Pollinators and Ecosystem Services in an Oil Palm Transformation Landscape

Dissertation
to attain the degree Doctor of Philosophy (Ph. D.)
of the Faculty of Agricultural Sciences
Georg-August-Universität Göttingen

Submitted by

Kevin Li

born on the fourth of January 1986 in Margate, Florida, USA

Göttingen, July 2020

Thesis committee

Professor Dr. Teja Tscharntke, Agroecology, Department of Crop Sciences, University of Göttingen, Germany

Professor Dr. Ingo Grass, Department of Ecology of Tropical Agricultural Systems, University of Hohenheim, Stuttgart, Germany

Professor Dr. Kerstin Wiegand, Department of Ecosystem Modelling, University of Göttingen, Germany

Date of oral examination: 19 August 2020

Submitted 6 July 2020. This version was updated 19 August 2022.

The DOI of this electronic dissertation is doi:10.53846/goediss-9410.

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: the impacts of adjacent forest on pollination services 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 from an adjacent forest border. I found that exclusion of all visitors significantly decreased fruit set compared to other treatments, confirming insect pollination is necessary for adequate yield. Forest proximity had a significant positive effect on fruit set when large visitors were excluded. This effect was not significant for treatments that minimized pollinator contributions, suggesting this trend was not due to abiotic factors. However, insect abundances associated with oil palm inflorescences were not strongly related to distance from forest, and only *E. kamerunicus* had a significant relationship with fruit set. These results could suggest that non-consumptive ecological spillover from forests may influence oil palm pollination, though more experimental work is needed to identify these interactions.

In my **third chapter**, I explore how enriching the oil palm agricultural matrix with up to six tree species played a role in driving insect-mediated ecosystem functions. Within a plantation-scale, long-term oil palm biodiversity enrichment project, I disentangled 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 changes in canopy openness, 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 the fruit production 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 can be affected. These effects are mediated by decreasing canopy openness; however, these relationships may change as enrichment communities continue to 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 pollinating function of stingless bees, understanding how this trade-off translates to landscape and population scales 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. 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

Human activity, enabled by fossil fuels and technology, is accelerating its impact on the global environment, bringing about an unprecedented era of anthropogenic global change (Crutzen 2002). Our environmental impacts have resulted in ecological collapses such as desertification (Kéfi et al. 2007), fisheries collapses (Jackson et al. 2001), insect and pollinator declines (Potts et al. 2010, Hallmann et al. 2017), and 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, because 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 complex issue that affects ecosystems worldwide (Newbold et al. 2015). While conservation and agriculture are often presented as opposing forces, they can find 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 monocultures). Within the following chapters, these interfaces occur spatially, via spillover from forest into monocultural oil palm; over levels of biodiversity restoration; and interacting between local and landscape scales.

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

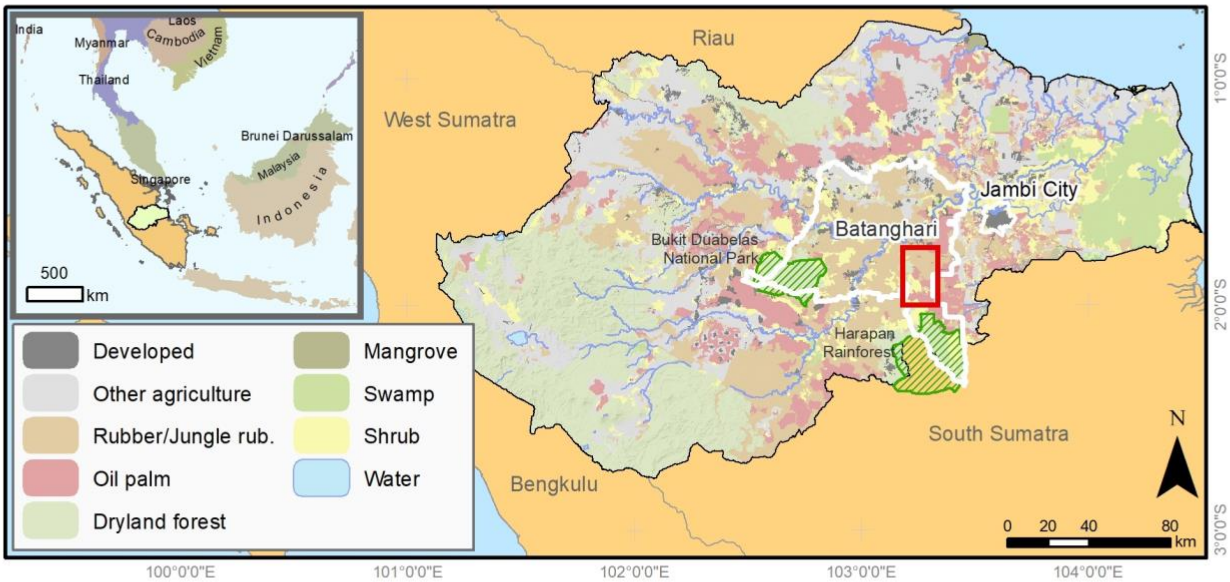

Figure 1. Map of Jambi province and surrounding context. The study region is located within the red rectangle, which corresponds to the extent of the map in **Figure 2a**. General land use categories are based on 2013 Landsat data classified by D. Melati.

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 with 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 change accompanied a transmigration program that increased the area's population and encouraged the conversion of land to cash crop production (Miyamoto 2006, 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, more open canopy, and lower leaf litter and tree biomass carbon than forest (Drescher et al. 2016, Meijide et al. 2018). Oil palm also often 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 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).

It is also important to consider the economic significance of these transformations for local communities. Within Jambi, preferences for rubber or oil palm by smallholders 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 change over gradients from simplified, high-intensity agricultural conditions to complex, biodiverse, natural or semi-natural habitats. Following a review of the state of oil palm pollinator research in my first chapter, I examine the ecological spillover effects of an interface between a forest border and an oil palm plantation in my second chapter. In my third chapter, I disentangle the effects of interacting biodiversity and plot size gradients in an oil palm biodiversity enrichment experiment. In my fourth chapter, I examine the effects of habitat simplification at landscape and local scales on the survival and colony health of a native stingless bee species.

Spatial interface: Ecological 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 of oil palm pollination in my **first chapter** with a review of the drivers of insect pollination in oil palm. Maintaining adequate fruit set has been a major concern in palm oil production historically, and agronomists have only recently understood the critical function of insects in oil palm pollination (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 pollination by the introduced weevil. However, despite concerns about the stability and resilience of introduced weevil populations, there appears to be little research on oil palm pollinators within the larger agroecosystem, or on landscape effects on pollinator services.

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 pollinator 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 fruit set and associated insect biodiversity patterns.

Biodiversity and patch size gradients in oil palm agroforestry enrichment

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 improves the diversity and stability of ecosystem functions (Aerts and Honnay 2011, Grossman et al. 2018) and could help mitigate the impacts of biological and physical habitat 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 (Teuscher et al. 2016). I quantified the abundance and ecosystem functions of insect herbivores, natural enemies, and pollinators using vegetation and insect surveys and phytometer plants. I then investigated how the biodiversity enrichment treatments influenced these variables, using statistical methods to disentangle the direct and indirect effects of the treatments on downstream ecosystem functions.

Scale interface: Pollinator response to local and landscape drivers

Eusocial bees and other wild pollinator taxa 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 high quality habitats are important, the types of land use in the matrix separating habitat patches

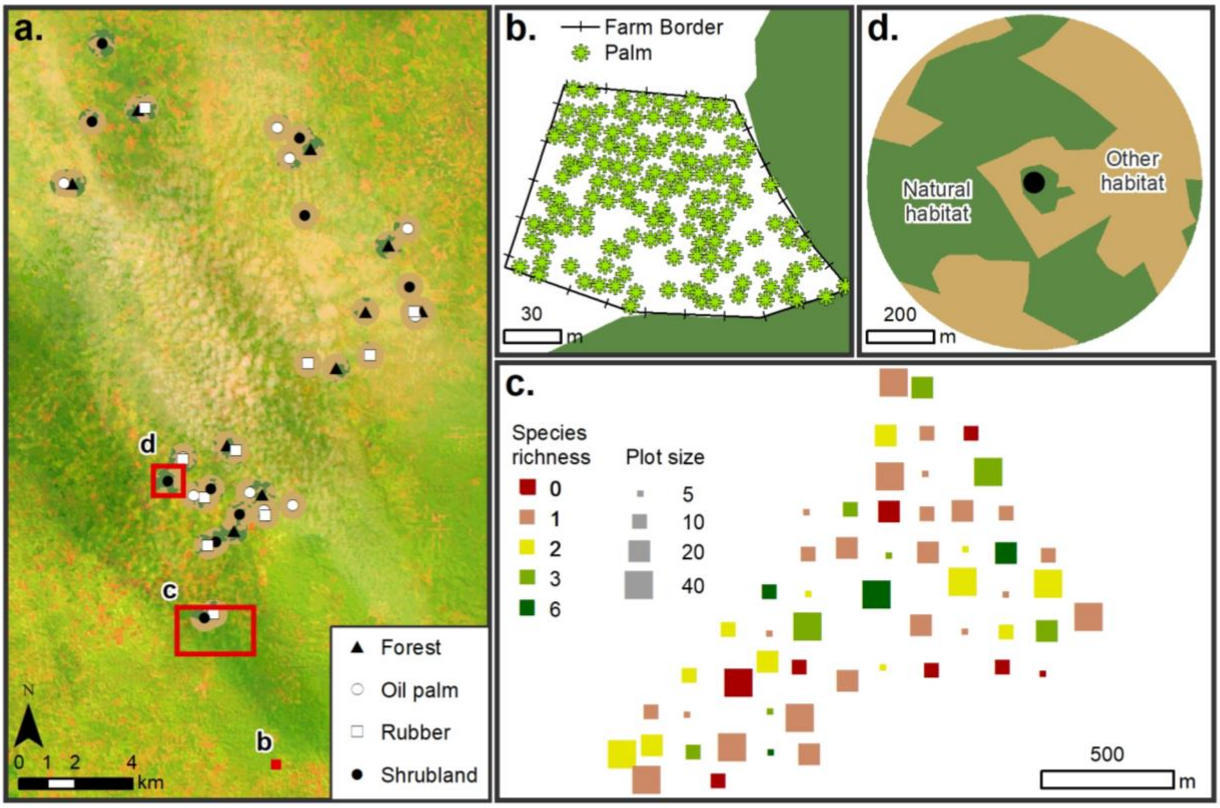

Figure 2. Maps of study areas for (a) landscape hives project in Chapter 4, (b) oil palm pollinators project in Chapter 2, (c) the biodiversity enrichment experiment (EFForTS-BEE) in Chapter 3, and (d) an exemplary map of a hive foraging area from Chapter 4. Background land cover in (a) is from a 2013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

also play a significant role in the survival and growth of wider-ranging organisms (e.g., for natural enemy insects in a fragmented urban landscape, 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 of how a eusocial bee adapts to and is impacted by local and landscape habitat quality. 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 the approach in my experimental chapters is that biodiversity and ecosystem function will benefit from closer association (physical or conceptual) with 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 influence insect-mediated pollination services to oil palm through ecological spillover (Tscharntke et al. 2012), though conditionally upon interactions with pollinator antagonists. In my third chapter, I hypothesized that the restoration effects on vegetation, insect groups, and insect-mediated ecosystem functions would reflect the flow of their ecological relationships. Based on the conceptual framework of ecological restoration (Teuscher et al. 2016), I implicitly expected that these relationships would more closely resemble natural forest conditions with greater biodiversity enrichment (more tree species and larger plots). 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. Over 1991-2011, annual temperatures in this region averaged 26.7±0.2°C and average mean precipitation was 2235±381mm (Drescher et al. 2016).

The oil palm pollination experiment in chapter two took place on a smallholder oil palm farm (Figure 2b) and was conducted 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 (Apidae: Meliponini), 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 was 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 placed above inflorescences.

In my third chapter, I conducted insect and vegetation surveys and a phytometer experiment in the biodiversity enrichment plots (Figure 3e) of a long-term biodiversity enrichment experiment (EFForTS-BEE, Teuscher et al. 2016) arrayed within an approximately 150 ha area of an oil palm plantation (Figure 2c). I conducted insect and vegetation surveys and pollinator and phytometer monitoring within a limited period to minimize variability due to seasonal or environmental differences (and for phytometer plants, to accomplish sufficient repetitions

Figure 3 (next page). Photos of 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 (T. Fung). Biodiversity enrichment and insect-mediated ecosystem functions 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) an experimental site in the forest destroyed by wildlife.


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before blooming ended). This required the help of several teams of assistants working simultaneously to cover the many plots in the experiment. We raised phytometer plants (chili pepper, *Capsicum annuum*) from seed in Jambi city and transferred them as seedlings to the field station in the plantation (Humusindo) where they reached sexual maturity (Figure 3f), after which we placed them in the plots for pollinator observation (Figure 3g). Assistants harvested chili fruits from the phytometer plants once fruits turned red. In my analyses, I 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). I tested cascading (i.e., linked direct and indirect) relationships between the variables using structural equation models (Grace 2008).

My fourth chapter took place over an approximately 200 km^2 area in the Batang Hari Regency (Figure 2a). The project purchased colonies of *T. laeviceps* from Bengkulu Province, to the southwest of Jambi, which were delivered overnight (Figure 3h). With the help of multiple teams of assistants, we placed colonies into sites distributed over the study region within the same day they were delivered. At each site we placed three hives inside a shelter that had been installed beforehand (Figure 3i). We allowed hives to acclimate for several weeks before we began foraging behavior surveys (Figure 3i), which the master’s student Sonja Schröck conducted. We standardized foraging survey methods by training with our project’s Indonesian counterpart, Professor Dr. Rika Raffiudin, whose master’s students also conducted studies in a subset of the hive sites. A challenge in fieldwork was the loss of hives due to damage by wildlife and people (Figure 3j). Multiple teams of assistants conducted colony foraging surveys with Sonja from August to November 2018 to cover all plots once a month. These teams also conducted flowering vegetation surveys at each plot before and after the foraging survey period. At the end of the four months, our team collected the surviving hives and measured hive structure and colony size.

Major findings

Chapter 1

In addition to the introduced pollinator *Elaeidobius kamerunicus*, other insect taxa 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 to growing regions worldwide. Management research also could take pollinator population dynamics into account by optimizing male and female inflorescence densities. Further, research should 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 there was also a non-significant trend under open pollination. This distance effect was not apparent with treatments that minimized the pollination contributions of flower visitors, suggesting that the effect was not abiotic. Only higher *E. kamerunicus* abundance was positively associated with higher fruit set under open pollination, and negatively associated with fruit set when large organisms were excluded. The other two major visitors, from the family Gelechiidae (Lepidoptera) and two families of Thysanoptera, were not significantly associated with fruit set. Insect abundance and fruit set patterns over the distance-to-forest gradient suggest unexamined ecological interactions, such as predation and non-consumptive effects, could also play a role in influencing oil palm pollination near forest, but further research is needed.

Chapter 3

Oil palm biodiversity enrichment treatments had the strongest direct effect on abiotic and vegetation variables in enrichment plots. One fast-growing species, *Peronema canescens*, strongly affected canopy openness. In turn, canopy openness, and to a lesser extent 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. The importance of canopy openness in mediating most of these relationships demonstrates how restoration affects ecosystem functions at an early stage and suggests that canopy gaps may play an important role in maintaining habitat heterogeneity and increasing insect-mediated ecosystem functions in ecological restoration.

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, we also measured higher floral richness and density in these last two types of habitats. Among the surviving colonies, local surrounding floral richness was associated with more hive pollen, which in turn drove bee and colony size. As *T. laeviceps* is a common native pollinator in the tropics, understanding how the trade-off between landscape availability of floral resources and suitable nesting habitat impacts this species can help us understand more broadly how deforestation in transforming tropical landscapes may impact pollinator diversity and function.

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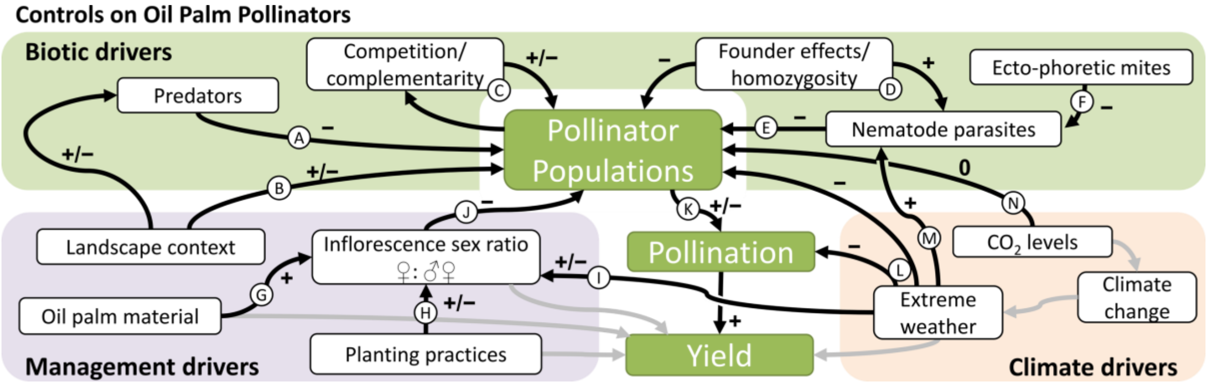
Chapter 1

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



Kevin Li[1]*, Teja Tscharntke[1,3], Barbara Saintes[1], Damayanti Buchori[2], Ingo Grass[1]

[1]Agroecology, Department of Crop Sciences, University of Göttingen, Göttingen, Germany

[2]Department of Plant Protection, Bogor Agricultural University, Bogor, Indonesia

[3]Centre of Biodiversity and Sustainable Land Use (CBL), University of Göttingen, Göttingen, Germany

Published in *Agriculture, Ecosystems and the Environment* 280 (2019) 152–160.
https://doi.org/10.1016/j.agee.2019.05.001

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.

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

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).

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.

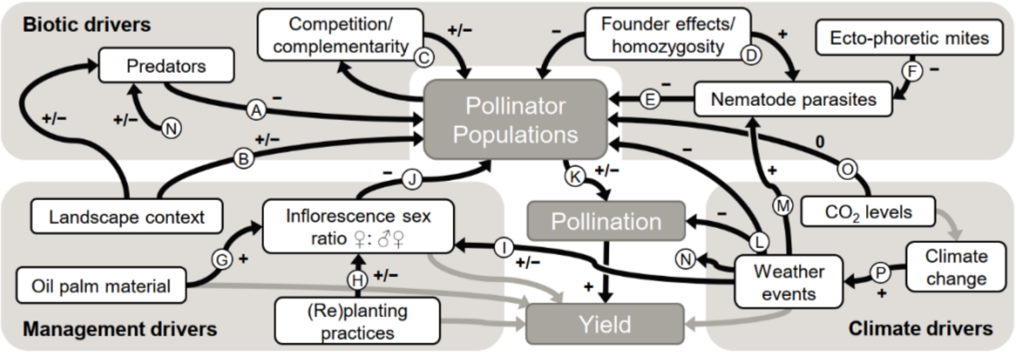
1.3.2. Controls on oil palm pollination

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 subvittatus* 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.

Acknowledgements

This study was financed by the Deutsche Forschungsgemeinschaft (DFG) in the framework of the collaborative German-Indonesian research project CRC 990 (Collaborative Research Centre 990: Ecological and Socioeconomic Functions of Tropical Lowland Rainforest Transformation Systems (Sumatra, Indonesia). R. N. Long, M. P. Hoffmann and C. R. Donough provided invaluable advice and resources. We thank E. Turner and an anonymous reviewer for their constructive feedback.

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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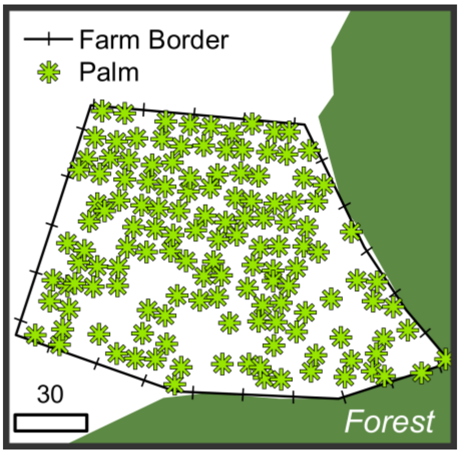
Chapter 2
Adjacent forest moderates insect pollination of oil palm



Kevin Li[1], Ingo Grass[2], Tien-Yi Fung[3], Riko Fardiansah[1,a], Marko Rohlfs[3], Damayanti Buchori[4,5], Teja Tscharntke[1,6]

[1]Agroecology, Department of Crop Sciences, University of Göttingen, Göttingen, Germany

[2]Department of Ecology of Tropical Agricultural Systems, University of Hohenheim, Stuttgart, Germany

[3]Population and Evolutionary Ecology, University of Bremen, Bremen, Germany

[4]Department of Plant Protection, Bogor Agricultural University, Bogor, Indonesia

[5]Center for Transdisciplinary and Sustainability Sciences, Bogor Agricultural University, Bogor, Indonesia

[6]Centre of Biodiversity and Sustainable Land Use (CBL), University of Göttingen, Göttingen, Germany

Published in *Agriculture, Ecosystems and the Environment* 338 (2022) 108108.
https://doi.org/10.1016/j.agee.2022.108108

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[a] Current address: Nature Conservation and Landscape Ecology, University of Freiburg, Freiburg im Breisgau, Germany

Abstract

Natural habitat plays a role in many agroecosystems as a source of pollination services and other ecological spillover, but these effects are largely unquantified in oil palm (*Elaeis guineensis*), a globally important crop linked to deforestation. In a field experiment in Sumatra, Indonesia, we manipulated floral visitor access to female oil palm inflorescences over a 100 m distance gradient from forest into oil palm and sampled insects with sticky traps placed above male and female inflorescences. Full exclusion of floral visitors decreased mean oil palm fruit set to 12%, demonstrating that insect pollination was necessary to maintain favorable fruit set and yield. Treatment group means of fruit set under open pollination (62%) and when excluding large (>1.4 mm diameter) organisms (72%), did not differ significantly from open pollination augmented with hand pollination (61%), suggesting no difference in pollen limitation. In contrast, when we examined change in fruit set with distance from forest, we found a significant trend of higher fruit set in oil palms closer to the forest when large organisms were excluded, which increased estimated fruit set at the forest edge to 87%, compared to open-pollinated palms (70%). This trend with distance from forest was absent when we fully excluded floral visitors, showing that the effect of forest was not likely due to an abiotic gradient (e.g., changing soil nutrients). Of the arthropod taxa collected from sticky traps, Drosophilidae (Diptera) and Gelechiidae (Lepidoptera) decreased and increased with distance from forest, respectively. The taxa *Elaeidobius kamerunicus* (Coleoptera: Curculionidae), Gelechiidae, and the families Thripidae and Phlaeothripidae (Thysanoptera) were abundant on both male and female inflorescence sticky traps. *Elaeidobius kamerunicus*, an introduced oil palm pollinator, had the only significant relationship with fruit set. Our results confirm pollination by insects as a key ecosystem service for oil palm production. Although further work is needed to clarify the relationship between fruit set, biodiversity, and distance from forest, we speculate that excluding large organisms could have increased fruit set closer to forest by mediating interactions between pollinators, forest predators, and farm mesopredators. Understanding the relationships between nearby forest and pollination services could better connect oil palm production to its landscape context and associated biodiversity. This would be important for landscape-scale conservation planning that considers both the ecosystem service needs and ecological impacts of oil palm agriculture.

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

2.1. Introduction

The tropical crop oil palm (*Elaeis guineensis*) 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). Oil palm expansion has been linked to deforestation and biodiversity loss (Koh and Wilcove 2008, Clough et al. 2016), but at the same time, the role of biodiversity in providing ecosystem services to oil palm and the relationship of biodiversity in oil palm to nearby natural habitats is still little understood. The contributions of wild pollinators have important economic implications in many major crops (Klein et al. 2007, Garibaldi et al. 2013). While insects are known to mediate oil palm pollination (Syed 1979, Wahid and Kamarudin 1997), the relationship between insect diversity and pollination function with nearby natural habitat is still not well understood (Li et al. 2019).

Research in oil palm pollination outside its region of origin (West Africa) has focused mainly on the introduced African weevil, *Elaeidobius kamerunicus*, the introduction of which resulted in fruit set and bunch weight increases in the 1980s (Syed et al. 1982, Greathead 1983, Pardede 1990). However, more recently, regions where oil palm has been introduced have observed fluctuations in weevil populations and fruit set rates, while drivers of oil palm pollination variability are still little understood (Donough et al. 1996, Wahid and Kamarudin 1997). The alternative to pollination ecosystem services historically has been hand pollination, which is labor and resource intensive (Wurz et al. 2021). The loss of these pollination services would have a significant impact on producers, especially smallholder farmers, who have fewer resources to implement hand pollination methods, and make up 40% of growers in the region of our study (Qaim et al. 2020).

Individual oil palms produce both male and female inflorescences (monoecy), but because only one inflorescence is in bloom at any given time, cross pollination is necessary (Corley and Tinker 2016). Effective pollinators must therefore be able to transport pollen from anthesizing male inflorescences to receptive female inflorescences. Most visits by pollinating insects to female oil palm inflorescences are brief (Syed 1979, Anggraeni et al. 2013), because female inflorescences offer none of the resources found on male inflorescences (including nectar) and only share a similar fennel-like scent that attracts pollen-bearing insects from male inflorescences (Dhileepan 1994, Tandon et al. 2001). Furthermore, as the flowers on both sexes of inflorescence open asynchronously over the course of several days (Tandon et al. 2001), pollinators must visit a female inflorescence over the entire bloom period for it to achieve a maximal fruit set rate. This also limits the effectiveness of hand pollination as the sole mechanism for pollinating oil palm (Harun and Noor 2002).

Developing a better understanding of the larger ecological context of oil palm pollination services that incorporates biodiversity within the surrounding landscape may help uncover drivers of variability. The cross-habitat spillover hypothesis (Tscharntke et al. 2012) proposes that organisms and associated ecological functions may spill over from neighboring habitats. Research on spillover of natural enemies to oil palm suggests that nearby natural and semi-natural habitats can affect parasitoid wasp community composition (Rizali et al. 2019a) and increase predation pressure on defoliating pests (Nurdiansyah et al. 2016), though riparian forest fragments appear to be unlikely to provide pest control services (Gray and Lewis 2014).

However, research on oil palm is only beginning to consider such spillover effects on pollination services. Across many agricultural systems, natural and semi-natural habitats can support important wild pollinator populations (Klein et al. 2003, Garibaldi et al. 2013, Albrecht et al. 2020). Higher pollinator diversity in turn can promote higher yield if functionally complementary pollinating species are promoted (Woodcock et al. 2019). However these natural habitats can also be a source of antagonists, such as predators of pollinators (Klein et al. 2006, Maas et al. 2015) or floral antagonists that decrease pollination success, e.g., through delivering heterospecific pollen (Vamosi et al. 2006). Though previous work has explored the role of nearby natural habitat in influencing the floral visitor community in oil palm (Mayfield 2005, Egonyu et al. 2021), a further connection to the associated effects on pollination ecosystem services for the farmer is needed (Li et al. 2019).

In this study, we jointly assessed the importance of flower-visiting organisms and proximity to nearby forest for oil palm fruit set, as an estimate of pollination services (Corley and Tinker 2016). We did this by limiting the access of larger organisms to female oil palm flowers with an experimental exclusion treatment over a distance gradient of 0-100 m from a neighboring forest edge. We also sampled the insect community over this gradient by placing sticky traps above the experimental oil palm inflorescences and on control palms without a blooming inflorescence. Our questions were: 1.) How does limiting the floral visitor community affect fruit set rate? 2.) How does fruit set rate change with distance from forest? 3.) How do insect communities change with distance from forest and comparing between inflorescence sexes? and 4.) How does fruit set rate vary with major floral visitor taxa?

For our first question, we hypothesized that excluding larger organisms (i.e., “partial exclusion”) would result in higher fruit set if pollinator antagonists (e.g., predators or competitively dominant, but poor pollinators) are excluded, or in lower fruit set if beneficial

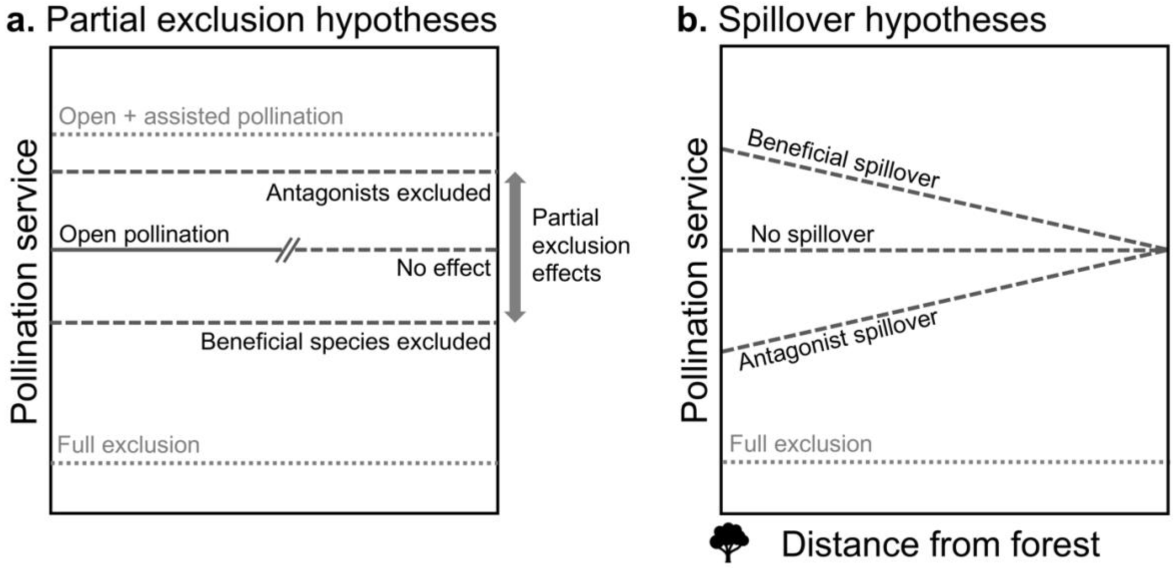


Figure 2-1. Illustrations of the hypothesized outcomes of: (a) partial exclusion, including if pollinator antagonists are excluded, if there is no effect of partial exclusion, or if beneficial species are excluded; and (b) outcomes of ecological spillover if forest is a source of beneficial species, not a source of spillover interactions, or a source of pollinator antagonists.

species are excluded, when compared to open pollination (Figure 2-1a). We expected treatments that fully excluded floral visitors (i.e., “full exclusion”) or supplemented open conditions with hand pollination (“assisted pollination”) would achieve minimum and maximum fruit set levels, respectively. For our second question, we hypothesized that fruit set near the forest would increase if the forest served as a spillover source of beneficial species, and fruit set would decrease if the forest was a spillover source of antagonists (Figure 2-1b). We predicted fruit set would not vary with distance from forest under the full exclusion and assisted pollination treatments, since these conditions should minimize the influence of floral visitors. To address our third question, we conducted a multivariate regression of the floral visitors collected from the sticky traps against our independent variables, distance from forest and inflorescence sex. To address our fourth question, we identified insect taxa that were found in sufficient number on both male and female inflorescences, suggesting they could significantly affect pollination services, and related their abundance to the fruit set of the open pollination and partial exclusion palms in a regression model.

2.2. Methods

2.2.1. Study region and site

From August 2018 to April 2019, we monitored oil palms within a 1.5-ha site, which covered most of a smallholder farm in the Batang Hari Regency of Jambi Province, Sumatra, Indonesia. The study site bordered a 7-ha forest patch to the east and south and a large-scale plantation and smallholder farms to the west and north (Figure 2-2). The neighboring forest was a remnant of the characteristic lowland dipterocarp forests in the region (Laumonier et al. 2010). The temperature and relative humidity of the site during the experimental part of our study, from August to October 2018, was calculated from readings by an iButton logger (Fawcett et al. 2019). Mean daily temperature and humidity were 27.2ºC and 84.1%, respectively, and mean daily minimum and maximum temperature and humidity were 22.9ºC and 34.6ºC, and 56.6% and 98.2%, respectively. Jambi Province receives a mean annual rainfall of 2235 ± 385 mm (Teuscher et al. 2016).

The site is located within a smallholder farm managed by a single household. Prior to the beginning of the study, the farmer removed undergrowth vegetation by weeding and herbicide

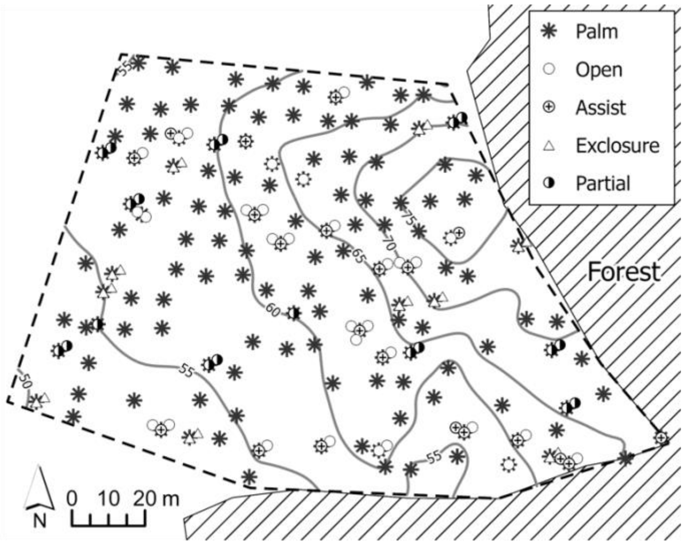


Figure 2-2. Map of the study area, shown enclosed within the dashed lines. Hatched area to the East shows the forested area. Within the study area, gray lines and numbers represent the contour lines on the plot. Symbols for palm tree locations and experimental treatments are shown in the legend.

application, which is common management practice. We mapped all individual oil palms and the forest edge with a handheld GPS (Garmin GPSMap 67). Mapping indicated a planting density of approximately 92 palms per hectare and an estimated 40 m elevation difference across the site (Figure 2-2). We used the ArcGIS geoprocessing tool “calculate distance” (ESRI 2011) to estimate the Euclidian distance of each palm to the nearest point on the forest edge. We categorized each palm to one of six distance bins that subdivided the range of possible distances from forest edge (0-100 m) into six bins of equal distance brackets (e.g., 0-16 m, 16-32 m, etc.).

Oil palm fruit bunch size increases with palm age (Corley and Tinker 2016), so we considered the importance of palm age in exploratory modeling of fruit set. As the managing household did not keep formal records of planting history, we estimated the approximate age of each palm by counting leaf scars, shown in Figure 2-3a. This method is useful for comparing relative ages of palms within a site in short-term studies (Pinard 1993).

2.2.2. Oil palm floral visitor exclusion treatments

From August to October 2018, we monitored for maturing female inflorescences throughout the site. We assigned the maturing inflorescences proportionally over the distance brackets described in Section 2.1 to four experimental treatments, maintaining an approximately balanced distribution of palm distances from forest edge over treatment groups. In two of the experimental treatments, we restricted flower access by completely enclosing the inflorescence in a mesh exclosure that was sealed at the base of the inflorescence (example in Appendix Figure 2-1a). For one type of exclosure (i.e., “full exclusion”), we used a 0.1 mm mesh that essentially isolated the inflorescence from all visitors, and for the other type (i.e., “partial exclusion”) we used a coarser 1.4 mm mesh that was penetrable by small insects such as *E. kamerunicus*, stingless bees (Apidae: *Tetrigona*), or thrips (Thysanoptera). Exclosures were put in place at least one week before flower receptivity, which we anticipated by characteristic changes in color and tearing in the peduncular bract (Forero et al. 2011). In addition to the exclusion treatments, we also assigned an “open pollination” treatment, which allowed full access to floral visitors, and an “assisted pollination” treatment, which supplemented open pollination with pollen applied by hand following industry practices (method described in Appendix A Text A.1). We used hand pollination to only supplement open pollination rather than serve as the sole source of pollen because our goal was to maximize pollination, and hand pollination alone is not as effective as insects at delivering pollen to the inner structure of the inflorescence, or over the entire asynchronous blooming period (Harun and Noor 2002). At the end of the flowering period, indicated by darkened, dry flowers (Forero et al. 2011), we removed exclosure treatments and placed bamboo or wire cages around the developing fruit bunches to prevent damage or theft until we assessed fruit set.

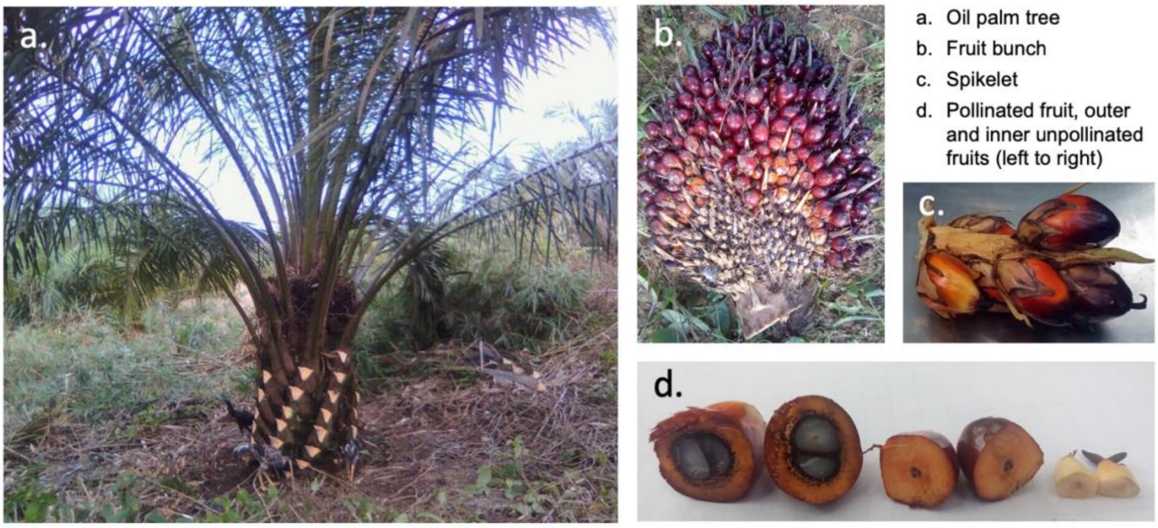


Figure 2-3. Example photos of: (a) a typical young oil palm tree used in this study. Note the triangular leaf scars, which we used to estimate relative palm age across the site. (b) A ripe fruit bunch after harvest. (c) A spikelet removed from the fruit bunch. (d) Cross sections of (left to right): a pollinated fruit and two forms of unpollinated (parthenocarpic) fruits. Credit: N. Marbun.

In total, our experiment included 92 female inflorescences grown on 45 unique palms, which we allocated to the four treatments (20 full exclusion, 20 partial exclusion, 31 open pollination, and 21 assisted pollination). The mean distance from forest between the treatment group palms was not significantly different ($F(3, 88) = 0.86$, $p = 0.47$) and groups did not differ in altitude ($F(3, 88) = 0.35$, $p = 0.79$), or our age proxy ($F(3, 88) = 1.92$, $p = 0.13$). There were moderate but statistically significant correlations between distance from forest and altitude (Pearson's r = -0.45, $p < 0.01$) and distance from forest and number of leaf scars (Pearson's r = 0.40, $p < 0.01$), which likely reflects the topography and management history at the extremes of the distance from forest gradient.

2.2.3. Assessment of fruit set

To investigate the experimental effects on fruit set rate, we estimated fruit set in each oil palm fruit bunch (Figure 2-3b) by counting the number of pollinated versus unpollinated fruits. Because fruit bunches can contain several hundred to several thousand fruits, we took a stratified random sample of approximately one-third of the entire bunch. Fruit bunches are branched into spikelets that hold clusters of individual fruits developed from flowers (Figure 2-3c). We randomly subset one third of the total spikelets in each bunch for sampling. Within this subset we counted pollinated fruits and unpollinated fruit types (Figure 2-3d), which can be clearly differentiated by their morphology and the presence of a kernel inside (Mathews et al. 2009).

2.2.4. Floral visitor community sampling

We planned to set sticky traps on all treatment (female) inflorescences to sample arthropod visitors over 24-hour periods during flowering. However, our results do not include traps from all experiment inflorescences, or from all flowering days, due to difficulty accessing the site in time for blooming or due to loss of traps. We recovered traps from 85% (78 of 92) of the experiment inflorescences, which included 43 of the 45 experiment palms. We also placed traps on six female inflorescences that we did not harvest as part of the experiment, either due to logistical reasons or loss of the fruit, so we only included these in our analysis of abundances over ecological gradients. Overall, we sampled 128 replicates representing the first and/or second days of blooming of these female inflorescences. We also placed traps on non-blooming palms over the distance from forest gradient (10 replicates/palms) and on male inflorescences that we found blooming during the experiment (six replicates in five palms). In total, we collected from 144 unique palm/day replicates.

We constructed sticky traps by applying non-drying glue to the bottoms of 100 mm diameter petri dishes and hanging them approximately 10 cm above the inflorescence, to not block access to flowers (Appendix Figure 2-1b). This placement was outside of any exclosures so that the collected abundances represented natural conditions reflecting ecological gradients rather than effects of exclusion treatments. Each trap was installed near mid-day and collected the next day at the same time. We initially placed two petri dishes per inflorescence replicate (n = 13 on female inflorescences and one on a male inflorescence), but we switched to one dish per replicate and accounted for differences in sampling effort in our statistics. We identified arthropods collected in the traps to family using a binocular microscope, consulting general and region-specific guides (Goulet et al. 1993, Johnson and Triplehorn 2004, Bosuang et al. 2017).

2.2.5. Statistical analyses

We performed all statistical analyses using the software R (R Core Team 2021). We fit generalized linear mixed effects models (GLMM) using the packages “glmmTMB” (Brooks et al. 2017). We computed marginal effects with “emmeans,” using the Tukey method of multiple testing adjustment for pairwise comparisons (Lenth 2019). We checked appropriateness of mixed model assumptions by comparing to simulated residuals using the package “DHARMa” (Hartig 2019). Mixed effects model fit metrics, including variance inflation factor and variance explained by fixed effects (i.e., marginal R^2, Nakagawa and Schielzeth 2013) were calculated using the package “performance” (Lüdecke et al. 2021).

Question 1: Pollen limitation and effect of floral visitor exclusion on fruit set rate

We modeled percent fruit set using a mixed effects beta regression model with a logit link (Ferrari and Cribari-Neto 2004). We included the four treatments as fixed effect factors and palm identity as a random effect, the latter to account for variability shared between inflorescences from the same palm.

Question 2: Effects of distance from forest and palm covariates

To consider the effect of distance from forest on fruit set rate, we updated the experimental treatment model to include distance from forest as a continuous variable, with an interaction with the exclusion treatment factor. We used likelihood ratio tests to compare models representing the effect of the exclusion treatment only, the effect of distance from forest regardless of treatment, and differing effects of distance from forest between treatments (i.e., the interaction between treatment and distance from forest). We also looked for evidence of nonlinear relationships over the distance from forest gradient by refitting the model with the distance from forest variable as a thin-plate spline with treatment group-level smoothers that estimated individual penalties for each group, using the package “mcgv” (Wood 2011). We compared this model to the original mixed effects model using AICc (Pedersen et al. 2019). Distance from forest was significantly correlated with the covariates altitude and palm age, and preliminary model fitting suggested these variables would be strongly multicollinear when included in the same model (VIF > 10). We therefore compared the relative fits of the treatment × distance from forest model to similarly structured treatment × altitude and treatment × palm age models by their AICc.

Question 3: Floral visitor community over ecological gradients

To look at drivers of covarying community composition collected from the sticky traps, we modeled taxa abundances in the 144 unique palm/day replicates surveyed from the female and male inflorescence and control palm sticky traps described in Section 2.4. We used a multivariate regression method, generalized linear latent variable models (GLLVM), from the package “gllvm” (Niku et al. 2019). Focusing on the subset of 23 taxa that were present in at least 10 palm/day replicates, we fit coefficients for effects of distance from forest and inflorescence sex assuming a negative binomial error distribution. Inflorescence sex coefficients included categorical variables for first and second-day female blooms and male blooms, which were estimated in reference to control palms as the baseline. We included one latent variable in this model, based on preliminary comparisons of models with 0-5 latent variables by AICc (Niku et al. 2019). We modelled the total abundance of each taxon across all the traps set on an inflorescence in a day, using the offset ln(n) in the model formula to account for sampling effort, where n is the number of traps set on a palm and day. Based on our multivariate analysis of the insect community, we identified insect families that were potential pollinators, or may have been associated with pollinator communities, by significant association with both male and female inflorescences, as compared to the control traps on nonflowering palms.

Question 4: Associations between major floral visitors and fruit set in open and partial exclusion treatments

Focusing on a subset of the open and partial exclusion treatment inflorescences, we modelled the correlation between fruit set and abundance of taxa that are known or potential pollinators. Based on the literature or prominent representation in the sticky traps (more details presented in the Results), we selected Curculionidae, Gelechiidae, and the combined families of Thripidae and Phlaeothripidae (“Thysanoptera”) as independent variables in the regression. The dataset for this model included 38 fruit bunches, excluding one fruit bunch with uniquely high Curculionidae abundance (230 individuals, compared to the mean 22.9±28.0 S.D.). We combined Thripidae and Phlaeothripidae families in the regression because they were highly correlated (Pearson r = 0.73, $p < 0.001$). We only used abundance data from first-day traps to standardize for potentially changing inflorescence attractiveness over time, taking the average in cases where we placed multiple traps on an inflorescence in a day. We fit separate slopes for effect of abundance of each taxon under open or partial exclusion treatments using an interaction between treatment factor and each taxon abundance variable. We included palm identity as a random effect.

2.3. Results

2.3.1. Question 1: Pollen limitation and effect of floral visitor exclusion on fruit set rate

We present marginal means and confidence intervals of each treatment as estimated by the first GLMM, which models fruit set means over each treatment group (Table 2-1a). The mean fruit set under the full exclusion treatment was 11.7% (95% CI = 7.0 – 18.9%). This was significantly lower ($p < 0.001$, adjusting for comparison of a family of four estimates) than the estimated mean fruit set of the assisted pollination (60.5%, 95% CI = 51.1 – 69.2%), open pollination (61.8, 95% CI = 52.9 – 69.9%), and partial exclusion treatments (72.2%, 95% CI = 60.9 – 81.3%). Aside from contrasts with the exclusion treatment, the experimental treatment means did not differ significantly from each other at the $\alpha = 0.05$ level (Figure 2-4a).

Table 2-1. Results of fruit set GLMM (beta regression link) with (a) pollination exclusion treatment and (b) distance from forest by exclusion treatment fixed effects variables. Coefficient estimates and their 95% confidence interval (CI) are reported in the log-odds scale, with the assisted pollination treatment as the baseline.

	a. **Treatment**			**b.** **Treatment × Distance from Forest**		
Predictors	*Estimates*	*95% CI*	*p-value*	*Estimates*	*95% CI*	*p-value*
(Intercept)	0.43	0.05 – 0.81	0.027	0.223	-0.418 – 0.865	0.495
Treatment [Exclosure]	-2.45	-3.12 – -1.77	<0.001	-2.169	-3.321 – -1.016	<0.001
Treatment [Open]	0.05	-0.25 – 0.35	0.733	0.464	-0.066 – 0.995	0.086
Treatment [Partial]	0.53	-0.10 – 1.16	0.100	1.605	0.433 – 2.778	0.007
Distance				0.006	-0.008 – 0.020	0.417
Treatment [Exclosure] * distance				-0.008	-0.032 – 0.016	0.519
Treatment [Open] * distance				-0.011	-0.023 – 0.001	0.068
Treatment [Partial] * distance				-0.023	-0.045 – -0.001	0.038
Random Effects						
Random intercept variance (TreeID)	0.58			0.56		
N (TreeID)	45 $_{\text{TreeID}}$			45 $_{\text{TreeID}}$		
Observations	92			92		
Marginal R^2	0.680			0.702		
AIC	-99.750			-100.096		

2.3.2. Question 2: Effects of distance from forest and other covariates

Modeling the effect of distance without accounting for differences between exclusion treatments did not improve model fit over a model with treatments only ($\chi^2 = 1.70$ (1), $p = 0.19$). Fitting separate effects of distance from forest for each treatment improved model fit marginally over the model without an interaction ($\chi^2 = 6.65$ (3), $p = 0.08$). Based on the fitted model coefficients presented in Table 2-1b, we estimated the marginal effect of distance from forest for each treatment. As expected, the fully excluded fruit bunches did not show a trend with distance from forest (log-odds ratio = -0.0022, 95% CI = -0.0224 – 0.0180, $p = 0.83$) (Figure 2-4b). The effect of distance from forest was also not significant for assisted pollination (0.0059, 95% CI = -0.0085 – 0.02024, $p = 0.42$). However, under the partial exclusion treatment, the distance from forest had a significant negative effect, i.e., fruit set was higher closer to the forest (-0.0175, 95% CI = -0.0347– -0.00038, *p* = 0.045) (Figure 2-4c). The estimated effect was also negative for open pollination, but it did not differ significantly from zero (-0.0050, 95% CI = -0.0186 – 0.0086, *p* = 0.46). Next to forest (distance = 0), the model-estimated mean fruit set was 87.2% (95% CI = 81.3 – 91.4%) for partial exclusion; 69.9% (95% CI = 62.6 – 76.4%) for open pollination; 60.7% (95% CI = 52.4 – 68.4%) for assisted pollination; and 12.3% (95% CI = 7.7 – 19.0%) for full exclusion (Figure 2-4c).

Fitting the distance from forest variable as thin plate splines (independently varying by exclusion treatment) in a generalized additive mixed effects model did not indicate a significant nonlinear pattern. Compared to the linear model, this nonlinear model increased the AICc score by ΔAICc = 19.5, suggesting no significant gain in information explained (see Appendix Table 2-1 for model details). We also fit alternative GLMMs replacing distance from forest with altitude or palm age, as these covariates were significantly correlated with distance from forest. The differences in AICc among these models did not exceed ΔAICc = 2 (Appendix Table 2-1), suggesting that the effect we observed closer to forest was not significantly better explained by these other covariates.

2.3.3. Question 3: Floral visitor community over ecological gradients

From the sticky traps, we collected 63,618 individual arthropods, which we classified into 84 taxa (Table 2-2 and Appendix Table 2-2). Represented in these samples were 13 orders, dominated by Coleoptera (3,453), Diptera (2,347), Lepidoptera (1,578), and Thysanoptera (55,716). The sampled individuals of the Coleoptera family Curculionidae were completely composed of the introduced *E. kamerunicus* weevil (3,185 individuals), so we equated the family to this species. We caught a limited numbers of predatory arthropods in our traps, including salticid spiders (Araneae, n = 8) and earwigs (n = 4) from three family of Dermaptera (Appendix Table 2-2).

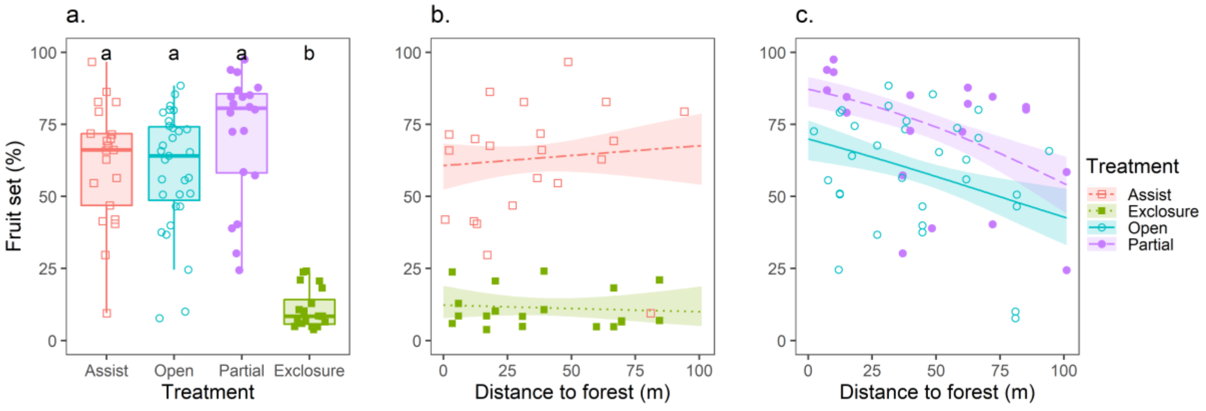


Figure 2-4. Fruit set rates of oil palm inflorescences in (a) the four pollination exclusion treatments, and estimated trend over distance from forest for (b) assisted pollination and full exclusion treatments, and (c) open pollination and partial exclusion treatments. In panel (a), significant differences (α = 0.05) between exclusion group means, as modeled by a GLMM, are indicated by the letter groupings. Boxplot box shows the median and first and third quartiles; points show actual fruit set values. In panels (b-c), marginal trends and 95% confidence intervals over the distance from forest gradient with the four exclusion treatments are estimated from a more complex GLMM.

Table 2-2. Summary statistics of taxa found on over 10 sticky traps. The abundances of these taxa were modeled as the multivariate response of the GLLVM. Significant effects supported by the GLLVM (α = 0.05) are indicated by the codes: DF (distance from forest), M (male inflorescence), F1 (female inflorescence day 1), and F2 (female inflorescence day 2), along with the direction of the significant effect (+/-).

				Female traps (n = 144)		**Male traps** (n = 7)		**Control traps** (n = 10)	
Order	*Family*	*GLLVM significant effects*	*Total*	*% Traps present*	*Mean when present (s.d.)*	*% Traps present*	*Mean when present (s.d.)*	*% Traps present*	*Mean when present (s.d.)*
Coleoptera	Chrysomelidae	M(+), F1(+), F2(+)	21	11	1.3 (0.6)	14	1 (-)	0	-
	Curculionidae	M(+), F1(+), F2(+)	3185	87	22.7 (28.1)	86	53.3 (39)	20	15 (19.8)
	Nitidulidae	DF (+)	74	24	1.9 (1.8)	43	1.7 (1.2)	10	1 (-)
	Ptiliidae		64	13	2.7 (2.7)	14	1 (-)	30	5 (4)
	Staphylinidae		38	19	1.3 (0.8)	14	1 (-)	20	1.5 (0.7)
Diptera	Cecidomyiidae		285	51	3.3 (3.5)	43	2.7 (2.9)	90	4.2 (1.5)
	Ceratopogonidae	M(-), F1(-), F2(-)	49	3	1 (0)	0	-	80	5.6 (3.2)
	Chironomidae	F1(-), F2(-)	47	12	1.9 (1)	14	2 (-)	60	2 (1.3)
	Culicidae		33	11	1.8 (1.8)	14	2 (-)	10	3 (-)
	Dolichopodidae	DF (+), M(+), F1(+), F2(+)	53	13	2.5 (2)	57	2 (1.4)	0	-
	Drosophilidae	DF (-), M(+), F1(+), F2(+)	440	37	8.1 (10.7)	29	5.5 (6.4)	10	1 (-)
	Phoridae		699	76	5.9 (9.9)	71	2.6 (1.8)	100	3.2 (1.9)
	Psychodidae	F1(+), F2(+)	616	76	5.5 (6.7)	57	2 (0.8)	30	1.7 (1.2)
	Sphaeroceridae	M(+), F1(+), F2(+)	71	15	2.2 (1.6)	43	8 (7.9)	0	-
Hemiptera	Cicadellidae	M(-)	28	10	1.6 (0.9)	0	-	20	2 (0)
Hymenoptera	Braconidae	M(-), F1(+), F2(+)	14	8	1.2 (0.4)	0	-	0	-
	Diapriidae	M(-), F1(+), F2(+)	16	10	1.1 (0.4)	0	-	0	-
	Encyrtidae	M(+)	140	26	2.1 (2.4)	43	19 (20.7)	40	1.3 (0.5)
	Formicidae		118	26	3 (3.7)	29	1 (0)	40	1 (0)
	Mymaridae		35	20	1.1 (0.4)	29	1.5 (0.7)	10	1 (-)
Lepidoptera	Gelechiidae	DF (+), F1(+), F2(+)	1578	90	11.8 (13.5)	71	7.6 (1.8)	80	2.8 (2.8)
Thysanoptera	Phlaeothripidae	M(+), F1(+), F2(+)	34810	90	262.2 (532)	100	129.6 (118.1)	40	18.8 (33.5)
	Thripidae	M(+), F1(+), F2(+)	20906	90	151.1 (274.8)	100	173.9 (127.9)	30	13.7 (21.9)

The generalized linear latent variable model (GLLVM) of the sticky trap taxa explained 24.3% of the variation in taxa abundance. Estimated coefficients for the model terms (Appendix Figure 2-2 and summarized in Table 2-2) showed that three families, Nitidulidae (Coleoptera), Drosophilidae (Diptera), and Gelechiidae (Lepidoptera), were positively correlated with distance from forest, while only Drosophilidae (Diptera) was modeled to increase in abundance closer to the forest. The abundances of seven taxa were significantly positively correlated with both male and female inflorescences, compared to the control traps, including Coleoptera families Chrysomelidae and Curculionidae, Diptera families Drosophilidae, Dolichopodidae, and Sphaeroceridae, and Thysanoptera families Phlaeothripidae and Thripidae. Two families of parasitic wasps (Hymenoptera), Braconidae and Diapriidae, were positively associated with female inflorescences while negatively associated with male inflorescences. Gelechiidae (Lepidoptera) and the Dipteran Pyschodidae were positively associated with female inflorescences but trends with male inflorescences were not significantly different from zero. Six taxa (Curculionidae, Thripidae, Phlaeothripidae, Gelechiidae, Dolichopodidae, and Drosophilidae) had higher positive correlations between their model residuals (Appendix Figure 2-3), indicating that these taxa co-occurred in our survey traps more than the model-estimated effects of distance from forest and inflorescence sex could explain.

Table 2-3. Results of fruit set GLMM (beta regression link) multiple regression of fruit set against the abundances of Curculionidae (*E. kamerunicus*), Gelechiidae, and Thysanoptera in the open pollination and partial exclusion treatments. Coefficient estimates and their 95% confidence interval (CI) are reported in the log-odds scale, with the open pollination treatment as the baseline.

Predictors		*Estimate*	*95% CI*	*p-value*
(Intercept)		0.1682	-0.4908 – 0.8273	0.617
Treatment [Partial]		0.9360	-0.1925 – 2.0645	0.104
Curculionidae		0.0141	0.0005 – 0.0278	0.043
Gelechiidae		-0.0175	-0.0604 – 0.0255	0.426
Thysanoptera		0.0000	-0.0004 – 0.0004	0.883
Treatment [Partial] * Curculionidae		-0.0330	-0.0521 – -0.0139	0.001
Treatment [Partial] * Gelechiidae		0.0449	-0.0217 – 0.1114	0.186
Treatment [Partial] * Thysanoptera		0.0002	-0.0004 – 0.0008	0.505
Random effects				
Random intercept variance (TreeID)	0.86			
N (TreeID)	26			
Observations	38			
Marginal R^2	0.278			

2.3.4. Question 4: Associations between main floral visitors and fruit set rate

Of the seven taxa we identified as significantly associated with both male and female inflorescences, we focused on the taxa Curculionidae and Thysanoptera as possible pollinators, which had high prevalence (over 80% of male and female inflorescence sticky traps) and abundance (>3000 total individuals captured). We also considered the family Gelechiidae in our analysis because it had the highest abundance after Curculionidae, and its prevalence on both male and female inflorescences was also high (71% and 90%, respectively). Other significant floral visitors to both sexes (Chrysomelidae, Drosophilidae, Dolichopodidae, and Sphaeroceridae) had much lower prevalence, i.e., presences on fewer than 50% of traps (Table 2-2).

The GLMM of fruit set with separate independent coefficients for Curculionidae, Gelechiidae, and Thysanoptera abundance under open and partial exclusion treatments accounted for 27.8% of variability (marginal R^2). This model (Table 2-3) performed better than a null model including only factors for open or partial exclusion treatments (χ^2 = 13.349 (6), p = 0.038, marginal R^2 = 15.5%). Fruit set showed the clearest trend with Curculionidae abundance (Figure 2-5a). The estimated marginal effect of Curculionidae abundance on fruit set was positive in the open pollination treatment (log-odds ratio = 0.0141, 95% CI = 0.000002 – 0.0283, p = 0.05), but was negative under partial exclusion (-0.0189, 95% CI = -0.0327 – -0.0051, p = 0.009). These values differed significantly at the α = 0.05 level (Table 2-3). The abundances of Gelechiidae (Figure 2-5b) and Thysanoptera (Figure 2-5c) did not have significant trends with fruit set at α = 0.05. Fitting a thin plate spline to the relationship between Thysanoptera abundance and fruit set did not reveal any further support for a nonlinear trend (Appendix Table 2-3).

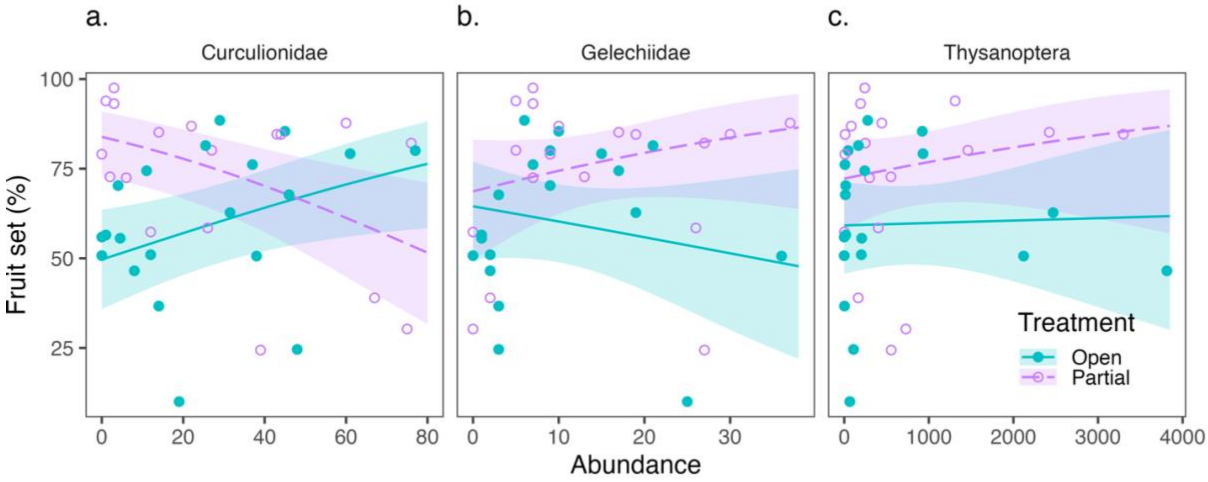


Figure 2-5. Marginal effects of major inflorescence visitor taxa on fruit set, under open (solid line) and partial exclusion (dashed line) treatments, estimated in a GLMM. These taxa were: (a) Curculionidae, which consisted solely of *E. kamerunicus*, (b) Gelechiidae, and (c) Thysanoptera, which combined the abundances of Thripidae and Phlaeothripidae families. Lines show estimated effects with other visitor taxa held at their observed mean values. Points represent actual abundance and fruit set values under open pollination (solid circles) and partial exclusion (open circles) treatments.

2.4. Discussion

Oil palm is a major crop, but our understanding of the role and drivers of insect-mediated pollination is incomplete. Using field experimental exclusion methods, we assessed the effects of flower visitor access (Question 1) and distance to nearby forest (Question 2) for oil palm fruit set. We found that, without flower visitor access, oil palm fruit set was reduced approximately fivefold, to 12%. On the other hand, the open and partial exclusion treatments did not differ in mean fruit set from the assisted pollination treatment, where we augmented natural pollination with hand pollination. When we included the effect of distance from forest in our model of fruit set, we found a trend of higher fruit set nearer the forest when larger organisms were excluded with partial exclusion.

In our analysis of the insect community from the sticky trap survey (Question 3), we found that most of the taxa we analyzed did not vary with distance from forest, and for those that did, the majority increased further from forest. The Lepidopteran family Gelechiidae, which increased with greater distance from the forest, was the most abundantly distributed of these taxa. We identified a co-occurring subset of taxa that were found in high abundance on both male and female inflorescences (*E. kamerunicus*, Gelechiidae, and Thysanoptera). Although the Dipteran family Drosophilidae also occurred with this group and increased closer to forest, it was not as widely prevalent. We modeled the association between *E. kamerunicus*, Gelechiidae, and Thysanoptera abundances and fruit set in open and partial exclusion treatments (Question 4). Only *E. kamerunicus*, a well-known oil palm pollinator, had strong associations with fruit set ($p \leq 0.05$), with a positive relationship under open pollination and a negative relationship under partial exclusion treatments. We synthesize and interpret these results in the following discussion.

2.4.1. Role of insect pollination in oil palm

One concern in oil palm production is yield gaps from pollination limitation (Woittiez et al. 2017). The palms within the smallholder farm of this study appear to not be pollen limited when comparing the fruit set under open pollination to supplementing open pollination with hand pollination. This comparison is important because supplementing with hand pollination has precedence in practice, as oil palm production outside Africa prior to the introduction of *E. kamerunicus* required augmenting natural pollination with similar methods (Syed et al. 1982). Effective insect pollination is advantageous for production, however, as insect pollination activity can take place continuously over the female inflorescence's multi-day, asynchronous bloom period (Tandon et al. 2001), while farm workers and researchers cannot conduct hand pollination with similar consistency. This is reflected historically, when fruit set generally increased following the introduction of *E. kamerunicus* in regions that previously used labor-intensive manual pollination (Li et al. 2019).

Comparing the relative difference in fruit production between natural pollination conditions and manually-applied pollen aligns with the typical definition of pollination limitation (Wurz et al. 2021). However, because oil palm produces parthenocarpic fruit types from unpollinated flowers, the sum of the pollinated and unpollinated fruits can be used to estimate a theoretical maximum fruit set for each fruit bunch (Lecoustre and Reffye 1987). Taking this theoretical maximum as the baseline for assessing pollination limitation rather than the assisted pollination treatment reveals that both open pollination and assisted pollination treatments fall short of the theoretical maximum pollination, and in some cases the partial exclusion treatment achieved the highest fruit set.

The results of our experiment suggest that additional factors related to the forest may moderate the important role floral visitors play in oil palm pollination and production. Our finding that the partial exclusion treatment had a significant increasing trend in fruit set closer to the forest is consistent with the hypothesis that benefits to oil palm pollinators spill over from nearby forest (Figure 2-1b). Our results also suggest that fruit set under partial exclusion exceeded open pollination next to forest (ca. 87% and 70%, respectively, Figure 2-4c), which we hypothesized would happen if antagonists were excluded by the partial exclusion treatment (Figure 2-1a). On the other hand, forest proximity had no effect when we completely excluded floral visitors, or when we supplemented natural pollination with hand pollination. Since the full exclusion and hand pollination treatments were meant to standardize the effect of pollinators, this suggests that the effect of distance from forest under the partial exclusion treatment was not standing in for an abiotic gradient that influenced pollination success, such as water or nutrient supply (Bos et al. 2007). Therefore, the significant pattern in fruit set over the gradient of distance from forest in the partial exclusion treatment most likely reflects changes in pollination function.

Oil production efficiency is thought to peak between 60% and 80% fruit set (Harun and Noor 2002), which is what we found on average for all but the full exclusion treatment fruit bunches. Under the full exclusion treatment, fruit set was well below the 40% level that Harun and Noor (2002) consider to be minimally sufficient to maintain an acceptable oil-to-bunch ratio of 20%. That the fruit set was still significantly above zero, even with full visitor exclusion, could reflect pollination resulting from wind dispersal, which was believed to be the main mode of pollination for oil palm prior to the discovery of insect pollination (Syed 1979). Our experiment was not designed to quantify the effect of wind pollination, however, as wind-dispersed pollen could also be influenced by the exclusion netting. Nevertheless, another study that excluded oil palm flower visitors similarly with a mesh net found a fruit set rate of 37%, which was also attributed to wind pollination (Dhileepan and Nampoothiri 1989).

2.4.2. Interpreting the role of forest in the floral visitor community

Our analysis of insect taxa observed on the sticky traps suggests that distance from forest plays a relatively small role in structuring the floral visitor community of oil palm for smallholder farms. Among the assemblage of insects associated with *E. kamerunicus*, only Drosophilidae was more abundant near forest. A Drosophilid species in Borneo, *Scaptodrosophila sp.*, may be attracted to fungi growing in decomposing oil palm flowers left by feeding adult and larval *E. kamerunicus* (Rizali et al. 2019b). However, unlike the most predominant taxa, i.e., Curculionidae, Gelechiidae, and Thysanoptera, we found Drosophilidae individuals in fewer than half of the traps over inflorescences, which suggests a limited role in pollination. Drosophilidae abundance can vary by species habitat specialization in tropical transformation landscapes (Furtado and Martins 2018); so the pattern we observed may reflect forest specialists declining away from their habitat.

Floral visitor taxa that increased further from forest may have favored oil palm plantations as a habitat, using resources associated with inflorescences such as pollen or flower parts, since areas further from the forest were closer to the neighboring large-scale oil palm plantation that had a densely planted oil palm monocrop. For example, Nitidulidae species that feed on pollen are noted as possible oil palm pollinators in West African and neotropical plantations (Li et al. 2019). Rizali et al. (2019b) also noted the presence of Gelechiidae on oil palm flowers. Previous research on Lepidoptera spillover in oil palm has shown that neighboring forest can have a positive effect on diversity, though some species increased within the oil palm habitat (Lucey and Hill 2012). Aside from Gelechiidae, these taxa had lower abundances and prevalence on the sticky traps and may be limited in their role in influencing pollination.

The overall relationship between the insect community and forest reflects the findings of Mayfield (2005), who determined that neither diversity nor visitation rate to oil palm flowers increased when comparing between near (0-15 m) and far (100-200 m) sites in relation to neighboring forest in Costa Rica. Forest is not thought to play a role in the natural history of *E. kamerunicus*, which relies solely on oil palm for habitat, breeding sites, and food (Syed 1982). However, a comparison between similar distances in Uganda found significantly higher abundances of *E. kamerunicus* in sites nearer forest, as well as higher visitor diversity (Egonyu et al. 2021). These contrasting results, taken with our own, demonstrate the variability in the role that neighboring vegetation may play in affecting the floral visitor community. Our own findings from the partial exclusion treatment suggest forest may play a moderating role in pollination services to oil palm. However, we were limited to a shorter distance gradient due to the size of the smallholder farm; future studies may find stronger relationships over a longer distance.

2.4.3. Relating trends in the floral visitor community and fruit set

We focused on the taxa Curculionidae (i.e., *E. kamerunicus*) and Thysanoptera to correlate with fruit set because they were present in nearly all the female inflorescence traps in high abundance, and are also noted pollinators in the literature (Li et al. 2019). Under open pollination, we found a trend that was consistent with *E. kamerunicus*’s role as a pollinator, but under the partial exclusion treatment, higher *E. kamerunicus* abundance was associated with lower fruit set. Other researchers have reported lower fruit set in farms with very high *E. kamerunicus* populations, which they attribute to intraspecific competition (Wahid and Kamarudin 1997). Our traps were placed outside of the exclosure treatments, so they cannot tell us directly about weevil abundance on the inflorescence. However, if higher trap abundances reflect higher visitation rates to the inflorescence itself, the effect of the partial exclosure may have created an enclosed environment where weevils could remain on the inflorescence longer and without disruption (e.g., by large predators), perhaps inducing this effect. Additional observations taken from within the exclosure would be needed to confirm this behavior.

There was no significant association between Thysanoptera and fruit set, but it is notable that very high Thysanoptera abundance (>1000) seemed to accompany higher and less variable fruit set (Figure 2-5c). Prior to the introduction of *E. kamerunicus*, a Thripidae species, *Thrips hawaiiensis*, was thought to be the main pollinator of oil palm in Southeast Asia (Syed 1979, Donough et al. 1996). This species can occur at high abundances, but its small size prevents individuals from carrying more than a few grains of pollen (Syed 1979). Its behavior is thought to be complementary to that of *E. kamerunicus*, with different active periods during the day (Anggraeni et al. 2013) and different seasonal population patterns that could contribute to long-term pollination stability (Wahid and Kamarudin 1997). We found that the abundance of Thripidae was strongly correlated with Phlaeothripidae, another Thysanopteran family that has so far not been identified as a pollinator in the literature.

Other species were orders of magnitude lower in abundance on the sticky traps, except for Gelechiidae, which we also included in the multiple regression model. Although another moth species, *Pyroderces* sp., is believed to be an oil palm pollinator (Syed 1979, Wahid and Kamarudin 1997), we did not find evidence that Gelechiidae had a significant relationship with fruit set. Though Gelechiidae had high abundances on both male and female inflorescence sticky traps, their presence on male inflorescences was not significantly higher than on non-flowering palms. This could indicate that Gelechiidae were generally prevalent throughout the farm and not targeting male flowers. Although two Gelechiid species have been reported to pollinate Phyllanthaceae (Luo et al. 2011), Gelechiidae have mainly been noted as crop pests (Picanço et al. 1998).

2.4.4. The role of nearby forest and antagonists of oil palm pollination

Based on our hypotheses for the exclusion experiment, we can infer that antagonists were excluded by the partial exclusion treatment, leading to the observed increase in fruit set closer to the forest edge. Antagonist agents that could decrease fruit set include floral antagonists that reduce pollination success, or predators of pollinators (Knight et al. 2005). In the first case, insect visitors could act as floral antagonists by depositing heterospecific pollen grains that decrease pollination success and fruit set (Wilcock and Neiland 2002). Plant communities with more co-flowering species, such as forest, could potentially increase pollination limitation by acting as a source of heterospecific pollen (Vamosi et al. 2006). However, none of the major floral visitor abundances that we found had a significant negative relationship with fruit set under open pollination that might reflect a floral antagonist role. Further, the exclusion of floral antagonists does not explain why fruit set decreased with greater distance from forest in the partial exclusion treatment. On the other hand, the lack of insect abundance relationships with distance from forest could suggest that a trait-mediated interaction, rather than a density-mediated interaction, influenced pollination services over this gradient (Benoit and Kalisz 2020). In particular, predation risk can strongly decrease flower visitation rates and time spent on flowers by pollinators, especially for smaller insects (Romero et al. 2011). This may be the case for oil palm pollinators such as *E. kamerunicus*, which must be small enough to enter the flowers of the female inflorescence. Further, given the short period that pollinators typically spend on a female inflorescence (Tandon et al. 2001), factors that modify these visits may play an important role in pollination effectiveness.

Future research should investigate how forest might increase pollination success, possibly through trait-mediated indirect interactions. For example, the positive effect of nearby forest on fruit set might be explained by intraguild predators (i.e., consumers of both mesopredators and their shared pollinator prey), such as birds and bats that spill over from the forest (Martin et al. 2013, Karp and Daily 2014). Though such larger predators can potentially disrupt pollination services by consuming *E. kamerunicus* (Ponnamma et al. 2006, Yue et al. 2015, Amit et al. 2015), they could also decrease overall predation pressure on *E. kamerunicus* and other pollinators if they simultaneously reduce mesopredators that more effectively suppress pollinator activity (Polis and Holt 1992). In a bird and bat exclusion experiment in oil palm in Jambi, Denmead et al. (2017) found that increased bird activity was associated with lower arthropod predator abundance and higher *E. kamerunicus* abundance, consistent with a release effect. This effect could decrease farther from forest for forest obligate intraguild predators, even within distances as short as 100 m (Hohlenwerger et al. 2022), while abundances of arthropod mesopredators may be less affected in oil palm (Lucey and Hill 2012, though diversity is often reduced; Junggebauer et al. 2021). The partial exclusion treatment may have also allowed floral visitors to spend more time on the inflorescence, which in turn increased pollination effectiveness (Chinchilla and Richardson 1991, Ivey et al. 2003), provided intraspecies competition was not too high (Wahid and Kamarudin 1997).

Further work would be needed to determine if intraguild predators are indeed suppressing arthropod mesopredators of pollinators and indirectly benefiting fruit set. We found spiders (Araneae) and earwigs (Dermaptera) in the sticky traps, which can prey on *E. kamerunicus* (Ponnamma et al. 2006, Yue et al. 2015) and would have been excluded by the partial exclusion treatment. However, we did not conduct further analysis on these groups, since our sticky traps were designed to sample flying insects and would not have been representative for these predators. Future work should also compare the relative negative impacts of intraguild versus arthropod predators on pollinators. Though arthropod predators can negatively influence pollination services (Suttle 2003, Romero et al. 2011), the overall outcome of intraguild predation often suppresses both arthropod predators and herbivores (Mooney et al. 2010). However, the effect of intraguild predation can depend on the predator taxa and landscape context (Martin et al. 2013, Karp and Daily 2014, Librán-Embid et al. 2017). Experimental tests to disentangle the effects of these two levels of predators in oil palm in relation to nearby forest could clarify their influence on pollination.

2.5. Conclusions

Oil palm is an economically significant crop, but its production is also a driver of deforestation and biodiversity loss. Our study underscores the critical role pollinators and associated insects play for this important crop, as excluding floral visitors severely limited fruit set. We also find trends that suggest ecological spillover from nearby forest may affect pollinating activity, perhaps through intraguild predation by forest predators on arthropod mesopredators of pollinators within the farm. Predation spillover from natural habitat can also provide biological control in oil palm (Nurdiansyah et al. 2016, Rizali et al. 2019a, but see Gray and Lewis 2014) so the tradeoff between these potential ecosystem services should be quantified (Saunders et al. 2016). Our findings demonstrate that a fuller understanding of ecosystem functions and services associated with biodiversity and habitat conservation should include the multiple and interacting functions of wildlife in agroecosystems. This broader understanding could help develop mutually beneficial agroecological practices and landscape conservation planning initiatives to support both biodiversity and farmer livelihoods (Koh et al. 2009, Grass et al. 2019, Perfecto et al. 2019).

Authors' contributions

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

Acknowledgements

We thank CR Donough for help on hand pollination methods; F Nurdiansyah for contributing field expertise; N Marbun, S Baktiar, and R Prihartini for field assistance; Arini, IPJ Yustia, and F Herawani for identification assistance; and MT Sitompul for the use of his farm. Very helpful comments by Edgar Turner and two anonymous reviewers improved the paper. This study was funded by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) – project ID 192626868 – SFB 990 in the framework of the collaborative German-Indonesian research project CRC 990.

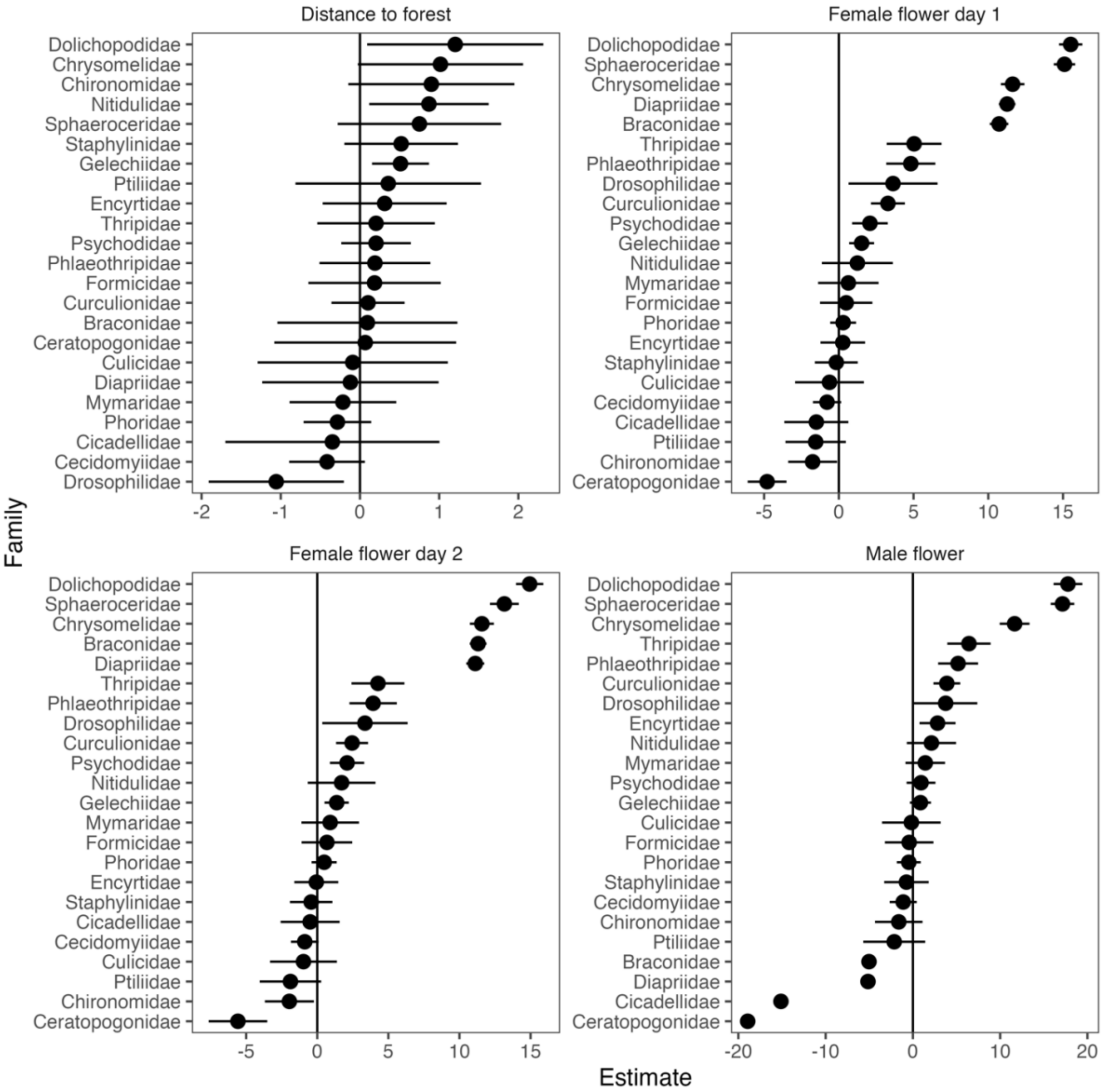
Data availability

Data available from: https://doi.org/10.6084/m9.figshare.20322423.v1

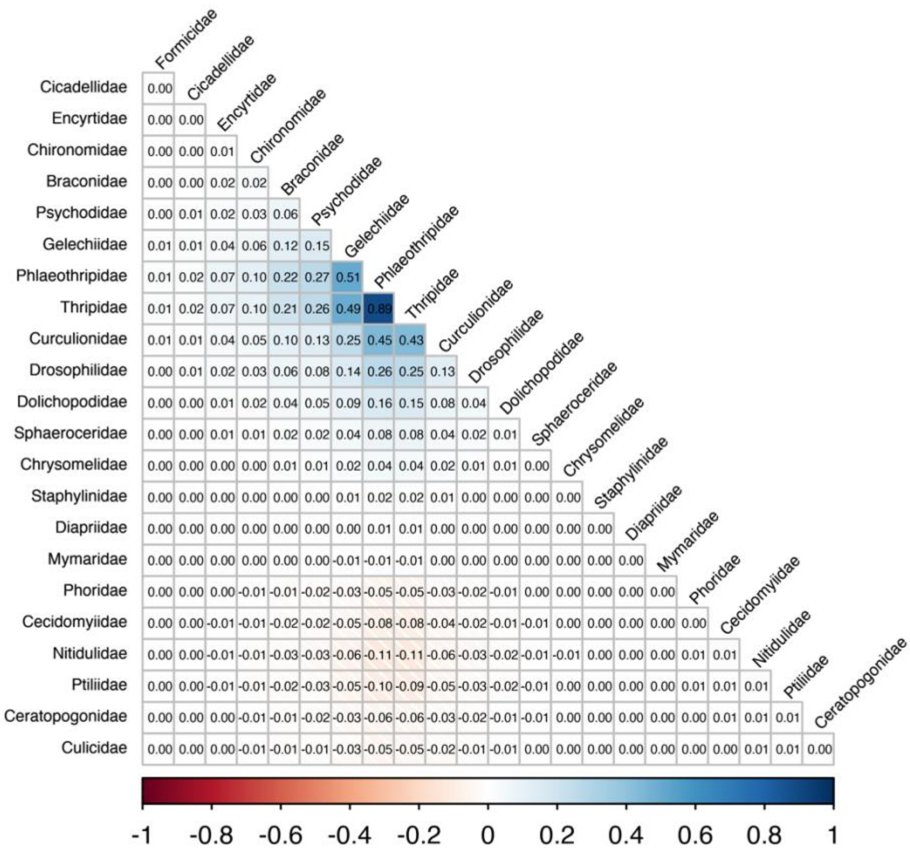
2.6. Supporting Information

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 Figure 2-2. Coefficient estimates for the generalized linear multivariate model of floral visitor families and 95% confidence intervals. Distance to forest is a continuous variable (distance in meters) divided by two standard deviations to rescale the effect sizes to match the rest of the (categorical) variables. The categorical variables "Female flower day X" is the log increase in taxa abundance predicted on a female flower on the X day of opening, compared to the control (nonflowering) palms. Likewise, "Male flower" is the log increase in taxa abundance on male flowers. Large magnitudes of effect size in the flower sex variables suggest that the associated taxon was either absent in the control palms (giving a strongly positive estimate) or absent in the inflorescence (giving a strongly negative estimate).



	Formicidae	Cicadellidae	Encyrtidae	Chironomidae	Braconidae	Psychodidae	Gelechiidae	Phlaeothripidae	Thripidae	Curculionidae	Drosophilidae	Dolichopodidae	Sphaeroceridae	Chrysomelidae	Staphylinidae	Diapriidae	Mymaridae	Phoridae	Cecidomyiidae	Nitidulidae	Ptiliidae	Ceratopogonidae
Cicadellidae	0.00																					
Encyrtidae	0.00	0.00																				
Chironomidae	0.00	0.00	0.01																			
Braconidae	0.00	0.00	0.02	0.02																		
Psychodidae	0.00	0.01	0.02	0.03	0.06																	
Gelechiidae	0.01	0.01	0.04	0.06	0.12	0.15																
Phlaeothripidae	0.01	0.02	0.07	0.10	0.22	0.27	0.51															
Thripidae	0.01	0.02	0.07	0.10	0.21	0.26	0.49	0.89														
Curculionidae	0.01	0.01	0.04	0.05	0.10	0.13	0.25	0.45	0.43													
Drosophilidae	0.00	0.01	0.02	0.03	0.06	0.08	0.14	0.26	0.25	0.13												
Dolichopodidae	0.00	0.00	0.01	0.02	0.04	0.05	0.09	0.16	0.15	0.08	0.04											
Sphaeroceridae	0.00	0.00	0.01	0.01	0.02	0.02	0.04	0.08	0.08	0.04	0.02	0.01										
Chrysomelidae	0.00	0.00	0.00	0.00	0.01	0.01	0.02	0.04	0.04	0.02	0.01	0.01	0.00									
Staphylinidae	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.02	0.02	0.01	0.00	0.00	0.00	0.00								
Diapriidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00							
Mymaridae	0.00	0.00	0.00	0.00	0.00	0.00	-0.01	-0.01	-0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00						
Phoridae	0.00	0.00	0.00	-0.01	-0.01	-0.02	-0.03	-0.05	-0.05	-0.03	-0.02	-0.01	0.00	0.00	0.00	0.00	0.00					
Cecidomyiidae	0.00	0.00	-0.01	-0.01	-0.02	-0.02	-0.05	-0.08	-0.08	-0.04	-0.02	-0.01	-0.01	0.00	0.00	0.00	0.00	0.00				
Nitidulidae	0.00	0.00	-0.01	-0.01	-0.03	-0.03	-0.06	-0.11	-0.11	-0.06	-0.03	-0.02	-0.01	-0.01	0.00	0.00	0.00	0.01	0.01			
Ptiliidae	0.00	0.00	-0.01	-0.01	-0.02	-0.03	-0.05	-0.10	-0.09	-0.05	-0.03	-0.02	-0.01	0.00	0.00	0.00	0.00	0.01	0.01	0.01		
Ceratopogonidae	0.00	0.00	0.00	-0.01	-0.01	-0.02	-0.03	-0.06	-0.06	-0.03	-0.02	-0.01	-0.01	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.01	
Culicidae	0.00	0.00	0.00	-0.01	-0.01	-0.01	-0.03	-0.05	-0.05	-0.02	-0.01	-0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.00

Appendix Figure 2-3. Pairwise residual correlations between taxa from the GLLVM with model terms distance to forest, inflorescence sex, and day of flowering (for female inflorescences). Higher correlation values qualitatively indicate pairwise associations between taxa, after accounting for the effects of the model variables. Positive values of residual correlation between taxa (blue) indicate positive correlation in occurrence. Likewise, negative (red) values indicate negative correlation in occurrence.

Appendix Text 2-1. 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) by puffing with a clean handheld pump applicator.

Appendix Table 2-1. Comparison in information criteria scores (IC) between alternative models for fruit set in exclusion treatment experiment: (a) between generalized linear mixed effects model (GLMM) modeling a linear effect of forest distance, and generalized additive mixed effects model (GAMM) modeling a nonlinear effect of forest distance; and (b) with other environmental gradient variables that were correlated with distance to forest distance on the site: altitude and palm age. Information criteria scores of the forest distance GLMM in (a) differ from those presented in (b) and the main text because the scores in (a) are calculated from a model estimated with a different r package, "mgcv" (Wood 2011), which allows direct comparison of IC scores with the nonlinear model also estimated by that package. Models in (b) are estimated with the package "glmmTMB" (Brooks et al. 2017).

a.	AICc	AIC	BIC
Treatment × Forest distance (GLMM)	-79.295	-141.572	-41.873
Treatment × Forest distance (GAMM)	-59.801	-135.184	-28.431
b.			
Treatment × Forest distance (main text)	-97.380	-100.096	-74.878
Treatment × Altitude	-98.917	-101.633	-76.415
Treatment × Palm age	-97.949	-100.665	-75.447

Appendix Table 2-2 (next page). Table of family-level summary statistics of arthropods collected from sticky traps.

Order/Taxon	Family	Sub-group	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.)
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	Curculionidae	*E. kamerunicus*	3185	87	22.7 (28.1)	86	53.3 (39)	20	15 (19.8)
	Anthicidae		7	5	1 (0)	0	-	0	-
	Bothrideridae		1	1	1 (-)	0	-	0	-
	Brentidae		2	1	2 (-)	0	-	0	-
	Carabidae		1	1	1 (-)	0	-	0	-
	Chrysomelidae		21	11	1.2 (0.6)	14	1 (-)	0	-
	Cicindelidae		1	1	1 (-)	0	-	0	-
	Coccinellidae		9	6	1 (0)	0	-	0	-
	Elateridae		10	6	1.1 (0.3)	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		74	24	1.9 (1.8)	43	1.7 (1.2)	10	1 (-)
	Phalacridae		1	1	1 (-)	0	-	0	-
	Ptiliidae		64	12	2.7 (2.7)	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	-
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	Anthomyiidae		1	1	1 (-)	0	-	0	-
	Camillidae		2	1	2 (-)	0	-	0	-
	Cecidomyiidae		285	51	3.3 (3.5)	43	2.7 (2.9)	90	4.2 (1.5)
	Ceratopogonidae		49	3	1 (0)	0	-	80	5.6 (3.2)

Order/Taxon	Family	Sub-group	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.)
Diptera	Chironomidae		47	12	1.9 (1)	14	2 (-)	60	2 (1.3)
	Chloropidae		20	3	2 (2)	0	-	50	2.4 (0.9)
	Culicidae		33	11	1.8 (1.8)	14	2 (-)	10	3 (-)
	Dolichopodidae		53	12	2.5 (2)	57	2 (1.4)	0	-
	Drosophilidae		440	37	8.1 (10.7)	29	5.5 (6.4)	10	1 (-)
	Lauxaniidae		2	1	1 (-)	0	-	10	1 (-)
	Micropezidae		9	6	1 (0)	0	-	0	-
	Muscidae		1	1	1 (-)	0	-	0	-
	Mycetophilidae		4	1	1.5 (0.7)	14	1 (-)	0	-
	Phoridae		699	76	5.9 (9.9)	71	2.6 (1.8)	100	3.2 (1.9)
	Psychodidae		616	76	5.5 (6.7)	57	2 (0.8)	30	1.7 (1.2)
	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	-
	Unknown Diptera		2	1	2 (-)	0	-	0	-
Hemiptera	Aleyrodidae		1	1	1 (-)	0	-	0	-
	Alydidae		1	1	1 (-)	0	-	0	-
	Aphididae		11	7	1.1 (0.3)	0	-	0	-
	Cicadellidae		28	10	1.6 (0.9)	0	-	20	2 (0)
	Miridae		14	7	1.3 (0.9)	14	1 (-)	0	-
Hymenoptera	Agaonidae	Other Hymenoptera	1	1	1 (-)	0	-	0	-
	Formicidae		118	26	3 (3.7)	29	1 (0)	40	1 (0)
	Mutilidae		2	1	2 (-)	0	-	0	-
	Mymaridae		35	20	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	-
	Aphelinidae	Parasitic wasps	1	1	1 (-)	0	-	0	-
	Braconidae		14	8	1.2 (0.4)	0	-	0	-

				Female traps (n = 144)		Male traps (n = 7)		Control traps (n = 10)	
Order/Taxon	Family	Sub-group	Total	% Traps present	Mean when present (s.d.)	% Traps present	Mean when present (s.d.)	% Traps present	Mean when present (s.d.)
Hymenoptera	Ceraphronidae	Parasitic wasps	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		140	26	2.1 (2.4)	43	19 (20.7)	40	1.2 (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		4	1	1 (0)	0	-	20	1 (0)
	Scelionidae		9	3	1.2 (0.5)	14	2 (-)	20	1 (0)
	Torymidae		3	2	1 (0)	0	-	0	-
	Trichogrammatidae		39	6	1 (0)	29	15.5 (17.7)	0	-
Lepidoptera	Gelechiidae		1578	90	11.8 (13.5)	71	7.6 (1.8)	80	2.8 (2.8)
Orthoptera	Gryllidae		1	1	1 (-)	0	-	0	-
	Orthoptera		1	1	1 (-)	0	-	0	-
Psocoptera	Elipsocidae		1	1	1 (-)	0	-	0	-
	Pachytroctidae		6	3	1.2 (0.5)	0	-	10	1 (-)
	Psocidae		1	0	-	0	-	10	1 (-)
Thysanoptera	Phlaeothripidae		34810	90	262.2 (532)	100	129.6 (118.1)	40	18.8 (33.5)
	Thripidae		20906	90	151.1 (274.8)	100	173.9 (127.9)	30	13.7 (21.9)

Appendix Table 2-3. Generalized additive model exploring nonlinear relationship between Thysanoptera abundance and fruit set. Separate smooth terms were fit to open pollination (the baseline) and partial exclusion treatment bunches using the r package "mgcv" (Wood 2011). These nonlinear effects were not significant.

Predictors	Estimates	CI	*p*
(Intercept)	1.46	0.91 – 2.36	0.119
Treatment [Partial]	1.85	0.89 – 3.86	0.099
Smooth term (Thysanoptera) × Treatment [Open]			0.812
Smooth term (Thysanoptera) × Treatment [Partial]			0.454
Random effect (TreeID)			**<0.001**
Observations	38		
R^2	0.686		

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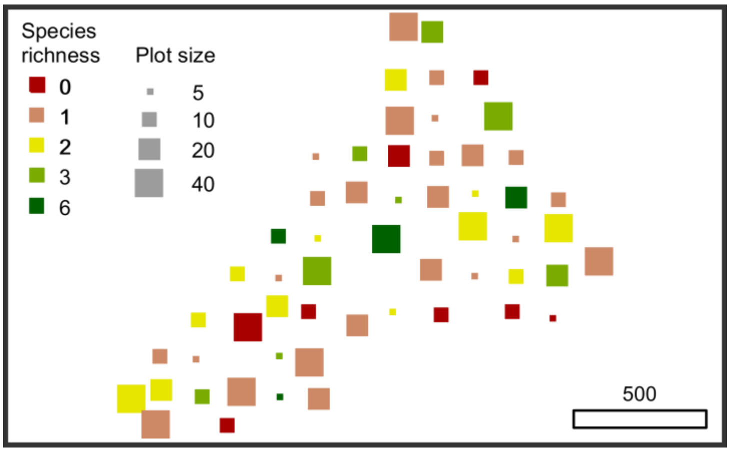
Chapter 3

Canopy openness drives insect-mediated ecosystem functions in oil palm biodiversity enrichment experiment in Indonesia



Kevin Li[1] *, Ingo Grass[2], Delphine Clara Zemp[3,b], Hendrik Lorenz[4], Lena Sachsenmaier[3,c], Fuad Nurdiansyah[5], Dirk Hölscher[4], Holger Kreft[3,6], Teja Tscharntke[1,6]

[1]Agroecology, Department of Crop Sciences, University of Göttingen, Göttingen, Germany

[2]Department of Ecology of Tropical Agricultural Systems, University of Hohenheim, Stuttgart, Germany

[3]Biodiversity, Macroecology and Biogeography, University of Göttingen, Göttingen, Germany

[4]Tropical Silviculture and Forest Ecology, University of Göttingen, Göttingen, Germany

[5]Faculty of Agriculture, Jambi University, Jambi City, Indonesia

[6]Centre of Biodiversity and Sustainable Land Use (CBL), University of Göttingen, Göttingen, Germany

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[b] Current address: Conservation Biology Laboratory, Institute of Biology, University of Neuchâtel, Switzerland.
[c] Current address: German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Germany / Systematic Botany and Functional Biodiversity, Leipzig University, Germany

Abstract

As the extent of oil palm (*Elaeis guineensis*) cultivation has expanded at the expense of tropical rainforests, enriching conventional large-scale oil palm plantations with native trees has been proposed as a strategy for restoring biodiversity and ecosystem function. However, how tree enrichment affects insect-mediated ecosystem functions is unknown. We investigated impacts on insect herbivory and pollination functions in the fourth year of a plantation-scale, long-term oil palm biodiversity enrichment experiment in Jambi, Sumatra, Indonesia. Within 48 plots systematically varying in size (25-1600 m^2) and planted tree species richness (1-6 species), we collected data on vegetation structure, understory insect abundances, and pollinator and herbivore activity on chili peppers (*Capsicum annuum*), a widespread home garden crop, as phytometer plants to quantify insect-mediated ecosystem functions. We examined the independent effects of plot size, tree species richness, and tree identity using the linear model for random partition design. These experimental treatments had the most relationships with vegetation structure: the tree species *Peronema canescens* strongly decreased (by approximately one standard deviation) both canopy openness and understory vegetation cover; the smallest plots had the lowest understory flower density and richness; and total planted tree species richness decreased flower density. Enrichment influenced herbivorous insects and natural enemies in the understory to a lesser extent: both groups had higher abundances in plots with two enrichment species planted, while herbivores decreased with increasing tree species richness. We found no strong direct relationships between experimental treatments and pollinator activity or most phytometer plant variables, except for lower leaf damage in the smallest plot size. Linking relationships in structural equation models shows that the negative association between *P. canescens* and understory vegetation cover was mediated through canopy openness. Likewise, canopy openness mediated increases in herbivore and pollinator insect abundances. Higher pollinator visitation increased phytometer yield, while impacts of insect herbivores on yield were not apparent. Our results demonstrate that even at an early stage, ecological restoration influences insect-mediated ecosystem functions, mainly through canopy openness. These findings suggest that maintaining some canopy gaps while enrichment plots develop may be beneficial for increasing habitat heterogeneity and insect-mediated ecosystem functions.

Key words: biodiversity, restoration, ecosystem functions, ecosystem services, pollinators, natural enemies, herbivores, chili pepper (*Capsicum annuum*), TreeDivNet, EFForTS-BEE

3.1. Introduction

In landscapes dominated by oil palm (*Elaeis guineensis*, Arecaceae), biodiversity is much lower than in natural forests (Savilaakso et al. 2014, Barnes et al. 2017), which negatively 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 declining, 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), adding 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, oil palm landscapes are a compelling priority for ecological restoration (Mittermeier et al. 2011, Meijaard et al. 2018). Therefore, methods of improving biodiversity and ecosystem function in these landscapes are needed (Koh et al. 2009, Foster et al. 2011, Darras et al. 2019).

The link between biodiversity and ecosystem function is an important topic in ecological research (Cardinale et al. 2006, Benayas et al. 2009), with practical relevance in conservation and agroecology (Manning et al. 2019). Diversified agroecosystems can contribute significantly to the provision of important ecosystem functions 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, Grossman et al. 2018). Understanding trade-offs in such services and disservices from increasing semi-natural habitat is important in restoration and agricultural management, but research rarely examines the associated ecological processes and interactions behind these outcomes (Saunders 2020).

Insects play an important role in providing ecosystem services and disservices in agroecosystems. Pollination by insects contributes to the yield of nearly 70% of major crops (Klein et al. 2007), while biocontrol of agricultural pests by insect natural enemies also plays a major role in agricultural production, especially in tropical agroecosystems. Oil palm cultivation has been found to have a negative impact on pollinator and biocontrol-associated insect species (Lucey and Hill 2012, Nurdiansyah et al. 2016, Rizali et al. 2019). Recent conservation efforts around oil palm have promoted the introduction of high-value conservation areas (Senior et al. 2015) but the conditions under which conservation measures are effective in promoting ecosystem functions are not well known. Remnant riparian fragments within oil palm landscapes do not appear to promote biocontrol services, but also do not increase herbivory disservices (Gray and Lewis 2014, Woodham et al. 2019). However, the outcome of enrichment or restoration of tree biodiversity in oil palm plantations for insect-mediated ecosystem functions is still an area of developing research (Luke et al. 2020).

In this study, we investigate the effects of mixed-species tree planting on pollination, biocontrol, and herbivory functions from flying insects using an experimental tree biodiversity framework. Our study makes use of a long-term biodiversity enrichment experiment (Teuscher et al. 2016) in Sumatra, Indonesia, within the Ecological and Socio-economic Functions of Tropical

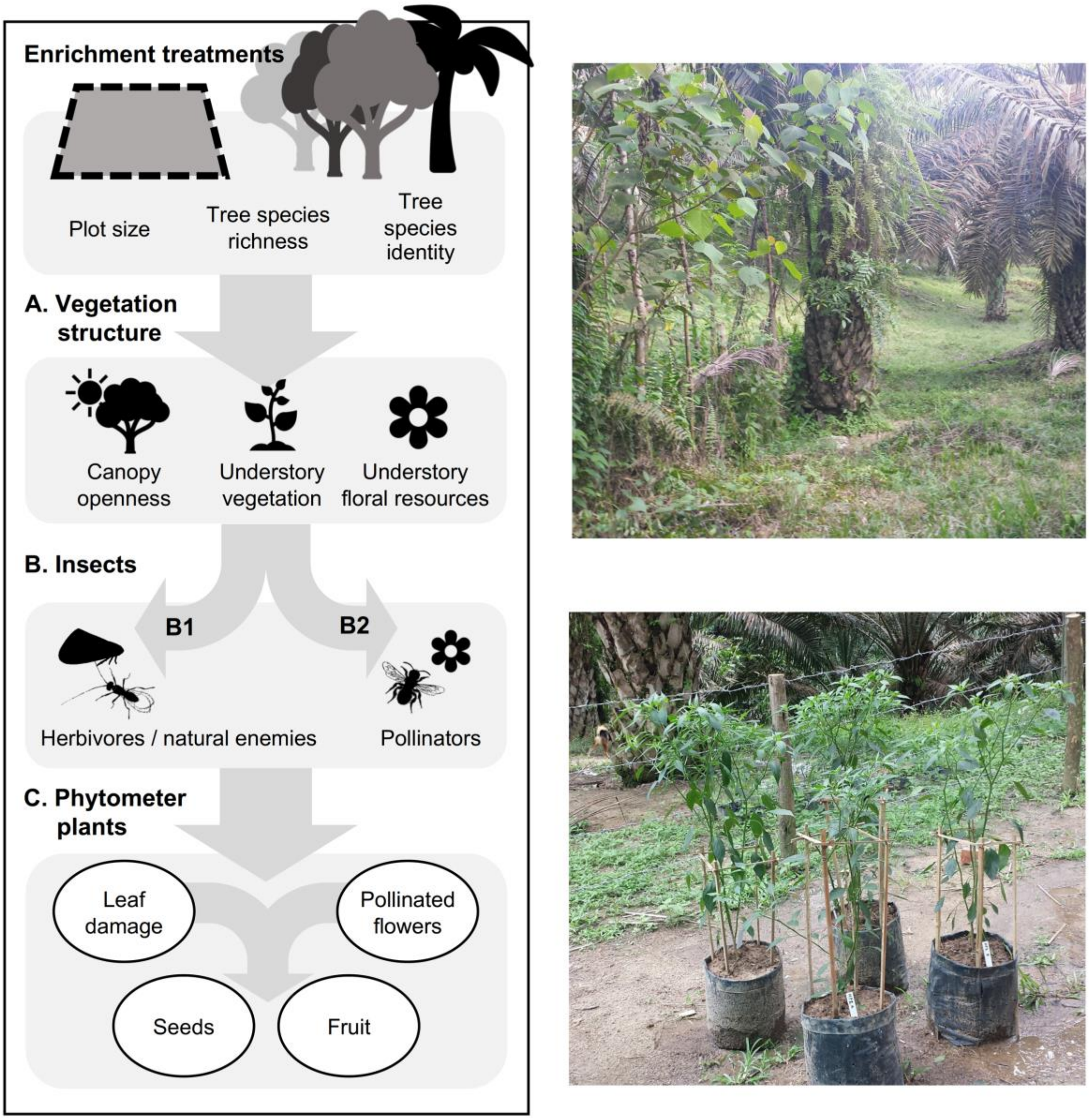


Figure 3-1. Diagram of hypothesized flow of effects from enrichment treatments to levels of endogenous variables: (A) vegetation structure, (B) insects-level ecosystem functions, and (C) phytometer plant-level ecosystem functions. Upper-right photo shows example of an enrichment plot (left side of photo) within oil palm context. Plot is 20 x 20m and is planted with one enrichment tree species, *Parkia speciosa* (Fabaceae). Lower-right photo demonstrates phytometer plant setup as it would be in each enrichment plot.

Lowland Rainforest Transformation Systems (EFForTS) collaborative research center (Drescher et al. 2016). In the experiment, an oil palm monoculture has been enriched with multiple native tree species in experimental plots, systematically varying plot size and planted tree species richness, allowing for the partitioning of the effects of tree species richness, identity, and plot size (Teuscher et al. 2016). We used chili pepper (*Capsicum annuum*, Solanaceae) as a phytometer (or sentinel) plant to serve as a sensor for pollination and herbivory ecosystem functions related to yield (fruit and seed counts). To explore the ecological pathways of the observed effects of enrichment, we tested hypothesized relationships of ecosystem functions outlined in Figure 3-1 and Table 3-1, using covariance-based structural equation models (SEM). This approach can help disentangle interrelated ecological variables by comparing the covariance of observed data to the theoretical covariance of a proposed system of relationships (Grace 2008).

3.2. Methods

3.2.1. Study site

We conducted our study in the fourth year of the EFForTS biodiversity enrichment experiment (EFForTS-BEE), which was established 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) and receives on average 2235±385mm of annual rainfall (Drescher et al. 2016).

The biodiversity enrichment experiment uses an array of 48 enrichment plots established within a conventional oil palm monoculture (exemplary photo in Figure 3-1) to test the effects of mixed-species tree planting and natural regeneration as strategies for increasing biodiversity and ecosystem functioning (Teuscher et al. 2016). The experiment systemically varies plot size and planted tree species richness following a random partition design (Teuscher et al. 2016). The plots were assigned among four categories of sizes (quadrats of 5x5, 10x10, 20x20, and 40x40 m) and were further partitioned into levels of planted tree species richness (1, 2, 3, and 6 species), which forms blocks where each species is represented in equal proportion. At intermediate levels of diversity (2 and 3 species), plot species composition was assigned randomly without replacement from the species pool. This setup allows for separation of the effects of plot size, tree species richness, and tree species identity without the need for a full factorial design (Bell et al. 2009).

Enrichment plots were established by thinning oil palms in the plots by 40% on average, although the number of felled oil palms depended on the plot size (Gérard et al. 2017). Enrichment tree seedlings were planted in a 2 m grid within the plot and the plot was protected by a perimeter fence. Planted tree species were *Archidendron jiringa* (Fabaceae), *Parkia speciosa*, (Fabaceae), *Peronema canescens* (Lamiaceae), *Durio zibethinus* (Malvaceae), *Dyera polyphylla* (Apocynaceae), and *Shorea leprosula* (Dipterocarpaceae). After tree planting, typical oil palm plantation management, including fertilizer and pesticide applications were halted within the plots for the experiment. Weeding was continued within the plots until 2.5 years after plot establishment, which allowed 1.5 years of natural vegetation development before the earliest sampling of this study, in November 2017. Further details about the experiment can be found in Teuscher et al. (2016) and Zemp et al. (2019b).

3.2.2. Plot field data collection

Vegetation structure variables

We estimated average flower density of each plot from 228 flower transect surveys (six transects per plot), conducted November-December. 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 these transects to also estimate plot flower richness, supplemented with a spatially stratified quadrat in January 2018. We conducted 5x5 m quadrat surveys of flower richness, sampling the entirety of the 25 m^2 plots and placing one quadrat in the 100 m^2 plots, three quadrats in the 400 m^2

plots, and 13 quadrats in the 1600 m^2 plots, the latter subplots representing 25%, 19%, and 20% of the total plot area, respectively. The quadrats were stratified in space so that one quadrat was always placed in the plot center and additional quadrats were placed randomly within equal divisions of the enrichment plot. We estimated the plot flower 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).

In March-May 2018, we estimated percent coverage of vegetation below a height of 1.3 m in 5x5 m subplots nested within each enrichment plot (Sachsenmaier 2018). Vegetation coverage estimation was based on consensus by two observers and excluded coarse woody debris, bare ground, senescent plants, leaf litter, or the phytometer plants. Canopy openness, which quantifies the fraction of sky not blocked by vegetation, was measured in April-May 2018 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). 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.

Survey of understory flying insects

We estimated abundances of herbivorous and natural enemy (predatory and parasitoid) insects from sweep net surveys of the herbaceous vegetation layer, conducted in the enrichment plots from November to December 2017. Within the understory vegetation of each plot, a surveyor made five evenly spaced sweeps, covering ca. 1 m of vegetation each, along a randomly placed 5 m transect using a 32 cm diameter sweep net (BioForm, Nuremburg, Germany). All flying insects (i.e., excluding Formicidae) were collected and individually preserved on site in 1.5 ml Eppendorf tubes with 70% ethanol. We identified samples to family using a binocular microscope and 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 functional groups (Section 3.6 Appendix S1, Appendix Table 3-1), which form the basis of the herbivore and natural enemy abundance variables in our models. We conservatively excluded families with mixed trophic niches (approximately one-third of families) from our counts of herbivore and natural enemy abundances.

3.2.3. Phytometer plants

We estimated the ecosystem functions of pollination and herbivory using phytometer plants, which we set in the enrichment plots. We selected *Capsicum annuum* (chili pepper) as a phytometer plant species because of its potential shade tolerance (Pouliot et al. 2012), its widespread home garden cultivation in this region (Prabowo et al. 2016), and the potential for generalist pollinators to increase fruit quality and yield (Roldán Serrano and Guerra-Sanz 2006). We raised 1500 individuals of a locally available variety of *C. annuum* from seeds. During a 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.

In early February 2018, we selected four healthy individuals of comparable size to place in each of the 48 enrichment plots (192 total). We halted fertilizer and pesticide application one week prior to placement in the plots and only watered as conditions required thereafter. Immediately prior to placement, we removed any flowers that had already opened to ensure pollination could be attributed to plot conditions. We placed four chili plants together with plant stems forming a 60 cm square at approximately the plot center in a location receiving at least partial sunlight and free from encroaching vegetation (exemplary photo in Figure 3-1). Plants were kept in their original polyethylene containers to isolate them from local soil conditions.

Monitoring insect functions and phytometer plants

During five weeks from February to March 2018, we conducted flower visitor observations while the chili plants bloomed in the field. Once a week for each plot on non-rainy days, a pair of observers counted flower visits by flying insects over a 5-minute period between 9:00 and 15:00, for a total of 25 observation minutes. We allowed a one-minute acclimatization period before each observation to reduce the effect of disturbance. After each observation session, we counted the number of chili flowers and estimated the proportion of leaves with damage, including insect herbivory, discoloration, or distortion.

We began harvesting ripe fruits after week five, continuing until all fruits were collected. 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 pollination and fruiting success by calculating the mean fruit-flower ratio of the plot, which was the mean number of fruits per plant divided by the mean number of flowers per plant over five weeks prior to harvest.

3.2.4. Analysis

We modeled the direct relationships between the experimental enrichment treatments and the response variables in Table 3-1 by applying the random partition linear modeling procedure (Bell et al. 2009). We then tested hypothesized ecological pathways (summarized in Table 3-1) with structural equation models (SEMs) within the levels of direct and indirect effects proposed in Figure 3-1: (A) the effects of experimental enrichment treatments on plot vegetation structure; (B1) effects on herbivore and natural enemy insects, and (B2) on pollinator insects; and (C) herbivory and pollination functions in the phytometer plants.

Analyses were conducted with R statistical software (R Core Team 2021). We estimated flower richness using the “vegan” package (Oksanen et al. 2019). Following recommended practices (Gotelli and Ellison 2004, Warton and Hui 2011), we applied appropriate transformations (Table 3-1) to the response 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). All variables were mean centered and unit variance scaled for comparability of effect sizes.

Random partition analysis

The experimental treatments were assigned according to the linear model for random partition design (Bell et al. 2009), which was adapted to EFForTS-BEE (Zemp et al. 2019a) and analyzed using code made available by Bell et al. (2009). The design allowed us to separately quantify the effects of tree species identity, tree species richness (linear and nonlinear effects), and plot size on the ecological response variables. The overall model is specified as:

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

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, which does not require the contribution of each species to the response to be directly measurable. Because the non-linear species richness term β_{NLR} is orthogonal to species identity effects (β_i), it quantifies the deviation from the linear richness expectation that is not attributed to tree species identity, hence representing species interaction strength.

Table 3-1. Ecological response (endogenous) variables, with transformation used, interaction level, and hypothesized driver in structural equation models. Interaction levels correspond to those presented in Figure 3-1: A = Vegetation structure; B1 = Herbivore and natural enemy insects; B2 = Pollinator insects; C = Insect-mediated ecosystem functions in phytometer plants. Asterisk (*) indicates significant biodiversity enrichment treatment from random partition results.

Endogenous variable	Transformation	Level	Hypothesized relationships
Canopy openness	Logit	A	Plot size, tree species identity*
Understory vegetation cover	None	A	Canopy openness, tree species identity*
Understory flower richness	Log	A	Canopy openness, understory vegetation cover, plot size*
Understory flower density	Log	A	Canopy openness, understory vegetation cover, tree species richness*, plot size*
Herbivore abundance	Log	B1	Understory vegetation cover, canopy openness, natural enemy abundance, tree species richness*, non-linear tree species richness*
Natural enemy abundance	Log	B1	Understory vegetation cover, canopy openness, herbivore abundance, non-linear tree species richness*
Chili pollinator abundance	Log	B2	Understory flower richness, understory flower density, canopy openness, understory vegetation cover
Chili flower visits	Log	B2	Chili pollinator abundance, understory flower richness, understory flower density, canopy openness, understory vegetation cover
Chili fruit-flower ratio	Log	C	Chili flower visits, chili leaf damage, canopy openness
Chili leaf damage	None	C	Herbivore abundance, plot size*
Fruit per chili plant	Log	C	Chili fruit-flower ratio, chili leaf damage, canopy openness
Seeds per chili fruit	None	C	Chili flower visitors, chili leaf damage

Structural equation models

We built four separate structural equation models representing the hypothesized flow diagram of enrichment treatment effects (Figure 3-1), presented in Table 3-1 as the drivers of each endogenous response variable. These hypotheses and supporting information are described in more detail in Section 3.6 Appendix S3. We followed a "weight of evidence" approach (Grace 2020), which involves building models based on prior knowledge and making ecologically-sound adjustments using multiple lines of evidence. After removing unsupported links, we compared plausible intermediate models to test whether the significant effects of tree enrichment treatments identified in the random partition analysis (Table 3-1, marked with asterisks) were mediated by ecosystem function variables.

We fit structural equation models by maximum likelihood estimation using the 'lavaan' package (Rosseel 2012). We assessed model distinguishability with the Vuong variance (ω^2) test using the package "nonnest2" (Merkle et al. 2016b). For distinguishable models, we used robust alternative likelihood ratio test variants for nested (LR) and non-nested (z) model comparisons (Vuong 1989, Merkle et al. 2016a). We report the χ^2 exact fit index of the final models, as well as the Swain small sample size correction adjusted for our sample size (n=48) (Rosseel 2020). In Section 3.3 we present overviews of the final models and a narrative summary of the comparisons testing alternative model structures. Full model results, additional approximate fit measures, and details about model comparisons are presented in Section 3.6 Appendix S3.

3.3. Results

3.3.1. Plot data summaries

Across all plots and transects, we found a total of 21 understory vegetation species with flowers. At this stage of the experiment, the planted enrichment tree species had not matured enough to produce flowers except for a few individuals of *A. jiringa*. The two most abundant flower species were the invasive species *Miconia crenata* (Melastomataceae) and *Asystasia gangetica* (Acanthaceae) which accounted for 57 and 21% of all flower units, respectively. 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 SD) % in 5x5m subplots. Plot canopy openness had a mean of 10 (±8.2 SD) %.

On the 48 transects, we identified a total of 934 insect individuals representing 68 families in 11 orders. Of these, 231 individuals were from 20 families (6 orders) that were exclusively herbivorous, and 260 individuals were from 23 families (6 orders) that were exclusively predatory or parasitic, i.e., natural enemies (more information in Section 3.6 Appendix S1, Appendix Table 3-1). Mean sweep net herbivore count was 4.8 (±4.5 SD) and mean natural enemy count was 5.4 (±3.6 SD). From the cumulative 25 minutes of phytometer plant monitoring at each plot, we observed 89 pollinators (plot mean = 1.9 ±2.2 SD) making a total of 327 chili flower visits (plot mean = 6.8 ±9.5 SD).

Phytometer plants produced an average of 0.56 (±0.39 SD) fruits per observed flower (fruit-flower ratio). We harvested 3108 fruits (plant mean = 18.9 ±23.2 SD). Based on a subset of the fruit harvested (n= 1287), we calculated a mean of 41.1 (±12.8 SD) seeds per fruit. We excluded six outlier plants that never produced any flowers from fruit and seed calculations.

3.3.2. Enrichment treatment effects from the random partition analysis

Tree species richness as a linear predictor (“linear richness”) explained significant variability in flower density (Section 3.6 Appendix S2, Appendix Table 3-2) and herbivore abundance (Appendix Table 3-3) in random partition models. In both cases, linear richness had a negative effect (Figure 3-2a). The linear richness model coefficient for flower density was β_{LR} = -0.21±0.10 standard error (p= 0.03) and the coefficient for herbivore abundance was β_{LR} = -0.20±0.10 (p= 0.050).

Planted tree species identity had a significant effect on canopy openness and vegetation cover (Appendix Table 3-2). *Peronema canescens* significantly decreased canopy openness (β_i = -1.0±0.25, p< 0.001) while *Shorea leprosula* contributed to significant increase in canopy openness (β_i = 0.65±0.26, p= 0.02) (Figure 3-2b). These same species identity effects were

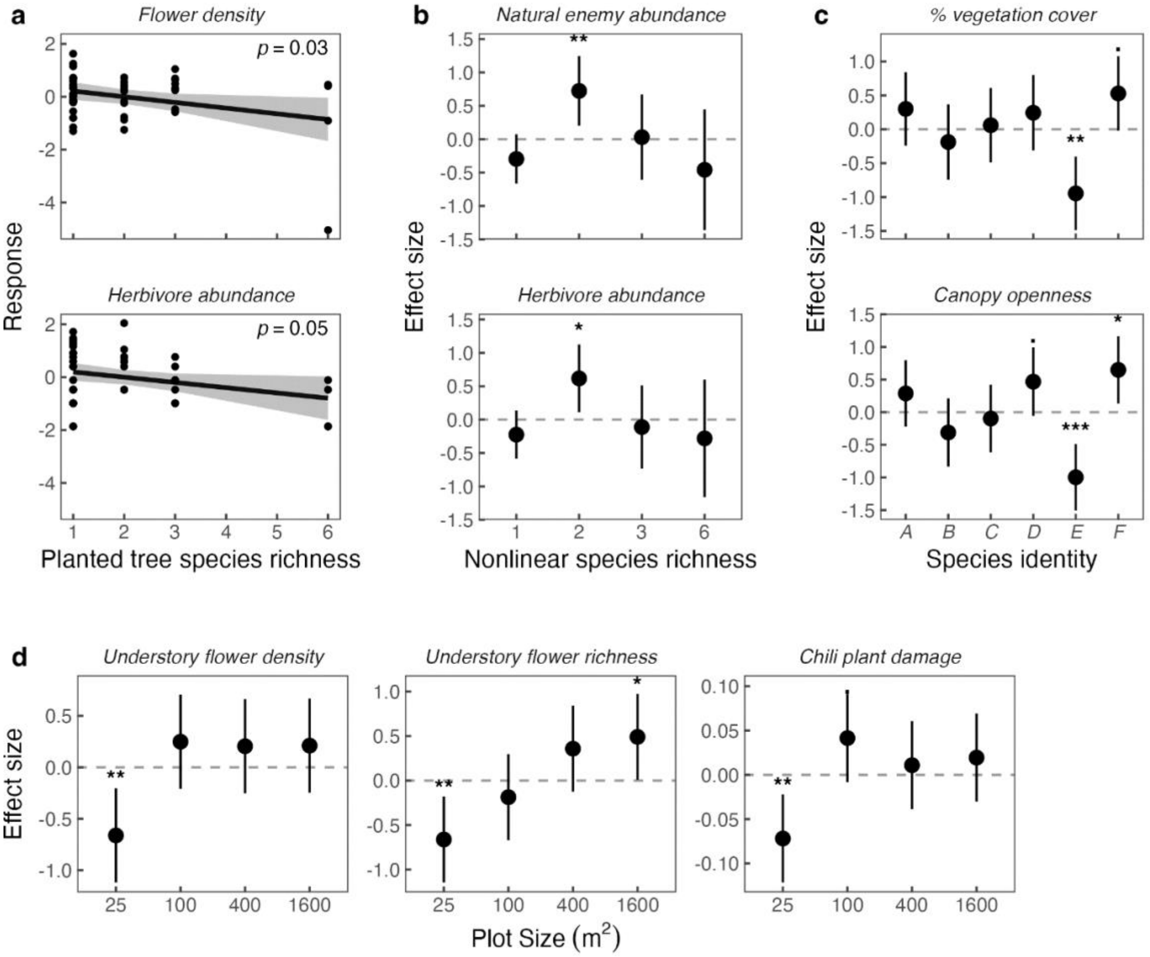


Figure 3-2. Contributors (p < 0.05 in Appendix Tables 3-2 to 3-4) for (a) linear richness effect (illustrated by estimated regression slope and 95% confidence interval), (b) species identity effect coefficients, (c) nonlinear richness effect coefficients, and (d) plot size effect coefficients. All effect sizes are for normalized, mean-centered, and unit variance-scaled variables. Letter codes for species identities are A: *Parkia speciosa*, B: *Archidendron jiringa*, C: *Durio zibethinus*, D: *Dyera polyphylla*, E: *Peronema canescens*, F: *Shorea leprosula*. Effect coefficients are shown with 95% confidence intervals. Symbols indicate p-value levels: *** p < 0.001, ** p < 0.01, * p < 0.05, . p < 0.10.

mirrored in vegetation cover, though only the negative effect of *P. canescens* was significant (β_i = -0.95±0.27, *p*= 0.001) while the positive effect of *S. leprosula* was marginally significant (Figure 3-2b).

The number of tree enrichment species as a categorical variable ("non-linear species richness") also explained significant variability in herbivore and natural enemy insect abundance (Appendix Table 3-3). Two-tree species treatments had a significant positive effect on herbivores (β_{NLR} = 0.62±0.25 *p*= 0.02) and natural enemies (β_{NLR} = 0.72±0.26, *p*= 0.008) (Figure 3-2c).

Plot size significantly affected flower density, flower richness, and chili plant damage (Appendix Table 3-2 and Appendix Table 3-4). For all these variables, the smallest plot size, 25 m^2, had a significant negative effect (flower density: β_P = -0.66±0.23, *p*= 0.006; flower richness: β_P = -0.66±0.24, *p*= 0.008; and chili plant damage: β_P = -0.67±0.23, *p*= 0.006) (Figure 3-2d). For flower density and chili plant damage, only this level of plot size had a significant effect. The effect on flower richness was significant at the largest plot size, 1600 m^2 (β_P = 0.49±0.24, *p*= 0.047).

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

3.3.3. Structural equation model results

The final vegetation structure SEM suggests that tree species identity directly drove canopy openness, which in turn affected understory vegetation (Figure 3-3a). Species identity is represented by *P. canescens* presence in our SEMs since this species had the most consistent effect in the random partition analysis. We found strong support that canopy openness fully mediated a positive effect of *P. canescens* on understory vegetation coverage, as an alternative SEM with only a direct effect of *P. canescens* on understory vegetation coverage fit significantly worse than the final model (z= -2.60, *p* = 0.005, see Section 3.6 Appendix S3, Appendix Figure 3-1a and Appendix Table 3-5 for more details). We found that canopy openness contributed positively to flower richness, but plot size also remained a significant positive variable in model comparisons. Tree species richness as a continuous variable had a significant negative relationship with understory flower richness, as was the case in the random partition analysis results. There was marginal evidence that canopy openness partially mediated the effect of plot size on understory flower richness, as the final model with both canopy openness and plot size influencing flower richness fit marginally better than an alternative model where plot size was removed (LR= 3.390, *p*= 0.0542); however, this difference was only marginally distinguishable (ω^2= 0.061, *p*= 0.095). Effects of plot size on canopy openness and of canopy openness on understory flower density were marginally significant ($p < 0.10$) in the final model. The global fit index of the final model was $\chi^2(7)$= 4.558, *p*= 0.714; Swain $\chi^2(7)$= 3.986, *p*= 0.875, indicating an adequate model fit to the data, with no omitted relationships.

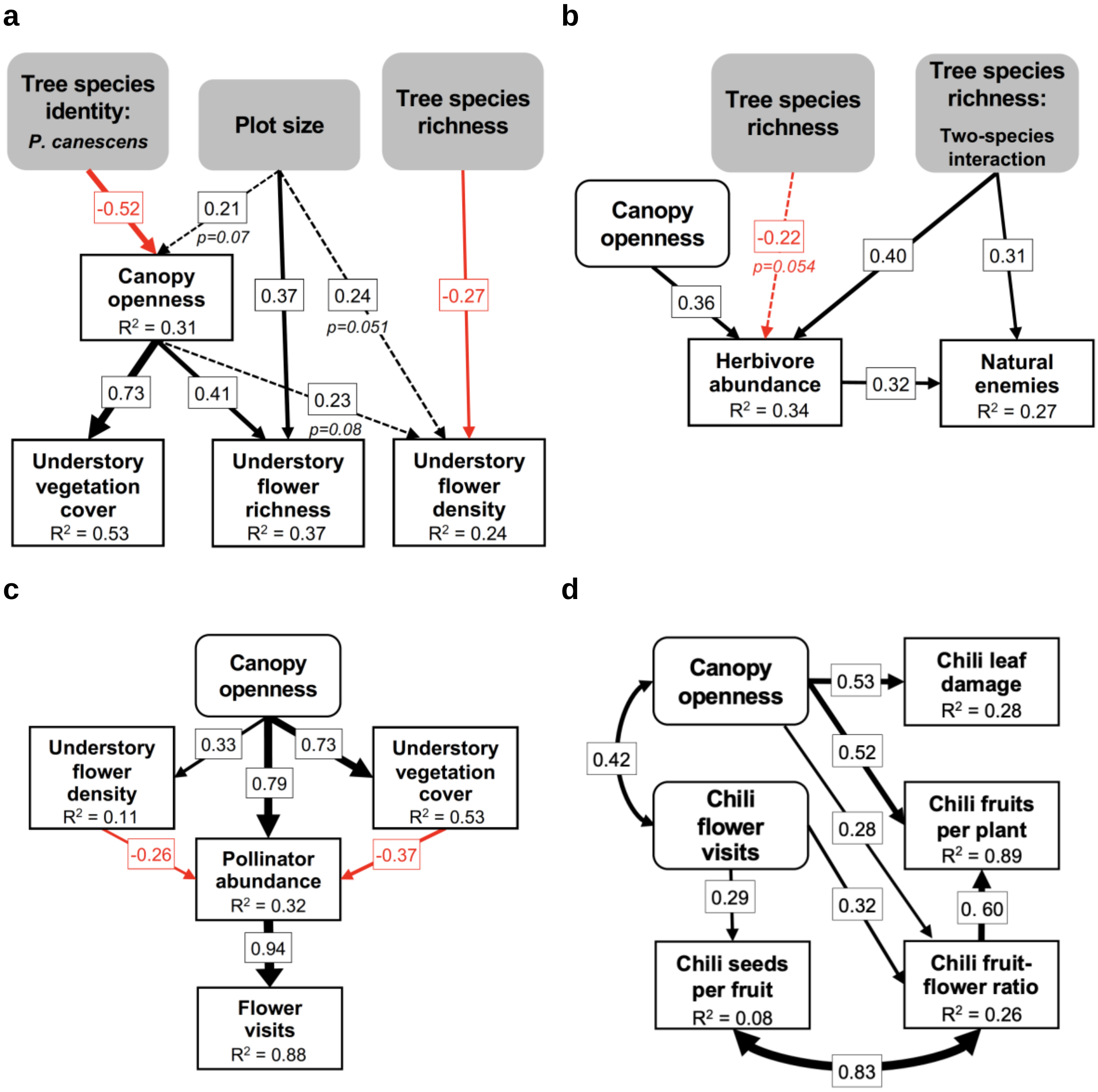


Figure 3-3. Diagrams of structural equation models of (a) vegetation structure, (b) herbivore and natural enemy ecosystem functions, (c) pollinator ecosystem functions, and (d) phytometer ecosystem functions. Rounded boxes represent exogenous variables in the model, i.e., those without regressions, and those with grey fill represent enrichment treatment variables. Square boxes represent endogenous variables, i.e., dependent variables in regressions. All effect sizes are for normalized, mean-centered, and unit variance-scaled variables. Single-headed arrows represent independent variable relationship with the standardized effect size in the associated box. Double-headed arrows represent model-fitted standardized covariance terms. Arrow widths are scaled by effect size. Solid arrows indicate relationships with $p < 0.05$ and dashed arrows indicate marginally significant ($p < 0.10$) relationships, with the p-value given beneath the effect size.

In the herbivore and natural enemy insects SEM, two-species tree richness remained a significant positive predictor of both herbivore and natural enemy insect abundance (Figure 3-3b), supporting the links indicated by the random partition analysis. Tree species richness as a continuous predictor variable of herbivore abundance was marginally supported ($p = 0.054$) and our results did not suggest any mediating pathways through other hypothesized links. Canopy openness was also a positive predictor of herbivore abundance but did not have a significant direct link to natural enemy abundance. We did not find significant relationships with understory vegetation cover or understory flower richness. In comparing alternative SEM formulations (Appendix Figure 3-1b and Appendix Table 3-5), we found significant support against natural enemy abundance fully mediating the effect of two-species tree richness on herbivore abundance (LR= 4.608, p= 0.02). In our final model, herbivores partially mediate the effects of two-species tree richness on natural enemies with a significant positive effect (Figure 3-3b), consistent with a bottom-up hypothesis (Scherber et al. 2010). Our final model had the best global fit of all candidate models considered ($\chi^2(5)$= 2.241, p= 0.815, Swain $\chi^2(5)$= 2.126, p= 0.832) and is consistent with one of our ecologically-based hypotheses, though Vuong variance tests (see Section 2.4.2) indicated that our data could not distinguish between fits with other intermediate models (Appendix Table 3-5).

In the pollinator insects SEM, we find that flower density 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. There was not strong evidence that other variables played significant mediating roles. An alternative SEM in which canopy openness did not have a direct link to pollinator abundance and only influenced vegetation cover and flower density did not fit better (z= 16.054, p< 0.001, Appendix Figure 3-1c and Appendix Table 3-5), suggesting that the two understory vegetation variables only partially mediated the effect of canopy openness. The final pollinator insect global fit was $\chi^2(4)$= 1.177, p= 0.882, Swain $\chi^2(4)$= 1.115, p= 0.892.

The final phytometer SEM (Figure 3-3d) supported a significant positive link between pollinator visits to chili flowers and the chili fruit-flower ratio; the latter in turn having a positive effect on the seeds per fruit. We fitted a covariance term between canopy openness and flower visits, which was significant, reflecting the finding of the pollinator SEM. Based on modification indices, we added a covariance term between seeds per fruit and the fruit-flower ratio. This additional term indicated high correlation (0.83) and may reflect shared mechanisms related to pollination success and plant resource allocation (Knight et al. 2006). On the other hand, flower visits explained only 8% of variance in seeds per fruit. Canopy openness had significant positive effects on the fruit-flower ratio and the number of fruits per plant. We did not find significant relationships between herbivore abundance and plant damage. In intermediate models we included enrichment plot size as a predictor of plant damage (Appendix Figure 3-1d, Appendix Table 3-5), which was suggested by the random partition results. However, we found that an SEM where canopy openness fully mediated the effect of plot size on leaf damage had moderately better fit than an SEM where plot size was the only driver (LR= -1.628, p= 0.052). When both variables were included in the leaf damage regression, the model was indistinguishable from the full mediation model (ω^2= 0.031, p= 0.164) but plot size was not a significant predictor (p> 0.10). We therefore removed plot size as a variable from the final model, which had a global fit of $\chi^2(4)$= 5.610, p= 0.230, Swain $\chi^2(4)$= 5.253, p= 0.262.

3.4. Discussion

We investigated the biodiversity enrichment effects of the EFForTS-BEE (Teuscher et al. 2016) on ecosystem functioning with random partition analysis (Bell et al. 2009) and tested for indirect effects using structural equation models. Through the random partition approach, we found negative and positive effects of the enrichment treatments (tree species diversity, identity and plot size) on plot vegetation structure variables (canopy openness, understory vegetation cover and flower richness and density) and evidence for tree species interaction effects on understory herbivore and natural enemy insects, while effects on pollinator activity and phytometer plant functions were mostly not significant. However, structural equation models revealed that the vegetation structure variables, namely canopy openness, mediated enrichment effects on insect abundances and functions to phytometer plants. Our results demonstrate that the effects of biodiversity enrichment, focusing on ecosystem functions associated with understory herbivore, natural enemy, and pollinator insects, are not always directly correlated with enrichment treatments, but rather may be mediated through multiple interacting pathways.

3.4.1. Effects on vegetation structure variables

Canopy openness explained different degrees of variability in the understory vegetation variables in the SEM. Understory vegetation cover was completely mediated by canopy openness. Flower richness was directly positively related to plot size, as predicted by island biogeography theory (MacArthur and Wilson 1963), but this effect was also partially mediated through canopy openness. This indirect effect can be explained by oil palm thinning that was part of the experimental setup and design, as more palms were felled in larger plots initially, increasing canopy openness (Gérard et al. 2017, Khokthong et al. 2019). Likewise, canopy openness also influenced understory flower density in our SEM results.

Our final vegetation structure SEM results demonstrate that tree species identity can play an influential role in determining downstream effects. The SEM confirms that the presence of *P. canescens* directly affected canopy openness, which in turn played important mediating roles for herbaceous vegetation variables. This fast-growing, early successional species performed very well in experimental plots (Zemp et al. 2019b) and was an important driver of stand structural complexity, a measure of vegetation structure that is correlated to canopy openness (Zemp et al. 2019a). On the other hand, *S. leprosula* is a primary forest species and had low survival rates (Zemp et al. 2019b). Mortality-induced canopy gaps may therefore explain this species’ positive association with canopy openness in the random partition analysis results. Species identity can be a key factor in tree biodiversity experiments associated with selection effects (Ebeling et al. 2008, Grossman et al. 2018); nevertheless, it is not commonly considered in comparing ecosystem functions across agroforestry systems (e.g., Steffan-Dewenter et al. 2007). Measures to diversify agricultural landscapes may therefore do well to consider life history traits and performance of enrichment tree species when anticipating downstream effects on insect-mediated ecosystem functions.

3.4.2. Effects on insect abundance and ecosystem functions

We found evidence that canopy openness played a role in herbivore and pollinator abundance. Some studies have found positive herbivore responses to increased canopy openness in forests, which is attributed to increased understory leaf growth or changes in microclimate (Basset et al. 2001, Franc and Götmark 2008). Indeed, our SEM showed that canopy openness was an important variable for herbivore and pollinator abundance, though the latter was partly mediated by the negative effect of understory vegetation cover. This negative effect may reflect additional aspects of habitat outside of understory vegetation that were favorable for pollinators, for example availability of nesting sites in bare soil or dead wood (Proctor et al. 2012, Rodríguez and Kouki 2015). A negative effect of flower density also partially mediated the relationship between canopy openness and pollinator abundance. This may suggest that co-flowering species in the plot competed with phytometer plants for pollinators (Knight et al. 2005). This dilution effect could indicate a depauperate pollination landscape where pollination services are a finite resource due to limited pollinator populations, leading to pollination competition (Knight et al. 2005, Veddeler et al. 2006, Holzschuh et al. 2011). Besides increasing vegetation growth, canopy openness may also promote warmer, sunnier environments that can create favorable ovipositioning sites and reduce larval development times of herbivore and pollinating insects (Wirth et al. 2008).

Two-species enrichment treatments had a significant effect on both functional groups of understory insects, which was not mediated through canopy openness. As this factor represents species interactions in the random partition framework (Bell et al. 2009), this suggests interactions between two species of trees have additional effects not associated with canopy openness. Zemp et al. (2019b) concurrently analyzed planted tree performance within these plots and found that trees in two-species plots experienced higher mortality. This may have contributed to habitat conditions such as increased dead wood (Seibold et al. 2016), which promoted higher insect populations.

We represent the connection between herbivore and natural enemy abundances as a bottom-up relationship in our final SEM, i.e., herbivores drive natural enemies. This model had the best global fit, but we could not formally compare alternative models based on our data. Nevertheless, the positive bottom-up relationship between herbivore and natural enemy abundances was consistent with a lack of a density-dependent relationship that might be expected in top-down control; though this can also depend on other controlling factors of predator and prey populations, such as environmental sensitivity (Levins and Schultz 1996) or spatial heterogeneity (Tscharntke 1992). The negative effect of tree species richness on herbivore abundance, though marginal, is also consistent with hypothesized associational effects of plant species diversity on insect herbivores, in which the likelihood of a host plant being found by pests increases with low diversity due to host concentration and increased plant apparency (Grossman et al. 2018).

These results suggest that insect herbivores respond more strongly to habitat changes related to biodiversity enrichment than natural enemies. Although stronger top-down effects may be more prevalent generally (Vidal and Murphy 2018), this is not always the case (Denno et al. 2003, Scherber et al. 2010, Schuldt et al. 2017). This might be related to the young age of plant biodiversity experiments, to heterogeneity across natural enemy groups, as well as other moderating effects such as intraguild predation (Grossman et al. 2018, Staab and Schuldt 2020).

3.4.3. Effects on ecosystem functions in phytometer plants

Our results suggest that the variation in pollination ecosystem service was attributed to flower visits in the enrichment plots. We found positive effects of flower visits on the fruit-flower ratio, which in turn increased the number of fruits produced. As flower visits were a positive driver of successful development from flowers to fruit, we may infer that fruit loss during development was not a major factor for the phytometer chili plants (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 fruit and seed variables. Pollinator visits only explained a small portion of seeds per fruit, though a study in sweet peppers has shown this has a major effect (Roldán Serrano and Guerra-Sanz 2006). However, we also found a strong correlation between the fruit-flower ratio and seeds per fruit, which could indicate our model may not be capturing more complex interactions due to plant resource allocation in response to pollination and other biotic or abiotic effects (Knight et al. 2006, Bos et al. 2007).

We found no relationships between herbivore abundance and phytometer plant damage or the fruit to flower ratio. We note that our herbivore samples were not taken at the same time as phytometer fruit development, so short-term temporal variability may have masked an effect. However, we did find some evidence that increased canopy openness could explain a positive effect of plot size on leaf damage. Light gaps can mediate herbivory effects on plants by promoting leaf growth, which presents a target for more herbivore attack (Norghauer et al. 2008), reflecting the “plant vigor hypothesis” (Price 1991). Canopy openness also had positive relationships with fruiting success indicators in the phytometer plants (fruit flower ratio and number of fruits), suggesting that canopy openness did indeed increase plant vigor. Nevertheless, plant tolerance of herbivory may depend on many factors, including environmental stress and nutrients (Wise and Abrahamson 2007), which may explain why leaf damage did not have significant impacts on fruit and seed production.

3.4.4. Canopy openness mediates early biodiversity enrichment effects on ecosystem functions

At four years, the progression of this enrichment experiment was still relatively early (Zemp et al. 2019a), and our finding of the importance of canopy openness reflects an early successional forest (Holmes and Matlack 2017). Canopy openness appears to play an important role in driving ecosystem functions at all the ecosystem levels we examined. In many cases, canopy openness was both a direct and indirect driver of ecosystem functions (e.g., on pollinator abundance and through flower density and vegetation cover). In other cases, canopy openness appears to fully mediate the effect of an enrichment treatment variable (e.g., canopy openness explained the negative correlation between understory vegetation cover and *P. canescens*). Based on the ecosystem functions we observed affecting the phytometer plants, the trends in our findings could suggest an eventual trade-off between net beneficial insect activity, namely from pollination services, and other ecosystem functions related to tree growth, as exemplified by the fast-growing species *P. canescens*, which lead to canopy closure (Zemp et al. 2019a). 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 resulting from oil palm thinning, which may change in the long term.

Decreased canopy openness is an expected effect of forest restoration, as it is associated with structural complexity and productivity that is characteristic of mature natural forests (Lamb et al. 2005, Zemp et al. 2019a). As tree growth continues to close canopy gaps, our results suggest understory vegetation cover and flower richness, which was strongly driven by canopy openness, may decrease, though decreases in flower richness may be dampened for large plots.

Our findings also suggest herbivore abundance may decrease with decreasing canopy openness, which in turn may lead to lower natural enemy abundance. These patterns highlight the important role canopy gaps play in enrichment ecosystems, as they do in natural forest habitats (Bouget and Duelli 2004). Methods of maintaining patches of canopy openness, such as through selective tree felling (Basset et al. 2001), could be one way to increase favorable environments for insect-mediated ecosystem functions in restoration projects, though further research is needed on which ecosystem functions may be favored and how this relates to specific restoration goals.

However, on a longer timescale, predominant dynamics may shift based on changing communities (Luong et al. 2019). Plot understories were dominated by invasive pantropical plants (Rembold et al. 2017). However, continued tree growth and spontaneous establishment of shade-adapted plant species through seed dispersal may add complexity and diversity to plots (Arroyo-Rodríguez et al. 2009, Staab and Schuldt 2020). This could create more heterogeneous habitats for insects, in turn promoting higher diversity of specialist herbivores and more stable populations of associated natural enemies (Root 1973). Larger-scale dynamics may also play a role as plot communities become more established. For example, as some plots develop into sources for pollinator populations, this could shift the dynamic between flower density and pollination services from dilution to resource concentration in nearby plots, reflecting processes closer to that observed in more natural heterogeneous landscapes (Jauker et al. 2009).

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 effects of biodiversity enrichment treatments on ecosystem functions of herbivory, natural enemy biocontrol, and pollination may be mainly indirect, i.e., mediated by changes in vegetation structure or canopy cover. In addition, enrichment species traits may play an important role, as we found that fast-growing trees (i.e., *Peronema canescens*) drove decreasing canopy openness, which in turn mediated effects on herbivores, natural enemies, and pollinators. We observed a net benefit for phytometer plants through insect-mediated pollination function with no apparent negative effect of herbivory; however, as this was driven by canopy openness, an eventual trade-off with forest complexity and the emergence of new patterns will likely occur as biotic communities continue to develop. Our results demonstrate that, even at early stages of restoration of highly simplified oil palm environments, tree biodiversity enrichment can have a substantial effect on ecosystem functioning. As our findings of the influence of canopy demonstrate, the ability of enrichment to enhance vegetation complexity had the greatest effect, reflecting the dynamics of forest succession, while tree species richness *per se* played less of a role in ecosystem functioning at this stage. Moving forward, our results suggest that maintaining heterogeneity in canopy openness in restoration plots may be important for supporting increased ecosystem functioning and improving habitat diversity.

Authors' contributions

KL, IG, and TT designed the study. DH, HK designed the enrichment experiment, which was maintained under the supervision of DCZ. 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.

Acknowledgements

We thank the assistance of Arini, Fahrurrozi, R Fardiansah, A Mellivera, JS Maranatha, N Marbun, R Mareta, AM Riany, Rony, and D Warisman. We also thank P.T. Humusindo for granting access to the property. This study was funded by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) – project ID 192626868 – SFB 990 in the framework of the collaborative German-Indonesian research project CRC 990.

Data availability

Data available from: 10.6084/m9.figshare.20339112

3.6. Supporting Information

Appendix S1
Insect taxonomic summary

Appendix Table 3-1. Summary of taxonomic and feeding guild groups on insects collected from understory vegetation. The "Functional group" column indicates the classification used for the analysis dataset, where empty cells indicate a mixed functional group that we excluded in our analyses.

Order	Family	Feeding guild	Functional group	Total individuals
Blattodea	Ectobiidae	omnivore		2
Coleoptera	Chrysomelidae	herbivore	herbivore	12
Coleoptera	Mordellidae	herbivore	herbivore	1
Coleoptera	Phalacridae	herbivore	herbivore	2
Coleoptera	Staphylinidae	predatory	natural enemy	4
Diptera	Asteiidae	herbivore	herbivore	3
Diptera	Camillidae	mixed		8
Diptera	Cecidomyiidae	mixed		25
Diptera	Celyphidae	herbivore	herbivore	4
Diptera	Ceratopogonidae	mixed		62
Diptera	Chironomidae	nectarivore		52
Diptera	Chloropidae	parasitic	natural enemy	58
Diptera	Culicidae	omnivore		27
Diptera	Dolichopodidae	predatory	natural enemy	34
Diptera	Drosophilidae	mixed		16
Diptera	Empididae	predatory	natural enemy	13
Diptera	Ephydridae	mixed		2
Diptera	Lauxaniidae	saprophagous		24
Diptera	Lonchaeidae	herbivore	herbivore	1
Diptera	Muscidae	mixed		2
Diptera	Mycetophilidae	mixed		5
Diptera	Phoridae	mixed		66

Order	Family	Feeding guild	Functional group	Total individuals
Diptera	Psychodidae	mixed		7
Diptera	Scatopsidae	saprophagous		1
Diptera	Sciaridae	fungivore		13
Diptera	Sphaeroceridae	saprophagous		4
Diptera	Stratiomyidae	saprophagous		7
Diptera	Tipulidae	mixed		15
Ephemeroptera	Baetidae	saprophagous		3
Hemiptera	Aleyrodidae	herbivore	herbivore	4
Hemiptera	Aphididae	herbivore	herbivore	6
Hemiptera	Cicadellidae	herbivore	herbivore	114
Hemiptera	Coreidae	herbivore	herbivore	2
Hemiptera	Delphacidae	herbivore	herbivore	5
Hemiptera	Derbidae	herbivore	herbivore	5
Hemiptera	Lygaeidae	herbivore	herbivore	30
Hemiptera	Miridae	mixed		34
Hemiptera	Nymph			26
Hemiptera	Pentatomidae	herbivore	herbivore	1
Hemiptera	Schizopteridae	predatory	natural enemy	3
Hemiptera	Tingidae	herbivore	herbivore	8
Hymenoptera	Aphelinidae	parasitic	natural enemy	1
Hymenoptera	Apidae	nectarivore		1
Hymenoptera	Braconidae	parasitic	natural enemy	36
Hymenoptera	Chalcididae	parasitic	natural enemy	1
Hymenoptera	Crabronidae	parasitic	natural enemy	3
Hymenoptera	Diapriidae	parasitic	natural enemy	8
Hymenoptera	Encyrtidae	parasitic	natural enemy	13
Hymenoptera	Eulophidae	parasitic	natural enemy	35
Hymenoptera	Evaniidae	parasitic	natural enemy	1
Hymenoptera	Mymaridae	parasitic	natural enemy	5
Hymenoptera	Platygastridae	parasitic	natural enemy	2
Hymenoptera	Pompilidae	parasitic	natural enemy	1
Hymenoptera	Pteromalidae	parasitic	natural enemy	3
Hymenoptera	Scelionidae	parasitic	natural enemy	23
Hymenoptera	Sphecidae	parasitic	natural enemy	1
Hymenoptera	Tiphiidae	parasitic	natural enemy	1
Hymenoptera	Vespidae	predatory	natural enemy	9
Lepidoptera	Gelechiidae	herbivore	herbivore	3
Lepidoptera	Pyralidae	herbivore	herbivore	2
Mantodea	Mantidae	predatory	natural enemy	3
Orthoptera	Acrididae	herbivore	herbivore	21
Orthoptera	Gryllidae	omnivore		38
Orthoptera	Pyrgomorphidae	herbivore	herbivore	4
Orthoptera	Tettigoniidae	predatory	natural enemy	2
Psocoptera	Pachytroctidae	saprophagous		1
Psocoptera	Trichopsocidae	saprophagous		2
Thysanoptera	Phlaeothripidae	herbivore	herbivore	3

Appendix S2
Random partition model results

Appendix 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 mean centered and unit variance scaled.

	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		
Understory 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		
Understory vegetation 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		
Understory 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		

Appendix Table 3-3. Random partition model results for insect-level ecosystem function effects (level B in Figure 3-1 and Table **3-1**). Variables are transformed according to Table **3-1** mean centered and unit variance scaled.

	Df	**Sum.Sq**	**Mean Sq.**	**F-value**	**p-value**
Insect 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		
Chili pollinator abundance					
Linear richness	1	0.628	0.628	0.575	0.453
Species identity	5	4.829	0.966	0.885	0.501
Non-linear richness	2	0.616	0.308	0.282	0.756
Plot size	3	1.655	0.552	0.506	0.681
Residuals	36	39.273	1.091		
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		

Appendix 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 mean centered and unit variance scaled.

	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	0.164	0.164	0.161	0.690
Species identity	5	8.353	1.671	1.642	0.174
Non-linear richness	2	1.213	0.607	0.596	0.556
Plot size	3	0.649	0.216	0.213	0.887
Residuals	36	36.620	1.017		
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		

Appendix S3
Proposed structural equation models and model results

The following sections report (1) proposed structural equation models (SEM) and (2) final SEM results and fit metrics.

1. Proposed structural equation models

The proposed relationships at the levels of vegetation structure, insect ecosystem functions, and phytometer plant functions are presented in Table 3-1 of the main text. The significant tree enrichment treatments identified in the random partition analysis were also added as hypothesized connections in the proposed SEMs (Table 3-1 in main text, marked with asterisks).

In the vegetation SEM (Table 3-1 in main text, level A), our hypothesized structure assumed that canopy openness influenced understory vegetation variables (vegetation cover, flower richness, and flower density), while vegetation cover also would affect flower variables. Additionally, we expected flower richness to increase with plot size due to the habitat size-species diversity relationship (MacArthur and Wilson 1963).

For the insect herbivore and natural enemy SEM (Table 3-1 in main text, level B1), we hypothesized that understory vegetation would influence herbivore and natural enemy insect abundance by providing habitat and, in the case of herbivores, resources (Langellotto and Denno 2004, Moreira et al. 2016). We also tested alternative model structures where herbivore abundance mediated habitat effects on natural enemies, reflecting bottom-up effects, or natural enemy abundance drove herbivores, reflecting top-down effects.

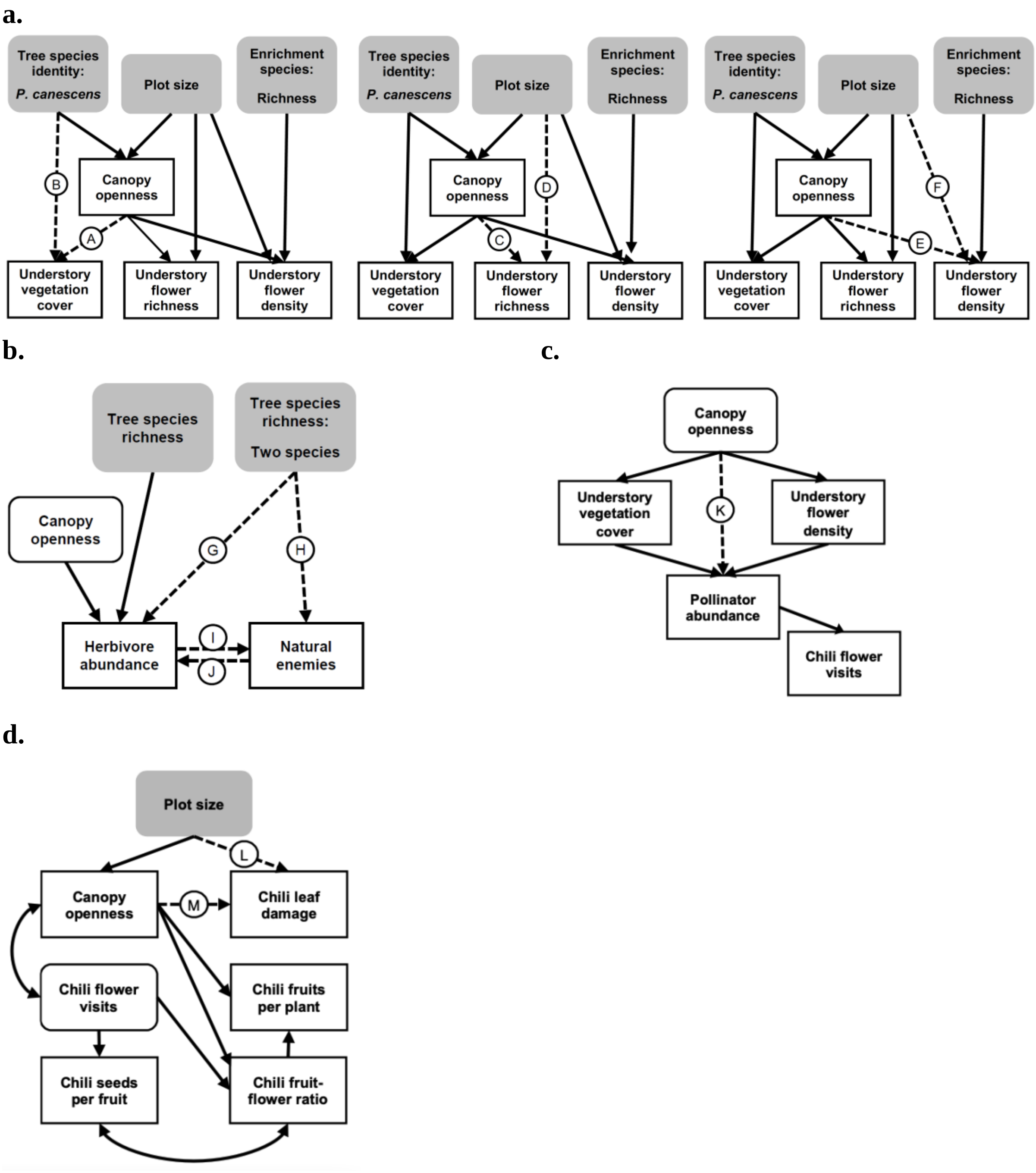
For the insect pollinators SEM (Table 3-1 in main text, level B2), we hypothesized that plot flower richness and flower density would affect pollinator abundance in a relationship that could be positive, by enriching floral resources and attracting more pollinators (Johnson et al. 2003), or negative, by diluting the effectiveness of a limited pollinator pool (Knight et al. 2005, Veddeler et al. 2006, Holzschuh et al. 2011), while vegetation cover could provide additional resources such as habitat.

For both insect SEMs, we also proposed canopy openness could play an indirect role through influencing vegetation variables, or a more direct role through affecting the thermal environment. Canopy openness is strongly negatively correlated with the structural complexity in these plots (Zemp et al. 2019), which may represent additional habitat niches (Langellotto and Denno 2004); canopy openness is also positively correlated with the thermal environment (Donfack et al. 2021), which can drive insect activity in fragmented habitats (Tuff et al. 2016).

In the phytometer plant SEM (Table 3-1 in main text, level C), we linked insect functions to relevant phytometer plant functions, i.e., pollinator flower visits to chili fruit-flower ratio and seeds per fruit, and herbivore abundance to leaf damage. We hypothesized leaf damage would impact seed and fruit production, while canopy openness would represent sunlight and associated microclimatic conditions.

We identified alternative intermediate models (Appendix Figure 3-1) by following a “weight of evidence” approach (Grace 2020) to remove unsupported links and make ecologically-based model adjustments. We compared between alternative candidate SEM model structures that proposed direct links to the significant enrichment treatments identified through the random partition analysis, or through other pathways based on ecological theory. In “downstream” SEMs flowing from the vegetation structure SEM (i.e., within levels B1, B2, or C in Figure 3-1 and Table 3-1 in main text), we fit covariance terms for exogenous variables (SEM variables with no independent variables) if we found direct or indirect relationships between these variables in higher-level SEMs that we did not include in the focal SEM.

We compared these alternative model structures to the final models presented in the main text, first assessing model distinguishability with the Vuong variance test (Vuong 1989). We compared distinguishable models using robust alternative likelihood ratio test variants for nested and non-nested model comparisons that do not make an assumption that the “true” model is included in the comparison set (Vuong 1989, Merkle et al. 2016).



Appendix Figure 3-1. Illustrations of alternative structural equation models for (a) vegetation structure, (b) herbivore and natural enemy insects, (c) pollinator insects, and (d) phytometer plants. These were tested against the final model structures presented in the main text. Within each panel, circled letters and dotted arrows represent alternative links that we tested by removing or adding that link. Comparisons and test results are presented in Appendix Table **3-5**.

Appendix Table 3-5. Comparison tests between alternative model structures shown in Appendix Figure **3-1** and the final models presented in the main text. The Vuong variance test (ω^2) indicates model comparison distinguishability based on the data. For distinguishable model comparisons, we present robust alternative likelihood ratio test results, using nested and non-nested versions depending on the model comparison.

Model	Comparison - letters indicate included links	Distinguish-ability (ω^2)	Distinguish-ability *p*	Likelihood ratio	Likelihood ratio *p*	Test type and conclusion
a.	A (final model) vs. B	0.417	0.00176	2.599	0.00467	Non-nested, A fits better
a.	CD (final model) vs C	0.133	0.00718	8.872	0.00243	Nested, CD fits better
a.	CD (final model) vs. D	0.210	0.00412	11.104	0.00143	Nested, CD fits better
a.	EF (final model) vs. E	0.061	0.0954	3.390	0.0542	Nested, EF fits better (marginal)
a.	EF (final model) vs. F	0.059	0.412			Not distinguishable
b.	GH vs. GHI (final model)	0.015	0.464			Not distinguishable
b.	GH vs. GI	0.108	0.132			Not distinguishable
b.	GH vs. GHJ	0.000	0.5			Not distinguishable
b.	GH vs. HJ	0.076	0.0186	4.608	0.0238	Nested, GH fits better than HJ
c.	K (final model) vs. without K	0.296	0.00248	16.054	0.000334	Nested, model fits better with K
d.	L vs. M	0.270	0.00299	-1.628	0.05177	Not nested, M fits better (marginal)
d.	M vs. LM	0.031	0.164			Nested, not distinguishable

2. Final SEM results and fit metrics

Final model output parameters are reported in Appendix Tables 3-7 to 3-10, including the χ^2 exact fit index and the Swain small sample size correction adjusted for our sample size (n = 48) (Rosseel 2020). We report three approximate fit indices: the root mean square error of approximation (RMSEA) and 95% confidence interval and *p*-value of RMSEA ≤ 0.05; the comparative fit index (CFI); and the standardized root mean square residual (SRMR). Variable abbreviations are explained in Appendix Table 3-6. In Appendix Tables 3-7 to 3-10, column 'lhs' represents response variables and 'rhs' represents predictor variables. The 'op' column indicates effect types: (~) is a direct effect, i.e., regression, and (~~) represents error correlation or variance. Error correlation between enrichment treatment variables were fixed as exogenous variables. Numeric columns represent the standardized effect estimate (est.std), standard error (se), z-statistic (z), *p*-value (pvalue), and upper and lower 95% confidence interval (ci.lower and ci.upper).

Appendix Table 3-6. Model variable codes used in the SEM outputs

Code	Explanation
sungkai	Tree species *Peronema canescens* planted in the plot
size.ord	Plot size (ordinal variable)
planted.R	Planted tree richness
planted.2	Two tree species planted in the plot
scaleveg	Understory vegetation cover
logitgap	Canopy openness
logfl.chao	Understory vegetation richness (Chao estimation)
logfl.d	Understory flower density
logher.a	Herbivore abundance
lognen.a	Natural enemy abundance
logpoll.a	Pollinator abundance
logflrvis	Total flower visits
damage.mn	Mean leaf damage
frflr.mn	Mean fruit to flower ratio
scalefrtseed	Mean seeds per fruit
logfruit	Mean total fruit per plant

Appendix Table 3-7. Final vegetation structure (level A) SEM results. Table heading codes are as follows: lhs = formula left-hand side (response variable); op = operator type (~ indicates regression, ~~ indicates correlation); rhs = formula right-hand side (predictor variable); est.std = standardized coefficient estimate (mean-centered and scaled by standard deviation); se = standard error of standardized estimate; z = z-score statistic; pvalue = coefficient p-value; ci.lower = coefficient estimate lower 95% confidence interval; ci.upper = coefficient estimate upper 95% confidence interval.

lhs	op	rhs	est.std	se	z	pvalue	ci.lower	ci.upper
logitgap	~	sungkai	-0.515	0.096	-5.343	0.000	-0.703	-0.326
logitgap	~	size.ord	0.208	0.116	1.787	0.074	-0.020	0.437
scaleveg	~	logitgap	0.731	0.066	11.016	0.000	0.601	0.861
logfl.chao	~	size.ord	0.365	0.107	3.407	0.001	0.155	0.576
logfl.chao	~	logitgap	0.414	0.109	3.814	0.000	0.201	0.627
logfl.d	~	planted.R	-0.267	0.125	-2.146	0.032	-0.512	-0.023
logfl.d	~	size.ord	0.242	0.124	1.949	0.051	-0.001	0.485
logfl.d	~	logitgap	0.228	0.131	1.744	0.081	-0.028	0.485
logitgap	~~	logitgap	0.692	0.102	6.785	0.000	0.492	0.892
scaleveg	~~	scaleveg	0.466	0.097	4.800	0.000	0.276	0.656
logfl.chao	~~	logfl.chao	0.632	0.106	5.968	0.000	0.424	0.839
logfl.d	~~	logfl.d	0.764	0.102	7.481	0.000	0.564	0.964
scaleveg	~~	logfl.chao	-0.066	0.144	-0.456	0.648	-0.347	0.216
scaleveg	~~	logfl.d	0.015	0.144	0.101	0.920	-0.268	0.297
logfl.chao	~~	logfl.d	-0.006	0.144	-0.043	0.966	-0.289	0.277
sungkai	~~	sungkai	1.000	0.000			1.000	1.000
sungkai	~~	size.ord	0.000	0.000			0.000	0.000
sungkai	~~	planted.R	0.500	0.000			0.500	0.500
size.ord	~~	size.ord	1.000	0.000			1.000	1.000
size.ord	~~	planted.R	0.000	0.000			0.000	0.000
planted.R	~~	planted.R	1.000	0.000			1.000	1.000

Global fit indices (df)

$\chi^2(7) = 4.558$, $p = 0.714$

Swain $\chi^2(7) = 3.986$, $p = 0.875$

Approximate fit indices

RMSEA = 0.000 (95% CI = 0.000-0.133, $p(\leq 0.05) = 0.773$)

CFI= 1.000

SRMR= 0.040

Appendix Table 3-8. Final herbivore and natural enemy insects (level B1) SEM results. Table heading codes are as follows: lhs = formula left-hand side (response variable); op = operator type (~ indicates regression, ~~ indicates correlation); rhs = formula right-hand side (predictor variable); est.std = standardized coefficient estimate (mean-centered and scaled by standard deviation); se = standard error of standardized estimate; z = z-score statistic; pvalue = coefficient p-value; ci.lower = coefficient estimate lower 95% confidence interval; ci.upper = coefficient estimate upper 95% confidence interval.

lhs	**op**	**rhs**	**est.std**	**se**	**z**	**pvalue**	**ci.lower**	**ci.upper**
logher.a	~	planted.R	-0.222	0.116	-1.925	0.054	-0.449	0.004
logher.a	~	planted.2	0.396	0.110	3.601	0.000	0.180	0.612
logher.a	~	logitgap	0.364	0.111	3.265	0.001	0.145	0.582
lognen.a	~	planted.2	0.306	0.129	2.364	0.018	0.052	0.559
lognen.a	~	logher.a	0.320	0.129	2.486	0.013	0.068	0.572
planted.R	~~	planted.2	0.000	0.000			0.000	0.000
logher.a	~~	logher.a	0.661	0.105	6.286	0.000	0.455	0.867
lognen.a	~~	lognen.a	0.727	0.109	6.673	0.000	0.513	0.941
planted.R	~~	planted.R	1.000	0.000			1.000	1.000
planted.2	~~	planted.2	1.000	0.000			1.000	1.000
logitgap	~~	logitgap	1.000	0.000			1.000	1.000

Global fit indices (df)

$\chi^2(5) = 2.241$, $p = 0.815$

Swain $\chi^2(5) = 2.126$, $p = 0.832$

Approximate fit indices

RMSEA = 0.000 (95% CI= 0.000-0.123, $p(\leq 0.05)$= 0.850)

CFI= 1.000

SRMR= 0.056

Appendix Table 3-9. Final pollinator insects (level B2) SEM results. Table heading codes are as follows: lhs = formula left-hand side (response variable); op = operator type (~ indicates regression, ~~ indicates correlation); rhs = formula right-hand side (predictor variable); est.std = standardized coefficient estimate (mean-centered and scaled by standard deviation); se = standard error of standardized estimate; z = z-score statistic; pvalue = coefficient p-value; ci.lower = coefficient estimate lower 95% confidence interval; ci.upper = coefficient estimate upper 95% confidence interval.

lhs	op	rhs	est.std	se	z	pvalue	ci.lower	ci.upper
scaleveg	~	logitgap	0.73	0.07	10.88	0.00	0.60	0.86
logfl.d	~	logitgap	0.33	0.13	2.52	0.01	0.07	0.58
logpoll.a	~	logitgap	0.79	0.16	4.94	0.00	0.47	1.10
logpoll.a	~	scaleveg	-0.37	0.17	-2.16	0.03	-0.71	-0.03
logpoll.a	~	logfl.d	-0.26	0.12	-2.08	0.04	-0.50	-0.01
logflrvis	~	logpoll.a	0.94	0.02	52.35	0.00	0.90	0.97
scaleveg	~~	scaleveg	0.47	0.10	4.74	0.00	0.27	0.66
logfl.d	~~	logfl.d	0.89	0.08	10.64	0.00	0.73	1.06
logpoll.a	~~	logpoll.a	0.69	0.11	6.27	0.00	0.47	0.91
logflrvis	~~	logflrvis	0.12	0.03	3.71	0.00	0.06	0.19
logitgap	~~	logitgap	1.00	0.00			1.00	1.00

Global fit indices (df)

$\chi^2(4) = 1.177$, $p = 0.882$

Swain $\chi^2(4) = 1.115$, $p = 0.892$

Approximate fit indices

RMSEA = 0.000 (95% CI = 0.000-0.105, $p(\leq 0.05) = 0.903$)

CFI= 1.000

SRMR= 0.013

Appendix Table 3-10. Final phytometer plant (level C) SEM results. Table heading codes are as follows: lhs = formula left-hand side (response variable); op = operator type (~ indicates regression, ~~ indicates correlation); rhs = formula right-hand side (predictor variable); est.std = standardized coefficient estimate (mean-centered and scaled by standard deviation); se = standard error of standardized estimate; z = z-score statistic; pvalue = coefficient p-value; ci.lower = coefficient estimate lower 95% confidence interval; ci.upper = coefficient estimate upper 95% confidence interval.

lhs	op	rhs	est.std	se	z	pvalue	ci.lower	ci.upper
logfrflr	~	logflrvis	0.32	0.12	2.73	0.01	0.09	0.56
logfrflr	~	logitgap	0.28	0.08	3.58	0.00	0.13	0.44
damage.mn	~	logitgap	0.53	0.10	5.03	0.00	0.32	0.73
logfruit	~	logfrflr	0.60	0.06	9.94	0.00	0.48	0.71
logfruit	~	logitgap	0.52	0.06	8.99	0.00	0.41	0.64
scalefrtseed	~	logflrvis	0.28	0.13	2.15	0.03	0.03	0.54
logflrvis	~~	logitgap	0.42	0.12	3.53	0.00	0.19	0.65
logfrflr	~~	scalefrtseed	0.83	0.04	18.73	0.00	0.74	0.92
logfrflr	~~	logfrflr	0.74	0.10	7.26	0.00	0.54	0.94
damage.mn	~~	damage.mn	0.72	0.11	6.59	0.00	0.51	0.94
logfruit	~~	logfruit	0.11	0.03	3.82	0.00	0.05	0.17
scalefrtseed	~~	scalefrtseed	0.92	0.08	12.16	0.00	0.77	1.07
logflrvis	~~	logflrvis	1.00	0.00	NA	NA	1.00	1.00
logitgap	~~	logitgap	1.00	0.00	NA	NA	1.00	1.00
damage.mn	~~	logfruit	0.07	0.14	0.51	0.61	-0.21	0.36
damage.mn	~~	scalefrtseed	-0.02	0.08	-0.26	0.79	-0.18	0.14
logfruit	~~	scalefrtseed	-0.02	0.08	-0.30	0.76	-0.18	0.13

Global fit indices (df)

$\chi^2(4) = 5.610$, $p = 0.230$

Swain $\chi^2(4) = 5.253$, $p = 0.262$

Approximate fit indices

RMSEA = 0.092 (95% CI = 0.000-0.251, $p(\leq 0.05) = 0.287$)

CFI = 0.992

SRMR = 0.089

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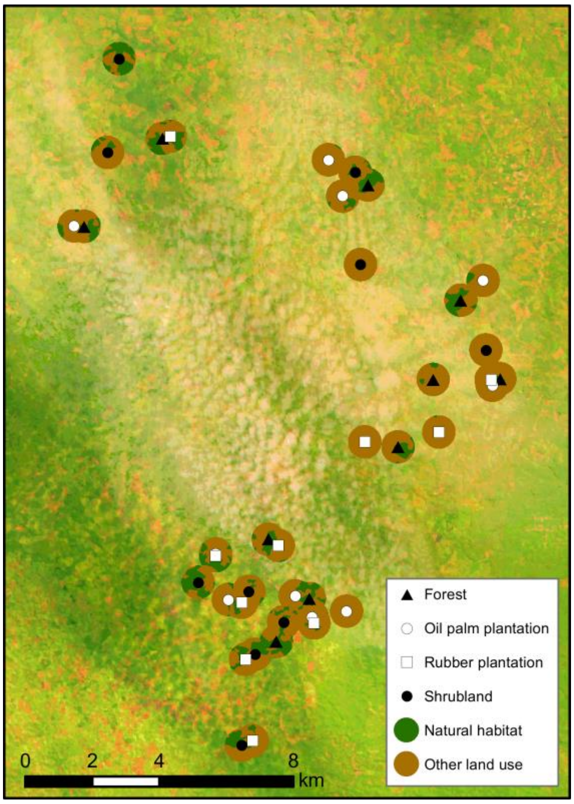
Chapter 4

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



Kevin Li[1], Sonja Schröck[2], Ingo Grass[3], Rika Raffiudin[4], Teja Tscharntke[1,5]

[1]Agroecology, Department of Crop Sciences, University of Göttingen, Göttingen, Germany

[2]Department of Animal Ecology and Tropical Biology, University of Würzburg, Würzburg, Germany

[3]Department of Ecology of Tropical Agricultural Systems, University of Hohenheim, Stuttgart, Germany

[4]Department of Biology, Bogor Agricultural University, Bogor, Indonesia

[5]Centre of Biodiversity and Sustainable Land Use (CBL), University of Göttingen, Göttingen, Germany

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 two habitats 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 in the landscape. We also observed negative correlations between hive resin and both resin foraging activity 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 should include clarifying the overall impact of increasing open habitats, at both the landscape and population levels.

Key words: stingless bees, floral resources, landscape scale, local scale, forest, oil palm, rubber, shrubland, *Tetragonula laeviceps*

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. 2017). 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. 2017, 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).

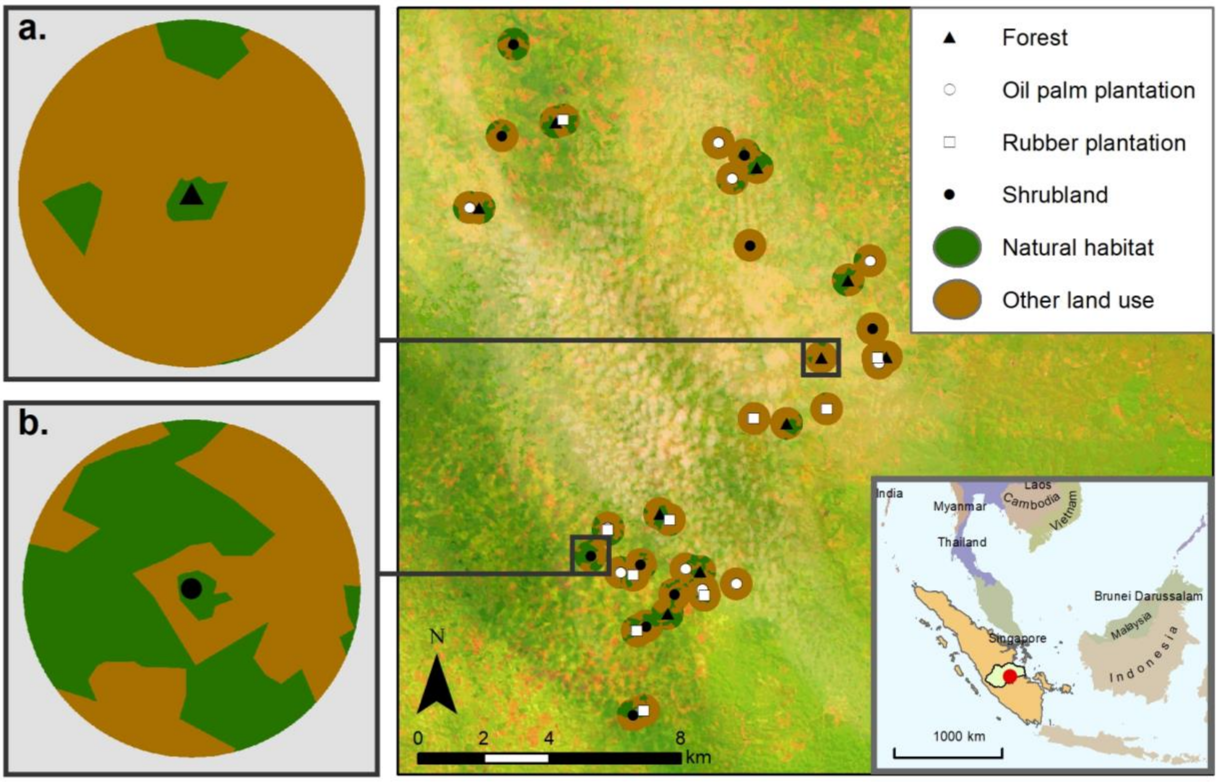


Figure 4-1. Map of study region in Batang Hari Regency, which is in Jambi Province, Sumatra, Indonesia (inset map). Call-outs show examples of (a) a forest plot with low surrounding natural habitat in the landscape and (b) a shrub plot with high surrounding natural habitat. Buffers are 500 m radius. 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 functions 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: 1.) plot land use ("land use") and 2.) 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 the survival 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 in turn whether these relationships implied indirect effects from 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 exploratory 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 include resin weight in the SEM, as prior biological knowledge does not suggest a relationship with flower resources, which our hive resin model also 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 still had hives at the end of the study period. 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. Mean landscape habitat around forest plots (29.8 ± 14.3% standard deviation) differed significantly from the mean around 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.

Mean landscape habitat did not differ significantly between plot types at the end of the study ($p > 0.05$, Section 4.6 Appendix B1. Landscape habitat), but ranges 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. Forest and rubber plots did not experience meaningful changes in floral density or richness. Though the change in forest richness was statistically 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 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

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**

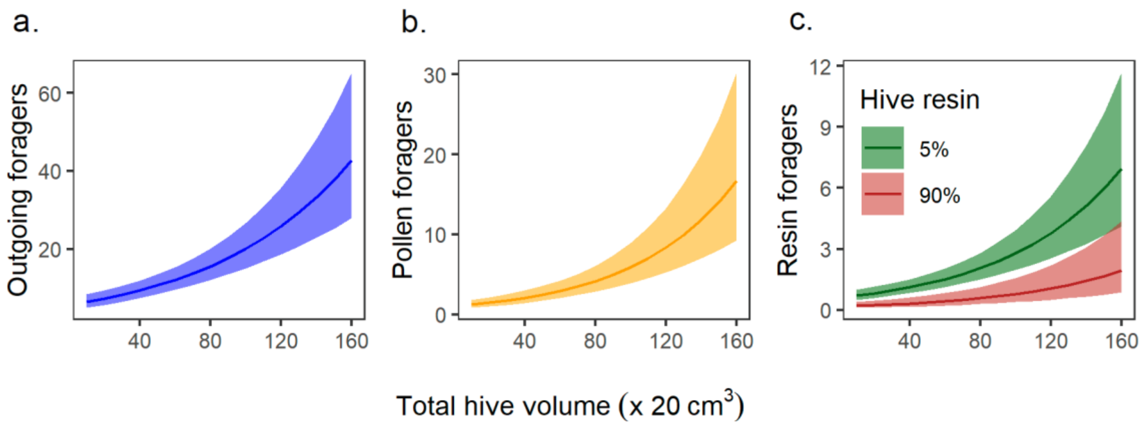


Figure 4-2. Estimated marginal mean forager counts and 95% confidence intervals over increasing hive volume for (a) outgoing foragers, (b) returning pollen foragers, and (c) returning resin foragers. Resin foragers also decreased with increasing proportion of hive occupied by resin (shown for 5% and 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		
τ_{00} Hive:Plot	113.85		
τ_{00} Plot	21.18		
ICC	0.34		
N Hive	3		
N Plot	31		
Observations	224		
Marginal R^2 / Conditional R^2	0.211 / 0.483		

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

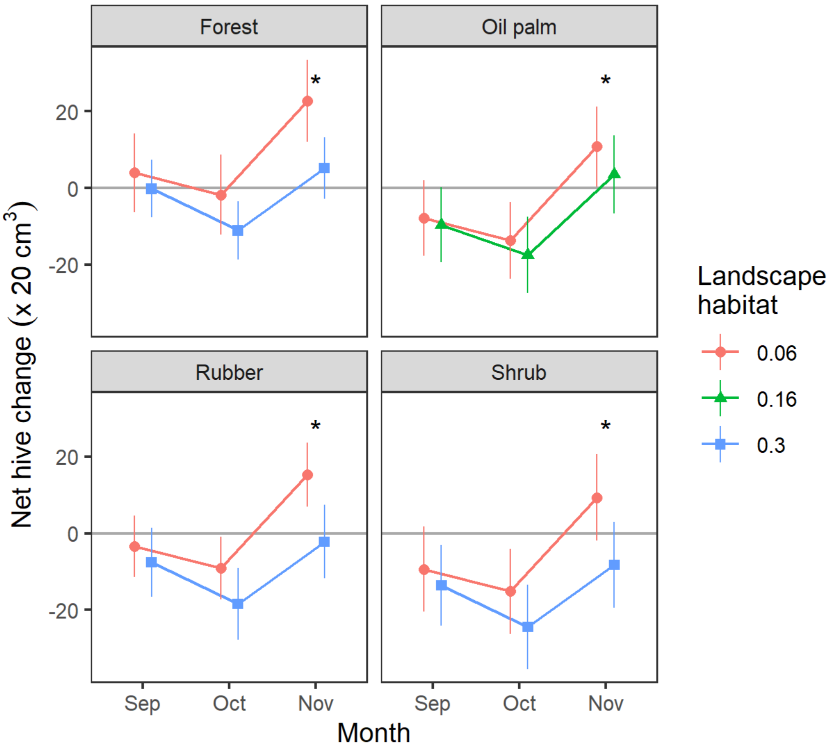


Figure 4-3. Modeled effect of plot land use (panels) and the interacting effects of month (x-axis) and proportion of habitat in the landscape on change in hive volume from initial size in August (net hive volume, y-axis). Note that hive change was estimated with the proportion of landscape habitat at 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.

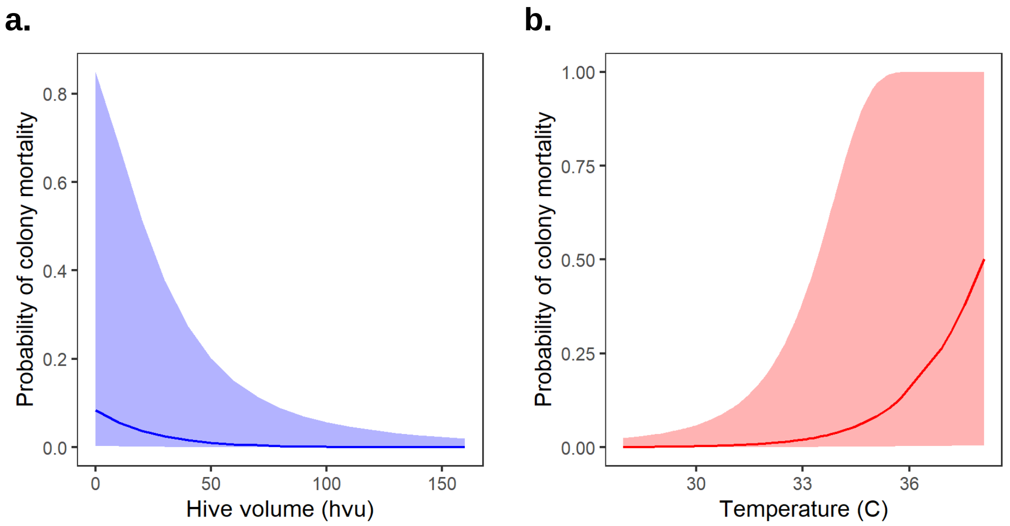


Figure 4-4. Estimated probability of colony mortality with increasing hive volume (a) and increasing temperature (b) and 95% confidence interval from survival analysis model.

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		
$\tau_{00\ \mathrm{Hive:Plot}}$	1.14		
$\tau_{00\ \mathrm{Plot}}$	6.58		
ICC	0.82		
N_{Hive}	3		
N_{Plot}	31		
Observations	292		
Marginal R^2 / Conditional R^2	0.395 / 0.894		

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 land use and landscape habitat. Other variables were not significant predictors of hive mortality at the a=0.05 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, 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

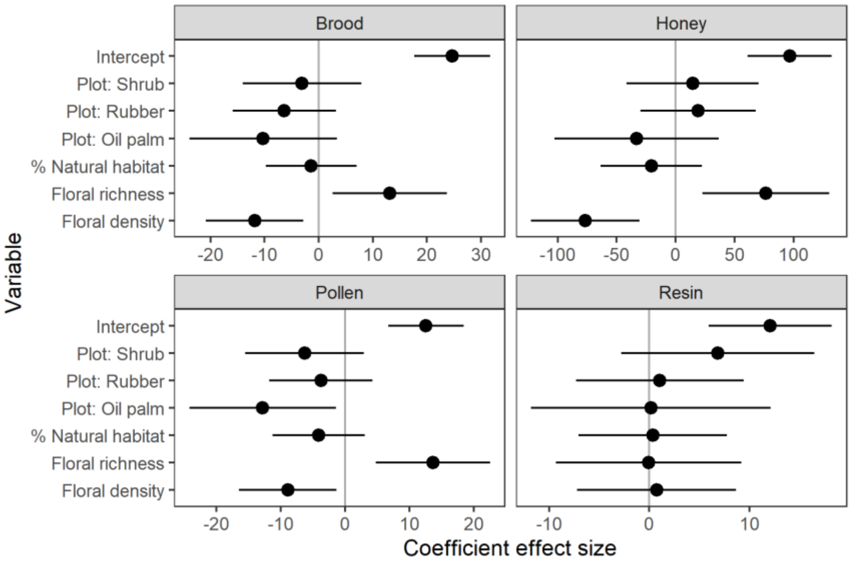


Figure 4-5. Effects estimates from linear (mixed) effects models of brood, honey, pollen, and resin weights at the end of the study in November. Estimates are compared to a forest plot baseline and continuous variables have been mean-centered and scaled by two standard deviations. Information about random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

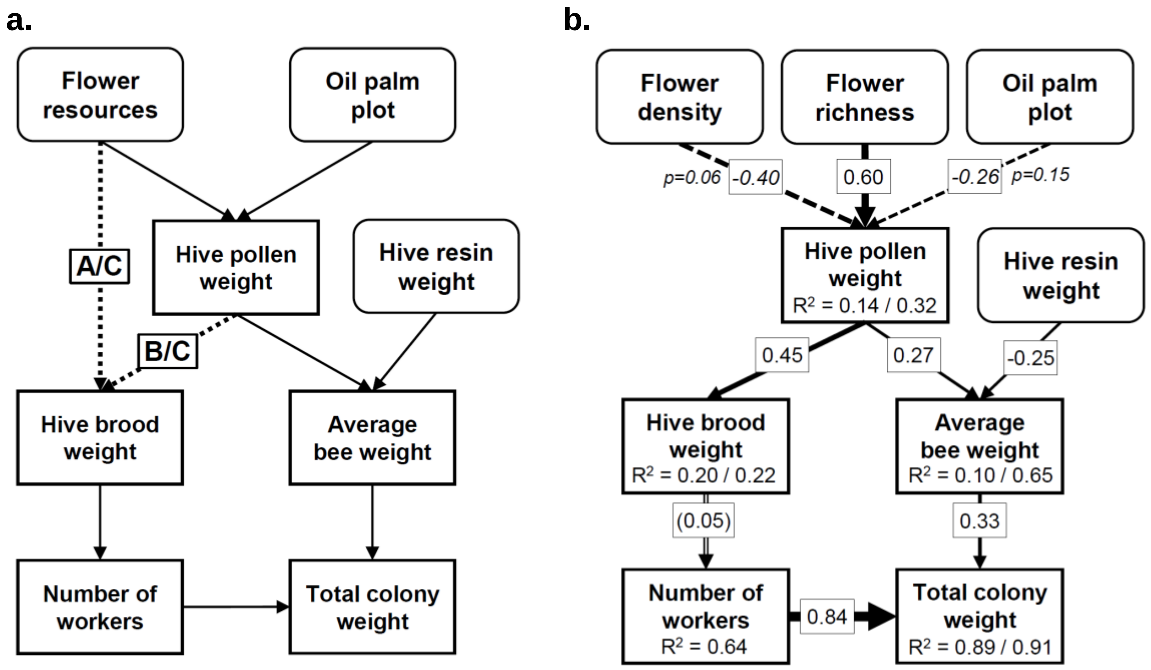


Figure 4-6. Hypothesized (a) and final (b) structural equation models of hive and colony variable relationships. Square boxes represent an exogenous model variable whose drivers are modeled in the SEM. Round boxes are exogenous variables that are not modeled. In (a), dotted arrows represent the alternative 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 by 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, in oil palm and shrub plots respectively, compared to forest, 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 overheat stingless bees, damage brood, and require 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 relationships with hive structure, which 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.

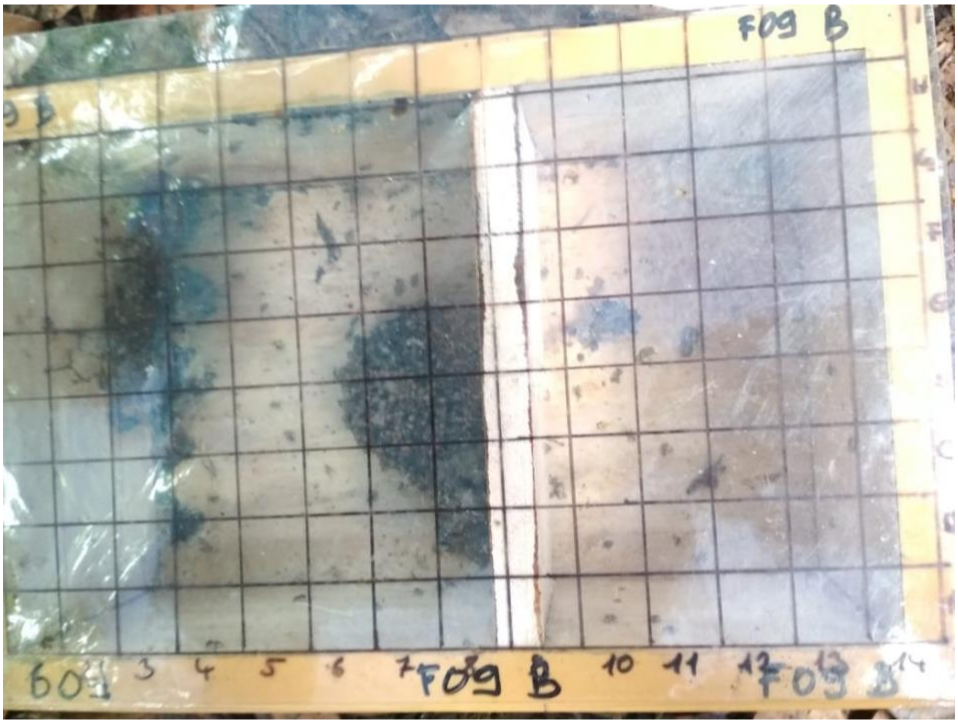
Acknowledgements

We are grateful for the assistance of Fahrurrozi, Davig Warisman, Wildan, and Ayu in the field and laboratory in Jambi. We would also like to thank the late Rustama Saepudin for arranging the purchase and delivery of the bees, and Teddy for assisting in assisting in delivery. This study was funded by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) – project ID 192626868 – SFB 990 in the framework of the collaborative German-Indonesian research project CRC 990.

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

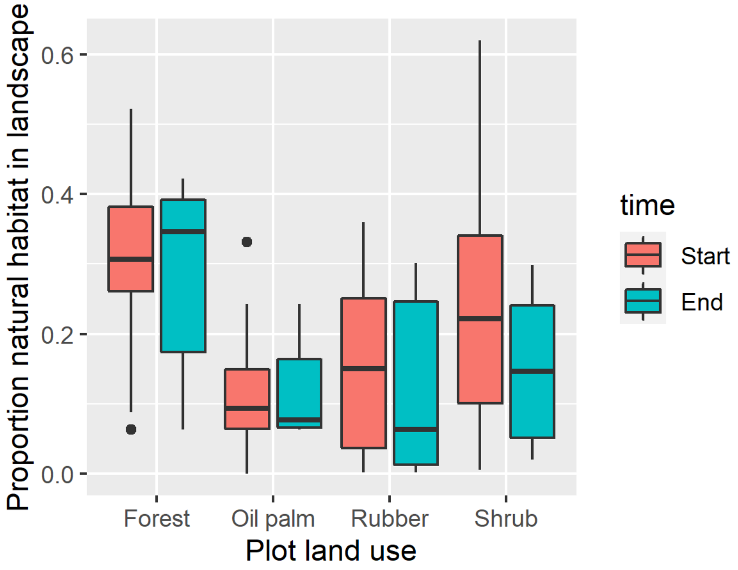
P value adjustment: tukey method for comparing a family of 4 estimates
```

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		

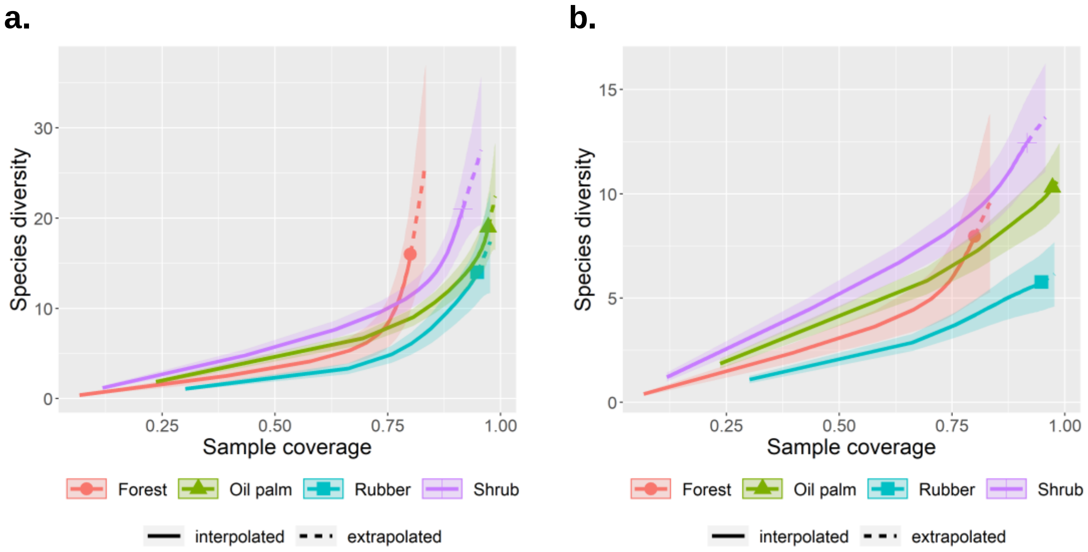
```
contrast          ratio     SE  df z.ratio p.value
 Forest / Oil palm 0.784 0.4430 Inf -0.431  0.9732
 Forest / Rubber   1.261 0.6948 Inf  0.422  0.9748
 Forest / Shrub    0.180 0.1016 Inf -3.036  0.0128
 Oil palm / Rubber 1.609 0.8862 Inf  0.864  0.8237
 Oil palm / Shrub  0.229 0.1296 Inf -2.605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

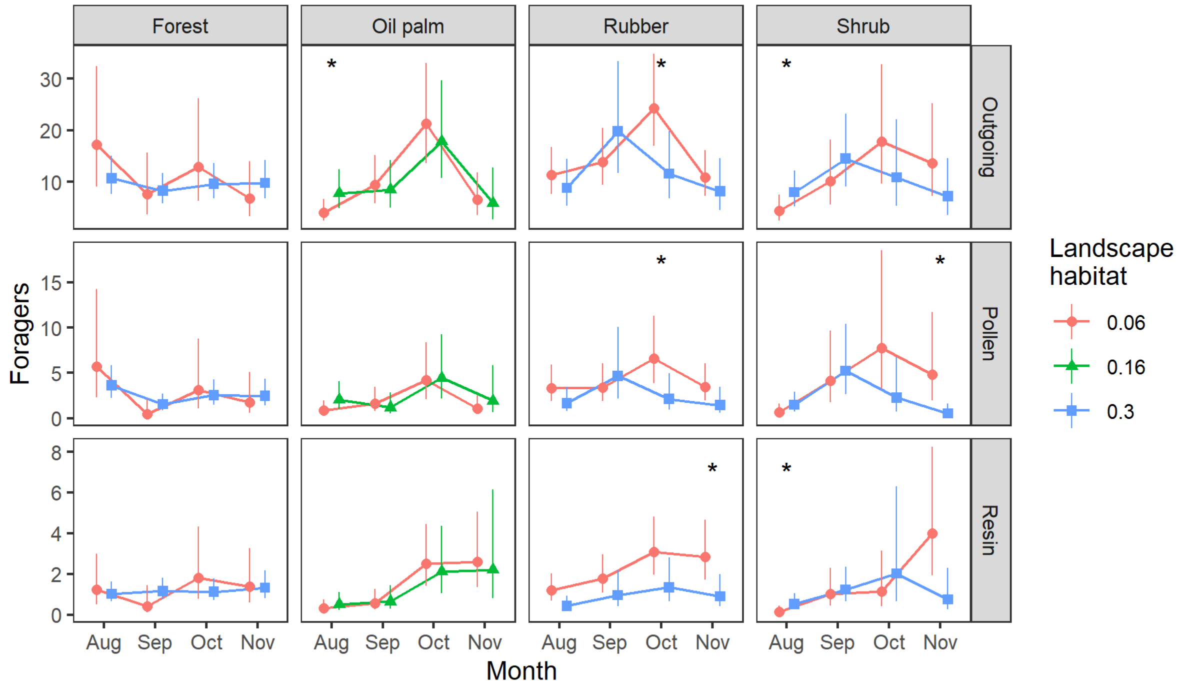
Appendix Table 4-9. Estimated coefficients for generalized linear mixed models of outgoing foragers, returning pollen foragers, and returning resin foragers. Models had a negative binomial link and random effects of hive identity nested within plot. Incidence rate ratios (IRR) are the exponentiated coefficients 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 $_{\text{Plot}}$			0.18 $_{\text{Plot}}$			0.10 $_{\text{Plot}}$		
	0.03 $_{\text{Timefac}}$			0.07 $_{\text{Timefac}}$			0.04 $_{\text{Timefac}}$		
ICC	0.32			0.32			0.18		
N	3 $_{\text{Hive}}$			3 $_{\text{Hive}}$			3 $_{\text{Hive}}$		
	37 $_{\text{Plot}}$			37 $_{\text{Plot}}$			37 $_{\text{Plot}}$		
	5 $_{\text{Timefac}}$			5 $_{\text{Timefac}}$			5 $_{\text{Timefac}}$		
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 enrichment treatments, or at multiple spatial scales.

I examined the interacting effects of landscape transformation at two different spatial scales 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 that were 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 effects on 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 canopy openness, which was strongly influenced by fast-growing enrichment tree species. 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 a forest border into an oil palm plantation, I found evidence of increasing oil palm pollination closer to forest that was moderated through partially excluding larger flower visitors. Pollination rate was associated with the introduced pollinator *Elaeidobius kamerunicus* 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 fruit set, demonstrating the importance of insect pollination services and the significant moderating role of forest.

Overall, the effects of landscape transformation on ecosystem functions and services were not easily simplified into basic gradients. Forest proximity moderated pollination services, but only under conditions that excluded some visitors; tree enrichment most directly affected light availability through canopy openness, which was directly and indirectly linked to higher pollination services; and forest conversion to open habitats was beneficial or detrimental to stingless bee colonies depending on whether it was providing habitat or floral resources. Clearly, the processes that occur in transformation landscapes are 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 can spur further research. For example, the influence of species interactions, such as predation, competition, or non-consumptive effects, 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., biocontrol in coffee (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. This includes the insect communities and ecological functions associated with gaps during biodiversity restoration and the role of gaps resulting from land conversion on the availability of floral and habitat resources for pollinators 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, as highlighted by the “Decade on Ecosystem Restoration” by the United Nations (Gann et al. 2019). The Roundtable on Sustainable Palm Oil has already adopted a “high conservation value” approach in certification schemes to promote biodiversity (Senior et al. 2015). Oil palm is an economically important crop that can bring benefits to local communities (Meijaard et al. 2018, Qaim et al. 2020), so consideration must 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 about the functions of biodiversity in relation to 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 has endeavored to contribute to these goals by investigating agroecosystem functions at different scales and connecting them to a context of landscape transformation.

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Acknowledgements

I would like to thank my advisor Teja for guiding me through the process leading up to this dissertation. His door was always open, and he taught me how to see the positive in my results, which brought clarity. Thank you also to my second advisor, Ingo for his support and feedback. I wish him the best of luck as a new professor, where I know he will be excellent. Thank you as well to Kerstin, for welcoming me to her spatial statistics class and her support on my advisory committee.

Thank you to the Indonesian counterparts for their support of my research: Ibu Dami for our meetings and discussions in Bogor; Fuad, for introducing me to Jambi; and Ibu Rika for accompanying me to the field and her expertise in bees.

I would also like to thank my two master's students, Sonja and Jonathan. Without their incredible work in the field, two of these chapters would not have been possible. I would also like to recognize the hard work of laboratory and field assistants in Indonesia and Germany: Arini, Ayu, Davig, Indah, Juwita, Meisi, Nahlia, Nurman, Ozy, Rico, Rosmalia, Weni, and Wildan made invaluable contributions in Indonesia and Hanna, Rebekka, Sonja, and Yasmin provided excellent assistance in Göttingen. My gratitude also goes out to M'lis in Michigan, and to Emmeline in Germany, for their help with my dissertation during the pandemic.

I thank my colleagues at EFForTS in Germany and Indonesia, some of whom are acknowledged in the preceding chapters. I am also grateful for the expertise and patience of Siria and Christina in the palynology department, and Ibu Aiyen for help in navigating Indonesian permits and bureaucracy. I thank the Deutsche Forschungsgemeinschaft for supporting my research.

I am grateful to Heike for helping me manage German bureaucracy even before arriving in Germany; Susanne and Brigitte for their help in the office; and Catrin for her kindness and generosity.

I am glad I got to know the cohort of PhD students, master's students, and postdocs who shared the third floor and this journey with me. Thank you, Manu, Kevin D, Emmeline, Felix Klaus, Arne, Felipe, Felix Kirsch, Nicole, Annemarie, Svenja, Anoush, Annika, Yvonne, Mina, Carolina, Gabriel, Max, Mike, Tara, and Viviana for: trips near and far, discussion on (Bayesian) statistics and coffee, running with me, alternative journal club, nightmare before Christmas, sharing chocolate, kitchen and Mensa conversations, and 2PM sport. Thanks for making Agroecology/Functional Agro-Biodiversity such a great place.

I am grateful for the generosity of Patty and Don, who welcomed me to their home whenever I came back to Michigan and helped Rachel and me make our own home in Lansing.

I would like to thank my parents Susie and Liang and my sister Lauren for encouraging me to embark on this journey, for their support from afar, and for editing help during the pandemic.

I feel lucky that I have had a partner who has shown love and support through this whole thing, no matter where I was, or where she was, or if we were stuck in Oman. Thank you, Rachel.

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, ………………………..

……………………………………
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, ………………………..

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Kevin Li