-way interaction between month, plot land use, and landscape (Appendix Table 4-11 to 4-13). The significant interaction between these three variables suggests that the effect of landscape habitat changed between months, and these changes differed between plot land uses

Table 4-1. Type-III analysis of variance (ANOVA) tables of Wald chi-square statistics, degrees of freedom, and significance of model coefficients for generalized linear mixed models (negative binomial link) of outgoing forager, returning pollen foragers, and returning resin foragers.

	Outgoing foragers			Pollen foragers			Resin foragers		
Predictors	*Chisq*	*df*	*p*	*Chisq*	*df*	*p*	*Chisq*	*df*	*p*
Intercept	156.00	1	**<0.001**	26.31	1	**<0.001**	0.20	1	0.659
Hive volume	59.55	1	**<0.001**	60.41	1	**<0.001**	53.09	1	**<0.001**
Month	10.40	3	**0.015**	24.02	3	**<0.001**	3.96	3	0.266
Land use	8.07	3	**0.045**	11.91	3	**0.008**	7.92	3	**0.048**
Landscape habitat	2.25	1	0.134	1.07	1	0.301	0.24	1	0.622
Floral density	0.55	1	0.457	0.32	1	0.574	0.00	1	0.982
Floral richness	2.57	1	0.109	0.26	1	0.607	0.08	1	0.778
Month:Land use	35.12	9	**<0.001**	55.53	9	**<0.001**	15.96	9	0.068
Month:Landscape habitat	8.67	3	**0.034**	8.99	3	**0.029**	6.42	3	0.093
Land use:Landscape habitat	15.97	3	**0.001**	14.58	3	**0.002**	19.47	3	**<0.001**
Month:Land use:Landscape habitat	30.45	9	**<0.001**	32.58	9	**<0.001**	22.05	9	**0.009**
Hive proportion pollen and honey				0.04	1	0.847			
Hive proportion resin							13.82	1	**<0.001**

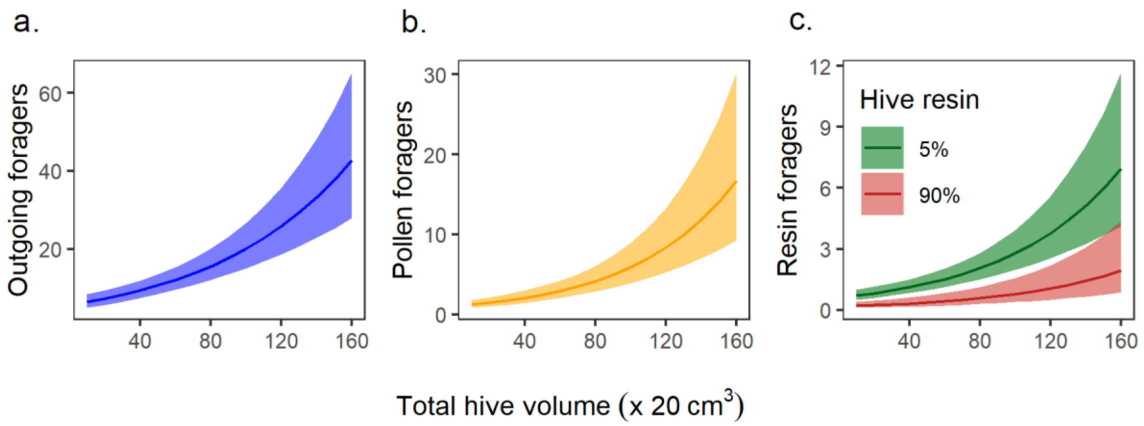

Figure 4-2. Estimated marginal mean forager counts and 95% confidence intervals over increasing hive volume for (a) outgoing foragers, (b) returning pollen foragers, and (c) returning resin foragers. Resin foragers also decreased with increasing proportion of hive occupied by resin (shown for 5% and 90% resin hives). Estimates are drawn.

Table 4-2. Results of the final linear mixed effects model of monthly net change in hive volume from the initial volume in August. Fixed effect coefficients are in units of 20 cm^3 volume change. Land use coefficients are given in relation to a forest plot baseline. Month and habitat interaction coefficients are relative to September values. Continuous variables have been centered and scaled by two standard deviations.

	Net hive volume change		
Predictors	*Estimate*	*95% C.I.*	*p*
Intercept	1.87	-5.97 – 9.70	0.640
Land use [Oil palm]	-11.88	-25.32 – 1.55	0.083
Land use [Rubber]	-7.36	-17.49 – 2.76	0.154
Land use [Shrub]	-13.36	-24.99 – -1.73	**0.024**
Month [Oct]	-8.29	-13.31 – -3.27	**0.001**
Month [Nov]	12.02	6.65 – 17.39	**<0.001**
Landscape habitat	-4.67	-14.46 – 5.12	0.350
Flower richness	1.79	-8.39 – 11.98	0.730
Flower density	-4.21	-11.64 – 3.23	0.268
Month [Oct] * Landscape habitat	-5.64	-15.85 – 4.56	0.278
Month [Nov] * Landscape habitat	-14.75	-25.46 – -4.04	**0.007**
Random effects			
σ^2	257.30		
$\tau_{00\ \mathrm{Hive:Plot}}$	113.85		
$\tau_{00\ \mathrm{Plot}}$	21.18		
ICC	0.34		
N_{Hive}	3		
N_{Plot}	31		
Observations	224		
Marginal R^2 / Conditional R^2	0.211 / 0.483		

for all three foraging activities (Table 4-1). Foraging activity patterns in forest plots did not change with increasing landscape habitat at a significance level of *p*=0.05 (Appendix Figure 4-5). In the first month of the study, activity increased with more landscape habitat for outgoing foragers in shrub and oil palm plots and for resin foragers in shrub plots (*p*<0.05). In the latter two months (October and November), foraging tended to be decreasing with greater landscape habitat proportion for rubber and shrub plots, though these trends were not always significant at an adjusted *p*=0.05 significance level (Appendix Table 4-10).

All forager activity types increased with hive size (Figure 4-2, a-c). The smallest hives were estimated to have marginal means of 10 outgoing foragers and two returning pollen foragers in an observation period (Figure 4-2a), while the largest hives had a mean of more than 40 outgoing foragers and 15 returning pollen

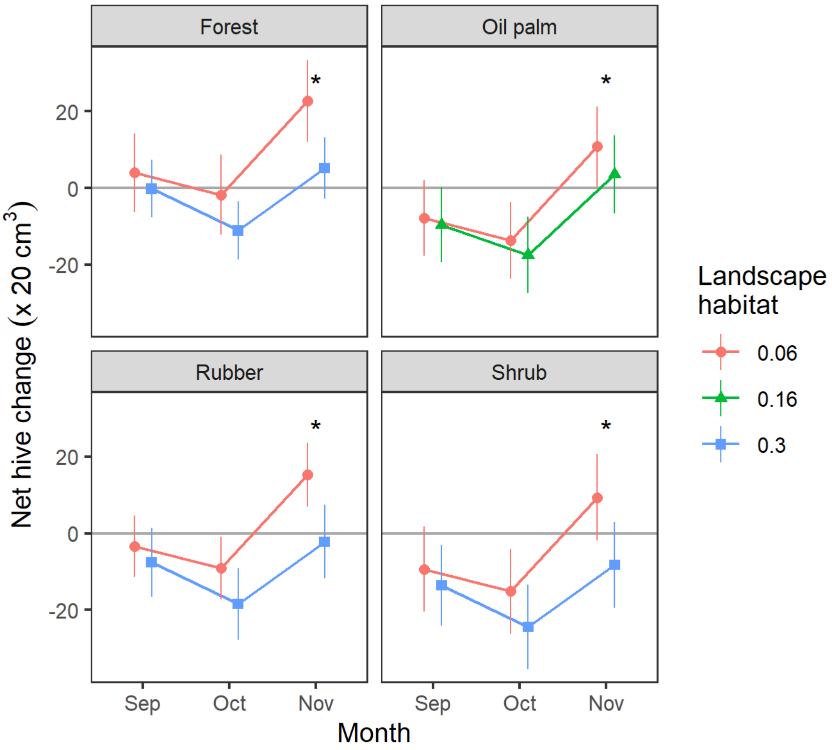

Figure 4-3. Modeled effect of plot land use (panels) and the interacting effects of month (x-axis) and proportion of habitat in the landscape on change in hive volume from initial size in August (net hive volume, y-axis). Note that hive change was estimated with the proportion of landscape habitat at 0.30 for all plot groups except oil palm, which was estimated at 0.16, the highest consistent value for this group for the entire study period. The effect of landscape habitat proportion was significant in November (*). October and shrub land use factors also had significant negative effects (**Table 4-2**).

foragers (Figure 4-2b). Resin forager activity increased with hive size but decreased with the relative amount of resin in the hive (Figure 4-2c). The remaining covariates did not explain significant additional variance (Table 4-1). The fixed effects variables explained 26.2%, 30.0%, and 39.7% of variability in the outgoing foragers, pollen foragers, and resin foragers models, respectively. Further model coefficients are found in Section 4.6 Appendix D.

4.3.3. Hive volume change over time

Land use, month, and landscape habitat were significant predictors of hive volume change (Table 4-2). Forest plot hives did not change significantly from August to September (*p*=0.625). Compared against forest hives, shrubland hive changes were significantly more negative (*p*=0.025), while a negative contrast with oil palm was marginally significant (*p*=0.081). The most parsimonious model included an interaction between landscape habitat and month (Appendix Table 4-14). Model estimated means indicate that hive change was significantly negative at a 95% confidence interval in October for all land uses except forest plots with low landscape habitat (Figure 4-3). In November, landscape habitat had a negative trend (*p*<0.01). This indicated that forest and rubber hives with low habitat landscapes increased significantly above their initial August size in November. The model did not estimate significant effects for flower resource covariates.

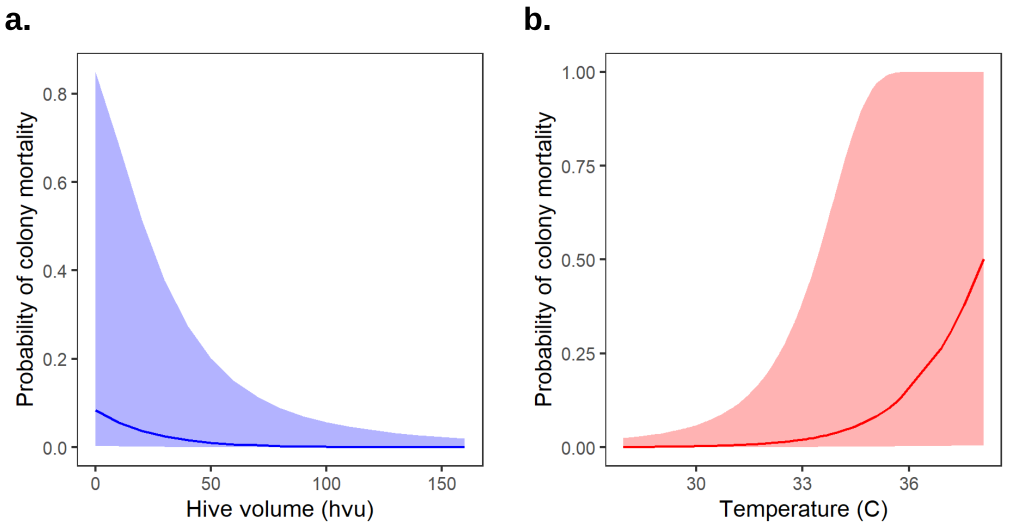

Figure 4-4. Estimated probability of colony mortality with increasing hive volume (a) and increasing temperature (b) and 95% confidence interval from survival analysis model.

4.3.4. Colony survival

Hives in rubber and forest land uses had the lowest rate of mortality by November, with six out of 30 rubber hives (20%) and eight out of 24 forest hives (33%). Mortality of hives in shrub and oil palm land uses was higher. Of the 24 hives placed in each of these land uses, 13 (54%) died in shrubland and 14 (58%) died in oil palm. Based on the survival model results (Table 4-3), the probability of colony mortality significantly decreased with increasing hive volume by approximately 90% with a hive volume increase of two standard deviations, or about 100 cm^3 (Figure 4-4a). With an increase in mean midday temperature by 4.4°C the model estimated a 21-fold increase in mortality risk (Figure 4-4b). Probability of hive mortality with time (hazard) was 1.11, which did not suggest an increasing hazard with time (p=0.80). The likelihood ratio test (Appendix Table 4-15) did not support including an interaction between plot

Table 4-3. Estimated coefficients for the survival analysis model. Coefficients represent the log of the proportional increase in risk with a unit increase in the independent variable. Plot land use effects are given in relation to a forest baseline. Continuous variables, except time, have been mean-centered and scaled by two standard deviations.

	Colony mortality		
Predictors	*Estimate*	*95% C.I.*	*p*
(Intercept)	-4.78	-8.75 – -0.82	**0.018**
Total hive volume	-2.22	-3.96 – -0.48	**0.012**
Time (months)	0.11	-0.67 – 0.88	0.784
Land use [Oil palm]	2.93	-1.43 – 7.30	0.187
Land use [Rubber]	-1.93	-5.91 – 2.05	0.342
Land use [Shrub]	0.46	-3.66 – 4.59	0.825
Landscape habitat	1.62	-0.11 – 3.35	0.066
Flower density	0.16	-1.44 – 1.76	0.846
Flower richness	-1.85	-5.24 – 1.54	0.284
Mean midday temp	3.02	0.48 – 5.56	**0.020**
Random effects			
σ^2	1.64		
τ_{00} Hive:Plot	1.14		
τ_{00} Plot	6.58		
ICC	0.82		
N_{Hive}	3		
N_{Plot}	31		
Observations	292		
Marginal R^2 / Conditional R^2	0.395 / 0.894		

land use and landscape habitat. Other variables were not significant predictors of hive mortality at the $p=0.05$ significance level (Table 4-3). The fixed effects explained 40.1% of variance and the area under the receiver-operator characteristic curve was 0.99.

4.3.5. Hive and colony size in November

The models of hive structure weights indicated that flower richness and flower density were significant predictors ($p<0.05$) for pollen, brood, and honey weight (Figure 4-5). Flower richness predicted an increase in these three types of hive structures, while flower density predicted a decrease. The pollen model also estimated significantly less pollen in oil palm plot hives ($p=0.021$). Other treatment effects were not significant for any model. The fixed effect variables together explained the greatest proportion of variance in the pollen weight model (22%), followed by the brood model (15%) and honey model (adjusted R^2 = 12%). None of the predictors in the resin model were significant, and their effects explained less than 5% of variance. An interaction between treatments was also not supported for these models (Appendix Tables Appendix Table 4-16 to Appendix Table 4-19). Further model information is found in Section 4.6 Appendix F.

The plot land use and landscape habitat treatments and floral resource covariates were not significant predictors of colony worker numbers (Appendix Table 4-21). However, floral resources were significant predictors of total colony weight in a similar pattern to the pollen, brood, and honey weight models (Appendix Table 4-22).

4.3.6. Hive and colony relationships to habitat variables

We fit data from 55 of the hives collected in November to structural equation models. We excluded six hives because we could not calculate average individual bee weight due to sample loss from ant damage. Among the alternative SEMs we considered (Figure 4-6a), we found the most support for a direct connection between flower resource variables and hive pollen weight (model B in Figure 4-6a). Model C did not support a partially mediated effect of floral resources on brood weight. Model fits and comparisons are shown in Table 4-4. The best model (Figure 4-6b) suggests that the exogenous variable floral richness positively affected pollen hive weight directly, which in turn drove brood size and individual bee weight. All links were significant

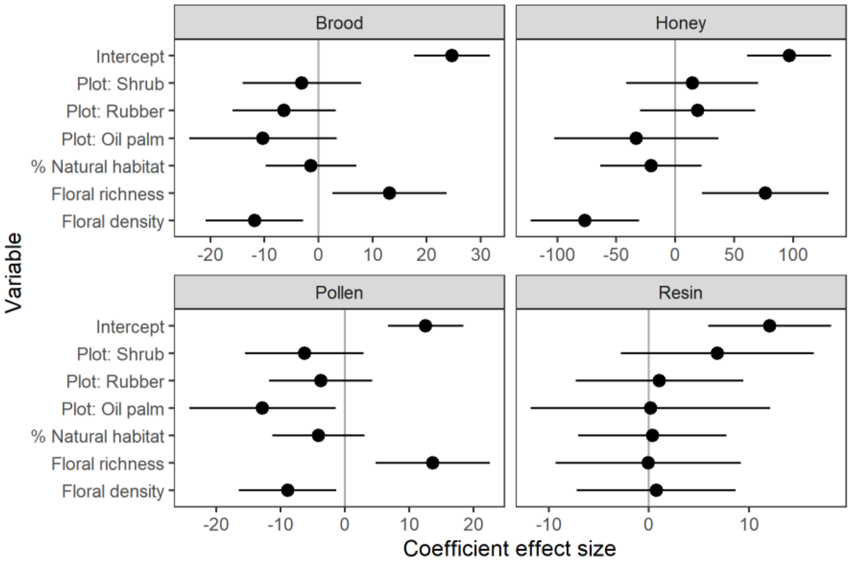

Figure 4-5. Effects estimates from linear (mixed) effects models of brood, honey, pollen, and resin weights at the end of the study in November. Estimates are compared to a forest plot baseline and continuous variables have been mean-centered and scaled by two standard deviations. Information about random effects are found in Appendix F.

Table 4-4 Comparison of structural equation model fits.

Model	*AIC*	*BIC*	*Fisher's C*	*Model comparison*	*Fisher's C difference*	*df difference*	*p*
A	88.528	136.704	40.528				
B	77.102	123.271	31.102	a vs. b	9.426	2	0.009 **
C	78.673	128.856	28.673	b vs. c	2.429	4	0.6574

except for floral density (*p*=0.06) and oil palm (*p*=0.15), which were negatively associated with hive pollen weight. Further model outputs are presented in Section 4.6 Appendix H.

The exogenous variables driving hive pollen weight explained 14% of variance (marginal R^2) while plot-level random effects allowed the model to account for 32% of total variability (conditional R^2). Though pollen and resin weight were significant predictors of average bee weight, they only accounted for 10% of variability, while more than half of total variability was attributed to plot random effects. In contrast, pollen weight accounted for 20% of brood weight variability as its sole predictor, which was not much improved by plot-level random effects. Total worker weight was strongly driven by the number of workers, though the variation in individual bee weights still had more than a third of the standardized effect size of worker numbers. Together, these variables accounted for 89% of colony weight variability.

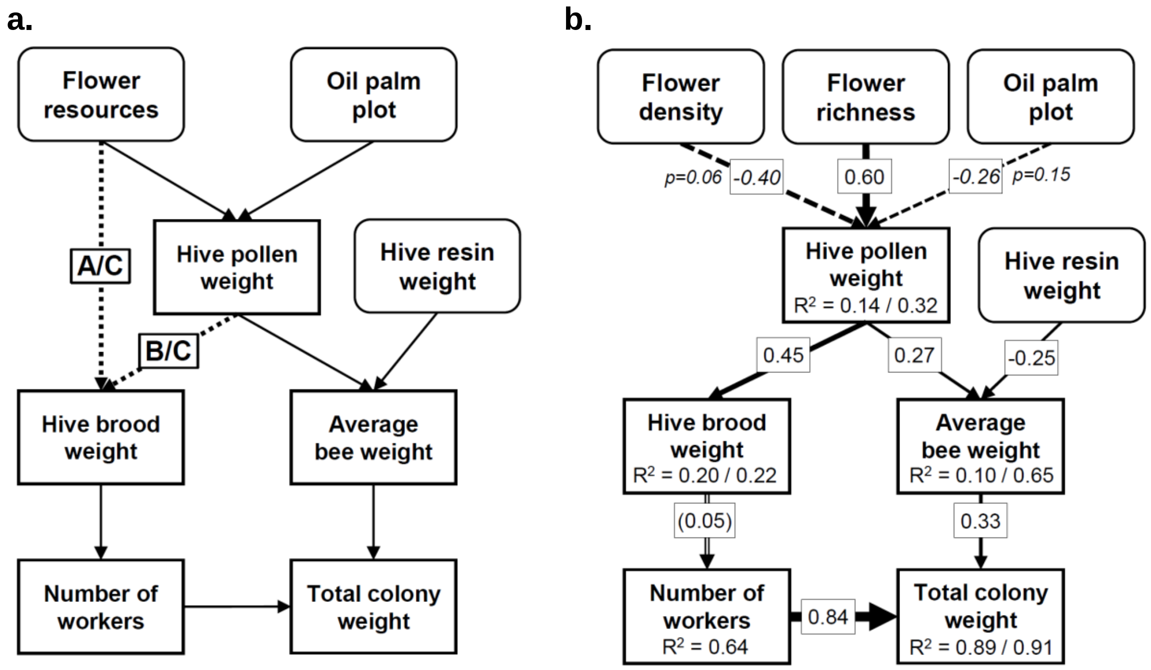

Figure 4-6. Hypothesized (a) and final (b) structural equation models of hive and colony variable relationships. Square boxes represent an exogenous model variable whose drivers are modeled in the SEM. Round boxes are exogenous variables that are not modeled. In (a), dotted arrows represent the alternative hypotheses tested. All dotted arrows with the same capital letter (A, B, or C) were included together in a hypothesis. In (b), arrow widths correspond to standardized effect size, which is also given in the associated box. Dashed arrows represent relationships that were not significant at α=0.05, with the associated *p*-value given. For mixed effects models, the marginal and conditional R^2 values are given. Note that the link between hive brood weight and worker numbers represents the untransformed coefficient of a negative binomial generalized linear model and is not directly comparable to other effects.

4.4. Discussion

In this landscape-scale field experiment, we investigated the effects of natural habitat intensification on colonies of a tropical stingless bee species (*Tetragonula laeviceps*). We used site selection to manipulate local land use and the landscape amount of habitat (forest and shrub cover) around hives. We found that colonies in forest and rubber plots had lower mortality and gained more in size over the study. Hives in oil palm and shrub plots had high mortality and did not significantly gain in size. The effects of land use type and amount of landscape habitat explained significant forager activity and changed (interacted) with time. Though there were not universal forager activity patterns with plot land use and landscape habitat, the effect of landscape habitat tended to be negative in later months, predicting lower activity in plots with greater amounts of natural habitat in the landscape. We also found a similar pattern predicting greater gains in hive size with less landscape habitat in November. Larger colonies consistently predicted more of all types of foraging activity, while greater proportion of hive resin predicted less resin foraging. Our final structural equation model indicates that floral richness directly influenced pollen amount in the hives, which in turn drove brood weight and bee size and eventually total colony weight. Hive resin also had a negative relationship with bee weight.

4.4.1. Effects of land use intensification

We hypothesized that more intensified (i.e. less natural) land uses at the local and landscape scale would have a detrimental effect on colony foraging activity, hive growth, and survival. As we expected, colonies performed well in their natural forest habitat, as these hives had low mortality and grew the most at the end of the study. Forests are the natural habitat of stingless bees (Roubik 2006), including *T. laeviceps* (Inoue et al. 1984). Although we observed higher plot-level means of floral richness and density than forest in oil palm and shrub plots respectively, we estimated the highest coverage-standardized species richness for forest overall. Stingless bees are fitter and reproduce more in florally diverse environments (Kaluza et al. 2018) and attempt to maximize their resource collection diversity (Kaluza et al. 2017). As we mainly focused on flowering vegetation within 10 m of hives, a survey of forest floral resources at a larger patch scale and in the canopy may have better reflected the local resources available to bees.

Oil palm and shrub plot hives had higher mortality rates and grew less over the study period. This may have been partly due to higher temperatures, which significantly increased mortality risk in the survival analysis. Land use intensification has been found to alter microclimate (Drescher et al. 2016), which our results affirm. Small species of stingless bees especially require a suitable range of ambient temperature for survival (Pereboom and Biesmeijer 2003). High temperatures can harm stingless bees through overheating, damage brood, and cause the colony to dedicate more energy to active thermal regulation responses such as fanning (Vollet-Neto et al. 2015). Furthermore, Sakagami (1983) observed that *T. laeviceps* may have limited thermoregulatory capacity. As *T. laeviceps* may be more reliant on passive thermal regulation strategies such as nest site selection and orientation (Jones and Oldroyd 2006), land conversion could further drive habitat loss and colony mortality through increasing more open, hotter land use types such as shrubland (Drescher et al. 2016).

Our results suggest that, in addition to reducing biodiversity through conversion to monocultures, another aspect of intensification that impacts *T. laeviceps* may be the creation of more exposed environments, which is exemplified by the shrub and oil palm land uses. In terms of habitat loss, rubber and oil palm plantations are sometimes considered similarly, as they are monocultural high-impact land uses with lower biodiversity (Clough et al. 2016, Rembold et al. 2017b). However, oil palm colonies had much higher rates of mortality and lower hive size than rubber plantation colonies even though oil palm had higher plot-level floral richness and similar mean midday temperatures. The difference may have been oil palm's higher level of exposure and simpler vegetation structure (Fitzherbert et al. 2008, Zemp et al. 2019), which it shared with shrubland, and which can affect Hymenopteran species (Loyola and Martins 2008). This could have contributed to and exacerbated the effects of high temperature in these plots. Similar to gradients of shade in coffee polyculture systems (Moguel and Toledo 1999), decreasing vegetation structural complexity from forest through rubber plantation, oil palm, and shrub may represent a decreasing gradient of nest habitat suitability for *T. laevicipes* and other social pollinators that warrants further investigation.

4.4.2. Landscape and temporal effects

We also hypothesized that bees might benefit more from natural habitat in the landscape if the local land use of the hive was more intensified. Our analysis of forager activity found some support for this interaction, as increased landscape habitat was associated with higher forager activity for shrub and oil palm plots in August. Greater amounts of natural and seminatural habitats can promote bumblebee (*Bombus terrestris* L) colony growth in temperate farmland (Bukovinszky et al. 2017) and has been shown in many studies to promote bee abundance and richness (Klein et al. 2003a, Ricketts et al. 2008, Brosi 2009, Kennedy et al. 2013).

However, patterns with landscape habitat appeared to change over time. In the latter two months of the study, more landscape habitat was associated with less foraging activity in rubber and shrub plots. Similarly, more landscape habitat was also associated with less overall hive growth at the end of the study. This latter pattern was the most apparent for forest and rubber plantation plots, as hives with less landscape habitat in these land uses increased significantly in volume over their initial size by the end of the study.

Changes in floral resource availability could explain some of the temporal variability we observed in the effect of landscape habitat. Flowering can be associated with increased rainfall in the tropics (Bawa et al. 2003, Boulter et al. 2006). In Jambi, one of the rainy periods typically peaks in December (Drescher et al. 2016), though in 2018 we already observed increased rain in October. By comparing flower surveys before and after the study period (August and January), we found evidence for an increase in floral density in shrub and oil palm land uses, but no strong patterns in forest or rubber plots. The amount of shrub and oil palm land cover within the hive landscape may have thus become more important during the second half of the study. We did not include oil palm in the landscape habitat metric of our original study design, but together with other agriculture types, oil palm comprises about 55% of the non-forested area in Jambi (Grass et al. 2020). Mass-flowering crops around hives can provide a temporary increase in floral resources in temperate (Holzschuh et al. 2013, Bänsch et al. 2020) and tropical (Fisher et al. 2017) systems. Stingless bees in Southeast Asia also increase resource collection during supra-annual “general flowering” events in which many plant species flower simultaneously over a large region (Eltz et al. 2001, Nagamitsu and Inoue 2002). However, further research is needed to determine whether a similar smaller-scale effect also occurs with flowering changes in open land uses due to seasonal factors, and whether this in turn counterbalances the landscape effects of forest cover.

4.4.3. Colony and hive response to exogenous conditions

Behavioral responses to environmental and landscape conditions are important to bee reproduction and survival in variable transformation landscapes. We found that hive pollen weight was significantly associated with increased flower richness in the plot. This effect may have been masked in our other analyses by stronger contrasts between months or land use categories, which were removed or diminished in our SEM analysis subset of surviving November hives. Our SEM results demonstrate that floral diversity indirectly increased the colony size at the end of the study, through the amount of collected pollen in the hive. This corroborates other stingless bee experiments, which find that higher floral diversity increases stingless bee fitness, while overall abundance appears to be less important (Kaluza et al. 2018, Trinkl et al. 2020).

A distinguishing behavior of stingless bees is mass provisioning, wherein workers fill brood cells with enough food for the complete development of the larva (Roubik 2006). This contrasts with *Apis* species, which must feed brood daily and are therefore directly impacted by restrictions in pollen supply (Biesmeijer et al. 1999). In our SEM results we found that exogenous habitat variables most directly affected the weight of stored pollen, which mediated effects on colony size through influencing individual bee weights and the amount of brood. Biesmeijer et al. (1999) found that mass provisioning allowed stingless bee colonies to react conservatively under pollen stress. As existing brood is not affected by low pollen conditions, colonies can reduce the allocated number of pollen foragers to minimize the risk of forager loss until foraging conditions improve. This may partly explain why larger hives had significantly lower colony mortality risk. Larger hives may not only reflect healthier colonies and larger pollen and honey stores, they may also have more brood, which ensures the continued reproduction of colony workers in the short term, regardless of current resource conditions.

We found that less resin in hives predicted higher resin foraging, while more resin correlated significantly with smaller bees. Resin plays an important role in nest construction and defense against predators, parasites, and pathogens (Roubik 2006). Terpene compounds in fresh resin may contribute to hive defense (Junker and Blüthgen 2008) as well as chemical defense on bee bodies (Lehmberg et al. 2008), especially against ants (Leonhardt and Blüthgen 2009). Increased hive resin may therefore be the result of stressors to the colony and hive. As resin collection can also come at a cost to food intake (Leonhardt and Blüthgen 2009), it may be indicative of past trade-offs between bee health and colony defense. Resin availability may be affected by landscape intensification, as stingless bees only collect from certain trees (Leonhardt and Blüthgen 2009); however, our results do not indicate clear land use or landscape effects. We also found that the cumulative volume of pollen and honey stores did not predict pollen foraging, although we note our analysis did not relate pollen foraging directly to pollen stores because we could not separately count pollen and honey pots in the field.

Nevertheless, though colonies may allocate more pollen foragers when pollen stores are low, this response may also be influenced by the perceived availability of pollen in the environment (Biesmeijer et al. 1998, 1999).

4.4.4. Trade-offs in transforming landscapes

Heterogeneous landscapes resulting from rainforest transformation present *T. laeviceps* and other tropical social bees with critical trade-offs that merit further research. Open habitats such as oil palm and shrubland have higher disturbance and light availability, which may increase their floral resource value in the landscape. On the other hand, as nesting sites, these environments have increased risk of colony mortality due to higher temperature and increased exposure. More research would help us understand how stingless bees may balance this trade-off to adapt to transformation landscapes. Furthermore, it is unknown how the predominantly non-native flowering community in open and intensified land uses affect stingless bee resource collection or nutrition. In general, little is known about the effects of exotic floral resources on wild bees. In a temperate system in Northern California, USA, wild bees appear to favor native species (Morandin and Kremen 2013) and in subtropical South Africa, more intensified land use and exotic floral abundance both decreased interactions between native plants and their pollinators (Grass et al. 2013).

On the other hand, although rubber plantations had lower floral richness and higher temperatures, hives performed comparably to forest. Rubber cultivation in Jambi has traditionally existed on a gradient of intensification from diversified “jungle rubber”, which is similar to forest, to monocultural plantations; however, in recent years most jungle rubber has been converted to either the more profitable monocultural form or oil palm (Clough et al. 2016). Rubber plantations, and more so jungle rubber, share a number of vegetation structure characteristics with forest, such as higher tree and understory density (Rembold et al. 2017a). Our own plots were rubber monocultures at the canopy layer, though they had varying degrees of sapling growth in the understory. Identifying the habitat characteristics that enable *T. laeviceps* to survive and grow in rubber plantations could help inform pollinator conservation practices in intensified landscapes.

4.5. Conclusions

Like many regions of the tropics, the forest cover of Jambi province, Sumatra, Indonesia, has decreased dramatically (Laumonier et al. 2010). Forest has primarily been replaced with monocultural rubber and oil palm plantations, as well as fallow shrubland (Drescher et al. 2016). Though the succeeding intensified land uses are more profitable for small holders, they come at a cost to biodiversity and ecosystem services (Clough et al. 2016, Grass et al. 2020). Understanding how key groups such as stingless bees respond to altered landscapes is important for planning diversified, ecologically functional alternative landscapes that also serve human needs (Grass et al. 2019, Perfecto et al. 2019). From our multiscale crossed study design, we found that oil palm and shrubland were poor habitats at the local level but might provide more floral resources at the landscape scale. On the other hand, colonies in rubber plantations performed comparably to colonies in natural forest habitat, despite land use intensification. Colonies also exhibited responses to local floral richness and internal hive conditions that demonstrated other aspects of colony and environment interlinkages. Further investigation of the mechanisms behind these relationships can help us understand the habitat and resource landscape of stingless bees and promote healthy ecosystem functioning in a transforming region.

Authors' contributions

KL, TT, and IG conceived of the study. KL and RR set up the experiment and SoS conducted fieldwork and lab work. KL and SoS conducted analysis and prepared the manuscript.

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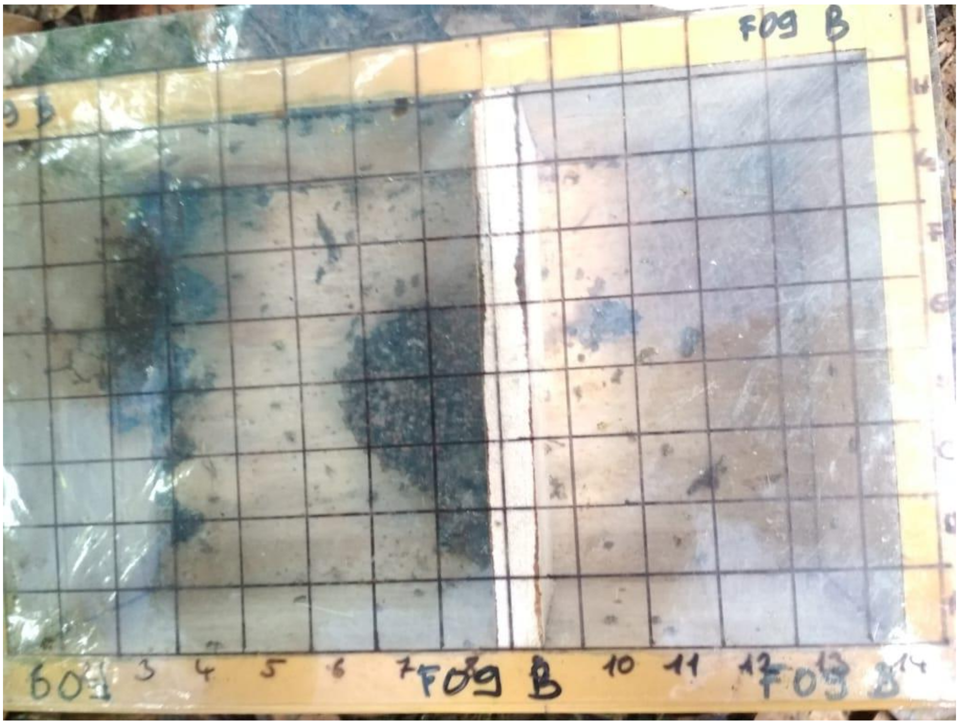
4.6. Supporting Information

Appendix A

Appendix Figure 4-1. Hive shelter setup. Shelter raised hives off the ground by approximately 1 m. A temperature logger was fixed under the roof above the middle hive. Shelters were oriented east where site conditions allowed.



Appendix Figure 4-2. Opened hive box with measuring grid placed on top of hive window for estimating hive volume.

Appendix B

1. Landscape habitat

Appendix Table 4-1. Model terms for linear model of landscape habitat by plot land use at the start of the study, followed by pairwise comparisons with Tukey's post-hoc tests.

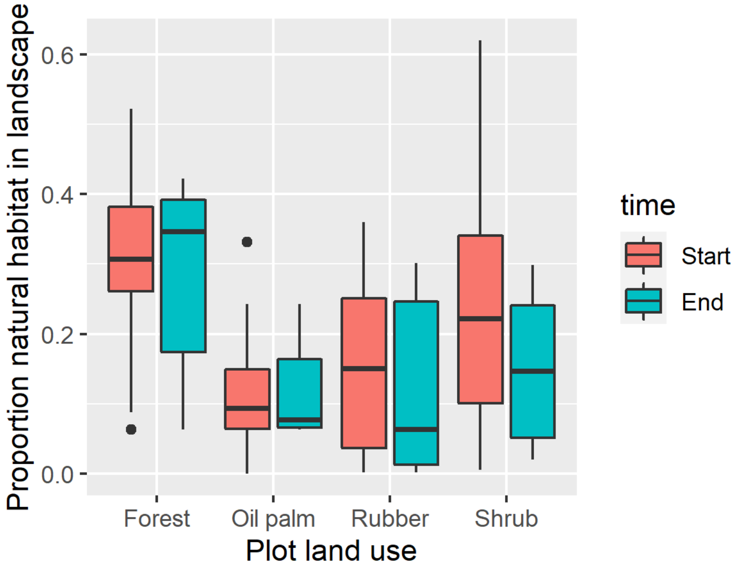
	Landscape habitat		
Predictors	*Estimates*	*95% CI*	*p*
(Intercept)	0.30	0.20 – 0.39	**<0.001**
type [Oil palm]	-0.18	-0.32 – -0.04	**0.010**
type [Rubber]	-0.14	-0.28 – -0.01	**0.041**
type [Shrub]	-0.05	-0.19 – 0.09	0.462
Observations	40		
R^2 / R^2 adjusted	0.204 / 0.137		

```
contrast          estimate     SE df t.ratio p.value
 Forest - Oil palm   0.1803 0.0668 36  2.700  0.0492
 Forest - Rubber     0.1417 0.0668 36  2.122  0.1655
 Forest - Shrub      0.0496 0.0668 36  0.743  0.8790
 Oil palm - Rubber  -0.0386 0.0668 36 -0.578  0.9381
 Oil palm - Shrub   -0.1306 0.0668 36 -1.957  0.2232
 Rubber - Shrub     -0.0921 0.0668 36 -1.379  0.5203

P value adjustment: tukey method for comparing a family of 4 estimates
```

Appendix Table 4-2. Model terms for linear model of landscape habitat by plot land use at the end of the study, followed by pairwise comparisons with Tukey's post-hoc tests.

	Landscape habitat		
Predictors	*Estimates*	*95% CI*	*p*
(Intercept)	0.27	0.19 – 0.36	**<0.001**
type [Oil palm]	-0.18	-0.32 – -0.04	**0.014**
type [Rubber]	-0.14	-0.26 – -0.02	**0.029**
type [Shrub]	-0.10	-0.25 – 0.05	0.187
Observations	25		
R^2 / R^2 adjusted	0.297 / 0.196		

```
contrast          estimate     SE df t.ratio p.value
 Forest - Oil palm   0.1776 0.0665 21  2.670  0.0636
 Forest - Rubber     0.1371 0.0583 21  2.350  0.1184
 Forest - Shrub      0.0974 0.0715 21  1.363  0.5350
 Oil palm - Rubber  -0.0405 0.0665 21 -0.608  0.9283
 Oil palm - Shrub   -0.0802 0.0783 21 -1.024  0.7373
 Rubber - Shrub     -0.0397 0.0715 21 -0.556  0.9439

P value adjustment: tukey method for comparing a family of 4 estimates
```



Appendix Figure 4-3. Comparison of proportion habitat in the landscape between plot land use types at the beginning and end of the study

2. Comparison of plot floral richness

Appendix Table 4-3. Model terms for linear model of estimated flower richness by plot land use, followed by pairwise comparisons with Tukey's post-hoc tests

	Species richness		
Predictors	*Estimates*	*95% CI*	*p*
(Intercept)	4.71	1.60 – 7.81	**0.004**
type [Oil palm]	7.24	2.85 – 11.63	**0.002**
type [Rubber]	-0.14	-4.42 – 4.14	0.948
type [Shrub]	2.16	-2.23 – 6.55	0.324
Observations	37		
R^2 / R^2 adjusted	0.321 / 0.259		

```
contrast            estimate   SE df t.ratio p.value
 Forest - Oil palm    -7.238 2.16 33 -3.353  0.0104
 Forest - Rubber       0.137 2.10 33  0.065  0.9999
 Forest - Shrub       -2.161 2.16 33 -1.001  0.7497
 Oil palm - Rubber     7.375 2.10 33  3.505  0.0070
 Oil palm - Shrub      5.076 2.16 33  2.352  0.1069
 Rubber - Shrub       -2.298 2.10 33 -1.093  0.6965

P value adjustment: tukey method for comparing a family of 4 estimates
```

3. Comparison of plot floral density

Appendix Table 4-4. Model terms for gamma-link generalized linear model of flower density by plot land use, followed by pairwise comparisons with Tukey's post-hoc tests.

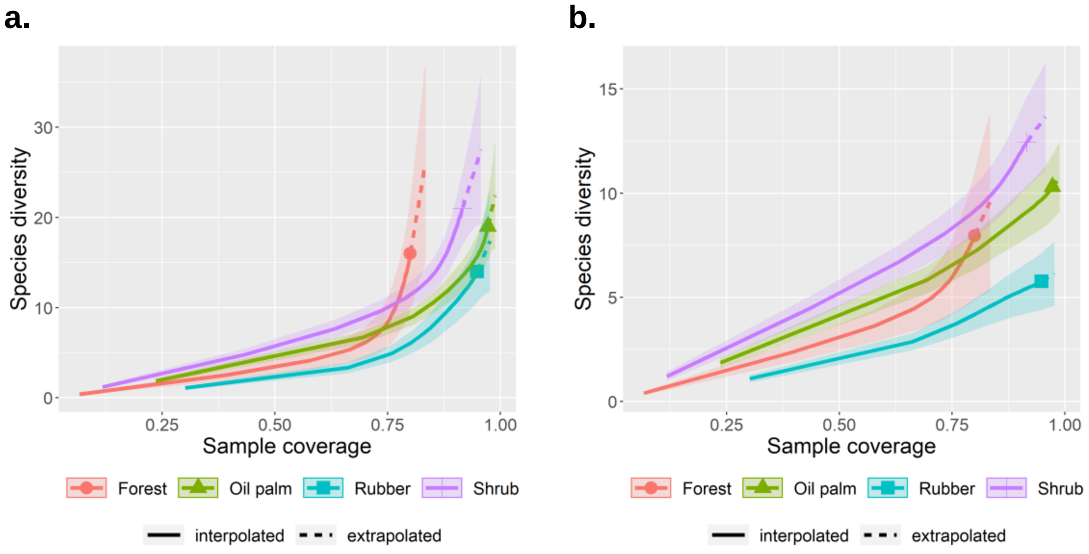
	Floral density		
Predictors	*Estimates*	*95% CI*	*p*
(Intercept)	0.79	0.39 – 1.93	0.551
type [Oil palm]	1.28	0.41 – 3.97	0.669
type [Rubber]	0.79	0.26 – 2.37	0.676
type [Shrub]	5.56	1.79 – 17.32	**0.005**
Observations	37		
R^2 / R^2 adjusted	0.544		

```
contrast           ratio     SE  df z.ratio p.value
 Forest / Oil palm 0.784 0.4430 Inf -0.431  0.9732
 Forest / Rubber   1.261 0.6948 Inf  0.422  0.9748
 Forest / Shrub    0.180 0.1016 Inf -3.036  0.0128
 Oil palm / Rubber 1.609 0.8862 Inf  0.864  0.8237
 Oil palm / Shrub  0.229 0.1296 Inf -2.605  0.0454
 Rubber / Shrub    0.143 0.0785 Inf -3.537  0.0023

P value adjustment: tukey method for comparing a family of 4 estimates
Tests are performed on the log scale
```

4. Sampling coverage-based richness

Appendix Table 4-5. Coverage-standardized richness and effective species (exponentiated Shannon diversity) estimated across land use group, at a coverage of 80%.

Land use	*n*	*Observed overall richness*	*Coverage-standardized richness (95% C.I.)*	*Coverage-std. effective species (95% C.I.)*
Forest	140	16	16 (10.3, 21.7)	8 (4.9, 11)
Shrub	96	21	11.3 (9.7, 12.9)	9.1 (7.7, 10.5)
Rubber	88	14	6.1 (5.0, 7.3)	4.2 (3.4, 5)
Oil palm	88	19	9.0 (8.0, 10.1)	7.3 (6.4, 8.1)



Appendix Figure 4-4. Estimated (a) species richness based on sample coverage and (b) Shannon effective species richness based on sample coverage.

5. Seasonal floral resource differences

Appendix Table 4-6. We performed 10,000 resamplings of the plot-level differences in flower abundance and richness between August and January flower surveys (n=37). The differences that were bootstrapped were calculated from the aggregation of the survey quadrats described in the methods, which were taken at cardinal directions 10 m from each hive shelter. Bootstrapped means by land use and associated confidence intervals, standard error, and p-value were estimated with a linear model fit over each resampling.

Flower metric	*Land use*	*Mean*	*95% CI*	*Standard error*	*p*
Abundance (flower units/25 m^2)	Forest	-3.78	(-8.67, -0.22)	2.32	0.102
	Oil palm	125.17	(-1.44, 284.23)	72.63	0.085
	Rubber	-20.53	(-73.4, 40)	28.89	0.477
	Shrub	780.96	(148.77, 1574.17)	373.46	0.037
Richness (species)	Forest	-0.45	(-0.89, -0.11)	0.23	0.049
	Oil palm	0.77	(-1.33, 2.78)	1.05	0.463
	Rubber	0.10	(-0.4, 0.6)	0.26	0.702
	Shrub	0.25	(-1.89, 2.44)	1.13	0.823

6. Temperature

Appendix Table 4-7. Model terms for linear model of midday temperature by plot land use, followed by pairwise comparisons with Tukey's post-hoc tests.

		Temperature	
Predictors	*Estimates*	*95% CI*	*p*
(Intercept)	30.21	30.00 – 30.42	<**0.001**
type [Oil palm]	2.21	1.87 – 2.55	<**0.001**
type [Rubber]	2.51	2.21 – 2.80	<**0.001**
type [Shrub]	3.02	2.68 – 3.37	<**0.001**
Observations	2695		
R^2 / R^2 adjusted	0.134 / 0.133		

```
contrast           estimate    SE   df t.ratio p.value
 Forest - Oil palm   -2.212 0.172 2691 -12.865 <.0001
 Forest - Rubber     -2.505 0.152 2691 -16.443 <.0001
 Forest - Shrub      -3.025 0.174 2691 -17.383 <.0001
 Oil palm - Rubber   -0.293 0.174 2691  -1.691 0.3285
 Oil palm - Shrub    -0.813 0.193 2691  -4.216 0.0002
 Rubber - Shrub      -0.519 0.176 2691  -2.959 0.0164

P value adjustment: tukey method for comparing a family of 4 estimates
```

Appendix C

Appendix Table 4-8. Flower species list and prevalence among sampling plots. * indicates a species is non-native or alien to Sumatra (Rembold et al. 2017).

Species	Forest	Shrub	Rubber	Oil palm
*Ageratum conyzoides**	-	0.40	0.20	0.80
*Asystasia gangetica**	-	0.30	0.50	0.80
*Centrosema pubescens**	-	-	0.10	-
*Chromolaena odorata**	-	0.10	-	-
*Cleome rutidosperma**	-	-	-	0.20
Clerodendrum paniculatum	0.11	-	-	-
*Clibadium surinamense**	-	0.60	0.30	0.20
*Clidemia hirta**	0.33	0.60	0.90	0.90
Cratoxylum cf. formosum	-	0.10	-	-
Cyanthillum cinereum	-	-	-	0.10
Globba pendula	0.11	-	-	-
*Hevea brasiliensis**	-	-	0.10	-
Hibiscus macrophyllum	-	0.10	-	-
*Hyptis capitate**	-	0.40	0.40	0.80
*Lantana camara**	-	0.40	0.10	0.20
*Lindernia diffusa**	-	-	-	0.10
Maesa ramentacea	-	0.10	-	-
Melastoma malabathricum	-	0.60	0.30	0.30
*Mikania micrantha**	-	0.30	-	0.10
Mussaenda frondosa	-	0.10	-	-
*Oxalis barrelieri**	-	-	-	0.10
*Passiflora foetida**	-	0.10	-	-
*Polygala paniculate**	-	-	-	0.50
Rolandra fructiosa	-	-	-	0.10
*Solanum jamaicense**	-	0.10	0.10	-
*Spermacoce alata**	-	0.10	-	0.60
*Spermacoce cf. ocymifolia**	-	0.10	0.10	0.20
*Stachytarpheta indica**	-	0.30	-	0.30
*Synedrella nodiflora**	-	-	-	0.30
Tabernaemontana pauciflora	-	-	0.10	-
Urena lobata	-	-	0.10	-
Urophyllum cf. arboreum	0.11	0.10	-	-
Unidentified Asteraceae sp. 1	-	0.10	-	-
Unidentified Fabaceae sp. 1	-	-	-	0.10
Unidentified Fabaceae sp. 2	0.11	-	-	-
Unidentified Malvaceae sp. 1	-	0.10	-	-
Unidentified sp. 01	-	-	0.10	-
Unidentified sp. 02	0.22	-	-	-
Unidentified sp. 03	0.22	-	-	-
Unidentified sp. 04	0.11	-	-	-
Unidentified sp. 05	0.11	-	-	-
Unidentified sp. 06	0.11	-	-	-
Unidentified sp. 07	0.11	-	-	-
Unidentified sp. 08	0.11	-	-	-
Unidentified sp. 09	0.11	-	-	-
Unidentified sp. 10	0.56	-	-	-
Unidentified sp. 11	0.11	-	-	-
Unidentified sp. 12	0.11	-	-	-

Appendix D

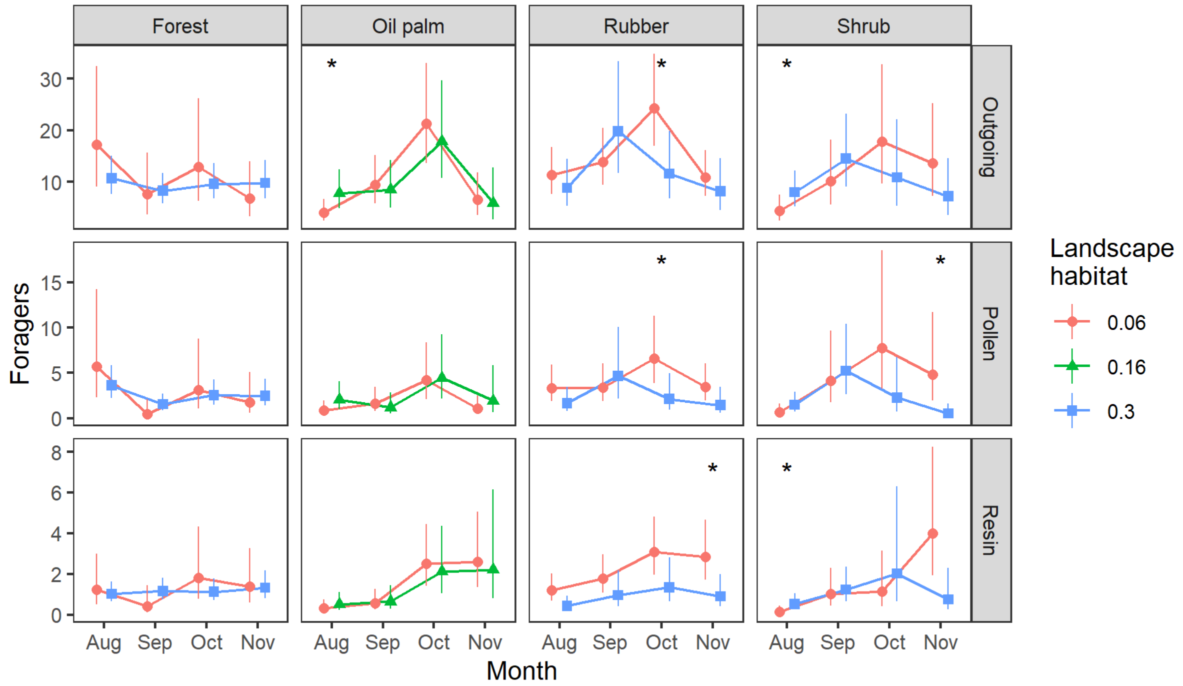
Appendix Table 4-9. Estimated coefficients for generalized linear mixed models of outgoing foragers, returning pollen foragers, and returning resin foragers. Models had a negative binomial link and random effects of hive identity nested within plot. Incidence rate ratios (IRR) are the exponentiated coefficients of the negative binomial model and represent the multiplicative increase in rate, i.e. number of foragers observed within a 5-minute survey. Variables were mean-centered and standardized by two standard deviations. Interacting effects of plot land use, landscape habitat, and month are shown in **Appendix Figure 4-5** in original data scale.

	Outgoing foragers			**Pollen foragers**			**Resin foragers**		
Predictors	*Log-Mean*	*95% CI*	*p*	*Log-Mean*	*95% CI*	*p*	*Log-Mean*	*95% CI*	*p*
(Intercept)	2.59	2.18 – 3.00	<**0.001**	1.50	0.93 – 2.08	<**0.001**	0.12	-0.43 – 0.68	0.659
Total hive volume	0.66	0.49 – 0.83	<**0.001**	0.91	0.68 – 1.14	<**0.001**	0.80	0.59 – 1.02	<**0.001**
Month [Sep]	-0.52	-0.89 – -0.16	**0.005**	-1.67	-2.43 – -0.91	<**0.001**	-0.46	-1.18 – 0.26	0.212
Month [Oct]	-0.20	-0.56 – 0.17	0.290	-0.48	-0.96 – 0.00	0.051	0.23	-0.32 – 0.78	0.405
Month [Nov]	-0.49	-0.88 – -0.10	**0.014**	-0.77	-1.33 – -0.22	**0.006**	0.19	-0.39 – 0.76	0.525
Land use [Oil palm]	-0.37	-1.02 – 0.29	0.273	-0.59	-1.54 – 0.36	0.222	-0.69	-1.69 – 0.31	0.178
Land use [Rubber]	-0.30	-0.77 – 0.17	0.211	-0.67	-1.34 – -0.00	**0.050**	-0.46	-1.15 – 0.22	0.187
Land use [Shrub]	-0.81	-1.37 – -0.25	**0.005**	-1.53	-2.41 – -0.65	**0.001**	-1.41	-2.41 – -0.41	**0.006**
Landscape habitat	-0.53	-1.23 – 0.16	0.134	-0.53	-1.52 – 0.47	0.301	-0.24	-1.20 – 0.72	0.622
Floral density	-0.10	-0.36 – 0.16	0.457	-0.12	-0.53 – 0.29	0.574	0.00	-0.37 – 0.38	0.982
Flora richness	0.29	-0.07 – 0.65	0.109	0.14	-0.41 – 0.70	0.607	-0.07	-0.53 – 0.40	0.778
Month [Sep] * Land use [Oil palm]	0.43	-0.19 – 1.05	0.172	0.85	-0.27 – 1.97	0.136	0.60	-0.66 – 1.86	0.348
Month [Oct] * Land use [Oil palm]	0.83	0.25 – 1.41	**0.005**	1.08	0.30 – 1.87	**0.007**	1.02	-0.05 – 2.10	0.062
Month [Nov] * Land use [Oil palm]	0.04	-0.90 – 0.98	0.939	0.67	-0.68 – 2.02	0.333	1.11	-0.34 – 2.56	0.134
Month [Sep] * Land use [Rubber]	1.04	0.57 – 1.51	<**0.001**	2.21	1.34 – 3.08	<**0.001**	1.07	0.15 – 1.98	**0.022**
Month [Oct] * Land use [Rubber]	0.70	0.23 – 1.17	**0.003**	0.94	0.26 – 1.61	**0.006**	0.81	0.04 – 1.58	**0.040**
Month [Nov] * Land use [Rubber]	0.43	-0.08 – 0.93	0.096	0.72	-0.01 – 1.44	0.052	0.61	-0.17 – 1.39	0.125
Month [Sep] * Land use [Shrub]	1.23	0.66 – 1.81	<**0.001**	3.23	2.22 – 4.24	<**0.001**	1.86	0.68 – 3.04	**0.002**
Month [Oct] * Land use [Shrub]	1.03	0.44 – 1.61	**0.001**	1.91	1.03 – 2.79	<**0.001**	1.48	0.36 – 2.60	**0.009**
Month [Nov] * Land use [Shrub]	0.98	0.39 – 1.57	**0.001**	1.23	0.31 – 2.15	**0.009**	1.63	0.52 – 2.74	**0.004**
Month [Sep] * Landscape habitat	0.64	-0.06 – 1.34	0.073	1.95	0.55 – 3.34	**0.006**	1.39	0.09 – 2.70	**0.037**
Month [Oct] * Landscape habitat	0.20	-0.47 – 0.88	0.557	0.30	-0.66 – 1.27	0.540	-0.33	-1.37 – 0.70	0.529
Month [Nov] * Landscape habitat	0.95	0.28 – 1.62	**0.005**	0.92	-0.02 – 1.86	0.056	0.17	-0.85 – 1.18	0.744
Land use [Oil palm] * Landscape habitat	2.32	0.85 – 3.79	**0.002**	2.81	0.58 – 5.05	**0.014**	1.44	-0.96 – 3.85	0.240
Land use [Rubber] * Landscape habitat	0.24	-0.74 – 1.22	0.633	-0.28	-1.72 – 1.17	0.707	-0.91	-2.31 – 0.49	0.201
Land use [Shrub] * Landscape habitat	1.21	0.35 – 2.08	**0.006**	1.50	0.20 – 2.80	**0.023**	1.78	0.51 – 3.05	**0.006**
(Month [Sep] * Land use [Oil palm]) * Landscape habitat	-2.73	-4.33 – -1.12	**0.001**	-5.13	-8.06 – -2.20	**0.001**	-2.22	-5.42 – 0.98	0.174

	Outgoing foragers			**Pollen foragers**			**Resin foragers**		
Predictors	*Log-Mean*	*95% CI*	*p*	*Log-Mean*	*95% CI*	*p*	*Log-Mean*	*95% CI*	*p*
(Month [Oct] * Land use [Oil palm]) * Landscape habitat	-2.47	-3.86 – -1.08	**<0.001**	-2.44	-4.55 – -0.33	**0.023**	-1.32	-3.93 – 1.29	0.322
(Month [Nov] * Land use [Oil palm]) * Landscape habitat	-3.01	-5.54 – -0.48	**0.020**	-1.57	-5.29 – 2.15	0.408	-1.84	-5.62 – 1.94	0.340
(Month [Sep] * Land use [Rubber]) * Landscape habitat	0.05	-0.91 – 1.02	0.914	-0.79	-2.47 – 0.89	0.359	-0.94	-2.72 – 0.84	0.299
(Month [Oct] * Land use [Rubber]) * Landscape habitat	-0.77	-1.68 – 0.15	0.100	-0.81	-2.18 – 0.56	0.245	0.55	-0.92 – 2.01	0.466
(Month [Nov] * Land use [Rubber]) * Landscape habitat	-0.99	-1.94 – -0.03	**0.043**	-1.13	-2.49 – 0.23	0.104	-0.33	-1.82 – 1.17	0.669
(Month [Sep] * Land use [Shrub]) * Landscape habitat	-0.90	-1.91 – 0.10	0.077	-2.65	-4.45 – -0.86	**0.004**	-2.70	-4.43 – -0.98	**0.002**
(Month [Oct] * Land use [Shrub]) * Landscape habitat	-1.45	-2.75 – -0.15	**0.029**	-2.69	-4.67 – -0.72	**0.007**	-0.55	-2.89 – 1.78	0.641
(Month [Nov] * Land use [Shrub]) * Landscape habitat	-2.35	-3.67 – -1.04	**<0.001**	-4.42	-6.40 – -2.44	**<0.001**	-3.64	-5.64 – -1.63	**<0.001**
Honey-pollen proportion				-0.02	-0.27 – 0.22	0.847			
Resin proportion							-0.44	-0.68 – -0.21	**<0.001**
Random Effects									
σ^2	0.52			0.92			0.98		
τ_{00}	$0.15_{\text{Hive:Plot}}$			$0.19_{\text{Hive:Plot}}$			$0.06_{\text{Hive:Plot}}$		
	0.06_{Plot}			0.18_{Plot}			0.10_{Plot}		
	0.03_{Timefac}			0.07_{Timefac}			0.04_{Timefac}		
ICC	0.32			0.32			0.18		
N	3_{Hive}			3_{Hive}			3_{Hive}		
	37_{Plot}			37_{Plot}			37_{Plot}		
	5_{Timefac}			5_{Timefac}			5_{Timefac}		
Observations	652			652			652		
Marginal R^2 / Conditional R^2	0.261 / 0.496			0.300 / 0.526			0.397 / 0.502		

Appendix Table 4-10. Comparison of estimated marginal trends of landscape habitat over the four months within each land use type for models of outgoing foragers, pollen foragers, and resin foragers. The *p*-values within each land use type was adjusted to account for multiple comparisons using the multivariate t distribution method in the "emmeans" package (Lenth 2019).

	Outgoing foragers					**Pollen foragers**					**Resin foragers**				
Month	*Trend*	*SE*	*df*	*t ratio*	*p*	*Trend*	*SE*	*df*	*t ratio*	*p*	*Trend*	*SE*	*df*	*t ratio*	*p*
Forest															
Aug	-1.96	1.28	613	-1.53	0.34	-1.95	1.81	612	-1.08	0.65	-0.96	1.81	612	-0.53	0.96
Sep	0.36	1.44	613	0.25	1.00	5.27	2.89	612	1.82	0.21	4.08	2.38	612	1.72	0.27
Oct	-1.23	1.39	613	-0.88	0.78	-0.85	2.03	612	-0.42	0.98	-2.01	1.80	612	-1.12	0.66
Nov	1.49	1.36	613	1.09	0.63	1.46	2.01	612	0.73	0.88	0.08	1.78	612	0.05	1.00
Oil palm															
Aug	6.49	2.33	613	2.78	**0.02**	8.23	3.61	612	2.28	0.08	4.50	4.11	612	1.10	0.70
Sep	-1.07	2.47	613	-0.43	0.98	-3.45	4.30	612	-0.80	0.86	0.95	4.11	612	0.23	1.00
Oct	-1.73	2.38	613	-0.73	0.89	0.54	3.45	612	0.16	1.00	-1.05	3.38	612	-0.31	1.00
Nov	-0.98	4.51	613	-0.22	1.00	5.35	6.52	612	0.82	0.85	-1.45	5.97	612	-0.24	1.00
Rubber															
Aug	-1.05	1.19	613	-0.88	0.77	-2.83	1.74	612	-1.63	0.29	-4.29	1.79	612	-2.39	0.06
Sep	1.48	1.28	613	1.16	0.58	1.27	1.84	612	0.69	0.89	-2.57	1.96	612	-1.31	0.51
Oct	-3.08	1.23	613	-2.50	**0.04**	-4.74	1.89	612	-2.51	**0.04**	-3.45	1.69	612	-2.04	0.14
Nov	-1.16	1.36	613	-0.86	0.79	-3.58	1.97	612	-1.81	0.20	-5.08	1.83	612	-2.77	**0.02**
Shrub															
Aug	2.48	0.91	613	2.72	**0.03**	3.58	1.46	612	2.46	0.05	5.54	1.51	612	3.66	**0.00**
Sep	1.51	1.23	613	1.23	0.60	0.88	1.90	612	0.46	0.98	0.90	1.73	612	0.52	0.97
Oct	-2.06	1.92	613	-1.07	0.71	-5.20	2.78	612	-1.87	0.21	1.65	3.44	612	0.48	0.98
Nov	-2.63	1.98	613	-1.33	0.53	-9.30	2.89	612	-3.22	**0.01**	-6.57	2.83	612	-2.33	0.08



Appendix Figure 4-5. Modeled interacting effects of Month (Aug-Nov), land use type (forest, oil palm, rubber, and shrub) and contrasting levels of natural habitat (forest and shrub) in the landscape on outgoing foragers, returning pollen foragers, and returning resin foragers. Forager numbers were estimated at a high and low level of landscape habitat for each land use, with associated 95% confidence interval. Note that proportion of landscape habitat was estimated at 0.30 for all plot land uses except oil palm, which was estimated at 0.16, which was the highest consistent value for this group across the entire study period. Significant landscape hive trends are indicated by (*).

Appendix E

Appendix Table 4-11. Likelihood ratio test comparison between candidate outgoing forager models.

```
Models:
outmod.nb5: outgoing.n ~ total.hvu +  Month + type + pcForShrub + flr.den 
+ flr.rich + (1 | Plot/Hive) + (1 | Timefac)
outmod.nb2: outgoing.n ~ total.hvu +  Month + type * pcForShrub + flr.den 
+ flr.rich + (1 | Plot/Hive) + (1 | Timefac)
outmod.nb4: outgoing.n ~ total.hvu + type +  Month * pcForShrub + flr.den 
+ flr.rich + (1 | Plot/Hive) + (1 | Timefac)
outmod.nb3: outgoing.n ~ total.hvu +  Month * type + pcForShrub + flr.den 
+ flr.rich + (1 | Plot/Hive) + (1 | Timefac)
outmod.nb: outgoing.n ~ total.hvu +  Month * type * pcForShrub + flr.den +
 flr.rich + (1 | Plot/Hive) + (1 | Timefac)

           Df    AIC    BIC  logLik deviance   Chisq Chi Df Pr(>Chisq)    
outmod.nb5 15 4510.5 4577.7 -2240.3   4480.5                              
outmod.nb2 18 4512.3 4592.9 -2238.1   4476.3  4.2647      3    0.23427    
outmod.nb4 18 4484.6 4565.2 -2224.3   4448.6 27.6981      0  < 2.2e-16 ***
outmod.nb3 24 4480.1 4587.6 -2216.1   4432.1 16.4684      6    0.01145 *  
outmod.nb  39 4460.0 4634.8 -2191.0   4382.0 50.0648     15  1.175e-05 ***
```

Appendix Table 4-12. Likelihood ratio test comparison between candidate returning pollen forager models.

```
Models:
polmod.nb5: pollen.n ~ total.hvu +  Month + type + pcForShrub + HP.hvu + f
lr.den + flr.rich + (1 | Plot/Hive) + (1 | Timefac)
polmod.nb2: pollen.n ~ total.hvu +  Month + type * pcForShrub + HP.hvu + f
lr.den + flr.rich + (1 | Plot/Hive) + (1 | Timefac)
polmod.nb4: pollen.n ~ total.hvu + type +  Month * pcForShrub + HP.hvu + f
lr.den + flr.rich + (1 | Plot/Hive) + (1 | Timefac)
polmod.nb3: pollen.n ~ total.hvu +  Month * type + pcForShrub + HP.hvu + f
lr.den + flr.rich + (1 | Plot/Hive) + (1 | Timefac)
polmod.nb: pollen.n ~ total.hvu +  Month * type * pcForShrub + HP.hvu + fl
r.den + flr.rich + (1 | Plot/Hive) + (1 | Timefac)

           Df    AIC    BIC  logLik deviance   Chisq Chi Df Pr(>Chisq)    
polmod.nb4 16 2941.4 3013.1 -1454.7   2909.4                              
polmod.nb5 16 2952.5 3024.2 -1460.3   2920.5  0.0000      0     1.0000    
polmod.nb2 19 2954.6 3039.7 -1458.3   2916.6  3.9159      3     0.2707    
polmod.nb3 25 2935.0 3047.0 -1442.5   2885.0 31.5944      6  1.951e-05 ***
polmod.nb  40 2911.2 3090.4 -1415.6   2831.2 53.8623     15  2.770e-06 ***
```

Appendix Table 4-13. Likelihood ratio test comparison between candidate returning resin forager models.

```
Models:
resmod.nb5: resin.n ~ total.hvu +  Month + type + pcForShrub + Resin.hvu +
 flr.den + flr.rich + (1 | Plot/Hive) + (1 | Timefac)
resmod.nb2: resin.n ~ total.hvu +  Month + type * pcForShrub + Resin.hvu +
 flr.den + flr.rich + (1 | Plot/Hive) + (1 | Timefac)
resmod.nb4: resin.n ~ total.hvu + type +  Month * pcForShrub + Resin.hvu +
 flr.den + flr.rich + (1 | Plot/Hive) + (1 | Timefac)
resmod.nb3: resin.n ~ total.hvu +  Month * type + pcForShrub + Resin.hvu +
 resmod.nb3:     flr.den + flr.rich + (1 | Plot/Hive) + (1 | Timefac)
resmod.nb: resin.n ~ total.hvu +  Month * type * pcForShrub + Resin.hvu + 
flr.den + flr.rich + (1 | Plot/Hive) + (1 | Timefac)

           Df    AIC    BIC  logLik deviance   Chisq Chi Df Pr(>Chisq)    
resmod.nb5 16 2108.4 2180.1 -1038.2   2076.4                              
resmod.nb2 19 2103.0 2188.1 -1032.5   2065.0 11.4395      3  0.0095719 ** 
resmod.nb4 19 2089.9 2175.0 -1025.9   2051.9 13.1232      0  < 2.2e-16 ***
resmod.nb3 25 2097.5 2209.5 -1023.7   2047.5  4.3914      6  0.6238659    
resmod.nb  40 2084.2 2263.3 -1002.1   2004.2 43.3395     15  0.0001394 ***
```

Appendix Table 4-14. Likelihood ratio test comparison between candidate models of net hive volume change.

```
Models:
totaldif.lme2
: total.dif ~  Month + type + pcForShrub + flr.rich + flr.den + (1 | Plot/
Hive)
totaldif.lme5
: total.dif ~ type +  Month * pcForShrub + flr.rich + flr.den + (1 | Plot/
Hive)
totaldif.lme4
: total.dif ~  Month + type * pcForShrub + flr.rich + flr.den + (1 | Plot/
Hive)
totaldif.lme3
: total.dif ~  Month * type + pcForShrub + flr.rich + flr.den + (1 | Plot/
Hive)
totaldif.lme
: total.dif ~ type *  Month * pcForShrub + flr.rich + flr.den + (1 | Plot/
Hive)

              npar    AIC    BIC  logLik deviance   Chisq Df Pr(>Chisq)
totaldif.lme2   12 1982.0 2023.0 -979.02   1958.0
totaldif.lme5   14 1978.9 2026.7 -975.44   1950.9  7.1439  2     0.0281 *
totaldif.lme4   15 1985.7 2036.9 -977.86   1955.7  0.0000  1     1.0000
totaldif.lme3   18 1990.7 2052.1 -977.36   1954.7  1.0024  3     0.8007
totaldif.lme    29 1998.6 2097.5 -970.29   1940.6 14.1357 11     0.2256
```

Appendix Table 4-15. Likelihood ratio test comparison between candidate survival models with and without interaction.

```
T.hivesurv1: event ~ total.hvu + time + type + pcForShrub + flr.den + flr.
rich + mnMidTemp + (1 | Plot/Hive)
T.hivesurv2: event ~ total.hvu + time + type * pcForShrub + flr.den + flr.
rich + mnMidTemp + (1 | Plot/Hive)

            Df    AIC    BIC  logLik deviance  Chisq Chi Df Pr(>Chisq)
T.hivesurv1 12 144.77 188.89 -60.385   120.77
T.hivesurv2 15 143.85 199.00 -56.923   113.85 6.9234      3    0.07438 .
```

Appendix Table 4-16. Likelihood ratio test comparison between candidate models of pollen weight.

```
Models:
polleng.lme: pollen.g ~ pcForShrub + type + flr.den + flr.rich + (1 | Plo
t)
polleng.lme2: pollen.g ~ pcForShrub * type + flr.den + flr.rich + (1 | Plo
t)

             npar    AIC    BIC  logLik deviance Chisq Df Pr(>Chisq)
polleng.lme     9 459.28 478.27 -220.64   441.28
polleng.lme2   12 460.39 485.73 -218.20   436.39  4.88  3     0.1808
```

Appendix Table 4-17. Likelihood ratio test comparison between candidate models of brood weight.

```
Models:
broodg.lme: brood.g ~ pcForShrub + type + flr.den + flr.rich + (1 | Plot)
broodg.lme2: brood.g ~ pcForShrub * type + flr.den + flr.rich + (1 | Plot)

            npar    AIC    BIC  logLik deviance  Chisq Df Pr(>Chisq)
broodg.lme     9 504.85 523.85 -243.42   486.85
broodg.lme2   12 510.37 535.70 -243.18   486.37 0.4797  3     0.9233
```

Appendix Table 4-18. Likelihood ratio test comparison between candidate models of resin weight.

```
resing.lme: honey.g ~ pcForShrub + type + flr.den + flr.rich + mnTemp
resing.lme2: honey.g ~ pcForShrub * type + flr.den + flr.rich + mnTemp

            npar    AIC    BIC  logLik deviance  Chisq Df Pr(>Chisq)
resing.lme     9 473.43 492.43 -227.72   455.43
resing.lme2   12 478.11 503.44 -227.06   454.11 1.3185  3     0.7248
```

Appendix Table 4-19. Likelihood ratio test comparison between candidate models of honey weight.

```
Models:
Model 1: honey.g ~ pcForShrub + type + flr.den + flr.rich + mnTemp
Model 2: honey.g ~ pcForShrub * type + flr.den + flr.rich + mnTemp

  Res.Df    RSS Df Sum of Sq Pr(>Chi)
1     53 237277
2     50 227067  3     10209   0.5225
```

Appendix F

Appendix Table 4-20 (next page). Effects estimates by linear mixed effects models of pollen, brood, honey, and resin weights at the end of the study in November. Estimates are compared to a forest plot baseline and continuous variables have been mean-centered and scaled by two standard deviations. Random effects statistics are given where a mixed model was fit. Otherwise, R^2 and adjusted R^2 are given.

	Pollen weight			Brood weight			Honey weight			Resin weight		
Predictors	*Est.*	*95% C.I.*	*p*	*Est.*	*95% C.I.*	*p*	*Est.*	*95% C.I.*	*p*	*Est.*	*95% C.I.*	*p*
(Intercept)	12.55	6.67 – 18.42	**<0.001**	24.67	17.69 – 31.65	**<0.001**	96.64	61.00 – 132.28	**<0.001**	12.08	5.95 – 18.21	**<0.001**
Land use: Oil palm	-12.85	-24.25 – -1.45	**0.027**	-10.27	-23.90 – 3.35	0.140	-32.98	-102.61 – 36.64	0.346	0.16	-11.80 – 12.12	0.979
Land use: Rubber	-3.77	-11.78 – 4.24	0.356	-6.36	-15.89 – 3.18	0.191	19.00	-29.70 – 67.69	0.438	1.05	-7.32 – 9.42	0.806
Land use: Shrub	-6.30	-15.52 – 2.91	0.180	-3.07	-14.04 – 7.89	0.583	14.39	-41.61 – 70.38	0.609	6.84	-2.80 – 16.48	0.164
Landscape habitat	-4.12	-11.32 – 3.07	0.261	-1.39	-9.80 – 7.01	0.745	-20.55	-63.42 – 22.33	0.341	0.35	-7.08 – 7.77	0.927
Flower density	-8.92	-16.52 – -1.33	**0.021**	-11.82	-20.81 – -2.83	**0.010**	-76.66	-122.55 – -30.77	**0.001**	0.73	-7.19 – 8.64	0.857
Flower richness	13.65	4.78 – 22.53	**0.003**	13.12	2.59 – 23.65	**0.015**	76.34	22.56 – 130.11	**0.006**	-0.08	-9.34 – 9.18	0.987
Random Effects												
σ^2	61.67			168.26						106.60		
τ_{00}	24.85 $_{\text{Plot}}$			3.06 $_{\text{Plot}}$						11.38 $_{\text{Plot}}$		
ICC	0.29			0.02						0.10		
N	25 $_{\text{Plot}}$			25 $_{\text{Plot}}$						25 $_{\text{Plot}}$		
Observations	61			61			61			61		
Marginal R^2 / Conditional R^2	0.213 / 0.439			0.141 / 0.156			0.215 (R^2) / 0.128 (adj. R^2)			0.046 / 0.138		

Appendix G

Appendix Table 4-21. Coefficient estimates from a generalized linear model with a negative binomial link predicting number of workers in a colony. Incidence rate ratios (IRR) are the exponentiated coefficients of the negative binomial model and represent the multiplicative increase in rate, i.e. number of foragers observed within a 5-minute survey. Variables were mean-centered and standardized by two standard deviations.

	Number of workers		
Predictors	*Incidence Rate Ratios*	*95% CI*	*p*
(Intercept)	1194.18	574.71 – 2795.91	<0.001
Land use [Oil palm]	0.72	0.28 – 1.93	0.498
Land use [Rubber]	0.81	0.41 – 1.56	0.521
Land use [Shrub]	0.92	0.43 – 2.02	0.826
Landscape habitat	0.30	0.03 – 2.72	0.261
Floral richness	1.06	0.99 – 1.15	0.081
Floral density	0.81	0.59 – 1.10	0.193
Observations	61		
R^2 Nagelkerke	0.093		

Appendix Table 4-22. Coefficient estimates from a linear model of total colony weight. Variables were mean-centered and standardized by two standard deviations.

	Total colony weight		
Predictors	*Estimates*	*95% CI*	*p*
(Intercept)	4.98	3.19 – 6.76	<0.001
Land use [Oil palm]	-1.86	-5.34 – 1.62	0.296
Land use [Rubber]	-1.22	-3.66 – 1.22	0.327
Land use [Shrub]	-1.18	-3.98 – 1.63	0.411
Landscape habitat	-1.11	-3.25 – 1.04	0.313
Floral richness	3.18	0.49 – 5.88	0.020
Floral density	-2.76	-5.06 – -0.46	0.019
Random Effects			
σ^2	11.00		
$\tau_{00\ \mathrm{Plot}}$	0.20		
ICC	0.02		
N_{Plot}	25		
Observations	61		
Marginal R^2 / Conditional R^2	0.118 / 0.133		

Appendix H

Appendix Table 4-23. PiecewiseSEM final model output

```
Call:
  workers.n ~ brood.g
  bees.g ~ beewt.mg + workers.n
  beewt.mg ~ pollen.g + resin.g
  pollen.g ~ flr.den + flr.rich + oilpalm
  brood.g ~ pollen.g

    AIC      BIC
 77.102   123.271

---
Tests of directed separation:

              Independ.Claim Test.Type      DF Crit.Value P.Value
    pollen.g ~ resin.g + ...      coef 49.7752     1.1685  0.2482
     brood.g ~ resin.g + ...      coef 51.5988     0.7009  0.4865
   workers.n ~ resin.g + ...      coef 52.0000     0.8147  0.4152
      bees.g ~ resin.g + ...      coef 50.8965     0.4976  0.6209
     brood.g ~ flr.den + ...      coef 12.0559    -1.0186  0.3284
    beewt.mg ~ flr.den + ...      coef 22.1728    -0.6613  0.5152
   workers.n ~ flr.den + ...      coef 52.0000     0.5520  0.5809
      bees.g ~ flr.den + ...      coef 19.5810    -0.7110  0.4855
    brood.g ~ flr.rich + ...      coef 13.9026    -0.0641  0.9498
   beewt.mg ~ flr.rich + ...      coef 22.9229    -0.4808  0.6352
  workers.n ~ flr.rich + ...      coef 52.0000     0.6783  0.4976
     bees.g ~ flr.rich + ...      coef 21.3800    -0.3957  0.6963
     brood.g ~ oilpalm + ...      coef 19.9506     0.1188  0.9066
    beewt.mg ~ oilpalm + ...      coef 25.6962    -0.8732  0.3906
   workers.n ~ oilpalm + ...      coef 52.0000     1.1152  0.2648
      bees.g ~ oilpalm + ...      coef 27.1494    -0.6762  0.5046
  workers.n ~ pollen.g + ...      coef 49.0000     1.3915  0.1641
     bees.g ~ pollen.g + ...      coef 47.7795     0.6759  0.5024
    beewt.mg ~ brood.g + ...      coef 41.9864     0.2260  0.8223
      bees.g ~ brood.g + ...      coef 49.9005     1.0501  0.2987
  workers.n ~ beewt.mg + ...      coef 50.0000    -0.5351  0.5926

Global goodness-of-fit:

  Fisher's C = 31.102 with P-value = 0.892 and on 42 degrees of freedom

---
Coefficients:

   Response Predictor Estimate Std.Error      DF Crit.Value P.Value Std.Estimate    

  workers.n   brood.g   0.0510    0.0064 53.0000     7.9385  0.0000            - ***
     bees.g  beewt.mg   1.0096    0.1457 46.2052     6.9290  0.0000        0.328 ***
     bees.g workers.n   0.0039    0.0002 48.7441    19.2038  0.0000       0.8385 ***
   beewt.mg  pollen.g   0.0295    0.0128 45.7589     2.3072  0.0256       0.2683   *
   beewt.mg   resin.g  -0.0349    0.0151 40.6141    -2.3151  0.0257      -0.2479   *
   pollen.g   flr.den  -4.1649    2.0775 18.1210    -2.0048  0.0602      -0.3983    
   pollen.g  flr.rich   1.1521    0.4381 19.2680     2.6299  0.0164       0.6018   *
   pollen.g   oilpalm  -7.2819    4.8312 21.6633    -1.5073  0.1462      -0.2649    
    brood.g  pollen.g   0.6240    0.1722 46.6965     3.6245  0.0007       0.4473 ***

  Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05

---
Individual R-squared:

   Response     method Marginal Conditional
  workers.n nagelkerke     0.64          NA
     bees.g       none     0.89        0.91
   beewt.mg       none     0.10        0.65
   pollen.g       none     0.14        0.32
    brood.g       none     0.20        0.22
```

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Synthesis

Like much of Southeast Asia, the rainforests of Jambi Province, Sumatra, Indonesia have experienced a dramatic scale of forest conversion (Laumonier et al. 2010) to hotter, more open habitats with lower biodiversity and ecosystem function (Drescher et al. 2016, Rembold et al. 2017, Grass et al. 2020). My thesis contributes to understanding the implications of these changes from contrasting perspectives. In three experimental studies, I examined this transformation over different gradients and interfaces. This included measuring oil palm pollination services over a spatial gradient from primary forest; identifying direct and indirect relationships to biodiversity enrichment gradients in oil palm biodiversity restoration; and comparing intensification at the interface between spatial scales. Generally, I expected ecosystem functions and services to benefit from closer proximity to natural forest ecosystems, whether this proximity was spatial, over biodiversity restoration treatments, or across multiple spatial scales.

I examined the interacting effects of scales in landscape transformation by studying the response of *Tetragonula laeviceps*, a native stingless bee, to land use intensification of the bees' local nesting habitat and within their foraging landscape. I found contrasting implications of landscape transformation dependent on spatial scale. Locally, *T. laeviceps* colonies had higher survival and nest growth in suitable habitats types such as forest. Hotter, open habitats such as oil palm and shrubland had high colony mortality and less hive growth, despite supporting higher flower richness. However, colonies may benefit from the floral resources in converted open habitats within their foraging landscape. As shown in other studies (Kaluza et al. 2017, 2018), stingless bees prefer and benefit from diverse floral resources, in our case by increasing pollen stores and supporting more brood and larger bee and colony sizes. Future research may identify the net impact of the contrasting effects of open habitats at different scales and relate them to landscape patterns of pollination function.

Within the tree biodiversity enrichment experiment (EFForTS-BEE, Teuscher et al. 2016), I found that the experimental gradients (planted tree diversity and plot size) led to indirect effects to understory vegetation, herbivores, natural enemies, and pollinators. These functions were often not directly driven by the experimental enrichment treatments. Instead, indirect effects were mediated by light availability and structural complexity, which was controlled by canopy openness and strongly influenced by planted enrichment tree species identity. Within this early stage of restoration, pollinators provided ecosystem services that increased the yield of phytometer chili plants, while there were no apparent disservices from herbivory. However, it is likely that these processes will change as the ecological community responds to decreasing canopy openness with continued tree growth.

Over a spatial gradient from forest in an oil palm plantation, I found evidence of increasing oil palm pollination with forest proximity that was mediated by partially excluding larger flower visitors. Pollination rate was associated with different flower visitor groups under the two experimental conditions in which they could affect yield. However, further research is needed to understand the ecological processes that link these visitors to forest and higher pollination rates. Nevertheless, pollination had a significant effect on oil palm yield, demonstrating the importance of insect pollination services and the positive mediating role of forest.

Overall, the effects of landscape transformation on ecosystem functions and services were not easily simplified into basic gradients. Forest proximity conferred pollination services, but under conditions that excluded some visitors; tree enrichment most directly affected light availability, which was directly and indirectly linked to higher pollination services; and forest conversion to open habitats could potentially be beneficial or detrimental to stingless bee colonies depending on its context. Clearly, the processes that occur in transformation landscapes are more complex, and advancing ecological theory suggests that additional conceptual approaches may be necessary (Vandermeer and Perfecto 2017). However, by comparing my observations against simple linear hypotheses, I hope I have revealed more mechanisms that may spur further research. For example, the influence of species interactions, such as predation, competition, or parasitism, on pollinator populations and behaviors over the spatial gradient from forest may be relevant to oil palm pollination services, and have been shown to be relevant in other agroecological systems, e.g. coffee biocontrol (Vandermeer et al. 2019). Similarly, interactions among understory insect communities with increasing biodiversity and patch size in restoration experiments may also have important effects. Light availability played an important role in open and disturbed habitats, which was in some ways similar to forest gaps (Schnitzer and Carson 2001, Richards and Windsor 2007). Further parallels to this natural phenomenon could be explored, such as characteristic communities and processes, as well as implications to a larger scale, e.g. increases in floral resources and open habitats in the landscape.

The expansion of oil palm cultivation has been a major factor in deforestation (Vijay et al. 2016). However, with over 17 million hectares in Malaysia and Indonesia already occupied by oil palm (Meijaard et al. 2018), conservation advocates stress the importance of promoting biodiversity and ecosystem processes within oil palm plantations (Foster et al. 2011). The importance and prevalence of restoration approaches will likely increase for oil palm and other ecologically simplified land uses with the upcoming “Decade on Ecosystem Restoration” by the United Nations (Gann et al. 2019). The Roundtable on Sustainable Palm Oil has already adopted the high conservation value approach in certification schemes to promote biodiversity (Senior et al. 2015). However, as oil palm is an economically important crop that can bring benefits to local communities (Meijaard et al. 2018, Qaim et al. 2020), consideration must also be given to the human benefit associated with oil palm and carefully balance human and ecological needs (Clough et al. 2016, Grass et al. 2020). As my review and experiment on oil palm pollinators demonstrate, much of the functions and ecosystem services of biodiversity in oil palm remain to be understood, and further benefits may potentially be gained from biodiversity and diversified landscapes, e.g. biocontrol (Nurdiansyah et al. 2016). On a landscape scale, natural habitat can be integrated with diversified and higher production agriculture, incorporating aspects of both “land sparing” and “land sharing”, which may buffer effects of more intensified land uses and provide connected diversified habitats for wildlife (Koh et al. 2009, Grass et al. 2019). The work of this thesis contributes to these goals by providing preliminary groundwork for understanding the effects of landscape transformation on ecosystem functions and services.

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Dissertation topic: Pollinators and Ecosystem Services in an Oil Palm Transformation Landscape

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2010-2015 **University of Michigan, School of Natural Resources & the Environment**
Master of Science in Natural Resources and Environment, Conservation Ecology
Master of Landscape Architecture
Certificate of Graduate Studies in Spatial Analysis
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Master's Thesis: Endogenous and Exogenous Spatial Dynamics of the Keystone Ant *Azteca Sericeasur* in an Intensifying Coffee Agroecosystem

- Committee members: Prof. Ivette Perfecto and Prof. John Vandermeer

2004-2008 **University of North Carolina at Chapel Hill (UNC-CH)**
Bachelor of Science, Biology
Minors: Sustainability, Chinese

- Carolina Scholars Fellow
- Honors Program
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PUBLICATIONS

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Li, K., I. Grass, D.C. Zemp, H. Lorenz, L. Sachsenmaier, F. Nurdiansyah, D. Hölscher, H. Kreft, T. Tscharntke. Trade-offs of ecosystem services and disservices in an oil palm biodiversity enrichment experiment in Sumatra, Indonesia. *In preparation*.

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ORAL AND POSTER PRESENTATIONS AT CONFERENCES

2019 **Li, K.**, I. Grass, J. Fung, F. Nurdiansyah, D. Buchori, T. Tscharntke. Spillover of pollinator diversity and services from forest to oil palm in Jambi, Indonesia. Oral presentation at the International Association for Landscape Ecology (IALE) World Congress

2019 **Li, K.**, A. Power, J. Fisher, A. Evans, A. Iverson. Creating a spatially and temporally-explicit model of floral resources for pollinators in the agricultural landscape of Central New York, USA. Poster presented at the IALE World Congress

2018 **Li, K.,** T. Tscharntke, B. Saintes, D. Buchori, I. Grass. Pollination: A missing link to sustainable oil palm agroecology? Poster, Association for Tropical Biology and Conservation Annual Meeting

2016 **Li, K.**, B. Otero Jimenez**.** Mice in a maze of coffee: How agricultural management and landscape affects the genetic structure of a forest rodent. Poster, IALE US symposium.

2015 **Li, K.**, I. Perfecto, J. Vandermeer. Evidence of endogenous processes in the spatial patterns of an arboreal ant in an intensifying agroecosystem. Oral presentation, Ecological Society of America (ESA) meeting.

2013 **Li, K.**, I. Perfecto, J. Vandermeer. Protecting coffee: Exploring endogenous and exogenous factors behind spatial patterns of biological control processes in an agroecosystem. Poster, ESA meeting.

2013 **Li, K.** I. Perfecto, J. Vandermeer. Arboreal ant response to an agroecological gradient of intensification. Poster, IALE 2013 US annual symposium.

2011 **Li, K.**, H. Wu, S. Chen. Migration of flying fox to recovering Pacific island forest ecosystems. Poster, IALE World Congress.

PROFESSIONAL EXPERIENCE

2017-2020 **Agroecology, University of Göttingen and EFForTS, *Doctoral Researcher* (Göttingen, Germany)**

- Contributed to the "Ecological and Socio-economic Functions of Tropical Lowland Rainforest Transformation Systems" (EFForTS) collaborative research group in Germany and Indonesia

2015-2017 **NC State University, *Post-graduate Researcher* (Raleigh, NC)**

- Modeled lead and arsenic bioaccessibility in soils in collaboration with US Environmental Protection Agency
- Modeled the effects of environmental stressors on fish presence in Pacific coast estuaries in project with US National Oceanic and Administrative Association

Aug. 2016 **Cornell University*, GIS Consultant* (Ithaca, NY)**

- Used GIS to map floral resources in an agricultural landscape to model wild pollinator diversity and pollination ecosystem services

2011-2012, Sum. 2015 **Matthaei Botanical Gardens, *GIS Technician* (Ann Arbor, MI)**

- Used GPS and GIS to assess habitat quality and evaluate invasive species management for threatened species conservation and habitat restoration projects

- Developed smartphone app projects to support management and sharing of Natural Areas GIS data

Sum. 2014 **Cooperative Institute for Limnology & Ecosystems Research, *Intern* (Ann Arbor)**

- Conducted multidimensional scaling analysis of Lake Michigan plankton biodiversity and presented results in symposium

2012-2013 **Nichols Arboretum, *Arboretum Caretaker* (Ann Arbor)**

- Performed grounds maintenance and led ecological restoration workdays of 9-25 participants to remove invasive plants and perform habitat restoration activities

Sum. 2011 **Yellowstone Ecological Research Center, *Research Intern* (Bozeman, MT)**

- Developed research project on snowfall changes and ecosystem impacts in the Northwest US that compared snowfall changes in the region by topographical, ecological, and conservation categories

Fall 2010 **Graham Sustainability Institute, *Student Researcher* (Ann Arbor)**

- Contributed literature research on biodiversity and stormwater management for sustainability planning recommendations in a Campus Integrated Assessment, presented to University regents and president

2009-2010 **Taiwan Forestry Bureau, *Research Field Assistant* (Taipei, Taiwan)**

- Radio-tracked and mapped Formosan flying fox roosts in behavioral study on Turtle Island, Taiwan
- Developed research protocol and wrote manual for continuing assistants

Sum. 2009 **Yellowstone Ecological Research Center, *Field Technician* (Cook City, MT)**

- Conducted radio-tracking of coyotes and contributed over 200 observation hours to 20-year study on coyote ecology in response to fire disturbance and wolf reintroduction
- Hosted activities for two urban youth outreach programs including Project Exploration (Chicago)

Fall 2008 **Institute for the Environment, *Student Researcher* (Chapel Hill, NC)**

- Conducted life cycle analysis on two types of frozen food packaging for a manufacturing company and presented environmental impact and carbon footprint findings in a public seminar (sustainability capstone group project)

Sum. 2007 **Taipei Zoo Conservation Research Center, *Field Technician* (Taipei, Taiwan)**

- Mapped and assessed roosts of Taiwanese tube-nosed bats and horseshoe bats, developed data collection protocol

2007 **UNC Biology Dept., Undergraduate Research Assistant (Chapel Hill)**

- Conducted phonotaxis behavioral observation experiments for neurobiology study on frog mate choice
- Conducted PCR and electrophoresis to identify enzyme expression in frog behavior study

QUALIFICATIONS AND SKILLS

Statistical analysis	• Hierarchical/Mixed effects modeling • Spatial analysis • Structural equation modeling • R statistical software
Geographic information systems	• ESRI ArcGIS software • QGIS
Microsoft Office	• Proficient in Microsoft Word, Excel, and Powerpoint

AWARDS AND FELLOWSHIPS

2015	UM Rackham and SNRE Conference Travel Awards, $1000
2015	Charles Lathrop Pack Foundation Award for Best MS Essay, $500
2015	American Society of Landscape Architects Certificate of Merit, MI Chapter
2014	Jeffrey Lund Forest Ecology Award, $500
2013	UM Rackham Conference Travel Award, $700
2013	NASA-MSU Professional Enhancement Travel Award, $700
2013	Improving MI Access to Geog. Information Networks Paper Competition Finalist
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2012	UM Rackham Thesis Research Award, $1,800
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2011	Doris Duke Conservation Fellowship, $30,000
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2011	UM Rackham International Conference Travel Award (Beijing), $2,100
2010	Clarence and Ruth Roy Bequest Award, $15,000
2008	UNC-CH William D. Weir Fellowship in Asian Studies, $15,000
2004-2008	UNC-CH Carolina Scholars Program, $7,500 annually
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TEACHING

Fall 2013, Winter 2015	**ENVR 309: Explorations in GIS** (Dr. J. Breck)
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SERVICE

Apr. 2013 & 2015	**Bioblitz Biodiversity Survey**, *Organizer and Volunteer* (Detroit, MI)
Mar. 2015	**Teach-in +50**: End the War Against the Planet, *Organizer* (Ann Arbor)
2015	**Landscape Arch. Faculty Search Committee**, *Student Representative* (UM SNRE)
Summer 2010	**Beijing Green Cross**, *Volunteer Intern* (Beijing, China)
Summer 2008	**Friends of Nature**, *Intern* (Beijing)
2005-2008	**UNC-CH Carolina Navigators Program**, *Trained Presenter* (Chapel Hill)

LANGUAGES

English	Native speaker
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French	Intermediate speaking/reading/writing
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Spanish	Basic speaking/reading/writing

Declarations

1. I hereby declare that this Ph.D. dissertation, entitled "Pollinators and Ecosystem Services in an Oil Palm Transformation Landscape" (board of examiners: Prof. Dr. Tscharntke, Prof. Dr. Grass, and Prof. Dr. Wiegand) has not been presented to any other examining body either in its present or a similar form.

Furthermore, I also affirm that I have not applied for a Ph.D. at any other school of higher education.

Göttingen, 06.07.2020

Kevin Li

2. I hereby solemnly declare that this dissertation was undertaken independently and without any unauthorized aid, and that all aid has been appropriately acknowledged.

Göttingen, 06.07.2020

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