GEORG-AUGUST-UNIVERSITÄT
GÖTTINGEN

ZENTRUM FÜR BIODIVERSITÄTSFORSCHUNG UND ÖKOLOGIE

SEKTION BIOLOGISCHE DIVERSITÄT UND ÖKOLOGIE

EXPERIMENTAL BIODIVERSITY ENRICHMENT IN AN OIL-PALM PLANTATION

Dissertation

zur Erlangung des mathematisch-naturwissenschaftlichen Doktorgrades

"Doctor rerum naturalium"

der Georg-August-Universität Göttingen

im Promotionsprogramm "Biologische Diversität und Ökologie"
der Georg-August University School of Science (GAUSS)

vorgelegt von M.Sc.

Anne Gérard

aus

Wiesbaden

Göttingen, 2016

Betreuungsausschuss

Prof. Dr. Holger Kreft

Prof. Dr. Dirk Hölscher

Dr. Katja Rembold

Mitglieder der Prüfungskommission

Referent: Prof. Dr. Holger Kreft

Koreferent: Prof. Dr. Dirk Hölscher

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Tag der mündlichen Prüfung: 15.11.2016

Conservation is sometimes perceived as stopping everything cold, as holding whooping cranes in higher esteem than people. It is up to science to spread the understanding that the choice is not between wild places or people, it is between a rich or an impoverished existence for Man.

— Thomas Lovejoy —

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Summary

Large-scale conversion of tropical forests has led to dramatic losses of biodiversity and associated ecosystem services and functions. One particularly severe example of forest and biodiversity loss is Indonesia. The country's exceptionally high biodiversity is seriously threatened by land conversion, for which oil-palm cultivation is a major driver. To increase biodiversity and ecosystem functioning in oil-palm-dominated landscapes, reduced-impact farming systems such as agroforestry systems have been proposed. But in regions where oil-palm plantations already dominate the landscape, this increase can only be achieved through systematic ecological restoration. However, knowledge about the underlying ecological and socio-economic processes, constraints, and trade-offs of ecological restoration in oil-palm landscapes is very limited.

To bridge this gap, I established a long-term biodiversity enrichment experiment, together with colleagues from Germany and Indonesia. We planted experimental tree islands in a conventional oil-palm plantation and systematically varied plot size, tree diversity, and tree species composition. We used six multi-purpose tree species that are native to the region. To enhance the light availability for the planted trees, we reduced the oil-palm density within the tree islands by thinning.

In this thesis, I present the design of the experiment and give a broad picture of initial effects induced by the experiment, taking into account initial ecological effects and changes in oil-palm yields. The initial phase after planting is most critical to achieve restoration goals in the future, as it constitutes a bottleneck that trees have to surpass for long-term establishment. In addition, from the farmer's perspective, the initial phase can be a decisive hindrance, given the time delay from the establishment of the tree islands to the emergence of benefits.

First, I describe environmental variables and biotic characteristics of the associated vegetation, invertebrates, and birds of the experimental sites prior to the establishment of the experiment, as well as initial experimental effects on the fauna. One year after establishment of the experiment, tree plantings had an overall positive effect on the bird and invertebrate communities at the plantation scale. Diversity and abundance of invertebrates also responded at smaller scales, and were positively affected by the size of the tree islands. Based on these results, I expect a further increase of biodiversity and associated ecological functions in the future.

Subsequently, I report on the establishment success of the trees, and identify the most important determinants for tree growth and survival. Most trees established well; however, I found strong differences between the tree species considering relative height increment, relative basal area increment and survival. Most species with high growth rates also showed high survival rates. At the plot level, site conditions, plot size, and diversity level of the planted trees only weakly affected mean tree growth and survival. At the level of individual trees, I found significant neighborhood effects between the species. Tall neighboring trees and distance to living oil palms significantly benefitted tree performance. It is yet too early to decide on the overall suitability of tree species regarding their effectiveness to achieve restoration goals, but differences in initial tree performance are an important information to evaluate the species in the future.

Lastly, I present effects of the experiment on oil-palm yields. After two years, I found enhanced yields on the individual level of oil palms both inside and directly adjacent to the experimental plots. Estimating net yield changes for different sizes of tree islands including foregone yield of removed oil palms and spillover effects, I found evidence that – in particular for larger tree islands – yield gains at least compensate for the reduced number of oil palms. These results, obtained during the early phase of tree island establishment, are promising in terms of identifying sustainable management options for oil-palm plantations that reconcile ecological and economic functions.

Initial effects were stronger and, particularly from the economic point of view, more beneficial than I had expected. However, so far, I observed mostly weak neighborhood effects and a weak influence of experimentally altered variables, and I expect these effects to become more pronounced over time. Insights gained from future long-term monitoring of the experiment I present in this study may bridge knowledge gaps towards the elaboration of management guidelines for oil-palm landscapes that are both ecologically improved and economically viable. As one part of the puzzle, this thesis represents an important contribution to an overall evaluation of the experiment, and can thus, moreover, add new insights beyond our project that help to advance restoration science.

Zusammenfassung

Die großflächige Umwandlung von tropischen Wäldern hat zu dramatischen Verlusten von Biodiversität und assoziierten Ökosystemdienstleistungen und –funktionen geführt. Indonesien ist ein besonders schwerwiegendes Beispiel für den Verlust von Waldflächen und Biodiversität. Landumnutzungen, in starkem Maße durch den Anbau von Ölpalmen vorangetrieben, stellen eine erhebliche Bedrohung für die außergewöhnlich hohe Biodiversität des Landes dar. Landwirtschaftssysteme, wie Agroforstsysteme, können hingegen genutzt werden, um die Biodiversität und Ökosystemfunktionen in von Ölpalmen dominierten Landschaften zu erhöhen. In Regionen, in denen Ölpalmplantagen bereits die Landschaft dominieren, kann diese Erhöhung nur durch systematische Renaturierung erfolgen. Die zugrunde liegenden ökologischen und soziökonomischen Prozesse und damit verbundene Beschränkungen und Kompromisse von Renaturierungsmaßnahmen in von Ölpalmen dominierten Landschaften sind jedoch weitgehend unbekannt.

Um diese Wissenslücke zu schließen, habe ich mit Kollegen aus Deutschland und Indonesien ein Langzeitexperiment zur Erhöhung der Biodiversität aufgebaut. Wir haben experimentell Bäume in Form von „Inseln“ in eine konventionelle Ölpalmplantage gepflanzt und hierbei systematisch die Flächengröße, das Diversitätslevel und die Artzusammensetzung variiert. Wir haben hierfür sechs multifunktionale heimische Baumarten ausgewählt. Auf der Fläche der Bauminseln haben wir einen Teil der Ölpalmen gefällt, um die Lichtverfügbarkeit für die gepflanzten Bäume durch eine reduzierte Ölpalmdichte zu erhöhen.

In dieser Doktorarbeit stelle ich den Aufbau des Experiments vor und gebe einen breiten Einblick in anfängliche Auswirkungen des Experiments, indem ich ökologische Aspekte in Betracht ziehe, sowie Veränderungen hinsichtlich des Ernteertrags. Da die Zeit kurz nach der Pflanzung ein Nadelöhr für die Langzeitetablierung der Bäume darstellt, ist sie sehr kritisch, um die erwünschten Renaturierungserfolge in der Zukunft zu erzielen. Des Weiteren kann die Anfangszeit auch aus der Sicht der Landwirte eine entscheidende Hürde darstellen, da der Nutzen der Bauminseln erst lange Zeit nach ihrer Pflanzung entsteht.

Zuerst beschreibe ich Umweltvariablen und biotische Charakteristika der den experimentellen Flächen assoziierten Vegetation, Invertebraten und Vögel vor der Errichtung des Experiments, sowie anfängliche Auswirkungen des Experiments auf die Fauna. Ein Jahr nach der Errichtung des Experiments hatten die Baumpflanzungen einen insgesamt positiven Effekt auf die Artengemeinschaften von Vögeln und Invertebraten in der Plantage. Die Größe der Bauminseln wirkte sich lediglich auf die Diversität und Abundanz von Invertebraten positiv aus, die somit auf kleinskalige Veränderungen reagierten. Ausgehend von diesen Ergebnissen erwarte ich einen weiteren Anstieg der Biodiversität und Ökosystemfunktionen in der Zukunft.

Danach berichte ich über den Anwuchserfolg der Bäume und ermittle die wichtigsten Determinanten für den Wuchs und das Überleben der Bäume. Insgesamt sind die Bäume gut angewachsen, jedoch gab es große Unterschiede zwischen den Baumarten hinsichtlich relativer Höhenwachstums-, Dickenwachstums- sowie Überlebensraten. Arten mit hohen Wachstumsraten wiesen vorwiegend auch hohe Überlebensraten auf. Auf Versuchsflächenebene hatten Standortbedingungen, Flächengröße und Diversitätslevel der gepflanzten Bäume lediglich einen geringen Einfluss auf das mittlere Baumwachstum und die Überlebensrate. Auf Individuenebene habe ich signifikante Nachbarschaftseffekte festgestellt. Hohe benachbarte Bäume und die Distanz zu verbleibenden Ölpalmen begünstigten die Entwicklung der Bäume. Noch ist es zu früh zu entscheiden, welche der Baumarten sich generell am besten eignen, um Renaturierungsziele zu erreichen. Unterschiede in der anfänglichen Entwicklung liefern jedoch wichtige Informationen für eine zukünftige Bewertung der Arten.

Zuletzt präsentiere ich Auswirkungen des Experiments auf den Ölpalmertrag. Nach zwei Jahren waren die Erträge pro Ölpalmindividuum erhöht, sowohl auf als auch direkt neben den Versuchsflächen. Die geschätzten Ertragsänderungen für die verschiedenen Flächengrößen unter Einbezug von Ernteverlusten durch gefällte Ölpalmen sowie Effekte auf benachbarte Ölpalmen deuten darauf hin, dass die erhöhten Ernteerträge insbesondere in großen Bauminseln mindestens das Fällen von Ölpalmen kompensiert haben. Diese Ergebnisse, die in der frühen Phase der Bauminseletablierung erzielt wurden, sind vielversprechend für die Erarbeitung nachhaltiger Managementoptionen für Ölpalmplantagen, die ökologische und ökonomische Funktionen in Einklang bringen.

Die anfänglichen Auswirkungen waren stärker und insbesondere aus ökonomischer Perspektive profitabler als ich erwartet habe. Die Nachbarschaftseffekte und die Auswirkungen der experimentell veränderten Variablen waren bislang jedoch überwiegend schwach. Ich erwarte, dass diese Auswirkungen mit der Zeit stärker ausgeprägt sein werden. Durch Erkenntnisse, die aus zukünftigen Langzeitbeobachtungen des Experiments, das ich in dieser Doktorarbeit vorstelle, gewonnen werden, können Wissenslücken geschlossen werden. Somit kann die Ausarbeitung von Managementrichlinien für von Ölpalmen dominierten Landschaften ermöglicht werden, die sowohl ökologisch verbessert als auch ökonomisch lohnenswert sind. Diese Doktorarbeit stellt einen wesentlichen Beitrag zur generellen Beurteilung des Experiments dar, wodurch darüber hinaus auch neue Erkenntnisse für die Renaturierungswissenschaft gewonnen werden können.

Author contributions

Chapter 2: Experimental biodiversity enrichment in oil-palm-dominated landscapes in Indonesia

Miriam Teuscher*, **Anne Gérard***, Ulrich Brose, Damayanti Buchori, Yann Clough, Martin Ehbrecht, Dirk Hölscher, Bambang Irawan, Leti Sundawati, Meike Wollni, Holger Kreft

MT and **AG** equally contributed to the article (*). The experiment was designed by UB, YC, DH, HK and MW. MT, ME and **AG** planned, MT and **AG** carried out the establishment of the experimental plots with support from DB, LS, and BI. Soil data were collected by **AG**; all other environmental data by MT and **AG**. Hemispherical photographs were taken by **AG**. The plant survey was designed by **AG** and HK and carried out by **AG**. Faunal surveys were designed by MT, YC and UB and carried out by MT. MT and **AG** analyzed the data. The text was written by MT and **AG** with comments from UB, HK, YC, DH, MW and ME.

Chapter 3: Initial tree performance in a biodiversity enrichment experiment in an oil-palm landscape

Anne Gérard, Dirk Hölscher, Bambang Irawan, Leti Sundawati, Miriam Teuscher, Holger Kreft

The study was designed by **AG**, DH, and HK. Data collection was done by **AG** with support from MT, BI, and LS. Analyses were conducted by **AG** with support from DH and HK. The manuscript was written by **AG**, revised by DH and HK, and all authors contributed to improve the manuscript.

Chapter 4: Oil-palm yields in diversified plantations: initial results from a biodiversity enrichment experiment in Sumatra, Indonesia

Anne Gérard, Meike Wollni, Dirk Hölscher, Bambang Irawan, Leti Sundawati, Miriam Teuscher, Holger Kreft

The study was designed by **AG**, MW, HK, DH, and MT. Data collection and analyses were done by **AG** with support from MT, BI, and LS. The text was written by **AG** with comments from BI, LS, HK, MW, MT, and DH.

Affiliations of co-authors

Ulrich Brose	German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, 04103, Leipzig, Germany Institute of Ecology, Friedrich Schiller University Jena, Dornburger-Str. 159, 07743, Jena, Germany
Damayanti Buchori	Department of Plant Protection, Bogor Agricultural University, Bogor, Indonesia
Yann Clough	Centre for Environmental and Climate Research, Lund University, Lund, Sweden Department of Crop Sciences, Agroecology, Georg-August-University Göttingen, Göttingen, Germany
Martin Ehbrecht	Silviculture and Forest Ecology of the Temperate Zones, Georg-August-University Göttingen, Göttingen, Germany
Dirk Hölscher	Tropical Silviculture and Forest Ecology, Georg-August-University Göttingen, Göttingen, Germany
Bambang Irawan	Faculty of Forestry, University of Jambi, Jambi, Indonesia
Holger Kreft	Biodiversity, Macroecology and Biogeography, Georg-August-University Göttingen, Göttingen, Germany
Leti Sundawati	Department of Forest Management, Faculty of Forestry, Bogor Agricultural University, Bogor, Indonesia
Miriam Teuscher	Department of Systemic Conservation Biology, J.F. Blumenbach Institute for Zoology and Anthropology, Georg-August-University Göttingen, Göttingen, Germany
Meike Wollni	Department of Agricultural Economics and Rural Development, Georg-August-University Göttingen, Göttingen, Germany

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1 Introduction

1.1 Biodiversity: crucial for ecosystem functioning and humanity alike

In recent years, there has been increasing concern about the alarming state of our planet's ecosystems among researchers and the general public alike. Given the great dimension to which humans have been altering the Earth's ecosystems, the current geological era has been termed the "Anthropocene" (Crutzen, 2002). The most serious human-induced concerns include the tremendous degree of global species loss, which is viewed as the beginning of the sixth mass extinction in the Earth's history (Ceballos et al., 2015). The biodiversity decline has already exceeded a tolerable level, defined by the "planetary boundaries" (Rockström et al., 2009), and could thus threaten its stability. Moreover, consequences associated to species loss are predicted to jeopardize human well-being in the long term (Balvanera et al., 2006; Cardinale et al., 2012).

In the light of this serious situation, it is surprising that the crucial role of biodiversity for ecosystem functioning and humanity was only recognized 30 years ago (Franco, 2013). At that time, various publications, e.g. by Myers (1979), drew attention to the massive dimension of species extinction caused by humanity. Having reached scientists and society likewise, a "National Forum on BioDiversity" was held in the US in 1986. The results were published in a book titled "Biodiversity", where the neologism – a deduction from "biological diversity" – first occurred (Wilson, 1988). At the same time, conservation biology established as a distinct field of science (Franco, 2013). In 1992, the "Convention on Biological Diversity" was published by the United Nations with the aim of integrating conservation and sustainable use of biological diversity into global politics. It also contains one of the most cited definitions on biological diversity (Box 1.1).

Meanwhile, researchers started to conduct experiments to investigate the consequences of species extinction (e.g. Naeem et al., 1995; Tilman and Downing, 1994) or, in turn, the importance of biodiversity for ecosystem functioning (see Box 1.1 for definition). In experimental plots, artificial systems were created, including different levels of species numbers. After a given time, various ecosystem processes were quantified and linked to the initial levels of species richness. To date, hundreds of similar biodiversity-ecosystem functioning experiments have followed, using different organisms in different biomes all over the globe. Through these experiments, positive effects of biodiversity on many aspects of ecosystem functioning were confirmed (reviewed e.g. in Balvanera et al., 2006; Cardinale et al., 2012; Hooper et al., 2012). These positive effects have mostly been attributed to improved resource use due to niche complementarity and positive interactions between species (e.g. Hector, 1999). A closely related and partly overlapping research branch emphasized an anthropocentric perspective, which led to the development of the conceptual framework of ecosystem services (see Box 1.1 for definition). Evidence was found that losing species can deteriorate the provision of ecosystem services that are crucial for human well-being (reviewed in e.g. Cardinale et al., 2012). The complex interplay between individuals, species, and their environments, however, still makes it difficult to fully understand and predict the consequences associated with species loss. However, such predictions are fundamental to inform decision-making for effective ecosystem protection (Cardinale et al., 2012).

The current extent of biodiversity loss may already be too severe to safeguard the stability of the Earth's ecosystems in the long term (Rockström et al., 2009). Land conversion, one of the biggest threats to biodiversity and ecosystem functioning, is projected to increase in the future and to further aggravate the situation (Foley, 2005). Thus, besides the importance of protecting the remaining biodiversity (Balvanera et al., 2006; Tilman and Downing, 1994), there is a need for integrating restoration activities into conservation strategies to enhance biodiversity (Kueffer and Kaiser-Bunbury, 2014). In his book "The Diversity of Life", first published in 1992, the famous biologist E.O. Wilson wrote: "Here is the means to end the great extinction spasm. The next century will, I believe, be the era of restoration in ecology."

Box 1.1 | Definitions

"*Biological diversity* means the variability among living organisms from all sources, including, inter alia, terrestrial, marine and other aquatic ecosystems, and the ecological complexes of which they are part: this includes diversity within species, between species and of ecosystems." (United Nations, 1992)

"*Ecosystem functioning* reflects the collective life activities of plants, animals, and microbes and the effects these activities – feeding, growing, moving, excreting waste, etc. – have on the physical and chemical conditions of their environment." (Naeem et al., 1999)

"*Ecosystem services* are the benefits people obtain from ecosystems. These include provisioning services such as food and water; regulating services such as regulation of floods, drought, land degradation, and disease; supporting services such as soil formation and nutrient cycling; and cultural services such as recreational, spiritual, religious and other nonmaterial benefits." (Millenium Ecosystem Assessment, 2003)

Strategies to conserve and restore biodiversity, ecosystem functioning, and ecosystem services are particularly urgently needed in the tropics (Lamb et al., 2005). Biodiversity is not equally distributed across the Earth's terrestrial ecosystems: tropical rainforests harbor by far the highest species richness (Corlett and Primack, 2005). Sadly, the tropics also face the world's highest deforestation rates (Hansen et al., 2013), putting high pressure on the remaining biota. Thus, most of the biodiversity hotpots, i.e. areas of high conservation priority (Myers et al., 2000), can be found here, and the tropics contribute disproportionally to the global biodiversity crisis (Bradshaw et al., 2009).

1.2 Need for new approaches to biodiversity conservation

Much of the deforested area is now used by humans. Therefore, the implementation of pure conservation concepts may be conflicting or even unethical in many cases (Kareiva and Marvier, 2012). Traditional restoration strategies in the tropics emphasizing economic outcomes, such as monoculture plantings with exotic species, have been criticized to provide only a small fraction of the functioning and services of the primary ecosystem (Lamb et al., 2005). Thus, novel approaches need to combine conservation and restoration with natural resource management and socio-economic perspectives at the landscape scale (Hobbs and Cramer, 2008). Such designed landscapes may be an effective and realistic way to achieve conservation goals in the future while accounting for local livelihoods (Kueffer and Kaiser-Bunbury, 2014). Yet, careful planning is required; sharp edges between components of the land-sparing concept, in which areas of high conservation value are separated from intensively managed agricultural land, could be buffered by integrating components of wildlife-friendly farming and thus increase the connectivity across the landscape (Koh et al., 2009).

1.3 From theory to practice: oil-palm-dominated landscapes as model landscapes

The cultivation of oil palms has become a major conservation concern (see Box 1.2 for more information). Oil-palm plantations cover large areas of South-East Asia, with Indonesia having the highest percentage of area cultivated with oil palm (FAO, 2016). In large scale, tropical rainforests have been directly or indirectly converted to monoculture oil-palm landscapes (Abood et al., 2015). This has resulted in a severe decline in biodiversity (Drescher et al., 2016; Fitzherbert et al., 2008; Foster et al., 2011; Savilaakso et al., 2014) and ecosystem functioning (Dislich et al., 2016). Therefore, oil-palm plantations have become a big threat to the region's exceptionally rich biodiversity (Sodhi et al., 2004). With a steadily rising demand for palm oil, further land conversion is expected in the future, which may increase the threat to remaining tropical rainforests (Fitzherbert et al., 2008).

As part of my PhD, I, together with my colleagues, experimentally test the concept of designer landscapes introduced by Koh et al. (2009) in an oil-palm-dominated landscape. Our study region, the province of Jambi, Indonesia, induced some strong adjustments of Koh et al. (2009)'s concept, however: there, the large-scale land transformation has already widely been completed, leaving few options for reasonable landscape planning right from the beginning. Remaining forest patches are scarce. Space for buffer zones may be created mainly by re-transforming oil-palm plantations, which could however be highly conflicting with local oil-palm farmers and estates. This situation is likely to be comparable with many other parts of the globe, given the degree to which unmanaged terrestrial ecosystems have already been converted to land-use systems (Foley, 2005).

In an existing agricultural landscape, area-effective, small-scale restoration measures would be advantageous and are more likely to be realizable, since opportunity costs of foregone harvesting acreage are minimized. It has been suggested to plant islands with native trees to enhance the conservation value of existing agricultural landscapes and to accelerate restoration (Rey Benayas et al., 2008). In abandoned pastures, tree islands were found to be similarly effective in enhancing biodiversity as large-scale monoculture plantings, but less costly (Zahawi et al., 2013). In agricultural landscapes, however, this concept remains largely untested (Rey Benayas et al., 2008). The most favorable trade-off with regard to area- and cost-effectiveness will strongly depend on two unknown variables: the minimum size of the islands, and the spatial arrangement of islands needed to adequately benefit biodiversity. Using native species in mixed-species stands may effectively contribute to enhance ecosystem functioning and services, and planting multi-purpose species can simultaneously benefit the local economy (Lamb et al., 2005). However, there is little knowledge on which species should be chosen, and which species composition is the most beneficial to achieve restoration goals. Although an overall positive effect of biodiversity on ecosystem functioning was found, the effect intensity differed between specific species compositions (Hooper and Vitousek, 2007). Moreover, some species were found to be more productive in monocultures than in mixed-species stands (Cardinale et al., 2007). The most favorable species composition and the minimum adequate number of species required for enhancing ecosystem functioning may therefore strongly depend on the characteristics of the chosen species, their interactions, and local site conditions. Furthermore, the species` effectiveness may vary with regard to the respective ecosystem function that is to be enhanced.

Box 1.2 I Why is the oil palm so popular?

Elaeis guineensis Jacq., the oil palm, is native to West and Central Africa, but is nowadays mainly cultivated in South-East Asia (Corley and Tinker, 2003). It has become one of the most important sources of vegetable oil worldwide (Carter et al., 2007). Compared to other major oil crops, it has the highest output value (Basiron, 2002). Regular palm oil is extracted from the outer pulp surrounding the fruit kernel, and higher quality palm kernel oil is derived from kernels themselves (Corley and Tinker, 2003). Given high cash value and relatively low labor-input requirements (Drescher et al., 2016), it is a very popular crop to cultivate. Palm oil offers various desired qualities to purchasers alike: the produce is fairly resistant to oxidation, which increases the shelf life of end products, and a solid fat content of 20-22% at 20°C is favorable for food products requiring a plastic consistency (Basiron, 2002). Furthermore, compared to other major oil crops, it is relatively cheap (Carter et al., 2007). At a global scale, palm oil is mainly used as cooking/frying oil, as shortening, margarine and confectionery fat but also in non-food products such as soaps, detergents, pharmaceutical products, and cosmetics (Basiron, 2002). In addition, it is among the most important crops for biodiesel production (Koh et al., 2009).

1.4 Research framing within the umbrella project "EFForTS"

I conducted my PhD thesis in a sub-project under the umbrella of the interdisciplinary "EFForTS" project ("Collaborative Research Centre 990: Ecological and Socio-economic Functions of Tropical Lowland Rainforest Transformation Systems (Sumatra, Indonesia)") (Drescher et al., 2016; http://www.uni-goettingen.de/en/310995.html). Along a gradient of management intensity from intact tropical lowland rainforest (not managed), to agricultural systems, i.e. jungle rubber (extensively managed), and rubber and oil-palm monocultures (both intensively managed), my colleagues investigate effects of land transformation on environmental processes, plants, animals, and local socio-economics. Once widely covered with rainforests, the study region Jambi province is among the regions currently strongly affected by land use change (Laumonier et al., 2010). Similar to my colleagues, the main research objective of my sub-project focusses on the investigation of changes in biodiversity and ecosystem functioning and services along the gradient of management intensity, but in reverse direction. In departing from a highly intensively managed oil-palm plantation, my overarching research question is: how much biodiversity and ecosystem functioning can be gained via ecological restoration whilst minimizing socio-economic losses?

To investigate this question, I established a biodiversity enrichment experiment within an oil-palm plantation in Jambi province together with colleagues from Germany and Indonesia. We planted tree islands and systematically varied tree species identity, diversity level (0, 1, 2, 3, and 6) of the planted tree species, and plot size (25 m^2, 100 m^2, 400 m^2, and 1600 m^2). Following the random partitions design by Bell et al. (2009), this resulted in 48 plots planted with trees. Additionally, we established four plots without planted trees which are subject to natural succession, and another four control plots in the oil-palm plantation under management-as-usual. For the tree species, we chose six multi-purpose species that are native to the study regions and used by local people; including two timber species, one latex-providing, and three fruit-providing species.

We expect that the enrichment planting will induce an overall higher associated biodiversity and ecosystem functioning compared to the surrounding oil-palm plantation. We furthermore hypothesize that, given the positive BEF-relationship, ecosystem functioning increases over time stronger with higher initial tree species diversity and with larger plot size. In the course of a planned runtime of 12 years, extensive monitoring of ecological and socio-economic factors within the experiment will help to evaluate the effectiveness of enrichment planting to restore biodiversity and associated ecosystem functioning and services, and may help to identify planting strategies under which enhanced ecosystem services positively affect oil-palm economics. The experiment is a long-term interdisciplinary research platform, and many researchers will have the chance to contribute to shed light on the broad picture of effects initiated by the enrichment plantings. In the framework of my thesis, I contributed to the project with the actual establishment of the tree islands and with the scientific insights that I gained during the initial phase of the experiment. In the following chapters 2, 3, and 4, I present my findings.

1.5 Study objectives and outline

The initial phase is crucial for the overall success of the long-term experiment: due to the sensitivity of saplings to environmental stresses, tree mortality is likely to be high (Evans and Turnbull, 2004). For long-term establishment, young trees must reach the canopy level and develop their root system as fast as possible to safeguard their access to resources (Evans and Turnbull, 2004; Peet and Christensen, 1987). This means badly-performing individuals may not survive the first years after planting. The initial phase of enrichment planting is also critical from the farmers' perspective, since the planted trees do not yet provide additional income, but generate establishment costs. The experiment aims at identifying restoration strategies that farmers will be willing to adopt. In this respect, potential economic losses during the initial phase can be a decisive hindrance.

In my thesis, I focus on the conditions of the oil-palm plantation prior to establishment and study early impacts of the biodiversity enrichment experiment on ecological and agro-economic factors.

In chapter 2, I introduce the experimental design and I present baseline data on the site conditions, the understory vegetation and the faunistic composition that were present at the experimental sites in the plantation prior to the establishment of the experiment. Additionally, I present changes in the faunistic composition one year after establishment.

In chapter 3, I analyze the performance of the planted trees: I compare tree growth parameters and survival between the different species, and I investigate the influence of plot-specific environmental factors on tree performance. Furthermore, I study initial signs of tree-tree and tree-oil-palm interaction.

In chapter 4, I compare the yields of oil palms within the experimental plots with yields of three oil palms in increasing distance adjacent to each plot. I also analyze the farmers' potential yield losses or gains from the establishment of a plot in the respective plot size classes in comparison with the oil-palm plantation under management-as-usual.

In chapter 5, I discuss the main findings of my PhD studies, integrate my results in the state-of-the-art of science and give an outlook to the future of the experiment.

2 Experimental biodiversity enrichment in oil-palm-dominated landscapes in Indonesia

Miriam Teuscher†, Anne Gérard†, Ulrich Brose, Damayanti Buchori, Yann Clough, Martin Ehbrecht, Dirk Hölscher, Bambang Irawan, Leti Sundawati, Meike Wollni and Holger Kreft

† These authors have contributed equally to this work.

published in *Frontiers in Plant Science* (2016),7:1538. doi: 10.3389/fpls.2016.01538

1.1 Abstract

Tropical biodiversity is threatened by the expansion of oil-palm plantations. Reduced-impact farming systems such as agroforests, have been proposed to increase biodiversity and ecosystem functioning. In regions where oil-palm plantations already dominate the landscape, this increase can only be achieved through systematic ecological restoration. However, our knowledge about the underlying ecological and socio-economic processes, constraints, and trade-offs of ecological restoration in oil-palm landscapes is very limited. To bridge this gap, we established a long-term biodiversity enrichment experiment. We established experimental tree islands in a conventional oil-palm plantation and systematically varied plot size, tree diversity, and tree species composition. Here, we describe the rationale and the design of the experiment, the ecosystem variables (soil, topography, canopy openness) and biotic characteristics (associated vegetation, invertebrates, birds) of the experimental site prior to the establishment of the experiment, and initial experimental effects on the fauna. Already one year after establishment of the experiment, tree plantings had an overall positive effect on the bird and invertebrate communities at the plantation scale. The diversity and abundance of invertebrates was positively affected by the size of the tree islands. Based on these results, we expect a further increase of biodiversity and associated ecological functions in the future. The long-term interdisciplinary monitoring of ecosystem variables, flora, fauna, and socio-economic aspects will allow us to evaluate the suitability of tree islands as a restoration measure. Thereof, guidelines for ecologically improved and socio-economically viable restoration and management concepts could be developed.

2.2 Introduction

A major driver of the current biodiversity crisis in South-East Asia is the large-scale transformation of natural rainforest into simplified production systems such as oil palm (Fitzherbert et al., 2008; Immerzeel et al., 2014). As a consequence of the resulting dramatic losses of biodiversity, losses in ecosystem functioning are expected (Edwards et al., 2014; Sodhi et al., 2004; Wilcove et al., 2013) that can disproportionally exceed the loss in species diversity (Barnes et al., 2014). The degradation of important ecosystem functions such as pollination success, or the impairment of soil fertility and water quality also puts human well-being at risk (Cardinale et al., 2012; Dislich et al., 2016).

Besides the importance of protecting tropical forests for biodiversity conservation, integrating biodiversity conservation into the management of existing large-scale oil-palm plantations seems imperative (Foster et al., 2011; Koh et al., 2009; Luskin and Potts, 2011; Teuscher et al., 2015). Designer plantation landscapes in which agroforestry zones buffer the natural vegetation from monoculture plantations have been proposed as one strategy to satisfy livelihood needs while increasing biodiversity and ecological functions (Koh et al., 2009). By enhancing the habitat complexity, the negative environmental impacts of intensively managed cash-crop production systems such as oil palm could be mitigated. Currently, institutions like the Roundtable for Sustainable Palm Oil (RSPO) focus on non-deforestation policy, conservation of large expanses of high valuable habitat, and threatened species (RSPO, 2013). However, in a region where most forest is lost (Margono et al., 2014) and where species diversity in the agricultural landscape is declining (Fitzherbert et al., 2008), options for conservation and reasonable landscape planning are already limited. Restoring habitat heterogeneity at local and landscape scales might thus be an option to maintain or even enhance biodiversity in oil-palm landscapes (Azhar et al., 2011).

Planting native trees has been considered a restoration measure to increase biodiversity (Chazdon, 2008). Planted tree islands can act as focal areas of recovery, or recruitment nuclei, and may initiate natural succession inside the islands and in its surroundings, as dispersers are attracted and establishment of new plant recruits is facilitated (Corbin and Holl, 2012; sensu Yarranton and Morrison, 1974). Such nuclei were found to have similar effects on biodiversity compared to tree plantings over large areas, but are more cost-effective (Zahawi et al., 2013). Even small tree islands can act as recruitment nuclei as they increase bird activity and hence seed rain (Cole et al., 2010). For instance, seedling species richness was increased within a short period and seedling establishment was facilitated due to a more favorable microclimate in experimental tree islands in Honduras (Zahawi and Augspurger, 2006). Most restoration planting experiments took place in abandoned agricultural land, pastures, and logged-over forests (Cole et al., 2010; Hector et al., 2011; Zahawi and Augspurger, 2006), but tree islands were also suggested to enrich biota in agricultural landscapes (Rey Benayas et al., 2009). To date there is no consensus on which is ecologically and economically the most effective tree island size and how to transfer insights from island biogeography into a landscape context (Mendenhall et al., 2014).

To our knowledge, restoration efforts have rarely been made in an existing plantation; empirical support on how oil palm performs in polyculture comes from a few studies of intercropping systems (see Box 2.1). Furthermore, there is not much knowledge on how biodiversity enrichment affects biodiversity and socio-economics.

Numerous experiments investigating the relationship between biodiversity and ecosystem functioning (BEF) have shown that adding a few species can already lead to a disproportionate increase in ecosystem functioning (Balvanera et al., 2006; Cardinale et al., 2006; Quijas et al., 2010). This suggests that adding species to an extremely depauperate system can result in relatively high gains in ecosystem functioning (Figure 2.1), both as the added species directly contribute to enhanced ecosystem functioning and increase the heterogeneity in resources and structure that could attract other organisms (Tews et al., 2004).

Box 2.1 | Oil palm polycultures

In West Africa and Brazil, smallholders traditionally practice extensive oil-palm-based agroforestry to make up their livelihood. In South-East Asia, however, mainly high-productive, profit-maximizing monocultures dominate the landscapes (Corley and Tinker, 2003). Nevertheless, in all growing areas some smallholders intercrop oil palm seedlings with non-permanent food crops like maize, manioc, yam, cocoyam, soy bean, or cassava to bridge the income gap until the oil palms start fruiting (Corley and Tinker, 2003; Erhabor and Filson, 1999; Lal et al., 1992; Okpala, 1995; Salako et al., 1995). This, however, contributes little to a more heterogeneous structure which would benefit biodiversity (Foster et al., 2011; Phalan et al., 2009).

In a few experiments, oil palm was intercropped with trees, thereby creating permanent agroforests: In oil palm-rubber mixtures, negative effects due to light competition were reported for both species (Corley and Tinker, 2003). Oil palm–teak mixtures resulted in lower oil palm yields but enhanced teak performance (Chia, 2011). No yield depression from oil palms was noticed when intercropped with cacao [Lee and Kasbi, 1980 (Malaysia), Amoah et al., 1995 (Ghana)], and in Nigeria, cacao yields were even higher when planted under oil palms (Egbe and Adenikinju, 1990). In Indonesia, native tree species, including *Aquilaria malaquensis* and *Shorea* sp., proved to grow well under oil palms (Muryunika, 2015). In our study region, in Jambi province, Sumatra, Indonesia, management intensity of smallholdings varies, as around 50% of the farmers retain trees in their plantation, which benefits biodiversity but results in oil-palm revenue penalties (Teuscher et al., 2015); only few farmers intentionally plant trees, i.e., intercropping or along the borders (Muryunika, 2015). Despite many smallholders being interested in enriching their plantations with other trees, there is neither an approved system with specific implication guidelines nor is there any knowledge about the ecological and socio-economic costs and benefits of an oil-palm-based agroforestry.

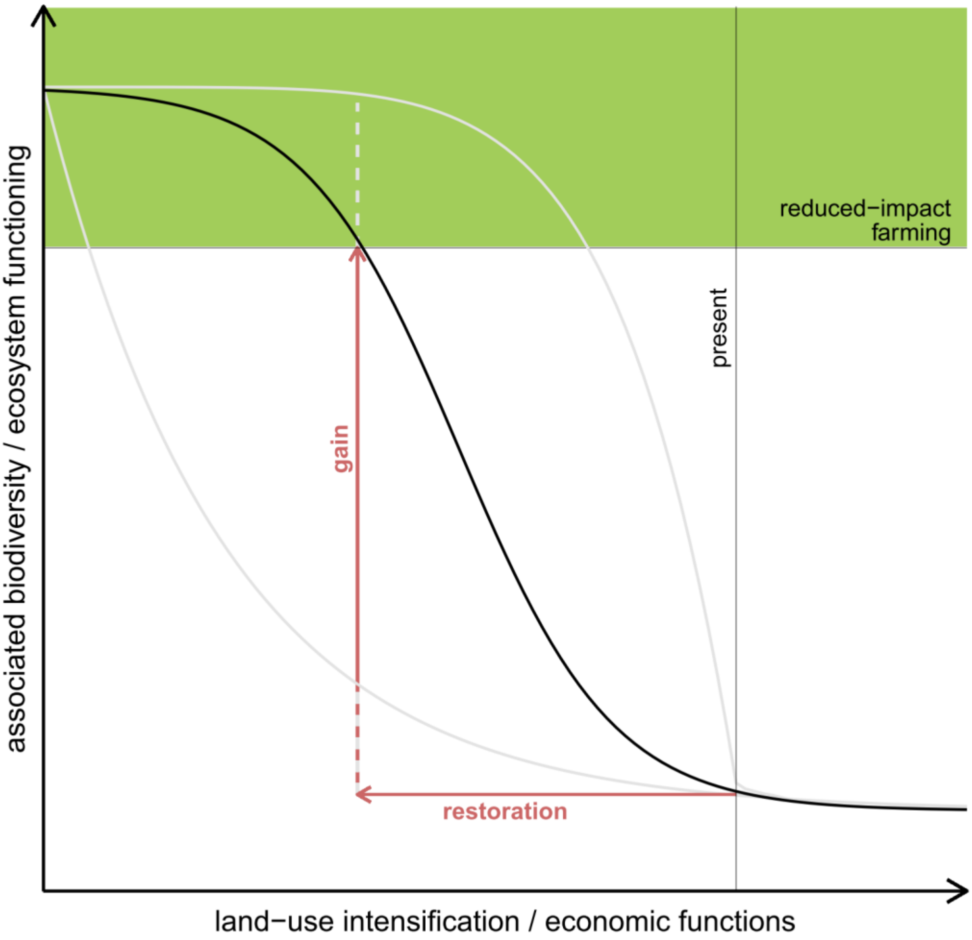

Figure 2.1 | Possible scenarios of changes in biodiversity and ecosystem functioning (BEF) as a consequence of land-use intensification assuming a negative and non-linear relationship between land-use intensification and BEF. Consequently, there is space for restoration measures in order to enhance ecosystem functioning while still allowing for profitable land use. The loss in ecosystem functioning is supposed to be relatively slow with extensive land use (shaded area) but reaches a critical point once the buffer ability of the ecosystem is exhausted. Further land-use intensification will then result in a severe decline in ecosystem functioning. The optimal trade-off situation between nature conservation and land use would be when intensification is stopped before the critical point is reached. In oil-palm-dominated landscapes, however, this point might already be exceeded, as BEF are severely degraded in oil-palm systems (Barnes et al., 2014; Dislich et al., 2016; Kotowska et al., 2015). To move back to the critical point, diverse habitats have to be restored.

Recently, insights from BEF research found their way into restoration ecology (Aerts and Honnay, 2011). However, most of the findings related to BEF have been obtained from small-scale studies in temperate grasslands and a number of large-scale tree planting experiments have only lately been established (Scherer-Lorenzen, 2005; Verheyen et al., 2015); six BEF experiments with trees are located in the tropics (Moreira et al., 2014; Petit and Montagnini, 2006; Verheyen et al., 2015). Early results from these experiments suggest that diverse plantings lead to a higher increase in ecosystem functions compared to monocultures (e.g., Potvin and Gotelli, 2008).

The knowledge gaps regarding the ecological consequences of restoration via enrichment plantings in oil-palm landscapes go along with limited knowledge about the impacts on the local socio-economy. In some parts of South-East Asia, the area of oil palms managed by smallholders is currently more rapidly increasing than the area managed by large estates (Euler et al., 2015b; Gatto et al., 2015), resulting in a growing number of households depending on palm-oil production. Therefore, it is essential to develop strategies that, at least partly, compensate potential income losses due to restoration plantings. In this regard, crop diversification may be one option, as it acts as insurance, e.g., as a buffer for world-market price-fluctuation, climate change impacts, or possible pest attacks (Lin, 2011). Additionally, it can have benefits in the short-term, e.g., by the provision of raw material or food for self-consumption or also financially through more efficient use of the available arable land. Further, enhanced biodiversity can improve the provision of ecosystem services that are beneficial to oil-palm management. Biological pest control, pollination, and litter decomposition (and thus soil fertility) are among the most important ecosystem services for productive oil-palm management (Foster et al., 2011) and can directly benefit the farmers' income (Tscharntke et al., 2011). This might raise the willingness to accept and adopt novel management forms.

We hypothesize that restoration plantings have the potential to help enhance biodiversity and ecosystem functions in impoverished landscapes whilst minimizing financial losses (Figure 2.1). Clear management strategies for restoration of intensively managed oil-palm landscapes toward ecologically improved and at the same time economically viable systems, however, are yet to be developed. Several questions have to be considered in this context: how many species need to be planted to gain a significant increase in ecosystem functioning? Which species composition and island size is the most effective? What are the trade-offs between BEF and socio-economics?

Here, we (1) present the design of a biodiversity enrichment experiment (BEE) in a monoculture oil-palm landscape (2) measure heterogeneity in the oil-palm plantation as a baseline for the experiment (3) describe abiotic and biotic characteristics of the plantation and (4) present first results of the effects of the enrichment plantings on birds and invertebrates one year after the establishment of the experiment.

2.3 Materials and methods

Study site

Our enrichment planting experiment was established on an oil-palm plantation of PT. Humusindo Makmur Sejati (01.95 °S and 103.25 °E, 47 ± 11 m a.s.l.) near Bungku village in the lowlands of Jambi province, Sumatra (Figure 2.2). The climate is humid tropical, with a mean temperature of 26.7 ± 1.0 °C and an annual rainfall of 2235 ± 385 mm (1991–2011; measured at Jambi Sultan Thaha airport of the Meteorological, Climatological and Geophysical Agency). The dominant soil type in the region is loamy Acrisol (Allen et al., 2015). Dipterocarp-dominated lowland rainforests are the primary natural vegetation (Laumonier et al., 2010; Whitten et al., 2000).

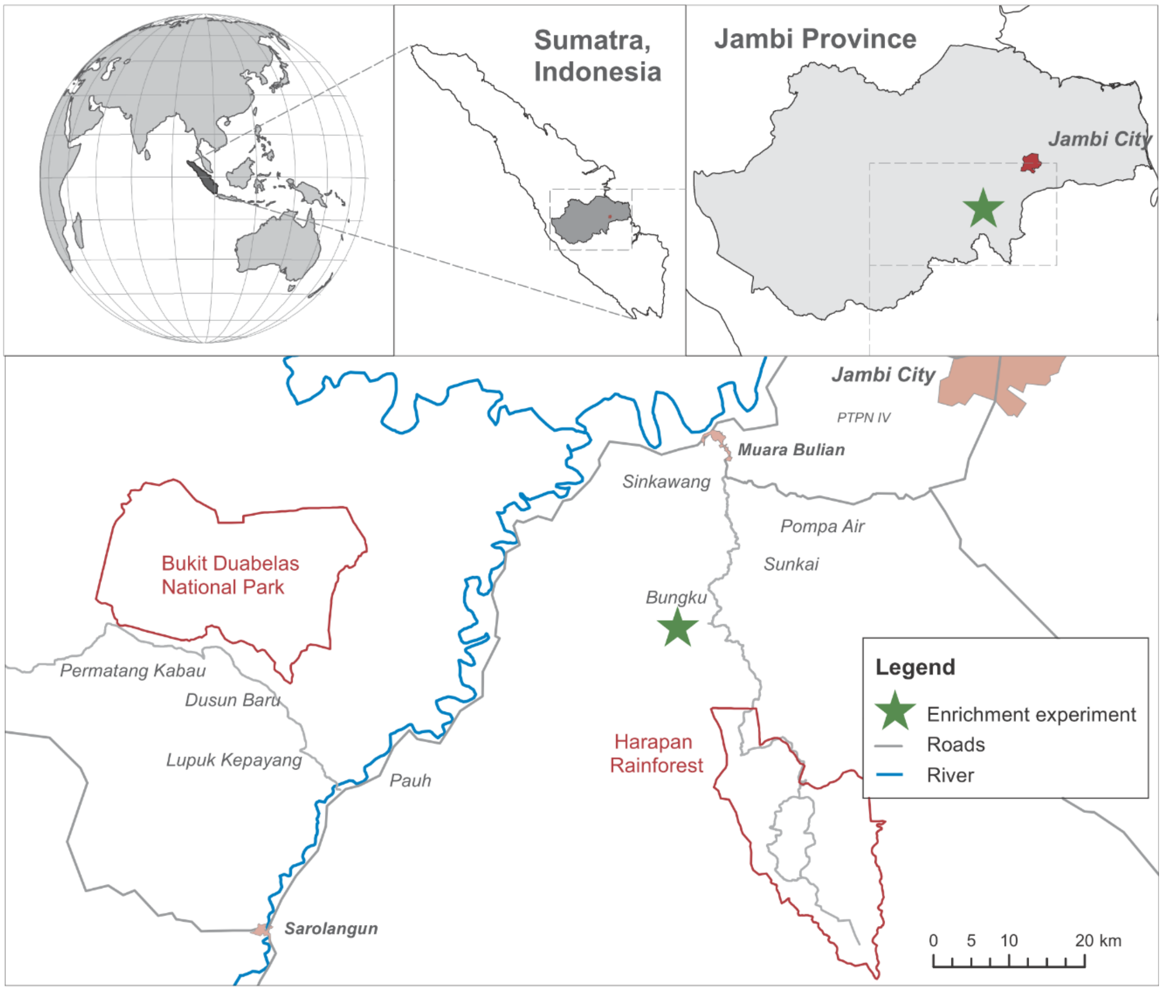

Figure 2.2 | Map of the study area (Drescher et al., 2016; modified). The green star indicates the location of the study site where the biodiversity enrichment experiment (EFForTS-BEE) was established.

The planting of oil palms in the plantation started in 2001 and, according to satellite images, ended approximately in 2006 or 2007 (Google Earth, 2015), leading to an inhomogeneous age structure of ca. 6–12 years. Oil palms are planted in 9 m x 9 m triangular grid resulting in ca. 143 oil palms per ha. In 2014, the average oil palm yield on the plantation was 22.74 metric tons of fresh fruit bunches ha^{-1} y^{-1}. The management of the plantation comprises fertilizer application [230 kg N (Urea), 196 kg P (Triple Superphosphate and rock phosphate), 142 kg K (KCl), 54 kg Mg (Kieserite and Dolomite), and 0.79 kg B (Borax), all in ha^{-1} year^{-1}; additionally S ($(NH_4)2SO_4$), Si (Zeolite), and Ca], regular manual weeding of the understory, and removal of epiphytes. Herbicides are only rarely used when there are not enough workers available for manual weeding. Livestock farming is also practiced on the plantation.

The biodiversity enrichment experiment (EFForTS-BEE)

We established a large-scale, long-term BEE within a monoculture oil-palm landscape as a sub-project of the EFForTS 1 [Ecological and socio-economic functions of tropical lowland rainforest transformation systems (Sumatra, Indonesia)] research initiative that investigates the impacts of transforming lowland rainforest into land-use systems such as oil-palm plantations (Drescher et al., 2016). Tree islands of varying species diversities and compositions were established with a minimum distance of 85 m between them. Across experimental plots, we varied the diversity and identity of the tree species planted, adopting a random partitions design (see Bell et al., 2009 for detailed information) (Figure 2.3). The design allows disentangling the linear effects of plot size, tree diversity, and non-linear effects of tree species composition. This approach analyzes gradients using stepwise linear regression models rather than comparing distinct groups. Thus, a full-factorial setup, which is usually not feasible, is not needed. The experiment comprises four partitions that differ in their plot size (5 m x 5 m, 10 m x 10 m, 20 m x 20 m, 40 m x 40 m). Each partition is divided into five blocks, one per tree diversity level (0, 1, 2, 3, and 6 species). Within each of these blocks, each species is randomly drawn from the species pool without replacement. Each species is thus selected exactly once at each diversity level and species compositions are random, with the restriction that no repetition across all plots was allowed (Figure 2.3). Additionally, there are four control plots of the same size without any experimental treatment and management-as-usual. This results in a total of 56 plots (Appendix Table A.1). The spatial arrangement of the plots in the plantation was random; i.e., plots were not aggregated according to partitions, blocks, or diversity level (Figure 2.4 A).

Figure 2.3 | Schematic overview of the experimental plots adopting a random partitions design (see Bell et al., 2009 for detailed information). 'P' stands for the four partitions that differ in plot size (P1 = 5 × 5 m, P2 = 10 × 10 m, P3 = 20 × 20 m, P4 = 40 × 40 m). Each partition 'P' is divided into five blocks 'Q' (Q1–Q20), one per tree diversity level 'R' (R = 0/1/2/3/6). Within each of these blocks, each species is randomly drawn from the species pool without replacement. Between the plots 'M' (M = 1–52; numbers represent the individual Plot IDs), no repetition of the species composition was allowed (tree species: A, *Parkia speciosa*, Fabaceae; B, *Archidendron pauciflorum*, Fabaceae; C, *Durio zibethinus*, Malvaceae; D, *Dyera polyphylla*, Apocynaceae; E, *Peronema canescens*, Lamiaceae; F, *Shorea leprosula*, Dipterocarpaceae). Additionally, there are four control plots (R = ctrl, M = 53–56) of the same size (10 m × 10 m). Trees were planted on plots with R = 1/2/3/6, but not on plots with R = 0/ctrl. A special experimental management (stop of herbicide/pesticide/fertilizer application and stop of weeding 2 years after establishment) is applied on the plots M = 1–52; plots M = 53–56 are managed-as-usual. The actual spatial arrangement of the plots in the plantation was random; plots were not aggregated according to partitions, blocks, or diversity level.

We selected six native multi-purpose tree species including three trees grown mainly for fruits (*Parkia speciosa*, Fabaceae; *Archidendron pauciflorum*, Fabaceae; *Durio zibethinus*, Malvaceae), two species used for timber (*Peronema canescens*, Lamiaceae; *Shorea leprosula*, Dipterocarpaceae), and one species which produces natural latex (*Dyera polyphylla*, Apocynaceae). To enhance the light availability in the experimental plots by ca. 40%, we removed selected oil palms prior to tree planting (not on the control plots in all sizes and not on the 5 m x 5 m plots which are in between oil palms).

In December 2013, trees were planted in a 2-m grid in alternating rows in north-south direction. On mixed-species plots, trees of the same species were planted as far away as possible from one another. We planted six trees on the 5 m x 5 m plots, 25 trees on the 10 m x 10 m plots, 100 trees on the 20 x 20 m plots and 400 on the 40 x 40 m plots. The total number of planted trees was 6354.

To enhance the establishment success of the trees, we applied inorganic (19 kg N, 8 kg P, 6 kg K, 3 kg Mg, all in ha^{-1}) and organic (11 kg N, 7 kg P, 10 kg K, 4 kg Mg, 20 kg Ca, all in ha^{-1}) fertilizer once inside the planting holes before we planted the trees on plots with diversity level 1-6 (note that this fertilizer treatment was not applied on 0-diversity plots but only on plots with trees planted).

The management of all experimental plots (diversity level 0-6) comprises manual weeding to prevent weeds from overgrowing the planted saplings (approximately every three months) but will, except for small circles around the trees on plots with diversity level 1-6, be stopped after two years to allow succession (Figure 2.4 C). The application of fertilizer, herbicide and pesticides inside plots stopped after planting. Fences around plots with diversity level 0-6 protect the plots, and particularly the planted trees, from damage by mammals. Dead trees were replaced during the first year after establishment.

The long-term monitoring of the EFForTS-BEE includes recording (a) the ecosystem variables (soil, canopy cover, surrounding matrix), (b) plants (tree mortality and growth, understory vegetation, seed rain, herbivory), (c) animals (bird and invertebrate community), and (d) socio-economics (oil-palm yields, benefits from the planted trees, incentive for enrichment planting).

In order to quantify potential ecological services or disservices from enrichment plantings on the surrounding oil palms, individual yield of three oil palm individuals in perpendicular direction from the plot are monitored (Figure 2.4 B). Additionally, the yield of each oil palm inside the plot is measured as part of the long-term monitoring.

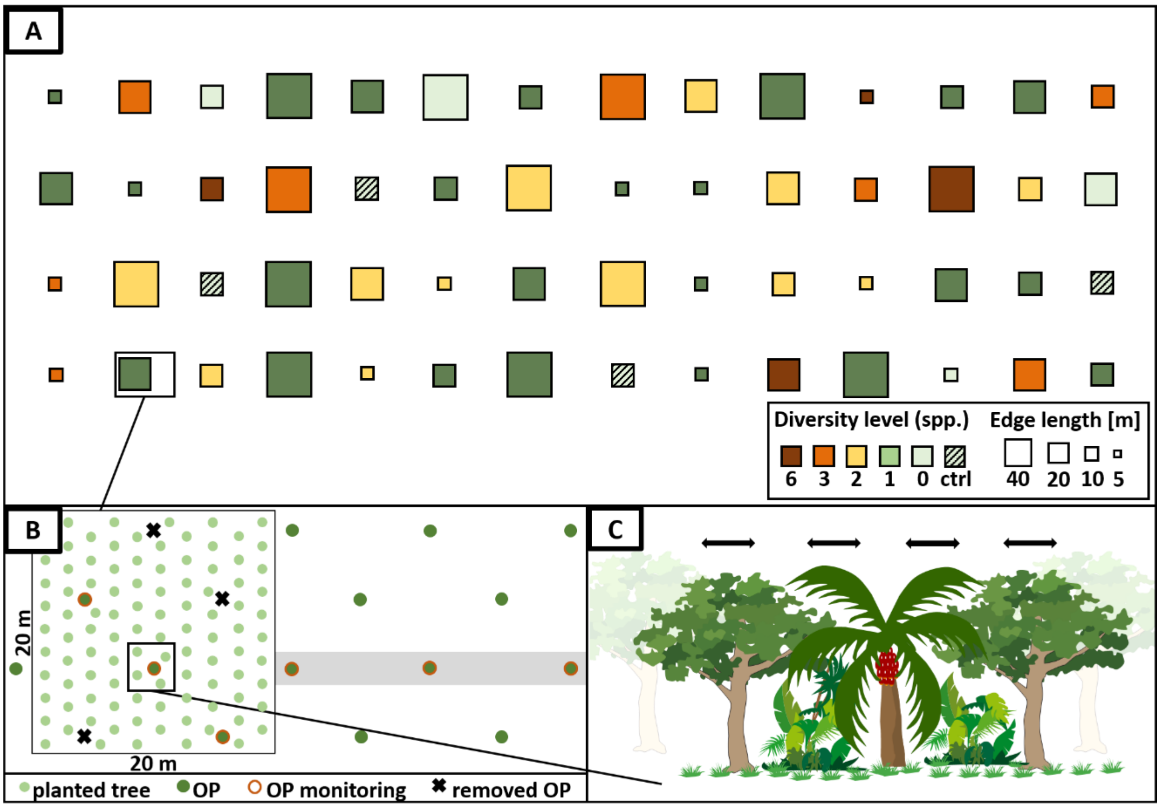

Figure 2.4 | Design of the biodiversity enrichment experiment (EFForTS-BEE). (A) Tree islands with systematically varying tree diversity (diversity level of 0, 1, 2, 3, and 6), identity and composition as well as plot size (5 m × 5 m, 10 m × 10 m, 20 m × 20 m, 40 m × 40 m) and species composition were established adopting a random partitions design (Bell et al., 2009). Partitions differ in their plot size and are subdivided into blocks of varying tree diversity levels. At each level of diversity, each tree species is represented exactly once. On plots with treatment (diversity level 0–6), a special management is applied (stop of fertilizer and pesticide application; manual weeding). Additionally, the experiment includes four control plots without treatment and with management-as-usual. In total, the experiment comprises 56 plots. **(B)** Oil palms (OP) were cut on the plot with treatments in order to enhance light conditions. Trees were planted in a 2 × 2 m grid. Perpendicular to each plot, three oil palms were selected to monitor services and disservices of the tree islands on surrounding oil palms. **(C)** Planted trees interact/compete with each other as well as with the oil palms (IAN Image, 2015; modified). Manual weeding will stop after two years to allow for natural succession.

Sampling of environmental variables, flora, and fauna

A baseline survey of the environment, vegetation, birds, and invertebrates was conducted in October 2013 prior to the establishment of EFForTS-BEE. In October 2014, bird and invertebrate surveys were repeated. Due to heavy disturbance in the ground vegetation layer during tree planting in December 2013, we did not repeat the vegetation survey; the data from 2013 would not have been comparable to the situation in 2014.

In each plot, slope was measured along all four plot edges and diagonal from the southwestern to the northeastern corner using a Vertex measuring instrument (Haglöf). We used the maximum slopes [in °] for further analyses.

Soil composite samples were taken on each plot at 0–10 cm depth. Samples were then oven-dried (40 °C, 48 h), ground and sieved (2 mm) for further analyses. Soil texture (20 g of soil) was analyzed using pipette methods. Soil organic C was measured with a CN analyzer (MT-1000, Yanako, Kyoto, Japan). Ten grams of dry soil were diluted in 25 ml H_2O to determine the pH-value. For bulk density (dry weight [g]/cylinder volume [cm^3]) analysis, a standardized soil volume (250 cm^3) was taken in 5–10 cm depth, oven dried (105 °C, 48 h), and immediately weighed.

On each plot, we established one randomly placed 2 m x 2 m subplot (random coordinates, X on south-north and Y on west-east axis with a minimum of 1.5 m distance to the plot edges). We estimated the percentage of bare soil, i.e., the area without any vegetation cover in the subplot.

Prior to oil-palm cutting, hemispherical photographs were taken at the subplot-center of each plot using a Canon 700D camera and a fisheye lens (SIGMA 4.5/2.8 EX DC HSM) and different exposure settings (see Beckschäfer et al., 2013). The gap fraction was calculated using the best picture per plot (maximum exposure time without being over-exposed) using 'ImageJ' (version 1.48v). One year after the establishment, hemispherical photographs were repeated, but covered the whole plot area with varying number of spots depending on the plot size (one spot in 5 x 5, one in 10 x 10, three in 20 x 20, seven in 40 m x 40 m) and gap fraction was calculated as means per plot to control for inhomogeneous canopy densities due to oil-palm cutting.

Individual-based vegetation surveys of all vascular plants ≥5 cm were conducted on each subplot. Herbarium specimens (Collection Numbers AG01-AG167, deposition and identification in SEAMEO BIOTROP institute, Bogor, Indonesia) were collected for plant identification.

Point counts of birds took place from 6 am to 10.30 am when weather conditions were appropriate (no rain). Birds within a 75 m radius around each plot center were recorded visually and acoustically using 15-min point counts (following the taxonomy of MacKinnon et al., 1993). Each sampling point was visited twice. For each species, we recorded the maximum number of individuals present simultaneously on the plot. For all recorded species, body mass was obtained from the literature (Wilman et al., 2014) to calculate bird biomass. Species were assigned to five trophic groups (insectivores, frugivores/nectarivores, herbivores/granivores, piscivores/ scavengers, omnivores) and to their main natural habitat (primary and old secondary forest interior; forest gaps, edges or upper canopy; little wooded and cultivated areas). Information on diet was obtained from Wilman et al. (2014). Information on habitat was also taken from the literature (Beukema et al., 2007; Pappas, 2001; Robson, 2015; Thiollay, 1995; Yosef et al., 2015).

We extracted invertebrates from the leaf-litter (LL) by sieving the LL from 1 m^2 within each subplot through a coarse sieve (mesh width = 2 cm) (see Digel et al., 2014; Ott et al., 2014). Invertebrates in the herb layer (HL) were sucked in from 1 m^2 within each subplot using a modified vacuum cleaner.

Specimens were stored in 70% ethanol, identified to family level, and assigned to trophic groups (predators, omnivores, herbivores, and detritivores). Individual body length (accuracy of 0.1 mm) was converted to fresh body mass using length-mass allometric functions (Appendix Table A.2) and, where necessary, dry mass-fresh mass relationships from the literature (Appendix Table A.3). We summed up the fresh masses of the individuals to calculate the total biomass per plot. Samples were collected based on collection permit no. 648/KKH-2/2014 and 15/KKH-2/2013, recommended by LIPI and issued by the Ministry of Forestry (PHKA).

Statistical analysis

We conducted a principal component analysis (PCA) with the soil variables (texture, pH, C content, and bulk density; Appendix Table A.4) to reduce their predominance in the set of site-condition variables (Table 2.1) to generalized trends, and used the scores of the first three PCA axes for further analyses.

To check for unintended systematic correlations between the site-condition variables and the experimental factors, we ran linear models with the site-condition and biotic variables (Appendix Table A.5) as responses and 'tree diversity' and 'plot size' as predictors. Further, we investigated the spatial autocorrelation of the site-condition parameters using Moran's I correlograms (standard deviate with 100 permutations, distance classes of 150 m) to test whether the site-condition variables in our plots are spatially dependent.

We calculated α-diversity as 1 – Simpson-index; β-diversity was calculated as 1 – Sørensen-index based on true abundance data (Legendre and De Cáceres, 2013) for all organism groups [vegetation (subplot), birds (75 m radius around plot center), LL invertebrates (subplot), HL invertebrates (subplot)]. We estimated species/family richness for each organism group using 'Jackknife 2' due to high mean evenness-values (vegetation: 0.67, birds: 0.84, LL invertebrates: 0.72, HL invertebrates: 0.82) (Brose et al., 2003).

We tested for the overall effect of tree planting by comparing the baseline survey and year one of the richness, abundance, and biomass of birds as well as LL and HL invertebrates generalized least square models and Tukey *post hoc* tests. We compared data from plots with diversity level 1-6 with data from plots with diversity level 0 and control plots.

Furthermore, we tested for the effect of tree diversity (levels of 1, 2, 3, and 6) and plot size (25, 100, 400, and 1600 m^2; ln-transformed) on the difference in richness, abundance, and biomass of birds and LL/HL invertebrates in year one compared to the baseline survey, following the stepwise linear regression approach by Bell et al. (2009). We tested for linear, non-linear, and identity effects of plot size and tree diversity.

Table 2.1 | Ecosystem variables of the experiment. Per variable, means of all plots are given with the standard deviation, except for the pH-value, where the full variable range is shown in addition to the mean. We show the gap fraction prior to cutting (baseline) and after cutting (year 1; mainly above the planted trees). Average oil palm height was derived from all plots (N = 31) where oil palms remained.

Variable		Unit	**Mean** ± SD
Altitude		[m]	**46.9** ± 10.5
Slope		[°]	**8.6** ± 5.9
Bare soil		[%]	**11.0** ± 10.6
Gap fraction$_{baseline}$		[%]	**14** ± 10.0
Gap fraction$_{year1}$		[%]	**27.5** ± 14.9
Oil palm trunk height		[m]	**3.83** ± 0.6
Soil	Bulk Density	[g/cm^3]	**1.09** ± 0.1
	Sand	[%]	**29.9** ± 12.6
	Silt	[%]	**40.5** ± 8.3
	Clay	[%]	**29.5** ± 8.3
	pH (1:2.5 H_2O)		3.97 - **4.11** - 5.3
	C	[%]	**2.18** ± 0.6

We investigated the effect of 'plot size' and 'tree diversity' on possible shifts in the relative proportions of invertebrate biomass and abundance within trophic compartments in year one compared to the baseline survey. The analyses were based on the community-weighted mean of the biomass and abundance of HL and LL invertebrates per plot. For the calculation, scores were assigned for trophic levels (herbivores, detritivores '0'; omnivores '0.5'; predators '1'), multiplied with the biomasses of the individuals, summed up per plot, and divided by the total biomass per plot. Community-weighted mean was modeled using a linear mixed model; 'tree diversity,' 'plot size', and its second order polynomial term (to test for non-linear effects of plot size) as well as 'year' entered the full model as predictors in a three-fold interaction. 'Plot ID' was included as a random effect. A backward selection of the full model was done to identify the most important predictors. All analyses were conducted in R (R Core Team, 2015) using the following packages: vegan (Oksanen et al., 2015), FD (Laliberté et al., 2014), ncf (Bjornstad, 2013), nlme (Pinheiro et al., 2015).

2.4 Results

Ecosystem variables of the plantation

Some site-condition baseline characteristics (topography, gap fraction, proportion of bare soil, soil texture, and soil carbon content) varied greatly among plots, while bulk density and soil pH were rather homogenous (Table 2.1; Appendix Table A.4).

The first three PCA axes explained 80% of the variation in the measured soil characteristics (Appendix Figure A.1). Soil texture (silt, sand and clay) contributed most to the first PCA axis; soil texture (clay), carbon content, and bulk density to the second, and soil pH to the third (Appendix Table A.4).

The proportion of bare soil as well as silt and sand content are spatially dependent on short distances, clay and sand content on large distances, and soil pH in one medium-distance class with a low correlation coefficient (0.15) (Appendix Figure A.2). We detected systematic relationships between the two experimental factors 'tree diversity' and 'plot size' with some site-condition and some biotic variables. However, the strengths of the effects were in all cases negligible (R^2 values < 0.09) (Appendix Table A.6).

Flora and fauna

We recorded a total of 92 plant species, 21 bird species, 87 LL, and 94 HL invertebrate families on the experimental plots (Table 2.2). Jackknife 2-estimated richness was substantially higher for plant species (157 species; 58.6% sample representativeness) and invertebrate families (LL/HL: 137/148 families; 63.5% sample representative in both groups) but not for birds (26 species estimated; 80.8% sample representativeness). These findings were consistent with species accumulation curves (Appendix Figure A.3). The α-diversity was similar for all organism groups (0.62–0.76) (Table 2.2). The abundance based β-diversity ranged from 0.12 to 0.2 (Table 2.2).

a. Vegetation

Of the 92 plant morphospecies, 64 could be identified of which 25 were alien species (Appendix Table A.7). The three most frequent species, *Clidemia hirta* (Melastomataceae) followed by *Asystasia gangetica* (Acanthaceae) and *Paspalum* cf. *conjugatum* (Poaceae), were non-native species.

b. Birds

A total of 21 species were detected (Appendix Table A.8). All species are listed as "least concern" (IUCN, 2015). Of the recorded individuals, 48.8% were insectivores, 35.5% frugivores/nectarivores, 7.2% omnivores, 2.8% herbivores/granivores, and 5.8% were piscivores/scavengers. The main natural habitat for 1.6% of the sampled individuals is primary and old secondary forest interior, for 7.5% forest gaps, edges or upper canopy, and for 90.9% little woods and cultivated areas.

c. Invertebrates

From the LL, 87 families (Appendix Table A.9) were collected. The sampled individuals consisted of 24.8% predators, 61.2% omnivores, 1.8% herbivores, 9.7% detritivores, and 2.5% others. In the HL, 94 families were collected (Appendix Table A.10). The invertebrates sampled consisted of 18.7% predators, 46% omnivores, 18.3% herbivores, 11.6% detritivores, and 5.4% others.

Table 2.2 | Species/family numbers of the four organism groups monitored at the experimental sites in the baseline survey. LL, leaf litter; HL, herb layer.

	Vascular plants	Birds	LL invertebrates	HL invertebrates
Total species/family richness	92 (species)	21 (species)	87 (families)	94 (families)
Estimated species/family richness	157	26	137	148
Mean species/family number per plot (± SD)	16.67 ± 4.55	4.42 ± 2.11	9.4 ± 5.76	11.6 ± 6.34
β-diversity	0.12	0.18	0.19	0.2
α-diversity, mean per plot (± SD)	0.76 ± 0.12	0.63 ± 0.19	0.62 ± 0.23	0.76 ± 0.13

Overall effect of tree planting on the bird and invertebrate community one year after establishment

a. Birds

We recorded 20 species (Appendix Tables A.8 and A.11), whereof 15 species where the same as in 2013 and five species were new. All species are listed as "least concern" (IUCN, 2015). Of the recorded individuals; 44.5% were insectivores, 31.7% frugivores/nectarivores, 2.3% omnivores, 16.5% herbivores/granivores, and 5.0% were piscivores/scavengers.

In year one of the experiment, bird species richness was significantly higher on plots with diversity level 1-6 as compared to the control plots (management-as-usual) ($p < 0.001$) but not different from plots with diversity level 0 ($p > 0.05$) (Figure 2.5 A). Furthermore, there was no difference in richness between experimental plots and control plots ($p > 0.05$). The abundance and biomass of birds was not significantly affected by any experimental treatment ($p > 0.05$) (Figures 2.5 B, C).

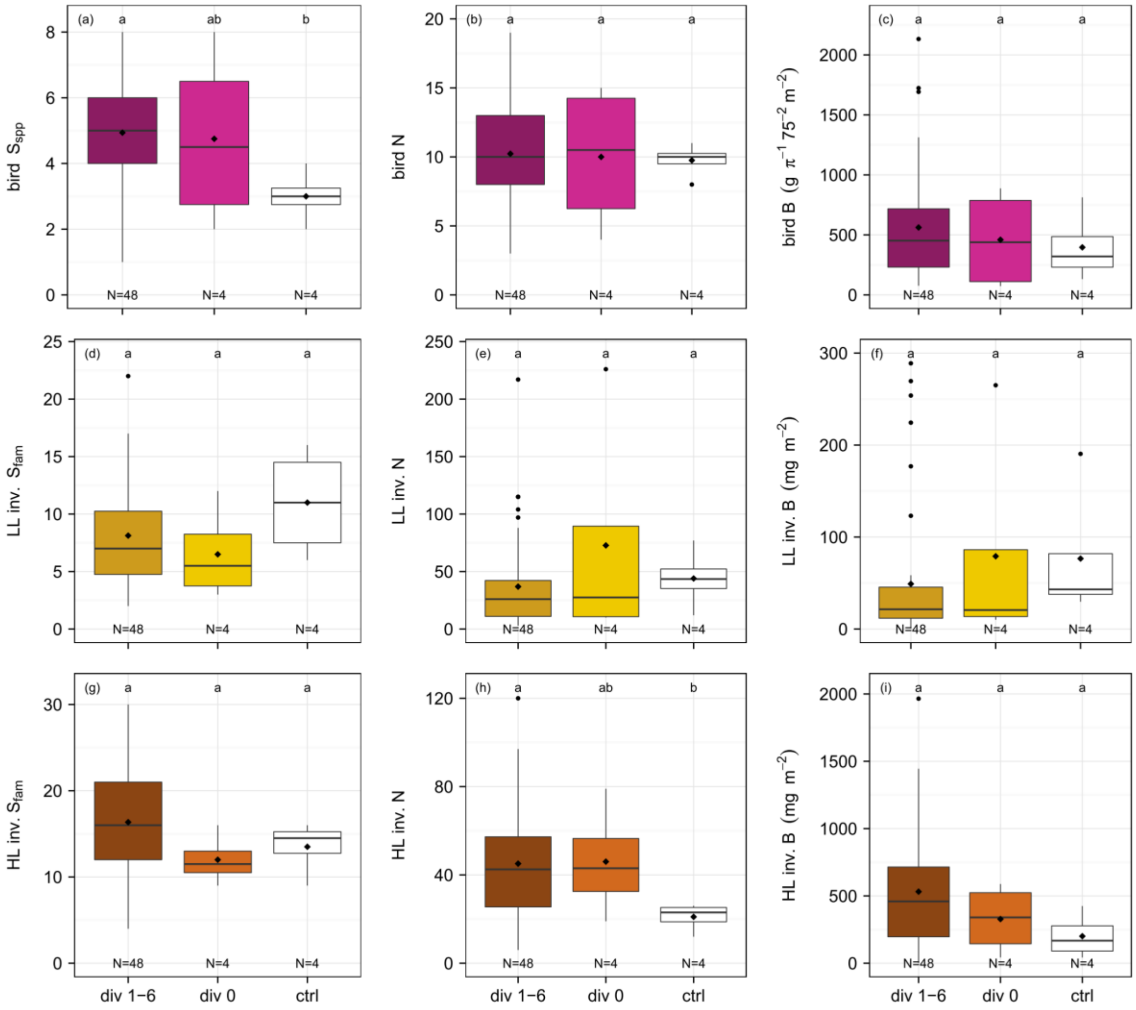

Figure 2.5 | Comparisons of the richness (S_{spp}, species level, S_{fam}, family level), abundance (N), and biomass (B) of birds (a,b,c), leaf-litter (LL) (d,e,f), and herb-layer (HL) (g,h,i) invertebrates (inv.) between plots with diversity level 1, 2, 3, and 6 (N=48), plots with diversity level 0 (N=4), and control plots (N=4) one year after establishment. Bird species richness and the abundance of HL invertebrates were significantly increased on plots with trees compared to control plots.

b. Invertebrates

A total of 74 families were collected in the LL (Appendix Tables A.9 and A.11) of which 48 were the same as in 2013, 26 were new, and 39 were not represented anymore. The sample comprised 17.1% predators, 70.7% omnivores, 3% herbivores, 7.3% detritivores, and 1.9% others. Family richness, abundance and biomass of the LL invertebrates did not differ between plots with diversity level 1-6, plots with diversity level 0 and control plots ($p > 0.05$) (Figures 2.5 D–F).

In total, 105 families were collected in the HL (Appendix Tables A.10 and A.11). Compared to the year before, 58 families were the same, 47 were new, and 36 were not present anymore. The invertebrates consisted of 17.2% predators, 48% omnivores, 15.3% herbivores, 11.5% detritivores, and 8% others.

Herb layer invertebrates were significantly more abundant on experimental compared to the control plots ($p < 0.01$), but there was no significant difference in HL invertebrate abundance between plots with diversity level 0 and those with diversity level 1-6 ($p > 0.05$) (Figure 2.5 H). Family richness and biomass were not affected by the experimental treatment ($p > 0.05$) (Figures 2.5 G, I).

Initial effects of tree diversity and plot size on the bird and invertebrate community

We found a significantly positive effect of plot size on the difference in diversity of LL family richness ($p < 0.05$) and the difference in abundance of HL invertebrates in year one compared to the baseline ($p < 0.05$) (Figure 2.6); Tree diversity, however, did not affect the difference in richness, abundance, and biomass of birds and invertebrates ($p > 0.05$) (Figure 2.7).

Shifts of invertebrate biomass and abundance within trophic compartments

We found non-significant effects ($p > 0.05$) of tree planting (factor ‘year’), plot size (plot size: year), and tree diversity (tree diversity: year) on the difference of the community-weighted mean trophic index and abundance of LL and HL invertebrates between year one and the baseline. This suggests that changes in the proportion of invertebrate biomass and abundance within the trophic compartments are likely to be driven by other than the experimental factors.

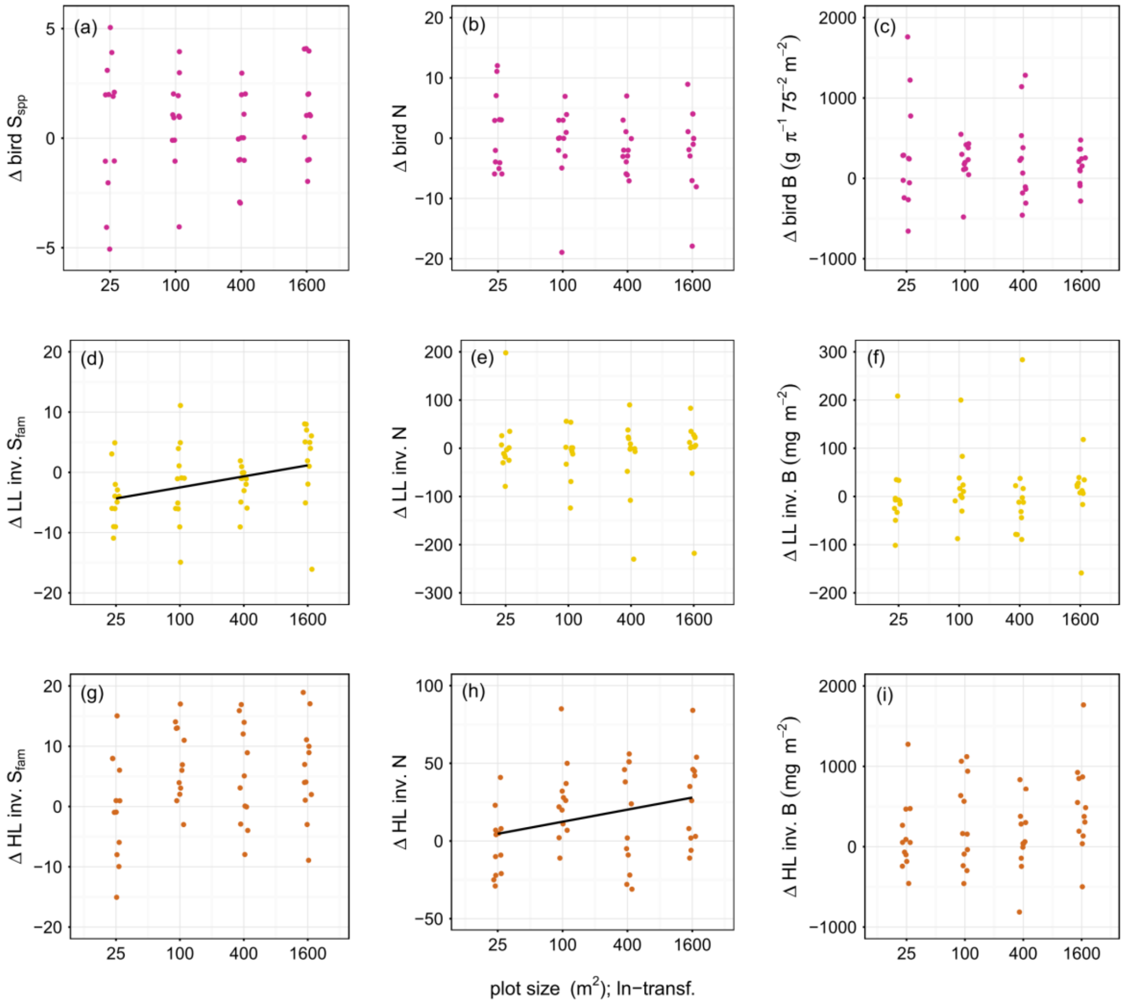

Figure 2.6 | Effect of plot size on the difference in richness (S_{spp} = species level, S_{fam}= family level), abundance (N), and biomass (B) of birds (a,b,c), leaf-litter (LL) (d,e,f) and herb-layer (HL) (g,h,i) invertebrates (inv.) between year one and the baseline. LL invertebrate family richness and HL invertebrate abundance was significantly positively related to plot size (indicated by a black line). Plot sizes (25, 100, 400, and 1600 m^2) were ln-transformed for improved representation in the figure. To avoid overplotting of data points, we used the 'jitter' function in R (R Core Team, 2015).

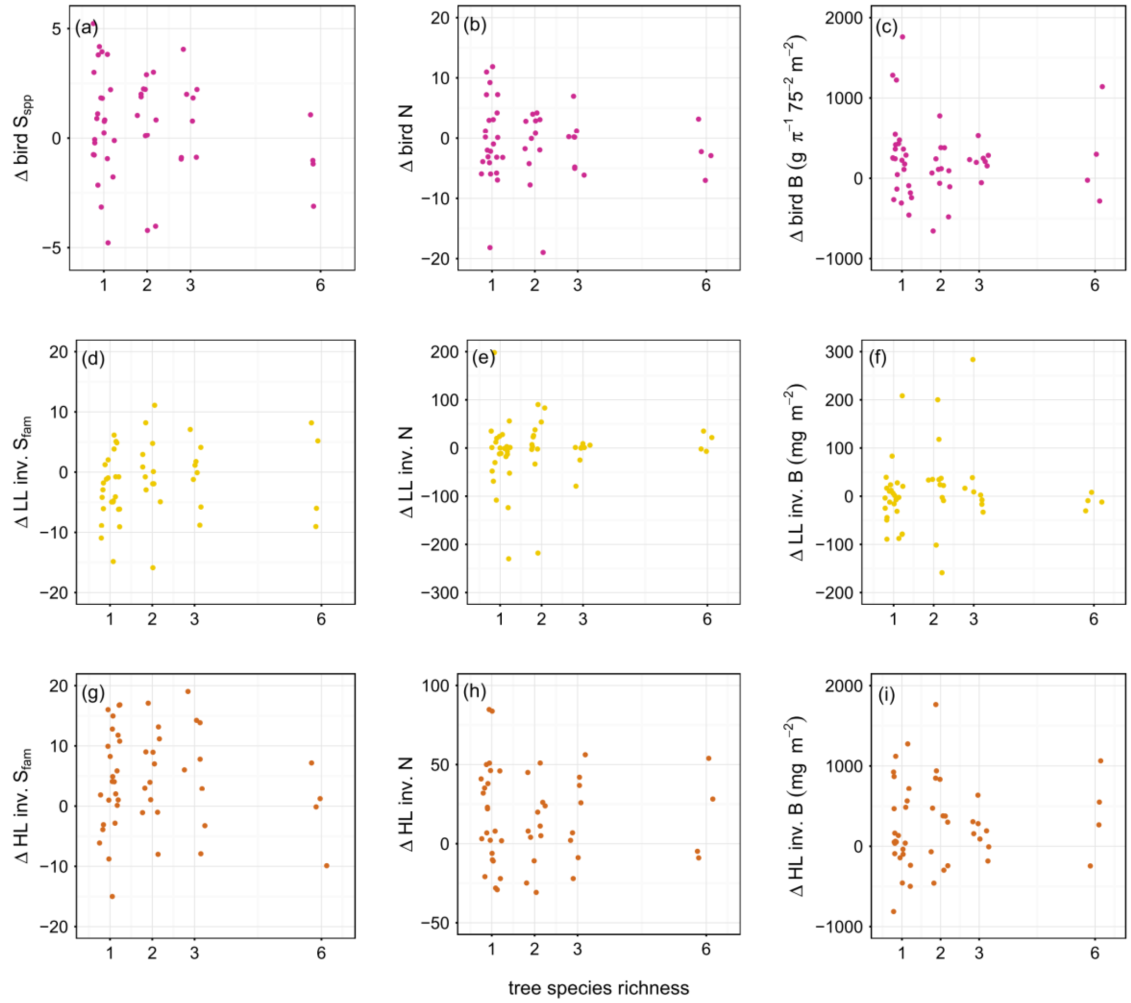

Figure 2.7 | Effect of tree diversity on the difference in richness (S_{spp} = species level, S_{fam}= family level), abundance (N), and biomass of birds (B) (a,b,c), leaf-litter (LL) (d,e,f), and herb-layer (HL) (g,h,i) invertebrates (inv.) between year one and the baseline. Birds were considered on species level, invertebrates on family level. There was no effect of tree diversity on any of the responses. To avoid overplotting of data points, we used the 'jitter' function in R (R Core Team, 2015).

2.5 Discussion

By experimentally investigating plot size and tree diversity – two key factors in a restoration context – EFForTS-BEE aims at shedding light on the ecological and socio-economic processes associated with ecological restoration of oil-palm landscapes. The controlled experimental design of EFForTS-BEE allows us to investigate the underlying mechanisms of enrichment plantings.

Our study site in Jambi province, Sumatra, is ideal for studying the long-term effects of enrichment plantings. We have chosen a medium-scale oil-palm plantation for the experiment that is embedded in an intensively oil-palm and rubber-dominated landscape. The average oil palm yield of 22.74 metric tons of fresh fruit bunches ha^{-1} y^{-1} is on the higher end compared to smallholder plantations in the region (18.02–23.72 t ha^{-1} y^{-1},Kotowska et al., 2015). This might be explained by a higher and more diverse fertilizer use compared to smallholders (Hassler et al., 2015; Kotowska et al., 2015). The management might hence be similar to other mid- or large-scale oil-palm plantations. Furthermore, the diversity of plants, birds, and invertebrates at the study site is comparable to and thus representative of the diversity in other oil-palm plantations in the region (Appendix Table A.12) (Drescher et al., 2016).

The results of our baseline survey showed that all plots are largely independent from each other. The spatial autocorrelation of some of the variables was only significant in single short- or large-distance classes or with a small correlation coefficient. Further, the α- and β-diversity was low for all organism groups and the relationship between the biotic and abiotic baseline variables and the experimental treatments negligible. Overall, this suggests that the ecosystem variables are appropriate for future statistical analyses to clearly distinguish experimental effects from other effects and that the experimental site is representative for other oil-palm plantations, making results transferable.

Interestingly, we already see significant effects of the enrichment plantings on the bird and invertebrate fauna one year after the establishment of the experiment. We chose birds and invertebrates as study organisms, as they are used as bio-indicators to monitor changes in habitat quality. Previous studies have shown that ecosystem functioning is negatively affected by the loss in birds (Sekercioğlu, 2006; Tscharntke et al., 2008) and invertebrate diversity (Barnes et al., 2014; Ewers et al., 2015), highlighting their importance in ecosystems and, hence, their key role in conservation or restoration measures. Comparing the overall species numbers between 2013 and 2014, there were one bird species (5% loss) and 13 insect families (15% loss) in the LL less, but a gain of 11 (12% gain) insect families in the HL. These differences may be due to annual fluctuations. In some cases, we see initial positive effects between the treatments (Figures 2.5 and 2.6).

The overall increase in bird richness on plots with trees compared to the control plots (Figure 2.5 A) might be due to an overall increase in heterogeneity within the plantation; some of the planted trees (i.e., *Archidendron pauciflorum* and *Parkia speciosa*) had already reached considerable heights (>4 m) after the first year and provide habitat for nesting, roosting, and foraging (Thiollay, 1995), and might facilitate movement through the agricultural landscape (Harvey, 2000). This result supports findings that habitat heterogeneity and the presence of native trees are important factors determining bird diversity and composition (Sekercioğlu, 2002; Teuscher et al., 2015; Walther, 2002). At the plot scale, however, responses of birds were non-significant, indicating that overall habitat complexity at the plantation scale might be more important than at a local scale at this early stage of the experiment. More birds, especially frugivorous species, might be attracted by the tree islands when trees grow bigger and bring in fruits. Frugivorous birds were the second-most abundant feeding guild and the key role of birds as seed dispersers in tropical systems is well documented (Sekercioğlu, 2006; Whelan et al., 2008). This might positively affect succession and spontaneous colonization of plants in the near future (Cole et al., 2010).

Invertebrates responded to the enrichment plantings on a much smaller scale. There was an overall increase in the abundance of HL invertebrates on plots with trees across the whole plantation in year one compared to the control, but the abundance on plots with diversity level 0 was not significantly different from either. Furthermore, we see a positive relationship between the plot size and the difference in family richness of LL invertebrates and the difference in abundance of HL invertebrates, respectively, in year one compared to the baseline. These results suggest that tree planting alone had no significant effect on invertebrate communities. Only the combination of stop of fertilizer and pesticide application, changes in the light environment, the creation of new small-scale habitat structures through the planting of trees, and the cutting of oil palms might explain these positive responses of the invertebrate communities (see Pywell et al., 2012; Tscharntke et al., 2011). The increase in LL invertebrate family richness with increasing plot size may be correlated to increased litter input (Gillison et al., 2003) and increased stoichiometric diversity in the leaves (Ott et al., 2014). The significant positive relationship between invertebrate family richness as well as abundance and plot size suggests, however, that structural effects might be more important than tree diversity. We did not observe any shifts in the relative proportion of invertebrate biomass and abundance within trophic compartments between the baseline and year one and this might indicate a time-lag in the response of important ecosystem processes to differences in plant diversity, which was also reported from other studies (Cardinale et al., 2012; Eisenhauer et al., 2012; but see Schuldt et al., 2015). Invertebrates fulfill many tasks that are essential for ecosystem functioning including litter decomposition, predation, pollination, and herbivory. The design allows to disentangle the effects of plot size and tree diversity on the diversity and structure of different organism communities such as plants, birds, and invertebrates, and, herewith, to draw conclusions on changes in ecosystem functioning. The initial positive effects on birds and invertebrates, two organism group's essential for the initiation of natural succession, are promising for further biodiversity enrichment in the future.

2.6 Conclusion

EFForTS-BEE is designed to directly address questions about the potential of enriched oil-palm landscapes to maintain or enhance biodiversity and ecosystem functions and services whilst aiming to minimize economic losses. An expected outcome of the experiment is a combination of island size, tree diversity level, and composition that is above-average cost-effective and productive to achieve high gains in ecosystem functioning. This involves identifying the most well-performing tree species in their most productive composition under the conditions of an oil-palm plantation, which do not negatively affect oil palm yields. Initial positive responses of birds and invertebrates to the biodiversity enrichment treatments are promising and suggest that tree islands can be a suitable measure to enhance biodiversity in impoverished landscapes. The concept of planting tree islands in oil-palm landscapes might be similarly relevant for oil-palm estates managing large monoculture plantations as well as for smallholders seeking to diversify their production to reduce risks and their dependence on oil palm. In this context, the development of 'Payment for Environmental Service' schemes could help to make biodiversity enrichment more attractive for farmers. Depending on the goals of involved stakeholders, tree plantings could be adjusted to management forms such as agroforests or secondary forests for production of timber or conservation. Another possible application might be the re-transformation of existing illegal oil-palm plantations inside nature conservation areas into a more natural habitat. Nevertheless, the EFForTS-BEE does not satisfy the need for areas of 'High Conservation Value' which are an integral part of the designed plantation landscapes concept. In their function as source habitats, 'High Conservation Value' habitats are essential to recruit biota from and initiate successful natural succession in the EFForTS-BEE or other reduced-impact farming systems. Our long-term objectives are to provide basic knowledge on how to improve landscape connectivity with stepping stones to provide habitat for migrating biota and to buffer the inhospitality of oil-palm landscapes to enhance BEF at the landscape scale. With the results of the experiment, we aim at evaluating the effectiveness of enrichment plantings as part of designer plantation landscapes and at developing clear restoration instructions for oil palm farmers toward a more sustainable management of oil palm.

2.7 Acknowledgements

We thank PT. Humusindo Makmur Sejati for permission to set up the experiment on their oil-palm plantation. Many thanks to Pak Hasbi and his family and all the people who helped us during the establishment phase of the EFForTS-BEE. Special thanks to Andi, Anshori, Zeri, Pak Lele, Ahzan, Dadang Dwi Putra, Walesa Edho Prabowo, Azka, Bayu, Dery, Eka, Fahmi, Huda, Juwita, Kevin, Happy and Judith for their commitment, endurance and good work in the field and/or lab. We thank the people in the lab in Palu, in the Indonesian Institute of Science (LIPI), and at Biotrop for assisting with analyses of samples. We are grateful to the following people who kindly provided data for this article: Ana Meijide, Andrew Barnes, Malte Jochum, Kevin Darras, Walesa Edho Prabowo, Katja Rembold and Robin Naumann. Thanks to Arne Erpenbach for creating the location map and to Philip Beckschäfer who helped us processing the hemispherical photographs. Logistical support was provided by the EFForTS staff and coordination. We acknowledge support by the Deutsche Forschungsgemeinschaft (DFG) and the Open Access Publication Funds of the Göttingen University. This study was financed by the DFG in the framework of the collaborative German-Indonesian research project CRC990.

3 Initial tree performance in a biodiversity enrichment experiment in an oil-palm landscape

Anne Gérard, Dirk Hölscher, Bambang Irawan, Leti Sundawati, Miriam Teuscher, Holger Kreft

3.1 Abstract

Large-scale conversion of tropical forest has led to dramatic losses of biodiversity and associated ecosystem services and functions. One particularly severe example of forest and biodiversity loss is Indonesia. Indonesia harbors a high biodiversity, which is seriously threatened by land conversion, for which oil-palm cultivation is a major driver. Restoration of biodiversity is urgently needed in many oil-palm-dominated landscapes, but there is a lack of empirical knowledge. To bridge this gap, we established an experiment of tree islands in an oil-palm plantation and systematically varied plot size, diversity level, and the composition of the planted tree species. We planted six multi-purpose native tree species. The initial phase after planting is most critical for a long-term establishment of the trees, which is decisive to achieve restoration goals in the future. Here, we report on the establishment success of the trees, and identify the most important determinants for tree growth and survival. We found strong differences between the tree species considering relative height increment, relative basal area increment and survival. Species with high growth rates mostly also showed high survival rates. At the plot level, site conditions, plot size, and diversity level of the planted trees only weakly affected mean tree growth and survival. At the level of individual trees, we found significant neighborhood effects between the species. Tall neighboring trees and the distance to living oil palms significantly affected tree performance and were beneficial. Though it is too early to decide on the overall suitability of the tree species regarding their effectiveness to achieve restoration goals, differences in initial tree performance are an important information to translate the findings of the experiment into management instructions in the future.

3.2 Introduction

The large-scale conversion of tropical forest (Hansen et al., 2013) has led to dramatic losses of biodiversity and associated ecosystem services and functions (Bradshaw et al., 2009) that exceed the boundaries of a stable Earth system (Rockström et al., 2009). Therefore, activities such as tree plantings are crucially needed to effectively restore biodiversity and ecosystem functioning (Lamb et al., 2005).

Indonesia is among the countries where restoration efforts are of high priority: it harbors a high biodiversity (Sodhi et al., 2004), which is threatened by high rates of habitat loss, as the country faces the world's highest estimated deforestation rates (Margono et al., 2014). Land conversion for oil-palm cultivation is considered as one of the strongest drivers of forest loss (Abood et al., 2015). Further plans to substantially increase the production may increase the pressure on remaining forests (Koh and Ghazoul, 2010). Conventional large homogeneous oil-palm dominated landscapes only host a minor fraction of the rainforest species (Drescher et al., 2016; Fitzherbert et al., 2008; Foster et al., 2011; Wilcove et al., 2013), and experience a decline of a wide range of ecosystem functions (Dislich et al., 2016). Though many researchers stress the importance for diversified oil-palm landscapes (Bhagwat and Willis, 2008; Foster et al., 2011; Koh et al., 2009), there is a lack of empirical knowledge on adequate management strategies.

Ecologically effective restoration and conservation of ecosystem functioning in existing agricultural systems such as oil-palm-dominated landscapes is a challenge, as it needs to benefit the biodiversity and, at the same time, maintain a high level of agricultural productivity to avoid economic losses. Large-scale conservation projects are related to high opportunity costs and may disregard local livelihoods (Kareiva and Marvier, 2012). To minimize such negative consequences, tree islands have been suggested as potentially area- and cost-effective enrichment components in agricultural landscapes (Rey Benayas et al., 2008). In abandoned pastures, for instance, tree islands were similarly effective in achieving restoration goals than afforestation in plantation-like monocultures (Zahawi et al., 2013). Though enrichment planting cannot be seen as an alternative to high-conservation-value areas (Rey Benayas and Bullock, 2012), its application could be one first step towards reduced-impact oil-palm cultivation. However, the minimum adequate size of the tree islands, spillover effects to the surrounding plantation, and the compatibility with the surrounding agricultural system remains largely unstudied (Rey Benayas et al., 2008).

The use of native multi-purpose tree species in mixed-species restoration plantings has the potential to both benefit local people and increase biodiversity and ecosystem functioning (Lamb et al., 2005). Mixed-species plantings were found to increase ecosystem functioning in a range of biodiversity-ecosystem functioning (BEF)-experiments which were mostly conducted in grasslands

(Cardinale et al., 2012; Quijas et al., 2010). In contrast to grassland experiment, tree-based BEF-experiments are still scarce (but see Forrester, 2014; Forrester and Pretzsch, 2015; Jucker et al., 2014; Scherer-Lorenzen et al., 2005; Verheyen et al., 2015). However, BEF-experiments with trees suggest a positive effect of tree diversity on biomass production, (Morin et al., 2011; Potvin and Gotelli, 2008), resource-use efficiency (Richards et al., 2010), and temporal stability (Morin et al., 2014). Such BEF-effects have mainly been traced back to complementarity effects between the species (e.g. Forrester, 2014; Morin et al., 2011; Richards et al., 2010). Positive effects of tree diversity on e.g. this and that may carry a big, but yet largely unstudied potential to advance restoration ecology (Aerts and Honnay, 2011).

The initial phase of a tree planting experiment can be seen as a bottleneck that trees have to surpass for a successful establishment. Mortality is often particular high shortly after planting (De Steven, 1991; Evans and Turnbull, 2004), which can be a consequence of the stress that seedling experience from being transplanted (Burdett, 1990). Saplings are particularly sensitive to insect and animal damage and to environmental stress during the establishment phase (Evans and Turnbull, 2004). Evaluating their performance in the initial phase may thus already indicate the species' general suitability to the local site conditions, which strongly depends on its autecology on the one hand, and its synecology, i.e. interactions with the surrounding vegetation, on the other (Günter et al., 2009). Competition for limited resources may lead to reduced growth and survival rates, and facilitation, e.g. by shade provision or enhanced nutrient input, can in turn benefit growth and survival rates (Günter et al., 2009). When planting tree species with different ecological requirements, complementarity between species can reduce competition (Li et al., 2014).

Growth rates can be high in the initial phase after planting: for a successful long-term establishment, reaching the canopy as fast as possible is crucial for saplings of light-demanding species; once the canopy is closed, the light might not be sufficient for small trees that remain in the understory (Peet and Christensen, 1987). Similarly, to safeguard access to nutrients and water, the roots have to expand quickly to occupy the available space in the soil (Evans and Turnbull, 2004). Species that are unsuitable to grow at specific sites or in specific compositions may not survive the initial phase.

Here we investigate the establishment success of the first two years of trees planted in a biodiversity enrichment experiment (EFForTS-BEE) in an oil-palm landscape (Teuscher et al., 2016). EFForTS-BEE integrates a BEF-component to test the effectiveness of tree islands as enrichment restoration strategy. Based on different autecological and synecological properties between the species, we expect the initial performance to differ between species. Complementary effects between the species could benefit trees that were planted in mixed-species plots. Edge effects with the surrounding oil-palm plantations are less in bigger plots, which could affect the performance of trees planted in plots of differing sizes. Trees, including oil palms, may interact already in the initial phase, for which neighborhood effects could influence the performance of the trees. Contrary to the young trees, the roots and crowns of the oil palms on the experimental site are already fully developed. With a water use of oil palms that can be very high (Röll et al., 2015), hampering effects on the young trees are possible, but its magnitude may vary between the species. This study may contribute to an evaluation of the planted tree species in the future regarding their ecological and economic effectiveness.

Therefore, we first investigate differences in height and basal area increment and survival between the six planted tree species. Second, we test which plot characteristics, i.e. site conditions, the diversity of the planted trees, and the size of the plots, are beneficial for the plot-specific tree performance. Third, we study if plot edge effects and inter- and intraspecific interactions between the planted tree species and the oil palms have a significant effect on tree performance.

3.3 Materials and Methods

Study site

The biodiversity enrichment experiment EFForTS-BEE is located in Jambi province, Sumatra, Indonesia (01.95° S and 103.25° E, 47 ± 11 m a.s.l., Teuscher et al., 2016). EFForTS-BEE is part of the collaborative research project "Ecological and Socioeconomic Functions of Tropical Lowland Rainforest Transformation Systems" (EFForTS) (Drescher et al., 2016). In the study region, the predominant climate is humid tropical, with a mean temperature of 26.7 ± 0.2°C and an annual rainfall of 2235 ± 381 mm (Drescher et al., 2016). Loamy acrisol is the dominant soil type in the region (Allen et al., 2015). Dipterocarp-dominated lowland rainforest represents the natural vegetation in the region (Laumonier, 1997; Whitten, 2000). The experiment was established in a conventional, mid-sized oil-palm plantation with approximately 143 oil palms per hectare. The management includes regular manual weeding of the understory vegetation, regular application of organic and inorganic fertilizer and occasional application of herbicides and pesticides (Teuscher et al., 2016). The plantation is owned by the company PT. Humusindo Makmur Sejati and located in undulating terrain; elevation above sea level (ranging from 20-71 m a.s.l.) as well as the slope (ranging from 0.2-21.3°) differ between the plots (Tab. 2).

Experiment description

In December 2013, we established tree islands in the oil-palm plantation systematically varying the plot size of the tree islands (25 m², 100 m², 400 m², and 1600 m²), the species diversity level of the planted trees (0, equivalent to no tree planting, 1, 2, 3, and 6 species), and the composition of the planted tree species. We chose six multi-purpose tree species that are native to the study region and economically relevant: *Archidendron pauciflorum* (Fabaceae), *Parkia speciosa* (Fabaceae), and *Durio zibethinus* (Malvaceae), of which the fruits are consumed, *Dyera polyphylla* (Apocynaceae), which produces natural latex, *Shorea leprosula* (Dipterocarpaceae) and *Peronema canescens* (Lamiaceae), both used as timber. The experimental design follows the random partition design by Bell et al. (2009), resulting in a total of 48 experimental tree islands (plus four plots under experimental management without tree planting and four control plots under management-as-usual, which were not incorporated in this study). To enhance light availability, we systematically thinned the oil-palm planting density in the tree islands to reduce the canopy cover by ca. 40%. Due to different plot sizes and the plot-specific oil-palm arrangement, this resulted in different numbers of remaining (zero to 20) and removed (zero to eight) oil palms per plot (for details see chapter 4, Table 4.1). The trees were planted in a 2 x 2 m-grid in rows alternating in north-south direction, resulting in six planted trees in the 25 m²-plots, 25 in the 100 m²-plots, 100 in the 400 m²-plots, and 400 in the 1600 m²-plots. In mixed-species plots, we planted an equal number of trees per species and plot. Where necessary, we reduced the total number of planted trees to be able to plant exactly the same number of trees (e.g., with 6 species on a 1600 m² plot, we planted 6*66=396 trees instead of 400). This resulted in a total of 6354 planted trees, with 1059 individuals per species. Within each plot, we maximized the distance between trees of the same species. The six planted multi-purpose tree species differ in their habitat preferences, as some are more strictly constrained to primary lowland rainforest or swamp forests, while others occur rather in secondary forests primary swamp forest. Two species belong to the Fabaceae-family, which is able to fix nitrogen (Table 3.1). The planting material was bought at the local market and collected in the forest and around the city (Table 3.1). Therefore, the variability of the genetic material among individuals may differ between the tree species.

The management in the experimental plots comprised a total stop of fertilizer, herbicide and pesticide application. Manual weeding was done regularly in the time reported here. We established fences around the plots to protect the saplings from damage by wild boars, livestock, and humans.

Data collection and data base

All trees were measured shortly after planting in January 2014, and again 2 years later in January 2016. For each of the 6,354 planted tree individuals, we determined the height (H, cm) and the stem diameter (cm) 10 cm above ground. Based on the measured diameter, we calculated the basal area.

We calculated relative growth rates (Hunt, 2003) to control for the varying sizes of the tree individuals at the time of planting (Table 3.1). Relative height increment (rHi,cm cm^{-1} y^{-1}) for each individual z was calculated as

$$(1) \qquad rHi_z = 365\, x\, \frac{\ln(H_{z_{2016}}) - \ln(H_{z_{2014}})}{t_{z_{2016}} - t_{z_{2014}}}$$

with H = height [cm], t = Julian day of measurement in 2016 or 2014, respectively.

Relative basal area increment ($rBAi$) per year (cm² cm^{-2} y^{-1}) for each individual z was calculated as

$$(2) \qquad rBAi_z = 365\, x\, \frac{\ln(BA_{z_{2016}}) - \ln(BA_{z_{2014}})}{t_{z_{2016}} - t_{z_{2014}}}$$

with BA = basal area (cm²), t = Julian day of measurement in 2016 or 2014, respectively.

Table 3.1 | Overview of the planted species: family, ecological characteristics, usage, and differences between the species when planted.AgeJan14 = age of the seedlings in January 2014, H_{Jan14}= height measured in January 2014, H_{Jan16}= height measured in January 2016, BA_{Jan14}= basal area measured in January 2014, BA_{Jan16}= basal area measured in January 2016, SD= standard deviation.

species	family	local name	natural habitat	special traits	main usage	origin of planting material	Age_{Jan14} [months]	H_{Jan14} [cm]	±SD	H_{Jan16} [cm]	±SD	BA_{Jan14} [cm^2]	±SD	BA_{Jan16} [cm^2]	±SD
Archidendron pauciflorum (Benth.) I.C.Nielsen	Fabaceae	Jengkol	primary and secondary lowland rainforest[1]	N-fixing	fruit	seed, bought at the local market	19	52.3	15	319.6	150	0.13	0.1	8.96	0.1
Durio zibethinus L.	Malvaceae	Durian	lowland rainforests[2]		fruit (also timber, medicinal)	seed, bought at the local market	7	41.0	11	122.4	77	0.13	0.1	2.72	0.1
Dyera polyphylla (Miq.) Steenis	Apocynaceae	Jelutung	primary lowland swamp rainforest[3]		latex (also timber)	seed, collected in the forest	7-8	31.6	9	94.3	44	0.22	0.1	2.42	0.1
Peronema canescens Jack	Lamiaceae	Sungkai	profits from forest disturbance, not in primary forests, lowland[4]		timber (also medicinal)	cutting, from many trees close to city	19	54.2	21	294.1	173	0.19	0.1	8.68	0.1
Parkia speciosa Hassk.	Fabaceae	Petai	primary and secondary lowland rainforest[5]	N-fixing	fruit	seed, bought at the local market	19	52.0	20	415.4	143	0.29	0.2	28.19	0.2
Shorea leprosula Miq.	Dipterocarpaceae	Meranti	well-drained or swampy rainforest[6]		timber	wildling, collected in the forest	8-9	85.8	22	254.3	114	0.28	0.1	11.75	0.1

[1]Nielsen, 1992; [2]Yap et al., 1993; [3]Rudjiman et al., 1995; [4]De Graaf et al., 1993; [5]Wiriadinata and Bamroongrugsa, 1994; [6]Kochummen et al., 1993

Additionally, we monitored the survival of the tree individuals every month. During the first two years of the experiment, dead tree individuals were replaced. For this study, we only included trees that were initially planted.

To investigate possible interactions between planted tree species and oil palms, we determined the position of the trunks of removed oil palms and the remaining oil palms in the plots, plus all oil palms within 12 m to the plot edge. For each tree individual, we calculated the nearest distance to plot edge (m), the distance to nearest oil palm removed (m), the distance to nearest oil palm alive (m), the number of neighbors in ≤ 5 m distance per species, and the mean height of all neighbors (cm) in ≤ 5 m distance.

We measured a range of variables describing the plot-specific site conditions. In October 2014, we took a minimum of twelve soil samples in 10-30 cm depth covering the whole plot area. Per plot, we merged all soil samples to one composite. We analyzed soil texture (proportional sand, silt, and clay content), proportional carbon content and soil pH. Additionally, we took one standardized soil volume in 0-10 cm depth in the center of each plot, which we oven-dried and weighed to measure the bulk density (g cm^{-3}). For each plot, elevation above sea level (m) and maximum slope (degree) were determined. To calculate the plot-specific canopy openness, in October 2014, we took hemispherical photographs covering the whole plot area with varying numbers of spots depending on the plot size (one spot in 25, one in 100, three in 400, seven in 1600 m^2 plots). Prior to tree planting, we estimated the proportion of ground vegetation cover on each plot in October 2013. A more detailed description of the data collection for the site-specific variables can be found in Teuscher et al. (2016).

Due to tree mortality, the relative portion per species changed over time in each plot and lead to different proportions among plots of the same diversity level by the end of the study period. To take this into account, for each plot, we calculated the Shannon diversity of all tree individuals that were still alive in January 2016. Here, we also considered the presence of trees that were replanted during the first two years of the experiment to replace dead individuals.

Statistics

For analyses of height and basal area based on tree individual data, we excluded outlier values outside an interval of plus/minus three absolute standard deviations around the median (Leys et al., 2013).

We used Kruskal-Wallis-tests to test for difference between tree species in height and diameter and their performance measured as *rHi* and *rBAi*, respectively. In both cases, parametric tests could not be implemented as heteroscedasticity occurred. For pairwise comparisons between all species, we used a Bonferroni-adjusted pairwise Wilcoxon-test. To analyze the different survival probabilities of the species, we applied a chi^2-test and calculated subsequently pairwise comparisons of proportions with Bonferroni correction for multiple testing.

To determine the influence of plot-specific site conditions, plot size, and the diversity level of planted trees on the species performance, we calculated the mean relative height and the mean relative basal area increment, and the number of trees that survived or died per plot, respectively. Due to mortality of all originally planted trees in three plots, the number of plots that could be considered in the following analyses was reduced to N=45. We tested for collinearity between the site condition variables and removed sand content due to high collinearity with silt and clay content (Pearson's r > 0.7) (Dormann et al., 2012). All explanatory variable and the response variables *rHi* and *rBAi* were z-transformed by subtracting its mean and dividing by its standard deviation.

We used linear mixed effects models to model mean *rHi* per plot and mean *rBAi* per plot. In both models, we included the species identities as random effects and controlled for the different sample sizes (number of remaining trees per plot) from which the means were calculated, by allowing a higher variance for small sample sizes. Third, we modeled the survival probability per plot using generalized linear mixed effects models to account for its binomial distribution. We included the species and, as overdispersion occurred, the plot identifier as random effects. The same explanatory variables were used in all three models, including site conditions, plot size, and the diversity level of planted trees, and the presence or absence of each of the six tree species. To find the minimum adequate models based on the full models one, two and three, we calculated models in all possible variable combinations, respectively. The minimum adequate models were selected based on lowest Akaike Information Criterion adjusted for small sample sizes (AICc). We calculated the marginal R^2 for linear and pseudo-R^2 for generalized linear mixed effect models, which give the explained variance for all fixed effects, but without random effects.

To test for neighborhood effects, we scaled all explanatory variables, *rHi* and *rBAi* in the individual-based database. We tested for collinearity (Dormann et al., 2012) and excluded the maximum height of trees in the close vicinity which was collinear (Pearson's r>0.7) with mean height of trees in the close vicinity. For each species, we calculated two linear models with the response variable *rHi* of all individuals of the respective species in the first model, and with *rBAi* in the second. Third, we calculated a generalized linear model for each species with survival as binary response variable containing '0' (dead) and '1' (survival). In all three models, the same set of explanatory variables was used. To select a minimum adequate model, we followed the same procedure as previously explained, with the exception that no adjustment of the Akaike information criterion (AIC) was needed. For the generalized models, a pseudo-R^2 was calculated by dividing the difference between the null deviance and the residual deviance by the null deviance (Zuur et al., 2009).

All statistical analyses were conducted in R (R Core Team, 2016) using the packages vegan (Oksanen et al., 2016), MuMIN (Barton, 2016), nlme (Pinheiro et al., 2015), lme4 (Bates et al., 2015), lmerTest (Kuznetsova et al., 2016), and piecewiseSEM (Lefcheck, 2015).

3.4 Results

Tree species differed significantly in height (p<0.001, Appendix Table B.1) and diameter (p<0.001, Appendix Table B.2) when they were planted, and also their age varied. Height also differed between individuals of the same species (Table 3.1). The plots differed in site conditions (Table 3.2). The soil texture and the soil carbon content were variable, whereas pH and bulk density were similar across plots. The mean proportion of vegetation cover prior to tree planting was high, but differed between the plots. Oil palm thinning contributed to varying light conditions between the plots, expressed by canopy openness (ranging from 4 - 70%, Table 3.2).

Table 3.2 | Overview of explanatory variables. For plot size, categories are given, sd= standard deviation.

name	unit	mean	±sd
elevation	m	47.5	9.68
slope	°	8.91	5.92
clay-content	prop.	0.29	0.08
silt-content	prop.	0.41	0.08
C-content	prop.	0.02	0.01
pH		4.46	0.23
bulk density	g/cm³	1.08	0.13
vegetation cover	prop.	0.73	0.16
canopy openness	prop.	0.28	0.15
plot size	m²	25, 100, 400, 1600	
Shannon index		0.31	0.45

Species performance

The overall survival rate was 51.8 %. The tallest tree individual (*P. speciosa*) reached a height of 913 cm in January 2016, and the maximum diameter that was reached by one individual was 11.3 cm (*P. canescens)*. We found significant differences between the performance of the planted species considering *rHi*, *rBAi*, and survival rates (Figure 3.1). *D. polyphylla* and *D. zibethinus* showed low *rHi* and *rBAi,* combined with low survival rates. In contrast, *A. pauciflorum, P. speciosa* and *P. canescens* had high *rHi* and *rBAi,* and also high survival rates. *S. leprosula* had the third lowest rHi and survival rate, but the second highest *rBAi.*

Influence of plot characteristics on species performance

The site condition variables, plot size, and the diversity level of planted trees only explained a minor proportion (1 – 10%) of the variance in plot-specific tree performance, i.e. *rHi*, *rBAi*, and survival, between the plots (Table 3.3). Among the site condition variables, only slope had a small negative impact on relative height increment, and elevation on relative basal area increment. Among the experimentally altered variables, the Shannon index had a significantly negative effect on *rHi*, *rBAi*, and a significantly positive effect on survival. Plot size had a significant negative effect on *rBAi*.

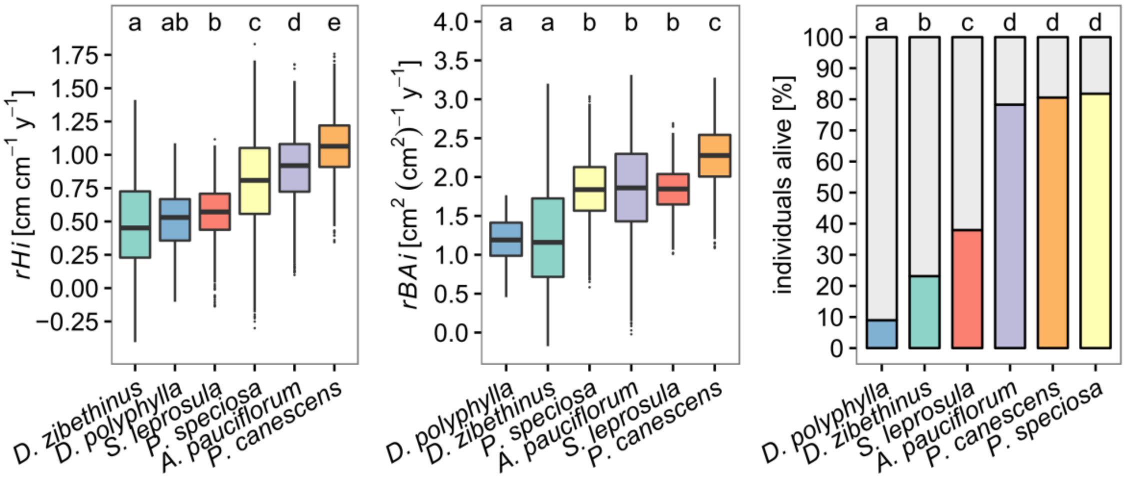

Figure 3.1 | Differences in species performance considering relative height increment (rHi), relative basal area increment (rBAi), and survival. Boxes show the interquartile range, which is the first and third quartile, and whiskers extend 1.5 times the interquartile

Table 3.3 | Minimum adequate models on plot level.
rHi = relative height increment, *rBAi* = relative basal area increment, and all explanatory variables are standardized and comparable. Species were included as random effects. est = model estimate, se = standard error. Significance levels are indicated by *: p<0.05, **: p<0.01, ***: p<0.001.

	rHi			*rBAi*			survival		
R²/pseudo R²	0.04			0.01			0.1		
variables	est	se	p	est	se	p	est	se	p
elevation				0.18	0.05	**			
slope	-0.21	0.07	**						
clay content									
silt content									
C content									
pH									
bulk density									
vegetation cover									
canopy openness									
plot size				-0.12	0.06	*			
Shannon index	-0.48	0.11	***	-0.16	0.07	*	0.87	0.28	**

Tree - tree and tree - oil-palm interaction

Neighborhood effects explained 7-38% of the variation in *rHi*, *rBAi*, and survival between individuals of the same species, and variation in *rHi* between individuals of *D. polyphylla* could not be explained by any of the variables (Figure 3.2).

Overall, distance to plot edge was generally not very important, but positively affected the height growth and survival of *D. zibethinus* and the survival of *A. pauciflorum*, whereas it negatively affected the survival of *D. polyphylla* (Figure 3.2). The distance to remaining oil palms had a consistently positive effect on tree performance on all species except for *P. speciosa,* which was not significantly affected. The effect of distance to trunks of removed oil palms was in some cases positive and in others negative, but generally weak. The mean height of neighboring trees in ≤ 5 m distance was an important variable for all species to explain the variation in individual tree growth and survival and had a throughout positive effect, with the exception of a negative effect on the survival of *D. polyphylla.* Regarding the interaction between the planted species, *A. pauciflorum* was positively affected by *P. speciosa* in the neighborhood in terms of *rHi* and *rBAi*, but, as by *A. pauciflorum* itself, negatively in terms of survival. *D. polyphylla* had a positive influence on *rHi* and survival of *A. pauciflorum*. The presence of any other species in the neighborhood was negative for *D. zibethinus*. The *rBAi* of *D. polyphylla* was negatively affected by *A. pauciflorum* and positively by *P. canescens*. Regarding the survival of *D. polyphylla*, *P. speciosa* had a strong positive effect, *D. zibethinus* had a weaker positive effect, and *S. leprosula* a negative influence. The rHi and rBAi of *P. speciosa* were positively affected by *D. polyphylla* in the close neighborhood and negatively by *P. canescens*, *A. pauciflorum. S. leprosula* negatively affected the *rBAi* of *D. polyphlla*. *P. speciosa* itself and *D. zibethinus* had a positive effect on survival of *P. speciosa*. The performance of *P. canescens* was not much affected by neighbors: *D. polyphylla* had a negative effect on rBAi of *P. canescens*, and *P. canescens* itself and *S. leprosula* on survival. *P. speciosa* had a positive effect on rHi and rBAi of *P. canescens,* and *A. pauciflorum* on rBAi. In all three models, the proportion of explained variance was low for *S. leprosula.* Its growth performance, i.e. *rHi* and *rBAi*, only responded to the presence of *A. pauciflorum* in a negative way. Considering survival, *D. polyphylla* and *P. speciosa* negatively affected *S. leprosula*, whereas *D. zibethinus* and *P. canescens* had a positive influence.

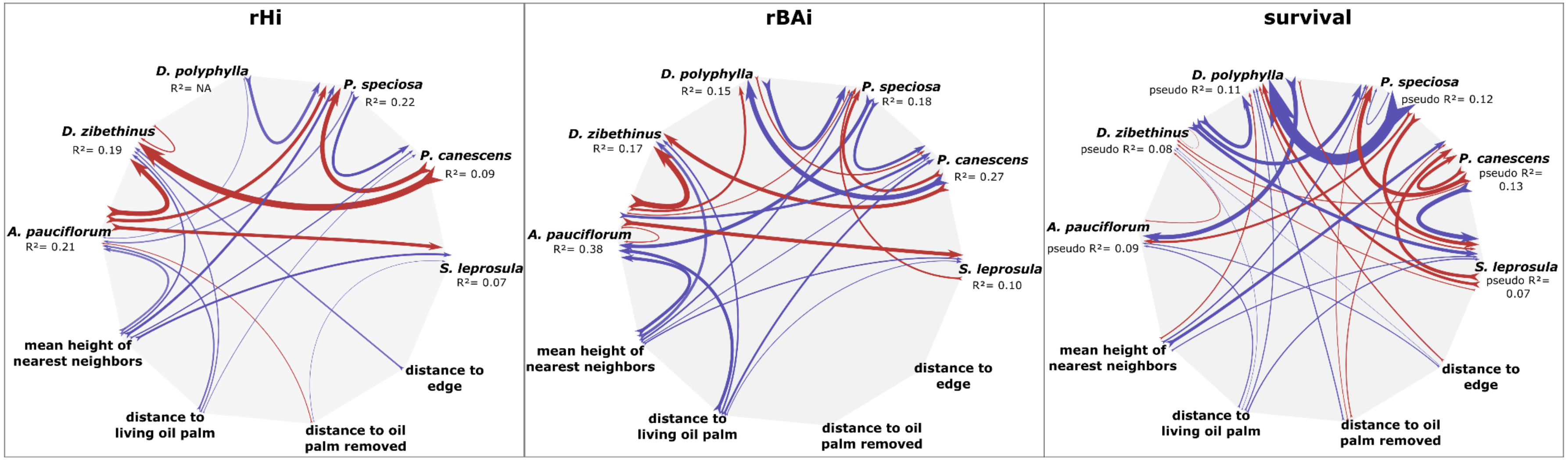

Figure 3.2. | **Model results on neighborhood effects** of trees, oil palms, and the plot edge on the performance of each of the six species, considering relative height increment (*rHi*), relative basal area increment (*rBAi*), and survival. We modeled *rHi*, *rBAi*, and survival for each species separately, always incorporating the whole set of explanatory variables shown in the figure, including species identity of the neighbors. Below each species name, R^2- or pseudo R^2-values are given of the respective model. Arrows are scaled according to their model estimates, which are comparable as we scaled the explanatory variables. The response variables *rHi* and *rBAi* were also scaled, but survival was not. Red arrows indicate a negative, blue arrows a positive influence. Arrows point from the influencing variable to the species influenced.

3.5 Discussion

Species identity was a strong determinant of the performance of the planted trees in the two initial years of the experiment. The large variation in tree performance, i.e. *rHi*, *rBAi*, and survival, between individuals of the same species (Figure 3.1) was only marginally explained by site condition variables on the plot level (compare estimates, Table 3.3). Among the experimentally altered variables, Shannon diversity of planted trees, and to a lower extent the plot size, had an impact on tree performance (Table 3.3). Interactions between trees and effects of oil-palm trunks and the plot edge were already noticeable, but in most cases weak (Figure 3.2).

We report on an overall successful establishment of the trees planted on the experimental plots despite large differences between the species-specific performances. The overall survival rate of 51.8% with a great variability between species (ranging from 9.0 - 82.8%, Fig. 1) is in line with other tree planting experiments with a comparable design. In the BEF-China experiment, 43% of individuals survived initially (Yang et al., 2013). In an experiment in Uganda, 58% of the seedlings survived (Piiroinen et al., 2015). In Costa Rica, species-specific survival rates varied between 5-80% (Ewel et al., 2015). Survival was highly species-specific in an experiment in Panama (Potvin and Gotelli, 2008), and for one species lower than 15% (Scherer-Lorenzen et al., 2007).

Although most of our species-specific results are similar to the performance of the species in other experiments, we also find differences (Table 3.4). For *A. pauciflorum* and *P. speciosa*, no similar studies were found. The weak performance of *D. polyphylla* in our experiment is striking (Table 3.4). *S. leprosula* showed average height growth, but had low survival rates and the basal area increment was almost twice as much as in another trial (Ådjers et al., 1995; Kochummen et al., 1993). In Java, first flowering of *P. canescens* was reported after c. five years (De Graaf et al., 1993), but occurred already after two years in our experiment. Even though fertilizer application in the experimental plots was stopped right after planting, we fertilized the trees once when planted (for details see Teuscher et al., 2016), and added nutrients may still be left in the soil, which could have speeded-up the tree development in some cases. This may also explain the exceptionally high diameter growth of *S. leprosula*, which responds strongly to fertilizer application (Nussbaum et al., 1995).

Much of the differences in performance might be explained species-specific life history traits. The plantation conditions seem to favor species which occur in secondary forests. Among the three best performing species, *A. pauciflorum* and *P. speciosa,* both also occur in secondary forests (Nielsen, 1992; Wiriadinata and Bamroongrugsa, 1994), and *P. canescens* is a common pioneer species in the area and benefits from forest disturbance (Kochummen et al., 1993). *S. leprosula* and *D. zibethinus* are more closely associated with primary forest, and performed worse. Alterations in the ecosystem

Table 3.4 | Comparison of the results of this study with findings in the literature. The respective height above ground [cm] for diameter measurement is given in parentheses.

species	indicator	our study (after 24 months)	literature	length of study period [months]	further information	reference
D. zibethinus	diameter increment	1.2 cm	0.3-0.5 cm	12	Sabah, Malyasia	Yap et al. (1993)
D. polyphylla	height diameter survival	94 cm 1.7 cm 9%	163/159 cm 3.2 cm (n.a.) 90%	18	Jambi, Indonesia; planted with oil palms on peat soil	Tata et al. (2015)
S. leprosula	height increment diameter increment survival	169 cm 3.1 cm 38%	174 cm 1.7 cm (10) 75%	24	South Kalimantan, Indonesia; planted in 2m distance	Ådjers et al. (1995)
	height increment	169 cm	100-113 cm	12	West Java, Indonesia	Kochummen et al. (1993)
P. canescens	max height max diameter survival	776 cm 11.3 cm 81%	485 cm 6.0 cm (5) 71%	19	South Kalimantan, Indonesia	Otsamo (2000)
	mean height mean diameter survival	415 cm 5.7 cm 81%	214 cm 3.9 cm (0) 68%	26	Jambi, Indondesia	Hatta (1999)

properties of oil-palm plantations in comparison to lowland rainforests might be responsible, such as a higher air temperature, lower relative humidity, higher canopy openness, less litter carbon input (Drescher et al., 2016), and, disregarding fertilizer input, an impoverished nutrient availability in the soil (Allen et al., 2015; Guillaume et al., 2015). *D. polyphylla*, which naturally occurs in swamp forests (Rudjiman et al., 1995), may have suffered from not being directly connected to groundwater.

Between the species, variable susceptibility to herbivory and plant diseases was observed in the field and was only pronounced for *S. leprosula*. In our study, this may have contributed to the unclear picture regarding its performance (Figure 3.1) and the low proportion of variation that could be explained with neighborhood interactions for this species (Figure 3.2).

Among the experimental factors, we found a slight negative effect of plot size and a strong negative influence of Shannon index on overall *rHi* and *rBAi* (Table 3.3). This finding is different compared to other BEF-experiments. Tree diversity was shown to have a positive influence on tree biomass, at least for specific species compositions (Erskine et al., 2006; Ewel et al., 2015; Kirui et al., 2012; Petit and Montagnini, 2006; Potvin and Gotelli, 2008). Li et al. (2014) did not find an effect of biodiversity on tree biomass.

In our experiment, tree diversity had a positive influence on survival (Table 3.3). Tree diversity did not affect survival rates in two other experiments (Potvin and Gotelli, 2008; Van de Peer et al., 2016). In one experiment, a negative effect of diversity level on the survival was observed in the very initial stage of the experiment, but disappeared soon (Yang et al., 2013).

Positive effects of mixed-species stands compared to monocultures such as an improved tree physiological efficiency (Richards et al., 2010) and alterations in ecosystem properties and processes (Bruelheide et al., 2014) might not yet exist, but could evolve in a later stage of the experiment. This could help achieving restoration goals faster and increase the amount of harvestable products. For example, in specific compositions, complementarity effects and facilitation between different species were found to induce an accumulation of more biomass than each of the single species in monoculture (e.g. Jucker et al., 2014; Potvin and Dutilleul, 2009). The accumulation of biomass and structural heterogeneity provided by native trees could substantially improve the hospitability for other plants and animals. A high number of species in the initial system was found to attract a higher level of associated biodiversity in other BEF-experiments (Balvanera et al., 2006), which is a main goal of ecological restoration (Rey Benayas et al., 2009).

Starting competition between the oil palms and the planted trees was indicated by a positive response of the tree performance to the distance to oil palms alive, which was the least pronounced for *P. speciosa*. Tall neighbors had a positive effect on the initial tree performance. Possibly, this may indicate small-scale environmental heterogeneity, which was found to be an important driver of tree growth and survival (Plath et al., 2011). With tall trees in the proximity, enhanced height growth rates could also be induced by competition for light, but this would likely go along with reduced stem diameter growth (Li et al., 2014). The two members of the Fabaceae-family, which features nitrogen-fixing properties, differed in their performance: *P. speciosa* had a predominantly positive effect on its neighbors, whereas *A. pauciflorum* had a rather negative effect. Overall, *D. polyphylla* and *P. speciosa* were mostly beneficial neighbors. *D. zibethinus* in the neighborhood was almost as often disadvantageous as favorable. *A. pauciflorum* and *P. canescens* were mostly disadvantageous as a neighbor, and *S. leprosula* throughout.

Some variation in performance between individuals of the same species remained unexplained. Damages by wild boars and livestock could play a role, which occurred when the fence was broken. Furthermore, harvesting of the oil palms within the plots continued, whereby some trees broke down due to dropping oil-palm leaves. This caused noise in the lower end of the data distribution, especially for *rHi*. Furthermore, different genetic endowments could have led to intraspecific differences (Table 3.1). The influence of site condition variables could become more significant when measured on smaller than on plot scale. For example, micro-topographic differences are crucial for the performance of *S. leprosula* seedlings (Born et al., 2014), and small-scale light interception are important for the performance of *S. leprosula* (Ådjers et al., 1995) and *P. canescens* (Otsamo, 2000).

Furthermore, weather events might have contributed to low survival of some species. During the rainy seasons, some experimental plots were flooded for several days. In June-October 2015, there was a pronounced drought in the study region which was associated with an El-Niño-Southern Oscillation event (Tacconi, 2016). However, extreme weather events and El-Niño-Southern Oscillation events are projected to become more frequent (Cai et al., 2014; IPCC, 2014), and might therefore be a bottleneck for the establishment of restoration plantings.

3.6 Conclusion

We report on a successful establishment of the trees planted to experimentally enrich an oil-palm plantation. Significant differences occurred between the tree species considering growth parameters and survival. On plot level, site conditions, plot size, and the diversity level of planted trees had a minor influence on tree performance. We already noticed starting interaction between the tree species, and an effect of the remaining oil palms. It is too early to decide on the overall suitability of the tree species regarding their effectiveness to achieve restoration goals while minimizing losses to the local socio-economics. However, the initial phase of the experiment is particularly critical. Therefore, differences in initial tree performance are important information to translate the findings of the experiment into management instructions for the future. Regarding the tremendous extent of land transformations for oil-palm plantations that has been occurring, restoration of ecosystem functioning is a necessity.

3.7 Acknowledgements

We thank the following persons and organizations for granting us access to and use of their properties: PT Humusindo Makmur Sejati and Pak Hasbi and his family. Special thanks to Andi, Adi, Teddy, Fadli, Azwin, Ahsan, Supadi, Anshori, and Zeri for their commitment and good work in the field. We thank the people in the lab in Palu and in the Indonesian Institute of Science (LIPI), for assisting with analyses of soil samples. Thanks to Philip Beckschäfer for helping us to process the hemispherical photographs. We are grateful for the logistical support by the EFForTS staff and coordination. This study was financed by the Deutsche Forschungsgemeinschaft (DFG) in the framework of the collaborative German - Indonesian research project Collaborative Research Centre 990 EFForTS.

4 Oil-palm yields in diversified plantations: initial results from a biodiversity enrichment experiment in Sumatra, Indonesia

Anne Gérard, Meike Wollni, Dirk Hölscher, Bambang Irawan, Leti Sundawati, Miriam Teuscher, Holger Kreft

4.1 Abstract

The expansion of oil-palm plantations threatens tropical biodiversity and ecosystem functioning. While oil palm expansion has been associated with positive welfare effects, the strong dependence of local livelihoods on a single crop species also entails social and economic risks. The importance of alternative management strategies has been stressed to mitigate negative ecological and socio-economic consequences. Yet, to date there is little empirical knowledge on the biological effectiveness and economic viability of such approaches. To bridge this gap, we experimentally established tree islands within a conventional oil-palm plantation and reduced the oil-palm density on these islands by thinning. After two years, we find enhanced yields per oil palm inside and also directly adjacent to the experimental plots. Estimating the net yield changes including opportunity costs and spillover effects for different sizes of tree islands, we find evidence that - in particular for larger tree islands - yield gains at least compensate for the reduced number of oil palms. These results obtained during the early phase of tree island establishment are promising in terms of identifying sustainable management options for oil palm that reconcile ecological and economic functions.

4.2 Introduction

The expansion of oil-palm (*Elaeis guineensis*) plantations is currently among the most serious threats to tropical ecosystems and biodiversity, and ongoing land conversion for oil-palm plantations is expected for the near future (Fitzherbert et al., 2008). Apart from the species loss directly associated with the conversion of forest into oil-palm plantations (Drescher et al., 2016; Fitzherbert et al., 2008; Foster et al., 2011), more indirect effects jeopardize the maintenance of local ecosystem functioning, e.g. through a decline of specific groups such as predators in the food web (Barnes et al., 2014) and a loss of regulative ecosystem services (Dislich et al., 2016). At larger scales, greenhouse gas emissions, mainly caused by preceding land conversion (Abood et al., 2015; Germer and Sauerborn, 2008), contribute to alter the global climate.

This development is particularly severe in Indonesia. In response to a steadily rising global demand for palm oil in the last decades (Sayer et al., 2012), the oil-palm area has increased more than eight-fold in Indonesia between 1990 and 2010 (FAO, 2016). At the same time, the country is currently experiencing the world's highest deforestation rates (Margono et al., 2014), with land transformations related to oil-palm expansion considered to be among the strongest direct and indirect drivers (Abood et al., 2015; Sodhi et al., 2010). The forest loss dramatically reduces the area of adequate habitat for Indonesia's unique flora and fauna, which is among the most species-rich on the globe (Sodhi et al., 2004).

Oil-palm adoption is associated with both opportunities and risks for local famers. Oil palm is the most productive oil crop on an area-basis (Basiron, 2007) and requires comparatively low labor input (Drescher et al., 2016). Consequently, oil-palm cultivation improved incomes and livelihoods of many Indonesian farmers (Euler et al., 2015a; Feintrenie et al., 2010). Currently, more than 40% of the oil-palm plantations are smallholder-owned, and this proportion is further increasing (Euler et al., 2015b; Gatto et al., 2015). Despite the economic benefits, the agricultural homogenization in the landscape is associated with a strong dependence on a single crop, minimizing the resilience to agronomic and economic shocks, such as pest outbreaks, climate variability (Lin, 2011) and fluctuating world market prices (Index Mundi, 2016). A range of ecosystem services are currently deteriorating (Dislich et al., 2016), notably those which are crucial for safeguarding agricultural productivity (De Groot et al., 2002). Moreover, local people face serious health threats that are directly related to the recent oil-palm intensification, including air pollution during recurring "haze"-episodes in Southeast-Asia due to land clearing (Behera et al., 2015; Gaveau et al., 2014) and declines in water quality and availability (Merten et al., 2016).

Many researchers highlight the need for more diversified oil-palm landscapes to mitigate the negative environmental consequences of this recent development (Fitzherbert et al., 2008; Foster et al., 2011; Koh, 2008; Koh et al., 2009). Oil-palm plantations enriched with trees could be a promising management option, as agroforestry-like systems increase the structural complexity and could thus make the landscapes more hospitable and permeable for native species (Bhagwat et al., 2008; Bhagwat and Willis, 2008; Koh et al., 2009). Yet, it is essential to take potential trade-offs between ecological and economic benefits into account. In this regard, specific tree species could potentially compensate for possible yield losses by adding social and economic value, e.g., they may provide food, timber and other resources, increase the resilience to environmental and economic change, and improve soil fertility (Tscharntke et al., 2011). For other crops such as cacao and coffee, well-managed agroforests have been shown to be both species-rich and economically viable (Clough et al., 2011; Perfecto et al., 2007). For oil palms, many scientists have questioned the economic viability of mixed-species stands of oil palm with other trees due to competition for resources (Corley and Tinker, 2003; Koh et al., 2009; Phalan et al., 2009). However, there is very little empirical evidence on the associated yield impacts of such alternative management approaches.

To shed light on the relationships between different plantation management strategies, oil-palm yields, and ecosystem functioning, we set up a long-term biodiversity enrichment experiment establishing tree islands in a conventional oil-palm plantation (Teuscher et al., 2016). Tree islands have been shown to be a cost-effective measure to enhance biodiversity and ecosystem functionality e.g. of abandoned pastures (Cole et al., 2010; Zahawi and Augspurger, 2006) and have also been suggested as components of agricultural landscapes (Rey Benayas et al., 2008). In the experiment, we planted tree islands with six multipurpose, native tree species, and systematically varied the size of the tree islands (25 m², 100 m², 400 m², and 1600 m²), the species diversity level of the planted trees (0, 1, 2, 3, and 6), and the composition of the planted tree species. Additionally, to enhance the light availability for the planted trees, we systematically thinned the oil-palm planting density in the tree islands.

In this study, we analyze the initial effects of the experiment on oil palm yields. First, we investigate the effects of agro-ecological and experimentally altered variables on yields per oil palm inside the experimental plots. Second, we analyze spillover effects of the experimental treatments to the yields of adjacent oil palms. Finally, from the farmers' perspective, it is relevant to consider not only the changes in per-oil-palm yields, but also the overall net effect at the plot level. Therefore, we analyze the net effects on yields at the aggregate plot scale. In this context, we consider yield changes inside the plots, spillover-effects to yields of surrounding managed-as-usual oil palms, and opportunity costs for farmers resulting from oil palm thinning. With our research, we aim to inform the development of more sustainable oil palm management strategies that can be implemented by large plantations and small-scale producers alike.

4.3 Materials and Methods

Study site and experimental design

We established a biodiversity enrichment experiment (EFForTS-BEE, 01.95° S and 103.25° E, 47 ± 11 m a.s.l., Teuscher et al., 2016) in Jambi province, Sumatra, Indonesia. EFForTS-BEE serves as an experimental platform for the collaborative research project "Ecological and Socioeconomic Functions of Tropical Lowland Rainforest Transformation Systems" (EFForTS) (Drescher et al., 2016). The experiment is located in a conventional, mid-sized oil-palm (OP) plantation where oil palms are planted in a 9x9 m triangular grid, i.e. with 7.8 m between rows of alternating oil palm arrangement, and an in-row distance of 9 m, resulting in approximately 143 oil palms per hectare. The mean yield in the plantation is 22.74 t/ha/year (Hasibuan, pers. comm.), equivalent to 159 kg/OP/year (hereafter referred to as plantation average). The management-as-usual is uniformly applied to the whole plantation surrounding the experimental plots and implies regular manual weeding of the understory vegetation, regular application of organic and inorganic fertilizer, and occasional application of herbicides and pesticides.

In December 2013, we established tree islands in the oil palm plantation with up to six different multi-purpose tree species native to Sumatra under various management options. The species are native to Sumatra and thus beneficial to local ecosystems, and were also selected based on their economic value to the local population. Three of the planted tree species produce edible fruits (*Parkia speciosa,* Fabaceae; *Archidendron pauciflorum*, Fabaceae; *Durio zibethinus,* Malvaceae), two species provide timber (*Peronema canescens,* Lamiaceae; *Shorea leprosula*, Dipterocarpaceae) and one species natural latex (*Dyera polyphylla,* Apocynaceae). To test a range of different management strategies, we systematically varied the plot size of the tree islands (25 m^2, 100 m^2, 400 m^2, and 1600 m^2), the species diversity level of the planted trees (0, equivalent to no tree planting, 1, 2, 3, and 6 species), and the composition of the six planted tree species. Further, to enhance light availability, we systematically thinned the oil-palm planting density in the tree islands. The experimental design follows the random partition design by Bell et al. (2009), which allows testing different management options without implementing a full-factorial approach. Following the random partition design, the combination of the different management factors resulted in a total of 52 experimental plots[1].

Oil-palm thinning in the tree islands resulted in different numbers of removed and remaining oil palms across and within the different plot size categories (Tab. 1). The 25 m^2 plots were established

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[1] Plus four control plots under management-as-usual, which were not monitored for this study.

in between the existing oil palms, implying that by design no oil palms were growing on these plots. On the 100 m^2 plots, we removed one oil palm per plot in the thinning process. In some cases, this entailed removing the only oil palm on the plot, resulting in a total of eight 100 m^2 plots without remaining oil palms. On the largest plots, up to 20 oil palms remained after thinning. Variations in the number of remaining oil palms on plots of the same size are a result of the specific oil-palm arrangement. Crop management was uniform across all experimental plots and comprised manual weeding and a total stop of fertilizer, pesticide and herbicide applications. A detailed description of the experiment can be found in Teuscher et al. (2016).

Table 4.1 | Number of plots per tree island size class and information on thinning, experimental tree enrichment, and remaining and removed oil palms.

tree island size	no plots	thinning		tree enrichment		no. of OP remaining				no. of OP removed				yield data for analysis	
[m^2]		y	n	y	n	min	med	max	total	min	med	max	total	inside plot	adjacent
25	13	0	13	12	1	0	0	0	0	0	0	0	0	N= 0	N=13*3
100	13	13	0	12	1	0	0	1	5	1	1	1	13	N= 5	N=13*3
400	13	13	0	12	1	1	2	5	31	1	3	4	32	N=13	N=13*3
1600	13	13	0	12	1	11	13	20	178	4	7	8	87	N=13	N=13*3
sum	52	39	13	48	4				214				132	31	156

Data collection

Between April 2015 and March 2016, fresh fruit bunches were weighed every one to two months to record oil-palm yields. Oil-palm yields were measured in kg/OP/year and recorded both for the remaining oil palms within the experimental plots (referred to as inside-plot yields) and for selected oil palms adjacent to the experimental plots (referred to as adjacent-to-plot yields). Inside-plot yields were calculated as the average yield of the remaining oil palms on the experimental plot (varying from one to 20 oil palms; Table 4.1, Figure 4.1). For the adjacent-to-plot yields, we recorded yields of three individual oil palms in increasing distance to the plot edge (distance positions one, two, and three) in order to monitor potential spillover effects of the experimental plots to the surrounding oil-palm plantation (Figure 4.1).

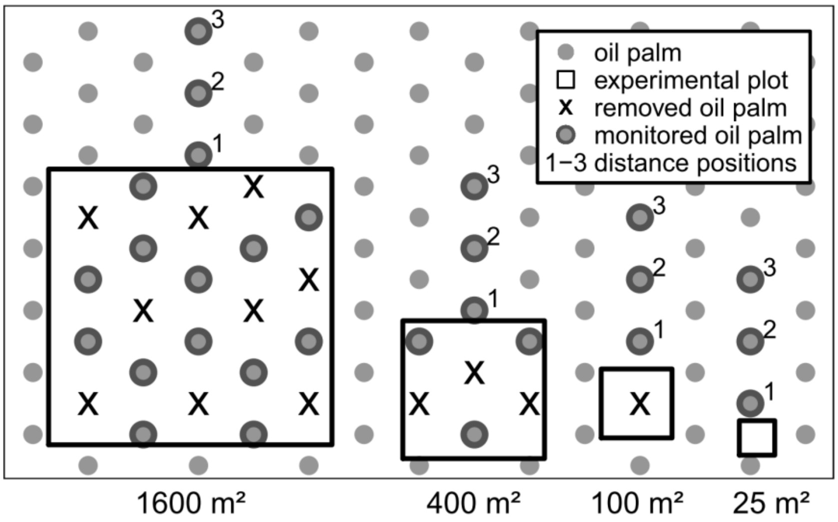

Figure 4.1 | Schematic overview of the yield (fresh fruit bunch weight) data collection of all oil palms inside, and of the three oil palms in increasing distance (mean distance position 1: 3.5m ±1.9, position 2: 12.2 m ±1.4, position 3: 21.8 m ±2.7) adjacent to each of the 52 experimental tree islands in an existing oil-palm plantation. In four different size categories, we established 13 tree islands respectively, which are here shown exemplarily (1600 m², 400 m², 100 m², and 25 m², f.l.t.r.). We find differences between the plot size categories regarding the number of remaining/ due to thinning removed oil palms per tree island size category (median 7/13, 3/2, 1/0, 0/0, f.l.t.r). The planted trees are not shown here. The minimum distance between the tree islands is 85 m.

To obtain agro-ecological data for each experimental plot, a minimum of twelve soil samples covering the whole plot area were taken in 10-30 cm depth in October 2014. Based on the plot-specific composites, we analyzed soil texture (proportional sand, silt, and clay content), proportional carbon content and soil pH. In the center of each plot, one standardized soil volume was taken in 0-10 cm depth, oven-dried and weighed to measure the bulk density (in g/cm³). Furthermore, elevation above sea level (in m) and maximum slope (in degree) were recorded for each plot. Canopy openness was calculated from hemispherical photographs taken one year after establishment for each experimental plot. Photographs covered the whole plot area with varying numbers of spots depending on the plot size (one spot in 25, one in 100, three in 400, seven in 1600 m² plots). A more detailed description of the data collection for the site-specific variables can be found in Teuscher et al. (2016).

Previous research has shown that oil-palm age is an important predictor of yields: during the first ~10 years of an oil-palm life, yield increases almost linearly with oil-palm age, then remains constant, until starting to decline again around the age of ~20 years (Corley and Tinker, 2003). At our study site, oil palm age ranged from approximately seven to twelve years. During this age range oil palm height has been shown to increase almost linearly with age (Röll et al., 2015), and can thus be considered a suitable proxy for age. Therefore, we measured the meristem height of the remaining oil palms on each experimental plot and calculated the plot-specific average oil-palm height in meters.

Finally, to capture the potential effects of experimental tree planting, we measured the height of all planted trees on each experimental plot in January 2016. Based on these measurements, we derived three indicators: (1) the maximum tree height based on the highest tree per plot; (2) the mean tree height per plot; and (3) the plot-specific coefficient of variation (CV tree height) calculated by dividing the standard deviation of all tree heights per plot by the mean tree height per plot.

Statistical analysis

a. *Determinants of inside-plot yields*

In a first step, we model inside-plot yields as a function of plot-specific agro-ecological and experimental variables:

$y_i = ß_0 + ß_1X_i + ß_2Z_i + e_i$

where y_i is the average yield per oil palm per year on experimental plot i; X is a vector of plot-specific agro-ecological characteristics including elevation, slope, canopy openness, average oil-palm height, and a number of soil quality parameters (C content, pH, clay content, silt content, bulk density); Z is a vector of plot-specific experimental variables including plot size, tree diversity level, coefficient of variation of tree height and maximum tree height; the betas are parameters to be estimated and e is a random error term.

Prior to estimating the model, we tested all variables for collinearity. Sand with silt content, sand with clay content, and max tree height with mean tree height showed collinearity above the critical Pearson’s r-value of 0.7 (Dormann et al., 2012) (Appendix Table C.1). Therefore, soil sand content and mean tree height were excluded from the model. Furthermore, we standardized all potential explanatory variables included in the model by subtracting the mean and dividing by the standard deviation. Additionally, we removed one yield outlier, which was outside the range of twice the standard deviation around the mean. To control for different sample sizes of oil palms from which the mean yield per plot was calculated, we allowed higher variances for small samples. We applied the ‘dredge’-algorithm (Barton, 2016) which computes models in all possible combinations of predictor variables. From the full set of models, we then identified the minimum adequate model based on the lowest Akaike Information Criterion adjusted for small sample sizes (AICc).

b. *Spillover effects of the experimental treatments on adjacent-to-plot yields*

To investigate potential spillover effects of the experimental treatments on the yields of adjacent oil palms, we calculate four different linear mixed effects models (Pinheiro et al., 2016). In all four models, Plot ID enters as random effect to control for the statistical dependence of data generated from around the same plot. In model one, we investigate the plot effect on yields by testing for differences between inside-plot yields vs. adjacent-to-plot yields. Again, to control for different sample sizes from which the mean yield per plot was calculated, we allow higher variance for small sample sizes. Models two, three and four are restricted to yield data from oil palms adjacent to the plots. Model two investigates the distance effect and tests for yield differences between oil palms located at increasing distance from the plots (distance positions one, two and three). In model three, we analyze the tree enrichment effect by testing whether there is a significant yield difference between oil palms adjacent to plots with (diversity level >0) and without (diversity level = 0) experimentally planted trees. We control for the large number of plots with planted trees compared to plots without planted trees allowing for a different variance structure. Additionally, we include an interaction term with distance position to test for heterogeneous tree enrichment effects across distance positions. Finally, in model four, we test whether yields differ between oil palms adjacent to plots with and without thinning. Again, we include an interaction term with distance position to test for heterogeneous thinning effects on yields across distance positions. Additionally, we test the average yield estimates of the sub-groups compared in the four models against the plantation average using a one-sample t-test. The comparison is based on the average yield data from the three adjacent oil palms for each plot, given that the data is not independent across adjacent palms.

c. *Estimation of net changes in yields at plot level*

To estimate the yield effects associated with the tree enrichment experiment by plot size class, we calculate the net changes in yields taking into account opportunity costs. First, the opportunity costs ($yield_{foregone}$) of tree enrichment resulting from the removal of oil palms are calculated as:

$$(1)\quad yield_{foregone} = OP_{removed} \times yield_{average}$$

where $OP_{removed}$ is the number of oil palms per plot removed during thinning and $yield_{average}$ is the plantation-level average yield per oil palm and year.

Next, we calculate the change in yield ($\Delta yield_{plot}$) for the remaining oil palms on the enriched plot:

$$(2)\ \ \Delta yield_{plot} = OP_{remaining} \times (yield_{measured} - yield_{average})$$

where $OP_{remaining}$ is the number of remaining oil palms on the plot after thinning and $yield_{measured}$ is the plot-specific average yield per oil palm and year.

To take spillover yield effects to adjacent oil palms into account, we first need to establish the number of adjacent oil palms for each plot size category. Given that we only find statistically significant spillover effects on directly adjacent palms, we only take oil palms at distance position one into account, representing a maximum distance of 7.9 meters from the plot. For each plot size class, we randomly placed 100 plots in a 9 x 7.8 m oil-palm planting grid, and randomly rotated each plot from zero to 90 degree. This rotation allows us to account for the varying orientation of the experimental plots relative to the oil-palm planting scheme. Based on these models, for each plot size category, we calculate the average number of oil palms directly adjacent to the plot (5.85 oil palms for 25 m^2 plots, 7.9 for 100 m^2, 12.41 for 400 m^2 and 21.39 for 1600 m^2 plots). We then multiply this number by the respective plot-specific change in yields of the adjacent oil palm in distance position one ($\Delta yield_{spillover}$) to extrapolate the total spillover effects.

$$(3)\ \ \Delta yield_{spillover} = (yield_{pos1} - yield_{average}) \times neighbors_{plot\ size}$$

where $yield_{pos1}$ is the measured yield of the adjacent oil palm in distance position one for each plot and year, and $neighbors_{plot\ size}$ is the extrapolated number of oil palms within a maximum distance of 7.9 m for each plot size category.

Based on these calculations, we obtain the net yield changes ($\Delta yield_{net}$):

$$(4)\ \ \Delta yield_{net} = \Delta yield_{spillover} + \Delta yield_{plot} - yield_{foregone}$$

Using a one-sample t-test, we test whether the average net yield estimates per plot size class differ from zero.

4.4 Results

Mean values and standard deviations of oil palm characteristics, site-specific conditions as well as experimental variables provide an overview of the variability across experimental plots (Table 4.2). Mean oil-palm height varies substantially across plots ranging from 2.7 to 5.4 m (Table 4.2). Located in a hilly area, the plantation is characterized by large variations in slope and elevation between plots (Table 4.2). Canopy openness ranges from 4 to 70% (Table 4.2) and is closely related to plot size and the respective extent of thinning: canopy openness is lowest for 25 m^2 plots (mean 13%), where no thinning was done, high for 100 and 400 m^2 plots (means 35% and 34%, respectively) and slightly lower again for 1600 m^2 plots (mean 28%) (Appendix Figure C.1). Regarding the soil variables, bulk density and pH are relatively constant across all plots, whereas carbon content and soil texture are relatively variable (Table 4.2). Differences in the structure of the planted trees per plot are pronounced, especially with respect to maximum tree height (Table 4.2), ranging from 0.32 to 9.13 m.

Table 4.2 | Summary statistics for agro-ecological and experimental variables.

variable			value		
group	name	unit	mean	±	SD
dependent	inside-plot yield	[kg/OP/year]	224.10		44
oil palm	OP height	[m]	3.83	±	1
site specific	elevation	[m]	46.90	±	11
	slope	[°]	8.60	±	6
	canopy openness	[%]	27	±	15
	bulk density	[g/cm^3]	1.09	±	0
	C content	[%]	2.17	±	1
	pH		4.44	±	0
	clay content	[%]	29.54	±	8
	silt content	[%]	40.54	±	8
experimental	diversity level		0,1,2,3,6		
	plot size	[m^2]	5^2, 10^2, 20^2, 40^2		
	CV tree height		0.46	±	0
	max tree height	[m]	4.89	±	2

Note: For diversity level and tree island size, categories are given.

Determinants of inside-plot yields

Considering the regression results on the influence of agro-ecological and experimental variables on inside-plot oil-palm yields (Table 4.3), the minimum adequate model (AICc=263.7) receives better model support than the full model (AICc=270.2) and explains 86% of the variation in yields. Oil-palm height, as a proxy for oil palm age, emerges as the most important predictor of yields, with an almost six-fold higher influence on yields compared to the second most important variables. The positive sign indicates that increasing height (and thus age) of oil palms is associated with higher oil-palm yields. Other agro-ecological variables that significantly contribute to explaining inside-plot yields include soil carbon content and bulk density, both having a positive influence on yields. With respect to the variables that we modified in the experiment, plot size and canopy openness have significantly positive effects, whereas maximum tree height has a significantly negative effect on per-oil palm yields inside the plots.

Table 4.3 | Results of linear models on inside-plot yields.

variable		full model (R^2_{adj}=0.84, AIC=270.2)		minimum adequate model (R^2_{adj}=0.86, AIC=263.7)	
group	name	estimate ± se	p	estimate ± se	p
oil palm	OP height	158.6 ± 20	***	133.5 ± 12	***
site specific	elevation	4.5 ± 4	0.31		
	slope	2.8 ± 5	0.55		
	canopy openness	19.6 ± 5	***	18.2 ± 4	***
	bulk density	13.3 ± 6	*	13.8 ± 3	***
	C content	24.2 ± 7	**	19.7 ± 3	***
	pH	-2.8 ± 4	0.48		
	clay content	2.3 ± 4	0.57		
	silt content	-1.5 ± 4	0.68		
experi-mental	diversity level	4.5 ± 7	0.53		
	plot size	24.3 ± 4	***	23.3 ± 4	***
	CV tree height	5.8 ± 9	0.51		
	max tree height	-23.6 ± 9	**	-14.2 ± 3	***

*Note: Significance levels are indicated by *($p \leq 0.05$), **($p \leq 0.01$) and ***($p \leq 0.001$).*

Spillover effects of the experimental treatments on adjacent-to-plot yields

In the following, we first describe the general plot effect (Figure 4.2 A) by comparing inside-plot yields with adjacent-to-plot yields, and thereafter focus on spillover effects to adjacent-to-plot yields (Figure 4.2 B-D).

We find a positive general plot effect with significantly higher inside-plot yields per oil palm compared to adjacent-to-plot yields ($p<0.001$) and to the plantation average ($p<0.001$). Adjacent-to-plot yields, in contrast, do not significantly differ from the plantation average ($p>0.1$, Figure 4.2 A). With an average value of 224.1 kg/OP/year, inside-plot yields are 36.1% higher than average adjacent-to-plot yields (164.7 kg/OP/year), and 40.9% higher compared to the plantation average of 159 kg/OP/year.

Furthermore, we find positive spillover effects: adjacent-to-plot yields decrease with increasing distance to the experimental plots (Figure 4.2 B). Adjacent-to-plot yields at position one are significantly higher compared to position two ($p<0.001$) and compared to position three ($p<0.01$). With a mean of 192.2 kg/OP/year at position one, yields are on average 31.2% higher than at position two (mean 146.5 kg/OP/year) and 23.7% higher than at position three (mean 155.4 kg/OP/year). Yields at distance position one are also significantly higher than the plantation average ($p<0.01$). Yields at distance position two do not differ significantly from distance position three ($p>0.1$), and neither of them differ from the plantation average ($p>0.1$ and $p>0.1$, respectively) (Figure 4.2 B).

There is no significant effect of tree enrichment on adjacent-to-plot yields (Figure 4.2 C): yields adjacent to plots with experimental trees (mean 165.3 kg/OP/year) are not significantly different ($p>0.1$) from yields adjacent to plots where no trees were planted (mean 157.8 kg/OP/year), and both mean values do not significantly differ from the plantation average ($p>0.1$ and $p>0.1$, respectively) (Figure 4.2 C). Furthermore, the effect of planted trees does not differ across distance positions one, two, and three (not shown in the figure).

Thinning of oil palms within the tree islands induces positive spillover effects (Figure 4.2 D): yields adjacent to plots where thinning took place (mean 173.0 kg/OP/year) are significantly higher ($p<0.05$) than yields adjacent to plots where no oil palms were removed (mean 139.7 kg/OP/year, Figure 4.2 D) and also significantly higher than the plantation average ($p<0.1$). Yields adjacent to plots without thinning in turn are not statistically different from the plantation average ($p>0.1$). Also, the effect of thinning does not differ across distance positions one, two, and three (not shown in the figure).

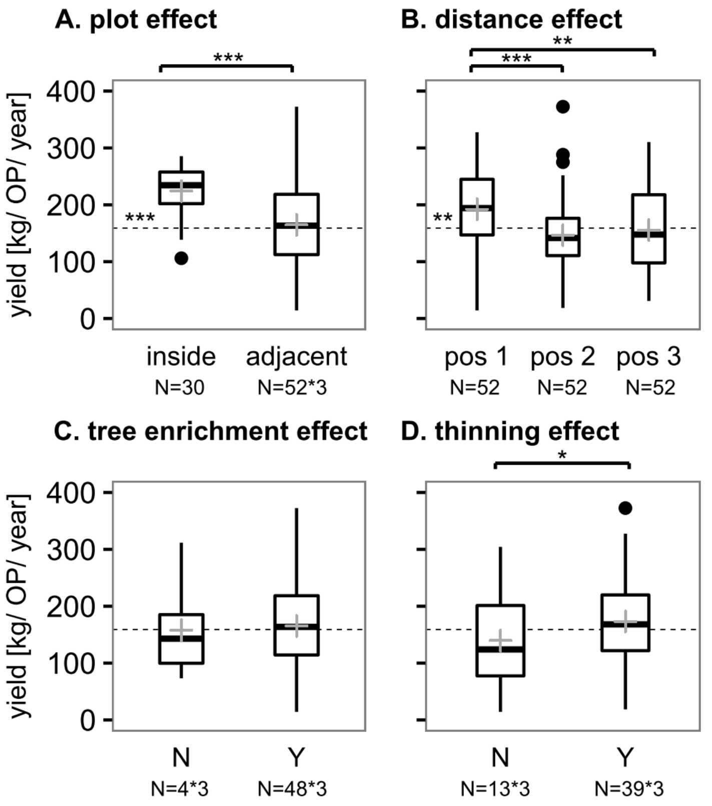

Figure 4.2 | Yields are positively affected by the experimental treatment. Panel A shows the overall plot effect, with inside-plot yields being significantly higher (plots with remaining oil palms: N=31) than adjacent-to-plot yields (per plot (N=52) three adjacent palms (*3)) and to the plantation average (horizontal dashed line, panel A). Panel B shows the distance effect to the experimental plots on yields: yields in short distances (position 1), are significantly higher than yields in positions 2 and 3 (N=52 respectively) and higher than the plantation average (horizontal dashed line). Panel C shows that tree planting has no significant effect on yields (three palms (*3) adjacent to plots without (N=4), and to plots with trees planted (N=48)), and none of the groups differs from the plantation average (horizontal dashed line). Panel D shows a positive thinning effect: yields adjacent to plots where thinning was undertaken (per plot (N=39) three palms (*3)) are significantly higher than yields adjacent to plots where no oil palm was removed (per plot (N=13) three palms (*3)), but none of the groups differ from the planation average (horizontal dashed line). Values of all subgroups are presented in boxplots with the median as continuous line and a "+" symbolizing the mean, the box showing the 25- and 75-percentiles, and the whiskers representing the lowest and the highest value within 1.5 times the inter-quartile range, respectively. Data beyond the end of the whiskers are outliers and plotted as points. Significance levels are indicated by * ($p<0.05$), ** ($p<0.01$), *** ($p<0.001$).

Estimated net changes in yields at plot level

We first estimate three distinct components of yield changes associated with the experiment, i.e., the yield foregone due to oil palm removal, the changes in yield inside the plots, and the spillover effects on yields adjacent to the plots (Figure 4.3 A-C). Based on these estimates, we analyze net yield changes at the plot scale (Figure 4.3 D).

Yield foregone per plot starts at zero for 25 m² plots (because no oil palms were removed) and then increases with plot size due to an increasing number of oil palms removed (Figure 4.3 A). Similarly, the changes in inside-plot yield (Figure 4.3 B) are zero for 25 m² plots (because no oil palms grow on these plots). The changes in inside-plot-yield (Figure 4.3 B) and the spillover effects on adjacent-to-plot yield (Figure 4.3 C) both increase with plot size. As a result, the average net yield effects of the experiment also increase with plot size. The net yield changes of the three smallest plot size classes (25, 100, and 400 m²) do not significantly differ from zero ($p>0.1$), implying neither losses nor gains on the average. For the largest plots (1600 m²), the average net yield change significantly differs from zero ($p<0.05$) and is positive with an average gain of more than 1,000 kg/plot including spillover-effects (Figure 4.3 D). It should be noted that the variance of plot-level estimates increases with plot size, thus also leading to increasing uncertainty in the magnitude of yield gains (Figure 4.3 D). In all plot size classes, we find some plots with negative net yield effects.

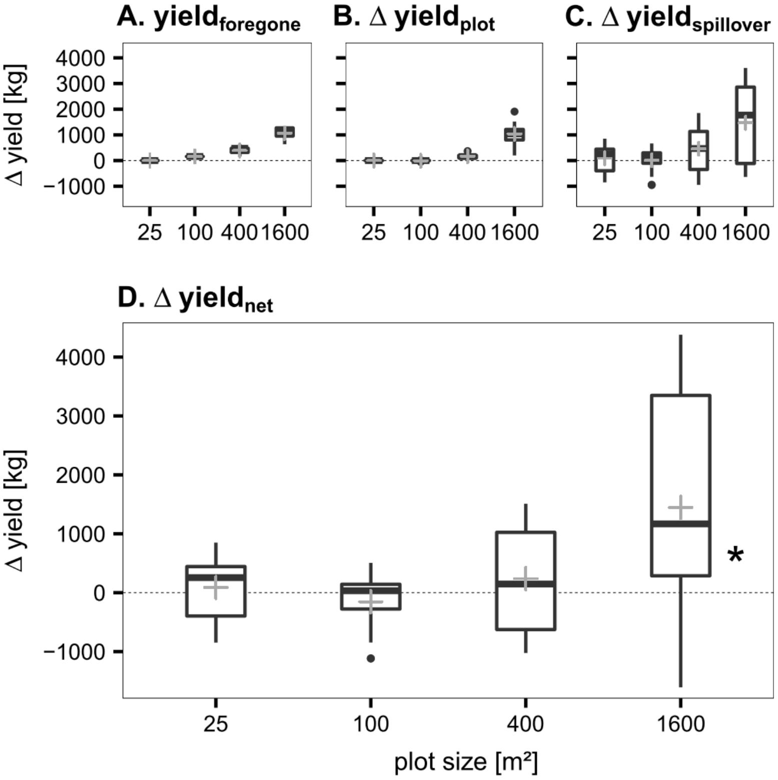

Figure 4.3 | Economic evaluation of yield changes induced by the experimental treatment. Panel A shows the estimated values of inside-plot yield loss due to oil-palm thinning, panel B of the inside-plot yield gain of the remaining oil palms and panel C of the adjacent-to-plot yield gain, all against the plot size. Panel D shows the resulting values of the sum of inside-plot (Panel B) and adjacent-to-plot yield changes (Panel C) minus inside-plot yield losses (Panel A) against the plot size. Values of all subgroups are presented in boxplots with the median as continuous line and a "+" symbolizing the mean, the box showing the 25- and 75-percentiles, and the whiskers representing the lowest and the highest value within 1.5 times the inter-quartile range, respectively. Data beyond the end of the whiskers are outliers and plotted as points. Each subgroup was tested against zero (dashed horizontal line), and resulting significance levels are indicated by * ($p<0.05$), ** ($p<0.01$), *** ($p<0.001$).

4.5 Discussion

Our study finds an initial increase in oil-palm yields inside the experimental tree enrichment plots in the EFForTS-BEE. Furthermore, we find positive spillover effects on yields of adjacent oil palms (Figure 4.2 A, B). Despite the yield foregone resulting from the removal of oil palms to plant trees, the estimated net yield changes per plot including spillover effects are unlikely to be negative, with overall neutral to positive effects, in particular for larger plots (Figure 4.3 D).

Generally, a trade-off is assumed between economic and ecological functions in oil palm cultivation, i.e., if farmers seek to improve ecological functions in their plantation, they need to sacrifice economic returns (Phalan et al., 2009). Our results indicate that, at least during the initial phase of the biodiversity enrichment experiment, this trade-off may not exist (Figure 4.3). In our study, we clearly find an increase in yields of the remaining oil palms, which is likely to at least compensate for the economic losses from removing oil palms. It is particularly noteworthy that these results were obtained despite a total stop of fertilizer, herbicide and pesticide applications on the experimental plots. Most likely, the increase in yields can be associated with thinning, leading to increased availability of light, nutrients and water (Table 4.3, Figure 4.2 D).

This is in line with previous findings showing that oil palms planted at low densities are more productive (Corley and Tinker, 2003; Henson and Dolmat, 2003; Nazeeb et al., 2008). Currently, the recommended planting scheme is 9 x 7.8 m resulting in a density of ~143 OP/ha (FAO, 1977). The recommended planting density is a compromise between different optima varying with age, and results from the highest cumulative yield over the lifespan of an oil palm. Yet, to maximize the yields on a hectare basis, Nazeeb et al. (2008) suggest high planting densities for young oil palms and thinning once the oil palms are fully developed. Regarding the results of our study, thinning is among the experimental factors that positively affect the productivity per oil palm. However, our data suggests that the net yield effect is only neutral to positive when also taking into account spillover effects on the plantation under management-as-usual, where no thinning took place. Furthermore, other factors related to the experiment may have also contributed to the yield increase.

Only two years after the establishment, our results represent the initial phase of the biodiversity enrichment experiment. As trees grow older, competition between trees and palms for water, nutrients and light is expected to increase and may lead to a reduction in oil-palm yields inside and also adjacent to the experimental plots. The significant negative effect of maximum tree height on inside-plot yields (Table 4.3) possibly indicates that this competition has already started. On the other hand, in other cropping systems, previous studies have shown that tree enrichment also has the potential to induce ecological benefits such as improved soil fertility, particularly when nitrogen fixing species are planted, reduced nutrient leaching and water run-off (Schroth et al., 2001), biological pest control, and a more favorable microclimate due to a more complex structure (Tscharntke et al., 2011). Such factors could enhance the ecosystem functioning in the oil-palm plantation and thus positively affect oil-palm productivity. In our experiment, there is no detectable impact of overall tree planting (Figure 4.2 C) and diversity level of the planted trees (Table 4.3) on oil-palm yields at this stage. The positive influence of plot size (Table 4.3) can probably be traced back to a higher number of removed oil palms around the remaining oil palms in larger plots, leading to an overall enhancement of resource availability. However, we also find higher yields at position 1 compared to 2 and 3 adjacent to plots where no oil palms were removed, indicating that the enhanced resource availability is not the only trigger among the experimental factors. We expect that over time potential effects related to tree planting will become more pronounced.

Currently, the neutralizing to positive net yield effects result exclusively from yield increases of the remaining oil palms. While these effects may or may not last in the long term (as discussed in the previous paragraph), direct benefits will sooner or later also accrue from the planted trees. The expected harvestable age of these trees ranges from approximately five years for the fruits of *Parkia speciosa* (Wiriadinata and Bamroongrugsa, 1994) to 30-35 years until tapping of *Dyera polyphylla* (Rudjiman et al., 1995). These benefits could then directly compensate potential losses in oil-palm yield. Furthermore, crop diversification could reduce the risk of large income fluctuations, help to increase the resilience to climate and other environmental change, and improve food security and nutritional quality for the local population. The long maturation periods of trees may be perceived as a barrier for cash-constrained (small-scale) farmers to adopt tree planting. In this context, our results of initial increases in oil-palm productivity in the enrichment plots are especially encouraging as they can buffer economic losses during the transition phase.

Presenting first results of a randomized experiment implemented under demanding conditions in rural Sumatra, some data limitations apply. In particular, given initial monitoring challenges in the first five months of data collection, the adjacent-to-plot oil palms may have been harvested occasionally in the usual plantation-management routine without weighing. While this would not affect the comparability between the three adjacent oil palms in different distance positions, it may lead to a slight underestimation of the adjacent-to-plot yields compared to the inside-plot yields. Yet, due to the pronounced difference between inside-plot and adjacent-to-plot yields (Figure 4.2 A) and the significantly higher yields in position 1 compared to position 2 and 3 (Figure 4.2 B), it is unlikely that such measurement error would change the general picture. Furthermore, the fact that the inside-plot yields as well as the yields in position 1 (Figures 4.2 A, B) are significantly higher than the plantation average, the control measure for yields under management-as-usual, confirm the results.

4.6 Conclusion

Our study provides evidence that biodiversity enrichment in oil palm can generate synergies between economic and ecological functions under certain conditions. In the initial phase, EFForTS-BEE significantly increased yields per oil palm, which at the plot scale even compensated for the yield losses from oil-palm removal. In our analysis of net yield changes, we find an overall neutral effect on yields for small plots and a very variable, but overall significantly positive effect for large plots (Figure 4.3). Given initial signs of a negative influence of high trees on oil palm yields, this positive effect may change in the long term. However, the results of this study are encouraging for further research aiming to identify more diversified management strategies for oil palm plantations that reconcile ecological and economic benefits. Such strategies could contribute to rehabilitate ecosystem functioning and increase local livelihood resilience in the face of world market price fluctuations and environmental change. Future results of our experiment will shed more light on whether tree islands are suitable to diversify the oil-palm landscape, and if so, which management strategies specifically.

4.7 Acknowledgements

We thank the following persons and organizations for granting us access to and use of their properties: PT Humusindo Makmur Sejati and Pak Hasbi and his family. Special thanks to Andi and Pak Dasam for their commitment and good work in the field. We thank the people in the lab in Palu, and in the Indonesian Institute of Science (LIPI), for assisting with analyses of samples. Thanks to Philip Beckschäfer who helped us processing the hemispherical photographs. We are grateful for the logistical support by the EFForTS staff and coordination. This study was financed by the Deutsche Forschungsgemeinschaft (DFG) in the framework of the collaborative German - Indonesian research project Collaborative Research Centre 990 EFForTS.

5 Synthesis

5.1 Framework of this thesis

Designer landscapes that reconcile ecological conservation and socio-economic structures have been proposed to reduce the negative impacts of monoculture oil-palm plantations (Koh et al., 2009), which hold, compared with forests, only a fraction of biodiversity and ecosystems functioning (Dislich et al., 2016; Drescher et al., 2016; Fitzherbert et al., 2008; Foster et al., 2011). However, where land conversion has already taken place, this can only be achieved through restoration measures, but knowledge on the effectiveness of such measures is lacking.

To gather such knowledge, I established a large-scale, long-term biodiversity enrichment experiment within an oil-palm-dominated landscape with colleagues from Germany and Indonesia. In my thesis, I report on the successful establishment of a biodiversity enrichment experiment (EFForTS-BEE) during its critical initial phase. I take into account ecological and socio-economic aspects, and hence give a broad picture of initial impacts induced by the experiment.

5.2 Establishment of the experiment and initial effects

The experimental site, a medium-scale oil-palm plantation, is embedded in an intensively managed oil-palm and rubber-dominated landscape, making it ideal to study long-term effects of biodiversity enrichment (chapter 2). I show that the experimental site I chose together with my colleagues is representative for other oil-palm plantations in the region, making results transferable. High statistical quality of analyses is given, as all experimental plots are largely independent from each other. This is particularly crucial for the future, as it qualifies the translation of insights gained from our experiment to more general management guidelines.

Effects on birds and invertebrates

Interestingly, effects of the enrichment plantings on the bird and invertebrate fauna were already significant one year after the establishment (chapter 2). Bird richness was higher on plots planted with trees compared to the oil-palm plantation under management as usual, but the experimentally altered variables plot size and diversity level had no effect on birds. Invertebrates, in contrast, also responded positively to plot size. For invertebrates, small-scale changes seem to be more crucial than for birds; the combination of a stop of fertilizer and pesticide application, changes in the light environment, and new small-scale habitat structures through the planted trees (see Pywell et al., 2012; Tscharntke et al., 2011) might explain the increase in invertebrate richness. Both organism groups fulfill many tasks that are essential for ecosystem functioning, including e.g. litter decomposition and predation for invertebrates; pollination and herbivory for both organism groups; and seed dispersal particularly for birds (Ewers et al., 2015; Sekercioğlu, 2006). Thus, an increase in bird and invertebrate richness is important to initiate the development of novel ecosystems.

The role of species identity for tree performance

I show that most planted trees established successfully within the two initial years of the experiment (chapter 3). However, I found large differences between the species regarding their performance: some species such as *D. polyphylla* and *D. zibethinus* had low survival rates as well as low relative height and basal area increment, which was, in all respects, contrary to *A. pauciflorum*, *P. speciosa*, and *P. canescens.* Only for *S. leprosula*, the picture was less clear. These differences in performance may be due to species-specific autecological properties, which are likely to be strong determinants for the establishment success (Günter et al., 2009).

Many ecosystem properties in oil-palm plantations are altered compared with forests (Allen et al., 2015; Drescher et al., 2016; Guillaume et al., 2015). Therefore, choosing suitable multi-purpose native tree species was challenging, as few knowledge existed on the species' abilities to grow under these conditions. Some individuals of each species established well in the oil-palm plantation. However, the overall performance seemed to be better for species that are not restricted to primary forests, or, like the worst performing species *Dyera polyphylla*, to swamp forests. Originally, we had chosen *Dyera costulata* for the experiment, which is adapted to mineral soils, but was unfortunately not available in the local tree nurseries. At another site in the region, *D. polyphylla* was reported to establish well, and a few individuals indeed performed well at the experimental site. Furthermore, opportunity costs for restoration measures could be reduced at sites where oil palms are less productive. For example, the oil palm does not tolerate sites where water stagnates above the soil surface (Corley and Tinker, 2003). At such sites, *D. polyphylla* could be more suitable than the other experimentally planted species.

Hence, based on my results from the initial phase, I conclude that species seem to be mostly well-chosen and that they are promising to add knowledge on biodiversity enrichment in oil-palm plantations with regard to different aspects. Now that the trees have established, a fruitful future of the experiment, which stands and falls with the planted trees, is most likely.

Neighborhood effects and the influence of experimentally altered variables on tree performance

On plot level, site conditions, plot size, and diversity level were weak but significant predictors for tree growth and survival. The most important determinant was diversity level with a significant positive effect on tree survival, and, contrary to my expectations, a significant negative effect on growth parameters (chapter 2). An improved tree physiological efficiency (Richards et al., 2010) and altered ecosystem properties and processes (Bruelheide et al., 2014) in mixed-species stands compared to monocultures enhanced tree growth in other studies (e.g., Erskine et al., 2006; Ewel et al., 2015; Kirui et al., 2012; Potvin and Gotelli, 2008). In our experiment, such positive diversity effects may become more pronounced in the future as trees grow older and interactions between the trees increase due to scarcity of resources (Peet and Christensen, 1987); though positive and negative neighborhood effects among planted tree species were already significant, the effect sizes were, so far, in most cases weak. Likewise, I expect the significantly negative, yet weak neighborhood effects between oil palms and the planted trees, which may indicate starting competition, to become more pronounced in the future. The evaluation of such interactions will be an important information on the suitability of the species to grow with oil palms.

Linkage between planted trees and associated biodiversity

The planted trees increase the structural heterogeneity in the oil-palm plantation, which is key to maintain high levels of species diversity (Stein et al., 2014; Teuscher et al., 2015). After the first study year, during which changes in bird and invertebrate richness were investigated (chapter 2), I observed a further increase in structural heterogeneity: maximum tree height had augmented from over four meters after the first year (chapter 2) to more than nine meters after two years, with a large variance between species and individuals (chapter 3). Compared to the oil-palm plantation under management-as-usual, I observed a higher litter accumulation in the experimental sites, which could benefit invertebrate diversity (e.g. Clough et al., 2011). Birds quickly occupied the newly created habitat: I observed several nests in the planted trees. One individual of the species *P. canescens* has already started flowering which may attract pollinators. In conclusion, based on the initial ecological effects together with the observed increase in structural heterogeneity, it seems likely that species richness on the experimental plots will further increase in the future.

Effects on oil-palm yields in the initial phase

Livelihoods and incomes of many Indonesian farmers have improved by adopting oil-palm cultivation (Euler et al., 2015a; Feintrenie et al., 2010) and these improvements should not be jeopardized by conservation or restoration interventions. In our experiment, I surprisingly found an increase in yield per remaining oil palm at the experimental tree islands and adjacent oil palms compared to oil palms under management-as-usual (chapter 4). Taking into account opportunity costs induced by oil palm thinning, increases in inside-plot yield and adjacent-to-plot yields, I found an overall net neutral to positive effect of the establishment of one experimental plot on oil-palm yields, respectively. Most probably, the increase in yields can generally be associated with thinning, leading to increased availability of light, nutrients and water per remaining oil palm. This was contrary to my expectations, particularly because the experimental treatment comprised a total halt of fertilizer, herbicide and pesticide application at the experimental plots. Furthermore, many scientists have questioned the economic viability of oil palms in mixed-species stands (Corley and Tinker, 2003; Koh et al., 2009; Phalan et al., 2009). These results are highly interesting and may advance the ongoing scientific debate about the profitability of oil palms in mixed-species stands (Bhagwat and Willis, 2008; Phalan et al., 2009).

Possible future economic output of the tree islands

The main long-term motivation for the experiment is to have a real impact on agricultural practices. Given these positive results of my study there is hope that diversifying management strategies may be adopted by local farmers, since to them, opportunity costs, i.e. losses in oil-palm yield, may be the biggest hindrance to diversification. However, the net zero to positive effect on oil-palm yields that I found in the initial years of the experiment may change over time: tall neighboring trees negatively affect oil-palm yields (chapter 3), and reversely, oil palms in the close vicinity negatively affects the performance of almost all tree species (chapter 4). Though the influence of positive determinants on oil-palm yields so far outweigh these negative effects, their significance suggest that competition could reduce economic gains in the long term. As these effects may be species-specific, some species may be more profitable to grow with oil palms than others. In the future, possible oil-palm yield reductions need to be counterbalanced with the direct economic benefits gained from the planted tree species and possible gains in ecosystem functioning and ecosystem services (Schroth et al., 2001; Tscharntke et al., 2011), which may or may not be translatable to monetary values. Further research will shed light on the species-specific benefits that can be gained from the ecological and the socio-economic point of view, and allow an evaluation on the suitability of the chosen tree species.

5.3 Limitations of my study

Initial effects were stronger and, particularly from the economic point of view, more beneficial than I had expected. However, so far, I observed mostly weak neighborhood effects and the experimentally altered variables, i.e. plot size and diversity level of planted trees, did not strongly affect ecological processes (chapters 2-4). This might be owing to the short time that has passed since tree planting. During my study period, some ecological key processes have not yet shown up, which may have limited the effects of the planted trees on the associated ecosystem and economics.

Although, to date, some trees are already surprisingly tall, their crowns and root systems have not yet fully developed. Shade provision may increase with crown expansion, which can alter microclimatic conditions and soil properties (Tscharntke et al., 2011). Interactions may not yet be pronounced to the extent that trees, including oil palms, influence each other with scarcer access to resources (Peet and Christensen, 1987). Thus, arising competition, complementarity, and facilitation between tree species including oil palms may induce new negative or positive ecological and economic effects, which I cannot predict yet. So far, only one tree individual has started flowering and may soon produce fruits. In the future, when all other trees will start with fruit production, economic gains from the planted trees will be measurable. Furthermore, with flowering and fruiting, new food sources may open up and attract animals. Once seed-dispersing bats and birds are attracted from longer distances, the seed bank in the plantation could become substantially enriched (Sekercioğlu, 2006; Wunderle, 1997). Currently, a lack of seed diversity in the oil-palm plantation may be a main limitation for the development of novel ecosystems in the experimental islands: seeds collected in seed traps that I established during my field studies to analyze seed rain mainly originated from the non-native species *Asystasia gangetica,* a frequent plant on the experimental plots (chapter 2).

In conclusion, several years may need to go by until novel ecosystems will have developed and until the overall socio-economic consequences will be measurable at the plantation scale. A study period of two years since tree planting did not allow me to fully evaluate the suitability of certain tree species, compositions, plot sizes or diversity levels, and, moreover, to draw conclusions on the overall restoration success of the experiment. Additional aspects beyond the scope of my thesis, such as the microclimate, the water-use efficiency, the soil seed bank, genetic and microbial diversity, herbivory, and more animal groups, need to be investigated. An extensive long-term monitoring is necessary to obtain results that qualify for an overall evaluation of the experiment. Before that, quantification of trade-offs between losses and benefits in the economic and the ecological point of view is strongly limited.

5.4 Challenges owing to the experimental design

Analyses of data collected in the experimental tree islands can be challenging owing to the experimental design, which is, according to Bell et al. (2009), not full-factorial. Moreover, we did not repeat the set of plot-specific combinations of plot size, diversity level, and species composition in our experiment, as this would have resulted in a high number of plots and thus hinder the implementation of the experiment. It is therefore obligatory to include every plot in the overall analyses. This can be difficult if, e.g., all trees of one plot die, or measurement errors occur, which would reasonably justify the exclusion of certain data points. As suggested by Bell et al. (2009), statistical analyses to test the influences of plot size, diversity level and species composition can only be done using linear models. This is challenging when the data basis does not suggest linearity.

The location of the experiment within the landscape represents a further challenge. In the concept of designer landscapes as suggested by Koh et al. (2009), buffer zones interconnect areas of high conservation value. Unfortunately, this is not the case for the experimental tree islands, which are far away from forest patches. Otherwise, they could act as "stepping stones" between such forest patches. A small nearby patch of logged-over forest had considerably diminished during my study period and was replaced by oil palms. The large distance to forest may be a serious obstacle for the migration of animals (Wunderle, 1997): animals would have to traverse large distances of monoculture oil-palm and rubber plantations to reach the tree islands. It is therefore difficult to integrate our experiment to a landscape context.

Furthermore, the experiment combines a range of concepts and theories, requiring conceptual compromises in some aspects. The economic profitability of the planted trees, as determined in the experiment, may not reflect the farmers' real-life conditions, given the total stop of fertilizer, pesticide, and herbicide application in the experimental plots, which is unlikely to be followed by farmers. As full succession is allowed, a dense understory vegetation layer may evolve, which may complicate the harvest process. Therefore, unmodified adoption of the experimental approach by farmers is questionable.

5.5 The potential of the experiment

The aforesaid challenges that result from the experimental design do not lessen the importance of the experiment. The experimental approach is novel and highly innovative, as it integrates existing knowledge and a range of theories into restoration science. First, the approach integrates the promising but rarely tested concept of planting tree islands within managed land as a potentially area-effective component to enrich biota (Rey Benayas et al., 2008). Second, the experimental approach makes use of the positive relationship between biodiversity and ecosystem functioning, which has to date only slowly found its way into restoration science (Aerts and Honnay, 2011), though restoration goals may thus be achieved faster. Third, as suggested by Lamb et al. (2005), planting native multi-purpose trees in restoration measures has generally the potential to satisfy livelihoods and to add ecological benefits simultaneously. However, the economic profitability of oil palms in mixed-species stands has generally been questioned (Corley and Tinker, 2003; Phalan et al., 2009). Therefore, the overarching questions may contribute to find answers to a large number of open questions that are relevant beyond oil-palm-dominated landscapes, such as: how many species need to be planted to gain a significant increase in ecosystem functioning? Which species composition and island size is the most effective? What are the trade-offs between an increase in ecosystem functioning and socio-economics?

To my knowledge, this experiment is among the first to test ecological restoration in existing agricultural landscapes, and, specifically, the first to test biodiversity enrichment in oil-palm-dominated landscapes. Gathering basic knowledge is crucial to find out the relevant aspects where further research is needed and reasonable, and is the basis to deepen the knowledge on such relevant aspects.

5.6 Outlook and further research

Large-scale planting of exotic and economically relevant tree species was traditionally considered a valid restoration strategy in the tropics but contributed little to improve ecosystem functioning (Lamb et al., 2005). Novel approaches are needed that take the positive relationship of biodiversity and ecosystem functioning into account (Aerts and Honnay, 2011). This is particularly urgent in existing agricultural landscapes, as croplands cover ~40% of the global land surface and contribute dramatically to the global decline in ecosystem functioning and services (Foley, 2005). Oil-palm cultivation in South-East Asia is just one example (Dislich et al., 2016).

Since a further increase of area under oil-palm cultivation is projected (Fitzherbert et al., 2008), the pressure on biota restricted to rainforests will aggravate. Thus, knowledge on effective restoration in agricultural landscapes or reduced-impact farming strategies is becoming increasingly existential for maintaining or increasing biodiversity and ecosystem functioning (Rey Benayas and Bullock, 2012). The experiment that I present in my thesis has the potential to bridge knowledge gaps towards the elaboration of management guidelines for oil-palm landscapes that are both ecologically improved and economically viable. For a translation into management guidelines, extensive monitoring of upcoming changes in biodiversity, ecosystem processes, and ecosystem properties is required. The desired effect of tree islands is not constrained to the core area but includes ecological spillover effects to the directly surrounding oil-palm plantation under management-as-usual, which need to be quantified to allow an extensive evaluation. To upscale the results to the landscape scale, the experiment could be expanded to a larger area and thus interconnect areas of high conservation value. Outcomes of the experiments have the potential to be transferable to other land use systems, but this requires further research in the target system. As one part of the puzzle, the results of this thesis could advance restoration ecology, which is, in E.O. Wilson's words, "the means to end the great extinction spasm" (Wilson, 2001).

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7 Appendix

A Supplementary material to chapter 2

Appendix Table A.1 | Plot infos.

Plot ID	Latitude	Longitude	Plot size (m²)	Tree diversity level	Number of fruit tree species	Number of timber tree species
1	-1.941619	103.251905	1600	1	1	0
2	-1.941743	103.252978	400	3	2	1
3	-1.943296	103.251765	400	2	1	1
4	-1.943206	103.253171	100	1	0	1
5	-1.944778	103.251792	1600	1	1	0
6	-1.944615	103.253150	25	1	0	1
7	-1.944689	103.255158	1600	3	1	2
8	-1.945868	103.249106	25	1	0	1
9	-1.945784	103.250588	100	3	2	1
10	-1.945945	103.251840	400	0	0	0
11	-1.945896	103.253220	100	1	0	1
12	-1.945888	103.254342	400	1	1	0
13	-1.945911	103.255925	100	1	0	1
14	-1.947283	103.249167	100	1	1	0
15	-1.947151	103.250424	400	1	1	0
16	-1.947333	103.251907	25	3	2	1
17	-1.947338	103.253148	400	1	0	1
18	-1.947168	103.254498	25	2	0	1
19	-1.947317	103.255865	400	6	3	3
20	-1.947337	103.257347	100	1	1	0
21	-1.948628	103.247800	100	6	3	3
22	-1.948734	103.249137	25	2	1	1
23	-1.948868	103.251317	1600	6	3	3
24	-1.948381	103.254313	1600	2	1	1
25	-1.948656	103.255886	25	1	1	0
26	-1.948487	103.257201	1600	2	0	1
27	-1.949921	103.246436	100	2	1	1
28	-1.950023	103.247777	25	1	1	0
29	-1.949964	103.248967	1600	3	2	1
30	-1.949809	103.252968	400	1	0	1
31	-1.949966	103.254488	25	1	1	0
32	-1.949976	103.255904	100	2	1	1
33	-1.950016	103.257276	400	3	1	2
34	-1.951426	103.245068	100	2	1	1
35	-1.951823	103.246590	1600	0	0	0
36	-1.951060	103.247721	400	2	1	1
37	-1.951176	103.248844	100	0	0	0
38	-1.951715	103.250417	400	1	0	1
39	-1.951383	103.251800	25	2	2	0
40	-1.951366	103.257142	25	0	0	0
41	-1.952674	103.243797	100	1	1	0
42	-1.952757	103.244984	25	1	0	1
43	-1.949631	103.258593	1600	1	1	0
44	-1.952709	103.247815	25	3	1	2
45	-1.953066	103.248695	1600	1	0	1
46	-1.954422	103.242421	1600	2	2	0
47	-1.953952	103.243710	400	2	1	1

48	-1.954103	103.245204	100	3	1	2
49	-1.953998	103.246627	1600	1	0	1
50	-1.954061	103.247820	25	6	3	3
51	-1.954249	103.249144	400	1	1	0
52	-1.955189	103.243481	1600	1	0	1

Appendix Table A.2 | Length-mass regression parameters for calculation of individual body masses from measured body lengths. For damaged individuals where body length could not be measured, body mass was substituted by species median body mass or order median body mass (for species with single individuals). 'Taxon' and 'Group' specify which animals the presented regression has been used for in this study. Regressions were available from the literature that estimate both dry and fresh mass ('Mass type') for different taxa. Appendix Table A.4 presents the dry mass-fresh mass conversion, used to convert all estimated body masses to fresh mass. The equations and regression parameters, 'a' and 'b', are presented, as well as the size range the regressions were calculated from ('Min' and 'Max'). All regressions were taken from the literature ('Reference'), with different specific definitions of how body length was measured ('Details of body length measurement') and specificity of the given regression ('Regression specificity'). (Barnes et al. 2014; modified and extended)

Taxon	Group	Mass type	Equation M[mg], L[mm]	a	b	Min [mm]	Max [mm]	Reference	Details of body length measurement	Regression specificity
All insect taxa		Dry mass	M = a * (L)^b	0.035	2.173	0.9	17.6	Gruner (2003)	Tip of abdomen to end of head or carapace, excl. any appendages	Inferred, all insect taxa
All insect taxa		Dry mass	M = exp(a + b * log(L))	-3.628	2.494	2.13	54.51	Sample et al. (1993)	From frons to tip of abdomen excluding appendages	Inferred, all insect taxa
Araneae	Araneae < 2.5 Mm	Fresh mass	M = exp(a + b * log(L))	-1.958	2.746	0.56	2.5	Höfer and Ott (2009)	Edge of prosoma (without chelicerae) to edge of opisthosoma (excl spinnerets)	Group specific
Araneae	Hunting	Fresh mass	M = exp(a + b * log(L))	-2.108	3.017	0.67	36	Höfer and Ott (2009)	Edge of prosoma (without chelicerae) to edge of opisthosoma (excl spinnerets)	Group specific
Araneae	Web-Building	Fresh mass	M = exp(a + b * log(L))	-1.784	2.255	0.56	10.67	Höfer and Ott (2009)	Edge of prosoma (without chelicerae) to edge of opisthosoma (excl spinnerets)	Group specific
Araneae	Spiders Random	Fresh mass	M = exp(a + b * log(L))	-1.844	2.711	1.8	21.5	Edwards (1996)	Clypeus to tip of spinnerets	Group specific
Araneae	Anapidae	Fresh mass	M = exp(a + b * log(L))	-1.784	2.255	0.56	10.67	Höfer and Ott (2009)	Edge of prosoma (without chelicerae) to edge of opisthosoma (excl spinnerets)	Inferred, web-building
Araneae	Araneidae	Fresh mass	M = exp(a + b * log(L))	-1.923	2.923	2.10	21.20	Edwards (1996)	Clypeus to tip of spinnerets	Group specific
Araneae	Clubionidae	Fresh mass	M = exp(a + b * log(L))	-2.156	2.653	2.5	9	Edwards (1996)	Clypeus to tip of spinnerets	Group specific
Araneae	Corinnidae	Fresh mass	M = exp(a + b * log(L))	-2.108	3.017	0.67	36	Höfer and Ott (2009)	Edge of prosoma (without chelicerae) to edge of opisthosoma (excl spinnerets)	Inferred, hunting spiders
Araneae	Ctenidae	Fresh mass	M = exp(a + b * log(L))	-1.758	2.894	1.3	36	Höfer and Ott (2009)	Edge of prosoma (without chelicerae) to edge of opisthosoma (excl spinnerets)	Group specific
Araneae	Deinopidae	Fresh mass	M = exp(a + b * log(L))	-1.844	2.711	1.8	21.5	Edwards (1996)	Clypeus to tip of spinnerets	Inferred, spiders random sample
Araneae	Dysderidae	Fresh mass	M = exp(a + b * log(L))	-2.108	3.017	0.67	36	Höfer and Ott (2009)	Edge of prosoma (without chelicerae) to edge of opisthosoma (excl spinnerets)	Inferred, hunting spiders
Araneae	Gnaphosidae	Fresh mass	M = exp(a + b * log(L))	-2.83	3.055	3	13.1	Edwards (1996)	Clypeus to tip of spinnerets	Group specific
Araneae	Linyphiidae	Fresh mass	M = exp(a + b * log(L))	-1.892	2.754	1.5	5.5	Edwards (1996)	Clypeus to tip of spinnerets	Group specific
Araneae	Lycosidae	Fresh mass	M = exp(a + b * log(L))	-2.043	2.842	2	23.5	Edwards (1996)	Clypeus to tip of spinnerets	Group specific
Araneae	Miturgidae	Fresh mass	M = exp(a + b * log(L))	-2.83	3.055	3	13.1	Edwards (1996)	Clypeus to tip of spinnerets	Inferred, Gnaphosidae
Araneae	Mysmenidae	Fresh mass	M = exp(a + b * log(L))	-1.784	2.255	0.56	10.67	Höfer and Ott (2009)	Edge of prosoma (without chelicerae) to edge of opisthosoma (excl spinnerets)	Inferred, web-building
Araneae	Ochyroceratidae	Fresh mass	M = exp(a + b * log(L))	-1.784	2.255	0.56	10.67	Höfer and Ott (2009)	Edge of prosoma (without chelicerae) to edge of opisthosoma (excl spinnerets)	Inferred, web-building
Araneae	Oonopidae	Fresh mass	M = exp(a + b * log(L))	-2.039	2.666	0.67	2.5	Höfer and Ott (2009)	Edge of prosoma (without chelicerae) to edge of opisthosoma (excl spinnerets)	Group specific
Araneae	Oxyopidae	Fresh mass	M = exp(a + b * log(L))	-2.108	3.017	0.67	36	Höfer and Ott (2009)	Edge of prosoma (without chelicerae) to edge of opisthosoma (excl spinnerets)	Inferred, hunting spiders
Araneae	Philodromidae	Fresh mass	M = exp(a + b * log(L))	-1.985	2.940	2.50	8.60	Edwards (1996)	Clypeus to tip of spinnerets	Group specific

Araneae	Pholcidae	Fresh mass	M = exp(a + b * log(L))	-1.784	2.255	0.56	10.67	Höfer and Ott (2009)	Edge of prosoma (without chelicerae) to edge of opisthosoma (excl spinnerets)	Inferred, web-building
Araneau	Pisauridae	Fresh mass	M = exp(a + b * log(L))	-2.108	3.017	0.67	36	Höfer and Ott (2009)	Edge of prosoma (without chelicerae) to edge of opisthosoma (excl spinnerets)	Inferred, hunting spiders
Araneae	Salticidae	Fresh mass	M = exp(a + b * log(L))	-2.184	2.901	4.00	13.00	Edwards (1996)	Clypeus to tip of spinnerets	Group specific
Araneae	Sparassidae	Fresh mass	M = exp(a + b * log(L))	-2.108	3.017	0.67	36	Höfer and Ott (2009)	Edge of prosoma (without chelicerae) to edge of opisthosoma (excl spinnerets)	Inferred, hunting spiders
Araneae	Tetrablemmidae	Fresh mass	M = exp(a + b * log(L))	-2.039	2.666	0.67	2.5	Höfer and Ott (2009)	Edge of prosoma (without chelicerae) to edge of opisthosoma (excl spinnerets)	Inferred, Oonopidae
Araneae	Tetragnathidae	Fresh mass	M = exp(a + b * log(L))	-2.615	2.574	3.50	9.00	Edwards (1996)	Clypeus to tip of spinnerets	Group specific
Araneae	Theridiidae	Fresh mass	M = exp(a + b * log(L))	-1.577	2.907	1.50	7.50	Edwards (1996)	Clypeus to tip of spinnerets	Group specific
Araneae	Theridiosomatidae	Fresh mass	M = exp(a + b * log(L))	-1.784	2.255	0.56	10.67	Höfer and Ott (2009)	Edge of prosoma (without chelicerae) to edge of opisthosoma (excl spinnerets)	Inferred, web-building
Araneae	Thomisidae	Fresh mass	M = exp(a + b * log(L))	-1.644	2.973	1.80	8.00	Edwards (1996)	Clypeus to tip of spinnerets	Group specific
Araneae	Zodariidae	Fresh mass	M = exp(a + b * log(L))	-2.108	3.017	0.67	36	Höfer and Ott (2009)	Edge of prosoma (without chelicerae) to edge of opisthosoma (excl spinnerets)	Inferred, hunting spiders
Blattodea	Blaberidae	Dry mass	M = exp(a + b * log(L))	-3.980	2.760	2.20	14.00	Wardhaugh (2013)	Front of labrum to tip of abdomen (excl. cerci or ovipositors) or tip of elytra (longest)	Inferred, Blattodea
Blattodea	Blattellidae	Dry mass	M = exp(a + b * log(L))	-3.980	2.760	2.20	14.00	Wardhaugh (2013)	Front of labrum to tip of abdomen (excl. cerci or ovipositors) or tip of elytra (longest)	Inferred, Blattodea
Blattodea	Blattidae	Dry mass	M = exp(a + b * log(L))	-3.980	2.760	2.20	14.00	Wardhaugh (2013)	Front of labrum to tip of abdomen (excl. cerci or ovipositors) or tip of elytra (longest)	Inferred, Blattodea
Coleoptera	Aderidae	Dry mass	M = exp(a + b * log(L))	-3.247	2.492	3.34	34.82	Sample et al. (1993)	From frons to tip of abdomen excluding appendages	Inferred, Coleoptera
Coleoptera	Anthicidae	Dry mass	M = exp(a + b * log(L))	-3.247	2.492	3.34	34.82	Sample et al. (1993)	From frons to tip of abdomen excluding appendages	Inferred, Coleoptera
Coleoptera	Anthribidae	Dry mass	M = exp(a + b * log(L))	-3.247	2.492	3.34	34.82	Sample et al. (1993)	From frons to tip of abdomen excluding appendages	Inferred, Coleoptera
Coleoptera	Carabidae	Dry mass	M = a * L^b	0.0237	2.7054	2.88	24	Lang et al. (1997)	Measured from anterior tip of head to posterior of abdomen excluding any appendages	Group specific
Coleoptera	Chrysomelidae	Dry mass	M = exp(a + b * log(L))	-2.427	2.171	3.34	7.84	Sample et al. (1993)	From frons to tip of abdomen excluding appendages	Group specific
Coleoptera	Corylophidae	Dry mass	M = exp(a + b * log(L))	-3.247	2.492	3.34	34.82	Sample et al. (1993)	From frons to tip of abdomen excluding appendages	Inferred, Coleoptera
Coleoptera	Colydiidae	Dry mass	M = exp(a + b * log(L))	-3.247	2.492	3.34	34.82	Sample et al. (1993)	From frons to tip of abdomen excluding appendages	Inferred, Coleoptera
Coleoptera	Discolomidae	Dry mass	M = exp(a + b * log(L))	-3.247	2.492	3.34	34.82	Sample et al. (1993)	From frons to tip of abdomen excluding appendages	Inferred, Coleoptera
Coleoptera	Hydraenidae	Dry mass	M = exp(a + b * log(L))	-3.247	2.492	3.34	34.82	Sample et al. (1993)	From frons to tip of abdomen excluding appendages	Inferred, Coleoptera
Coleoptera	Lagrioidinae	Dry mass	M = exp(a + b * log(L))	-3.247	2.492	3.34	34.82	Sample et al. (1993)	From frons to tip of abdomen excluding appendages	Inferred, Coleoptera
Coleoptera	Pselaphidae	Dry mass	M = exp(a + b * log(L))	-3.247	2.492	3.34	34.82	Sample et al. (1993)	From frons to tip of abdomen excluding appendages	Inferred, Coleoptera
Coleoptera	Scolytidae	Dry mass	M = exp(a + b * log(L))	-3.247	2.492	3.34	34.82	Sample et al. (1993)	From frons to tip of abdomen excluding appendages	Inferred, Coleoptera
Coleoptera	Curculionidae	Dry mass	M = exp(a + b * log(L))	-3.247	2.492	3.34	34.82	Sample et al. (1993)	From frons to tip of abdomen excluding appendages	Inferred, Coleoptera
Coleoptera	Elateridae	Dry mass	M = a * L^b	0.0138	2.595	1.65	10.3	Gruner (2003)	Tip of abdomen to end of head or carapace, excl. any appendages	Inferred, slender beetles
Coleoptera	Nitidulidae	Dry mass	M = exp(a + b * log(L))	-3.247	2.492	3.34	34.82	Sample et al. (1993)	From frons to tip of abdomen excluding appendages	Inferred, Coleoptera
Coleoptera	Phalacridae	Dry mass	M = exp(a + b * log(L))	-3.247	2.492	3.34	34.82	Sample et al. (1993)	From frons to tip of abdomen excluding appendages	Inferred, Coleoptera
Coleoptera	Ptiliidae	Dry mass	M = exp(a + b * log(L))	-3.247	2.492	3.34	34.82	Sample et al. (1993)	From frons to tip of abdomen excluding appendages	Inferred, Coleoptera

Coleoptera	Scarabaeidae	Dry mass	M = exp(a + b * log(L))	-2.448	2.494	4.24	24.79	Sample et al. (1993)	From frons to tip of abdomen excluding appendages	Group specific
Coleoptera	Scydmaenidae	Dry mass	M = exp(a + b * log(L))	-3.247	2.492	3.34	34.82	Sample et al. (1993)	From frons to tip of abdomen excluding appendages	Inferred, Coleoptera
Coleoptera	Silvanidae	Dry mass	M = a * L^b	0.0138	2.595	1.65	10.3	Gruner (2003)	Tip of abdomen to end of head or carapace, excl. any appendages	Inferred, slender beetles
Coleoptera	Staphylinidae	Dry mass	M = a * L^b	0.0134	2.26	2.2	13.6	Lang et al. (1997)	Measured from anterior tip of head to posterior of abdomen excluding any appendages	Group specific
Coleoptera	Tenebrionidae	Dry mass	M = exp(a + b * log(L))	-0.043	1.2	5.65	13.39	Sample et al. (1993)	From frons to tip of abdomen excluding appendages	Group specific
Dermaptera	Anisolabididae	Dry mass	M = exp(a + b * log(L))	-3.628	2.494	2.13	54.51	Sample et al. (1993)	From frons to tip of abdomen excluding appendages	Inferred, all insect taxa
Dermaptera	Labiduridae	Dry mass	M = exp(a + b * log(L))	-3.628	2.494	2.13	54.51	Sample et al. (1993)	From frons to tip of abdomen excluding appendages	Inferred, all insect taxa
Dermaptera	Labiidae	Dry mass	M = exp(a + b * log(L))	-3.628	2.494	2.13	54.51	Sample et al. (1993)	From frons to tip of abdomen excluding appendages	Inferred, all insect taxa
Dermaptera	Spongiphoridae	Dry mass	M = exp(a + b * log(L))	-3.628	2.494	2.13	54.51	Sample et al. (1993)	From frons to tip of abdomen excluding appendages	Inferred, all insect taxa
Dermaptera	Uniden	Dry mass	M = exp(a + b * log(L))	-3.628	2.494	2.13	54.51	Sample et al. (1993)	From frons to tip of abdomen excluding appendages	Inferred, all insect taxa
Diplura	Campodeidae	Dry mass	M = a * (L)^b	0.034	2.191	0.9	17.6	Gruner (2003)	Tip of abdomen to end of head or carapace, excl. any appendages	Inferred, general arthropod
Diplura	Japygidae	Dry mass	M = a * (L)^b	0.034	2.191	0.9	17.6	Gruner (2003)	Tip of abdomen to end of head or carapace, excl. any appendages	Inferred, general arthropod
Diplura	Stratiopmydae	Dry mass	M = a * (L)^b	0.034	2.191	0.9	17.6	Gruner (2003)	Tip of abdomen to end of head or carapace, excl. any appendages	Inferred, general arthropod
Diplura	Uniden	Dry mass	M = a * (L)^b	0.034	2.191	0.9	17.6	Gruner (2003)	Tip of abdomen to end of head or carapace, excl. any appendages	Inferred, general arthropod
Diptera	Adults	Dry mass	M = a * (L)^b	0.0153	2.573	1.75	8.6	Gruner (2003)	Tip of abdomen to end of head or carapace, excl. any appendages	Original, Diptera adult
Diptera	Asteiidae	Dry mass	M = a * (L)^b	0.0153	2.573	1.75	8.6	Gruner (2003)	Tip of abdomen to end of head or carapace, excl. any appendages	Original, Diptera adult
Diptera	Bibionidae	Dry mass	M = a * (L)^b	0.035	2.173	0.9	17.6	Gruner (2003)	Tip of abdomen to end of head or carapace, excl. any appendages	Inferred, all insect taxa
Diptera	Calliphoridae	Dry mass	M = a * (L)^b	0.0153	2.573	1.75	8.6	Gruner (2003)	Tip of abdomen to end of head or carapace, excl. any appendages	Original, Diptera adult
Diptera	Cecidomyiidae	Dry mass	M = a * (L)^b	0.035	2.173	0.9	17.6	Gruner (2003)	Tip of abdomen to end of head or carapace, excl. any appendages	Inferred, all insect taxa
Diptera	Ceratopogonidae	Dry mass	M = a * (L)^b	0.0153	2.573	1.75	8.6	Gruner (2003)	Tip of abdomen to end of head or carapace, excl. any appendages	Original, Diptera adult
Diptera	Chironomidae	Dry mass	M = a * (L)^b	0.0153	2.573	1.75	8.6	Gruner (2003)	Tip of abdomen to end of head or carapace, excl. any appendages	Original, Diptera adult
Diptera	Chloropidae	Dry mass	M = a * (L)^b	0.0153	2.573	1.75	8.6	Gruner (2003)	Tip of abdomen to end of head or carapace, excl. any appendages	Original, Diptera adult
Diptera	Clusiidae	Dry mass	M = a * (L)^b	0.0153	2.573	1.75	8.6	Gruner (2003)	Tip of abdomen to end of head or carapace, excl. any appendages	Original, Diptera adult
Diptera	Culicidae	Dry mass	M = a * (L)^b	0.0153	2.573	1.75	8.6	Gruner (2003)	Tip of abdomen to end of head or carapace, excl. any appendages	Original, Diptera adult
Diptera	Deuterophlebiidae	Dry mass	M = a * (L)^b	0.0153	2.573	1.75	8.6	Gruner (2003)	Tip of abdomen to end of head or carapace, excl. any appendages	Original, Diptera adult
Diptera	Dolichopodidae	Dry mass	M = a * (L)^b	0.0153	2.573	1.75	8.6	Gruner (2003)	Tip of abdomen to end of head or carapace, excl. any appendages	Original, Diptera adult
Diptera	Drosophilidae	Dry mass	M = a * (L)^b	0.0153	2.573	1.75	8.6	Gruner (2003)	Tip of abdomen to end of head or carapace, excl. any appendages	Original, Diptera adult
Diptera	Lauxaniidae	Dry mass	M = a * (L)^b	0.0153	2.573	1.75	8.6	Gruner (2003)	Tip of abdomen to end of head or carapace, excl. any appendages	Original, Diptera adult

Diptera	Muscidae	Dry mass	M = a * (L)^b	0.0153	2.573	1.75	8.6	Gruner (2003)	Tip of abdomen to end of head or carapace, excl. any appendages	Original, Diptera adult
Diptera	Mycetophylidae	Dry mass	M = a * (L)^b	0.0153	2.573	1.75	8.6	Gruner (2003)	Tip of abdomen to end of head or carapace, excl. any appendages	Original, Diptera adult
Diptera	Opomyzidae	Dry mass	M = a * (L)^b	0.0153	2.573	1.75	8.6	Gruner (2003)	Tip of abdomen to end of head or carapace, excl. any appendages	Original, Diptera adult
Diptera	Phoridae	Dry mass	M = a * (L)^b	0.0153	2.573	1.75	8.6	Gruner (2003)	Tip of abdomen to end of head or carapace, excl. any appendages	Original, Diptera adult
Diptera	Piophilidae	Dry mass	M = a * (L)^b	0.0153	2.573	1.75	8.6	Gruner (2003)	Tip of abdomen to end of head or carapace, excl. any appendages	Original, Diptera adult
Diptera	Psychodidae	Dry mass	M = a * (L)^b	0.0153	2.573	1.75	8.6	Gruner (2003)	Tip of abdomen to end of head or carapace, excl. any appendages	Original, Diptera adult
Diptera	Sciaridae	Dry mass	M = a * (L)^b	0.0153	2.573	1.75	8.6	Gruner (2003)	Tip of abdomen to end of head or carapace, excl. any appendages	Original, Diptera adult
Diptera	Simuliidae	Dry mass	M = a * (L)^b	0.0153	2.573	1.75	8.6	Gruner (2003)	Tip of abdomen to end of head or carapace, excl. any appendages	Original, Diptera adult
Diptera	Sphaeroceridae	Dry mass	M = a * (L)^b	0.0153	2.573	1.75	8.6	Gruner (2003)	Tip of abdomen to end of head or carapace, excl. any appendages	Original, Diptera adult
Diptera	Pipunculidae	Dry mass	M = a * (L)^b	0.0153	2.573	1.75	8.6	Gruner (2003)	Tip of abdomen to end of head or carapace, excl. any appendages	Original, Diptera adult
Diptera	Scatopsidae	Dry mass	M = a * (L)^b	0.0153	2.573	1.75	8.6	Gruner (2003)	Tip of abdomen to end of head or carapace, excl. any appendages	Original, Diptera adult
Diptera	Tipulidae	Dry mass	M = a * (L)^b	0.0153	2.573	1.75	8.6	Gruner (2003)	Tip of abdomen to end of head or carapace, excl. any appendages	Original, Diptera adult
Diptera	Uniden	Dry mass	M = a * (L)^b	0.0153	2.573	1.75	8.6	Gruner (2003)	Tip of abdomen to end of head or carapace, excl. any appendages	Original, Diptera adult
Ephemeroptera	Baetidae	Dry mass	M = a * (L)^b	0.035	2.173	0.9	17.6	Gruner (2003)	Tip of abdomen to end of head or carapace, excl. any appendages	Inferred, all insect taxa
Chilopoda	All	Dry mass	M = exp(a + b * log(L))	-4.049	2.18	4	47	Gowing and Recher (1984)	Not mentioned	Inferred, Chilopoda
Geophilomorpha	Dignathodontidae	Dry mass	M = exp(a + b * log(L))	-4.049	2.18	4	47	Gowing and Recher (1984)	Not mentioned	Inferred, Chilopoda
Geophilomorpha	Geophilidae	Dry mass	M = exp(a + b * log(L))	-4.049	2.18	4	47	Gowing and Recher (1984)	Not mentioned	Inferred, Chilopoda
Geophilomorpha	Mecistocephalidae	Dry mass	M = exp(a + b * log(L))	-4.049	2.18	4	47	Gowing and Recher (1984)	Not mentioned	Inferred, Chilopoda
Diplopoda	All	Dry mass	M = exp(a + b * log(L))	-4.591	2.543	11.0	47.0	Gowing and Recher (1984)	Not mentioned	Inferred, Diplopoda
Glomerida	Glomeridae	Dry mass	M = exp(a + b * log(L))	-4.591	2.543	11.0	47.0	Gowing and Recher (1984)	Not mentioned	Inferred, Diplopoda
Hemiptera	Aleyrodidae	Dry mass	M = exp(a + b * log(L))	-2.823	2.225	2.13	13.25	Sample et al. (1993)	From frons to tip of abdomen excluding appendages	Inferred, homoptera
Hemiptera	Alydidae	Dry mass	M = exp(a + b * log(L))	-4.784	3.075	3.2	40.23	Sample et al. (1993)	From frons to tip of abdomen excluding appendages	Original, Hemiptera
Hemiptera	Anthocoridae	Dry mass	M = exp(a + b * log(L))	-4.784	3.075	3.2	40.23	Sample et al. (1993)	From frons to tip of abdomen excluding appendages	Original, Hemiptera
Hemiptera	Aphididae	Dry mass	M = exp(a + b * log(L))	-2.823	2.225	2.13	13.25	Sample et al. (1993)	From frons to tip of abdomen excluding appendages	Inferred, homoptera
Hemiptera	Aradidae	Dry mass	M = exp(a + b * log(L))	-4.784	3.075	3.2	40.23	Sample et al. (1993)	From frons to tip of abdomen excluding appendages	Original, Hemiptera
Hemiptera	Ceratocombidae	Dry mass	M = exp(a + b * log(L))	-4.784	3.075	3.2	40.23	Sample et al. (1993)	From frons to tip of abdomen excluding appendages	Original, Hemiptera
Hemiptera	Cicadellidae	Dry mass	M = exp(a + b * log(L))	-3.735	2.561	2.13	13.25	Sample et al. (1993)	From frons to tip of abdomen excluding appendages	Group specific
Hemiptera	Cixiidae	Dry mass	M = exp(a + b * log(L))	-4.784	3.075	3.2	40.23	Sample et al. (1993)	From frons to tip of abdomen excluding appendages	Inferred, Hemiptera
Hemiptera	Coreidae	Dry mass	M = exp(a + b * log(L))	-4.784	3.075	3.2	40.23	Sample et al. (1993)	From frons to tip of abdomen excluding appendages	Inferred, Hemiptera
Hemiptera	Cydnidae	Dry mass	M = exp(a + b * log(L))	-4.784	3.075	3.2	40.23	Sample et al. (1993)	From frons to tip of abdomen excluding appendages	Inferred, Hemiptera

Hemiptera	Delphacidae	Dry mass	M = exp(a + b * log(L))	-2.823	2.225	2.13	13.25	Sample et al. (1993)	From frons to tip of abdomen excluding appendages	Inferred, homoptera
Hemiptera	Derbidae	Dry mass	M = exp(a + b * log(L))	-2.823	2.225	2.13	13.25	Sample et al. (1993)	From frons to tip of abdomen excluding appendages	Inferred, homoptera
Hemiptera	Dictyopharidae	Dry mass	M = exp(a + b * log(L))	-2.823	2.225	2.13	13.25	Sample et al. (1993)	From frons to tip of abdomen excluding appendages	Inferred, homoptera
Hemiptera	Dipsocoridae	Dry mass	M = exp(a + b * log(L))	-4.784	3.075	3.2	40.23	Sample et al. (1993)	From frons to tip of abdomen excluding appendages	Inferred, Hemiptera
Hemiptera	Eriosomatidae	Dry mass	M = exp(a + b * log(L))	-2.823	2.225	2.13	13.25	Sample et al. (1993)	From frons to tip of abdomen excluding appendages	Inferred, homoptera
Hemiptera	Flatidae	Dry mass	M = exp(a + b * log(L))	-2.823	2.225	2.13	13.25	Sample et al. (1993)	From frons to tip of abdomen excluding appendages	Inferred, homoptera
Hemiptera	Geocoridae	Dry mass	M = exp(a + b * log(L))	-4.784	3.075	3.2	40.23	Sample et al. (1993)	From frons to tip of abdomen excluding appendages	Inferred, Hemiptera
Hemiptera	Hydrometridae	Dry mass	M = exp(a + b * log(L))	-4.784	3.075	3.2	40.23	Sample et al. (1993)	From frons to tip of abdomen excluding appendages	Inferred, Hemiptera
Hemiptera	Largidae	Dry mass	M = exp(a + b * log(L))	-4.784	3.075	3.2	40.23	Sample et al. (1993)	From frons to tip of abdomen excluding appendages	Inferred, Hemiptera
Hemiptera	Lophopidae	Dry mass	M = exp(a + b * log(L))	-2.823	2.225	2.13	13.25	Sample et al. (1993)	From frons to tip of abdomen excluding appendages	Inferred, homoptera
Hemiptera	Lygaeidae	Dry mass	M = exp(a + b * log(L))	-4.784	3.075	3.2	40.23	Sample et al. (1993)	From frons to tip of abdomen excluding appendages	Inferred, Hemiptera
Hemiptera	Meenoplidae	Dry mass	M = exp(a + b * log(L))	-2.823	2.225	2.13	13.25	Sample et al. (1993)	From frons to tip of abdomen excluding appendages	Inferred, homoptera
Hemiptera	Miridae	Dry mass	M = exp(a + b * log(L))	-4.784	3.075	3.2	40.23	Sample et al. (1993)	From frons to tip of abdomen excluding appendages	Inferred, Hemiptera
Hemiptera	Nabidae	Dry mass	M = exp(a + b * log(L))	-4.784	3.075	3.2	40.23	Sample et al. (1993)	From frons to tip of abdomen excluding appendages	Inferred, Hemiptera
Hemiptera	Pentatomidae	Dry mass	M = exp(a + b * log(L))	-4.197	3.053	6.35	16.73	Sample et al. (1993)	From frons to tip of abdomen excluding appendages	Group specific
Hemiptera	Pseudococcidae	Dry mass	M = exp(a + b * log(L))	-2.823	2.225	2.13	13.25	Sample et al. (1993)	From frons to tip of abdomen excluding appendages	Inferred, homoptera
Hemiptera	Reduviidae	Dry mass	M = exp(a + b * log(L))	-4.784	3.075	3.2	40.23	Sample et al. (1993)	From frons to tip of abdomen excluding appendages	Inferred, Hemiptera
Hemiptera	Ricaniidae	Dry mass	M = exp(a + b * log(L))	-2.823	2.225	2.13	13.25	Sample et al. (1993)	From frons to tip of abdomen excluding appendages	Inferred, homoptera
Hemiptera	Schizopteridae	Dry mass	M = exp(a + b * log(L))	-4.784	3.075	3.2	40.23	Sample et al. (1993)	From frons to tip of abdomen excluding appendages	Inferred, Hemiptera
Hemiptera	Tingidae	Dry mass	M = exp(a + b * log(L))	-4.784	3.075	3.2	40.23	Sample et al. (1993)	From frons to tip of abdomen excluding appendages	Inferred, Hemiptera
Hemiptera	Tropiduchidae	Dry mass	M = exp(a + b * log(L))	-2.823	2.225	2.13	13.25	Sample et al. (1993)	From frons to tip of abdomen excluding appendages	Inferred, homoptera
Hemiptera	Uniden	Dry mass	M = exp(a + b * log(L))	-4.784	3.075	3.2	40.23	Sample et al. (1993)	From frons to tip of abdomen excluding appendages	Inferred, Hemiptera
Hymenoptera	Aphelinidae	Dry mass	M = exp(a + b * log(L))	-3.336	2.104	1	12	Gowing and Recher (1984)	Not mentioned	Inferred, Hym. Excl Formicidae
Hymenoptera	Bethylidae	Dry mass	M = exp(a + b * log(L))	-3.336	2.104	1	12	Gowing and Recher (1984)	Not mentioned	Inferred, Hym. Excl Formicidae
Hymenoptera	Braconidae	Dry mass	M = exp(a + b * log(L))	-3.336	2.104	1	12	Gowing and Recher (1984)	Not mentioned	Inferred, Hym. Excl Formicidae
Hymenoptera	Ceraphronidae	Dry mass	M = exp(a + b * log(L))	-3.336	2.104	1	12	Gowing and Recher (1984)	Not mentioned	Inferred, Hym. Excl Formicidae
Hymenoptera	Chalcididae	Dry mass	M = exp(a + b * log(L))	-3.336	2.104	1	12	Gowing and Recher (1984)	Not mentioned	Inferred, Hym. Excl Formicidae
Hymenoptera	Cynipidae	Dry mass	M = exp(a + b * log(L))	-3.336	2.104	1	12	Gowing and Recher (1984)	Not mentioned	Inferred, Hym. Excl Formicidae
Hymenoptera	Diapriidae	Dry mass	M = exp(a + b * log(L))	-3.336	2.104	1	12	Gowing and Recher (1984)	Not mentioned	Inferred, Hym. Excl Formicidae
Hymenoptera	Dryinidae	Dry mass	M = exp(a + b * log(L))	-3.336	2.104	1	12	Gowing and Recher (1984)	Not mentioned	Inferred, Hym. Excl Formicidae
Hymenoptera	Dryniidae	Dry mass	M = exp(a + b * log(L))	-3.336	2.104	1	12	Gowing and Recher (1984)	Not mentioned	Inferred, Hym. Excl Formicidae

Hymenoptera	Encyrtidae	Dry mass	M = exp(a + b * log(L))	-3.336	2.104	1	12	Gowing and Recher (1984)	Not mentioned	Inferred, Hym. Excl Formicidae
Hymenoptera	Eucoilidae	Dry mass	M = exp(a + b * log(L))	-3.336	2.104	1	12	Gowing and Recher (1984)	Not mentioned	Inferred, Hym. Excl Formicidae
Hymenoptera	Eulophidae	Dry mass	M = exp(a + b * log(L))	-3.336	2.104	1	12	Gowing and Recher (1984)	Not mentioned	Inferred, Hym. Excl Formicidae
Hymenoptera	Figitidae	Dry mass	M = exp(a + b * log(L))	-3.336	2.104	1	12	Gowing and Recher (1984)	Not mentioned	Inferred, Hym. Excl Formicidae
Hymenoptera	Formicidae	Dry mass	M = exp(a + b * log(L))	-3.996	2.489	2	18	Gowing and Recher (1984)	Not mentioned	Group specific
Hymenoptera	Ichneumonidae	Dry mass	M = exp(a + b * log(L))	-3.336	2.104	1	12	Gowing and Recher (1984)	Not mentioned	Inferred, Hym. Excl Formicidae
Hymenoptera	Mymaridae	Dry mass	M = exp(a + b * log(L))	-3.336	2.104	1	12	Gowing and Recher (1984)	Not mentioned	Inferred, Hym. Excl Formicidae
Hymenoptera	Mymarommatidae	Dry mass	M = exp(a + b * log(L))	-3.336	2.104	1	12	Gowing and Recher (1984)	Not mentioned	Inferred, Hym. Excl Formicidae
Hymenoptera	Platygastridae	Dry mass	M = exp(a + b * log(L))	-3.336	2.104	1	12	Gowing and Recher (1984)	Not mentioned	Inferred, Hym. Excl Formicidae
Hymenoptera	Scelionidae	Dry mass	M = exp(a + b * log(L))	-3.336	2.104	1	12	Gowing and Recher (1984)	Not mentioned	Inferred, Hym. Excl Formicidae
Hymenoptera	Sphecidae	Dry mass	M = exp(a + b * log(L))	-3.336	2.104	1	12	Gowing and Recher (1984)	Not mentioned	Inferred, Hym. Excl Formicidae
Hymenoptera	Tiphiidae	Dry mass	M = exp(a + b * log(L))	-3.336	2.104	1	12	Gowing and Recher (1984)	Not mentioned	Inferred, Hym. Excl Formicidae
Hymenoptera	Trichogrammatidae	Dry mass	M = exp(a + b * log(L))	-3.336	2.104	1	12	Gowing and Recher (1984)	Not mentioned	Inferred, Hym. Excl Formicidae
Hymenoptera	Vespidae	Dry mass	M = exp(a + b * log(L))	-3.336	2.104	1	12	Gowing and Recher (1984)	Not mentioned	Inferred, Hym. Excl Formicidae
Isopoda	All	Dry mass	M = exp(a + b * log(L))	-4.81	3.44	2.7	8	Wardhaugh (2013)	Front of labrum to tip of abdomen (excl. cerci or ovipositors) or tip of elytra (longest)	Original, Isopoda
Isopoda	Oniscidae	Dry mass	M = exp(a + b * log(L))	-4.81	3.44	2.7	8	Wardhaugh (2013)	Front of labrum to tip of abdomen (excl. cerci or ovipositors) or tip of elytra (longest)	Original, Isopoda
Isopoda	Philosciidae	Dry mass	M = exp(a + b * log(L))	-4.81	3.44	2.7	8	Wardhaugh (2013)	Front of labrum to tip of abdomen (excl. cerci or ovipositors) or tip of elytra (longest)	Original, Isopoda
Isopoda	Armadillidae	Dry mass	M = exp(a + b * log(L))	-4.81	3.44	2.7	8	Wardhaugh (2013)	Front of labrum to tip of abdomen (excl. cerci or ovipositors) or tip of elytra (longest)	Original, Isopoda
Isopoda	Termitidae	Dry mass	M = exp(a + b * log(L))	-4.81	3.44	2.7	8	Wardhaugh (2013)	Front of labrum to tip of abdomen (excl. cerci or ovipositors) or tip of elytra (longest)	Original, Isopoda
Isoptera	Rhinotermitidae	Dry mass	M = e^a * L^b	-5.802	3.177	3.30	5.60	Johnson and Strong (2000)	Head to end of abdomen	Inferred, Isoptera
Isoptera	Termitidae	Dry mass	M = e^a * L^b	-5.802	3.177	3.30	5.60	Johnson and Strong (2000)	Head to end of abdomen	Inferred, Isoptera
Lepidoptera	Acanthopteroctetidae	Dry mass	M = exp(a + b * log(L))	-5.036	3.122	2.76	40.73	Sample et al. (1993)	Frons to tip of abdomen (excl. antennae, ovipositors, wings etc.)	Inferred, Lepidoptera
Lepidoptera	Acanthopteroctetidae	Dry mass	M = exp(a + b * log(L))	-5.036	3.122	2.76	40.73	Sample et al. (1993)	Frons to tip of abdomen (excl. antennae, ovipositors, wings etc.)	Inferred, Lepidoptera
Lepidoptera	Gelechiidae	Dry mass	M = exp(a + b * log(L))	-5.036	3.122	2.76	40.73	Sample et al. (1993)	Frons to tip of abdomen (excl. antennae, ovipositors, wings etc.)	Inferred, Lepidoptera
Lepidoptera	Geometridae	Dry mass	M = exp(a + b * log(L))	-5.036	3.122	2.76	40.73	Sample et al. (1993)	Frons to tip of abdomen (excl. antennae, ovipositors, wings etc.)	Inferred, Lepidoptera

Lepidoptera	Gracillariidae	Dry mass	M = exp(a + b * log(L))	-5.036	3.122	2.76	40.73	Sample et al. (1993)	Frons to tip of abdomen (excl. antennae, ovipositors, wings etc.)	Inferred, Lepidoptera
Lepidoptera	Noctuidae	Dry mass	M = exp(a + b * log(L))	-5.036	3.122	2.76	40.73	Sample et al. (1993)	Frons to tip of abdomen (excl. antennae, ovipositors, wings etc.)	Inferred, Lepidoptera
Lepidoptera	Pyralidae	Dry mass	M = exp(a + b * log(L))	-5.036	3.122	2.76	40.73	Sample et al. (1993)	Frons to tip of abdomen (excl. antennae, ovipositors, wings etc.)	Inferred, Lepidoptera
Lepidoptera	Thyrididae	Dry mass	M = exp(a + b * log(L))	-5.036	3.122	2.76	40.73	Sample et al. (1993)	Frons to tip of abdomen (excl. antennae, ovipositors, wings etc.)	Inferred, Lepidoptera
Lepidoptera	Tineidae	Dry mass	M = exp(a + b * log(L))	-5.036	3.122	2.76	40.73	Sample et al. (1993)	Frons to tip of abdomen (excl. antennae, ovipositors, wings etc.)	Inferred, Lepidoptera
Lepidoptera	Tortricidae	Dry mass	M = exp(a + b * log(L))	-5.036	3.122	2.76	40.73	Sample et al. (1993)	Frons to tip of abdomen (excl. antennae, ovipositors, wings etc.)	Inferred, Lepidoptera
Lepidoptera	Zygaenidae	Dry mass	M = exp(a + b * log(L))	-5.036	3.122	2.76	40.73	Sample et al. (1993)	Frons to tip of abdomen (excl. antennae, ovipositors, wings etc.)	Inferred, Lepidoptera
Lepidoptera	Uniden	Dry mass	M = exp(a + b * log(L))	-5.036	3.122	2.76	40.73	Sample et al. (1993)	Frons to tip of abdomen (excl. antennae, ovipositors, wings etc.)	Inferred, Lepidoptera
Lithobiomorpha	Henicopidae	Dry mass	M = exp(a + b * log(L))	-4.049	2.18	4	47	Gowing and Recher (1984)	Not mentioned	Inferred, Chilopoda
Mantodea	Mantidae	Dry mass	M = exp(a + b * log(L))	-6.340	3.010	6.00	66.00	Wardhaugh (2013)	Front of labrum to tip of abdomen (excl. cerci or ovipositors) or tip of elytra (longest)	Group specific
Neuroptera	Chrysopidae	Dry mass	M = exp(a + b * log(L))	-4.483	2.570	3.45	54.51	Sample et al. (1993)	Frons to tip of abdomen (excl. antennae, ovipositors, wings etc.)	Inferred, Neuroptera
Opiliones	All	Fresh mass	M = exp(a + b * log(L))	-0.899	2.984	0.57	6.9	Höfer and Ott (2009)	Edge of prosoma (without chelicerae) to edge of opisthosoma (excl spinnerets)	Inferred, Opiliones
Orthoptera	Acrididae	Dry mass	M = exp(a + b * log(L))	-3.17	2.61	2.3	33	Wardhaugh (2013)	Front of labrum to tip of abdomen (excl. cerci or ovipositors) or tip of elytra (longest)	Inferred, Orthoptera
Orthoptera	Gryllidae	Dry mass	M = exp(a + b * log(L))	-3.17	2.61	2.3	33	Wardhaugh (2013)	Front of labrum to tip of abdomen (excl. cerci or ovipositors) or tip of elytra (longest)	Inferred, Orthoptera
Orthoptera	Tetrigidae	Dry mass	M = exp(a + b * log(L))	-3.17	2.61	2.3	33	Wardhaugh (2013)	Front of labrum to tip of abdomen (excl. cerci or ovipositors) or tip of elytra (longest)	Inferred, Orthoptera
Orthoptera	Gryllacrididae	Dry mass	M = exp(a + b * log(L))	-3.17	2.61	2.3	33	Wardhaugh (2013)	Front of labrum to tip of abdomen (excl. cerci or ovipositors) or tip of elytra (longest)	Inferred, Orthoptera
Orthoptera	Tettigoniidae	Dry mass	M = exp(a + b * log(L))	-3.17	2.61	2.3	33	Wardhaugh (2013)	Front of labrum to tip of abdomen (excl. cerci or ovipositors) or tip of elytra (longest)	Inferred, Orthoptera
Orthoptera	Tridactylidae	Dry mass	M = exp(a + b * log(L))	-3.17	2.61	2.3	33	Wardhaugh (2013)	Front of labrum to tip of abdomen (excl. cerci or ovipositors) or tip of elytra (longest)	Inferred, Orthoptera
Polydesmida	Paradoxosomatidae	Dry mass	M = exp(a + b * log(L))	-4.591	2.543	11.0	47.0	Gowing and Recher (1984)	Not mentioned	Inferred, Diplopoda
Polydesmida	Platyrhacidae	Dry mass	M = exp(a + b * log(L))	-4.591	2.543	11.0	47.0	Gowing and Recher (1984)	Not mentioned	Inferred, Diplopoda
Polydesmida	Cryptodesmidae	Dry mass	M = exp(a + b * log(L))	-4.591	2.543	11.0	47.0	Gowing and Recher (1984)	Not mentioned	Inferred, Diplopoda
Polydesmida	Dalodesmidae	Dry mass	M = exp(a + b * log(L))	-4.591	2.543	11.0	47.0	Gowing and Recher (1984)	Not mentioned	Inferred, Diplopoda
Polydesmida	Haplodesmidae	Dry mass	M = exp(a + b * log(L))	-4.591	2.543	11.0	47.0	Gowing and Recher (1984)	Not mentioned	Inferred, Diplopoda
Polydesmida	Opisotretidae	Dry mass	M = exp(a + b * log(L))	-4.591	2.543	11.0	47.0	Gowing and Recher (1984)	Not mentioned	Inferred, Diplopoda
Polydesmida	Pyrgodesmidae	Dry mass	M = exp(a + b * log(L))	-4.591	2.543	11.0	47.0	Gowing and Recher (1984)	Not mentioned	Inferred, Diplopoda
Polyxenida	Polyxenidae	Dry mass	M = exp(a + b * log(L))	-4.591	2.543	11.0	47.0	Gowing and Recher (1984)	Not mentioned	Inferred, Diplopoda

Pseudoscorpionida	All	Fresh mass	M = exp(a + b * log(L))	-1.892	2.515	0.86	2.10	Höfer and Ott (2009)	Edge of prosoma (without chelicerae) to edge of opisthosoma (excl spinnerets)	Group specific
Psocoptera	Uniden	Dry mass	M = a * (L)^b	0.014	3.115	1.50	3.15	Gruner (2003)	Tip of abdomen to end of head or carapace, excl. any appendages	Inferred, Psocoptera
Psocoptera	Psoquillidae	Dry mass	M = a * (L)^b	0.014	3.115	1.50	3.15	Gruner (2003)	Tip of abdomen to end of head or carapace, excl. any appendages	Inferred, Psocoptera
Psocoptera	Pachytroctidae	Dry mass	M = a * (L)^b	0.014	3.115	1.50	3.15	Gruner (2003)	Tip of abdomen to end of head or carapace, excl. any appendages	Inferred, Psocoptera
Psocoptera	Mesopsocidae	Dry mass	M = a * (L)^b	0.014	3.115	1.50	3.15	Gruner (2003)	Tip of abdomen to end of head or carapace, excl. any appendages	Inferred, Psocoptera
Psocoptera	Liposcelidae	Dry mass	M = a * (L)^b	0.014	3.115	1.50	3.15	Gruner (2003)	Tip of abdomen to end of head or carapace, excl. any appendages	Inferred, Psocoptera
Psocoptera	Ectopsocidae	Dry mass	M = a * (L)^b	0.014	3.115	1.50	3.15	Gruner (2003)	Tip of abdomen to end of head or carapace, excl. any appendages	Inferred, Psocoptera
Psocoptera	Epipsocidae	Dry mass	M = a * (L)^b	0.014	3.115	1.50	3.15	Gruner (2003)	Tip of abdomen to end of head or carapace, excl. any appendages	Inferred, Psocoptera
Psocoptera	Elipsocidae	Dry mass	M = a * (L)^b	0.014	3.115	1.50	3.15	Gruner (2003)	Tip of abdomen to end of head or carapace, excl. any appendages	Inferred, Psocoptera
Psocoptera	Hemipsocidae	Dry mass	M = a * (L)^b	0.014	3.115	1.50	3.15	Gruner (2003)	Tip of abdomen to end of head or carapace, excl. any appendages	Inferred, Psocoptera
Psocoptera	Lepidopsocidae	Dry mass	M = a * (L)^b	0.014	3.115	1.50	3.15	Gruner (2003)	Tip of abdomen to end of head or carapace, excl. any appendages	Inferred, Psocoptera
Psocoptera	Psyllipsocidae	Dry mass	M = a * (L)^b	0.014	3.115	1.50	3.15	Gruner (2003)	Tip of abdomen to end of head or carapace, excl. any appendages	Inferred, Psocoptera
Schizomida	Protoschizomidae	Fresh mass	M = exp(a + b * log(L))	-2.108	3.017	0.67	36	Höfer and Ott (2009)	Edge of prosoma (without chelicerae) to edge of opisthosoma (excl spinnerets)	Inferred, hunting spiders
Scolopendromorpha	Cryptopidae	Dry mass	M = exp(a + b * log(L))	-4.049	2.18	4	47	Gowing and Recher (1984)	Not mentioned	Inferred, Chilopoda
Symphyla	Scutegerillidae	Dry mass	M = a * (L)^b	0.035	2.173	0.9	17.6	Gruner (2003)	Tip of abdomen to end of head or carapace, excl. any appendages	Inferred, all insect taxa
Thysanoptera	Aeolothripidae	Dry mass	M = a * (L)^b	0.035	2.173	0.9	17.6	Gruner (2003)	Tip of abdomen to end of head or carapace, excl. any appendages	Inferred, all insect taxa
Thysanoptera	Phlaeothripidae	Dry mass	M = a * (L)^b	0.035	2.173	0.9	17.6	Gruner (2003)	Tip of abdomen to end of head or carapace, excl. any appendages	Inferred, all insect taxa
Thysanoptera	Thripidae	Dry mass	M = a * (L)^b	0.035	2.173	0.9	17.6	Gruner (2003)	Tip of abdomen to end of head or carapace, excl. any appendages	Inferred, all insect taxa
Thysanoptera	Merothripidae	Dry mass	M = a * (L)^b	0.035	2.173	0.9	17.6	Gruner (2003)	Tip of abdomen to end of head or carapace, excl. any appendages	Inferred, all insect taxa
Schizomida	Hubbardiidae	Fresh mass	M = exp(a + b * log(L))	-2.108	3.017	0.67	36	Höfer and Ott (2009)	Edge of prosoma (without chelicerae) to edge of opisthosoma (excl spinnerets)	Inferred, hunting spiders

Appendix Table A.3 | Dry-to-fresh mass conversion from the literature for transformation of dry body masses (DM) (from length-dry mass regression calculations) to fresh mass (FM).

Taxon	Equation FM[mg], DM[mg]	a	b	Reference	Regression specificity
All groups with dry-mass length-mass regressions (see Appendix Table A.1)	FM = exp(a+b * log(DM))	0.6111	1.0213	Mercer et al. (2001)	Insecta

Appendix Table A.4 | Soil data (soil depth 0-10 cm) that were used in the PCA-analysis (baseline; 52 plots; no controls), resulting PCA scores of the soil data and a set of variables that describe the site conditions.

PlotID	Sand [prop]	Silt [prop]	Clay [prop]	pH	Bulk Density [g/cm^3]	Total C [prop]	PC axis 1	PC axis 2	PC axis 3	Slope [°]	Bare soil [prop]	Gap fraction [prop]	Altitude [m a.s.l.]
1	0.29	0.43	0.28	4.47	1.10	0.0184	0.01	-0.03	0.02	12.20	0.60	0.05	61.2
2	0.33	0.41	0.26	4.61	1.01	0.0229	0.03	0.10	0.10	12.60	0.25	0.04	46.9
3	0.35	0.37	0.27	4.47	1.03	0.0201	0.05	0.04	-0.02	7.80	0.10	0.07	40.5
4	0.27	0.41	0.32	4.40	0.93	0.0239	-0.06	0.11	-0.05	7.60	0.15	0.04	55.3
5	0.35	0.45	0.20	4.41	1.18	0.0182	0.06	-0.03	0.01	6.80	0.15	0.08	54.2
6	0.37	0.35	0.28	4.26	0.99	0.0167	0.06	0.02	-0.21	18.80	0.08	0.17	44.8
7	0.33	0.33	0.34	4.37	1.02	0.0200	0.02	0.00	-0.11	8.90	0.02	0.34	37.6
8	0.34	0.37	0.29	4.08	1.17	0.0123	0.04	-0.16	-0.28	5.10	0.20	0.04	62.6
9	0.39	0.31	0.30	5.02	1.13	0.0209	0.17	0.00	0.33	17.80	0.20	0.05	50.7
10	0.28	0.33	0.39	4.21	1.15	0.0194	-0.03	-0.14	-0.16	7.60	0.30	0.06	57.2
11	0.24	0.42	0.34	4.68	1.02	0.0168	0.00	-0.04	0.12	18.30	0.60	0.04	57.3
12	0.35	0.45	0.20	4.50	0.94	0.0244	0.02	0.21	0.04	16.80	0.01	0.59	53.0
13	0.11	0.54	0.35	4.38	1.24	0.0216	-0.17	-0.16	0.11	9.50	0.25	0.14	53.5
14	0.35	0.35	0.30	4.68	1.33	0.0104	0.16	-0.27	0.12	10.60	0.17	0.04	51.5
15	0.24	0.48	0.28	4.26	0.97	0.0370	-0.05	0.03	-0.14	8.20	0.01	NA	64.8
16	0.28	0.47	0.25	4.21	1.02	0.0191	-0.05	-0.07	0.16	8.70	0.05	0.17	54.1
17	0.25	0.44	0.31	4.49	1.26	0.0257	-0.04	-0.05	-0.12	5.10	0.07	0.12	54.6
18	0.25	0.43	0.31	4.30	1.04	0.0163	-0.31	0.15	0.22	6.60	0.08	0.10	51.9
19	0.08	0.55	0.37	4.41	1.05	0.0394	-0.10	0.18	0.11	2.40	0.10	0.30	48.2
20	0.24	0.47	0.29	4.56	0.91	0.0275	-0.08	-0.27	-0.04	2.00	0.10	0.12	42.3
21	0.19	0.43	0.39	4.28	1.30	0.0165	-0.13	-0.27	0.16	16.20	0.25	0.08	64.6
22	0.10	0.44	0.47	4.58	1.23	0.0178	-0.15	-0.15	0.15	20.80	0.10	0.10	44.2
23	0.14	0.53	0.33	4.40	1.29	0.0238	0.24	0.10	-0.01	20.90	0.10	0.03	53.5
24	0.53	0.23	0.24	4.61	1.04	0.0209	-0.10	-0.17	-0.28	6.80	0.08	0.05	53.6
25	0.20	0.43	0.37	4.07	1.06	0.0124	0.09	0.11	0.01	11.10	0.15	0.18	45.7
26	0.26	0.36	0.38	5.28	1.10	0.0228	0.35	-0.06	-0.06	6.40	NA	0.17	44.7
27	0.15	0.41	0.43	4.61	1.02	0.0258	-0.02	-0.14	0.24	1.80	NA	0.16	45.1
28	0.41	0.32	0.27	4.51	1.04	0.0245	0.11	0.01	0.22	21.30	0.10	0.06	67.1
29	0.60	0.18	0.22	4.59	1.20	0.0141	-0.25	0.07	-0.12	5.40	0.08	0.11	47.8
30	0.23	0.35	0.42	4.75	1.20	0.0227	0.06	0.07	-0.10	2.00	0.25	0.13	62.5
31	0.39	0.44	0.16	4.62	1.28	0.0235	0.17	0.09	-0.07	14.90	0.20	0.09	52.1
32	0.13	0.58	0.29	4.04	1.03	0.0265	-0.03	0.09	-0.01	1.00	0.05	0.11	52.5
33	0.38	0.34	0.28	4.37	1.01	0.0217	0.27	0.13	-0.21	4.60	0.20	0.06	60.5
34	0.46	0.33	0.21	4.53	0.98	0.0162	0.18	-0.04	-0.18	2.10	0.03	0.17	44.7
35	0.35	0.42	0.22	4.22	1.20	0.0312	-0.01	0.22	-0.09	0.60	0.08	0.10	44.4
36	0.60	0.26	0.14	4.31	1.06	0.0182	0.10	-0.02	0.06	2.80	0.40	0.05	47.2
37	0.50	0.22	0.27	4.27	1.19	0.0206	-0.30	-0.13	-0.28	0.20	0.20	0.04	45.1
38	0.35	0.42	0.23	4.33	0.89	0.0256	0.14	-0.09	-0.04	0.40	0.01	0.13	38.9
39	0.37	0.41	0.22	4.55	1.14	0.0172	0.12	-0.04	-0.02	2.70	0.05	0.17	43.3
40	0.05	0.42	0.53	3.97	0.97	0.0222	0.13	0.31	0.19	11.10	0.01	0.15	52.6
41	0.41	0.32	0.26	4.44	1.20	0.0169	0.03	-0.02	0.11	8.90	0.10	0.06	54.5
42	0.39	0.38	0.23	4.46	1.15	0.0165	-0.20	0.30	-0.01	7.50	0.05	0.18	46.6
43	0.46	0.38	0.17	4.78	0.91	0.0280	-0.20	-0.09	0.11	14.90	0.20	0.03	52.2
44	0.31	0.44	0.26	4.56	1.14	0.0198	-0.01	0.03	0.08	8.30	0.05	0.48	45.8
45	0.21	0.44	0.34	4.36	0.79	0.0351	0.01	-0.17	-0.01	2.80	0.00	0.16	42.8
46	0.10	0.47	0.44	4.46	1.11	0.0252	0.07	-0.22	0.16	17.50	0.20	0.06	47.2
47	0.28	0.39	0.33	4.59	1.02	0.0223	-0.29	0.15	-0.10	7.40	0.05	0.44	51.2
48	0.29	0.36	0.35	4.40	1.24	0.0184	-0.08	0.24	0.03	2.20	0.30	0.04	46.2
49	0.31	0.50	0.20	4.50	1.43	0.0152	-0.01	0.06	-0.11	9.10	0.30	0.16	43.0
50	0.13	0.51	0.37	4.09	0.93	0.0332	0.01	-0.03	0.02	3.50	0.00	0.43	47.9
51	0.28	0.53	0.20	4.43	0.88	0.0255	0.03	0.10	0.10	10.60	0.00	0.07	46.8
52	0.32	0.47	0.20	4.24	1.05	0.0196	0.05	0.04	-0.02	8.20	0.25	0.10	54.4

Appendix Table A.5 | Biotic data (baseline; 52 plots; no controls). S_{spp} = species richness, N = abundance, B = biomass, S_{fam} = family richness, LL inv. = leaf-litter invertebrates, HL inv. = herb-layer invertebrates.

PlotID	Plant S_{spp}	Plant N	Bird S_{spp}	Bird N	Bird B	LL inv. S_{fam}	LL inv. N	LL inv. B	HL inv. S_{fam}	HL inv. N	HL inv. B
1	13	220	0	0	0.00	5	7	3.61	4	12	27.32
2	24	482	4	6	233.43	7	11	5.32	8	33	168.57
3	15	739	3	12	131.70	6	8	12.45	22	69	137.97
4	20	482	4	15	308.93	30	210	141.08	15	35	373.86
5	16	996	4	14	150.02	3	11	0.96	8	18	65.77
6	16	586	5	9	291.51	11	24	23.77	7	17	479.79
7	15	607	2	10	90.48	4	14	7.40	25	42	235.60
8	16	675	4	8	372.08	7	10	22.61	5	15	102.00
9	11	274	8	21	1115.02	6	9	8.22	8	16	55.82
10	20	542	5	18	614.89	6	25	146.13	8	24	45.64
11	12	284	3	4	92.55	12	30	7.88	7	25	972.55
12	9	573	6	11	312.99	13	151	98.40	14	40	1133.81
13	17	203	4	10	335.13	6	18	14.00	3	5	327.33
14	16	361	4	16	588.90	5	9	2.57	6	12	116.43
16	14	554	4	14	289.06	13	39	37.00	22	50	116.08
17	20	718	6	14	810.48	12	23	48.73	16	48	473.72
18	19	603	7	19	1115.99	8	9	110.47	11	47	346.00
19	24	872	9	14	582.17	12	38	45.80	15	35	258.98
20	21	642	5	7	252.04	6	23	11.58	19	44	201.39
21	20	330	4	8	353.96	14	33	68.23	20	49	205.17
22	22	595	3	8	202.69	5	6	8.21	6	9	74.77
23	21	646	6	18	789.38	8	11	5.73	18	35	119.64
24	20	632	4	12	360.60	8	14	5.02	9	20	331.77
25	13	525	1	3	29.04	13	37	91.60	6	8	21.23
28	18	384	5	15	570.60	12	19	45.60	19	29	36.28
29	20	444	6	13	565.84	10	20	33.78	5	10	88.11
30	20	750	4	12	296.83	4	4	12.84	15	38	165.46
31	19	438	7	10	317.63	13	27	31.21	4	9	118.56
32	23	507	2	4	56.84	12	46	21.70	10	31	147.92
33	13	734	5	8	467.71	4	9	2.15	6	25	102.52
34	14	474	7	25	701.73	6	29	34.44	12	39	805.17
35	21	492	3	4	118.86	3	35	35.09	14	53	233.24
36	15	594	4	5	223.50	6	14	10.69	4	13	101.92
37	13	1092	11	21	1244.57	6	7	0.76	6	13	193.15
38	20	851	7	18	542.43	15	42	53.03	12	18	268.28
39	19	414	4	14	224.08	6	9	25.17	11	17	57.79
40	21	304	5	13	342.32	8	20	17.41	9	22	512.67
41	8	120	2	4	74.96	14	83	94.65	15	27	39.08
42	10	399	2	3	27.46	9	23	11.30	23	68	685.27
43	18	340	2	6	50.18	3	4	1.18	7	13	106.69
44	17	514	6	15	330.03	11	112	78.22	9	19	289.24
45	16	379	7	32	676.98	16	83	149.17	27	54	746.31
46	17	268	3	6	128.98	26	224	180.06	5	36	159.10
47	16	254	1	1	27.80	14	25	9.33	6	16	610.80
48	14	230	3	6	140.92	3	5	2.47	5	6	30.08
49	12	223	3	6	261.76	3	7	5.05	13	23	145.71
50	14	369	3	7	221.96	17	69	49.84	22	46	302.90
51	26	682	5	15	420.08	16	63	90.36	19	39	78.98
52	19	455	4	8	156.66	1	3	0.61	6	13	63.74

Appendix Table A.6 | Summary tables from linear and generalized linear models testing the effects of plot size and tree diversity on the environmental variables. In case of overdispersion, we used the negative binomial distribution for modelling. Asterisks denote significance levels: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. TD = tree diversity, PS = plot size, S_{spp} = species richness, N = abundance, S_{fam} = family richness, B = biomass, LL inv. = leaf-litter invertebrates, HL inv. = herb-layer invertebrates.

Response	Fixed effects	Estimate	Std. Error	t-value	p-value		R^2
PCaxis1	TD	-0.046	0.034	-1.383	0.170		0.046
	PS	-0.002	0.014	0.127	0.899		
	TD: PS	0.004	0.006	0.726	0.470		
PCaxis 2	TD	0.063	0.033	1.925	0.057		0.080
	PS	0.047	0.014	3.290	0.001	**	
	TD: PS	-0.013	0.006	-2.138	0.035	*	
PCaxis 3	TD	0.020	0.033	0.593	0.555		0.056
	PS	0.022	0.014	1.545	0.126		
	TD: PS	-0.001	0.006	-0.089	0.929		
Slope	TD	-3.356	1.387	-2.413	0.018	*	0.064
	PS	-1.688	0.596	-2.833	0.006	**	
	TD: PS	0.699	0.251	2.779	0.007	**	
Bare soil	TD	-0.473	0.310	-1.526	0.130		0.008
	PS	-0.047	0.133	-0.352	0.726		
	TD: PS	0.073	0.056	1.299	0.197		
Gap fraction	TD	0.495	0.174	2.851	0.005	**	0.084
	PS	0.062	0.075	0.834	0.406		
	TD: PS	-0.079	0.031	-2.506	0.014	*	
Altitude	TD	-0.309	1.625	-0.190	0.849		-0.025
	PS	-0.468	0.698	-0.671	0.504		
	TD: PS	0.067	0.294	0.229	0.820		
Plant S_{spp} (nb)	TD	-0.157	0.065	-2.419	0.016	*	0.078
	PS	-0.066	0.028	-2.388	0.017	*	
	TD: PS	0.032	0.012	2.764	0.006	**	
Plant N	TD	0.048	0.100	0.476	0.634		0.021
	PS	0.010	0.043	0.225	0.822		
	TD: PS	-0.001	0.018	-0.075	0.940		
Bird S_{spp}	TD	-0.182	0.113	-1.611	0.107		0.056
	PS	-0.104	0.049	-2.106	0.035	*	
	TD: PS	0.040	0.020	1.989	0.047	*	
Bird N	TD	-0.130	0.336	7.891	0.368		0.009
	PS	-0.048	0.061	-0.783	0.433		
	TD: PS	0.024	0.026	0.946	0.344		
Bird B	TD	-0.226	0.225	-1.006	0.317		0.026
	PS	-0.176	0.097	-1.826	0.071		
	TD: PS	0.061	0.041	1.492	0.139		
LL inv. S_{fam}	TD	0.037	0.133	0.283	0.777		0.048
	PS	-0.072	0.059	-1.226	0.220		
	TD: PS	0.002	0.024	0.078	0.938		
LL inv. N	TD	0.049	0.234	1.829	0.067		0.037
	PS	0.195	0.101	1.937	0.053		
	TD: PS	-0.087	0.043	-2.048	0.041	*	
LL inv. B	TD	0.377	0.343	1.097	0.275		0.089
	PS	-0.150	0.148	-1.020	0.311		
	TD: PS	-0.060	0.062	-0.967	0.336		
	TD	0.202	0.123	1.644	0.100		0.071

Response	Fixed effects	Estimate	Std. Error	t-value	p-value	R^2
HL inv. S_{fam}	PS	0.055	0.055	1.001	0.317	
	TD: PS	-0.023	0.022	-1.010	0.312	
HL inv. N	TD	0.243	0.136	1.791	0.073	0.053
	PS	0.089	0.059	1.512	0.131	
	TD: PS	-0.034	0.025	-1.375	0.169	
HL inv. B	TD	0.008	0.237	0.035	0.972	0.001
	PS	-0.011	0.102	-0.112	0.911	
	TD: PS	-0.002	0.043	-0.039	0.969	

Appendix Table A.7 | List of plant species (baseline; 52 plots; no controls). N = abundance, F = frequence (number of plots present on).

Species	Family	N	F
Adiantum latifolium Lam.	Pteridaceae	264	32
Ageratum conyzoides (L.) L.*	Compositae	381	16
Alternanthera sessilis (L.) R.Br. ex DC.	Amaranthaceae	57	4
Asplenium normale D. Don	Aspleniaceae	109	17
cf. *Asplenium* spec.	Aspleniaceae	3	2
Asystasia gangetica (L.) T.Anderson*	Acanthaceae	5253	49
Bauhinia semibifida Roxb.	Fabaceae	1	1
Blechnum orientale L.	Blechnaceae	8	2
Breynia cernua (Poir.) Müll.Arg.	Phyllanthaceae	7	4
Centotheca lappacea (L.) Desv.	Poaceae	1714	42
Centrosema pubescens Benth.*	Fabaceae	38	5
Chromolaena odorata (L.) R.M.King & H.Rob.*	Compositae	9	5
Cleome rutidosperma DC.*	Cleomaceae	5	1
Clerodendrum spec.	Lamiaceae	2	2
Clidemia hirta (L.) D. Don*	Melastomataceae	3233	50
Commelina diffusa Burm.f.*	Commelinaceae	7	1
Coptosapelta flavescens Korth.	Rubiaceae	2	1
Crassocephalum crepidioides (Benth.) S.Moore*	Compositae	3	2
Croton argyratus Blume	Euphorbiaceae	1	1
Croton hirtus L'Hér.*	Euphorbiaceae	24	5
Cuphea carthagenensis (Jacq.) J.F.Macbr.*	Lythraceae	8	2
Cyclosorus heterocarpus (Blume) Ching	Thelypteridaceae	54	7
Cyclosorus megaphyllus Ching	Thelypteridaceae	1625	41
Cyperus diffusus Vahl	Cyperaceae	165	28
Cyrtococcum patens (L.) A.Camus	Poaceae	1286	40
Dicranopteris linearis (Burm. f.) Underw.	Gleicheniaceae	9	1
Dioscorea alata L.	Dioscoreaceae	3	2
Elaeis guineensis Jacq.*	Arecaceae	131	30
fern spec. 01		1	1
cf. *Ficus* spec.	Moraceae	1	1
Ficus cf. *variegata* Blume	Moraceae	19	7
grass spec. 01	Cyperaceae	4	1
grass spec. 02	Poaceae	18	6
herb spec. 01		1	1
herb spec. 02		2	1
herb spec. 03		2	1
herb spec. 04		1	1
herb spec. 05		1	1
Hyptis capitata Jacq.*	Lamiaceae	6	1
Imperata cylindrica (L.) Raeusch*	Poaceae	85	10
Lantana camara L.*	Verbenaceae	2	1
Lindernia crustacea (L.) F.Muell.	Linderniaceae	8	4
Lindernia diffusa (L.) Wettst.*	Linderniaceae	1	1
Ludwigia octovalvis (Jacq.) P.H.Raven*	Onagraceae	4	2
Lygodium circinatum (Burm. f.) Sw.	Lygodiaceae	91	23
Mallotus peltatus (Geiseler) Müll.Arg.	Euphorbiaceae	5	1
Melastoma malabathricum L.*	Melastomataceae	66	23
Merremia umbellata (L.) Hallier f.	Convolvulaceae	78	7
Microlepia speluncae (L.) T. Moore	Dennstaedtiaceae	76	22
Mikania micrantha (L.) Willd.*	Compositae	81	17
Mimosa cf. *pudica* L.*	Fabaceae	13	4
Nephrolepis cf. *acutifolia* (Desv.) Christ	Nephrolepidaceae	2299	42
Oplismenus compositus (L.) P.Beauv.	Poaceae	38	2
Ottochloa nodosa (Kunth) Dandy	Poaceae	1962	44
Oxalis barrelieri L.*	Oxalidaceae	6	1
Panicum cf. *laxum* Sw.*	Poaceae	2194	29
Paspalum cf. *conjugatum* P.J.Bergius*	Poaceae	1584	49

Species	Family	N	F
Peperomia pellucida (L.) Kunth*	Piperaceae	6	1
Pericampylus glaucus (Lam.) Merr.	Menispermaceae	1	1
Phyllanthus cf. *niruri* L.	Phyllanthaceae	19	4
Pronephrium triphyllum (Sw.) Holttum	Thelypteridaceae	35	4
Pteris cf. *armata* C. Presl	Pteridaceae	50	4
Pteris ensiformis Burm. f.	Pteridaceae	1	1
Pueraria phaseoloides (Roxb.) Benth.	Fabaceae	5	2
Salvia occidentalis Sw.	Lamiaceae	3	1
Schizostachyum sp.	Poaceae	1	1
Scleria levis Retz.	Cyperaceae	283	37
seedling spec. 1		1	1
Selaginella willdenowii (Desv. ex Poir.) Baker	Selaginellaceae	126	14
Solanum jamaicense Mill.*	Solanaceae	12	6
Spermacoce alata Aubl.*	Rubiaceae	1814	32
Stenochlaena palustris (Burm. f.) Bedd.	Blechnaceae	14	2
Strombosia javanica Thwaites	Olacaceae	11	1
Taenitis blechnoides (Willd.) Sw.	Pteridaceae	452	23
Tectaria vasta (Blume) Copel.	Tectariaceae	21	6
Urceola brachysepala Hook.f.	Apocynaceae	29	3
Urceola spec.	Apocynaceae	108	8
woody spec. 01		1	1
woody spec. 02		3	2
woody spec. 03		1	1
woody spec. 04		34	3
woody spec. 05		12	1
woody spec. 06		1	1
woody spec. 07		1	1
woody spec. 08		1	1
woody spec. 09		1	1
woody spec. 10		2	1
woody spec. 11		1	1
woody spec. 12		1	1
woody spec. 13		2	1
woody spec. 14		1	1
woody spec. 15		1	1

Species: * = alien species

Appendix Table A.8 | List of bird species recorded within a 75 m radius around the centre of each plot with information on diet and main habitat. Total abundance, total biomass and frequence of the bird species from the baseline survey (52 plots, no controls) as well as from year 1 (56 plots, control plots included) are given. Diet: Invertebrate = invertebrates; PlantSeed = plants and seeds; FruiNect = fruits and nectar (≥ 50% of their diet consists of fruit and/or nectar but they also feed on invertebrates, plants or seeds); VertFishScav = vertebrates, fish, carrion; Omnivore = omnivore (score of ≤ 50 in all four categories) (for detailed information on categories see Wilman et al. (2014)). Habitat: main natural habitat: 1 = primary and old secondary forests interior; 2 = forest gaps, edges, or upper canopy; 3 = little wooded and cultivated areas. All species are listed as 'Least Concern' (IUCN, 2015). Diet and biomass data was taken from Wilman et al. (2014). N = abundance, B = biomass, F = frequence (number of plots present on).

						Baseline			Year 1	
Species	Family	Diet	Habitat	Habitat source	N	B [g/75 m radius]	F	N	B [g/75 m radius]	F
Amaurornis phoenicurus	Rallidae	Omnivore	3	Beukema et al. (2007)	10	1440.00	5	-	-	-
Celeus brachyurus	Picidae	Invertebrate	2	Thiollay (1995)	1	85.94	1	-	-	-
Centropus sinensis	Cuculidae	Omnivore	3	Thiollay (1995)	1	280.70	1	1	280.70	1
Chalcophaps indica	Columbidae	Omnivore	1	Thiollay (1995)	9	1228.86	7	10	955.78	7
Coturnix chinesis	Phasianidae	PlantSeed	3	Pappas (2001)	-	-	-	1	40.41	1
Dicaeum trigonostigma	Dicaeidae	FruiNect	2	Thiollay (1995)	16	113.60	13	20	127.80	16
Eurystomus orientalis	Coraciidae	Invertebrate	2	Thiollay (1995)	2	286.04	2	-	-	-
Geopelia striata	Columbidae	PlantSeed	3	Thiollay (1995)	8	452.80	6	41	1811.20	18
Halcyon smyrnensis	Alcedinidae	VertFishScav	3	Thiollay (1995)	33	2924.80	22	19	1736.60	13
Lanius schach	Laniidae	Invertebrate	3	Yosef et al. (2015)	-	-	-	2	103.02	2
Lonchura punctulata	Estrildidae	PlantSeed	3	Thiollay (1995)	-	-	-	7	40.80	3
Megalaima haemacephala	Ramphastidae	FruiNect	3	Thiollay (1995)	2	88.98	2	-	-	-
Merops viridis	Meropidae	Invertebrate	3	Thiollay (1995)	3	34.80	1	-	-	-
Orthotomus atrogularis	Sylviidae	Invertebrate	3	Thiollay (1995)	-	-	-	1	7.68	1
Orthotomus ruficeps	Sylviidae	Invertebrate	3	Thiollay (1995)	61	429.30	27	45	210.60	20
Orthotomus sericeus	Sylviidae	Invertebrate	2	Thiollay (1995)	21	216.00	14	1	10.80	1
Prinia familiaris	Cisticolidae	Invertebrate	3	Thiollay (1995)	241	1810.16	48	252	1539.12	50
Pycnonotus aurigaster	Pycnonotidae	Omnivore	3	Thiollay (1995)	31	1019.59	14	6	221.65	3
Pycnonotus goiavier	Pycnonotidae	FruiNect	3	Thiollay (1995)	191	4698.20	38	198	4281.20	45
Pycnonotus plumosus	Pycnonotidae	FruiNect	3	Thiollay (1995)	14	453.05	7	6	174.25	4
Rhipidura javanica	Rhipiduridae	Invertebrate	3	Robson (2015)	2	25.00	2	5	62.50	4
Spilornis cheela	Accipitridae	VertFishScav	2	Thiollay (1995)	1	597.74	1	8	4781.92	6
Spizaetus cirrhatus	Accipitridae	VertFishScav	3	Thiollay (1995)	-	-	-	1	1475.12	1
Stigmatopelia chinensis	Columbidae	PlantSeed	3	Thiollay (1995)	8	1272.00	6	64	8904.00	28
Todiramphus chloris	Alcedinidae	Invertebrate	3	Thiollay (1995)	14	859.17	10	61	3634.95	32
Treron vernans	Columbidae	FruiNect	2	Thiollay (1995)	3	396.00	3	-	-	-

Appendix Table A.9 | List of families of leaf-litter invertebrates recorded on the plots. Total abundance, total biomass and frequence of the invertebrate families from the baseline survey (52 plots, no controls) as well as from year 1 (56 plots, control plots included) are given. Each family was assigned a feeding type which was taken from the literature. Data on biomass was calculated based on Appendix Table A.2. N = abundance, B = biomass, F = frequence (number of plots present on).

				Baseline			**Year 1**		
Family	Order	Feeding type (FT)	FT Source	N	B [mg/m^2]	F	N	B [mg/m^2]	F
Blattellidae	Blattodea	Detritivore	CSIRO (1991)	7	18.11	5	12	15.18	10
Corinnidae	Araneae	Predator	Jocqué and Dippenaar-Schoeman (2006)	17	79.22	14	15	64.10	14
Formicidae	Hymenoptera	Omnivore	CSIRO (2013)	1291	562.23	50	1551	1163.63	53
Gryllidae	Orthoptera	Omnivore	Schowalter (2009)	6	25.86	6	16	27.30	12
Oxyopidae	Araneae	Predator	Jocqué and Dippenaar-Schoeman (2006)	7	36.46	7	11	23.57	10
Theridiidae	Araneae	Predator	Jocqué and Dippenaar-Schoeman (2006)	45	43.31	23	39	31.61	23
Theridiosomatidae	Araneae	Predator	Jocqué and Dippenaar-Schoeman (2006)	19	4.36	13	1	0.17	1
Linyphiidae	Araneae	Predator	Jocqué and Dippenaar-Schoeman (2006)	28	9.91	18	64	20.29	23
Lycosidae	Araneae	Predator	Jocqué and Dippenaar-Schoeman (2006)	44	126.11	23	58	225.67	28
Mecistocephalidae	Geophilomorpha	Predator	Colloff et al. (2005)	-	-	-	3	39.98	3
Oonopidae	Araneae	Predator	Jocqué and Dippenaar-Schoeman (2006)	34	12.79	15	13	4.11	8
Phalacridae	Coleoptera	Fungivore	CSIRO (1991)	36	8.67	3	18	1.38	12
Staphylinidae	Coleoptera	Predator	CSIRO (1991)	113	24.53	20	34	7.27	17
Cicadellidae	Hemiptera	Herbivore	CSIRO (1991)	1	1.24	1	4	1.41	3
Gnaphosidae	Araneae	Predator	Jocqué and Dippenaar-Schoeman (2006)	36	16.40	24	4	3.25	4
Japygidae	Diplura	Predator	CSIRO (1991)	9	13.70	5	10	10.84	7
Mysmenidae	Araneae	Predator	Jocqué and Dippenaar-Schoeman (2006)	30	2.91	16	-	-	-
Acrididae	Orthoptera	Detritivore	CSIRO (1991)	-	-	-	2	233.96	1
Scolytinae	Coleoptera	Detritivore	CSIRO (1991)	3	0.74	3	1	0.11	1
Tetrigidae	Orthoptera	Detritivore	Kocarek et al. (2011)	4	14.90	4	3	37.38	2
Dipsocoridae	Hemiptera	Predator	CSIRO (2013)	22	2.66	10	14	1.40	9
Geophilidae	Geophilomorpha	Predator	CSIRO (1991)	16	207.48	10	1	12.15	1
Pyrgodesmidae	Polydesmida	Detritivore	CSIRO (1991)	70	62.15	20	65	63.11	20
Corylophidae	Coleoptera	Detritivore	CSIRO (1991)	-	-	-	6	1.23	5
Elateridae	Coleoptera	Herbivore	CSIRO (1991)	2	0.08	2	3	0.25	2
Blaberidae	Blattodea	Detritivore	CSIRO (1991)	10	19.14	7	9	3.59	6
Carabidae	Coleoptera	Herbivore	CSIRO (1991)	7	9.22	5	19	6.86	12
Dalodesmidae	Polydesmida	Detritivore	CSIRO (1991)	3	6.40	1	-	-	-
Aderidae	Coleoptera	Herbivore	CSIRO (1991)	-	-	-	10	2.10	5
Cydnidae	Hemiptera	Herbivore	CSIRO (1991)	8	3.42	2	11	3.33	6
Gracillariidae	Lepidoptera	Herbivore	CSIRO (1991)	-	-	-	3	0.97	3
Henicopidae	Lithobiomorpha	Predator	Colloff et al. (2005)	16	18.57	6	-	-	-

				Baseline			Year 1		
Family	Order	Feeding type (FT)	FT Source	N	B [mg/m^2]	F	N	B [mg/m^2]	F
Labiidae	Dermaptera	Omnivore	CSIRO (1991)	7	26.39	7	-	-	-
Largidae	Hemiptera	Herbivore	CSIRO (1991)	6	2.39	4	-	-	-
Mantidae	Mantodea	Predator	CSIRO (1991)	3	0.71	3	-	-	-
Oniscidae	Isopoda	Detritivore	Zimmer (2002)	1	0.18	1	-	-	-
Nabidae	Hemiptera	Predator	CSIRO (1991)	-	-	-	15	27.77	10
Pentatomidae	Hemiptera	Herbivore	CSIRO (1991)	-	-	-	5	543.95	4
Philosciidae	Isopoda	Detritivore	Zimmer (2002)	44	115.33	17	10	20.44	9
Salticidae	Araneae	Predator	Jocqué and Dippenaar-Schoeman (2006)	24	59.81	18	22	85.07	16
Scelionidae	Hymenoptera	Omnivore	CSIRO (1991)	-	-	-	2	0.10	2
Scutigerellidae	Symphyla	Detritivore	CSIRO (1991)	4	1.49	4	11	4.73	8
Phlaeothripidae	Thysanoptera	Fungivore	CSIRO (2013)	7	1.39	6	9	2.45	6
Protoschizomidae	Schizomida	Predator	Harvey (2015)	1	0.84	1	-	-	-
Silvanidae	Coleoptera	Predator	CSIRO (1991)	-	-	-	10	1.64	8
Pseudococcidae	Hemiptera	Herbivore	Ben-Dov (1994)	1	0.39	1	-	-	-
Sironidae	Opiliones	Predator	Pinto-da-Rocha et al. (2007)	1	14.35	1	-	-	-
Tenebrionidae	Coleoptera	Detritivore	CSIRO (1991)	13	56.57	9	-	-	-
Termitidae	Isoptera	Detritivore	CSIRO (1991)	10	8.93	1	1	1.48	1
Tetrablemmidae	Araneae	Predator	Jocqué and Dippenaar-Schoeman (2006)	10	1.50	6	2	0.51	2
Polyxenidae	Polyxenida	Detritivore	CSIRO (1991)	5	0.59	5	12	4.52	7
Rhinotermitidae	Isoptera	Detritivore	CSIRO (1991)	3	1.11	2	-	-	-
Thomisidae	Araneae	Predator	Jocqué and Dippenaar-Schoeman (2006)	13	39.57	10	12	22.65	8
Colydiidae	Coleoptera	Fungivore	CSIRO (1991)	2	0.33	2	-	-	-
Discolomidae	Coleoptera	Fungivore	CSIRO (1991)	-	-	-	1	0.39	1
Hydraenidae	Coleoptera	Herbivore	CSIRO (1991)	2	0.26	1	-	-	-
Miridae	Hemiptera	Herbivore	CSIRO (1991)	2	0.35	2	-	-	-
Pselaphidae	Coleoptera	Predator	CSIRO (1991)	-	-	-	7	1.48	7
Pachytroctidae	Psocoptera	Detritivore	Gruner (2004)	1	0.07	1	3	0.14	2
Schizopteridae	Hemiptera	Predator	Reagan and Waide (1996)	6	0.18	5	7	0.16	5
Reduviidae	Hemiptera	Predator	CSIRO (1991)	8	227.19	6	2	63.06	2
Zodariidae	Araneae	Predator	Jocqué and Dippenaar-Schoeman (2006)	-	-	-	5	19.51	5
Dignathodontidae	Geophilomorpha	Predator	CSIRO (1991)	1	0.25	1	1	0.25	1
Neobisiidae	Pseudoscorpion	Predator	Eisenbeis (2006)	1	0.29	1	1	0.24	1
Opisotretidae	Polydesmida	Detritivore	CSIRO (1991)	6	4.81	4	-	-	-
Cryptodesmidae	Polydesmida	Detritivore	David (2009)	1	0.70	1	2	2.10	2
Nitidulidae	Coleoptera	Herbivore	CSIRO (1991)	2	1.69	2	4	0.55	2
Aeolothripidae	Thysanoptera	Omnivore	CSIRO (2013)	-	-	-	2	0.27	2
Scydmaenidae	Coleoptera	Predator	CSIRO (1991)	3	0.08	1	4	0.69	3
Blattidae	Blattodea	Detritivore	CSIRO (1991)	8	7.08	7	2	0.66	2

				Baseline			**Year 1**		
Family	Order	Feeding type (FT)	FT Source	N	B [mg/m²]	F	N	B [mg/m²]	F
Delphacidae	Hemiptera	Herbivore	CSIRO (1991)	2	0.47	2	-	-	-
Lagrioidinae	Coleoptera	Herbivore	Costa et al. (1995)	-	-	-	1	0.26	1
Lygaeidae	Hemiptera	Herbivore	CSIRO (1991)	6	1.32	4	-	-	-
Drosophilidae	Diptera	Detritivore	McAlpine (1981)	1	0.50	1	-	-	-
Araneidae	Araneae	Predator	Jocqué and Dippenaar-Schoeman (2006)	3	7.66	3	7	25.20	7
Dryinidae	Hymenoptera	Parasite	Goulet and Huber (1993)	1	0.40	1	1	0.30	1
Glomeridae	Glomerida	Detritivore	David (2009)	4	11.06	3	-	-	-
Sparassidae	Araneae	Predator	Jocqué and Dippenaar-Schoeman (2006)	-	-	-	3	1.56	3
Ctenidae	Araneae	Predator	Jocqué and Dippenaar-Schoeman (2006)	2	15.84	2	4	16.92	3
Haplodesmidae	Polydesmida	Detritivore	CSIRO (1991)	-	-	-	6	1.65	4
Chrysomelidae	Coleoptera	Detritivore	CSIRO (1991)	2	13.02	2	15	1.98	2
Psoquillidae	Psocoptera	Detritivore	Gruner (2004)	3	0.96	3	-	-	-
Olpiidae	Pseudoscorpion	Predator	CSIRO (1991)	1	0.35	1	-	-	-
Ectopsocidae	Psocoptera	Detritivore	Gruner (2004)	-	-	-	12	0.49	3
Tetragnathidae	Araneae	Predator	Jocqué and Dippenaar-Schoeman (2006)	-	-	-	8	21.82	6
Labiduridae	Dermaptera	Omnivore	CSIRO (1991)	1	4.35	1	-	-	-
Pholcidae	Araneae	Predator	Jocqué and Dippenaar-Schoeman (2006)	1	0.21	1	-	-	-
Spongiphoridae	Dermaptera	Omnivore	CSIRO (1991)	22	84.49	2	-	-	-
Aphididae	Hemiptera	Herbivore	CSIRO (1991)	1	0.06	1	4	0.60	3
Heteroceridae	Coleoptera	Herbivore	Clarke (1973)	-	-	-	1	4.89	1
Liposcelidae	Psocoptera	Detritivore	Gruner (2004)	1	0.24	1	3	0.05	1
Tridactylidae	Orthoptera	Herbivore	CSIRO (1991)	1	2.54	1	-	-	-
Ptiliidae	Coleoptera	Fungivore	CSIRO (1991)	1	0.03	1	1	0.03	1
Tingidae	Hemiptera	Herbivore	CSIRO (1991)	3	0.30	2	-	-	-
Ceratocombidae	Hemiptera	Predator	CSIRO (2013)	-	-	-	1	0.01	1
Stratiomydae	Diptera	Detritivore	CSIRO (1991)	1	4.54	1	-	-	-
Armadillidae	Isopoda	Detritivore	Zimmer (2002)	3	29.15	1	-	-	-
Tettigoniidae	Orthoptera	Omnivore	CSIRO (1991)	1	3.11	1	-	-	-
Myrmeleontidae	Neuroptera	Predator	Gepp and Hölzel (1989)	1	2.00	1	-	-	-
Curculionidae	Coleoptera	Detritivore	CSIRO (1991)	-	-	-	1	1.62	1
Scarabaeidae	Coleoptera	Detritivore	CSIRO (1991)	-	-	-	1	8.66	1
Cryptopidae	Scolopendromorpha	Predator	Colloff et al. (2005)	4	13.23	2	-	-	-
Campodeidae	Diplura	Omnivore	CSIRO (1991)	1	0.34	1	-	-	-
Epipsocidae	Psocoptera	Detritivore	Gruner (2004)	2	0.08	1	-	-	-
Paradoxosomatidae	Polydesmida	Detritivore	David (2009)	1	0.54	1	-	-	-
Platyrhacidae	Polydesmida	Detritivore	David (2009)	1	22.35	1	-	-	-
Hubbardiidae	Schizomida	Predator	(Harvey, 2015)	1	9.90	1	-	-	-

				Baseline			**Year 1**		
Family	Order	Feeding type (FT)	FT Source	N	B [mg/m²]	F	N	B [mg/m²]	F
Phalangodidae	Opiliones	Predator	Pinto-da-Rocha et al. (2007)	4	7.15	2	-	-	-
Mesopsocidae	Psocoptera	Detritivore	Gruner (2004)	1	0.05	1	-	-	-
Hemipsocidae	Psocoptera	Detritivore	Gruner (2004)	-	-	-	3	0.09	1
Pyralidae	Lepidoptera	Herbivore	Stehr (2005)	-	-	-	1	1.82	1
Gelechiidae	Lepidoptera	Herbivore	Stehr (2005)	-	-	-	1	0.58	1
Anisolabididae	Dermaptera	Omnivore	Capinera (2008)	-	-	-	3	76.89	1

Appendix Table A.10 | List of families of herb-layer invertebrates recorded on the plots. Total abundance, total biomass and frequence of the invertebrate families from the baseline survey (52 plots, no controls) as well as from year 1 (56 plots, control plots included) are given. Each family was assigned a feeding type which was derived from the literature. Data on biomass was calculated based on Appendix Table A.2. N = abundance, B = biomass, F = frequence (number of plots present on).

				Baseline			**Year 1**		
Order	Family	Feeding type (FT)	FT Source	N	B [mg/m²]	F	N	B [mg/m²]	F
Hemiptera	Aphididae	Herbivore	CSIRO (1991)	14	0.81	5	38	3.32	21
Araneae	Corinnidae	Predator	Jocqué and Dippenaar-Schoeman (2006)	-	-	-	7	7.45	7
Hymenoptera	Formicidae	Omnivore	CSIRO (2013)	91	68.48	34	255	213.86	52
Orthoptera	Gryllidae	Omnivore	Schowalter (2009)	499	3064.30	51	764	7354.87	54
Araneae	Salticidae	Predator	Jocqué and Dippenaar-Schoeman (2006)	23	92.96	15	36	140.86	25
Diptera	Culicidae	Predator	CSIRO (1991)	26	21.68	20	5	1.21	5
Diptera	Tipulidae	Detritivore	CSIRO (1991)	23	25.59	14	5	2.75	5
Hymenoptera	Braconidae	Parasite	Goulet and Huber (1993)	8	2.94	8	32	15.95	17
Hymenoptera	Scelionidae	Omnivore	CSIRO (1991)	25	3.62	12	89	10.69	37
Orthoptera	Acrididae	Detritivore	CSIRO (1991)	58	6282.27	24	100	10985.43	38
Hemiptera	Cicadellidae	Herbivore	CSIRO (1991)	96	123.60	26	146	196.70	40
Hymenoptera	Eucoilidae	Omnivore	CSIRO (1991)	-	-	-	2	0.08	2
Araneae	Linyphiidae	Predator	Jocqué and Dippenaar-Schoeman (2006)	2	3.95	2	17	30.45	16
Mantodea	Mantidae	Predator	CSIRO (1991)	8	298.35	7	14	527.72	12
Hemiptera	Miridae	Herbivore	CSIRO (1991)	30	5.29	18	50	11.17	16
Araneae	Oxyopidae	Predator	Jocqué and Dippenaar-Schoeman (2006)	79	829.09	30	91	574.37	38
Araneae	Sparassidae	Predator	Jocqué and Dippenaar-Schoeman (2006)	-	-	-	4	22.34	4
Araneae	Lycosidae	Predator	Jocqué and Dippenaar-Schoeman (2006)	46	461.74	26	85	1273.62	36
Blattodea	Blattellidae	Detritivore	CSIRO (1991)	15	178.96	15	7	8.19	5
Hymenoptera	Diapriidae	Omnivore	CSIRO (1991)	3	0.46	3	-	-	-
Orthoptera	Tettigoniidae	Omnivore	CSIRO (1991)	19	703.32	11	20	2320.63	16
Thysanoptera	Aeolothripidae	Omnivore	CSIRO (2013)	-	-	-	7	0.25	7
Hemiptera	Aleyrodidae	Herbivore	Pappas et al. (2013)	-	-	-	23	1.80	14
Diptera	Cecidomyiidae	Detritivore	CSIRO (1991)	9	0.27	6	72	3.53	34
Hemiptera	Dictyopharidae	Herbivore	Wilson et al. (1994)	-	-	-	2	20.33	2
Hymenoptera	Mymaridae	Parasite	Goulet and Huber (1993)	2	0.06	2	59	1.26	27
Thysanoptera	Thripidae	Herbivore	CSIRO (1991)	-	-	-	22	1.28	13
Araneae	Theridiidae	Predator	Jocqué and Dippenaar-Schoeman (2006)	28	91.57	21	8	3.24	7
Araneae	Thomisidae	Predator	Jocqué and Dippenaar-Schoeman (2006)	22	76.50	14	8	22.93	6
Coleoptera	Staphylinidae	Predator	CSIRO (1991)	4	3.11	4	3	1.67	3
Diptera	Asteiidae	Fungivore	CSIRO (1991)	22	3.30	9	5	0.55	3

				Baseline			**Year 1**		
Order	Family	Feeding type (FT)	FT Source	N	B [mg/m^2]	F	N	B [mg/m^2]	F
Diptera	Ceratopogonidae	Detritivore	McAlpine (1981)	11	2.01	8	11	0.62	6
Diptera	Phoridae	Detritivore	CSIRO (1991)	2	0.10	2	-	-	-
Diptera	Piophilidae	Detritivore	McAlpine (1981)	3	0.21	3	-	-	-
Diptera	Psychodidae	Detritivore	CSIRO (1991)	4	0.13	4	1	0.03	1
Hemiptera	Anthocoridae	Herbivore	CSIRO (1991)	10	1.57	2	-	-	-
Hemiptera	Delphacidae	Herbivore	CSIRO (1991)	53	71.70	21	23	12.66	18
Hymenoptera	Trichogrammatidae	Omnivore	CSIRO (2013)	1	0.00	1	15	0.18	13
Lepidoptera	Thyrididae	Herbivore	CSIRO (1991)	4	21.64	4	-	-	-
Lithobiomorpha	Henicopidae	Predator	Colloff et al. (2005)	1	0.21	1	-	-	-
Araneae	Araneidae	Predator	Jocqué and Dippenaar-Schoeman (2006)	12	70.62	9	2	4.00	2
Hemiptera	Cixiidae	Herbivore	CSIRO (1991)	-	-	-	14	3.91	10
Hymenoptera	Encyrtidae	Parasite	Goulet and Huber (1993)	1	0.04	1	18	0.53	16
Hymenoptera	Eulophidae	Parasite	Goulet and Huber (1993)	12	1.86	9	22	2.75	17
Hemiptera	Nabidae	Predator	CSIRO (1991)	2	1.06	2	27	88.67	13
Thysanoptera	Phlaeothripidae	Fungivore	CSIRO (2013)	6	0.55	3	11	1.39	6
Lepidoptera	Pyralidae	Herbivore	Stehr (2005)	1	8.15	1	1	1.50	1
Orthoptera	Tetrigidae	Detritivore	Kocarek et al. (2011)	36	1010.79	22	37	978.99	23
Araneae	Theridiosomatidae	Predator	Jocqué and Dippenaar-Schoeman (2006)	8	1.14	7	75	24.19	34
Coleoptera	Aderidae	Herbivore	CSIRO (1991)	4	2.30	4	4	3.45	4
Diptera	Sciaridae	Detritivore	CSIRO (1991)	19	0.98	10	3	0.04	3
Diptera	Sphaeroceridae	Detritivore	CSIRO (1991)	5	0.76	4	-	-	-
Hemiptera	Tropiduchidae	Herbivore	CSIRO (1991)	10	44.55	6	2	2.23	2
Hymenoptera	Vespidae	Predator	Goulet and Huber (1993)	3	20.14	2	-	-	-
Lepidoptera	Tineidae	Omnivore	CSIRO (1991)	8	5.17	6	-	-	-
Polydesmida	Pyrgodesmidae	Detritivore	CSIRO (1991)	5	9.02	4	-	-	-
Hymenoptera	Ceraphronidae	Parasite	Goulet and Huber (1993)	5	0.10	4	27	0.72	17
Neuroptera	Chrysopidae	Predator	CSIRO (1991)	-	-	-	1	6.05	1
Lepidoptera	Gelechiidae	Herbivore	Stehr (2005)	-	-	-	3	2.06	3
Lepidoptera	Gracillariidae	Herbivore	CSIRO (1991)	-	-	-	12	3.57	11
Orthoptera	Gryllacrididae	Herbivore	CSIRO (1991)	-	-	-	4	325.74	3
Coleoptera	Phalacridae	Fungivore	CSIRO (1991)	1	0.30	1	2	0.60	2
Araneae	Pholcidae	Predator	Jocqué and Dippenaar-Schoeman (2006)	-	-	-	1	2.31	1
Diptera	Chloropidae	Detritivore	CSIRO (1991)	8	0.75	6	2	0.29	2
Diptera	Mycetophilidae	Fungivore	McAlpine (1981)	1	0.80	1	1	0.14	1
Araneae	Philodromidae	Predator	Jocqué and Dippenaar-Schoeman (2006)	-	-	-	1	30.76	1
Coleoptera	Carabidae	Predator	CSIRO (1991)	1	4.04	1	2	4.17	2
Diptera	Lauxaniidae	Detritivore	CSIRO (1991)	5	2.72	4	-	-	-
Hemiptera	Meenoplidae	Herbivore	CSIRO (1991)	2	2.18	2	-	-	-

				Baseline			Year 1		
Order	Family	Feeding type (FT)	FT Source	N	B [mg/m^2]	F	N	B [mg/m^2]	F
Hemiptera	Pseudococcidae	Herbivore	Ben-Dov (1994)	1	0.02	1	-	-	-
Hymenoptera	Ichneumonidae	Parasite	Goulet and Huber (1993)	16	5.72	12	1	2.02	1
Lepidoptera	Acanthopteroctetidae	Herbivore	CSIRO (1991)	1	6.09	1	-	-	-
Lepidoptera	Geometridae	Herbivore	Stehr (2005)	6	5.79	5	-	-	-
Hemiptera	Hydrometridae	Predator	CSIRO (1991)	-	-	-	2	17.94	2
Hemiptera	Derbidae	Herbivore	CSIRO (1991)	3	5.25	3	-	-	-
Hemiptera	Eriosomatidae	Herbivore	CSIRO (1991)	-	-	-	3	0.21	3
Diptera	Muscidae	Omnivore	CSIRO (1991)	3	0.61	3	3	1.31	3
Diptera	Deuterophlebiidae	Detritivore	Courtney 1997	-	-	-	1	0.01	1
Araneae	Dysderidae	Predator	CSIRO (1991)	-	-	-	1	5.79	1
Hemiptera	Reduviidae	Predator	CSIRO (1991)	5	34.31	5	5	606.11	4
Orthoptera	Tridactylidae	Herbivore	CSIRO (1991)	2	13.35	2	6	39.30	5
Hymenoptera	Bethylidae	Omnivore	CSIRO (1991)	-	-	-	3	1.86	3
Blattodea	Blaberidae	Detritivore	CSIRO (1991)	1	0.77	1	9	32.00	8
Diptera	Dolichopodidae	Predator	McAlpine (1981)	1	1.27	1	6	0.55	5
Diptera	Calliphoridae	Herbivore	CSIRO (1991)	2	1.19	1	-	-	-
Thysanoptera	Merothripidae	Detritivore	CSIRO (1991)	-	-	-	2	0.14	2
Lepidoptera	Noctuidae	Herbivore	Stehr (2005)	2	1.25	2	4	4.19	3
Hemiptera	Ricaniidae	Herbivore	CSIRO (1991)	-	-	-	1	0.26	1
Blattodea	Blattidae	Detritivore	CSIRO (1991)	1	5.42	1	8	177.08	8
Psocoptera	Pachytroctidae	Detritivore	Gruner (2004)	-	-	-	4	0.15	4
Diptera	Clusiidae	Detritivore	CSIRO (1991)	1	0.55	1	-	-	-
Ephemeroptera	Baetidae	Detritivore	CSIRO (1991)	3	4.52	3	1	1.86	1
Hymenoptera	Chalcididae	Parasite	Goulet and Huber (1993)	-	-	-	3	1.17	3
Hymenoptera	Platygastridae	Parasite	Goulet and Huber (1993)	2	0.05	2	1	0.03	1
Hemiptera	Schizopteridae	Predator	Reagan and Waide (1996)	-	-	-	6	0.52	6
Hemiptera	Coreidae	Herbivore	Schuh and Slater (1995)	1	41.75	1	-	-	-
Hymenoptera	Tiphiidae	Parasite	Goulet and Huber (1993)	2	4.76	1	-	-	-
Coleoptera	Chrysomelidae	Herbivore	CSIRO (1991)	4	30.50	4	3	4.45	3
Hemiptera	Tingidae	Herbivore	CSIRO (1991)	1	0.06	1	3	0.20	3
Lepidoptera	Zygaenidae	Herbivore	CSIRO (1991)	1	8.82	1	-	-	-
Araneae	Pisauridae	Predator	CSIRO (1991)	1	91.93	1	-	-	-
Hemiptera	Aradidae	Herbivore	CSIRO (1991)	1	1.46	1	1	0.44	1
Araneae	Anapidae	Predator	Jocqué and Dippenaar-Schoeman (2006)	-	-	-	3	4.51	3
Diptera	Simuliidae	Herbivore	CSIRO (1991)	-	-	-	4	0.18	4
Hemiptera	Lophopidae	Herbivore	CSIRO (1991)	1	0.68	1	-	-	-
Hymenoptera	Figitidae	Omnivore	CSIRO (1991)	1	0.06	1	-	-	-
Coleoptera	Anthicidae	Detritivore	CSIRO (1991)	-	-	-	1	1.10	1
Hymenoptera	Cynipidae	Herbivore	Goulet and Huber (1993)	-	-	-	2	0.25	1

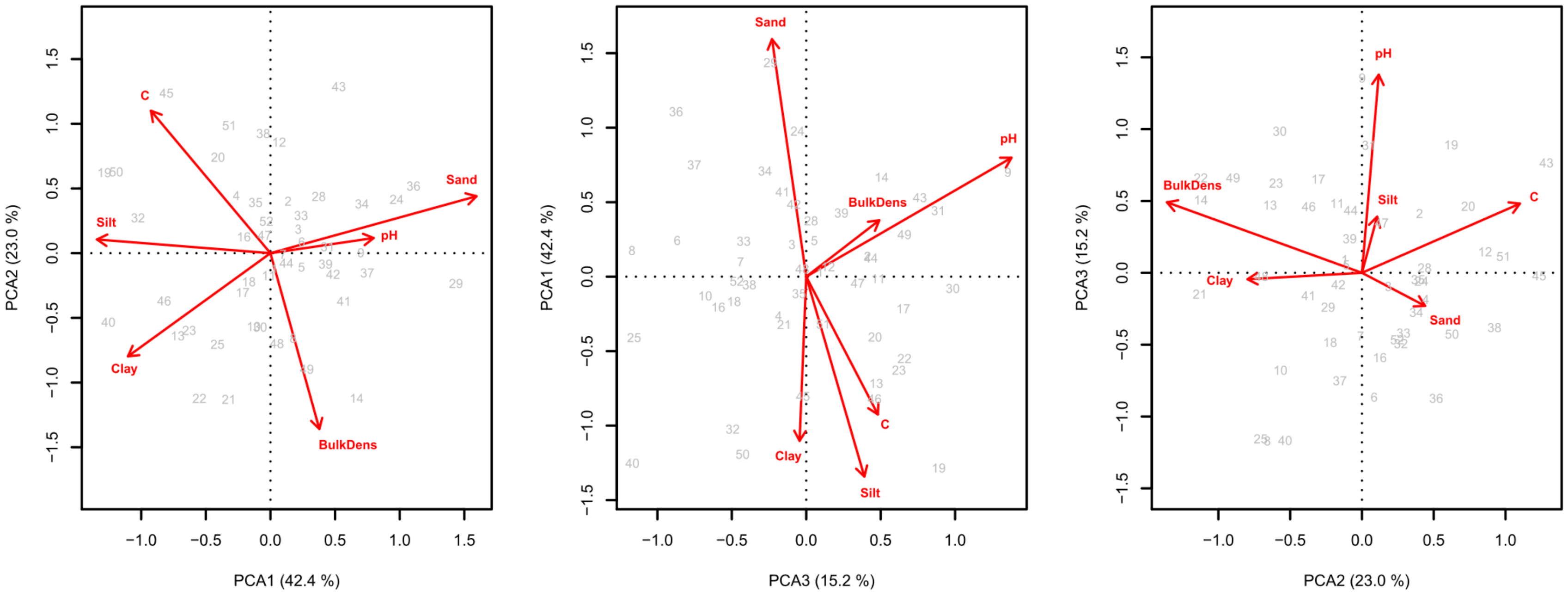
				Baseline			Year 1		
Order	Family	Feeding type (FT)	FT Source	N	B [mg/m²]	F	N	B [mg/m²]	F
Araneae	Deinopidae	Predator	Jocqué and Dippenaar-Schoeman (2006)	-	-	-	1	22.25	1
Polyxenida	Polyxenidae	Detritivore	CSIRO (1991)	-	-	-	2	0.64	2
Diptera	Bibionidae	Detritivore	CSIRO (1991)	1	11.80	1	-	-	-
Diptera	Drosophilidae	Detritivore	McAlpine (1981)	1	0.69	1	-	-	-
Hemiptera	Flatidae	Herbivore	CSIRO (1991)	4	3.72	3	-	-	-
Hemiptera	Geocoridae	Predator	Schuh and Slater (1995)	2	1.53	2	-	-	-
Diptera	Chironomidae	Detritivore	McAlpine (1981)	2	0.44	1	1	0.06	1
Araneae	Ochyroceratidae	Predator	Jocqué and Dippenaar-Schoeman (2006)	-	-	-	1	0.90	1
Araneae	Mysmenidae	Predator	Jocqué and Dippenaar-Schoeman (2006)	1	0.08	1	-	-	-
Diptera	Opomyzidae	Detritivore	McAlpine (1981)	3	0.61	3	-	-	-
Hymenoptera	Mymarommatidae	Fungivore	Goulet and Huber (1993)	-	-	-	3	0.04	3
Isoptera	Termitidae	Detritivore	CSIRO (1991)	-	-	-	1	2.67	1
Lepidoptera	Tortricidae	Herbivore	CSIRO (1991)	1	0.32	1	-	-	-
Psocoptera	Lepidopsocidae	Detritivore	Gruner (2004)	-	-	-	3	0.69	3
Phasmatodea	Phasmatidae	Herbivore	Bedford (1978)	-	-	-	1	1220.85	1
Araneae	Ctenidae	Predator	Jocqué and Dippenaar-Schoeman (2006)	-	-	-	1	10.97	1
Psocoptera	Elipsocidae	Detritivore	Gruner (2004)	-	-	-	2	0.08	2
Hemiptera	Alydidae	Herbivore	CSIRO (1991)	-	-	-	2	56.01	1
Psocoptera	Liposcelidae	Detritivore	Gruner (2004)	-	-	-	6	0.02	3
Hemiptera	Pentatomidae	Herbivore	CSIRO (1991)	-	-	-	1	117.74	1
Araneae	Tetragnathidae	Predator	Jocqué and Dippenaar-Schoeman (2006)	-	-	-	1	1.46	1
Araneae	Gnaphosidae	Predator	Jocqué and Dippenaar-Schoeman (2006)	-	-	-	2	5.18	2
Hymenoptera	Sphecidae	Predator	CSIRO (1991)	-	-	-	1	13.89	1
Psocoptera	Ectopsocidae	Detritivore	Gruner (2004)	-	-	-	1	0.02	1
Araneae	Clubionidae	Predator	Jocqué and Dippenaar-Schoeman (2006)	-	-	-	1	7.74	1
Hymenoptera	Aphelinidae	Parasite	CSIRO (1991)	1	0.06	1	2	0.14	1
Araneae	Miturgidae	Predator	Jocqué and Dippenaar-Schoeman (2006)	-	-	-	1	2.26	1
Diptera	Pipunculidae	Parasite	McAlpine (1981)	2	2.92	1	-	-	-
Diptera	Scatopsidae	Detritivore	McAlpine (1981)	1	0.06	1	-	-	-
Psocoptera	Psyllipsocidae	Detritivore	Gruner (2004)	-	-	-	2	1.91	2
Coleoptera	Curculionidae	Detritivore	CSIRO (1991)	1	0.50	1	-	-	-
Coleoptera	Anthribidae	Fungivore	CSIRO (1991)	2	0.58	1	-	-	-
Phthiraptera	Trichodectidae	Parasite	CSIRO (1991)	1	0.01	1	-	-	-

Appendix Table A.11 | Biotic data (first year; 56 plots). S_{spp} = species richness, N = abundance, B = body mass, S_{fam} = family richness, LL inv. = leaf-litter invertebrates, HL inv. = herb-layer invertebrates.

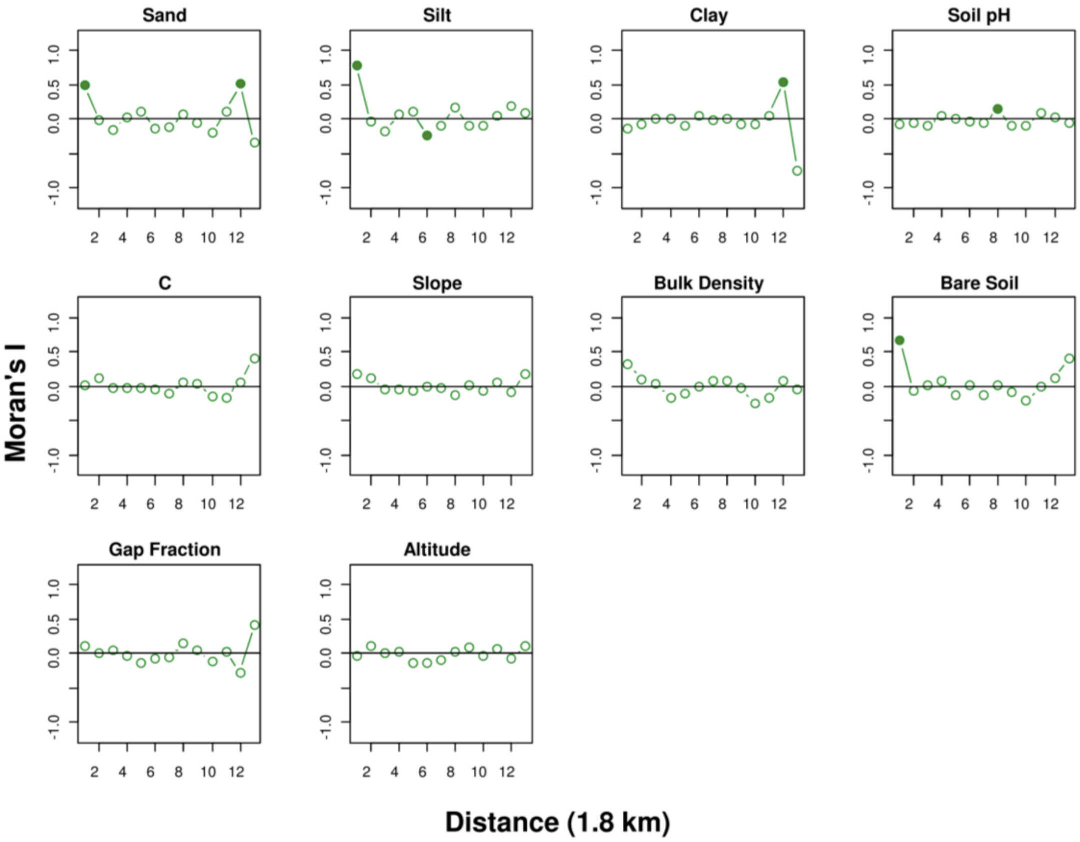
PlotID	Bird S_{spp}	Bird N	Bird B	LL inv. S_{fam}	LL inv. N	LL inv. B	HL inv. S_{fam}	HL inv. N	HL inv. B
1	4	10	243.42	10	42	42.95	5	6	64.52
2	6	13	765.44	9	20	288.91	11	24	161.83
3	6	11	513.33	7	31	9.86	14	42	438.59
4	5	13	739.86	15	88	224.38	26	120	282.16
5	5	13	514.29	5	35	21.33	10	21	199.73
6	7	16	579.26	7	14	19.93	22	58	532.47
7	6	10	299.32	11	15	16.42	22	45	428.10
8	8	19	2132.60	3	11	6.96	6	6	2.14
9	7	17	1313.05	7	10	46.52	22	53	692.00
10	6	14	887.65	4	10	14.69	12	37	178.17
11	7	11	641.10	6	30	18.36	24	57	735.88
12	5	8	178.96	12	43	19.45	30	86	320.63
13	7	10	753.19	10	74	11.79	16	57	490.74
14	4	13	699.06	4	10	4.45	10	19	79.50
15	6	13	1692.13	16	49	47.05	17	32	1086.18
16	6	10	234.05	4	14	29.50	14	28	206.38
17	5	7	352.63	7	16	4.66	12	20	513.22
18	3	15	459.39	5	6	9.14	12	22	103.47
19	6	11	1723.40	3	38	33.80	15	31	14.18
20	6	10	430.03	5	11	28.16	21	49	766.57
21	5	11	653.14	8	26	37.92	21	77	1268.84
22	5	11	444.66	3	15	42.93	5	13	6.64
23	5	11	506.14	16	33	13.55	25	91	669.98
24	5	9	298.20	6	97	123.11	20	65	707.65
25	6	15	1251.86	2	7	42.22	12	31	489.17
26	4	9	213.43	15	68	55.71	16	53	1965.31
27	7	10	967.46	10	115	269.54	21	56	409.00
28	3	9	304.58	7	217	253.83	4	8	89.81
29	7	13	720.56	14	26	17.11	24	52	394.15
30	5	10	115.40	3	3	0.72	12	16	22.44
31	2	6	76.20	4	9	6.35	12	17	1393.20
32	4	9	176.610	7	13	12.55	17	42	1087.27
33	4	8	716.70	4	9	18.57	20	81	384.49
34	3	6	221.240	17	27	58.33	15	28	507.55
35	2	4	73.37	12	44	26.66	11	49	588.41
36	4	6	117.91	5	52	48.07	21	37	480.15
37	8	15	754.06	3	226	265.06	16	79	502.26
38	4	12	234.39	13	62	21.62	24	69	307.77
39	7	17	1000.52	9	35	58.51	10	22	532.30
40	3	7	123.12	7	11	10.16	9	19	43.07
41	2	5	120.88	5	16	7.13	12	49	1159.40
42	4	6	276.35	3	10	3.89	17	39	228.19
43	6	10	305.30	9	16	25.02	24	97	975.05
44	5	9	615.08	5	33	45.23	17	26	105.81
45	6	16	1154.07	11	31	176.93	18	43	248.05
46	3	4	222.70	10	11	21.36	14	44	1007.57
47	3	4	93.55	14	115	31.61	15	67	1444.66
48	5	8	373.52	2	8	4.64	11	32	186.84
49	1	3	169.80	4	10	11.36	17	69	631.61
50	2	5	197.72	22	104	40.46	12	40	569.62
51	5	10	644.46	10	15	11.73	24	77	141.15
52	6	9	519.56	6	31	12.68	16	48	987.91
53	3	10	264.12	14	44	190.47	9	12	228.82
54	3	8	376.63	6	12	45.79	16	25	424.78
55	2	11	131.80	8	43	29.74	14	21	42.52
56	4	10	812.85	16	77	40.40	15	26	106.60

Appendix Table A.12 | Species/family numbers, beta diversity and Simpson index for plants, birds and leaf-litter invertebrates in forest, oil palm and the experimental site EFForTS-BEE.

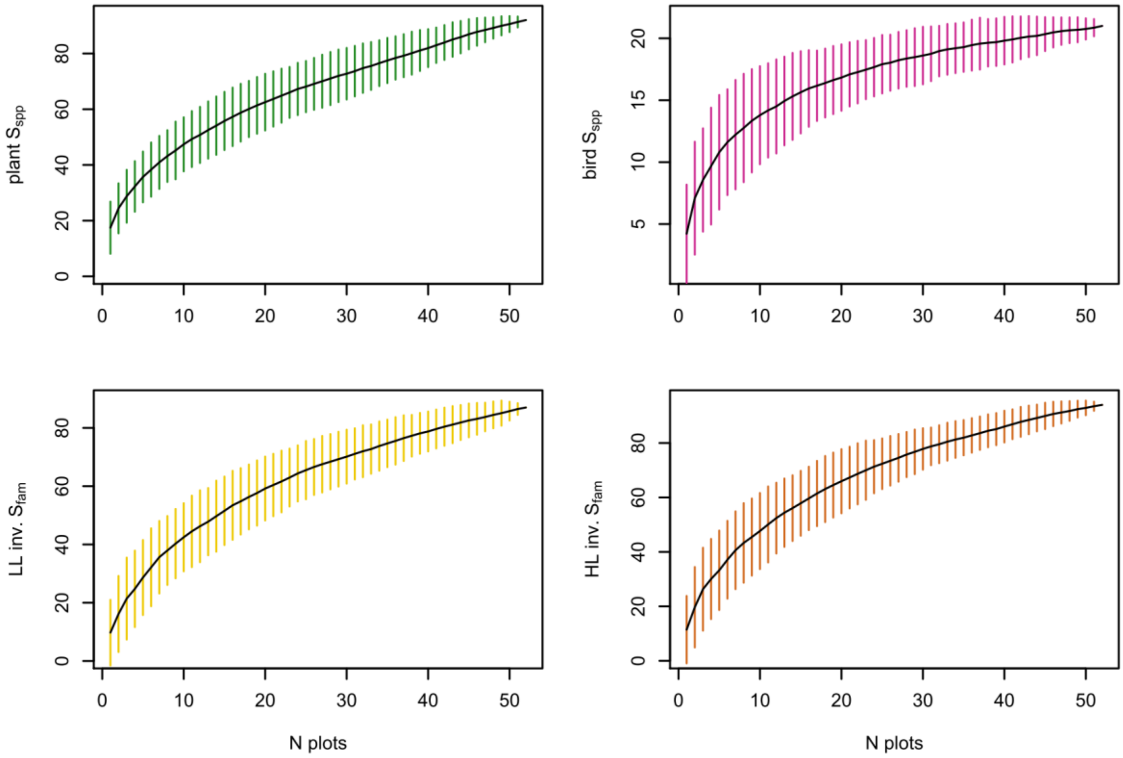
		Forest	Oil palm	EFForTS-BEE
Plants	species richness (total)		78	53
	mean species richness (±SD)		32.25 ± 13.05	25.25 ± 6.9
Birds	species richness (total)	30	9	6
	Mean species richness (±SD)	11 ± 4.08	4.5 ± 1.29	2.25 ± 1.5
	mean α- diversity (±SD)	0.87 ± 0.05	0.58 ± 0.07	0.34 ± 0.4
Leaf-litter invertebrates	family richness (total)	47	25	16
	mean family richness	19.5 ± 7.94	7.5 ± 8.35	5.5 ± 2.38
	mean α- diversity (±SD)	0.65 ± 0.06	0.47 ± 0.26	0.52 ± 0.23



Appendix Figure A.1| Principal component analysis of the soil data.



Appendix Figure A.2 | Spatial correlogram to check for spatial autocorrelation of the site-condition variables. Moran's I is given as a function of distance. Values significant at a nominal (two-sided) 5%-level are represented by filled circles and non-significant values by open circles.



Appendix Figure A.3 | Species accumulation curves for plant and bird species (S_{spp}) as well as for families (S_{fam}) of leaf-litter (LL) and herb-layer (HL) invertebrates (inv.).

Supplementary references to Appendix A

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B Supplementary material to chapter 3

Appendix Table B.1 | P-values of pairwise comparisons of differences in height between the species when planted.

	Archidendron pauciflorum	*Durio zibethinus*	*Dyera polyphylla*	*Parkia speciosa*	*Peronema canescens*
Durio zibethinus	0.000	NA	NA	NA	NA
Dyera polyphylla	0.000	0.000	NA	NA	NA
Parkia speciosa	1.000	0.000	0.000	NA	NA
Peronema canescens	1.000	0.000	0.000	0.116	NA
Shorea leprosula	0.000	0.000	0.000	0.000	0.000

Appendix Table B.2 | P-values of pairwise comparisons of differences in diameter between the species when planted.

	Archidendron pauciflorum	*Durio zibethinus*	*Dyera polyphylla*	*Parkia speciosa*	*Peronema canescens*
Durio zibethinus	1.000	NA	NA	NA	NA
Dyera polyphylla	0.000	0.000	NA	NA	NA
Parkia speciosa	0.000	0.000	0.141	NA	NA
Peronema canescens	0.000	0.000	0.000	0.000	NA
Shorea leprosula	0.000	0.000	0.000	0.000	1.000

Appendix Table B.3 | P-values of pairwise comparisons of differences in relative height increment (*rHi*) two years after planting.

	Archidendron pauciflorum	*Durio zibethinus*	*Dyera polyphylla*	*Parkia speciosa*	*Peronema canescens*
Durio zibethinus	0.000000	NA	NA	NA	NA
Dyera polyphylla	0.000000	1.000000	NA	NA	NA
Parkia speciosa	0.000000	0.000000	0.000000	NA	NA
Peronema canescens	0.000000	0.000000	0.000000	0.000000	NA
Shorea leprosula	0.000000	0.000416	1.000000	0.000000	0.000000

Appendix Table B.4 | P-values of pairwise comparisons of differences in relative basal area increment (*rBAi*) two years after planting.

	Archidendron pauciflorum	*Durio zibethinus*	*Dyera polyphylla*	*Parkia speciosa*	*Peronema canescens*
Durio zibethinus	0.0000000	*NA*	*NA*	*NA*	*NA*
Dyera polyphylla	0.0000000	1.0000000	*NA*	*NA*	*NA*
Parkia speciosa	1.0000000	0.0000000	0.0000000	*NA*	*NA*
Peronema canescens	0.0000000	0.0000000	0.0000000	0.0000000	*NA*
Shorea leprosula	1.0000000	0.0000000	0.0000000	1.0000000	0.0000000

Appendix Table B.5 | P-values of pairwise comparisons of differences in survival rates two years after planting.

	Archidendron pauciflorum	*Durio zibethinus*	*Dyera polyphylla*	*Parkia speciosa*	*Peronema canescens*
Durio zibethinus	0.0000000	*NA*	*NA*	*NA*	*NA*
Dyera polyphylla	0.0000000	0.0000000	*NA*	*NA*	*NA*
Parkia speciosa	0.7558510	0.0000000	0.0000000	*NA*	*NA*
Peronema canescens	1.0000000	0.0000000	0.0000000	1.0000000	*NA*
Shorea leprosula	0.0000000	0.0000000	0.0000000	0.0000000	0.0000000

Appendix Table B.6 | All data on plot level as incorporated to model plot-specific growth parameters and survival rates. Abbreviations and units: *A.pau= Archidendron pauciflorum, D. pol = Dyera polyphylla, D. zib= Durio zibethinus, P. can= Peronema canescens, P. spe = Parkia speciosa, S. lep= Shorea leprosula, rHi*= relative height increment [cm/ (cm*y)], *rBAi*= relative basal area increment [cm²/ (cm²*y)], elev= elevation [m a.s.l.], slope [°], clay-, silt-, sand-, and C-content [%], bulk d= bulk density [g/cm³], plot size [m²], Shannon = Shannon index, veg =vegetation cover [%], can op = canoy openness [proportional].

plot ID	*A. pau*	*D. pol*	*D. zib*	*P. can*	*P. spe*	*S. lep*	rHi	rBAi	dead trees	trees alive	elev	slope	clay	silt	sand	C	pH	bulk d	plot size	Shannon	veg	can op
1	0	0	0	0	1	0	0.84	1.83	39	361	55	12.2	27.8	43.3	28.9	1.84	4.47	1.10	1600	0.00	70	0.28
2	0	0	1	0	1	1	0.73	1.66	46	53	40	12.6	26.2	40.6	33.2	2.29	4.61	1.01	400	0.96	70	0.35
3	0	1	1	0	0	0	0.47	1.15	64	36	48	7.8	27.4	37.3	35.3	2.01	4.47	1.03	400	0.68	70	0.40
4	0	0	0	0	0	1	0.44	1.92	14	11	48	7.6	32.0	41.0	26.9	2.39	4.40	0.93	100	0.00	40	0.43
5	1	0	0	0	0	0	0.84	1.72	69	331	68	6.8	20.2	45.0	34.8	1.82	4.41	1.18	1600	0.00	70	0.44
6	0	0	0	1	0	0	1.20	2.08	0	6	39	18.8	27.7	35.0	37.3	1.67	4.26	0.99	25	0.00	65	0.11
7	0	0	0	1	1	1	0.76	1.92	176	223	35	8.9	33.6	33.2	33.2	2.00	4.37	1.02	1600	1.08	85	0.45
8	0	0	0	0	0	1	-0.64	0.60	5	1	56	5.1	29.0	37.2	33.8	1.23	4.08	1.17	25	0.00	55	0.05
9	1	1	0	0	1	0	0.90	1.95	6	18	45	17.8	30.0	30.7	39.3	2.09	5.02	1.13	100	1.03	40	0.18
11	0	1	0	0	0	0	0.93	1.14	24	1	52	18.3	33.8	41.9	24.3	1.68	4.68	1.02	100	0.00	50	0.18
12	0	0	1	0	0	0	0.42	1.26	80	20	58	16.8	19.7	45.1	35.2	2.44	4.50	0.94	400	0.00	90	0.36
13	0	0	0	1	0	0	0.97	2.20	1	24	51	9.5	34.7	54.3	11.1	2.16	4.38	1.24	100	0.00	40	0.70
14	0	0	1	0	0	0	0.20	0.55	24	1	46	10.6	30.4	34.5	35.1	1.04	4.68	1.33	100	0.00	40	0.30
15	1	0	0	0	0	0	0.95	2.04	16	84	70	8.2	27.9	47.8	24.4	3.70	4.26	0.97	400	0.00	60	0.49
16	0	1	1	0	1	0	NA	NA	6	0	58	8.7	25.3	46.8	27.9	1.91	4.21	1.02	25	0.64	80	0.19
17	0	0	0	0	0	1	0.56	1.85	38	62	37	5.1	31.2	44.1	24.7	2.57	4.49	1.26	400	0.00	80	0.42
18	0	1	0	1	0	0	0.95	1.99	3	3	40	6.6	31.5	43.1	25.4	1.63	4.30	1.04	25	0.00	80	0.17
19	1	1	1	1	1	1	0.86	2.07	42	54	54	2.4	37.2	54.8	8.0	3.94	4.41	1.05	400	1.42	65	0.41
20	1	0	0	0	0	0	0.78	1.69	9	16	39	2.0	29.4	47.0	23.5	2.75	4.56	0.91	100	0.00	75	0.34
21	1	1	1	1	1	1	0.96	2.21	7	17	56	16.2	38.9	42.5	18.6	1.65	4.28	1.30	100	1.58	75	0.31
22	1	0	0	0	0	1	0.12	0.28	4	2	44	20.8	46.7	43.8	9.5	1.78	4.58	1.23	25	0.00	65	0.04
23	1	1	1	1	1	1	0.80	2.04	165	231	38	20.9	33.1	53.0	13.9	2.38	4.40	1.29	1600	1.60	70	0.20
24	0	0	1	1	0	0	0.94	2.15	199	201	58	6.8	23.7	23.0	53.3	2.09	4.61	1.04	1600	0.28	85	0.36
25	0	0	0	0	1	0	0.95	1.87	0	6	44	11.1	37.4	43.1	19.5	1.24	4.07	1.06	25	0.00	95	0.07
26	0	1	0	0	0	1	0.45	1.89	351	49	46	6.4	37.7	36.4	25.9	2.28	5.28	1.10	1600	0.27	95	0.32
27	0	0	0	1	1	0	1.06	2.33	1	23	38	1.8	43.7	40.9	15.4	2.58	4.61	1.02	100	0.69	80	0.56
28	1	0	0	0	0	0	0.48	1.29	0	6	49	21.3	26.6	32.1	41.3	2.45	4.51	1.04	25	0.00	65	0.09
29	1	1	1	0	0	0	0.69	1.41	252	147	57	5.4	21.9	18.1	60.0	1.41	4.59	1.20	1600	0.84	40	0.14
30	0	0	0	1	0	0	1.14	2.15	1	99	51	2.0	42.1	35.4	22.5	2.27	4.75	1.20	400	0.00	90	0.15
31	0	0	1	0	0	0	0.57	1.50	1	5	38	14.9	16.3	44.3	39.3	2.35	4.62	1.28	25	0.00	85	0.09
32	0	0	1	0	0	1	0.35	1.74	20	4	52	1.0	28.8	57.9	13.3	2.65	4.04	1.03	100	0.00	80	0.33
33	1	1	0	1	0	0	1.04	2.16	32	67	49	4.6	28.1	33.6	38.3	2.17	4.37	1.01	400	0.81	60	0.18
34	1	1	0	0	0	0	0.88	2.20	14	10	52	2.1	21.0	33.2	45.8	1.62	4.53	0.98	100	0.00	85	0.53
36	0	0	0	0	1	1	0.81	1.77	45	55	43	2.8	13.7	26.4	59.9	1.82	4.31	1.06	400	0.34	60	0.38
38	0	1	0	0	0	0	0.50	1.24	74	26	44	0.4	22.6	42.2	35.3	2.56	4.33	0.89	400	0.00	60	0.43
39	0	0	1	0	1	0	NA	NA	6	0	38	2.7	22.2	40.5	37.2	1.72	4.55	1.14	25	0.56	70	0.10
41	0	0	0	0	1	0	0.71	1.98	5	20	54	8.9	26.4	32.4	41.2	1.69	4.44	1.20	100	0.00	75	0.44
42	0	1	0	0	0	0	0.58	1.29	2	4	34	7.5	23.1	37.5	39.4	1.65	4.46	1.15	25	0.00	95	0.13

plot ID	*A. pau*	*D. pol*	*D. zib*	*P. can*	*P. spe*	*S. lep*	rHi	rBAi	dead trees	trees alive	elev	slope	clay	silt	sand	C	pH	bulkd	plot size	Shannon	veg	canop
43	0	0	1	0	0	0	0.52	1.30	265	135	49	14.9	16.5	37.9	45.6	2.80	4.78	0.91	1600	0.00	65	0.26
44	1	0	0	1	0	1	NA	NA	6	0	36	8.3	25.6	43.8	30.7	1.98	4.56	1.14	25	0.64	85	0.26
45	0	0	0	1	0	0	0.99	2.18	140	260	50	2.8	34.4	44.4	21.3	3.51	4.36	0.79	1600	0.00	95	0.30
46	1	0	0	0	1	0	0.67	1.80	128	272	64	17.5	43.6	46.5	9.9	2.52	4.46	1.11	1600	0.69	80	0.21
47	1	0	0	1	0	0	0.87	1.97	19	81	41	7.4	32.9	39.2	28.0	2.23	4.59	1.02	400	0.69	90	0.18
48	0	0	1	1	0	1	0.58	1.70	6	18	39	2.2	35.1	36.4	28.5	1.84	4.40	1.24	100	0.96	70	0.17
49	0	0	0	0	0	1	0.48	1.81	263	137	71	9.1	19.8	49.7	30.5	1.52	4.50	1.43	1600	0.00	80	0.26
50	1	1	1	1	1	1	0.95	1.92	3	3	32	3.5	36.8	50.7	12.5	3.32	4.09	0.93	25	1.61	95	0.35
51	0	0	0	0	1	0	1.02	2.02	10	90	38	10.6	19.9	52.7	27.5	2.55	4.43	0.88	400	0.00	85	0.25
52	0	1	0	0	0	0	0.37	1.07	383	17	36	8.2	20.4	47.3	32.3	1.96	4.24	1.05	1600	0.00	70	0.22

Appendix Table B.7 | Correlations between site condition variables

	plot size	slope	bulk density	sand content	silt content	clay content	pH	C content	elevation	vegetation cover	canopy openness
slope	0.06										
bulk density	0.02	0.21									
sand content	0.13	-0.06	-0.04								
silt content	-0.08	0.03	-0.04	-0.79							
clay content	-0.13	0.07	0.11	-0.76	0.20						
pH	0.21	0.19	0.15	0.21	-0.36	0.05					
C content	0.10	-0.18	-0.51	-0.40	0.45	0.16	-0.02				
elevation	0.31	0.07	0.14	0.04	0.01	-0.08	-0.04	0.01			
vegetation cover	0.12	-0.18	-0.17	-0.19	0.21	0.08	-0.06	0.18	-0.19		
canopy openness	0.08	-0.36	-0.20	-0.11	0.18	-0.01	-0.03	0.36	0.17	-0.08	
Shannon Index	0.06	0.03	0.11	-0.20	0.01	0.31	-0.03	0.19	-0.19	0.01	0.02

Appendix Table B.8 | Correlations between neighborhood effect variables

	distance to plot edge	distance to remaining oil palm	distance to removed oil palm	*P. speciosa*	*D. zibethinus*	*S. leprosula*	*D. polyphylla*	*A. pauciflorum*	*P. canescens*
distance to remaining oil palm	0.02								
distance to removed oil palm	-0.17	-0.10							
P. speciosa	0.12	-0.04	-0.02						
D. zibethinus	0.15	0.04	0.05	-0.27					
S. leprosula	0.04	0.07	0.02	-0.14	-0.15				
D. polyphylla	0.02	-0.05	-0.06	-0.22	0.08	-0.03			
A. pauciflorum	0.13	0.02	-0.12	-0.22	-0.21	-0.26	-0.07		
P. canescens	0.04	0.01	-0.06	-0.32	-0.08	-0.16	-0.16	-0.31	
mean height nearest neighbor	-0.10	0.15	-0.07	-0.06	-0.26	-0.09	-0.18	-0.06	0.45

	A. pauciflorum			*Durio zibethinus*			*Dyera polyphylla*			*P. speciosa*			*P. canescens*			*S. leprosula*		
	rHi	***rBAi***	**survival**	***rHi***	***rBAi***	**survival**	***rHi***	***rBAi***	**survival**	***rHi***	***rBAi***	**survival**	**rHi**	**rBAi**	**survival**	**rHi**	**rBAi**	**survival**
R²/pseudo R²	0.21	0.38	0.09	0.19	0.17	0.08		0.15	0.11	0.22	0.18	0.12	0.09	0.27	0.13	0.07	0.10	0.07
	est p	est p	est p	est p	est p	est p	NA	est p	est p	est p	est p	est p	est p	est p	est p	est p	est p	est p
dEdge			0.27 **	0.23 **	0.11 n.s.	0.10 ***			-0.37 *									
dOPal	0.22 ***	0.46 ***	0.29 **	0.16 **	0.24 **	0.11 **		0.13 n.s.	0.29 *		0.04 n.s.		0.08 **	0.29 ***			0.11 ***	0.34 ***
dOPrem	-0.11 *	-0.10 n.s.				0.01 n.s.			0.32 **			-0.20 *			-0.29 *	0.06 *		
NNhgt	0.29 ***	0.45 ***	0.24 n.s.	0.23 *	0.40 ***				-0.33 *	0.36 ***	0.24 ***	0.41 **	0.18 ***	0.13 ***	0.85 ***	0.30 ***	0.19 ***	0.31 **
A. pauciflorum		-0.14 ***		-0.70 **	-0.81 **	-0.23 **		-0.33 *		-0.47 ***	-0.15 **			0.38 ***		-0.49 *	-0.55 **	
D. zibethinus			-0.97 n.s.	-0.17 *		-0.06 *			1.03 **			1.08 *		0.05 n.s.			0.13 n.s.	0.96 ***
D. polyphylla	0.10 **		1.29 **	-0.14 n.s.					0.29 n.s.	0.43 ***	0.54 ***	1.12 n.s.		-0.21 ***			0.06 n.s.	-0.41 **
P. speciosa	0.20 **	0.51 ***	-0.65 ***						3.27 ***			0.28 **	0.40 ***	0.41 ***				-1.05 ***
P. canescens				-0.99 ***	-0.55 *	-0.28 ***		0.73 *		-0.66 ***	-0.43 ***	-1.24 ***			-0.90 ***			1.30 ***
S. leprosula						-0.26 ***			-0.81 *	-0.11 n.s.	-0.25 ***				-0.98 ***			

Appendix Table B.9| Minimum adequate models per species on individual level. dEdge= shortest distance to plot edge, dOPal = distance to closest oil palm alive, dOPrem = distance to closest oil palm removed (now oil palm trunk), NNhgt = mean height of all neighbors in a maximum distance of 5 m.

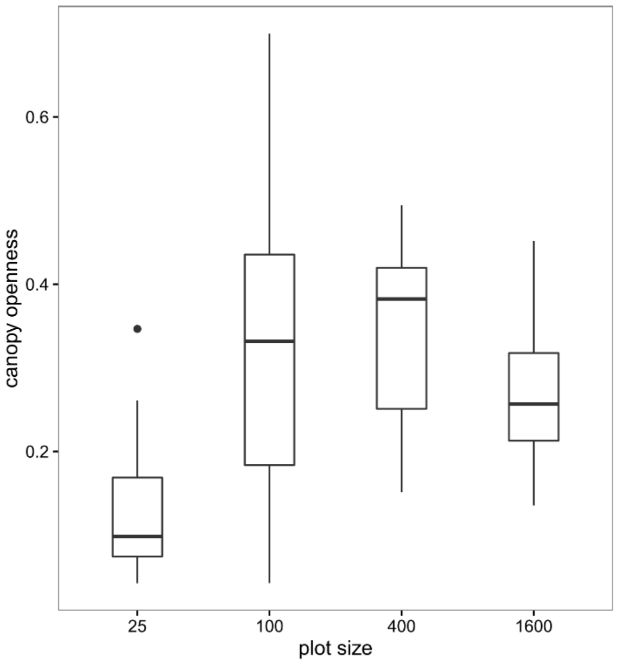
C Supplementary material to chapter 4

Appendix Table C.1 | Collinearity matrix of all explanatory variables measured using Pearson's r.

	plot size	OP height	diversity level	canopy openness	bulk density	elevation	slope	sand content	silt content	clay content	soil pH	C content	max tree height	mean tree height
OP height	-0.19													
diversity level	-0.03	-0.24												
canopy openness	-0.24	-0.23	-0.10											
bulk density	0.26	0.12	0.22	-0.28										
elevation	0.19	-0.28	-0.22	0.12	0.21									
slope	0.29	-0.29	0.19	-0.34	0.17	-0.01								
sand content	0.04	0.32	-0.22	0.04	-0.08	-0.02	-0.12							
silt content	-0.08	-0.29	0.04	0.11	0.00	0.07	0.14	-0.82						
clay content	0.04	-0.19	0.33	-0.21	0.15	-0.06	0.03	-0.70	0.18					
soil pH	0.12	0.16	0.02	-0.28	0.17	-0.06	0.26	0.18	-0.43	0.22				
C content	-0.20	-0.39	0.15	0.23	-0.45	0.05	-0.08	-0.59	0.52	0.37	-0.18			
max tree height	0.05	0.31	0.37	-0.27	0.22	0.01	0.08	0.02	-0.20	0.22	0.16	0.04		
mean tree height	-0.19	0.39	0.21	-0.12	0.08	0.06	-0.21	-0.08	-0.08	0.25	0.04	0.17	0.88	
cv tree height	0.43	-0.34	0.33	-0.21	0.11	-0.01	0.62	0.24	-0.25	-0.11	0.23	-0.28	-0.07	-0.47

Appendix Table C.2 | All data per plot of all variables and their unit as incorporated in the analyses.

		adjacent-to-plot-yield																		
Plot ID	inside-plot- yield	pos 1	pos 2	pos3	plot size	OP height	OPcut	OPalive	diversity level	canopy openness	bulk density	elevation	slope	silt content	clay content	soil pH	C content	max tree height	mean tree height	cv tree height
	[kg]	[kg]	[kg]	[kg]	[m^2]	[m]				[prop]	[g/cm^3]	[m]	[°]	[prop]	[prop]		[prop]	[cm]	[cm]	
1	246.12	129.20	122.83	110.63	1600	4.11	7	13	1	0.28	1.10	55	12.2	43.25	27.81	4.47	1.84	625	271.07	0.51
2	239.43	306.38	95.50	310.37	400	3.50	3	1	3	0.35	1.01	40	12.6	40.56	26.23	4.61	2.29	554	245.16	0.52
3	236.71	196.73	160.56	204.83	400	4.20	3	2	2	0.40	1.03	48	7.8	37.28	27.40	4.47	2.01	252	92.65	0.50
4	NA	188.27	251.82	136.09	100	0.00	1	0	1	0.43	0.93	48	7.6	41.03	32.03	4.40	2.39	417	242.83	0.59
5	285.52	311.78	107.53	72.44	1600	4.15	8	12	1	0.44	1.18	68	6.8	45.02	20.18	4.41	1.82	595	281.33	0.44
6	NA	238.17	46.35	88.76	25	0.00	0	0	1	0.11	0.99	39	18.8	35.01	27.69	4.26	1.67	620	437.33	0.29
7	219.82	241.79	141.10	217.01	1600	3.48	8	11	3	0.45	1.02	35	8.9	33.22	33.58	4.37	2.00	646	262.23	0.60
8	NA	234.80	114.69	118.18	25	0.00	0	0	1	0.05	1.17	56	5.1	37.23	28.98	4.08	1.23	32	32.00	0.00
9	138.60	40.15	142.20	221.61	100	3.60	1	1	3	0.18	1.13	45	17.8	30.66	30.03	5.02	2.09	740	338.11	0.51
10	223.53	161.92	169.65	231.94	400	3.90	3	1	0	0.42	1.15	59	7.6	33.18	39.21	4.21	1.94	0	0.00	0.00
11	NA	38.12	79.85	163.49	100	0.00	1	0	1	0.18	1.02	52	18.3	41.87	33.83	4.68	1.68	144	144.00	0.00
12	219.88	239.94	218.70	126.55	400	3.30	1	2	1	0.36	0.94	58	16.8	45.13	19.72	4.50	2.44	240	111.10	0.65
13	NA	168.05	101.79	99.51	100	0.00	1	0	1	0.70	1.24	51	9.5	54.28	34.65	4.38	2.16	524	389.92	0.18
14	NA	243.22	148.18	75.18	100	0.00	1	0	1	0.30	1.33	46	10.6	34.48	30.38	4.68	1.04	115	74.14	0.34
15	259.86	202.83	152.82	176.90	400	3.25	2	2	1	0.49	0.97	70	8.2	47.76	27.89	4.26	3.70	623	349.35	0.44
16	NA	154.42	113.44	223.71	25	0.00	0	0	3	0.19	1.02	58	8.7	46.81	25.32	4.21	1.91	124	100.67	0.30
17	226.58	308.21	118.16	301.20	400	4.10	3	2	1	0.42	1.26	37	5.1	44.07	31.23	4.49	2.57	522	275.90	0.32
18	NA	218.34	191.84	227.87	25	0.00	0	0	2	0.17	1.04	40	6.6	43.13	31.49	4.30	1.63	539	479.67	0.12
19	180.83	278.39	166.94	178.81	400	3.00	2	3	6	0.41	1.05	54	2.4	54.84	37.21	4.41	3.94	710	383.22	0.41
20	390.24	297.55	231.76	195.82	100	4.20	1	1	1	0.34	0.91	39	2.0	47.04	29.44	4.56	2.75	434	237.00	0.46
21	NA	191.57	198.22	39.78	100	0.00	1	0	6	0.31	1.30	56	16.2	42.50	38.86	4.28	1.65	630	297.33	0.51
22	NA	91.36	127.82	163.79	25	0.00	0	0	2	0.04	1.23	44	20.8	43.84	46.65	4.58	1.78	66	52.00	0.25
23	259.94	151.27	171.39	262.11	1600	3.83	8	12	6	0.20	1.29	38	20.9	53.01	33.07	4.40	2.38	797	324.61	0.68
24	240.24	327.61	372.57	150.31	1600	3.96	6	11	2	0.36	1.04	58	6.8	22.98	23.69	4.61	2.09	730	402.16	0.46
25	NA	254.89	199.86	279.77	25	0.00	0	0	1	0.07	1.06	44	11.1	43.12	37.42	4.07	1.24	880	500.67	0.49
26	279.24	292.73	288.22	246.13	1600	4.11	6	12	2	0.32	1.10	46	6.4	36.44	37.71	5.28	2.28	531	230.66	0.59
27	NA	178.30	167.04	145.11	100	0.00	1	0	2	0.56	1.02	38	1.8	40.92	43.72	4.61	2.58	642	416.83	0.41
28	NA	14.16	24.25	117.63	25	0.00	0	0	1	0.09	1.04	49	21.3	32.10	26.63	4.51	2.45	386	188.17	0.56
29	205.10	215.98	175.75	48.35	1600	3.85	8	20	3	0.14	1.20	57	5.4	18.14	21.88	4.59	1.41	683	223.42	0.76
30	279.83	82.67	190.91	121.83	400	5.40	2	2	1	0.15	1.20	51	2.0	35.38	42.08	4.75	2.27	776	502.70	0.28
31	NA	227.13	75.07	164.47	25	0.00	0	0	1	0.09	1.28	38	14.9	44.33	16.34	4.62	2.35	204	138.40	0.37
32	177.14	189.55	124.69	114.56	100	3.30	1	1	2	0.33	1.03	52	1.0	57.91	28.75	4.04	2.65	350	246.20	0.40
33	251.15	250.29	18.62	124.09	400	4.80	3	4	3	0.18	1.01	49	4.6	33.64	28.09	4.37	2.17	761	448.25	0.37
34	148.72	169.30	275.00	30.94	100	3.70	1	1	2	0.53	0.98	52	2.1	33.15	21.01	4.53	1.62	473	320.25	0.41
35	271.23	311.66	111.64	283.11	1600	3.31	5	17	0	0.19	1.20	50	0.6	42.42	22.20	4.22	3.12	0	0.00	0.00
36	264.82	131.14	33.92	90.96	400	4.60	3	1	2	0.38	1.06	43	2.8	26.42	13.69	4.31	1.82	820	370.85	0.50
37	106.05	78.83	106.70	167.50	100	3.00	1	1	0	0.04	1.19	30	0.2	22.29	27.43	4.27	2.06	0	0.00	0.00
38	264.31	112.60	180.68	172.23	400	4.17	4	3	1	0.43	0.89	44	0.4	42.15	22.58	4.33	2.56	182	83.48	0.43
39	NA	167.12	79.80	74.19	25	0.00	0	0	2	0.10	1.14	38	2.7	40.53	22.24	4.55	1.72	485	205.50	0.93
40	NA	73.48	123.96	73.29	25	0.00	0	0	0	0.07	0.97	20	11.1	42.26	53.12	3.97	2.22	0	0.00	0.00
41	NA	225.82	134.47	262.40	100	0.00	1	0	1	0.44	1.20	54	8.9	32.38	26.43	4.44	1.69	387	218.73	0.45
42	NA	304.39	126.60	37.63	25	0.00	0	0	1	0.13	1.15	34	7.5	37.49	23.09	4.46	1.65	126	75.20	0.42
43	232.11	249.72	161.60	75.10	1600	3.68	7	11	1	0.26	0.91	49	14.9	37.92	16.52	4.78	2.80	415	137.46	0.59
44	NA	82.65	73.32	106.90	25	0.00	0	0	3	0.26	1.14	36	8.3	43.76	25.57	4.56	2	467	428.33	0.09
45	200.91	184.84	163.00	92.85	1600	3.19	4	14	1	0.30	0.79	50	2.8	44.39	34.35	4.36	3.5	642	374.95	0.31
46	170.78	134.00	100.81	173.09	1600	2.70	8	17	2	0.21	1.11	64	17.5	46.49	43.59	4.46	2.5	586	208.54	0.63
47	190.05	159.44	177.80	177.85	400	3.86	1	5	2	0.18	1.02	41	7.4	39.19	32.86	4.59	2.2	540	247.58	0.46
48	NA	213.15	156.83	262.46	100	0.00	1	0	3	0.17	1.24	39	2.2	36.44	35.11	4.4	1.8	420	224.11	0.51
49	238.70	153.66	114.99	219.84	1600	3.75	5	15	1	0.26	1.43	71	9.1	49.74	19.79	4.5	1.5	550	267.20	0.41
50	NA	202.78	137.67	73.35	25	0.00	0	0	6	0.35	0.93	32	3.5	50.72	36.83	4.09	3.3	434	238.40	0.67
51	226.59	117.86	169.92	111.57	400	5.03	2	3	1	0.25	0.88	38	10.6	52.7	19.85	4.43	2.5	913	471.11	0.41
52	239.21	256.65	178.32	135.26	1600	3.73	7	13	1	0.22	1.05	36	8.2	47.27	20.42	4.24	2	145	72.09	0.48



Appendix Figure C.1 | Differences in canopy openness between and within plot size classes. The boxes show the 25- and 75-percentiles, and the whiskers representing the lowest and the highest value within 1.5 times the inter-quartile range, respectively.

Acknowledgements

Many people have helped and supported me during the course of this thesis, and without them, the last years would have been a lot more challenging.

First of all, I would like to thank my first supervisor Prof. Holger Kreft and my second supervisor Prof. Dirk Hölscher for their great support and commitment; for their inspiring input, constructive criticism, enthusiasm, and their time and availability for numerous discussion rounds. I also thank Dr. Katja Rembold for co-supervising this thesis. Also, I thank Katja and the whole working group for the enjoyable atmosphere at work.

Many thanks to the DFG who kindly provided the funding for this thesis in the framework of the CRC990. I enjoyed being part of a great and interdisciplinary research project; thanks to all my colleagues of the CRC 990 for inspiring knowledge exchange and pleasant moments in Indonesia and Göttingen alike. I am grateful for the logistic support of the CRC990 coordination team, who facilitated my work a lot. I acknowledge Martin Ehbrecht's great commitment in Indonesia before I started my PhD, his preparation helped me substantially to conduct my PhD thesis.

Special thanks to Miriam Teuscher, Dr. Mimi, for sharing so many difficult and so many nice moments with me, and that she decided to establish the experiment alongside me. Without her help, commitment, and jokes, I might have given up in many moments. I am very glad we are such a great team!

I am grateful that so many people helped me substantially during field work in Indonesia. First of all Juliandi, who reliably managed the experiment and collected data throughout the intital years. I thank Andi for his patience with my sometimes poor Bahasa Indonesia and for introducing me to his very friendly family and to the Indonesian culture. Thanks to the family of Pak Hasbi who kindly hosted us for week. Furthermore, thanks to Anshori who endured a long time with me in the field, and helped establishing the experiment, together with the 'team bagus' Andi, Zeri, Supadi, Ahsan, and many workers of the company Humusindo. I am grateful for the support of Adi, Teddy, Fadli, and Azwin for collecting tree data. Thanks to Judith and Happy for their hard work to get soil samples and the great time we had in the field, together with Liz, Andi, Ani, and the cat. I was pleased to find so many friends in Indonesia who shared their punk culture and experience with me; most notably Kadek and Happy.

Most special thanks to Jonni, who was always there for me despite the many ups and downs during the PhD years. Thanks for visiting me in the Indonesian haze, and also for a lot of scientific input.

I am very thankful that my family has always supported and believed in me throughout my whole life. Their backing has helped me a lot to achieve my personal aims. Thanks to so many of my friends and flatmates with whom I could laugh and talk in good and in bad moments.

Eidesstattliche Erklärung

Hiermit erkläre ich an Eides statt, dass ich die vorliegende Arbeit selbständig angefertigt, keine unerlaubten Hilfsmittel verwendet und bisher noch keinen Promotionsversuch unternommen habe.

Anne Gérard

21.10.2016