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Ecological impacts of biodiversity enrichment in oil palm plantations

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„Wer Bäume pflanzt, wird den Himmel gewinnen“

- *Konfuzius* -

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Summary

Land-use change is one of the major drivers of biodiversity loss. To satisfy the demand for palm oil in food and biofuel, complex, species-rich rainforests are converted into large, simply-structured mono-culture oil palm plantations. This has dramatic consequences for biodiversity and ecosystem functioning, thereby also putting human well-being at risk. Facing the severe decline in biodiversity, the re-establishment of diverse habitats and their multi-functionality through restoration measures could help biodiversity and ecosystem functioning recover faster. However, knowledge about the underlying ecological and socio-economic mechanisms of restoration in oil palm plantations and clear instructions towards a wildlife-friendly management of oil palm are lacking.

In this thesis, I provide initial insights into the relationship between ecology and economics when a wildlife-friendly farming strategy is applied in oil palm systems. Focusing on birds of smallholder oil palm-dominated landscapes in the Jambi province, Sumatra, Indonesia, I uncovered the ecological-economic relationship when having remnant or planted trees within oil palm plantations and estimated the costs for the conservation of bird diversity and abundance. The results suggest that bird diversity and abundance depends on the number of trees on the plot and that an increase in bird diversity and abundance results in revenue penalties, indicating that there is a win-lose relationship between ecological and economic outcomes. However, since the relationship was non-linear, an increase in bird diversity could be achieved at lower costs in highly intensified oil palm plantations as compared to extensively managed oil palm plantations. Furthermore, the costs for increased bird abundance were lower than for increased bird diversity. Overall, these findings illustrate that there is room for tree-based enrichment in intensively managed oil palm plantations as a measure to maintain a baseline level of biodiversity at relatively little costs.

In order to address various open questions and to effectively be able to shed light on additional ecological and socio-economic mechanisms linked to enrichment plantings, I established a long-term, large-scale biodiversity enrichment in a mono-culture oil palm plantation in the Jambi province, Sumatra, Indonesia. The establishment of the experiment comprised planting tree islands of different sizes and with varying tree diversity and composition within gaps of an oil palm plantation. I assessed initial environmental and biotic characteristics of the plantation prior to the tree planting against which the longitudinal data from the tree islands will be compared to throughout the years following the establishment. The design allows for disentangling the effects of tree diversity and island size on the diversity and composition of different organism groups such as plants, birds and invertebrates. Herewith, conclusions can be drawn on changes in ecosystem functioning. I investigated early effects of the tree plantings on the bird and invertebrate communities. Interestingly, birds and invertebrates responded positively to the enrichment plantings already one year after the establishment of the tree islands. Overall bird species richness and abundance of herb-layer invertebrates was increased on plots with trees. Invertebrates were not only positively affected by enrichment plantings on a landscape scale but also on plot level. In summary, these findings illustrate the great potential of restoration plantings to benefit biodiversity and associated ecosystem functioning as birds and invertebrates play a key role in initiating succession processes, thereby enhancing biodiversity. Both, birds and invertebrates fulfil many tasks that are essential for the functioning and resilience of ecosystems. The biodiversity enrichment experiment provides lucrative ground for further research in various disciplines in order to develop ecologically improved and socio-economically viable management strategies for oil palm plantations.

Overall, this thesis contributes substantially to make advances in BEF and restoration research in tropical agricultural landscapes. Scientific evidence on the costs and benefits of enrichment plantings provides the ground for future political decision-making towards increased ecological and socio-economic sustainability in oil palm management. Ultimately, the biodiversity enrichment experiment may contribute to increasing and conserving biodiversity in tropical agricultural landscapes without jeopardizing the food security of a growing human population.

Zusammenfassung

Landnutzungsänderung gilt als eine der wichtigsten Ursachen für den Verlust an biologischer Artenvielfalt. Um der Nachfrage nach Palmöl in Lebensmitteln und Biokraftstoffen nachzukommen, werden komplexe, artenreiche Regenwälder in große, einfach strukturierte Monokulturplantagen umgewandelt. Das hat dramatische Folgen für die biologische Vielfalt und die ökologische Funktionsfähigkeit dieser Systeme, was wiederum das menschliche Wohl gefährdet, da wir von Produkten (z.B. Holz, Früchte) und Funktionen (z.B. Bestäubung, Regulierung des Klimas und der Wasserqualität) unserer Ökosysteme abhängig sind. Breite Landstriche Indonesiens, die vorher aus tropischem Regenwald bestanden, wurden bereits komplett in Plantagen konvertiert, wodurch eine Reinitialisierung von natürlichen Gemeinschaften auf Kosten der Plantagenfläche zum Erhalt der ökologischen Funktionsfähigkeit notwendig wird. Die ökologischen und sozio-ökonomischen Prozesse im Zusammenhang mit dem Wiederaufbau natürlicher Ökotope in Ölpalmplantagen sind jedoch weitgehend unbekannt.

In dieser Arbeit beleuchte ich den Zusammenhang zwischen Ökologie und Ökonomie in von Kleinbauern bewirtschafteten Ölpalmplantagen. Der Fokus lag dabei auf Vögeln in einer Ölpalmlandschaft in der Provinz Jambi, Sumatra, Indonesien. Ich untersuchte, inwiefern die Artenvielfalt und Abundanz (Anzahl der Individuen) der Vögel von der Anzahl anderer übrig gebliebener oder gepflanzter Bäume auf der Plantage abhängt und wie das wiederum die Ökonomie der Plantage beeinflusst. Weiterhin errechnete ich die geschätzten Kosten für den Erhalt der Artenvielfalt und Abundanz von Vögeln. Die Ergebnisse legen nahe, dass die Vogelartenvielfalt und Abundanz der Vögel positiv mit der Anzahl von Bäumen zusammenhängt, dass allerdings eine Erhöhung der Artenvielfalt und Abundanz zu Gewinneinbußen führt. Aufgrund der Nichtlinearität der Beziehung zwischen diesen ökologischen und ökonomischen Funktionen ist eine Erhöhung der Vogelartenvielfalt auf einer intensiv bewirtschafteten Plantage mit geringeren Kosten verbunden, als dies auf bereits extensiv bewirtschafteten Ölpalmplantagen der Fall ist. Außerdem ist eine Erhöhung der Abundanz an Vögeln kostengünstiger als die Erhöhung ihrer Artenvielfalt.

Zusammenfassend zeigen die Ergebnisse, dass eine Baum-basierte Anreicherung in intensiv bewirtschafteten Ölpalmplantagen eine relativ kostengünstige Maßnahme darstellt, um ein Grundniveau an Biodiversität zu erhalten.

Um verschiedene offene Fragen bezüglich der ökologischen und sozio-ökonomischen Mechanismen im Zusammenhang mit Anreicherungsmaßnahmen in Ölpalmplantagen effektiv zu beleuchten, wurde ein Langzeit-Anreicherungsexperiment in einer Ölpalm-Monokulturplantage in der Provinz Jambi, Sumatra, Indonesien etabliert. Zu diesem Zweck wurden Bauminseln angepflanzt, wobei die Vielfalt und Identität der Bäume sowie die Größe der Inseln systematisch variiert. Das Design des Experiments ermöglicht eine Entflechtung der Auswirkungen der Baumartenvielfalt und -inselgröße auf die Vielfalt und Zusammensetzung verschiedener Organismengruppen, wie beispielsweise Pflanzen, Vögel und wirbelloser Tiere. Vor der Pflanzung wurden die biotischen und abiotischen Parameter der Plantage erhoben, um spätere Daten mit den Anfangsdaten zu vergleichen und Rückschlüsse auf Veränderungen in der Vielfalt und Zusammensetzung von Flora und Fauna oder den assoziierten Ökosystemfunktionen feststellen zu können. Weiterhin habe ich frühe Auswirkungen der Anreicherungspflanzungen auf Vögel und Wirbellose untersucht. Interessanterweise reagierten Vögel und wirbellose Tiere bereits ein Jahr nach Anpflanzung der Bauminseln positiv auf diese Veränderungen der Baumartenvielfalt und -anzahl innerhalb der Plantage. Insgesamt waren die Vogelartenvielfalt und die Abundanz der Wirbellosen in der Krautschicht auf den Versuchsflächen mit Bäumen erhöht. Außerdem wurde ein positiver Zusammenhang zwischen Anzahl und Vielfalt von Wirbellosen und der Größe der Versuchsflächen festgestellt. Zusammenfassend verdeutlichen diese ersten positiven Ergebnisse das große Potenzial der Bauminseln für die Wiederherstellung biologischer Vielfalt und der damit verbundenen Ökosystemfunktionen. Vögel und wirbellose Tiere spielen eine Schlüsselrolle bei der Initiierung wichtiger Sukzessionsprozesse innerhalb von Ökosystemen, was sich positiv auf die allgemeine Vielfalt im System auswirkt. Vögel und Wirbellose erfüllen zahlreiche Aufgaben, die für das Funktionieren und die Widerstandsfähigkeit der Ökosysteme essentiell sind. Das Anreicherungsexperiment bietet eine lukrative Basis für weitere Forschungsprojekte in verschiedenen Disziplinen, um ökologisch verbesserte und sozio-ökonomisch nachhaltige Strategien zur Bewirtschaftung von Ölpalmplantagen zu entwickeln.

Insgesamt trägt diese Arbeit wesentlich zu Fortschritten in der Biodiversitäts- und Ökosystemforschung sowie im Bereich der Forschung zur Wiederherstellung von vielfältigen Systemen in tropischen Agrarlandschaften bei. Wissenschaftliche Erkenntnisse über die Kosten und Nutzen der Anreicherungspflanzungen sind die Basis für künftige politische Entscheidungen hin zu erhöhter ökologischer und sozio-ökonomischer Nachhaltigkeit im Palmölmanagement. Nicht zuletzt kann das Anreicherungsexperiment zur Steigerung und Erhaltung der biologischen Vielfalt in tropischen Agrarlandschaften beitragen, ohne die Ernährungs- und Versorgungssicherheit einer wachsenden Weltbevölkerung zu gefährden.

Contributions to the chapters of this thesis

Chapter 2: Trade-offs between bird diversity and abundance, yields and revenue in smallholder oil palm plantations in Sumatra, Indonesia

Miriam Teuscher, Miriam Vorlaufer, Meike Wollni, Ulrich Brose, Yeni Mulyani, Yann Clough

All authors designed the study. The questionnaire for the household study was developed by MV, MW and MT. The vegetation and bird survey was carried out by MT, the household survey by MT and MV. MT and MV analysed the data with support form YC, UB and MW; MT and MV wrote the first draft of the manuscript and all authors contributed to revisions.

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Chapter 3: Biodiversity enrichment in oil palm landscapes: A tree planting experiment in Sumatra (Indonesia)

Miriam Teuscher, Anne Gérard, Ulrich Brose, Damayanti Buchori, Yann Clough, Martin Ehbrecht, Hendrayanto, Dirk Hölscher, Bambang Irawan, Yeni Mulyani, Prijanto Pamungkas, Leti Sundawati, Meike Wollni, Holger Kreft

The experiment was designed by UB, YC, DH, HK and MW. BI, LS, PP, DH, HK, YC, ME, MT and AG searched for possible oil palm plantations to set up the experiment and were involved in negotiations with plantation owners on-site. MT and AG planned and carried out the establishment of the experimental plots. DB, LS, PP, BI, H and YM provided scientific and logistical support in Indonesia during the establishment phase of the experiment. Soil data were collected by AG; all other environmental data by MT and AG. Hemisperical 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.

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PART I

GENERAL INTRODUCTION

Chapter 1: Introduction

1.1 Aims and scope of this thesis

Tropical ecosystems, especially rainforests, are known as the most species-rich habitats in the world (Whitmore 1998). However, rainforests are subject to extensive land-use transformation which results in loss of species (Newbold *et al.* 2015). One of the most common cultivation systems in the tropics are oil palm (Elaeis guineensis) plantations, which harbour very low biodiversity compared to natural tropical forest (Koh & Wilcove 2008; Fitzherbert *et al.* 2008; Fayle *et al.* 2010; Edwards *et al.* 2014), but are of utmost importance to Southeast Asian economies (Basiron 2007). Consequently, oil palm agriculture will most likely expand further in the future to satisfy a globally increasing demand for food and biofuel. This will put even more pressure on tropical biodiversity (Laurance, Sayer & Cassman 2014). In this context, conservation of natural habitat, alone, might not be sufficient to stop the severe decline in biodiversity. Restoration efforts are needed to help biodiversity recover faster and to maintain ecosystem functioning linked to biodiversity. Developing management strategies that jointly benefit biodiversity and economic returns are the key to balance these conflicting interests of ecology and economy. The main questions to be investigated in this context are: 1) “how do ecology and economics respond when having trees within or at the border of oil palm plantations?”; 2) “how much does is cost to conserve a diversity of species in oil palm habitats?”; 3) “can we enhance biodiversity and ecosystem functions through tree-based restoration in oil palm landscapes and at the same time keep economic losses low?” and 4) “what is the best planting strategy?”.

In this thesis, I shed light on how remnant or planted trees affect the ecology and economics in oil palm plantations in a combined field and household study on 120 smallholder oil palm plantations. Furthermore, I sat the scene for long-term research on restoration in oil palm landscapes to gain fundamental knowledge of the ecological and socio-economic impacts of such enrichment plantings in oil palm plantations. Together with researchers from Germany and Indonesia, I established a biodiversity enrichment experiment by planting tree islands in gaps in a mono-culture oil palm plantation in the province of Jambi on Sumatra, Indonesia. This biodiversity enrichment experiment provides a lucrative foundation for interdisciplinary research to investigate the effects of restoration in tropical landscapes on biodiversity, ecosystem functioning and socio-economics. The experiment aims at contributing to the development of ecologically improved and socio-economically viable management strategies. In the framework of this biodiversity enrichment project, my focus is on the taxonomic and functional diversity response of birds and invertebrates to such tree plantings.

Before I present my research objectives in detail and lead you through the chapters of my thesis, I will introduce some general topics. To begin with, I will talk about the main threats to biodiversity. Then, I elaborate on the complexity of biodiversity and ecosystem functioning, as well as on problems induced by biodiversity loss. Further, I illustrate proposed conservation strategies to retain biodiversity or even enhance it. To conclude my introduction, I elucidate opportunities and challenges of restoration in degraded ecosystems.

1.2 Threats to biodiversity

Biodiversity is lost and ecosystem functioning is being impaired by a vast array of human activities (Millenium Ecosystem Assessment 2005). Increasing human population and consumption pressures push ecosystems to the brink of their capacities and create conditions that greatly harm our environment. This leads to extinctions of species and populations, degradation of ecosystems, erosion of genetic diversity and evolutionary potential, loss of ecosystem services as well as to the erosion of support systems for human society (Millenium Ecosystem Assessment 2005). Five main drivers for biodiversity loss have been identified: land-use change, overexploitation, spread of invasive species, pollution, and climate change (Millenium Ecosystem Assessment 2005). An increased food demand has initiated an increase in food production, which was made possible by the expansion and intensification of agriculture (Matson *et al.* 1997; Laurance, Sayer & Cassman 2014), thereby imposing a huge impact on ecosystems. Forty percent of the Earth's land surface is, for instance, currently occupied by cropland and pastures (Foley *et al.* 2005). Such anthropogenic impacts have contributed to an unprecedented increase in the rate of global species extinctions (Barnosky *et al.* 2011; Monastersky 2014).

Obviously, these practices are unsustainable as we are erasing essential resources and natural capital, thereby endangering our own future. However, to better understand why we should be concerned with biodiversity loss and why this also puts our future well-being at risk, I provide some background on biodiversity and its importance for the functioning of ecosystems and humanity in the following section.

1.3 Biodiversity and its importance for humanity

1.3.1 Definition of biodiversity

Biodiversity (or biological diversity) describes the immense richness and variation of all living things in the world. It can be considered on many different levels of biological variation, ranging from genes – the ultimate source of biodiversity at all levels – to populations, species, ecosystems and entire biomes (Groom, Meffe & Carroll 2006). In the convention for biological diversity in Rio de Janeiro in 1992, biodiversity was defined as "[…] 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" (Box 1.1). This definition draws the attention to the many dimensions of biodiversity. It recognizes that all biota can be described by taxonomic or genetic diversity and that variation across space and time is a key feature of this diversity (Millenium Ecosystem Assessment 2005). When people hear or talk about biodiversity, however, they most often refer to it as species diversity, which indeed is one of the fundamental levels of biodiversity. Landscape heterogeneity is an important driver of biodiversity and it varies with spatial scales (Stein, Gerstner & Kreft 2014). Therefore, to understand the full picture of biodiversity, it is important to take account of it at different scales. In 1960, Rob Whittaker considered three diversity levels of natural communities across space. Alpha diversity describes local diversity, i.e. the species richness found in a habitat in which species are influenced by inherent biotic and abiotic characteristics. Beta diversity describes the spatial differentiation between communities in an area of interest and is high when two communities have very different species compositions, meaning they have very few species in common. The third level of diversity categorized by Whittaker (1960) is gamma diversity, which describes diversity on a regional scale. It is the sum of all alpha diversities in a region.

In my thesis I mainly focus on alpha diversity (species richness) and how it differs a) between oil palm plantations along a management intensity gradient and b) between planted tree islands of different plot size, tree diversity level and tree species compositions.

Box 1.1: Glossary

Biodiversity: variety of life. It is a measure of the variety of different organisms present in different ecosystems. This can refer to genetic variation, species variation or ecosystem variation within an area or entire biome.

Ecosystem functions: ecological processes that control the fluxes of energy, nutrients and organic matter through an environment. Examples include: primary production, which is the process by which plants use sunlight to convert in organic matter into new biological tissue; nutrient cycling, which is the process by which biologically essential nutrients are captured, released and then recaptured; and decomposition, which is the process by which organic waste, such as dead plants and animals, is broken down and recycled.

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.

Ecosystem service: a property or process in an ecosystem that confers either direct or indirect benefits to humans. We focus on the goods that are directly used by humans (e.g., food, fuel, and fiber) and the ecological processes that influence the provision of these goods (e.g., pollination, soil nutrient cycling, etc.).

1.3.2 Where do we find biodiversity?

Interestingly, biodiversity is not distributed evenly on our planet. There are places where astonishingly high biological diversity can be found: tropical rainforests – the ecosystems that blanket the Earth along the equator (Morley 2009). The stable climate in the tropics enables the establishment of heterogenic, multi-strata forests which harbour a tremendous, yet poorly understood, diversity of species and ecological processes (Whitmore 1998). The intrinsic value of tropical rainforests is much greater than, e.g. that of forests in temperate regions, as they harbour a much greater gene pool, necessary for securing a long future of plant and animal life (Morley 2009). Moreover, they are a major source of wood, plant and animal products, and form the economic base of many households (Grimes *et al.* 1994). Tropical rainforests also provide numerous services that make up crucial parts of the Earth's water, carbon and nutrient cycles (Bawa *et al.* 2004). These forests, above all, play an important role in regulating the global climate as they are a major absorber of atmospheric CO_2 (Morley 2009).

1.3.3 Why is biodiversity important?

The ecological value of species diversity is often characterized by the sum of functions that are fulfilled by the species present in an ecosystem. Biodiversity has been identified as being critical for maintaining ecosystem functions (Box 1.1) (Hooper, Chapin III & Ewel 2005). The biodiversity hypothesis states that a reduction in species diversity will ultimately lead to a reduction in ecosystem function (Srivastava & Vellend 2005). But how many species do we need to keep the system working? And, are all species equally important in their contributions to the functioning of the ecosystem? To address these questions, four major hypotheses have been developed regarding the relationship between biodiversity and ecosystem functioning (BEF):

- The *equally important species hypothesis* (Vitousek & Hooper 1997) posits that all species are equally important and thus contribute equally to ecosystem functioning. The relationship between species number and their function is linear and positive (Figure 1.1 a).
- The *species redundancy hypothesis* (Walker 1992) postulates that many species have similar functions. First, functioning will increase with increasing species number until it reaches a saturation point. After this point, a further increase in species richness does not result in an increase in function (Figure 1.1 b).
- The *rivet popper hypothesis* (Ehrlich & Ehrlich 1981) is similar to the species redundancy hypothesis, with the addition that many species can get lost unnoticed, but if a keystone species disappears, the function of the whole species community collapses (Figure 1.1 c).

- The *idiosyncratic hypothesis* (Lawton 1994) proposes no systematic relationship between the species number and the function that the species fulfils (Figure 1.1 d).

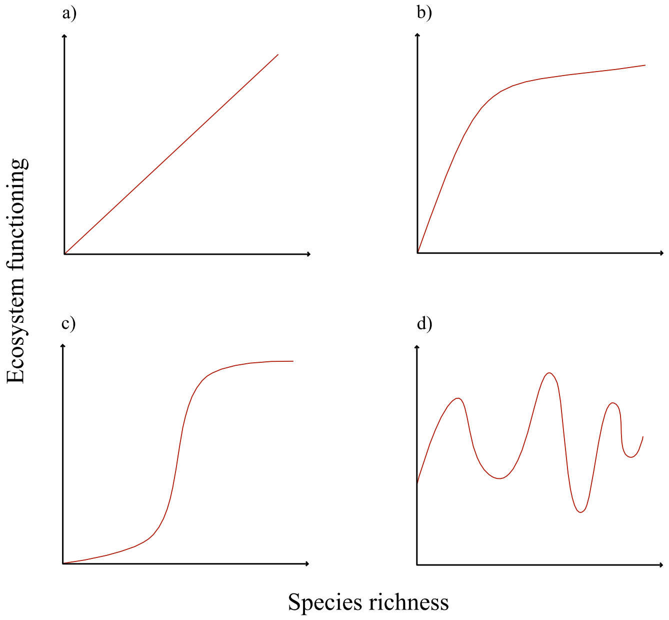

Figure 1.1: Graphic representation of four potential types of relationships between species richness and ecosystem functioning: a) linear (Vitousek & Hooper 1997); b) redundant (Walker 1992); c) rivet popper (Ehrlich & Ehrlich 1981); and d) idiosyncratic (Lawton 1994).

In the last few decades, the results of numerous studies and experiments that tested extinction scenarios in different spatial and temporal settings caused controversy over the influence of biodiversity on ecosystem functioning, stability and resource efficiency (Cardinale *et al.* 2006, 2012; Balvanera *et al.* 2006). However, considering the different dimensions of BEF in space and time allowed a more holistic understanding of the BEF relationship and provided strong support for the conclusion that species diversity tends to be positively related with ecosystem functioning in the shape of a saturating curve (Cardinale *et al.* 2012). This suggests that the species redundancy hypothesis is well supported (Figure 1.1 b). A low number of species should already provide a certain level of ecosystem function in a constant environment. However, if these species are negatively affected by a perturbation, this level of functioning will only be maintained, when other species with a similar effect on functioning are not affected or respond positively to the same perturbation (Naeem *et* *al.* 2009). Therefore, redundancy of species can be seen as a buffer, making an ecosystem more resilient and stable against unpredictable disturbances, as other species with similar functions can replace the lost species (Isbell *et al.* 2011). This highlights that the effects of species loss in already species-poor systems can be relatively more disadvantageous due to lacking redundancy of species for sustaining processes in an ecosystem compared to species-rich ecosystems (Hooper, Chapin III & Ewel 2005; Srivastava & Vellend 2005; Cardinale *et al.* 2012).

People often seek mainly economic justifications for the conservation of biodiversity and ecosystem functions. In the next paragraph I describe the essentiality of ecosystem functions for human well-being and why we therefore should be motivated to act in an environmentally friendlier way.

1.3.4 Ecosystem services

Humans have evolved as part of the world’s ecosystems and depend to a large degree on goods and services provided by them. These goods and other benefits are used, or required by humans and are referred to as ‘ecosystem services’ (Box 1.1). This term has often been used synonymously with the term ecosystem function. More precisely, however, ecosystem services can be described as a *selection* of ecosystem functions and components, that are related to human well-being (Costanza *et al.* 1997; Daily *et al.* 1997; Cardinale *et al.* 2012). For example, food production is an ecosystem service and the associated ecosystem function would be the part of gross primary production that can be extracted as food. Biological control—the reduction of herbivores by top-predators—is another example of an ecosystem service, provided via the trophic-dynamic regulation of populations which is also an ecosystem function (Costanza *et al.* 1997). In the Millenium Ecosystem Assessment (2005), ecosystem services were distinguished into four categories: 1) provisioning (e.g. food, timber, or genetic resources), 2) regulating (e.g. water purification or disease control), 3) supporting (e.g. nutrient cycling or pollination), and 4) cultural (e.g. recreational or spiritual benefits). The demand for ecosystem services has significantly increased in the last 50 years as the world population has doubled (Millenium Ecosystem Assessment 2005) and will increase further, as the human population is expected to approach 11 billion people this century (Laurance, Sayer & Cassman 2014).

Anthropogenic activities impact the biodiversity, and with it, the functions and services that ecosystems provide. As a result, there has been increasing interest in quantifying the value of ecosystem services as this is important for developing arguments and strategies for protecting these services (e.g. Storkey et al. 2013; Ojea & Martin-Ortega 2015; Zhang et al. 2015). Some services can be quantified easily, such as the production of food, fiber, pharmaceuticals, and fuel. For other services, like prevention of soil erosion, regulation of climate or services of cultural value, however, it is difficult to assign a monetary value, particularly because such values vary among countries and continents. Nevertheless, there are estimates that number the value of ecosystem services to be in the order of trillions (10^{12}) of US dollars annually, which is most likely an underestimation (Costanza *et al.* 1997, 2014). Nonetheless, if clean air and water or the production of food depends upon the maintenance of biodiversity, this definitely should be a powerful motivation for conserving it.

1.4 Land-use change in Indonesia

One of the key drivers of biodiversity loss worldwide is land-use change (Immerzeel *et al.* 2014; McGill 2015; Newbold *et al.* 2015). In the tropics, land-use change often implies the transformation of complex tropical rainforests into depauperate agricultural production systems (Gibbs *et al.* 2010). Although tropical forests cover less than 10% of the Earth’s land surface (FAO & JRC 2012), they harbor a huge amount of irreplaceable biodiversity (Gibson *et al.* 2011). Therefore, the transformation of tropical forest into other land-use systems is especially detrimental for biodiversity.

Indonesia is a distinct example of this transformation. It is known as one of the ‘hottest’ hotspots of biodiversity in the world (Myers *et al.* 2000), yet the ongoing proliferation of oil palm plantations in Indonesia is placing tremendous pressure on forest cover and, hence, on biodiversity. Between 2000 and 2012, a forest cover loss of 15.79 Mha (8.4 % of total land area) was reported for Indonesia (Hansen *et al.* 2013), where 6.02 Mha or 38% occurred within primary forest (Margono *et al.* 2014). In 2012, Indonesia underwent the largest increase in annual forest loss globally, even more than Brazil that had been the leader in deforestation of tropical forest before (Margono *et al.* 2014). The establishment of oil palm plantations has been identified as one of the key drivers for the loss of forest (but see Gatto, Wollni & Qaim 2015), thus heavily contributing to decline in biodiversity, ecosystem functioning of species communities, land degradation and rising greenhouse gas emissions (see Box 1.2) (Koh & Wilcove 2008; Fitzherbert *et al.* 2008; Wilcove & Koh 2010; Margono *et al.* 2014; Allen *et al.* 2015; Guillaume, Damris & Kuzyakov 2015). On Sumatra, where our biodiversity enrichment experiment is located, forest has traditionally been replaced by rubber (*Hevea brasiliensis*) and – in line with the trend in Indonesia in general – more currently predominantly by oil palm (Villamor, Pontius & van Noordwijk 2014), leaving behind only 28.3% of the original extent of primary forest on the island (Margono *et al.* 2014). Looking forward, one of the greatest challenges that we are facing in the 21st century is thus to meet the growing demand of food while simultaneously reducing agriculture's environmental impact. There are biodiversity conservation strategies that are proposed to protect or enhance biodiversity in agricultural landscapes. I will discuss them in the following paragraph and give some examples from oil palm plantations in particular.

Box 1.2: Facts about oil palms

The oil palm (*Elaeis guineensis*) originates from West and Central Africa and it was introduced to SE Asia in 1848. It is a perennial crop that starts yielding palm fruits for oil about three years after planting and has a continual productive lifespan of 25-30 years (Corley & Tinker 2003). With a total yield of about 4 t per ha, the oil palm is the most productive oil crop in the world, using proportionally less land compared to other oil crops (soybean, sunflower or rapeseed less produce less than 0.8 t per ha) (Sheil *et al.* 2009; UNCTAD 2015). Palm oil has therefore become the most important vegetable oil in the world (Phalan *et al.* 2013) and Indonesia is ranked second after Malaysia among the top five producers of palm oil globally (FAO 2015). As the secret in our shopping basket (Paddison 2014), palm oil is an ingredient in about one out of ten products available in the supermarket. Apart from that, oil palm is also the most relevant crop for biodiesel production (Koh *et al.* 2009). The Indonesian government used oil palm cultivation to improve the livelihood of rural households. But the high demand for palm oil did not only offer a potential pathway out of poverty but also created environmental and social problems (McCarthy, Gillespie & Zen 2012).

1.5 Conservation strategies for biodiversity in agricultural landscapes

Detrimental impacts of agricultural practices on the environment and the associated loss in ecosystem functions stress the need to develop strategies that conserve biodiversity and at the same time are economically viable (see also Box 1.3). Two models have been proposed to increase agricultural production whilst mitigating the negative consequences for biodiversity: ‘land sparing’ and ‘land sharing’. Land sparing relates to farming for high yield, potentially enabling the protection of non-farmland habitat, whereas the land sharing strategy is lower yielding farming with more biodiversity within the farmland (Green *et al.* 2005). The latter is also known as wildlife-friendly farming. The two models have often been controversially discussed (Edwards *et al.* 2010; Ghazoul, Koh & Butler 2010; Clough *et al.* 2011; Phalan *et al.* 2011b; Foster *et al.* 2011; Hulme *et al.* 2013). However, both strategies represent realistic solutions, depending on the local circumstances (Baudron & Giller 2014). A holistic view on the situation supported with results from field experiments is needed (Fischer *et al.* 2011).

Box 1.3: Incentives for nature conservation

The primary goal of landowners is to maximize profit to make up their livelihood. If there are differences in management strategies that favor conservation of biodiversity and those that favor economic output, returns must be reconciled (Banks 2004). Conservation efforts must be pragmatic and strategies have to be developed that are jointly beneficial for landowners and biodiversity. In order to increase the farmer’s motivation to adopt alternative management practices that are less harmful to biodiversity, incentives, such as ‘Payments for Ecological Services’ (PES) (Tscharntke *et al.* 2011), could be offered in exchange for managing their land sustainably (i.e. decreased use of pesticides and herbicides, enrichment of plantation with other trees, retaining forest fragments within their plantation). Certification schemes such as the ‘Roundtable for Sustainable Oil Palms’ (RSPO) are another motivation for farmers to manage their land in a wildlife-friendly way (RSPO 2013). However, the performance of the RSPO still needs to be improved for nature conservation, as their main focus is on the conservation of large areas of high conservation value and on already endangered species only. This scheme neglects that smaller habitat fragments with a lower habitat value as well as more common species are also contributing to biodiversity and thus are worth being protected (Laurance *et al.* 2010; Edwards, Fisher & Wilcove 2011; Edwards & Laurance 2012).

1.5.1 Land-sparing

Set-aside areas for conservation might indeed enhance habitat availability for wildlife and may thus benefit biodiversity. Land areas spared for nature, however, vary considerably in size and habitat quality, from contiguous forest to small forest fragments, and with or without buffer zones around intensively managed areas. Consequently, the magnitude of benefits of such forest patches on wildlife varies accordingly. Nevertheless, forest fragments can be important stepping stones between forest areas, increase the connectivity in the landscape and can have a ’spillover effect’ on adjacent agricultural land (Lucey & Hill 2012; Gilroy *et al.* 2015). In oil palm plantations, positive effects of forest fragments on biodiversity were reported for butterflies, birds (Koh 2008a; Edwards *et al.* 2010; Gilroy *et al.* 2015) and ants (Lucey & Hill 2012; Lucey *et al.* 2014). The potential of spared land to house a high level of biodiversity, however, might be negatively impacted by edge effects around forest fragments (Groom, Meffe & Carroll 2006). These edge effects increase with decreasing size of the fragments. To alleviate such negative consequences of hard borders between natural and intensively managed habitats, buffer zones are proposed (Koh *et al.* 2009; Barnes *et al.* 2014a). Furthermore, the survival of species largely depends on their dispersal ability – i.e., whether or not they are capable to move between the habitat patches (Lucey *et al.* 2014). Isolation of forest habitat within a hostile and simple-structured landscape matrix with large distances between the spared natural areas, can negatively affect a species’ survival due to lacking connectivity between protected sites and limited dispersal abilities of species (Lucey *et al.* 2014).

Despite many positive effects of forest fragments on biodiversity, land-sparing by increasing yields has not been very efficient in preventing further expansion of oil palm plantations and encroachment of forest (Ewers *et al.* 2009). It is an insufficient solution and not a panacea for all conservation problems, although forest fragments surely are essential for habitat conservation as they are still important source habitats of wildlife. Therefore, land-sharing wildlife-friendly approaches should in addition to land-sparing strategies be considered for protection of biodiversity in agricultural landscapes.

1.5.2 Land-sharing

There is increasing recognition that areas of conservation alone are not sufficient to slow down current declines in biodiversity and that, therefore, conservation outside protected areas is necessary (Bhagwat *et al.* 2008). Agroecosystems can contribute considerably to the diversity of landscapes (Perfecto & Vandermeer 2002; Tscharntke *et al.* 2011; Perfecto, Vandermeer & Philpott 2014). Sustainable management of agriculture with a reduced application of pesticides or active improvement of habitat promotes functional agrobiodiversity (Pywell *et al.* 2012). This in turn facilitates the increase of ecosystem services such as enhanced biological pest control or improved crop pollination; services that directly increase the farmers' income (Tscharntke *et al.* 2011). Benefits from biological pest-control services can be high for farmers, as they can greatly reduce damage by harmful insects on yield. Birds, for example, have been shown to reduce infestations by 50% in wildlife-friendly managed coffee plantations, thereby preventing US\$75-US\$310 $ha^{-1}yr^{-1}$ in damage (Karp *et al.* 2013). Several other studies have also shown that birds can reduce herbivore density, underlining their importance for pest control (Van Bael *et al.* 2008; Koh 2008b; Maas, Clough & Tscharntke 2013). Pest control not only delivers direct benefits to human-welfare but also provides economic incentives for crop producers to make plantations more hospitable for biodiversity (Koh 2008b).

Especially promising examples of wildlife-friendly farming methods that enhance biodiversity in combination with maintaining high yields are agroforests (Bhagwat *et al.* 2008; Clough *et al.* 2011; Maas, Clough & Tscharntke 2013). Agroforestry is defined as a "natural resource management practice, that, via the integration of trees and other tall woody plants on farms and in the agricultural landscape, diversifies production for increased social, economic, and environmental benefits" (Schroth *et al.* 2004). Agroforests have the potential to provide habitat outside protected habitats, connect nature reserves and alleviate resource-use pressure on conservation areas. Therefore, they play an important role in maintaining species diversity in human-dominated landscapes (Bhagwat *et al.* 2008). Furthermore, agroforests diversify the farmer's income due to mixed crop production, thereby reducing the negative impact of crop failure. Agroforestry with oil palms is rather uncommon in Southeast Asia; e.g. in Sumatra, large mono-cultural oil palm estates dominate the landscape. However, few examples exist, where oil palms were intercropped with trees, i.e. with rubber (Corley & Tinker 2003), teak (Chia 2011), or cacao (Lee & Kasbi 1980; Egbe & Adenikinju 1990; Amoah *et al.* 1995).

So far, I have discussed various methods for sustainable management of crops in order to protect or enhance biodiversity and simultaneously keep yields high. One strategy is sparing contiguous forest or forest fragments with buffer zones around them whilst increasing yield on agricultural land (Koh *et al.* 2009). The alternative strategy is wildlife-friendly farming where crops are produced in extensive management, i.e. agroforests, which can also result in a win-win for both, biodiversity and farmers (Waldron *et al.* 2012). Especially in Indonesia, where most of the forests have already been cleared to make way for large, biodiversity-impoverished oil palm landscapes, the attention should be on these wildlife-friendly strategies for biodiversity conservation. This will not only increase biodiversity value of anthropogenic landscapes but also decrease the pressure on conservation areas. In light of the ever-increasing decline of biodiversity, it might not be enough to just conserve what is remaining. Active restoration of degraded habitats through tree planting has been identified as a tool to help biodiversity recover and restore ecosystem functions and should additionaly be consiered. The following section therefore elucidates opportunities and challenges of tree-based restoration in degraded, agricultural systems.

1.6 Restoration of degraded ecosystems

As many parts of the world are facing severe biodiversity loss due to anthropogenic land transformation (Rockström *et al.* 2009), the restoration of biodiversity—and with it ecosystem functioning—has become equally important as biodiversity conservation. The saturating relationship between biodiversity and ecosystem functioning that has been discovered from extinction scenario experiments (i.e. analysis of the relationship in the direction of biodiversity loss) (Cardinale *et al.* 2012) indicates that if we simply turn the tables and add species to a system that is already extremely depauperate, we can expect a relatively rapid positive effect on biodiversity and ecosystem functioning. The added species in restoration plantings can directly contribute to increased biodiversity and ecosystem functioning and increase the structural heterogeneity that could attract other organisms (Tews *et al.* 2004; Stein, Gerstner & Kreft 2014). In the restoration context, collaboration of different disciplines is necessary to simultaneously tackle and ameliorate the consequences of environmental change on biodiversity and human well-being (Perring *et al.* 2015).

Restoration ecology is a sub-discipline of ecology that informs the "intentional activity that initiates or accelerates the recovery of an ecosystem with respect to its health, integrity and sustainability" (Wright *et al.* 2009). Restoration activities can also serve as powerful tools for exploring some of the central biodiversity-ecosystem functioning (BEF) questions. However, for BEF research to be useful for ecological restoration, ecosystem functions must be related to the ecosystem services desired as the outcome of restoration. In the following paragraphs I will discuss some factors related to restoration.

1.6.1 Tree plantings as nuclei for natural succession

Tree planting is considered an important measure to accelerate natural succession (Chazdon 2008a). Planted trees are likely to attract seed dispersing animals by e.g. providing habitat for foraging, nesting, or roosting (Thiollay 1995) and thus increasing seed rain. Even within small stands, trees may facilitate seedling establishment by creating a more favorable microclimate and enhancing the soil. One strategy that has been used in forest restoration is applied nucleation, which involves planting of tree islands as focal areas of recovery (sensu Yarranton & Morrison 1974; reviewed in Corbin & Holl 2012). Once these patches or nuclei are established, they attract seed dispersing animals and thereby facilitate recruitment of other woody plants (Corbin & Holl 2012). An example for this restoration method can be found in a pasture landscape of Honduras where small tree islands (64, 16, and 4 m^2) were planted as recruitment foci (Zahawi & Augspurger 2006). Within two years after planting, bird activity, seed rain, seedling establishment, and seedling species richness were elevated in the tree islands. In another study in southern Costa Rica, tree islands of 16-250 m^2 were planted and compared with an unplanted control in an agricultural landscape (Cole, Holl & Zahawi 2010). Two years after planting, seed rain was highest in the large plots, intermediate in the smaller tree islands, and lowest on the control plots. Planting design was more important than surrounding forest cover within a 500 m radius area. The advantage of applied nucleation over restoration of entire landscapes is that it is a promising restoration strategy to accelerate forest recovery to a similar extent as plantation-style restoration but is more economical (Zahawi *et al.* 2013).

1.6.2 Size of restoration plantings

In highly productive agricultural landscapes, such as oil palm-dominated landscapes, space for conservation is sparse and opportunity costs for the establishment of newly created conservation areas are very high. In this context, the question about the optimal size of tree islands to be planted arises: small enough to be reasonable in cost, but large enough to achieve reasonable positive effects on biodiversity and ecosystem functioning. In a macro-scale study within a human-dominated landscape, bats showed positive and negative responses to increasing size of fragments, suggesting that there is no clear pattern on how species richness responds to island size (Mendenhall *et al.* 2014). Hence, the most effective minimum tree island size as recruitment foci in the oil palm system to enhance biodiversity has yet to be identified.

1.6.3 Diversity of restoration plantings

Conventional tree planting in the tropics has mainly been based on exotic species from a few genera grown in single-species stands in the past. This practice has been criticized for contributing little to ecosystem functioning and biodiversity (Lamb, Erskine & Parrotta 2005). More recent approaches, however, propose the use of native species in mixed stands (Erskine, Lamb & Bristow 2005; Petit & Montagnini 2006; Hall *et al.* 2011; Bruelheide *et al.* 2014). Many positive effects of tree planting on biodiversity have been reported (Balvanera *et al.* 2006; Quijas, Schmid & Balvanera 2010) but most such studies took place in grasslands and outside the tropics. However, in a tropical tree biodiversity experiment in Panama, primary productivity was significantly higher in three-species mixtures than in monocultures (Potvin & Gotelli 2008a); tree species composition, however, did not affect productivity (Salisbury & Potvin 2015). Similar results regarding the diversity of plantings were found in a tree diversity experiment in Costa Rica, were mixed tree plantations had a higher productivity compared to mono-culture tree plantations (Petit & Montagnini 2006). In a large-scale forest biodiversity experiment in subtropical China, where 40 tree species were planted with varying tree diversity on plots of the same size (Bruelheide *et al.* 2014), the proportion of trophobioses, symbiotic associations between organisms where food is obtained or provided, increased with increasing tree diversity. This finding suggests that tree diversity could increase the robustness of insect associations against changing environmental conditions through bottom-up processes (Staab, Blüthgen & Klein 2015).

A limitation of many restoration projects has been the unknown effects of tree diversity because of missing experimental manipulations of the number of species. However, there is evidence that not only structure, which is essentially a function of age rather than diversity, is likely to be important for associated animal biota (Kanowski *et al.* 2003), but that birds and lizards benefit more from diverse rainforest restoration plantings than from species-poor timber plantations (Erskine, Lamb & Bristow 2006). This shows that diverse restoration plantings have a higher potential to increase animal diversity, which is not only important for animal biodiversity per se, but also for associated ecosystem functions, such as seed dispersal, which may affect successional trajectories and/or speed.

Overall, these examples illustrate the great benefits of tree islands for biodiversity and associated ecosystem functions. So far, however, no tree-based restoration experiment exists that a) simultaneously manipulates the size and the diversity of the tree plantings, b) considers socio-economic impacts of such plantings and c) is conducted in a plantation that is further maintained whilst restoaration effects are studied. In order to develop clear guidelines that can improve the management of agricultural systems such as oil palm plantations and benefit both, biodiversity and humanity, it is, however, essential to study the impacts of such tree plantings on both, ecology and socio-economics and find the most effective planting strategy. In the following section, I will introduce the concept of a biodiversity enrichment experiment that is designed to simultaneously address ecological and socio-economic aspects of tree enrichment in a mono-culture oil palm plantation.

1.7 Towards a better understanding of restoration effects on biodiversity and ecosystem functioning in oil palm landscapes

Ecological restoration has recently adopted insights from the biodiversity-ecosystem function perspective (Aerts & Honnay 2011). Currently, there are 19 tree diversity restoration experiments in 16 countries worldwide that also focus on BEF (‘TreeDivNet’ 2015). These experiments are connected via the informal research network of tree diversity experiments ‘TreeDivNet’ (www.TreeDivNet.ugent). Four experiments are located in the tropics: the UADY tree diversity experiment on pasture land in Mexico (Moreira *et al.* 2014), the Gazi Bay experiment in Kenyan mangrove forests (Kirui *et al.* 2008), the Sabah biodiversity experiment in Bornean tropical forests (Hector *et al.* 2011) and the Sardinilla experiment in Panama on pasture land (Scherer-Lorenzen, Bonilla & Potvin 2007). Furthermore, there is another tree diversity experiment which addresses BEF-questions in Costa Rica (Petit & Montagnini 2006) but it is not part of the TreeDivNet forum. To date, there is no such project in an oil palm plantation, which is already established and further maintained. While there is broad consensus that the re-establishment of diverse habitats and the restoration of ecological multi-functionality in oil-palm-dominated landscapes is an urgent need, there is little knowledge on how this can be implemented in a way that is both ecologically and economically effective.

To bridge this gap and in order to investigate the general underlying mechanisms and specific management strategies of biodiversity enrichment with trees, I established a combined biodiversity enrichment and biodiversity-ecosystem functioning experiment in collaboration with colleagues from Germany and Indonesia. Tree islands were planted as ‘recruitment foci’ within a large-scale, mono-culture oil palm plantation in the province of Jambi (Sumatra, Indonesia) in December 2013 within the framework of my PhD project. Plot size as well as species diversity and composition of six multi-purpose tree species native to Sumatra that deliver a variety of products (fruits, latex, timber) to local people were systematically varied (plot sizes: 5x5 m, 10x10 m, 20x20 m, 40x40 m); tree diversity levels of six, three, two and one). A random partitions design was followed (as described by Bell et al., 2009) with four partition series plus four plots without planting, subjected to natural succession. This experiment is planned to run for at least nine years. Monitoring of ecological processes focuses on seed rain, growth rates and survival of trees, and taxonomic and functional diversity responses of birds and arthropods. Parallel to the ecological studies, socio-economic surveys are planned to assess opportunities and constraints of enrichment plantings for local communities. With the results of this interdisciplinary biodiversity enrichment experiment, it is aimed to significantly contribute to the development of ecologically improved and socio-economically viable management strategies.

The three main hypotheses addressed with the experiment are:

- Gap enrichment plantings have a beneficial effect on biodiversity and ecosystem functioning in oil palm landscapes
- Tree islands act as recruitment foci and thereby have a positive effect on the colonization of flora and fauna
- Trade-offs between socio-economic and ecological functions are minimized a) due to the economic value of the planted trees and b) by increased provisioning of ecosystem services, which directly benefit farmers' income (e.g. ecological pest control, increased pollination)

1.8 Overarching project framework and study area

The study for my PhD thesis was carried out on the island of Sumatra, one of the 17,508 islands of Indonesia, and the second largest in the Malay Archipelago after Borneo. My project sits within the overarching framework of the collaborative research centre entitled 'Ecological and socio-economic functions of tropical lowland rainforest transformation systems on Sumatra, Indonesia' (EFForTS), which is a research initiative of the University of Göttingen in Germany and three universities in Indonesia (University of Jambi on Sumatra; University of Bogor on Java; and University of Tadulako on Sulawesi). The main goal of this international, interdisciplinary research program is to investigate the impacts and forces responsible for deforestation in the Province of Jambi, one of the most severely converted regions in Indonesia (Miettinen, Shi & Liew 2011), and to evaluate the ecological, economic and social consequences linked to the transformation of rainforest into other land-use systems.

1.8.1 Study area

Jambi province is located in the eastern part of central Sumatra. The climate is humid tropical with a mean annual rainfall of 26.7 ± 1.0°C and a mean annual rainfall of 2235 ± 385 mm (1991-2011; climate station at the Jambi Sultan Thaha airport of the Meteorological, Climatological and Geophysical Agency). There is a dry season from June to August, where rainfall can reach measures below 100 mm. The natural vegetation in the Jambi Province is dipterocarp dominated lowland rainforest in the centre and peat-swamp forest along the east coast (Laumonier 1997; Whitten 2000). Dominant soil types are loam and clay Acrisols, of which we find the first in the Bungku region (Allen *et al.* 2015).

1.9 Study objectives

The main focus of most of the projects within the EFForTS- project is on the consequences of lower diversity in e.g. oil palm plantations compared to tropical lowland rainforest. In my subproject, however, the focus is to investigate how ecological and socio-economic functions respond if habitat is restored within a mono-cultural oil palm plantation. The title of my subproject is ‘Biodiversity enrichment in oil palm plantations – ecological and socio-economic impacts’. My focus in this subproject is on the ecological impacts of enrichment plantings, in particular on bird and invertebrate communities. In my thesis I therefore a) studied the ecological and economic effects of remnant or planted trees in smallholder oil palm plantations to uncover the economic and ecological trade-offs and b) established a biodiversity enrichment experiment to study the effect of biodiversity enrichment plantings on bird and invertebrate communities in oil palm systems.

In a first step, I assessed the shape of the relationship between ecological (bird diversity, bird abundance) and economic outcomes (oil palm yield and revenue) of remnant or planted trees in smallholder oil palm plantations along a management intensity gradient (Figure 1.3). This interdisciplinary approach allowed me to study not only the ecological impacts of “natural” enrichment plantings on biodiversity but also to gain a deeper understanding of the potential economic constraints and opportunities to encourage increased use of enrichment plantings in the area. Furthermore, I aimed at estimating the costs for increased bird diversity/bird abundance in oil palm plantations. The analysis to answer these research questions is based on economic and ecological data from 120 smallholder oil palm plantations.

Figure 1.3: Smallholder oil palm plantations of different management intensity: a) high intensity, no trees b) intermediate management intensity, few trees c) extensive management, many trees within the oil palm plantation.

In a second step, I sat the scene for long-term research on ecological and socio-economic processes of enrichment plantings in oil palm plantations by establishing a biodiversity enrichment experiment in an oil palm plantation in the Province of Jambi, Sumatra, Indonesia (Figures 1.4–1.7). This long-term experiment is aimed at contributing to the development of management guidelines for an ecologically improved and socio-economically viable management of oil palm plantations. The establishment of the experiment comprised the planting of tree islands in gaps of an oil palm plantation. The design allows for disentangling effects attributed to island size and those to the diversity of plantings in order to find the best planting strategy for increased diversity and associated ecosystem functions, while simultaneously minimizing opportunity costs. My focus for the early phase of the experiment and within the timeframe of my PhD project was on the establishment of the tree islands, the assessment of the initial abiotic and biotic conditions prior to the tree planting on the plantation, as well as on monitoring the effects of enrichment plantings on bird and invertebrate communities one year after establishment.

The first part of my research project took place on smallholder oil palm plantations surrounding four villages in the Batanghari region in the province of Jambi, Sumatra, Indonesia. The second part of the study was conducted on the plantation of PT Humusindo near Bungku, also in the Jambi province.

Figure 1.5: Establishment process of the biodiversity enrichment experiment: a) plots were measured in a mono-cultural oil palm plantation; b) roughly 40% of the oil palms were cut to increase light conditions for better growth of freshly planted trees; c) marked plastic poles were set to assisted the adherence to the strict planting scheme; d) tree seedlings waiting to enrich the oil palm plantation; e) digging of holes; f) application of organic and an-organic fertilizer to enhance establishment of the planted trees; g) planted trees on the experimental plots.

Figure 1.4: Seedlings of the six multi-purpose tree species selected for the biodiversity enrichment experiment a) *Archidendron pauciflorum, b) Peronema canescens, c) Durio zibethinus, d) Dyera polyphylla, e) Shorea leprosula* and f) *Parkia speciosa*.

Figure 1.6: Tree growth over 17 months. The pictures show the same single-species plot planted with *Shorea leprosula* a) right after planting, b) ten months after planting, and c) 17 months after planting.

Figure 1.7: Tree islands 17 months after planting. a) A single-species plot planted with *Peronema canescens;* b) A mixed-species plot.

1.10 Outline

In the research chapters of this thesis, I investigate the effects of enrichment plantings in oil palm plantations on ecology and economics.

In Chapter 2 “Trade-off between bird diversity and abundance, yield and revenue in smallholder oil palm plantations in Sumatra, Indonesia”, I present a study on the economic–ecological relationship of remnant or planted trees in smallholder oil palm plantations along a management intensity gradient. In addition, I investigated different possibilities to estimate the price for increased bird species richness and abundance in oil palm plantations.

In Chapter 3 “Biodiversity enrichment in oil palm landscapes: A tree planting experiment in Sumatra (Indonesia)”, I give an introduction to the biodiversity enrichment experiment. The initial abiotic and biotic characteristics of the experimental plots prior to the tree plantings are presented and I also give first insights on early effects of the planted tree islands on the bird and invertebrate fauna one year after establishment.

Finally, Chapter 4 summarizes the main findings and concludes with suggestions for further research.

PART II

RESEARCH CHAPTERS

Chapter 2: Trade-offs between bird diversity and abundance, yields and revenue in smallholder oil palm plantations

2.1 Abstract

Global land-use change has drastic consequences for biodiversity leading to losses of ecological functioning, ecosystem services and human well-being. While species dependent on undisturbed natural habitat are most affected by conversion to agriculture, even populations of disturbance-tolerant species can be endangered in landscapes dominated by high-input mono-cultural cropping systems. This has raised the question of how, and at what cost, a diversity of species can be conserved in such habitats. Focusing on birds of smallholder oil palm-dominated landscapes, we investigated the relationship between the ecological and economic outcomes of remnant or planted trees in smallholder oil palm plantations. The study comprised a household and a field component. We gathered plot specific data on yields, revenue and inputs from 120 households owning productive oil palm plantations in the Jambi Province, Sumatra, Indonesia. Bird diversity and abundance as well as vegetation structure was assessed on the same oil palm plots. We tested the effects of a set of economic and ecological variables on measures of bird diversity, bird abundance, oil palm yield, and total revenue. Our results show that a gain in bird diversity and bird abundance conditional on increases in number of trees comes along with a loss in revenue for farmers indicating that there is a win-lose relationship between ecological and economic functions. However, since the relationship is non-linear, costs for bird species gain or gain in bird abundance change depending on the number of trees within an oil palm plantation: in a relatively extensively managed oil palm plantation (high number of trees, low oil palm yields), a further increase in the number of bird species or individuals leads to a relatively high loss in total revenue, whereas in an intensively managed oil palm plantation the same increase in number of bird species results in a smaller loss in revenue. An increase in bird abundance can be fostered at smaller costs when compared to the costs for increasing biodiversity. This suggests that thereis room for tree-based enrichment of intensively managed oil palm plantations, where a relatively high increase in bird species richness or bird abundance could be achieved at relatively low cost.

Keywords: ecological-economic trade-off, bird diversity, agro-ecosystems, oil palm, Southeast Asia

2.2 Introduction

Land-use change is globally the most important cause for biodiversity loss (Sala *et al.* 2000; Immerzeel *et al.* 2014). Both the transformation of natural or semi-natural habitats into mono-cultural annual or perennial cropping as well as agricultural intensification at local and landscape-scale lead to losses in biodiversity and ecosystem functioning of species communities (Sala *et al.* 2000; Sodhi *et al.* 2004; Steffan-Dewenter *et al.* 2007; Koh & Wilcove 2008; Wilcove *et al.* 2013; Edwards *et al.* 2014), with a risk of negative effects on human well-being (Cardinale *et al.* 2012; but see Raudsepp-Hearne *et al.* 2010). In the next few decades, the pressure on biodiversity will proceed or even amplify due to an increasing demand for food (Tilman *et al.* 2002) and biofuels (Koh & Wilcove 2007; Field, Campbell & Lobell 2008; Corley 2009; Koh & Ghazoul 2010). The mitigation of the loss of biodiversity and of land degradation is therefore one of the major challenges in the current decade (UN‘s ‘decade of biodiversity’) (Tscharntke *et al.* 2012a).

Almost two-third of the cropland expansion in tropical countries in the last decade can be attributed to the expansion of annual crops, such as soybean and maize. Oil palm (Elaeis guineensis), ranking the fifth of the most rapidly expanding crops in harvested area, is the most rapidly expanding perennial crop in the tropics (Phalan *et al.* 2013). Within 25 years, the total plantation area of oil palm has tripled, with current global estimates of over 15 million ha (Gilbert 2012). In Indonesia, the area under oil palm cultivation almost doubled from 4.2 million ha in 2000 to around 8 million ha in 2010, which account for 46% of the world’s crude oil production (Obidzinski *et al.* 2012). In 2009, the Indonesian government claimed that the oil palm area can be nearly doubled to 18 million ha “without disturbing […] forest preservation efforts” (The Jakarta Post 2009).

On the one hand, oil palm cultivation is an attractive pathway out of poverty for many rural households (The World Bank 2011) even though smallholder productivity (in 2010, 38% of the total oil palm area was managed by smallholders (Rianto, Mochtar & Sasmito 2012)) is approximately 35-40% lower than yields in the private and government sectors (Lee *et al.* 2013) and varies considerably conditional on institutional, agronomic and biophysical factors (McCarthy 2010; Rist, Feintrenie & Levang 2010; Koh & Ghazoul 2010; Budidarsono 2012; Lee *et al.* 2013). On the other hand, oil palm cultivation is also a pervasive threat to biodiversity (Belcher & Schreckenberg 2007; Fitzherbert *et al.* 2008). Large areas of Southeast Asia, where around 80% of palm oil are produced, belong to the most biologically diverse terrestrial ecosystems on earth, characterized by a high degree of endemicity (Fitzherbert *et al.* 2008). It is estimated that between 1990 and 2005 around 57% of the oil palm expansion occurred at the expense of tropical rainforest (Koh & Wilcove 2008; Wilcove & Koh 2010). Between 1990 and 2005, Indonesia reported an absolute decline in forested area of 280,000 km2, ranking second among the countries which face a significant decline in forested area (World Trade Organization 2010). Oil palm plantations are also often established on extensive complex smallholder production systems, such as “jungle rubber” (hutan karet), which is characterized by rubber trees mixed with other tree species forming a stand structure similar to secondary forest (Gouyon, Foresta & Levang 1993; Ekadinata & Vincent 2011). Both, forest and jungle rubber, are valuable habitats for conservation. Jambi Province in Indonesia is one of the provinces with the fastest and most complete transformation of tropical lowland rainforest and extensive traditional production systems into rubber or oil palm plantations worldwide (Laumonier *et al.* 2010). Compared to jungle rubber as a complex agroforestry system, oil palm production is characterized by a high degree of intensification at the landscape and habitat scale, including landscape simplification (Foster *et al.* 2011) and rather low structural habitat complexity (uniform stand age; low canopy; low ground layer vegetation cover; low-stability micro-climate).

Oil palm landscapes are among the poorest habitats for biodiversity in tropical regions (Fitzherbert *et al.* 2008) and the conversion of natural or logged forest to oil palm plantations leads to dramatic losses in biodiversity in the majority of taxonomic groups (Foster *et al.* 2011). Fayle et al. (2010), for example, report a decline of forest ant species of 81% as forest is converted to oil palm. This loss of species is mainly caused by a loss in habitat heterogeneity. Moreover, conversion of tropical forests into oil palm can lead to a loss in ecosystem functions that disproportionately exceeds the decline in species diversity (Barnes *et al.* 2014b). Edwards et al. (2013) showed that functional diversity of birds experiences severe declines along a gradient from unlogged forest to logged forest to oil palm. Similar results were found by Azhar et al. (2013) who found reduced bird functional diversity in oil palm compared to peat swamp forest. Species that dominantly colonized oil palm landscapes after conversion are mainly generalist disturbance-tolerant species with large geographical ranges and low conservation status (Peh *et al.* 2006; Edwards *et al.* 2013).

However, it has been highlighted that even in such impoverished landscapes, there can be significant variation in abundance and diversity of species, dependent on the management of the vegetation and the presence of nearby forests (Koh 2008a; Azhar *et al.* 2011), suggesting that the – from many species' perspective – inhospitable monoculture landscape can be softened up to some degree. Achieving this is valuable, not only in order to maintain populations of disturbance-tolerant species, which have been shown to keep declining elsewhere long after major changes in land use (e.g. farmland birds in Europe), but also to ensure ecosystem functions such as pest control. Birds, for instance, play an important role in an ecosystem as they maintain a wide range of ecosystem functions such as pest control, seed dispersal and pollination (Sekercioglu *et al.* 2002; Sekercioğlu, Daily & Ehrlich 2004; Van Bael *et al.* 2008; Karp *et al.* 2013). Birds were shown to contribute to the control of leaf-eating oil palm pests (Koh 2008a) and have a beneficial impact on agroforestry crops as they effectively suppressed arthropod densities leading to an increase of yield by about a third (Maas, Clough & Tscharntke 2013).

One wildlife-friendly option are designer plantation landscapes in which monocultural plantations are enriched with trees planted in gaps within the plantation or with agroforestry buffer zones to surrounding natural vegetation. They are proposed as a means to maintain livelihood needs while increasing biodiversity and ecological functions and thus to alleviate the negative environmental impacts of intensively managed transformation systems such as oil palm (Bhagwat *et al.* 2008; Bhagwat & Willis 2008; Koh *et al.* 2009; Clough *et al.* 2011). In particular, tree planting is considered an important measure. Planted trees are likely to attract seed dispersing animals by providing habitat for foraging, nesting, or roosting and thus increase seed rain and allow natural succession (Chazdon 2008b). Even within small stands, trees may alleviate stressful conditions and thus facilitate seedling establishment by creating a more favourable microclimate and amelioration of the soil (Zahawi & Augspurger 2006; Manning, Fischer & Lindenmayer 2006; Herrera & García 2009; Fischer, Stott & Law 2010; Cole, Holl & Zahawi 2010).

The evaluation of management options that aim to conserve biodiversity, both at the landscape and habitat scale, depends on the shape of relationship between ecological and economic outcomes (Perfecto *et al.* 2005; Steffan-Dewenter *et al.* 2007; Tscharntke *et al.* 2012a). The effect of mixed trees in oil palm plantations, controlling for management regimes (e.g. fertilizer and herbicides application) and habitat complexity (ground vegetation, shrubs) on yields and revenue has rarely been studied. On the one hand, oil palm yields most probably decrease with increasing number of other trees within the plantation because of competition for light and nutrients (Corley & Tinker 2003), and depending on the method of establishment, on space forgone for planting oil palm. On the other hand, Miccolis *et al.* (2014) show, based on a study of oil palm grown in trial plots of ecologically diverse agroforestry systems in northern Brazil, that after five years oil palm yields in agroforestry systems were on average higher than those in mono-cultural systems. Thus, agro forests managed to be more "wildlife-friendly" do not necessarily result in a decrease in agricultural output.

Here, we investigate the relationship between the ecological and economic outcomes of remnant or planted trees in smallholder oil palm plantations, as a contribution towards the scientific basis for designing incentives for structurally complex oil palm plantations for enhanced species diversity. This study comprises a field and a household survey component. We conducted a bird and vegetation assessment and a socio-economic household survey from the same 120 smallholder oil palm plantations in four villages in the province of Jambi, Sumatra, Indonesia, along a gradient of habitat complexity and management intensity. This study aims to answer the following research questions: (1) Do remnant or planted trees within oil palm plantations affect bird diversity and bird abundance? (2) Do remnant or planted trees within oil palm plantations affect economic outcome variables, such as yield and revenue? (3) Is there a trade-off between ecological and economic functions? (4) What is the shape of the relationship between ecological and economic functions?

2.3 Material and methods

2.3.1 Study site

The survey was conducted in four villages (Bukit Harapan 1° 31' 25.9746" S, 102° 56' 3.3864" E; Bukit Sari 1° 31' 59.7606" S, 103° 10' 16.8882" E; Karmeo 1° 47' 39.7242" S, 103° 2' 38.1402"; Pulau Betung 1° 33' 41.4216" S, 103° 25' 41.6958" E) in the Batanghari region in the Province of Jambi, Sumatra, Indonesia, between February and April 2013. A map of the study area is provided in Figure 2.1. Total area of all 101 plots used in the analyses (excluding missing data points) was 164 ha (70 ha in Bukit Harapan; 53 ha in Bukit Sari; 27 ha in Karmeo; 14 ha in Pulau Betung). The climate is humid tropical, with a mean temperature range from 25.9–26.8°C and an annual rainfall of 2268.3 mm year-1 (1960–1990 average). To establish mono-cultural oil palm and rubber cultivation area, natural lowland rainforest was cut massively in the 1970's and 1980's by concession logging. Hence, large areas of lowland rainforest do no longer exist in the Batanghari region but only small patches of jungle rubber or secondary forest. This transformation of lowland rainforest into mono-cultural rubber and oil palm plantations was fostered by the transmigration program, which was launched by the Indonesian government in the 1980's (Fearnside 1997; Elmhirst 1999). Within the framework of this program, households were resettled from the over-populated islands of Java or Bali to the less-populated islands of Kalimantan and Sumatra. These settlements were established in Nucleus Estates and smallholder plantations (NES), where a company-owned refinery and estate is surrounded by smallholder-owned plantations. Besides access to credit and oil palm technology, early transmigrant households obtained certified land entitlements, which include 2 ha of already established oil palm plantation within the NES plantation (McCarthy, Gillespie & Zen 2012). Transmigrant smallholder oil palm plantations intend to be intensively used agricultural systems characterized by high input use and contribute to landscape homogenization. Oil palm plantations within one NES plantation are similar in terms of oil palm age, oil palm density, and management practices and form a large mono-cultural oil palm plantation by bordering each other.

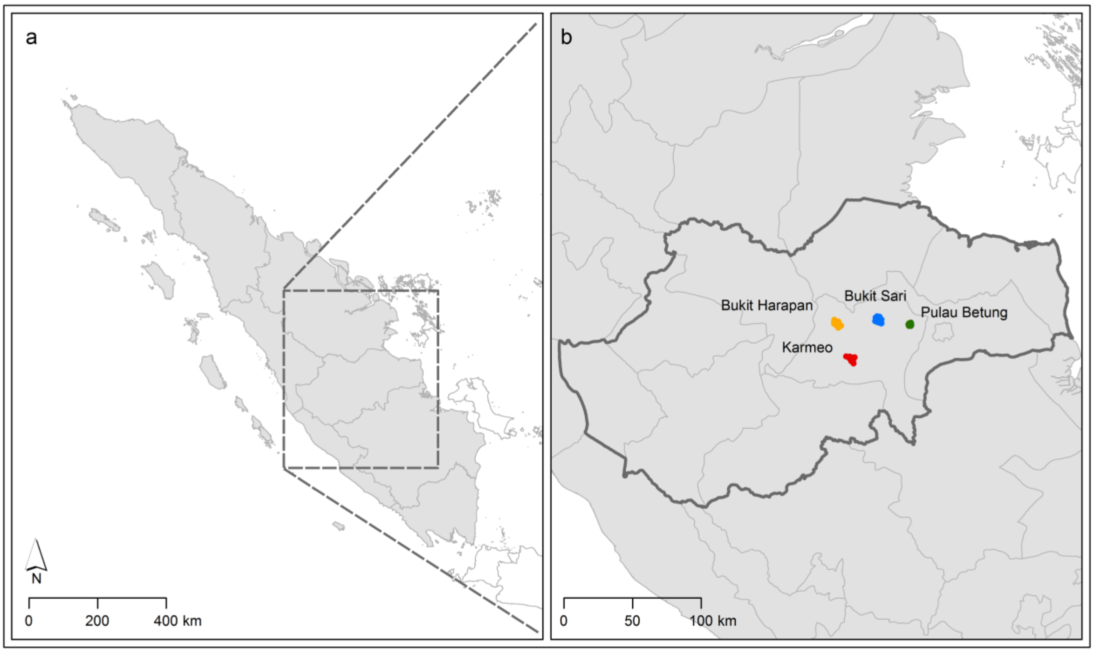

Figure 2.1: Map of the study area: (a) Sumatra (b) Location of the study plots in the four study villages Bukit Harapan (yellow), Bukit Sari (blue), Pulau Betung (green) and Karmeo (red) in the Jambi province.

In the last 10 years, however, the expansion of smallholder oil palm area has been mainly driven by independent smallholders, who are located in autochthonous, rather than transmigrant villages (Ekadinata & Vincent 2011). These independent smallholders are either locals or spontaneous migrants (e.g. from other parts of the Jambi province). Autochthonous oil palm plots are considerably different compared to the transmigrant ones in terms of oil palm age, oil palm density and management practices. The landscape of autochthonous villages is characterized by oil palm plantations that incorporate a management intensity gradient and small patches with different land use types (e.g. rubber mono-culture, jungle rubber, bush fallow land, home garden etc.).

To capture a wide range of variability in structural complexity on the habitat and landscape scale among oil palm plantations and accounting for the gradient in agricultural intensity in that region, the survey was carried out in two autochthonous villages (Pulau Betung, Karmeo) and two transmigrant villages (Bukit Sari, Bukit Harapan).

2.3.2 Household survey

Based on a village census, a total of 120 households that individually manage productive oil palm plots were randomly selected. In the case that a household owned more than one productive oil palm plot, the largest oil palm plot was selected for further consideration. In the transmigrant villages, 70 oil palm cultivating households were interviewed. Due to the lower number of households owning productive oil palms, only 50 plots were selected in the autochthonous villages. Information on farm and household characteristics including plot specific data was obtained from the household heads. The standardized questionnaire contains information on plot characteristics (plot size, oil palm age, oil palm density, location etc.), abundance and use of trees within or along the border of the specific plot, costs and benefits of oil palm cultivation and cultivation of trees, respectively. All plot characteristics and management related information refer to the calendar year 2012. Afterwards, we accompanied the farmer to the plot that he/she was interviewed about to take GPS coordinates and tracked the borders of each plot by surrounding it with a GPS device. Plots sizes ranged from 0.19 ha to 9.26 ha (mean plot size: 1.62 ± 0.98).

2.3.3 Bird sampling

Birds were recorded visually and acoustically, and by systematic tape recordings in accordance with a standardized observation method using 15 minutes point counts at the centre of each plot. We did only one point count per plot, independent of the plot size, as we only wanted to assess the local bird diversity and the sum of observations at the centre of each plot. Each plot was visited twice from 6 am to 10.30 am and there was a minimum of six days between the first and the second sampling period on plots within each of the villages. Point counts were only done when weather conditions were appropriate (no rain). For every species, we recorded the maximum number of individuals present simultaneously on the plot. Individuals flying only above the canopy were excluded from analyses. Migratory species were not recorded. For taxonomy we followed MacKinnon et al. (1993). To get a standardized measure for all plots for the analyses, we used bird observations within a 25 m radius only, as this was the maximum area that could fit into every plot. For vulnerability status, we used the species' IUCN (International Union for Conservation of Nature) classification (IUCN 2014).

2.3.4 Vegetation assessment

Vegetation structure was assessed on 100 m x 6 m transects on each plot starting from the centre of the plot proceeding into northerly, southerly, westerly and easterly direction. We distinguished between trees and shrubs and noted the distance of each vegetation structure from the centre. The height and percentage cover of ground vegetation was assessed within circles (radius=3 m) at the centre point and along each of the four transects at 50 m and 100 m distance from the centre. Density measures for vegetation variables were calculated only from data that was collected within each plot. Vegetation data collected outside the plot were not considered.

2.3.5 Data analysis

Using mixed effects models, we tested the effect of a set of economic and ecological variables on bird diversity, bird abundance (sum of bird observations in two sampling periods), yields (ton year -1 ha-1) and revenue (US$ year-1 ha-1), with village as a random effect to control for unobserved heterogeneity between the four study villages. Table 2.1 depicts the set of variables used, as well as their range.

For the bird models, we pooled the observations from the two sampling periods and ran a glmm with a Poisson distribution and a log-link function using the "glmer" function (R Core Team 2014). There was no over-dispersion in the bird diversity model whereas the bird abundance model was highly over-dispersed. To deal with the over-dispersion in the abundance model, we included an observation level random effect.

Table 2.1: Explanatory variables considered in the full models to explain bird abundance (number of bird individuals within a 25 m radius around the centre point), bird diversity (number of bird species within a 25 m radius around the centre point), yields (ton fresh bunches of oil palm ha-1y-1) and revenue (IDR ha-1y-1); transformed values in parentheses. Offsets used for log transformation of variables including zeros in parentheses.

Variable name	Description	Min	Mean	Max
Village	Factor with four levels, Bukit Harapan, Bukit Sari, Karmeo and Pulau Betung, entered the model as random effect	-	-	-
Number of trees (ecology models)	Number of all trees > 2 m per ha, log transformed (offset: 2.51)	0	27.93	314.72
Number of trees (economic models, negative input)	Number of trees per ha, log transformed (offset: 0.22)	0	12.26	125.67
Number of oil palms	Number of oil palms per ha, log transformed	86.98	159.26	349.99
Forest border	Factor with two levels, forest patch bordering the oil palm plot (1) and no forest patch at the border of the plot (0)	0	-	1
Shrubs	Number of shrubs > 1.5 m per ha, untransformed	0	30.63	193.72
Height ground vegetation	Factor with five levels: (1) 0-15 cm, (2) 16-30 cm, (3) 31-50 cm, (4) 51-100 cm, (5) 101-150 cm	0	-	5
Age	Age of oil palms	1	12.39	21
Age, squared	Age of oil palms, squared transformed	1	189.41	441
Quantity of fertilizer	Total amount of applied fertilizer (kg) per ha and year, log transformed (offset: 1.14)	0	771.10	2493.22
Value of herbicides	Total value of applied herbicides (IDR) per ha and year, log transformed (offset: 14127.2)	0	184094.6	3461947
Labour hours	Total working hours of family and non-family labourers per ha and year, log transformed	32.43	286.31	2190.72
Marehat	Factor with two levels, marehat clones plantes (1) and no marehat clones planted (0)	0	-	1

For the economic models, we estimated a Cobb-Douglas production function, which was specified as a linear relationship between the log-transformed outcome variables and a range of log-transformed input variables. The “lme” function was used assuming a normal distribution and fitting the models by maximum likelihood estimation (R Core Team 2014).

Oil palm yields were calculated as the total output of oil palm bunches divided by oil palm area. The total revenue comprises the revenue generated both from marketed oil palm bunches and from fruit and timber products of the remnant or planted trees within or at the border of the oil palm plantation. In addition, the opportunity costs of fruits and timber products generated from remnant or planted trees and consumed by the household were valued using the respective market prices. For the oil palm revenue, for each individual farmer the average fresh oil palm bunch price was calculated based on the average fresh oil palm bunch price received in the dry and in the rainy season weighted by the length of each season.

The choice of explanatory variables considered in the economic models was guided by the production technologies and practices hypothesized to influence oil palm output and output generated from remnant or planted tree stands. Oil palm smallholders use three main discretionary inputs: herbicides, fertilizer and labour. Since herbicides are partly used as concentrates, we considered the total value of the applied herbicides in the analyses, assuming a positive correlation between the concentration of active substances and price. For fertilizers, it was feasible to use the total amount of applied fertilizer. Labour reflects the total working hours of family and hired labourers spent on weeding of ground layer vegetation and epiphytes, herbicide, fertilizer and soil amendment applications and harvesting. All management-related explanatory variables are given per hectare and year. Previous studies have shown that the yield potential is determined by the quality of the seedlings (Phalan et al., 2009) and that transmigrant smallholders tended to receive better quality seedlings (McCarthy et al., 2012). While most of the transmigrant oil palm plantations in our sample were planted with Marehat clones, the variety can be found on a significantly lower share of the autochthonous plots. To control for differences in yields and revenues conditional on the seedling quality, we considered a dummy for Marehat clones.

As for the ecological predictors, besides height and percentage cover of ground vegetation as well as number of trees, a forest factor describing whether or not a forest patch (> 1 ha) was bordering the plot was included because we assumed that forest patches at the border should function as source habitats and influence bird diversity and abundance on the plot (Anand, Krishnaswamy & Das 2008; Clough *et al.* 2009). Nearest fragment distance or nearest forest fragment size could not be adequately assessed as there were neither suitable maps with a detailed enough land-use classification, nor recent enough aerial pictures available from which size and distance of forest fragments could have been derived. Collecting this information in the field was not possible due to time and labour constraints.

We used two different tree variables – one for the economic models and one for the bird models – because in the economic survey all the information (e.g. number of oil palms, amount of fertilizer) relates to an entire plot, whereas the ecological variables were derived from only part of a plot (100 x 6 m transects for vegetation, 25 m radius for birds). As the tree variable is our determining factor and links the economic and ecological parts of the study, we decided to maintain the same scales for the tree variable as for the corresponding response variables (data on bird diversity and abundance for only part of the plot; data on yield and revenue for the whole plot). Hence, for the bird models we used the tree densities that were derived from data collected on transects. In the economic models we included a tree variable, which was based on household survey data and related to the area of the whole plot; it is the number of trees which the farmer recalled having within his plot. The field and household based data on number of trees is significantly correlated ($p = 0.008$). In the economic models we included the tree variable as a negative input given that this better described the data (lower AIC). Additionally, we multiplied the tree variable with a constant term (1.05), as this better approximated the correct shape of the function. In the case of the bird models, the tree variable was entered as a positive input.

Due to incomplete data we only considered 101 of the originally 120 observations in the analysis (37 plots in autochthonous villages, 64 plots in transmigrant villages).

We checked for correlations between the explanatory variables. Not surprisingly, correlation between percentage cover and height of ground vegetation was relatively high (Pearson's $r = 0.59$). Both variables are known to be important structural parameters for birds (Atkinson *et al.* 2005; Clough, Kruess & Tscharntke 2006; Azhar *et al.* 2013), but due to the correlation we only included height of ground vegetation. All of the other variable pairs were not strongly correlated (Pearson's $r < 0.5$).

Number of oil palms, number of trees (both variables), labour hours, amount of fertilizer, and value of herbicides were log-transformed. As those variables – except for number of oil palms – contained zeros, we added the smallest value of each variable divided by two to each value of the variable in order to be able to do the log-transformation. Age of oil palms entered the model untransformed and with an additional squared term, as we expected optimal yields at intermediate palm age. All other terms entered the models without transformation. To avoid a leverage effect of some explanatory variables as compared to others, we normalized all predictors by subtracting the mean and dividing by the standard deviation (Schielzeth 2010).

We checked for spatial autocorrelation by calculating Moran's I values for each of the model's residuals. Using the Moran's I standard deviate in the 'spdep' package in R (R Core Team 2014), we tested for spatial autocorrelation but found no support for spatial autocorrelation of variation in any of the response variables (Moran's I test results yielded $p>0.1$).

Model adequacy of full and best models, including normality, homoscedasticity of the residuals, and whether a linear relationship was likely to be appropriate, was checked graphically using diagnostic plots. A forward and backward selection was done with each full model. The best models were chosen on the basis of the Akaike Information Criterion (AIC). All analyses were conducted in R (R Core Team 2014), with additional functions provided by the packages lme4 and nlme.

2.4 Results

2.4.1 Household survey: trees

For almost half of the sampled oil palm plantations (47.9%) trees were reported by the respondents. 1843 trees were recorded on all plots in total. The five most common tree species in the oil palm plantations were rubber Hevea brasiliensis (N=1495), banana Musa spec. (N=120), durian Durio zibethinus (N=46), langsat Lansium domesticum

(N=42) and alstonia Alstonia scholaris (N=30), which account for 94% of the total number of trees. Some other species occurred infrequently; overall 35 species of trees were found. Of those, 19 tree species could be classified as fruit trees and 15 tree species as timber trees (and rubber). When considering only the plantations with trees, on average 1.9286 (SD=0.1817) different tree species were cultivated, indicating a rather low level of tree species diversity. Even though the number of trees and the number of tree species are significantly correlated, the strength of the relationship is relatively weak (Pearson’s r = 0.31). Respondents indicated that 85.8% of the trees were planted, while the remaining 14.2% are remnants from former cultivation systems. Unfortunately, the data does not contain information on the age of the trees to assess whether the trees were planted before or after the establishment of the oil palm plantation. With respect to the management of the trees, results revealed that 40% of the trees were pruned, herbicides were applied to 27.9% of the trees and only 2.7% of the trees received fertilizer application. Manure and pesticides were not used.

2.4.2 Bird species composition and abundance

727 birds of 33 species were detected across all plots within a 25 m radius around the centre point of each plot. The Yellow-Vented Bulbul Pycnonotus goiavier was the most common species (N=197), followed by the Olive-Winged Bulbul Pycnonotus plumosus (N=156) and the Bar-Winged Prinia Prinia familiaris (N=127). There was one observation of the Green Iora Aegitina viridissima, which was the only recorded species listed as “nearly threatened” according to the IUCN. All other recorded species are listed as “least concern” (IUCN 2014) (Table S 2.1).

The three most important parameters for explaining variation in bird diversity were number of trees, height of ground vegetation and whether or not high quality oil palm seedlings (Marehat) were planted on the plot, as depicted in Table 2.2. The number of trees and height of ground vegetation had a positive effect on species richness, whereas the presence of high quality seedlings had a negative effect on species diversity. Similar results were found for bird abundance, which was also positively affected by number of trees and height of ground vegetation. However, the

Marehat variable did not enter the model. Instead, the number of oil palms was included and had a negative effect on the number of bird observations.

Table 2.2: Coefficients of variables (± SE) included in the bird and economic models.

	Bird species	Bird abundance	Yield	Revenue
Village	random effect	random effect	random effect	random effect
Number of trees (ecology models, positive input)	0.243 ± 0.059	0.277 ± 0.093	-	-
Number of trees (economic models, negative input)	-	-	0.404 ± 0.053	0.256 ± 0.143
Number of oil palms	-	-0.205 ± 0.099	-	-
Forest border	-	-	-	-
Shrubs	-	-	-0.068 ± 0.049	-
Height ground vegetation	0.144 ± 0.056	0.194 ± 0.097	-0.123 ± 0.051	-0.131 ± 0.052
Age of oil palm			1.247 ± 0.272	1.655 ± 0.299
(Age productive oil palm)2	-	-	-1.016 ± 0.271	-1.226 ± 0.297
Quantity of fertilizer	-	-		-
Value of herbicides	-	-	-	-
Labour hours	-	-	0.309 ± 0.053	0.344 ± 0.056
Marehat	-0.227±0.141	-	0.212 ± 0.127	-

The predicted bird diversity conditional on the number of trees ranged from 2.58 species (N tree ha-1 = 0) to 5.15 species (N tree ha-1 = 125) (Figure 2.2 a). Predicted sums of bird observations ranged from 3.66 individuals (N tree ha-1 = 0) to 8.05 individuals (N tree ha-1 = 125) (Figure 2.2 c). Bird diversity and the sum of bird observations showed a positive nonlinear response to an increase in the number of trees (Figure 2.2 a and Figure 2.2 c), with a decrease in the marginal effect of trees on bird diversity and abundance, respectively, with increasing number of trees (Figure 2.2 b and Figure 2.2 d). This implies that a further increase in the number of trees in a plantation with low numbers of remnant or planted trees has a larger effect on bird diversity and abundance than the same increase in the number of trees on an oil palm plot with high numbers of remnant or planted trees.

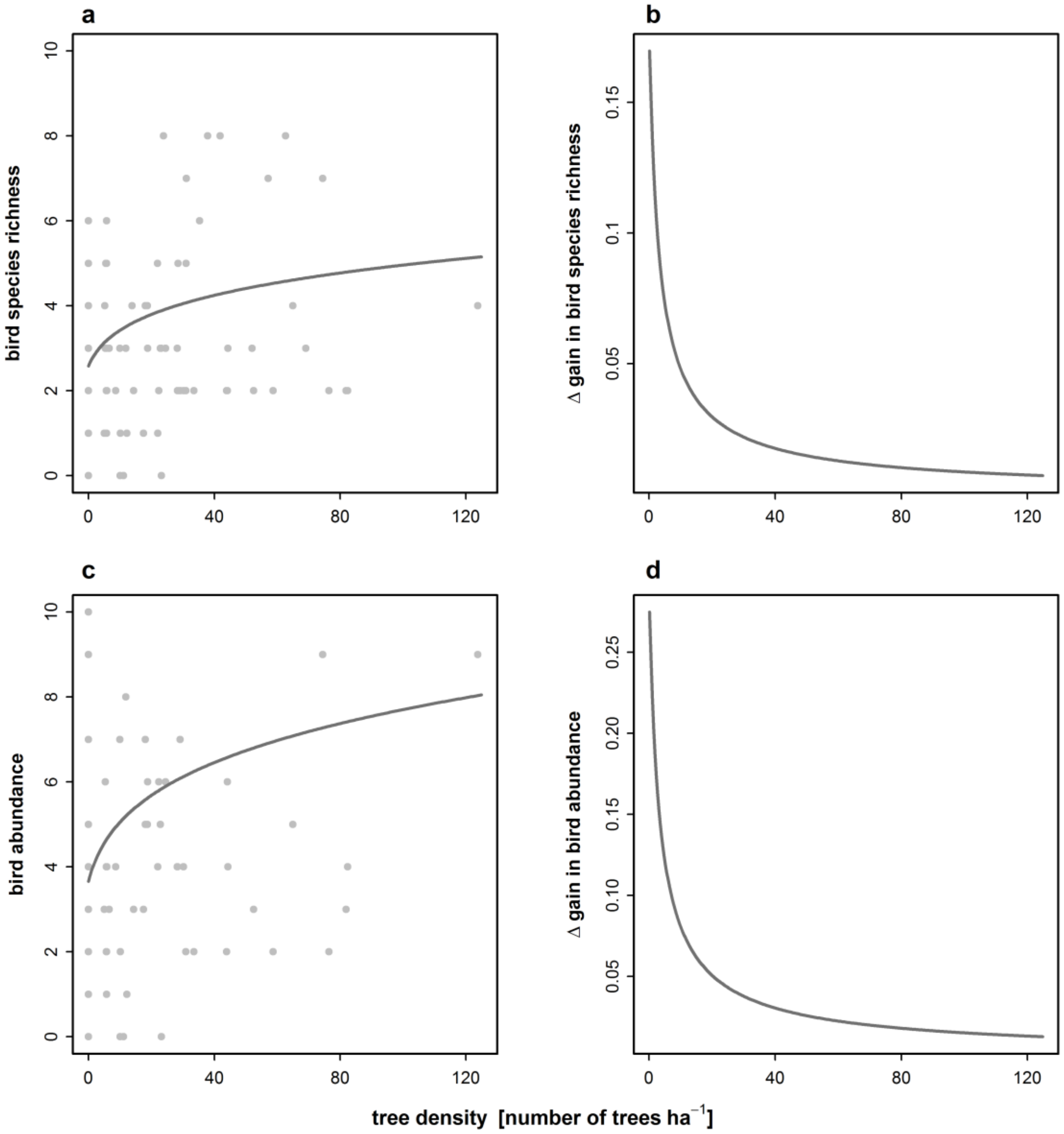

Figure 2.2: Effects of trees within oil palm plantations on bird species richness (a), as well as bird abundance (c). The marginal gain in bird species (b) and bird abundance conditional on the number of trees are given. Grey dots indicate original observations.

2.4.3 Determinants of yields

As expected, yields were highest at intermediate oil palm age, as both the age of the oil palm plantation and its squared value were significant in the best model, as depicted in Table 2.2. Oil palm yields were positively affected by the amount of labour hours (family and hired labour hours) spent on weeding of ground layer vegetation and epiphytes, herbicide, fertilizer and soil amendment applications and harvesting. The cultivation of Marehat clones (improved oil palm seedlings) positively affected oil palm yields. Further management parameters such as the amount of applied fertilizers and the value of applied herbicides did not enter the best model. Yields were not affected by landscape variables, such as the dummy for neighbouring forest patches, which was not considered in the best model. In contrast, both variables capturing the habitat complexity determined the yields of the oil palm plantation; the height of the ground vegetation layer and the number of shrubs >1.5 m negatively affected the yields. We found the number of trees within or at the border of the oil palm plantation to negatively affect yields, too. The predicted oil palm yields conditional on the number of trees ranged from 11.15 ton ha-1y-1 (N tree ha-1 = 0) to 1.80 ton ha-1y-1 (N tree ha-1 = 125) (Figure 2.3 a). Testing for the functional form of the relation between yields and number of trees, results indicated that the predicted yields conditional on the number of trees follow a non-linear pattern, with an increase of the marginal effect of trees on yields with increasing numbers of trees.

2.4.4 Trees and revenue

To test whether or not the benefits generated from trees compensated for the loss in oil palm yield, we tested the effect of the set of predictors on total revenue (US$ ha-1y-1) (Phalan *et al.* 2011b). Again, results outlined in Table 2.2 revealed that the total revenue was highest at intermediate age of the oil palm as both, the age and the squared term of age, entered the model. Similar to yields, revenue was not affected by neighbouring forest patches, the amount of applied fertilizer or the value of applied herbicides. Revenue was positively affected by the amount of labour hours (considering family and hired labour hours) and negatively by height of ground vegetation, being one of the proxies for habitat complexity As opposed to the yield model, the cultivation of Marehat clones and shrubs were not important parameters to explain variation in revenue. Again, we found that the number of trees within or at the border of the oil palm plantation negatively affected the total revenue. The predicted revenue conditional on the number of trees ranged from 1010.83 US$ ha-1y-1 (N tree ha-1 = 0) to 222.87 US$ ha-1y-1 (N tree ha-1 = 125). Similar to the functional form of the production function for yield, the relation between predicted revenue and number of trees is non-linear, with an increase in the marginal effect of trees on predicted revenue with increasing tree stands (Figure 2.3 b).

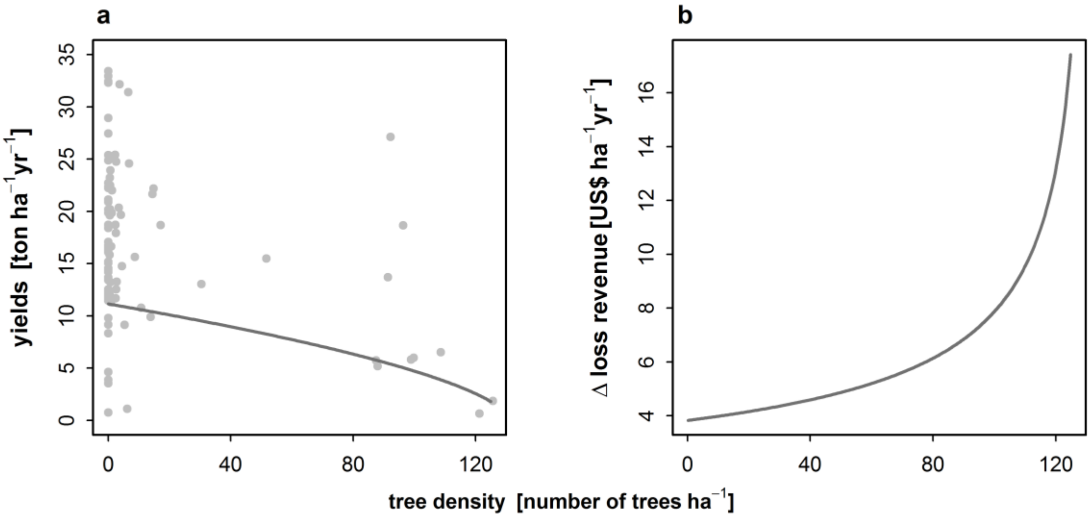

Figure 2.3: Effects of trees within oil palm plantations on oil palm yields (a). The marginal loss in revenue (b) conditional on the number of trees are given. Grey dots indicate original observations.

2.4.5 Bird diversity and abundance – revenue relationship

The predicted bird diversity and the predicted revenue can be defined as a “yield set”, since both outcome variables can be parameterized with respect to trees (Perfecto *et al.* 2005). The functional form of the “yield set” revealed a trade-off between the revenue and the bird diversity (Figure 2.4 a). Thus, the bird diversity loss can only be mitigated at the cost of revenue. It implies that external incentives have to be provided to encourage profit-maximizing farmers to conserve (Kragt & Robertson 2014). The slope, also called marginal rate of transformation (MRT), measures how much of revenue is given up for one more unit of bird diversity or vice versa. It also reflects the (marginal) shadow prices of bird diversity (the shadow prices of bird diversity in terms of revenue at the margin). The “yield set” curve is convex, indicating that the MRT increases with increasing revenue (agricultural intensification). Given a relatively extensively managed oil palm plantation (high number of trees, low revenue), a further increase in number of bird species leads to a distinct loss in revenue. In contrast, given a relatively intensively managed oil palm plantation (relatively low number of tree stands and high revenue), the same increase in number of bird species results in a smaller revenue loss. Thus, up to a certain level of intensification, bird diversity shows a relatively low sensitivity to an increase in intensification.

Similar results were found for the bird abundance - revenue relationship. There was also a trade-off between bird abundance and revenue (Figure 2.4 c) with distinct losses in revenue when bird abundance is increased on relatively extensively managed oil palm plantations and only small losses in revenue with increases in bird abundances on intensively managed plantations. However, in general, the revenue loss for additional bird individuals is smaller than for additional bird species, meaning that for the same amount of funds more individuals could be locally conserved compared to species.

2.4.6 Marginal shadow price of bird species richness and abundance – tree relationship

To evaluate potential target groups of conservation programs that aim to foster bird diversity and abundance by giving external incentives to establish or expand the number of trees within oil palm plantations, we illustrate the marginal loss in revenue with every unit increase in bird diversity (Figure 2.4 b) and bird abundance (Figure 2.4 d) conditional on the trees within or at the border of the oil palm plantation. Results revealed that the marginal loss in revenue induced by a one unit increase in bird diversity, and hence the shadow price of bird diversity expansion, increases with increasing numbers of trees (extensification of oil palm cultivation). We calculated the percentage of revenue that has to be given up for an additional bird species exemplified for a plantation with 10 and 50 trees per ha, respectively. A farmer that has ten trees within his/her plantation experiences a 20% loss of total revenue for an additional bird species, whereas on a plantation with 50 remnant or planted trees the same increase in bird species results in a 67% loss of total revenue. Similarly, for every unit increase in bird abundance, the marginal loss in revenue increased with increasing number of trees. However, a farmer that has ten trees within his/her plantation experiences a 12% loss of total revenue for an additional bird individual, whereas on a plantation with 50 remnant or planted trees the same increase in bird individuals results in a 39% loss of total revenue. This shows, that an increase in bird abundance can be enhanced at smaller costs when compared to the costs for increasing bird diversity.

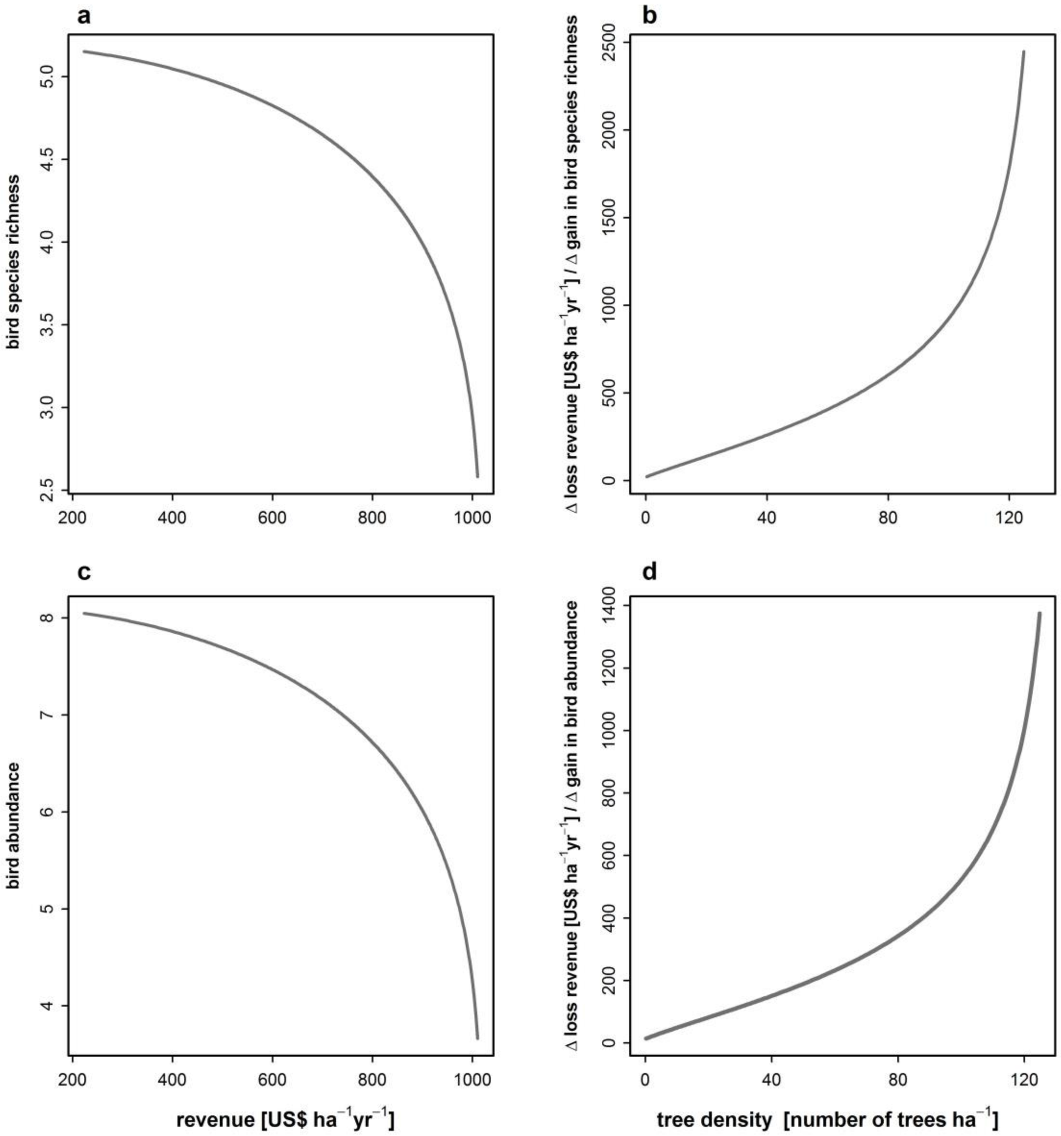

Figure 2.4: Relationship between predicted revenue and predicted bird diversity (a) and predicted bird abundance, respectively (c). Marginal loss in revenue with every one-unit change in bird diversity (b) and bird abundance (d), respectively, conditional on the tree stands within or at the border of the oil palm plantation.

2.5 Discussion

Forests and traditional cultivation systems with a high degree of habitat complexity in Southeast Asia are being converted to oil palm plantations at high rate and there is growing interest in oil palm agriculture in other tropical regions, such as South America and Western Africa. Besides the obvious need to conserve large expanses of natural habitats, this raises the question on how to maintain a baseline level of biodiversity in oil palm-dominated landscapes. Focusing thus on a “wildlife-friendly” strategy of having remnant or planted trees within or at the border of oil palm plantations, we investigated the relationship of bird diversity and bird abundance with oil palm yields and total revenue along a gradient from low-intensity oil palm plantations enriched with trees to intensively managed mono-cultural oil palm plantations. Consistent with our expectations, we found a win-lose relationship between these ecological and economic functions indicating that a gain in bird diversity and bird abundance conditional on an increase in the number of trees comes along with a loss in revenue for farmers. It implies that profit-maximizing farmers do not have a private incentive to conserve. However, incremental increases in bird diversity and bird abundance come at different costs depending on the initial number of trees (and therefore the initial level of bird species diversity or bird abundance).

Overall, our study confirmed that bird communities supported by oil palm plantations are extremely impoverished in comparison to natural forests (Peh et al., 2006). Only a few common and widespread species are found in this type of habitat and there is a loss of species with high conservation status and restricted ranges. We observed one forest species and five edge-tolerant species besides mostly edge-tolerant, open habitat and generalist species (for definitions see Rotenberg and Stouffer, 2007) (see Table S 2.1). With one exception, all sampled bird species had low conservation status. Oil palm sites, however, differed significantly in their bird diversity and abundance depending on the vegetation in the plantation.

Even though oil palm plantations are often pure monocultures, especially in large estates (Foster et al., 2011), almost half of the sampled smallholder oil palm plantations had remnant or planted trees on them, and varying levels of ground vegetation. We found that the number of trees and the height of ground vegetation were important parameters in explaining variation in bird abundance and species richness. Structural complexity is in general known to positively affect avian community structure (Tews *et al.* 2004; Gordon *et al.* 2007; Van Bael *et al.* 2007; Stein, Gerstner & Kreft 2014). Azhar et al. (2011) showed that oil palm plantation estates and smallholdings supported similar bird assemblages, but the latter supported slightly more species due to higher complexity of vegetation structure compared to a typical mono-cultural plantation estate. However, our findings suggest that large-scale plantations could also create similar situations like in smallholdings by planting trees for conservation outcomes. A positive effect of trees on bird diversity was also found in the studies by Abrahamczyk et al. (2008) and Clough et al. (2009), where cacao plantations in Sulawesi, Indonesia, with interspersed trees harboured more bird species than plantations without trees. On oil palm plantations in Thailand, Peninsular Malaysia and Guatemala bird species richness was enhanced by a well-developed understory vegetation (Aratrakorn et al., 2006; Azhar et al., 2011; Nájera and Simonetti, 2010). While we observed a considerable range in density of different fruit and timber trees (0–314.7 trees ha-1 (trees >2 m)), the average number of tree species per hectare was low compared to traditional agroforestry crop plantations, such as coffee and cacao, where tree abundance and diversity can be much higher (8–128 trees h-1 (trees >10m); 12–104 tree species ha-1) (e.g., Clough et al., 2009). In our study, bird diversity and abundance showed a positive non-linear response to increasing numbers of remnant or planted trees. With increasing numbers of trees, however, there was a decreasing marginal effect of trees on predicted bird diversity and abundance.

In line with findings by Azhar et al. (2011), landscape-level attributes such as small secondary forest patches bordering the oil palm plantation, which we included as a landscape parameter, did not explain any variation in bird diversity and abundance in our study. This may be attributed to the low dependency of the majority of bird species (non-forest species) in oil palm plantations on forest habitats and resources as they find food within the plantations (Azhar *et al.* 2013), and the limited value of neighbouring small secondary forest patches as a source habitat for birds. The study region is characterized by highly isolated forest fragments in wide areas of homogenous oil palm monocultures. Harapan rainforest and the National Park Bukit Duabelas are the only two significant forest areas left in the study area and are not bordering the study sites.

While the number of trees benefited bird diversity and bird abundance, they negatively affected oil palm yields. Assuming that trees within or at the border of the oil palm plantation compete with oil palm for nutrients and light, we included the tree variable in the economic models as a negative input. Indeed, controlling for management practices, landscape, and habitat complexity, the results of the analyses showed that the oil palm yield (ton ha-1 y-1) decreased with increasing number of remnant or planted trees within or at the border of the oil palm plantation. Results indicated that the predicted yield conditional on the number of trees follow a non-linear pattern, with an increase of the marginal effect of trees on predicted yields with increasing numbers of trees. This is in accordance with findings by Corley and Tinker (2003) who stated that oil palm productivity is low when they are shaded by trees (also see Phalan et al., 2009). Oil palm, as a water-demanding plant with high light requirements would likely face intensive competition with intercropped trees for water, nutrients and light (Koh et al., 2009).

The use of a proxy measure for yields such as management intensity indices (e.g. number of trees) would not give the quantitative information on yields necessary to assess the trade-off between economic outcome and bird diversity (Phalan et al., 2011a; Steffan-Dewenter et al., 2007).

Since the economic outcome generated from the remnant or planted trees may compensate for the oil palm yield penalties, we considered the total revenue including the opportunity costs of fruit and timber products consumed by the household, even though this measure is affected by market fluctuations (Phalan et al., 2011a). The predicted total revenue also decreases with increasing number of trees within or at the border of the oil palm plantation (with increasing marginal loss in revenue).

2.5.1 Implications for conservation

The win-lose trade-off between the bird diversity and total revenue conditional on the number of remnant or planted trees within or at the border of the oil palm plantation implies that profit-maximizing farmers do not have, at least in economic terms, a private incentive to mitigate bird diversity loss by extensifying the oil palm cultivation. As in Europe, where land-sharing is encouraged by agri-environment payments for farmers (Kleijn et al. 2006), one could imagine that economic incentives could be implemented to foster the extensification of oil palm cultivation in terms of increasing the number of trees. The marginal loss in revenue with every unit increase in bird diversity conditional on the number of trees within or at the border of the oil palm plantation follows a positive non-linear pattern. Thus, with increasing extensification of the oil palm plantation in terms of the number of trees, the loss in revenue per additional bird species increases suggesting that conservation measures are relatively cheap at low abundances of trees within a plantation. While farmers of a rather intensively managed oil palm plantation (e.g. 10 trees per ha) lose 20% of their total revenue per additional bird species, farmers, who already harbour many trees (e.g. 50 trees per ha) on their oil palm plantation lose 67% of the total revenue per additional bird species. Similar results were found for bird abundance, but the loss in revenue per additional bird individual is in general lower than for an additional bird species. On an intensively managed oil palm plantation with 10 trees per ha the farmer experiences a loss in revenue of 11%; farmers of extensively managed oil palm plantations with 50 trees per ha lose 39% of their revenue. Given a fixed conservation payment, farmers of highly intensified oil palm plantations with no or few trees therefore have a relatively strong incentive to expand the number of trees within the oil palm plot compared to farmers of already extensively managed oil palm plantations with many trees on the plot. In fact, the absolute number of bird individuals and bird species would still be lower in relatively intensive plantations with only a few trees compared to a more extensive plantation with more trees to start with. But even a slight increase in bird abundance on intensively managed plantations might already contribute to the system being more stable and resilient towards disturbance or pests due to increased ecosystem functioning and provision of ecosystem services such as pest control and soil fertility. Interestingly, such a gain in ecosystem functioning may exceed the associated increase in diversity (Barnes *et al.* 2014b). Future studies need to address whether or not an increase in bird diversity also results in higher ecosystem functioning.

To compensate for a revenue loss associated with the increased abundance of trees within the oil palm plantation, both, the implementation of a premium price for eco-friendly certified palm oil products and relevant extension services financed through national or international environmental funds, are potential solutions. The rising public debate about the social and environmental impacts of oil palm cultivation prompted the establishment of the Round Table on Sustainable Palm Oil Production (RSPO, 2014). The RSPO certification requirements cover a range of sustainability criteria, such as controlling of soil erosion, groundwater and chemical pollution. However, specific certification schemes requiring foliage cover, tree height and diversity, like in the SMBC (Smithsonian Migratory Bird Centre) bird friendly coffee certification scheme, do not exist for palm oil. In Europe, palm oil, as the "secret in the shopping basket" has often been hidden as generic vegetable oil in processed food (Paddison 2014). In 2014, the EU launched the law on food information to consumers (FIC), determining that hiding ingredients under generic titles is no longer permitted. Whether the labelling of palm oil translates into a change in consumer preferences towards more eco-friendly produced palm oil products still remains to be seen (Smedley, 2014).

Critics of wildlife-friendly interventions argue that they tend to reduce actual or potential farmland yields compared to conventional farming and thereby increase encroachment on natural habitat (Donald 2004; Green *et al.* 2005; Clough *et al.* 2011; Phalan *et al.* 2011b; Tscharntke *et al.* 2012b). Indeed, in the majority of management intensity gradients ranging from no or minor management to high management intensity, biodiversity declines steeply in response to a slight increase in intensification (with a decreasing marginal rate of substitution), indicated by a concave function. It implies that the target species would benefit more from land-sparing associated with maximum attainable yield agriculture than from land-sharing (Phalan *et al.* 2011a; b; Baudron & Giller 2014). This shape holds for multiple taxa in Europe and the tropics (Gabriel et al., 2013; Hulme et al., 2013; Phalan et al., 2011b; Kleijn et al., 2009). Of course, also in our study region, large differences in bird diversity and abundance between forests and oil palm plantations suggest that when having to choose between diversification of oil palm and forest conservation (and assuming both are effective), the latter would be a more efficient way to maximise crop production and species conservation. The degree to which both the causal linkages (lower yields □ encroachment on natural habitat) implicit in the models as well as the model assumptions hold, and whether the focus on two desired outcomes rather than a breadth of ecosystem services is relevant for resource management and policy, are issues severely debated elsewhere (Baudron and Giller, 2014; Tscharntke et al., 2012b; Phalan et al., 2011a; Koh et al., 2009). The debate suggests that oil palm diversification, such as the maintenance of trees in oil palm plantations, while not an alternative to conserving forests, should not be rejected a priori.

Interestingly, our results show that farmer choices are not governed purely by economic considerations: although yield and revenue were negatively affected by density of trees on the plantation, a significant part of the smallholders have either implicitly or explicitly chosen to keep and/or plant trees on their plantation, despite the likely perceived standard of oil palm management as a pure monoculture, which can be easily observed on nearby estate plantations. In this study, long-term resilience, as opposed to short-term yield maximization, was not considered as an economic objective, even though it might be pursued by risk-averse decision-makers. In our rather simplistic approach, other factors, such as cultural services (spiritual enrichment, recreation and aesthetic experiences), are also neglected (Kragt & Robertson 2014). Further progress on understanding farmer choices and value systems is critical to inform possible conservation actions.

Further research is needed to provide more specific recommendations on how to design potential oil palm plantations with high habitat complexity provided through the presence of trees and a well-developed ground layer vegetation. While this study investigated the effect of the presence of remnant or planted trees on bird diversity and abundance as well as on yields and revenue, we did not distinguish between remnant and planted trees, fruit trees and other trees nor was the size structure of trees considered. Other studies suggest that factors such as tree age, tree diversity, presence of specific functional groups of trees or tall trees, are decisive when it comes to associated animal diversity (Kanowski *et al.* 2003; Erskine, Lamb & Bristow 2005; Clough *et al.* 2011). To test the effect of tree species diversity, size structure and composition on biodiversity and oil palm yields, a long term biodiversity enrichment experiment which systematically alters tree species richness and composition and the size of tree islands was established in the same region (Jambi Province, Sumatra, Indonesia). Monitoring the growth of trees, oil palm yield, bird and invertebrate diversity and abundance, this will allow us in the near future to address questions regarding the planting strategy under which biodiversity and ecosystem functions can be restored – which includes choosing the appropriate tree species for habitat enrichment – and how the economic functions of an oil palm plantation are affected by different types of enrichment plantings.

2.6 Conclusion

Our study confirmed that bird communities supported by oil palm plantations are extremely impoverished in comparison to natural forests. Nevertheless, the restoration of wildlife-friendly oil palm plantations associated with higher structural complexity can mitigate the loss of bird diversity with respect to edge-tolerant, open habitat and generalist species. Furthermore, we found a positive relationship between bird abundance and tree density. Thus, a slight increase in bird abundance on intensively managed plantations might already increase ecosystem functioning and provision of ecosystem services such as pest control and soil fertility. Studies, which investigate the ecological role of birds in oil palm plantations by identifying and analysing functional groups separately, are hence needed. The negative revenue - bird diversity and revenue - bird abundance relationship, respectively, suggests that profit-maximizing farmers do not have an incentive to establish or restore wildlife-friendly oil palm systems. However, since the relationship is non-linear, in a relatively extensively managed oil palm plantation (high number of trees, low oil palm yields), a further increase in the number of bird species and bird individuals leads to a relatively high loss in revenue, whereas in an intensively managed oil palm plantation the same increase in number of bird species and individuals results in a smaller loss in revenue. This indicates that there is room for tree-based enrichment of intensively managed oil palm plantations, where a relatively high increase in bird species richness and bird abundance could be achieved at relatively low cost.

2.7 Acknowledgements

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Chapter 3: Biodiversity enrichment in oil palm landscapes: A tree planting experiment in Sumatra (Indonesia)

3.1 Abstract

Tropical biodiversity is threatened by the expansion of oil palm plantations. Buffer zones around plantations such as agroforestry systems, have been proposed to increase biodiversity and ecosystem functioning. In regions where plantations already dominate the landscape, this can only be achieved through systematic restoration. However, our knowledge about underlying ecological and socio-economic processes, constraints and trade-offs is very limited and clear instructions for restoration towards a wildlife-friendly management are lacking. Here we present a large-scale, long-term biodiversity enrichment planting experiment. We planted tree islands in an oil palm plantation and systematically varied tree island size, tree species richness, and tree species composition. We describe the environmental (soil, climate, topography, light availability) and biotic (associated vegetation, invertebrates, birds) characteristics of the experimental site prior to the establishment of the experiment and first effects on the faunistic diversity. Already one year after the establishment of the experiment, tree plantings had an overall positive effect on the bird and invertebrate communities on the landscape scale. Moreover and on a local scale, we found the size of tree islands to be positively related to the diversity and abundance of invertebrates. The biodiversity enrichment experiment provides the basis for further research projects to uncover the ecological and economic long-term mechanisms associated to enrichment plantings. With the results of the experiment we aim on evaluating the effectiveness of the enrichment plantings as part of the proposed designer plantation landscapes and develop clear restoration instructions to realize a more sustainable management of oil palm.

3.2 Introduction

A major driver of the current biodiversity crisis in tropical South-East (SE) 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). In consequence of the resulting dramatic losses of biodiversity, losses in ecosystem functioning of species communities are expected (Sodhi *et al.* 2004; Wilcove *et al.* 2013; Edwards *et al.* 2014) that can even disproportionally exceed the decline in species diversity (Barnes *et al.* 2014b). This puts also a risk on human well-being as ecosystems are being degraded, leading to e.g. decreased pollination success, insufficient provision of goods, or impairment of soil and water quality (Cardinale *et al.* 2012).

Besides the importance of protecting primary and secondary tropical forests for biodiversity conservation, integrating biodiversity conservation and ecosystem restoration into management of existing large scale oil palm plantations seems reasonable (Koh *et al.* 2009; Luskin & Potts 2011; Foster *et al.* 2011; Teuscher *et al.* 2015). Designer plantation landscapes in which agroforestry zones buffer the natural vegetation from mono-culture plantations have been proposed as a means to maintain livelihood needs while increasing biodiversity and ecological functions (Koh *et al.* 2009). By adopting this strategy for enhanced habitat complexity, the negative environmental impacts of intensively managed cash-crop production systems such as oil palm could be mitigated. However, in a region where forest is nearly eradicated (Margono *et al.* 2014) and where the diversity of the species communities in the agrarian landscape is declining (Fitzherbert *et al.* 2008) with an increase of area under oil palm monocultures (Euler *et al.* 2015; Gatto, Wollni & Qaim 2015), it is too late for reasonable landscape planning right from the beginning. Restoring habitat heterogeneity at the local and landscape levels is highly recommended in oil palm landscapes to maintain or even enhance biodiversity (Azhar *et al.* 2011) but currently institutions like the ‘Roundtable for Sustainable Oil Palm’ (RSPO) rather focus on non-deforestation policy, conservation of large expanses of high valuable habitat, and threatened species (RSPO 2013).

From a restoration point of view, planting native trees has been considered an important measure to accelerate natural succession towards forests or agroforests (Chazdon 2008b). Tree island plantings as nuclei for natural succession have been proposed to initiate a cascading process in the surroundings (Corbin and Holl, 2012; sensu Yarranton and Morrison, 1974). Such nuclei were found to have similar effects on biodiversity compared to plantation-style restoration plantings but are more economic (Zahawi *et al.* 2013). Even small tree islands can act as „recruitment foci" as they increase the bird activity, which contributes to elevated seed rain (Cole, Holl & Zahawi 2010). Furthermore, seedling species richness was found to be increased within a short period and seedling establishment was facilitated due to a more favorable microclimate and amelioration of the soil (Zahawi & Augspurger 2006). Most restoration plantings took place in abandoned agricultural land, pastures or logged forests (Zahawi & Augspurger 2006; Cole, Holl & Zahawi 2010; Hector *et al.* 2011), but tree islands were also suggested to enrich agricultural landscapes (Rey-Benayas *et al.* 2009). Regarding the size of restoration plantings there is no consensus yet on which is ecologically and economically the most effective. Further research is needed as the approved biogeographic assumptions for marine islands cannot simply be transferred to tree islands (Mendenhall *et al.* 2014). To our knowledge, restoration efforts have rarely been made while maintaining an existing plantation and, in particular, there is no experience in oil palm landscapes. Furthermore, there is not much experience of oil palm in polyculture (see Box 3.1).

Numerous experiments investigating the relationship between biodiversity and ecosystem functioning (BEF) showed that already few species can have a disproportionaly high impact on ecosystem functioning (Cardinale *et al.* 2006; Balvanera *et al.* 2006; Quijas, Schmid & Balvanera 2010). The saturating relationship between biodiversity and ecological functioning that resulted from BEF experiments in the direction of biodiversity loss (Cardinale *et al.* 2012) indicates that, if we simply turn the tables and add species to a system that is already extremely depauperate, we can expect a relatively high positive effect on ecosystem functioning, 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 3.1: Oil palm in polyculture

In West Africa and Brazil, smallholders traditionally practice extensive oil palm-based agroforestry, but this system could economically not compete with the high-productive monocultures in SE Asia. To bridge the income gap until the oil palms start fruiting, oil palm seedlings are intercropped with food crops, e.g. maize, manioc, yam, cocoyam, soy bean and cassava, until the oil palm canopy closes (Okpala 1995; Salako, Lal & Swift 1995; Erhabor & Filson 1999; Corley & Tinker 2003). However, this contributes little to a more heterogeneous structure which would benefit biodiversity (Phalan *et al.* 2009; Foster *et al.* 2011). Several experiments investigated services and disservices in permanent polycultures: Enhanced pest attraction harming the oil palms could not be confirmed (Dhileepan 1991). Negative effects due to light competition were reported from oil palm-rubber mixtures (Corley & Tinker 2003) and oil palm–teak mixtures resulted in oil palm yield depression, whereas an enhanced teak performance could compensate the losses (Chia 2011). No yield depression from oil palms was noticed when intercropped with cacao (Lee & Kasbi, 1980 (Malaysia), Amoah et al., 1995 (Ghana)). In Nigeria, cacao yields were even higher when planted under oil palms (Egbe & Adenikinju 1990). In conclusion, negative and positive experiences were made with intercropping oil palms, suggesting that there might be suitable crops to plant with oil palms. More research is needed to identify the right best intercropping scheme, also with regard to possible differences on a regional scale.

Recently, BEF research-insights found their way into restoration ecology (Aerts & Honnay 2011). Most of the findings related to BEF have been obtained in grasslands outside the tropics and mainly in small-scale studies, but recently, a number of large-scale tree planting experiments have emerged (Scherer-Lorenzen *et al.*, 2005; “TreeDivNet”, 2015); four tree diversity experiments are located in the tropics (Petit & Montagnini 2006; Kirui *et al.* 2008; Potvin & Gotelli 2008b; Moreira *et al.* 2014). Results from such experiments suggest that diverse plantings are more beneficial for BEF than monocultures (e.g. Potvin and Gotelli, 2008).

The knowledge gap of the ecological consequences of restoration via enrichment plantings in oil palm landscapes goes along with a lack of experience of the impacts on the local socio-economy. The area under oil palm hold by small-scale farmers is more rapidly increasing than the area under estate (Euler *et al.* 2015; Gatto, Wollni & Qaim 2015) meaning that there is a growing number of households depending on palm-oil production. Therefore, it is essential to develop a management strategy that, at least, compensates potential income losses due to restoration plantings and, in the best case, even increase the farmers’ income. Crop diversification can act as an insurance for the future, 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 control of pests, pollination as well as 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 and at the same time contribute to a more heterogeneous landscape.

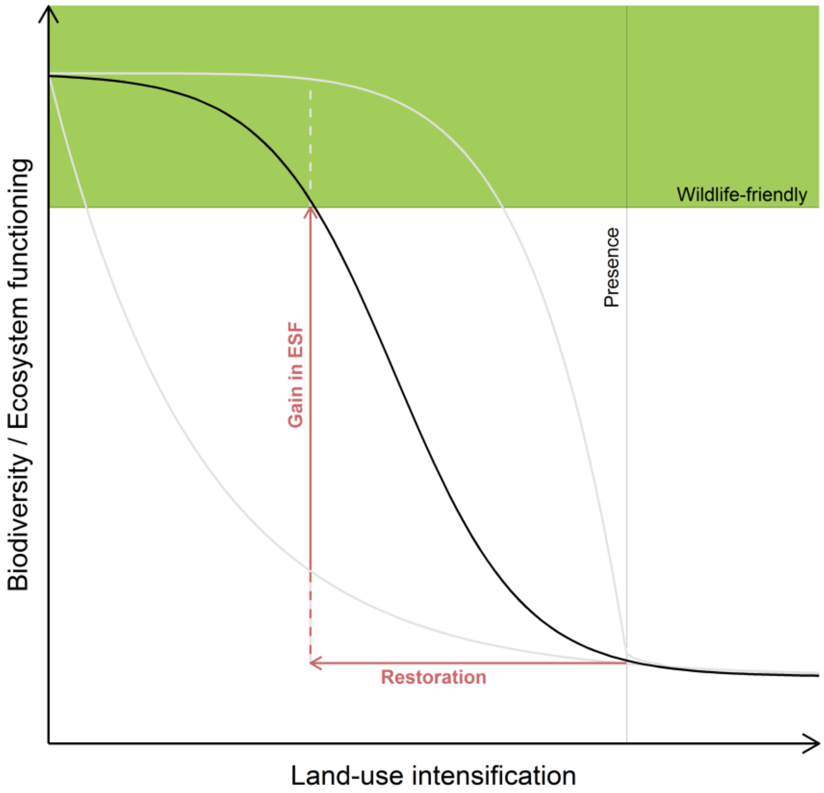

Figure 3.1: A conceptual diagram with possible scenarios of changes in ecosystem functions (ESF) as a consequence of land-use intensification. We assume a negative and non-linear relationship between ecosystem functioning and land-use intensification in the shape of the black line. Consequently, there is space for restoration measures in order to enhance ESF while still allowing for profitable land use. The loss in ESF 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 ESF. The optimal trade-off situation between nature conservation and land use would be when intensification is stopped before the critical point is reached. In the oil-palm-dominated landscapes, however, this optimal point might already be exceeded as biodiversity and ESF are severely degraded in oil palm systems (Barnes *et al.* 2014b; Dislich *et al.* 2015; Kotowska *et al.* 2015). To move back to the optimal point, diverse habitats have to be restored.

We assume that there is room for restoration plantings that have the potential to help restore biodiversity and ecosystem functions in impoverished landscapes whilst minimizing negative impacts on the local socio-economy (Figure 3.1). Clear implications for restoration of highly intensively managed oil palm systems towards wildlife-friendly and at the same time economically attractive systems, however, are yet to be developed. Several questions have to be considered in this context: How many species need to be planted to significantly gain ecosystem functions? Assuming non-linear effects due to facilitation or competition among species, which species composition and island size is the most effective? Which strategy results in the best relationship between BEF and socio-economics?

Here, we 1) present the design of a biodiversity enrichment experiment in a mono-culture oil palm plantation 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.

3.3 Methods

3.3.1 Study site

The experiment (ca. 140 ha in size) was established on an oil palm plantation owned by PT Humusindo (01.95° S and 103.25° E, 46.9 ± 10.46 a.s.l.) near the village Bungku in the lowlands of the Jambi province, Sumatra, Indonesia (Figure 3.2). 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; climate station at the Jambi Sultan Thaha airport of the Meteorological, Climatological and Geophysical Agency). The natural vegetation is dipterocarp dominated lowland rainforest in the centre and peat-swamp forest along the east coast (Laumonier, 1997; Whitten, 2000). Dominant soil types in the Bungku region are loam Acrisols (Allen *et al.* 2015).

The oil palms on the plantation were planted in the year 2002. The management of the plantation comprises the application of fertilizer and herbicides, regular manual weeding of the understory herb layer and removal of the epiphytes. In the center of the experimental area Rambutan trees (*Nephelium lappaceum*, Sapindaceae) are cultivated as a second source of income. Buffalo and cattle farming are practiced on the plantation, too

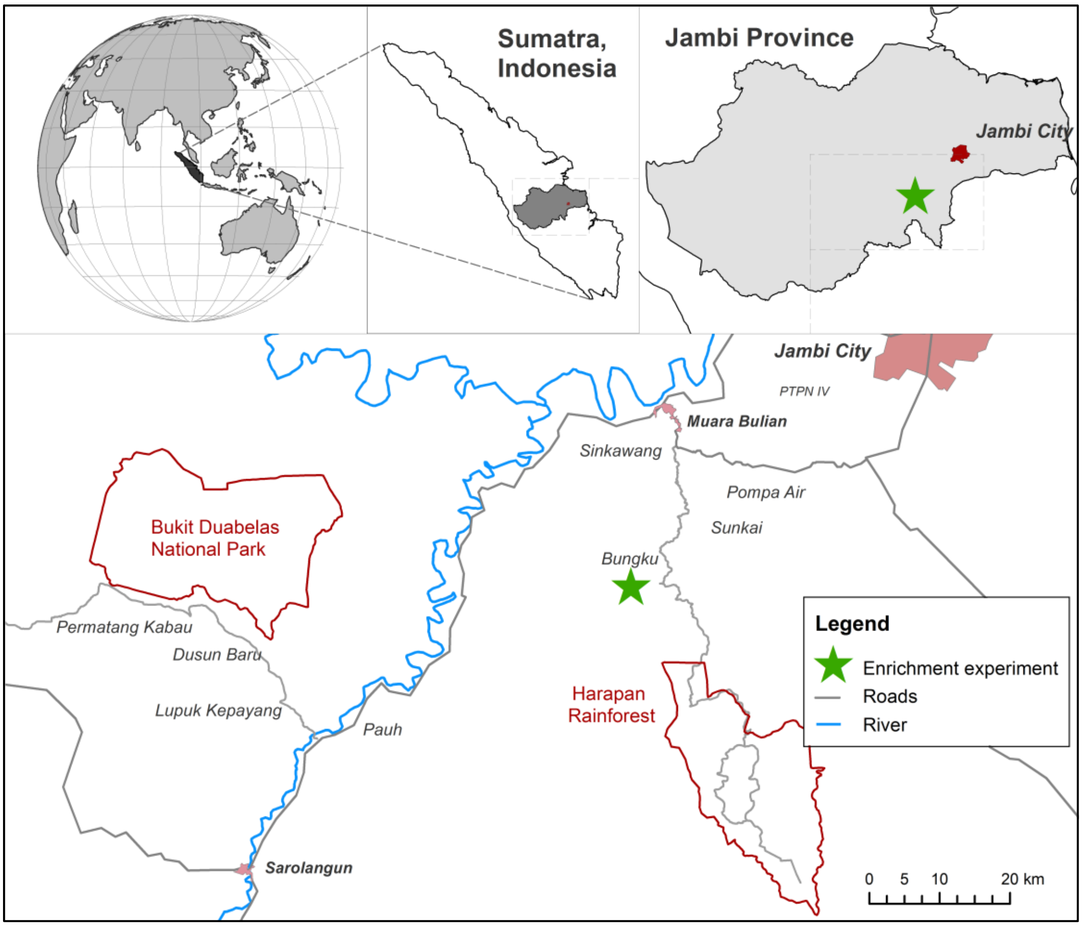

Figure 3.2: Location map of the study area. The green star indicates the location of the study site where the biodiversity enrichment experiment was established.

3.3.2 The biodiversity enrichment experiment (BEE)

We established a large-scale, long-term biodiversity enrichment experiment (BEE) within a mono-culture oil palm plantation. Tree islands of varying species diversities and compositions were established. Across experimental plots, we varied the diversity and identity of the tree species planted adopting a random partitions design (Bell *et al.* 2009) (Figure 3.3 A). The experiment comprises four partitions that differ in their plot size (5x5 m, 10x10 m, 20x20 m, 40x40 m). Each partition is subdivided into five blocks, one per tree diversity level (six, three, two, one, and zero). Within each of these blocks, every species is drawn at random from the species pool without replacement. This means that each species is selected exactly once at each diversity level and species compositions are random, with the restriction that no repetition across all plots was allowed (Table S 3.1). Additionally, there are four control plots without any experimental treatment and management-as-usual. This results in a total of 56 plots (Table S 3.2).

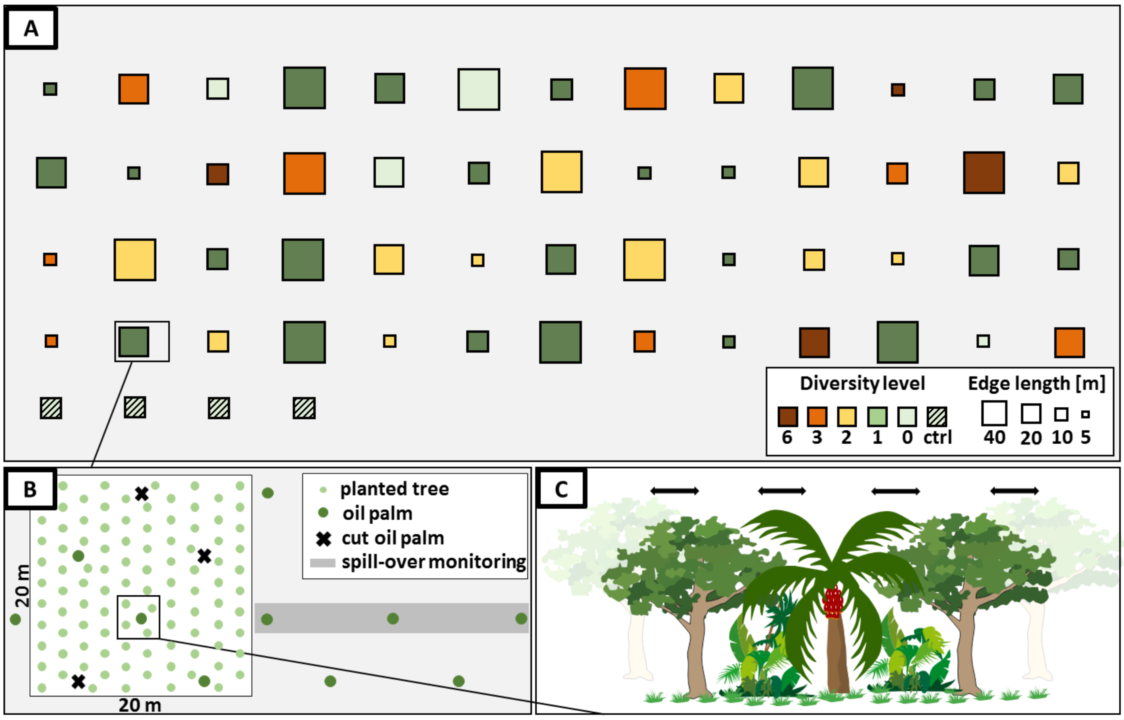

Figure 3.3: *A)* Design of the biodiversity enrichment experiment (BEE). Tree islands with systematically varying tree species richness (diversity level of 0,1,2,3 and 6), identity and composition as well as plot size (5x5 m, 10x10 m, 20x20 m, 40x40 m) and species composition were established adopting 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. The experiment includes four control plots without treatment and with management-as-usual. In total, the experiment comprises 56 plots. *B)* Oil palms were cut on the plot with treatments in order to enhance light conditions. Trees were planted in a 2x2 m grid. Perpendicular to each plot, three oil palms were selected to monitor services and disservices (‘spill-over effects’) of the tree islands on surrounding oil palms. *C)* Planted trees interact/compete with each other as well as with the oil palms.

We selected six multi-purpose tree species including three fruit trees (*Parkia speciosa*, Fabaceae; *Archidendron pauciflorum*, Fabaceae; *Durio zibethinus*, Malvaceae), two timber species (*Peronema canescens*, Lamiaceae; *Shorea leprosula*, Dipterocarpaceae) and one rubber species (*Dyera polyphylla,* Apocynaceae). The trees are all native to Sumatra and used by local people. The two nitrogen-fixing Fabaceae-species may further enhance nitrogen availability. To enhance the light availability in the plots with experimental treatment, 40% of the initial oil-palm-crown cover was reduced by cutting oil palms prior to tree planting (not on the control plots).

Trees were planted in a 2 m grid in alternating rows in north-south direction. On plots with mixed species, the trees of the same species were planted as far away as possible from one another to avoid clustering of species. We planted six trees on the 5x5 m plots, 25 trees on the 10x10 m plots, 100 trees on the 20x20 m plots and 400 on the 40x40 m plots. The total number of planted trees is 6354. To enhance the establishment success of the trees, we applied organic (250 g; BIOST: N = 1.4%, C = 12%, P_2O_5 = 1.82%, K_2O= 1.57%) and inorganic (50 g; NPK Mutiara: N = 15%, P_2O_5 = 5%, K_2O = 6%, MgO = 4%) fertilizer once when we planted the trees. The management of the experimental plots comprises manual weeding to control weeds that may overgrow the planted saplings, but will be stopped after two years to allow natural succession (Figure 3.3 C). The application of fertilizer, herbicide and pesticides stopped. Fences around all plots protect the trees from feeding damage by mammals. Dead trees were replaced during the first year after establishment.

In order to quantify potential ecological services or disservices from enrichment plantings on the surrounding oil palms, three oil palm individuals in perpendicular direction from the plot are used as indicators (Figure 3.3 B). For each oil palm individual yield is monitored. Additionally, the yield of each oil palm individual inside the plot is measured, too.

The monitoring within the framework of the BEE includes monitoring of a) the environment (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).

3.3.3 Sampling

The baseline survey of the environment, vegetation, birds and invertebrates was done in October 2013 prior to the establishment of the BEE. One year after the establishment, in October 2014, bird and invertebrate surveys were repeated.

Per plot, soil composites of two depths (0-10 cm and 10-30 cm) were taken. Samples were air dried (40°C, 2 days), grounded and sieved (2 mm). Soil texture (20 g soil) was analyzed using the Pipette Method. Ten grams of dry soil were diluted in 25 ml H2O to analyze the pH-value. For bulk density (dry weight [g] / cylinder volume [cm^3]) analysis, a standardized soil volume (250 cm^3) was taken, oven dried (105°C, 48 hours) and immediately weighed. Hemispherical photographs were taken in the center of randomly placed 2x2 m subplot per plot using a Canon 700D camera and a fisheye lens (SIGMA) (see Beckschäfer et al., 2013). The gap fraction was calculated in the best picture per subplot (maximum exposure time without being over-exposed) using 'ImageJ' (version 1.48v).

In the same subplots (2x2 m), individual-based vegetation surveys of plants ≥5 cm were done. Herbarium specimens were collected for plant identification.

Bird sampling took place from 6 am to 10.30 am when weather conditions were appropriate. Birds within a 75 m radius around each plot center were recorded visually and acoustically using 15 minutes point counts. Each sampling point was visited twice. For every species, we recorded the maximum number of individuals present simultaneously on the plot. For taxonomy we followed MacKinnon et al., (1993) and for vulnerability status, we used the species' International Union for Conservation of Nature (IUCN) classification (IUCN 2015). Body masses were obtained from the literature (Wilman *et al.* 2014) to calculate bird biomass per species.

We extracted invertebrates from the leaf-litter (LL) by sieving the LL from 1 m^2 subplot per plot 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 subplot using a modified vacuum cleaner. Animals were stored in 70% ethanol. Specimens were 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-regressions (Table S 3.3) and, where necessary, dry mass-fresh mass relationships from the literature (Table S 3.4). We summed together the fresh masses of the individuals to calculate the total biomass per plot.

3.3.4 Statistical analysis

Correlating all environmental variables (Table 3.1) showed strong relations between the two soil depths (soil texture, soil pH, C and N; Table S 3.5).

Table 3.1: Environmental variables

Variable name	Description	Scale	Min	Mean ± SD	Max
Altitude	Height a.s.l. [m]	plot	20	46.9 ± 10.46	71
Slope	Slope (SW to NE)	plot	-20.80	-0.37 ± 7.38	20.90
Bare soil	Soil without any vegetation [%]	subplot	0	10.98 ± 10.56	50
Gap fraction	Relative gap fraction in the canopy [%]	subbplot	0.03	0.14 ± 0.14	0.59
Bulk Density	250 cm³ soil sample [g/cm³]	plot	0.79	1.09 ± 0.13	1.43
Soil texture sand (1)	[%]	plot	4.62	29.93 ± 12.59	59.95
Soil texture sand (2)	[%]	plot	3.60	29.07 ± 13.28	63.18
Soil texture silt (1)	[%]	plot	18.14	40.54 ± 8.28	57.91
Soil texture silt (2)	[%]	plot	15.06	39.21 ± 8.61	62.88
Soil texture clay (1)	[%]	plot	13.69	29.54 ± 8.26	53.12
Soil texture clay (2)	[%]	plot	15.39	31.72 ± 8.84	56.06
Soil pH (1)	(1 (soil) : 2.5 (1M KCl))	plot	3.970	4.11 ± 0.23	5.28
Soil pH (2)	(1 (soil) : 2.5 (1M KCl))	plot	4.10	4.42 ± 0.16	4.96
C (1)	[%]	plot	1.04	2.18 ± 0.60	3.94
C (2)	[%]	plot	0.41	1.37 ± 0.41	2.31
N (1)	[%]	plot	0.33	0.44 ± 0.08	0.63
N (2)	[%]	plot	0.34	0.41 ± 0.06	0.55
CN (1)		plot	2.93	5.01 ± 1.14	7.84
CN (2)		plot	1.18	3.36 ± 0.95	6.1

To reduce their predominance to general trends, we conducted a PCA with the soil variables and used the scores of the first three PCA axes in all further analyses. In case plots are spatially dependent, we would have to control for that in further statistical analyses. Spatial autocorrelation of the environmental parameters was tested by calculating Moran's I values (standard deviate with 100 permutations, distance classes of 0.15 km). To check for unintended systematic correlations between the environmental variables and the experimental factors, we ran linear models with the environmental variables as responses and 'tree diversity' and 'plot size' as predictors.

Alpha-diversity was calculated with the Simpson-index; beta-diversity was calculated with the Sørensen-index based on true abundance-data (Legendre & De Cáceres 2013). We estimated species 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, Martinez & Williams 2003). We tested for the overall effect of tree planting by comparing the means of the baseline survey and year one of the richness, abundance and biomass of birds as well as LL and HL invertebrates with generalized least square models and applying a Tukey post-hoc test.

Further, 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). Tree diversity and plot size were taken into the models separately whilst controlling for the other variable in each model. We tested for linear, non-linear and ID-effects of plot size and tree diversity.

Shifts of invertebrate biomass and abundance within trophic compartments in year one compared to the baseline survey and how these shifts are affected by 'plot size' and 'tree diversity' were investigated based on the community weighted mean (CWM) 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 together per plot and divided by the total biomass per plot. A linear mixed model was run with the CWMs as responses; '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.

All analyses were conducted in R using the following packages: vegan, FD, spdep, nlme (R Core Team 2015).

3.4 Results

3.4.1 Oil palm yields

In 2014, the average oil palm yield on the plantation was 22.74 tons of fresh fruit bunches ha^{-1}.

3.4.2 Environmental characteristics of the plantation

Some of the environmental characteristics varied a lot between the plots (topography, light availability, proportion of bare soil, soil texture and soil carbon content, while others were rather stable (bulk density, soil pH, nitrogen content) (Table 3.1; Figure S 3.1, Table S 3.6). The first three PCA axes explained 69.6% (from 1st to 3rd axis: 36%, 20%, 13.5%) of the overall variation of the measured soil characteristics (Figure S 3.2). Soil texture (silt, sand) and carbon content contributed most to the first PCA axis; soil texture (clay), carbon content, and bulk density to the second and; nitrogen content to the third. Soil pH was not very important on any of the three PCA axes. (Table S 3.6). We found no support for spatial autocorrelation of the variation in any of the variables (Figure S 3.3). We detected systematic relationships between the two experimental factors ‘tree diversity’ and ‘plot size’ with some environmental and some biotic variables. However, the strengths of the effects were in all cases negligible (R^2 values <0.17) (Table S 3.7).

Table 3.2 shows diversity indices for the different organism groups. Plants and birds were identified on species level, invertebrates on family level. We found 99 plant species, 21 bird species, 87 LL (litter layer) and 148 HL (herb layer) invertebrate families. The estimated numbers of total species richness were substantially larger for plant species (168 species estimated; 58.9% sample representativeness) and invertebrate families (LL/HL: 137/148 families estimated; 63.5% sample representative in both groups), but not for birds (26 species estimated; 80.8% sample representativeness). These findings are congruent with the results from the species accumulation curve (Figure 3.4). The Simpson index was similar for all organism groups (0.62 to 0.76). The abundance based β-diversity ranged from 0.14 to 0.2.

Table 3.2: Species/family numbers of the four organisms groups monitored at the experimental plots. LL = leaf litter, HL = herb layer.

	Plants	Birds	LL invertebrates	HL invertebrates
Total species/family richness	99 (species)	21 (species)	87 (families)	94 (families)
Estimated species/family richness	168	26	137	148
Mean species/family number per plot (± SD)	16.87 ± 4.59	4.42 ± 2.11	9.4 ± 5.76	11.6 ± 6.34
β-diversity	0.14	0.18	0.19	0.2
Mean Simpson Index mean per plot (± SD)	0.77 ± 0.11	0.63 ± 0.19	0.62 ± 0.23	0.76 ± 0.13

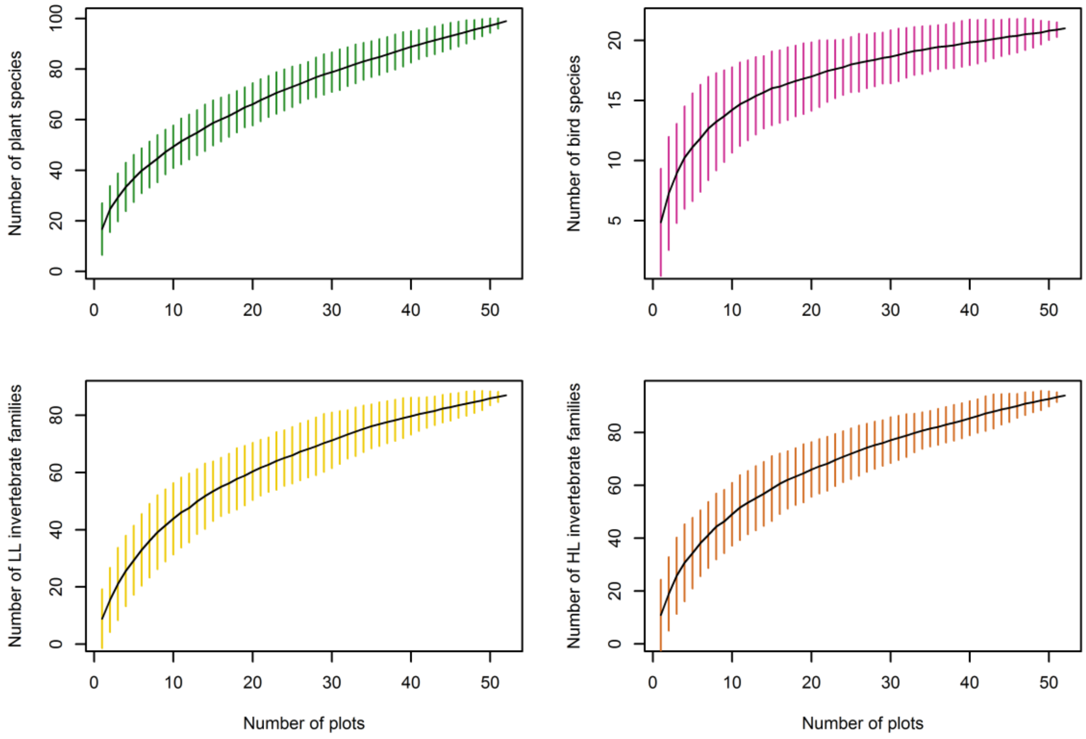

Figure 3.4: Species accumulation curve for plant and bird species as well as for families of leaf-litter (LL) and herb-layer (HL) invertebrates.

3.4.3 Biotic characteristics of the plantation

Vegetation

Overall, 99 plant species were recorded in the understory herb layer (Table S 3.8 and S 3.9). The three most frequent species were *Clidemia hirta* (Melastomataceae), followed by *Asystasia gangetica* (Acanthaceae) and *Paspalum* cf. *conjugatum* (Poaceae). The three most abundant species are also among the most frequent species: *A. gangetica* was the most abundant species with 5253 individuals in the plots, followed by *C. hirta* (3233 individuals) and *Nephrolepis* cf. *acutifolia* (Nephrolepidaceae) (2299 individuals). *A. gangetica* und *C. hirta* were both introduced to Sumatra.

Birds

A total of 590 bird individuals of 21 species were detected (Table S 3.8 and S 3.10). Three species that were the three most frequent species were also the three most abundant ones: The Bar-Winged Prinia *Prinia familiaris* (N=187), followed by the Yellow-Vented Bulbul *Pycnonotus goiavier* (N=169), and the Ashy Tailorbird *Orthotomus rufices* (N=53). All species are listed as least concern (IUCN 2015).

Leaf-litter invertebrates

We hand-collected 2173 individuals from 87 families (Table S 3.8 and S 3.11) out of the sieving samples of the LL. Individuals from the family Formicidae (Hymenoptera) were most abundant (N=1291). The second most abundant family was Staphilinidae (N=113) (Coleoptera), followed by Pyrgodesmidae (N=70) (Polydesmida). The sampled individuals consisted of 24.8 % predators, 61.2 % omnivores, 1.8 % herbivores and 9.7 % detritivores.

Herb layer invertebrates

1407 individuals from 94 families were collected in the HL (Table S 3.8 and S 3.12). Individuals from the family Gryllidae (Orthoptera) (N=499) were the most abundant ones, followed by Cicadellidae (Hemiptera) (N=96) and Formicidae (Hymenoptera) (N=91). The invertebrates sampled consisted of 18.7% predators, 46% omnivores, 18.3% herbivores, 11.6% detritivores.

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

Birds

We recorded 531 birds of 20 species (Table S 3.13 and S 3.14), whereof 15 species where the same as in 2013. Six species that where present in 2013 where not recorded in 2014 anymore. *P. familiaris* (N=149) was the most abundant species, followed by *P. goiavier* (N=146), and *Todiramphus chloris* (N=51). All species in 2014 are listed as "least concern" (IUCN 2015).

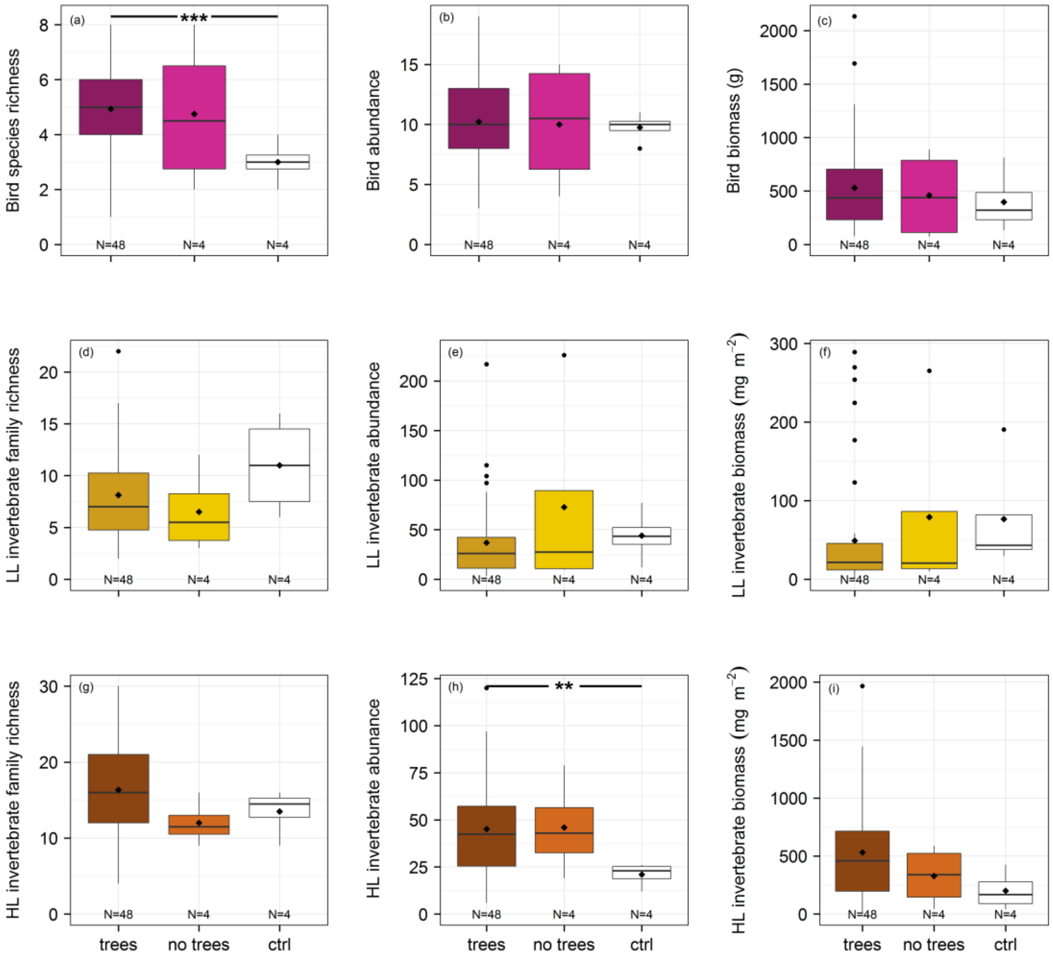

Figure 3.5: Comparison of the richness, abundance and biomass of birds, leaf-litter (LL) invertebrates and herb-layer (HL) invertebrates between plots with trees (N=48), plots without trees (N=4) and control plots (N=4). For birds we considered species richness, for invertebrates richness is accounted for on family level only. We found a significantly higher species richness of birds on the plots with trees as compared to the control plots (a). Furthermore, the abundance of HL invertebrates was significantly higher on plots with trees compared to the control.

In year one of the experiment, bird species richness was significantly higher on plots with trees (diversity levels one to six) as compared to the control plots (management-as-usual) but not different to plots with diversity level zero (oil palms cut; no trees planted; manual weeding; no application of fertilizer, herbicides and pesticides) (Figure 3.5 a). There was no significant effect of tree planting on the abundance and biomass of birds (Figure 3.5 b and c).

Leaf-litter invertebrates

A total of 2062 individuals from 74 families were collected in the LL (Table S 3.13 and S 3.15) of which 48 were the same as in the baseline survey in 2013, 26 were new and 39 families that were found in 2013 were not represented in 2014 anymore. Most abundant were individuals from the family Formicidae (Hymenoptera) (N=1437). Animals from the family Lyniphiidae (Aranea) were second most abundant (N=63), followed by Pyrgodesmidae (Polydesmida) (N=62). The sample comprised 17.1% predators, 70.7% omnivores, 3% herbivores and 7.3% detritivores.

We found no difference in overall family richness, abundance and biomass of the LL invertebrates in year one between plots with trees (diversity level one to six), plots with diversity level zero and control plots (Figure 3.5 d, e and f).

Herb-layer invertebrates

2349 individuals from 105 families were collected in the HL (Table S 3.13 and S 3.16). 58 families were the same as in the year before, 47 were new and 36 families that were present in 2013 were not present in 2014. Animals of the families Gryllidae (Orthoptera) (N=749), Formicidae (Hymenoptera) (N=250) and Cicadellidae (Hemiptera) (N=139) were most abundant. The invertebrates consisted of 17.2% predators, 48% omnivores, 15.3% herbivores and 11.5% detritivores.

We found a significantly higher abundance of HL invertebrates on plots with trees (diversity level one to six) as compared to the control plots in year one (Figure 3.5 h). Family richness and biomass were not affected by tree planting (Figure 3.5 g and i).

3.4.5 Effect of tree diversity and plot size on the bird and invertebrate community after one year

We found a significantly positive effect of plot size on the difference in diversity of LL family richness and the difference in abundance of HL invertebrates in year one compared to the baseline (Figure 3.6); Tree diversity, however, did not have any effect on the difference in richness, abundance and biomass of birds and invertebrates (Figure 3.7).

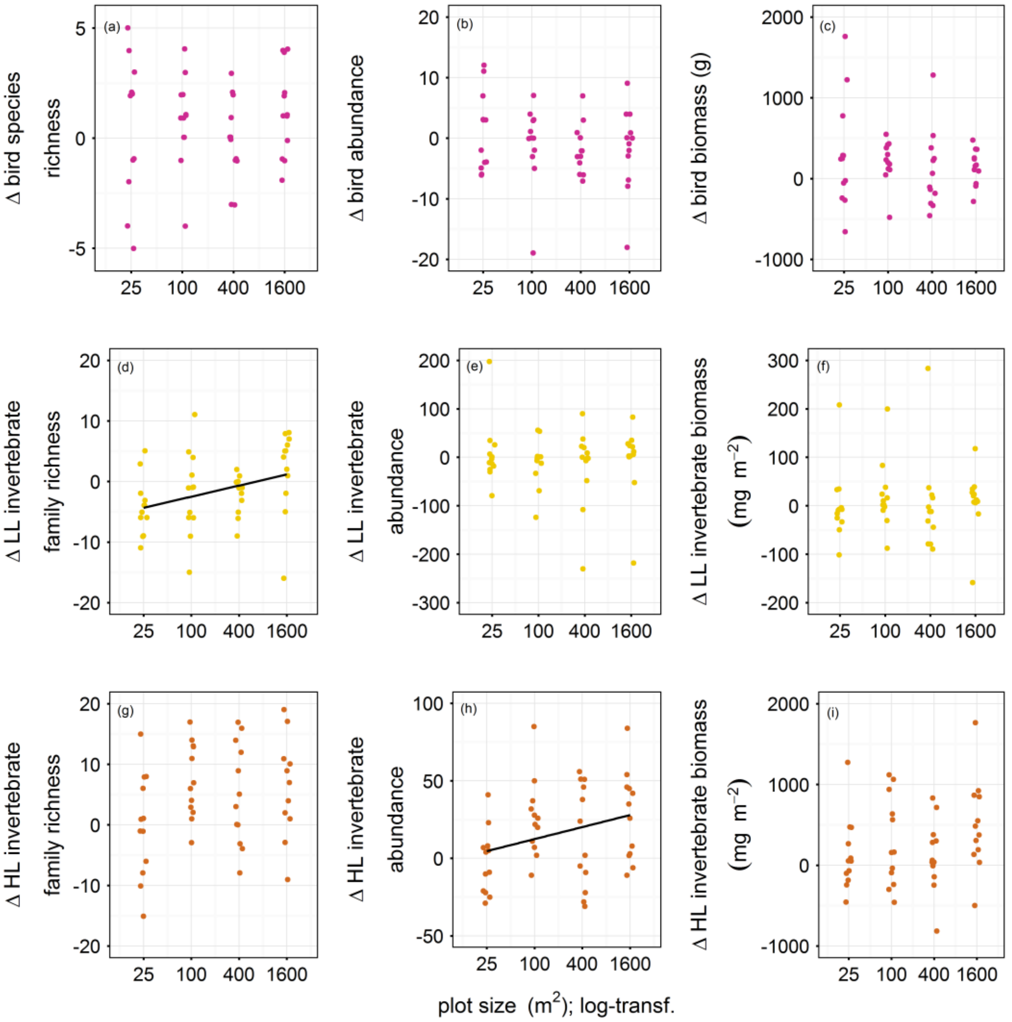

Figure 3.6: Effect of plot size on the difference in richness, abundance and biomass of birds as well as leaf-litter (LL) and herb-layer (HL) invertebrates between year one and the baseline. Birds were considered on species level, invertebrates on family level. LL invertebrate family richness (d) and HL invertebrate abundance (h) was significantly positively related to plot size (indicated by a black line).

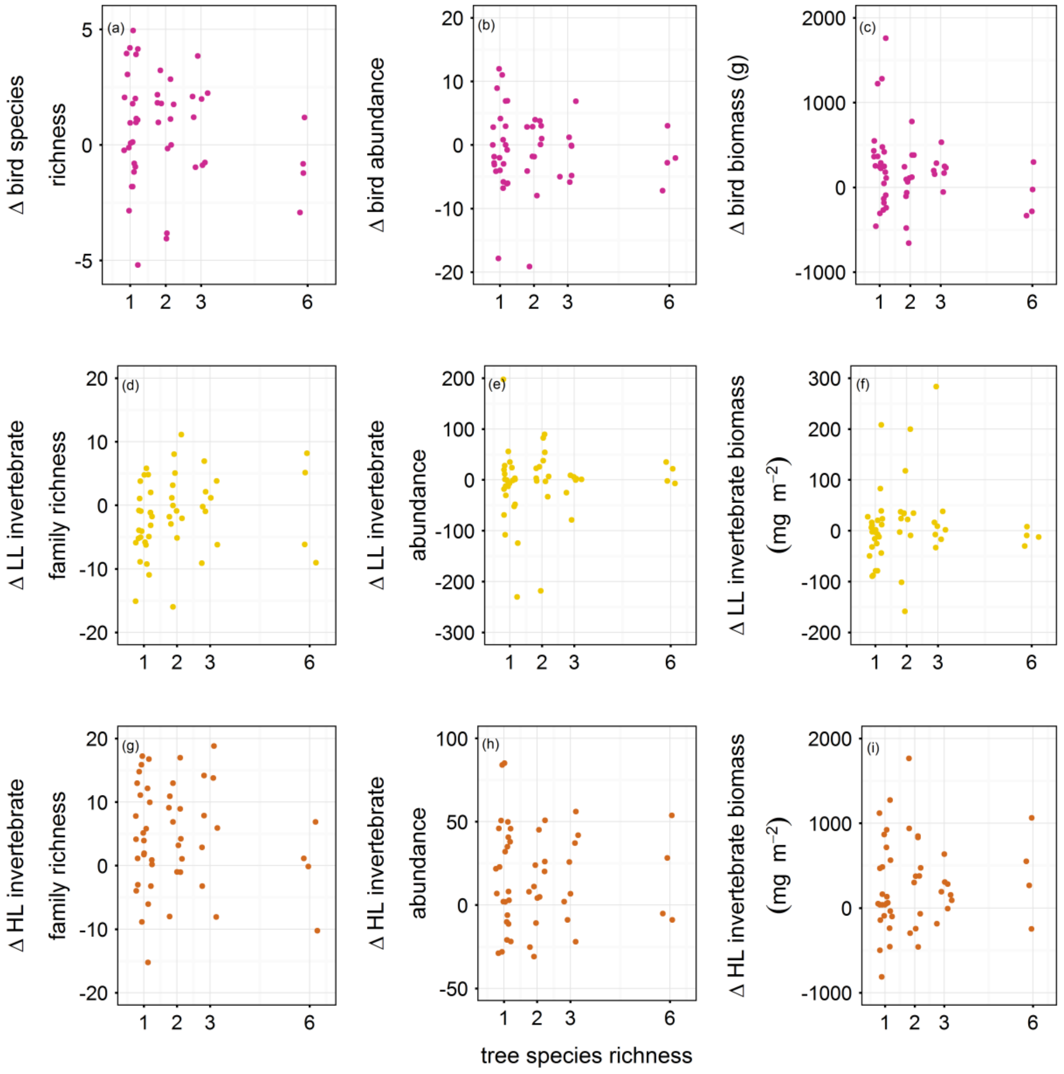

Fig. 3.7: Effect of tree diversity on the difference in richness, abundance and biomass of birds as well as leaf-litter (LL) and herb-layer (HL) invertebrates between year one and the baseline. Birds were considered on species level, invertebrates on family level. There was no effect of tree diversity on any of the responses.

3.4.6 Shifts of invertebrate biomass and abundance within trophic compartments

Variation in the community weighted mean (CWM) trophic index and CWM abundance of LL and HL invertebrates, respectively, between the baseline and year one of the experiment could neither be explained by tree planting in general (factor 'year') nor by plot size (plot size : year) or tree diversity (tree diversity : year). This suggests that the changes within the trophic compartments of the invertebrate communities are likely to be driven by other than the experimental factors.

3.5 Discussion

By addressing the effects of two important factors in a restoration context – tree island size and tree diversity – in an experimental approach, we aim at shedding light on the ecological and socio-economic processes associated with a wildlife-friendly, oil-palm-based agroforestry. A controlled experimental design, rather than an observational design, gives also more power to learn about the underlying mechanisms of enrichment plantings.

Our study site in Jambi province, Sumatra, is an ideal place to study the long-term effects of enrichments plantings. Sumatra has experienced huge losses in biodiversity due to the transformation of lowland rainforest into rubber and oil palm plantations in the past decades (Fitzherbert *et al.* 2008; Margono *et al.* 2014), and in Jambi province, the already large proportion of area under oil palm cultivation is still increasing (Euler *et al.* 2015; Gatto, Wollni & Qaim 2015). We have chosen a medium-scale oil palm plantation for the experiment that is representative for the area. Oil palm yields, management and fertilizer application are comparable to other oil palm plantations (Hassler *et al.* 2015; Kotowska *et al.* 2015). 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 (Table S 3.17). The results of our baseline survey showed that all plots are independent from each other as we did not find support for spatial autocorrelation, despite detecting variation in the environmental characteristics. Further, the relationship between the biotic and abiotic baseline variables and the two experimental treatments ‘plot size’ and ‘tree diversity’ is negligible. Overall, we can conclude that the site conditions are appropriate for future statistical analyses to clearly distinguish experimental impacts and that our site is representative for other oil palm plantations so that results from the BEE are transferable to other plantations.

Interestingly, we already see positive effects of the enrichment plantings on the bird and invertebrate fauna one year after the establishment of the experiment. The overall increase in bird species richness across the plantation could be attributed to an overall increase in heterogeneity within the plantation due to some of the planted trees (i.e. *Archidendron pauciflorum* and *Parkia speciosa*) having already reached considerable heights (> 4 m) within the first year, which might provide habitat for nesting, roosting and foraging (Thiollay 1995). This result supports findings that habitat heterogeneity is a very important factor determining bird diversity and composition (Sekercioglu 2002; Walther 2002; Stein, Gerstner & Kreft 2014; Teuscher *et al.* 2015). At plot level, responses of birds were non-significant indicating that overall habitat complexity at the landscape scale is more important than at a local scale at this early stage of the experiment. Most likely, more birds, especially frugivorous species that were found to be absent in oil palm plantations (Prabowo *et al.* 2015), will be attracted by the tree islands when trees grow bigger and carry fruits. Birds serve as seed dispersers (Sekercioğlu 2006; Whelan, Wenny & Marquise 2008) and this might in turn positively affect succession and spontaneous colonization of the plants in the tree islands (see Cole et al., 2010). Due to an expected increase in the number of herbivorous insects feeding on the foliage of the planted trees (Schuldt *et al.* 2010), an increase in the proportion of insectivorous birds in a bottom-up effect is also expected as birds function as pest control agents (Sekercioğlu 2006; Koh 2008b).

Invertebrates responded to the enrichment plantings on a much smaller scale. We do not only see 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 also see a positive relationship between the tree island 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. The stop of fertilizer and pesticide application in combination with the creation of new small-scale habitat structures through the planting of trees might be the reason for these positive responses of the invertebrate communities (see Pywell et al., 2012; Tscharntke et al., 2011). The increase in leaf-litter invertebrate family richness could additionally 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 qualitative factors such as tree diversity. Lacking shifts in the relative proportion of invertebrate biomass and abundance within trophic compartments between year one and the baseline indicate that there may be 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. They are among the most important organism for litter decomposition and, moreover, prey, pollinators, herbivores and seed predators (Ewers *et al.* 2015).

We chose birds and invertebrates as study organisms, as they are used as bio-indicators to monitor changes in habitat quality. Ecosystem functioning was found to be negatively correlated with diversity loss of birds (Sekercioğlu 2006; Tscharntke *et al.* 2008) and invertebrates (Barnes *et al.* 2014b; Ewers *et al.* 2015), highlighting their key role in ecosystems and, hence, the need for their conservation or rather restoration. The early positive effects of the BEE on birds and invertebrates, two organism groups which are essential for the initiation of natural succession, are promising for further biodiversity enrichment in the future. 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.

3.6 Conclusions

Being aware of the limited contribution that some planted trees may have compared to high-value nature conservation, already some left-over trees can enhance the ecological value of a plantation by maintaining at least a baseline level of biodiversity (Teuscher et al. 2015). Tree islands are a promising restoration measure for impoverished landscapes (Rey-Benayas *et al.* 2009). Balancing ecosystem functioning (ESF) and the local socio-economy, one outcome of the experiment might be a combination of island size, tree diversity level and composition that is above-average cost-effective and productive to achieve high gains in ESF. This implies 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.

The concept of biodiversity enrichment might be similarly relevant for companies managing large scale mono-culture plantations as well as for small-scale farmers seeking to diversify their production to reduce risks and their dependence on palm oil.

In this context, ‘Payment for Environmental Service’ (PES)-schemes or a certificate for wildlife-friendly palm oil not exclusively focusing on non-deforestation policy and ‘High Conservation Value’ (HCV) habitats could make the biodiversity enrichment method more appealing. Depending on the goals of involved stakeholders, tree plantings could be adjusted to management forms such as agroforests, secondary forests for production of timber or for conservation. One realistic application is considered in the close-by Harapan rainforest, where an illegal oil palm plantation within the national park is supposed to be re-transformed to forest. In this case, tree islands could act as a smooth transition from plantation to forest: the plantings could make the plantation more hospitable for wildlife by reducing the land-use intensity and at the same time give farmers enough time to consider alternative means of income.

Our experiment 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 minimizing economic losses. However, this does not satisfy the need for areas of HCV which are an integral part of the aimed designed plantation landscapes. In their function as source habitats, HCV habitats are essential to recruit wildlife from and initiate successful natural succession in the BEE or other wildlife-friendly farming systems. Our long-term objectives are to improve landscape connectivity, to provide habitat for migrating biota and to buffer the inhospitality of oil palm plantations, thereby contributing to biodiversity conservation on a landscape scale. With the results of the experiment we aim on evaluating the effectiveness of the enrichment plantings as part of the proposed designer plantation landscapes and develop clear restoration instructions for oil palm farmers towards a more sustainable management of oil palm.

3.7 Acknowledgements

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PART III

GENERAL DISCUSSION

Chapter 4: discussion

Land-use change is widely recognized as one of the key drivers of global biodiversity loss (Sala *et al.* 2000; Rockström *et al.* 2009; Newbold *et al.* 2015). In Indonesia, land-use change is fueled by an increasing demand for food and biodiesel, leading to a proliferation of oil palm plantations (Turner *et al.* 2008; Fitzherbert *et al.* 2008). Oil palm has become one of the most rapidly expanding crops in the humid tropics and over 85% of the world's palm oil production originates from Indonesia and Malaysia (UNCTAD, 2015). Potentially, palm oil production can foster development of the rural poor but often is accompanied by environmental and social problems (Gilbert, 2012; McCarthy, Gillespie, & Zen, 2012). New establishment of oil palm plantations is often linked to deforestation (Koh & Wilcove 2008; Gibbs *et al.* 2010; Abood *et al.* 2015) and this conversion of highly diverse tropical rainforest ecosystems into simplified agricultural production systems has devastating impacts on biodiversity and ecosystem functioning (Wilcove & Koh 2010; Foster *et al.* 2011; Dislich *et al.* 2015). This puts a risk on human well-being, too, because ecosystem service degradation leads to e.g. insufficient provision of goods or impairment of water quality (Naeem *et al.* 1999; Cardinale *et al.* 2006, 2012).

Designer plantation landscapes where highly intensified oil palm plantations are surrounded by agroforestry buffer zones have been proposed as a measure to increase biodiversity and ecosystem functioning and simultaneously decrease negative effects on rural livelihood (Koh *et al.* 2009). This approach can be especially interesting in areas where new plantations are planned. However, in an already heavily deforested region it might already be too late for this kind of preventive landscape planning and re-establishing diverse habitats should be considered. Sumatra is an example of such a region, since very little forest is remaining (Margono *et al.* 2014) and the area under oil palm is increasing, leading to dramatic declines in biodiversity (Fitzherbert *et al.* 2008). To date, there are four experiments in the tropics that do research on the relationship between restoration via tree planting and associated effects on biodiversity and ecosystem functioning (Petit & Montagnini 2006; Kirui *et al.* 2008; Potvin & Gotelli 2008b; Moreira *et al.* 2014). These experiments were established in pastures, abandoned land and logged forest. However, there is no such project in an established oil palm plantation, where production/cultivation of oil palms is maintained while restoration effects are studied. Consequently, there is little knowledge on how the re-establishment of diverse habitats and the restoration of multi-functionality in oil-palm-dominated landscapes can be implemented in a way that is ecologically and economically sustainable at the same time.

The aim of this thesis was to contribute to a better understanding of the ecological and economic impacts of restoration via biodiversity enrichment plantings in oil palm plantations and to set the scene for long-term research in the field of restoration of oil-palm-dominated landscapes. First, I investigated the ecological and economic trade-offs when having remnant or freshly planted non-oil-palm trees within smallholder oil palm plantations in the province of Jambi, Sumatra, Indonesia. The costs to conserve bird species diversity and abundance in oil palm plantations were estimated (Chapter II). Second, I established a long-term, large-scale biodiversity enrichment and ecosystem functioning experiment by planting tree islands in an oil palm plantation. The complexity of this experiment creates a platform for interdisciplinary research on the effects of tree-based restoration in oil palm plantations on biodiversity, ecosystem functioning and human livelihood. It aims at contributing to the development of ecologically improved and socio-economically viable management strategies for oil palm systems. My particular research focus within the framework of the experiment was on the establishment of the tree islands, the assessment of the initial abiotic and biotic conditions prior to the tree planting on the plantation, the bird and invertebrate communities in the plantation and their taxonomical and functional diversity responses to tree islands one year after establishment (Chapter III).

4.1 Trade-off between ecology and economics in oil palm plantations

In Chapter II, I studied the ecological-economic trade-off of oil palm plantations with remnant or retroactively planted trees (non-oil-palm trees are always referred to as ‘trees’; oil palm trees are referred to as ‘oil palms’). I combined economic and ecological data from 120 smallholder oil palm plots in the Jambi province, Sumatra, Indonesia in a preliminary study to the biodiversity enrichment experiment. I assessed the monetary costs for the conservation of bird species richness and bird abundance when a wildlife-friendly farming system is applied in oil palm landscapes. The focus was on single remnant or planted trees within or at the border of oil palm plantations. These trees varied in number along an oil palm management gradient from high intensity management (low number of trees) to low intensity management (high number of trees). My results confirm that oil palm plantations are very poor in bird species richness compared to natural forest. However, retaining trees in oil palm plantations mitigated the loss of bird species richness and abundance of common and widespread species of low conservation status. This suggests that enhanced habitat complexity in oil palm plantations can at least maintain a baseline level of biodiversity. Besides tree presence, the height of ground vegetation was an important factor that explained variation in bird species richness and abundance. The increase in bird species richness and abundance was dependent on the number of trees and linked to a decrease in revenue, implying a win-lose relationship between ecological and economic outcomes.

Both, the marginal gain in bird species and bird abundance with increasing tree density as well as the marginal loss in revenue, were non-linear. Therefore, the marginal shadow price of bird species richness and bird abundance expansion changes depending on the initial number of trees present on the oil palm plantation, hence on the initial management intensity. In relatively extensively managed oil palm plantations (N trees = 50), an increase in bird species richness can only be achieved at the expense of relatively high revenue penalties (67% decline in total revenue), whereas in relatively intensively managed oil palm plantations (N trees = 10), the same increase in bird species richness can be achieved with a considerably smaller loss in revenue (20% loss of total revenue). Similarly, this was found for bird abundance as well, but where an increase in individual numbers implied lower costs compared to the costs for increased bird species richness. Furthermore, the study resolved that farmers' choices are not solely governed by economic reasons. Although remnant or planted trees negatively affected oil palm yield and revenue, farmers decided to maintain the trees within their plantations because of recreational, spiritual or aesthetic reasons. In summary, increasing bird diversity and abundance in highly intensified oil palm plantations is cheaper than in extensively managed oil palm plantations.

4.1.1 Limitations of the study

In chapter II, I obtained initial insights into the effects on ecology and economics when enrichment plantings such as remnant trees or planted trees are retained within oil palm plantations. Nevertheless, the limitations of my study have to be critically assessed.

The majority of oil palm plantations I considered for my study where highly intensively managed, containing only few remnant or planted trees; only few plantations had very large numbers of trees. This led to a high imbalance of plots with few trees compared to plots with many trees and consequently a high variability in the data. To better explain a larger proportion of variation in the data, further studies should therefore aim to cover the whole gradient from high to intermediate and low numbers of trees in the plantation. Furthermore, I did not distinguish between remnant and planted trees, fruit trees and other trees, nor was the size structure of trees considered. The study was limited to the analysis of quantitative changes in tree numbers. Qualitative factors such as tree diversity, their size structure and composition, and their economic value, however, are likely to have impacts on biodiversity and ecosystem functioning as well as on oil palm yields and revenue (see i.e. Clough et al., 2011; Erskine et al., 2006; Kanowski et al., 2003; Petit and Montagnini, 2006).

The study revealed that bird diversity increased with increasing number of trees in the oil palm plantation. It is important to remember that throughout all oil palm plantations, predominantly generalist, open-habitat and edge-tolerant bird species of low conservation status were found. Doubtless, these species also contribute to maintaining a baseline level of biodiversity. However, this also suggests that oil palm plantations enriched with single trees fail to retain forest bird species and a generally high level of biodiversity (also see Edwards et al., 2010). The overall conservation value of keeping single remnant or planted trees within oil palm plantations is therefore rather low. Nevertheless, although the absolute number of bird individuals and bird species would be lower in intensive plantations with few trees compared to a more extensive plantation with more trees to start with, even this slight increase in bird species richness and abundance might already lead to increased ecosystem functioning (Srivastava & Vellend 2005) and, thereby, to increased provision of ecosystem services such as pollination, seed dispersal and pest control (Foster *et al.* 2011). However, the benefits in ecosystem service provision due to marginal changes in bird species richness or abundance might depend on the initial number of bird species or individuals. Further studies should, therefore, address the form of the relationship between bird diversity and abundance and the associated provision of ecosystem services.

My study revealed that some farmers retained trees within the plantation for recreational, spiritual or aesthetic reasons. A ‘choice experiment’ to assess farmers’ willingness to plant or retain trees within their oil palm plots could be a useful extension to the household study to specify their motivation for a wildlife-friendly farming strategy. The design of the choice experiment could include different levels of compensation to elicit farmers’ willingness to accept such farming strategies. These results would be valuable for informing the design of ‘Payment for Ecosystem Service’ (PES) programs (see Vorlaufer 2015). Considering the negative relationship between biodiversity and economics, profit-maximizing farmers factually have no motivation to retain trees within their plantations. However, given a fixed conservation payment, farmers of highly intensive oil palm plantations would have a comparatively higher incentive to increase the number of trees on their plantation than farmers of already extensively managed oil palm plantations. Studies to investigate whether or not economic losses could entirely or to a relatively high extent be lessened by planting trees of high economic value would elucidate if PES are even necessary.

Thus, my study is a starting point and provides the basis for further research on enrichment plantings in oil palm plantations. In order to address various open questions and to effectively be able to shed light on additional ecological and socio-economic mechanisms linked to enrichment plantings, a long-term, large-scale experiment with a controlled design is needed, which will be more effective to gain a deeper understanding than further short-term, observational studies. Therefore, I established a biodiversity enrichment planting experiment with colleagues from Germany and Indonesia in a second step.

4.2 The biodiversity enrichment experiment

In Chapter III, I introduced the biodiversity enrichment planting experiment and presented some initial results. The experiment was established in a mono-culture oil palm plantation in the province of Jambi, Sumatra, Indonesia.

In total, colleagues and I planted 56 experimental tree islands in December 2013. Plot size as well as tree species diversity, identity, and composition were systematically manipulated. For the experiment, a random partitions design was adopted (Bell *et al.* 2009), with four partition series that differ in their plot size (5x5 m, 10x10 m, 20x20 m, 40x40 m). Each partition was subdivided into five blocks, one per tree diversity level (levels of six, three, two, one, and zero). Additionally, four control plots without any experimental treatment were set up. This resulted in a total of 56 pots. The set of trees chosen for the experiment comprised six multi-purpose tree species native to Sumatra that deliver products (fruits, timber latex) to local people. Prior to planting the trees, selected oil palms were cut on the experimental plots in order to reduce canopy cover to ensure that there was enough light for the planted trees to establish and grow. On the control plots no palms were cut. The management of the plots with treatments included manual weeding, but the application of fertilizer, pesticides and herbicides completely stopped. On the control plots, management-as-usual was applied. A fence was built around all plots to avoid large mammals to damage the tree islands. To assess services or disservices of the tree islands on the surrounding oil palms, three consecutive oil palms were marked outside each plot in perpendicular direction, for which yield and spillover of biota is monitored. Within the framework of the experiment, long-term monitoring includes the environment (soil, canopy cover, surrounding matrix), plants (growth performance and survival of trees, seed rain, understory vegetation), animals (functional and taxonomic changes in the composition of bird and invertebrate communities), and socio-economics (oil palm yields, benefits from planted trees, willingness to accept enrichment plantings by local people).

In a baseline survey, the initial abiotic and biotic characteristics of the experimental plots prior to the plantings were assessed. The focus was on environmental parameters as well as on canopy cover, floristic composition of understory vegetation, invertebrate community composition in the leaf litter and the herb layer, and on the bird community.

Results from the baseline survey showed that the experimental site very well exemplifies other oil palm plantations in the region in terms of their abiotic and biotic characteristics. There was no support for spatial autocorrelation and the relationships between measured abiotic and biotic variables and the two experimental factors ‘plot size’ and ‘tree diversity’ was negligible. This suggests a high reliability of the experimental effects on various parameters measured in the future. Interestingly, one year after the establishment of the experiment, positive effects of the tree plantings on the fauna could be reported. The overall bird species richness and abundance of herb-layer invertebrates in year one was significantly increased on plots with trees compared to control plots. Even on a local scale, plantings have affected the fauna within one year after tree planting: the difference in leaf-litter invertebrate family richness and herb-layer invertebrate abundance in year one compared to the baseline survey was significantly positively related to plot size. The test for relative shifts within trophic compartments of invertebrates in relation to plot size and tree diversity level, however, did not show any significant results.

Overall increase in bird species richness across the plantation but non-significant responses of birds at the plot level suggested that, at this early stage of the experiment, overall habitat complexity at the landscape scale is more important than tree identity, tree diversity, tree composition and plot size. This is in line with other studies that found habitat heterogeneity to be a very important factor determining bird diversity and composition (Sekercioglu 2002; Walther 2002; Teuscher *et al.* 2015). Trees provide habitat for birds for roosting, nesting and foraging (Thiollay 1995) and facilitate movement through the agricultural landscape (Harvey 2000). It is likely that frugivorous birds, that were found to be absent in oil palm plantations (Prabowo *et al.* 2015), will be attracted again as soon as the planted fruit trees start fruiting. Arriving birds, especially frugivorous and granivorous species, will then function as seed dispersers (Whelan, Wenny & Marquise 2008), accelerating the recruitment of plants within the plots. Insectivorous birds are also expected to increase in number and diversity due to an expected increase in numbers of herbivorous insects feeding on the foliage of the planted trees (Schuldt *et al.* 2010) that provide prey resources for the birds.

Invertebrates responded not only on a landscape scale but also locally to enrichment plantings. Stopping fertilizer and pesticide application in combination with the creation of new small-scale habitat structures by the planted trees is likely to have caused this positive impact on the herb layer invertebrate abundance and richness in leaf-litter family richness. Both variables were positively related to plot size. This is congruent with findings that large inputs of fertilizer and pesticides have negative effects on biodiversity (Geiger *et al.* 2010; Decourtye, Henry & Desneux 2013) and that, hence, a reduction of pesticide and fertilizer application protects functional agrobiodiversity (Tscharntke *et al.* 2011). The increase in leaf-litter invertebrate family richness could additionally be correlated to an increased litter input by the planted trees, as leaf-litter dwelling macroinvertebrates strongly depend on litter input from the vegetation (Gillison *et al.* 2003). Not only the quantity of resource availability, but also the increased stoichiometric diversity in the leaves might play an important role in affecting the diversity of leaf-litter invertebrates (Ott *et al.* 2014). The significant positive relationship between invertebrate family richness/abundance and plot size suggests, however, that landscape effects might be more important than qualitative factors such as tree diversity. Lacking shifts within trophic compartments of invertebrate communities between year one and the baseline indicate that there may be 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., 2010).

First results of the experiment showed that enrichment plantings can have positive effects on bird and invertebrate communities. However, my data collected on the experimental site represent only a snapshot in the early stages of the experiment. Over time, mechanisms and processes associated to enrichment plantings may change whilst the planted trees are growing and future findings might hence be different.

To gain a deeper understanding of the mechanisms and consequences of tree islands for environmental enrichment in mono-culture production systems, bird and invertebrate communities are of key importance. Both groups represent key bio-indicators and thus are a valuable tool for monitoring the impact of habitat changes on the functioning of ecosystems. In the following section, I discuss the importance of birds and invertebrates for ecosystem functioning.

4.2.1 The importance of birds and invertebrates as bio-indicators

In many studies, bird communities are used as bio-indicators to monitor the health of an ecosystem. Birds are easy to observe (during daytime), they are taxonomically well identified, sensitive to changes in habitat quality and play an important role in ecosystem functioning by acting as pollinators, predators, seed dispersers, scavengers, and ecosystem engineers (Sekercioğlu 2006; Tscharntke *et al.* 2008). Tropical studies suggest high importance of insectivorous birds in agricultural systems (Sekercioğlu 2006) because they can significantly reduce plant damage by insect herbivores (Van Bael, Brawn & Robinson 2003; Van Bael & Brawn 2005; Van Bael *et al.* 2008; Koh 2008b; Karp *et al.* 2013). Furthermore, birds are considered to be highly effective agents in the transportation of seeds (Darwin 1859; Sekercioğlu 2006). Zoochory (the dispersal of plant seeds by animals) is a very important dispersal mode, especially for tropical trees and plants, as in some forests up to 90% of tropical plant species seeds are dispersed by animals. Birds often outperform mammals in long-distance dispersal (Sekercioğlu 2006). High diversity and abundance of birds can thus increase seed rain and facilitate the recovery of degraded systems (Sekercioğlu 2006; Cole, Holl & Zahawi 2010). It is therefore suggested, that tree enrichment plantings, which have as such already been identified to increase bird diversity (Clough *et al.* 2009; Teuscher *et al.* 2015), are designed to facilitate avian seed dispersal (Lindell, Reid & Cole 2013). Another important function within ecosystems is pollination. Bird pollination, compared to insect pollination, is less common. Nevertheless, more than 900 bird species pollinate ~500 of the 13,500 vascular plant genera (Sekercioğlu 2006).

Invertebrates, in general, also represent a group that is essential for the maintenance of ecosystem functioning. They are the “little things, that run the world” (Wilson 1987) because they influence ecosystem functioning far out of proportion to their body mass and can both have direct and indirect effects on other organisms’ activity (Coleman & Hendrix 2000). Invertebrates act as prey resource, pollinators, biological control agents, soil ecosystem engineers and regulators, herbivores, and predators of seeds and other insects (Ewers *et al.* 2015). A loss in diversity and abundance of invertebrates due to forest conversion (Turner & Foster 2008; Fayle *et al.* 2010; Barnes *et al.* 2014b) has been found to negatively affect multitrophic ecosystem functioning (Barnes *et al.* 2014b). In particular, this can lead to a decrease in litter decomposition, seed predation and removal, and invertebrate predation (Ewers *et al.* 2015).

Overall, birds and invertebrates exemplify ideal focal taxa to study the effects of restoration on ecosystem functioning. Both groups function as bio-indicators, as they are sensitive to changes in habitat quality which also highlights the need for the conservation of their diversity and abundance.

4.2.2 Opportunities and constraints of the biodiversity enrichment experiment

The biodiversity enrichment experiment provides lucrative ground for interdisciplinary studies that can contribute to the development of specific recommendations on how to design economically realizable oil palm plantations that simultaneously harbor high biodiversity and maintain ecosystem functioning. However, interests of ecology and socio-economics can be opposing, making it difficult to satisfy all the expectations incumbent on this experiment. In the following, I discuss some points regarding the opportunities and constraints of this experiment.

In the biodiversity enrichment experiment, tree species identity, diversity, tree compositions and plot size were simultaneously manipulated. This exceeds most restoration and BEF experiments with trees, where often only one or two factors are manipulated (Hector *et al.* 2011; Holl *et al.* 2011; Bruelheide *et al.* 2014). Addressing multiple factors at the same time, however, allows for a faster identification of the best planting strategy, making it more economically effective than testing all the factors separately in different experiments. Monitoring the growth of trees, oil palm yield, animal and plant diversity and abundance as well as services and disservices of the tree islands on the surrounding oil palms will then elucidate which tree composition and size of islands can most effectively restore biodiversity and ecosystem functions. At the same time, however, the design could just as well turn out to be unsuitable for large-scale, long-term field experiments. The random partitions design was initially developed for lab experiments where only one factor was manipulated (species diversity) (Bell *et al.* 2009). Knowledge about the applicability of the random partitions design in the field is lacking. In the biodiversity enrichment experiment, each partition series is only represented once (one partition per plot size); hence there are no replicates at all. This could cause problems e.g. in case one plot gets destroyed or the trees within one plot are dying because of pest infestation. It would be impossible to distinguish whether experimental factors such as the species composition and plot size or other underlying mechanisms led to the death of the trees.

The set of trees chosen for the experiment includes native fruit and timber species (*Parkia speciosa*, Fabaceae; *Archidendron pauciflorum*, Fabaceae; *Durio zibethinus*, Malvaceae; *Dyera polyphylla*, Apocynaceae; *Peronema canescens*, Verbenaceae; *Shorea leprosula*, Dipterocarpaceae) which are available in local nurseries and are of economic value. The use of native trees is similarly beneficial for humans and native wildlife. The trees deliver economically valuable products to farmers (fruit, timber latex). Furthermore, the two Fabaceae species may enhance nitrogen availability by nitrogen fixation, thereby enhancing soil fertility and reducing the need for fertilizer use. The concept of biodiversity enrichment with native trees in oil palm plantations may be especially attractive for smallholders as they could benefit from increased diversification of their production and, hence, reduce their risk in case of crop failure. With additional trees in their plantation, the smallholders do not solely rely on oil palm output. Native wildlife will additionally benefit more from the use of native trees than from using exotic trees (Southwood *et al.* 2004). In particular, native trees have the potential to increase forest-dependent species (Douglas *et al.* 2014). So far, there is no experience on how the chosen tree species perform when planted within oil palm plantations. One year after establishment, differences in growth and survival rates between the tree species were evident (Anne Gérard, unpubl. data). *P. canescens* and *A. pauciflorum* had very high growth rates whereas *D. polyphylla* had a comparatively low growth rate. Growth performance might also depend upon water availability, which was found to be reduced in oil palm systems due to high transpiration rates by oil palms (Röll *et al.* 2015), or upon differences in soil texture and nutrients. Beyond that, planted tree species might differ in their susceptibility to pest infestations. Within the framework of the Master project by Jennifer Arns, which I have been co-supervising since the end of 2014, herbivory was estimated on the planted trees 17 months after the establishment of the tree islands. First results show that herbivory significantly differs between the tree species (Jennifer Arns, unpubl. data). Obviously, there are many ambiguities about the suitability of the chosen trees for restoration in oil palm systems. However, this experiment will help gather information on the usefulness of these trees for economically realizable restoration measures and will therefore facilitate further experiments in the future.

One problem linked to the management of the experimental plots is that the removal of fertilizer and pesticide application is not equally advantageous for ecology and economics. From an economic point of view, stopping the application of fertilizers does not seem reasonable, as high yields in agricultural systems are usually maintained and achieved through high fertilizer inputs (Matson *et al.* 1997). Furthermore, a farmer would use pesticides if the planted trees become infested by insects or fungi, in order to avoid death of trees that would lead to reduced income. For ecological research, however, it makes perfect sense to discontinue the application of fertilizer and herbicides in order to study natural succession and the pure benefits (and disadvantages) of tree islands on biodiversity and ecosystem functions within the oil palm system.

Moreover, from an economic perspective, it is not reasonable to cut oil palm trees once they are established and productive. For this experiment, however, oil palms were cut in order to increase light conditions for better growth performance and survival of the planted trees. This causes huge revenue penalties for the farmers, which have to be remedied by other means. In order to minimize economic losses, it seems reasonable to find other ways to introduce trees into oil palm plantations. In this respect it has to be considered that, if other trees are introduced too early or planted together with oil palms when a new plantation is established, trees may overgrow the surrounding oil palms. Consequently, the oil palm yield will decrease due to shading (Corley & Tinker 2003). Competition between trees and oil palms will probably have an impact on growth and yield of both, trees and oil palms, depending on planting design.

Generally, the long-term perspective of conservation efforts and short-term perspective of high yields and revenues are conflicting, as they have to be realized on the same piece of land. In order to optimize the revenues from oil palm management, rotation periods usually do not exceed 25 – 30 years. At the end of a rotation period, the management unit is usually clear-cut to plant the next generation of oil palms (Luskin & Potts 2011). Thus, the key to successful restoration of biodiversity and its conservation may lie in a commitment to a long term oriented management strategy that goes beyond a single rotation period of oil palms. A contribution of biodiversity enrichment to conservation can only be achieved if restored areas are not clear-cut after the end of oil palm rotation. A solution could be to create a patchwork of differently aged plantations, thereby diminishing the negative impacts of disturbances by large-scale clear-cuttings at the end of a rotation period (Luskin & Potts 2011). *In situ*, biodiversity might not be eliminated then. This concept appears to be highly suitable to be combined with biodiversity enrichment.

The examples suggest that outcomes from this experiment cannot directly be transferred to real-life situations that farmers are confronted with. In fact, the experiment is a tool to gather basic knowledge on restoration in agricultural landscapes by identifying the most effective island size and tree composition in both ecological and economic terms. Based on this information, pragmatic management guidelines can be developed. However, the implementation of the biodiversity enrichment concept requires a few more thoughts, such as at what time tree islands could be established; i.e. should this happen right at the beginning when an oil palm plantation is newly established, or when oil palms have reached the end of their life cycle and could then be replaced by trees? Despite some conflicts of interest, the biodiversity enrichment experiment is a valuable tool to gather in-depth knowledge on the effects of restoration via tree enrichment plantings in oil palm systems, based on which management implications can be developed.

4.3 Outlook and further research

This thesis has illustrated empirically that biodiversity enrichment plantings can have positive impacts on ecological conditions in agricultural production systems, but that there is a trade-off between ecological and economic functions. In order to develop pragmatic management guidelines that are ecologically beneficial and at the same time feasible in socio-economic terms, it is essential to understand the effects of tree plantings on biodiversity and ecosystem functioning, as well as on the socio-economics of oil palm plantations over time. In this thesis, I have only explored mechanisms of enrichment plantings over a short time and covered a fraction of the vast spectrum of studies possible with this experiment. Further research in various fields is needed to uncover the long-term mechanisms associated with enrichment plantings. In the following, I raise some topics that propose avenues for future research.

Conversion from forest to oil palm plantations leads to high losses in carbon stocks and also reduces of carbon sequestration (Kotowska *et al.* 2015). Further research is needed to understand which combination of tree species has the greatest potential for taking large amounts of carbon dioxide from the atmosphere and storing it in the wood of the trees or transporting it into the soil.

Numerous experiments have shown that microbial community composition contributes significantly to shaping aboveground biodiversity and the functioning of terrestrial ecosystems (Bardgett & van der Putten 2014). BEF research on microbial diversity is crucial because many of the most critical ecosystem services are underpinned by microbial processes, e.g. nutrient transformations that improve soil and water quality. How changes in plant and animal diversity induced by enrichment plantings alter microbial diversity as well as how this, in turn, affects ecosystem functioning andaboveground biodiversity through bottom-up effects, would therefore be an interesting topic to do research on.

Seed rain is expected to be higher in plots with higher initial tree diversity, as a consequence of both higher bird diversity (higher seed diversity in bird faeces) and longer period of attractiveness due to complementarity in leafing, fruiting, and flowering periods. Mist-netting studies collecting faecal samples of birds could shed light on seed rain and the identity of species that make substantial contributions to seed dispersal (Lindell, Reid & Cole 2013). In this context, other seed dispersing animals, such as bats in particular should be acknowledged as they also function as important seed dispersers in tropical systems (Kunz *et al.* 2011). In combination with studies on seed rain, studying shifts in plant communities seem reasonable as over time, a shift from plant communities dominated by weedy invasive species to communities with a high proportion of native species is expected. Ultimately, increased proportion of native plants as a consequence of increased seed rain may positively affect arthropod-mediated ecosystem services (Isaacs *et al.* 2009).

Studies on the effects of plant diversity on higher tropic levels, such as insect herbivores as primary consumers, provide further research possibilities. Most findings suggest that herbivory is reduced with increased plant diversity (Jactel & Brockerhoff 2007); others indicate that increased plant diversity promotes herbivory (Schuldt *et al.* 2010, 2015). Within the framework of the Master project by Jennifer Arns, herbivory was estimated on the planted trees 17 months after establishment of the tree islands. Results indicate that herbivory is tree species specific. In this context, studies aiming to identify insect herbivores responsible for plant damage, as well as whether herbivore communities differ between plots of various sizes and diversity levels would be interesting extensions. Furthermore, whether herbivory on the planted trees affects herbivory on oil palms and if that has any consequences for oil palm yields could be studied. Most likely, herbivory by arthropods will be higher in the first years (see Schuldt et al., 2015) due to a lag in successful colonization of higher trophic level species. One year after establishment, no shift in the invertebrate community was detected. To complete the picture of responses on various trophic levels, additional investigation whether or not there will be shifts within the functional groups of bird and bat communities is needed. This is important to consider as birds and bats function as pest control agents, thereby affecting herbivory (Sekercioğlu 2006; Kalka, Smith & Kalko 2008; Maas *et al.* 2015). Long-term monitoring of plant-insect interactions as well as top-down control by birds and bats is critical to understand consequences and opportunities of biological pest control and when it is most effective.

To investigate possible benefits of tree islands on the surrounding oil palms, studies on the spillover from native trees into the plantation system and the identity, diversity and functional importance of the added animals need to be conducted (see e.g. Lucey and Hill, 2012; Lucey et al., 2014). For example, invertebrate communities in the canopy or in the trunk of oil palms inside the plot could be compared to the communities in oil palms outside the plot and the spillover effect and the distance to the tree islands could be tested.

To assess the economic impacts of tree islands, it needs to be investigated if the emerging opportunity costs from planting fewer oil palms to create space for enrichment plantings can be compensated for by the output of the planted trees. Compensation could additionally be drawn from ecosystem services such as biological pest control, pollination, enhanced soil retention, litter decomposition and improved water quality (Foster *et al.* 2011) because these directly benefit the farmers' income (Tscharntke *et al.* 2011). In this context, the magnitude of an ecological function (e.g. invertebrate consumption) and that of the consequent ecosystem service benefiting humans (e.g. pest control) needs to be measured in order to provide 'exchange rates' between ecological functions and ecosystem services and to estimate the profit gained by enhanced ecosystem services. Based on knowledge of the combined socio-economic and ecological impact of enrichment plantings, payment schemes for ecosystem services (PES) can be designed that lead to higher levels of adoption of enrichment plantings in smallholder oil palm plantations.

The given examples illustrate the vast opportunity of the presented biodiversity enrichment experiment for future investigations on the effects of enrichment plantings on ecology and socio-economics. This highlights that this thesis has substantially contributed to make advances in BEF and restoration research in tropical agricultural landscapes. The biodiversity enrichment experiment is designed to directly address questions about the potential of enrichment plantings to restore biodiversity, their capacity to improve ecosystem functioning, and their ability to deliver increased ecosystem services whilst minimizing economic losses. With the results of the experiment, the effectiveness of the enrichment plantings will be evaluated to find the best planting strategy and to develop clear guidelines that will have direct relevance for high-profile policy issues. The concept of enrichment planting may be similarly attractive for large oil palm estate owners and smallholders; especially if newly developed PES-schemes not only focus on non-deforestation policy and high conservation value habitat. Eventually, the knowledge gained from this biodiversity enrichment experiment can be transferred to or considered by restoration projects in other oil palm plantations or even in other agricultural systems such as rubber plantations and rice paddies; land uses that are also very common in the tropics. Ultimately, this interdisciplinary biodiversity enrichment experiment may contribute to increasing and conserving biodiversity in tropical agricultural landscapes without jeopardizing the food security of a growing human population.

PART IV

APPENDIX

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Supplementary Information – Chapter 2

Supplementary table

Table S 2.1: List of bird species recorded within a 25 m radius around the centre of oil palm plantations

species name	family	common name	$_a$habitat	$_b$IUCN
Aegithina viridissima	Aegithinidae	Green Iora	gene	NT
Aegithina tiphia	Aegithinidae	Common Iora	gene	LC
Aethopyga siparaja	Nectariniidae	Crimson Sunbird	gene	LC
Amaurornis phoenicurus	Rallidae	White-breasted Waterhen	gene	LC
Anthreptes malacensis	Nectariniidae	Plain-throated Sunbird	openco	LC
Artamus leucorhynchus	Artamidae	White-breasted Woodswallow	openco	LC
Celeus brachyurus	Picidae	Rufous Woodpecker	edgetol	LC
Centropus bengalensis	Cuculidae	Lesser Coucal	openco	LC
Centropus sinensis	Cuculidae	Greater Coucal	openco	LC
Chalcophaps indica	Columbidae	Emerald Dove	edgetol	LC
Chrysocolaptes lucidus	Picidae	Greater Flameback	edgespec	LC
Cisticola exilis	Cisticolidae	Golden-headed Cisticola	openco	LC
Dicaeum cruentatum	Dicaeidae	Scarlet-backed Flowerpecker	edgetol	LC
Dicaeum trigonostigma	Dicaeidae	Orange-bellied Flowerpecker	edgetol	LC
Gallus gallus	Phasianidae	Red Junglefowl	openco	LC
Halcyon chloris	Alcedinidae	Collared Kingfisher	openco	LC
Halcyon smyrnensis	Alcedinidae	White-throated Kingfisher	openco	LC
Hirundo rustica	Hirundinidae	Barn Swallow	openco	LC
Lonchura leucogastra	Estrildidae	White-bellied Munia	openco	LC
Lonchura molucca	Estrildidae	Black-faced Munia	openco	LC
Lonchura punctulata	Estrildidae	Nutmeg Mannikin	openco	LC
Loriculus galgulus	Psittacidae	Blue-crowned Hanging-parrot	edgetol	LC
Megalaima haemacephala	Ramphastidae	Coppersmith Barbet	openco	LC
Orthotomus atrogularis	Sylviidae	Dark-necked Tailorbird	edgespe	LC
Orthotomus ruficeps	Sylviidae	Ashy Tailorbird	edgespe	LC
Orthotomus sericeus	Sylviidae	Rufous-tailed Tailorbird	edgespe	LC
Prinia familiaris	Cisticolidae	Bar-winged Prinia	openco	LC
Prinia flaviventris	Cisticolidae	Yellow-bellied Prinia	openco	LC
Pycnonotus aurigaster	Pycnonotidae	Sooty-headed Bulbul	edgespec	LC
Pycnonotus goiavier	Pycnonotidae	Yellow-vented Bulbul	gene	LC
Pycnonotus plumosus	Pycnonotidae	Olive-winged Bulbul	edgespec	LC
Rhipidura javanica	Rhipiduridae	Pied Fantail	forspec	LC
Streptopelia chinensis	Columbidae	Spotted Dove	gene	LC

a: Habitat affinities of birds as classified by Rotenberg and Stouffer (2007): forspec = forest specialist, edgetol = edge-tolerant forest species, edgespec = edge specialist, openco = open-semiopen species, gene=Generalist
b: IUCN status (IUCN 2014): LC = least concern, NT = near threatened

Questionnaire for household study: "tree enrichment"

We are students from Gottingen University-Germany, Universitas Jambi and IPB , Bogor, who are studying the impact of intercropping fruit and timber trees in oil palm plantations on bird biodiversity. Your participation in answering these questions is very much appreciated. Your responses will be COMPLETELY CONFIDENTIAL and will only be used for research purpose. Your responses will be added to those of 120 other households and analyzed together. If you indicate your voluntary consent by participating in this interview, may we begin?

1. Household Identification

QID	Question	Answer
1	Interviewer (Name)	
2	Respondent (Full name)	
3	Is the respondent HHhead? (1) Yes ; (2) No	
3.1	If QID 3=2 HHhead's Full name	
4	Village (Name)	
5	RT	
6	Date of interview (mm/dd/20YY)	_________/____________/20_________
7	Time of interview	From ___.____till____.____
8	Signature of interviewer	

2. General plot information (oil palm farmer)

[A plot is defined as a piece of land under one crop, which is not segmented spatially and where the managerial practices are common and palms/trees are of approximately the same age.]

How many oil palm plots do you have? ________

QID		Plot 1	Plot 2	Plot 3	Plot 4	Plot 5
1	Area of plot (ha)					
2	Number of oil palms in the plot (#)					
3	Year of planting					
4	Year of first harvest ever (YYYY)					
5	Year of last replanting in the plot (YYYY)					
6	If replanted, year of first harvest after replanting (YYYY)					

Selection criteria for the "specific plot": biggest (ha) one of all the plots and the plot must be already productive

Plot number: ____

7. Who is currently managing the plot? _______________(1) household; (2) entrusted to company; (3) entrusted to farmer cooperative; (4) others, specify:____

8. Is the plot managed by sharecropping?__________(1) Yes; (2) No

If QID 8>1 or 8=1, change plot.

3. Specific plot information

3.1 Ownership

The following questions refer to the specific plot. Now we would like to ask you some questions about your biggest plot, the one you mentioned that has ___ ha.

QID	Question	Answer
1	Ownership of land? (1) leased-in; (2) owned	
2	If land leased in: Amount of rent paid in last 12 months ('000 Rp)	

3.2. Oil palms on the specific plot

QID	Question	Answer
3	Number of different oil palm varieties	
4	Name of Variety 1 (number of oil palms per variety1)	
5	Name of Variety 2 (number of oil palms per variety2)	
6	Number of oil palms which are not productive in the plot	
7	Number of oil palms which are affected by diseases or pests	
8	What kind of pest or disease do you experience on your oil palm plot? (1) rats (2) pigs (3) pest insects (4) others, specify __________________ (Multiple answers possible)	
9	Distance between oil palm (____meters*____meters)	
10	Number of oil palm rows	
11	Number of oil palm trees per row	
12	Have you ever used fire for clearing the land? (1) Yes; (2) No	
13	If QID12=1, Year of last clearing using fire (YYYY)	
14	In the last 12 months did you keep the cut-off plants and crop residues on the plot? (1) Yes; (2) No	

3.3. Distance from the plot to other structures

Distance from the plot to (only if not more than 500 m away from the plot; if it is within the plot, please write 0 m)

QID	Distance from the plot to……………..	Answer
12.1	Nearest road (meters)	
12.2	Nearest secondary forest (meters)	
12.3	Nearest production forest (meters)	

12.4	Nearest jungle rubber (meters)	
12.5	Nearest rubber plantation (meters)	
12.6	Nearest fallow land/cleared land/revitalization (oil palm) (meters)	
12.7	Nearest paddy field (meters)	
12.8	Nearest home/kitchen garden (meters)	
12.9	Nearest river or lake (meters)	

4. Input use on this specific plot in the last 12 months

The following questions refer to the specific plot

QID	Input	Number of times used in last 12 months (#)	Name of input	Unit of measure-ment	Quantity used in plot in 12 months(QU/plot /year)	Average price of input as used in last 12 months (`000Rp./QU)
1	Seedlings (replanting)					
2	Manure: plant waste (from plants outside the plot)			Kg		
3	Manure: Animal waste			Kg/liters		
4	Soil amendments (Lime, gypsum)					
5	Chemical fertilizer			Kg/liters		
6				Kg/liters		
7				Kg/liters		

QID	Input	Number of times used in last 12 months (#)	Name of input	Unit of measurement	Quantity used in plot in 12 months(QU/plot /year)	Average price of input as used in last 12 months (`000Rp./QU)
9	Herbicides			liter		
10				liter		
11				liter		
12				liter		
13	Pesticides			liter		
14				liter		
15				liter		
16				liter		
17	Maschinery					
18	Transport Inputs					
19	Transport Outputs					

5. Labor Input in last 12 months (specific plot)

The following questions refer to the specific plot

QID	Activity	Number of operations in last 12 months	Average Time taken to complete one operation (Unit)	Number of hired laborers per operation	Total costs for laborers per operation (`000 Rp./operation)	Number of family laborers involved per operation (from owner* and from hired laborers)
1	Replanting					
2	Seedlings transportation					

3	Manure application					
4	Fertilizer application					
5	Herbicide Applicaion					
6	Pesticide application					
7	Manual weeding on ground					
8	Manual weeding on palm/tree (fill only if done separately)					
9	Harvesting					
10	Transportation harvest					
11	Marketing					

6. Outputs oil palm from the specific plot

The following questions refer to the specific plot

6.1 Last three sales from this specific plot.

QID	Sale ID (1= most recent sale)	Date of sale	Total quantity sold (kg)	Average price obtained for ouput (‘000 Rp/kg)
1	1			
2	2			
3	3			

6.2 Harvest in the last 12 months

QID	Total harvest in last 12 months from this specific plot (ton)	Total quantity sold (kg)
1/2		

6.3. Change of harvest last 12 months

Please indicate how the harvest changed throughout the last 12 months. Please distinguish between dry and rainy season.

QID		Frequency of harvest (once in how many days) on this specific plot ?	Quantity of harvest per month (kg/month) from this specific plot	Were there any shocks? Code A	Average prive obtained for output in this season ('000Rp /kg)
1	Dry season (April-October)				
2	Rain season (November-March)				
Code A: (1) None; (2) drought; (3) fire; (3) flood; (4) theft; (5) pest; (6) other, specify					

7. Intercropping with fruit and timber trees (perennial crops)

Questions refer to the specific plot

1Do you have fruit or timber trees on your oil palm plot (surrounded by oil palm trees; and not at the edge of oil palm plantation)? (1) Yes, (2) No ________ (if n=2, continue with section 9)

If yes, please specify in the table below:

QID	Name of tree species	Number of trees	Number of already productive trees	Are the trees (1) planted (ever) or (2) left-overs?	Did you maintain these trees at least in the last 12 months? (1) Yes, (2) No			
					Weeding	Fertilizer	Herbicides	Pesticides
2								
3								
4								
5								
6								
7								
8								
9								
10								
Number of trees, which cannot be specified:_________								

7.1 Input use intercropped trees in last 12 months

If the respondent maintained the trees by weeding, fertilizer, herbicide or pesticide application, in the last 12 months please continue with the following table.

Please sum it up for all trees. It just refers to trees in the oil palm plot.

QID	Input	Number of times used in last 12 months (#)	Name of input	Unit of measurement	Quantity used in plot in 12 months(QU/plot/year)	Average price of input as used in last 12 months (`000Rp./QU)
1	Seedlings (replanting)					
2	Manure: plant waste (from plants outside			Kg		

	the plot)					
3	Manure: Animal waste			Kg/liters		
4	Soil amendments (Lime, gypsum)					
5	Chemical fertilizer			Kg/liters		
6				Kg/liters		
7				Kg/liters		
8				Kg/liters		

QID	Input	Number of times used in last 12 months (#)	Name of input	Unit of measurement	Quantity used in plot in 12 months(QU/plot/year)	Average price of input as used in last 12 months (`000Rp./QU)
9	Herbicides			liter		
10				liter		
11				liter		
12				liter		
13	Pesticides			liter		
14				liter		
15				liter		
16				liter		
17	Maschinery					

18	Transport Inputs					
19	Transport Outputs					

7.2. Labor Input intercropped trees last 12 months

If the respondent maintained the trees by weeding, fertilizer, herbicide or pesticide application, in the last 12 months please continue with the following table.

Please sum it up for all trees. It just refers to trees in the oil palm plot.

QID	Activity	Number of operations in last 12 months	Average Time taken to complete one operation (Unit)	Number of hired laborers per operation	Total costs for laborers per operation (`000 Rp./operation)	Number of family laborers involved per operation (from owner* and from hired laborers)
1	Replanting					
2	Seedlings transportation					
3	Manure application					
4	Fertilizer application					
5	Herbicide Applicaion					
6	Pesticide application					
7	Manual weeding on ground					
8	Manual weeding on palm/tree (fill only if done separately)					
9	Harvesting					
10	Transportation harvest					
11	Marketing					

8. Tree by-products

Please do not include rubber here, separate table for rubber.

QID	Name of tree species	By-product type (Code A)	Unit of measurement (QU, name)	Production in the last 12 months (QU)	Quantity (QU) marketed in last 12 months	Average Price obtained in last 12 months ('000 Rp/QU)
1						
2						
3						
4						
5						
6						
7						
Code A: (1) fruit; (2) timber; (3) roots; (4) leaves (5) others: specify.____________________						

8.1 Labor input (for harvesting/marketing)

Please sum it up for all trees. It just refers to trees in the oil palm plot. Include rubber here.

QID		Number of operations in last 12 months	Time taken to complete one operation	Number of hired laborers per operation	Total costs for laborers per operation in last 12 months (`000 Rp./operation)	Number of family laborers involved per operation (from owner* and from hired laborers)
1	Harvesting					
2	Transport output					
3	Marketing					

8.2 Harvest rubber intercropped in oil palm

If the oil palm plot is intercropped with rubber, please continue with this table. Otherwise switch to section 8.

QID	Sale ID (1= most recent sale)	Date of sale	Total quantity sold (kg)	Average price obtained for output (‘000 Rp/kg)
1	1			
2	2			
3	3			

8.3. Harvest rubber intercropped in oil palm in the last 12 months

QID	Total harvest in last 12 months from this specific plot (ton)	Total quantity sold (kg)
1/2		

8.4 Change of harvest rubber intercropped in oil palm

Please indicate how the harvest changed throughout the last 12 months. Please distinguish between dry and rainy season.

QID		Frequency of harvest (once in how many days)?	Quantity of harvest per month (kg/month)	Were there any shocks? Code A	Average price obtained for output in this season ('000Rp /kg)
1	Dry season (April-October)				
2	Rain season (November-March)				
Code A: (1) None; (2) drought; (3) fire; (3) flood; (4) theft; (5) pest; (6) other, specify:_________________					

9. Arrangement of fruit and timber trees

Please show the pictures.

Could you please describe to us the arrangement of fruit and timber trees on the specific oil palm plot? Number:___________________

QID	What were the three main reasons for choosing this arrangement of trees within oil palm plantation? Code A	
1		
2		
3		
Code A : (1) increase of biodiversity; (2) pest control; (3) other: specify:_______________________		

10. Cut-off of fruit and timber trees on the specific plot

QID		
1	Have you ever cut any productive tree in the oil palm plantation (surrounded by oil palm) in the last 5 years (1) Yes; (2) No	
2	If QID1=1, number of cut productive trees	
3	If QID1=1, please name the main reason:____	

QID	What are the three main reasons for you for planting the above trees or not removing remnant trees in the oil palm plot? Code A	
4		
5		
6		
Code A: (1) to maintain soil fertility; (2) to reduce likelihood for soil erosion; (3) to increase rainfall absorption; (4) to preserve groundwater;; (6) to fulfill food/housing needs; (7) for other economic activities; (8) pest management; (9) weed management; (10) to make border with border to neighboring plots ; (11) others, specify:____		

QID	From your perspective, what are the three main problems associated with planting trees within the oil palm plantation? (general question) Code A	
7		
8		
9		
Code A: (1) no problems (2) competition for water (3) competition for nutrients (4) others, specify:____		

11. Perception about functions of fruit and timber trees within oil palm plantations

Now, we would like to know your perception on fruit or timber trees in oil palm plantations. We will read some statements. Please mention whether you (1) strongly disagree; (2) disagree; (3) agree; (4) strongly agree.

QID	Fruit and Timber trees within oil palm plantations……..	Strongly Disagree	Disagree	Agree	Strongly Agree	Don't know
1	Increase soil fertility					
2	Decrease soil erosion					
3	Decrease water availability					
4	Increase bird diversity					
5	Increase number of individuals per bird species					
6	Increase insect diversity					
7	Increase number of individuals per insect species					
8	Decrease likelihood of pest and disease in oil palm plantations					
9	Increase the oil palm yield					
10	Decrease oil palm yield					
11	Compete with oil palm trees for nutrients					

12. Cultivation of fruit and timber trees outside oil palm plot

Now we would like to know, if you cultivate any of the below mentioned fruit and timber trees outside oil palm plantations. If the respondent does not cultivate the following systems, please indicate is by N.A.

Please tick (√) the related blank box which shows the name of the trees and the type of the field where it's cultivated!

QID	Type of fields	The name of the trees				
		Jengkol	Durian	Petai	Jelutung	Sungkai
1	Home garden					
2	Rubber Plantation					
3	Individual owned production forest					
4	Other, specify:__________________					

13. Bird diversity, abundance and distribution in oil palm plantation

The following questions refer to the specific plot.

1.Have you ever observed any birds on your oil palm plot? __________(1) Yes, (2) No

If QID1=1, 2. how many different bird species have you observed on the plot? ___________

3.If you know the names of the birds observed on the plots, please write them down below:

QID	Name of birds
1	
2	
3	
4	

4. Have you observed birds feeding on the oil palm fruits? ___________(1) Yes, (2) No

If QID4=1, 5. and if you know the names of the birds feeding on oil palms, please write down below:

QID	Name of birds
1	
2	
3	
4	

6. According to your observation, is the number of bird species and/or the number of individuals per bird species in non-oil palm structures (fruit and timber tress, river, lake) larger, the same or smaller than in oil palm plantations? ______________________________________(1)larger, (2) smaller, (3)the same

7. Do you think that birds have a positive, negative, or no effect on the yield of oil palm?_______________________ (1) Positive effect, (2) Negative effect (3) No effect

8. Please specify why you think that birds have a ___________(see answer QID7) effect:
____
____

9. Do you currently own rubber or jungle rubber plantations?__________(1)Yes, (2) No

If QID9=1, 10. Have you observed more, less or the same number of birds on the rubber/jungle rubber plot compared to the oil palm plot?_________________(1) More, (2) the same (3) less

13. Birds caught at the specific oil palm plot

1. Have you caught any birds in the last 12 months?_____________(1) Yes, (2) No

If QID1=1 please fill out the table.

QID	Total number of birds caught in the last 12 months	Number of birds caught per location		
		On specific plot	Within 1 km around plot	Other location
2				

3.Do you know the species name of at least one caught bird? _______(1) Yes, (2) No

If QID3=1, 4 please fill out table

QID	Bird species	Number of caught birds per bird species (if known) in last 12 months	Number of sold birds per bird species	Average price per bird species (‘000 Rp)
1				
2				
3				
4				

4. We will read out three categories of bird sizes. Please, name the number of birds caught per category of bird size (not wingspan).

QID	Bird size	Number of caught birds per bird size category (if known) in last 12 months	Number of sold birds per bird size category	Average price per bird per bird size category (‘000 Rp)
1	< 15 cm			
2	15cm-25cm			
3	>25cm			

5. Which characteristics/features of birds increase the selling price? Order features according to importance.

QID	Characteristics
1	
2	
3	

6. Which method do you use to catch the birds?

QID	Method
1	
2	
3	

7. Number of birds that you keep as pet in your household?________

Thanks for your participation!

Supplementary Information – Chapter 3

Supplementary figures

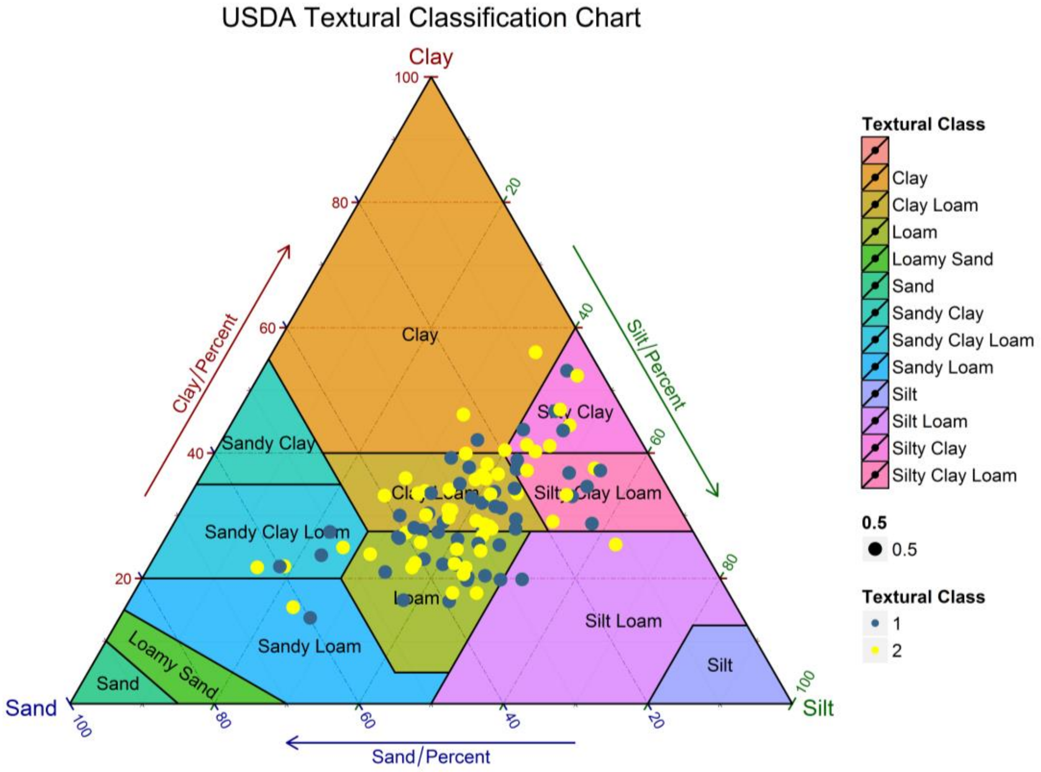

Figure S 3.1: Soil texture of all plots in two depths (1=0-10 cm (yellow points), 2=10-30 cm (grey points)) according to the USDA textural classification chart. We found a high variability among the plots and higher clay content in 10-30 cm than in 0-10 cm.

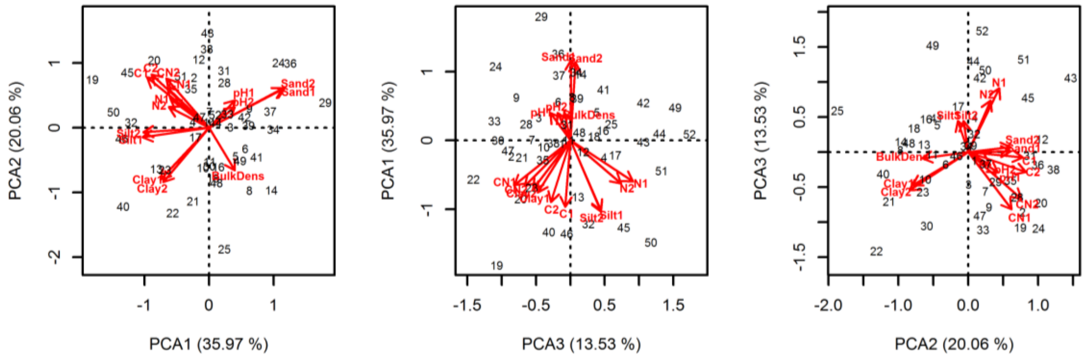

Figure S 3.2: Principal component analysis of the soil data.

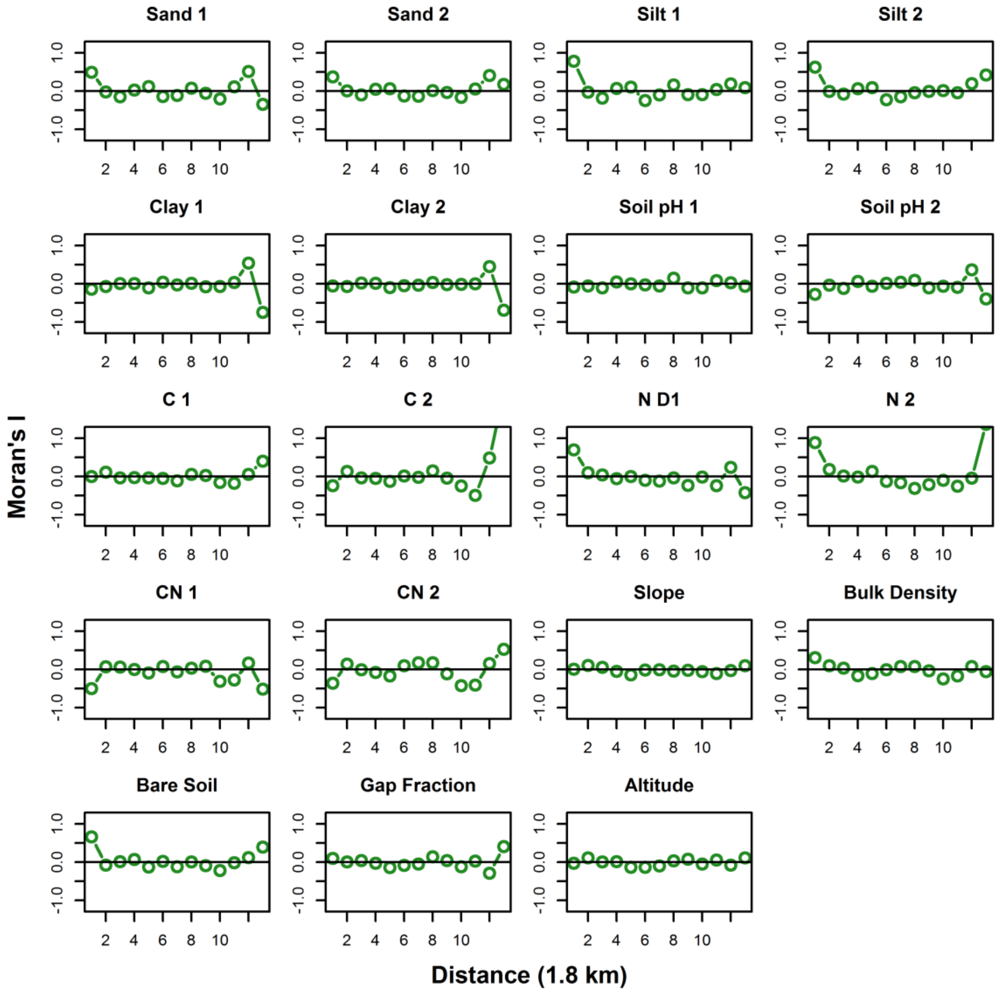

Figure S 3.3: Spatial correlogram to check for spatial autocorrelation of the environmental variables. Moran's I is given as a function of distance. Values significant at a nominal (two-sided) 5%-level are represented by filled circles and non-significant values by open circles.

Supplementary tables

Table S 3.1: Partitions of the experimental design (columns). Per partition, each species (A-F) is present in each diversity level (block) without replacement. Thus, there are different numbers of plots per diversity level (number in first row; species composition for each plot in the second row).

Plot size [m] **Diversity level**	**5x5**	**10x10**	**20x20**	**40x40**	**sum**
1	6	6	6	6	**24**
	A B C D E F	A B C D E F	A B C D E F	A B C D E F	
2	3	3	3	3	**12**
	AC BF DE	CF AE BD	AF BE CD	AB CE DF	
3	2	2	2	2	**8**
	AEF BCD	ABD CEF	ACD BEF	ACF BDE	
6	1	1	1	1	**4**
	ABCDEF	ABCDEF	ABCDEF	ABCDEF	
0	1	1	1	1	**4**
	no trees	no trees	no trees	no trees	
ctrl		4			**4**
sum	**13**	**13 +4**	**13**	**13**	**56**

Table S 3.2: Plot infos

Plot ID	Latitude	Longitude	Plot size	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
53			100	Control	-	-
54			100	Control	-	-
55			100	Control	-	-
56			100	Control	-	-

Table S 3.3: 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 mass (DM) and fresh mass (FM) ('Mass type') for different taxa. Appendix Tab. 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	Regression specificity
All insect taxa		DM	M = a * (L)^b	0.035	2.173	0.9	17.6	(Gruner 2003)	Inferred, all insect taxa
All insect taxa		DM	M = exp(a + b * log(L))	-3.628	2.494	2.13	54.51	(Sample *et al.* 1993)	Inferred, all insect taxa
Araneae	Araneae < 2.5 mm	FM	M = exp(a + b * log(L))	-1.958	2.746	0.56	2.5	(Höfer & Ott 2009)	Group specific
Araneae	Hunting	FM	M = exp(a + b * log(L))	-2.108	3.017	0.67	36	(Höfer & Ott 2009)	Group specific
Araneae	Web-building	FM	M = exp(a + b * log(L))	-1.784	2.255	0.56	10.67	(Höfer & Ott 2009)	Group specific
Araneae	Spiders random	FM	M = exp(a + b * log(L))	-1.844	2.711	1.8	21.5	(Edwards 1996)	Group specific
Araneae	Anapidae	FM	M = exp(a + b * log(L))	-1.784	2.255	0.56	10.67	(Höfer & Ott 2009)	Inferred, web-building
Araneae	Araneidae	FM	M = exp(a + b * log(L))	-1.923	2.923	2.10	21.20	(Edwards 1996)	Group specific
Araneae	Clubionidae	FM	M = exp(a + b * log(L))	-2.156	2.653	2.5	9	(Edwards 1996)	Group specific
Araneae	Corinnidae	FM	M = exp(a + b * log(L))	-2.108	3.017	0.67	36	(Höfer & Ott 2009)	Inferred, hunting spiders
Araneae	Ctenidae	FM	M = exp(a + b * log(L))	-1.758	2.894	1.3	36	(Höfer & Ott 2009)	Group specific
Araneae	Deinopidae	FM	M = exp(a + b * log(L))	-1.844	2.711	1.8	21.5	Edwards 1996	Inferred, spiders random sample
Araneae	Dysderidae	FM	M = exp(a + b * log(L))	-2.108	3.017	0.67	36	(Höfer & Ott 2009)	Inferred, hunting spiders
Araneae	Gnaphosidae	FM	M = exp(a + b * log(L))	-2.83	3.055	3	13.1	(Edwards 1996)	Group specific
Araneae	Linyphiidae	FM	M = exp(a + b * log(L))	-1.892	2.754	1.5	5.5	(Edwards 1996)	Group specific
Araneae	Lycosidae	FM	M = exp(a + b * log(L))	-2.043	2.842	2	23.5	(Edwards 1996)	Group specific
Araneae	Miturgidae	FM	M = exp(a + b * log(L))	-2.83	3.055	3	13.1	(Edwards 1996)	Inferred, gnaphosidae
Araneae	Mysmenidae	FM	M = exp(a + b * log(L))	-1.784	2.255	0.56	10.67	(Höfer & Ott 2009)	Inferred, web-building
Araneae	Ochyroceratidae	FM	M = exp(a + b * log(L))	-1.784	2.255	0.56	10.67	(Höfer & Ott 2009)	Inferred, web-building
Araneae	Oonopidae	FM	M = exp(a + b * log(L))	-2.039	2.666	0.67	2.5	(Höfer & Ott 2009)	Group specific
Araneae	Oxyopidae	FM	M = exp(a + b * log(L))	-2.108	3.017	0.67	36	(Höfer & Ott 2009)	Inferred, hunting spiders
Araneae	Philodromidae	FM	M = exp(a + b * log(L))	-1.985	2.940	2.50	8.60	(Edwards 1996)	Group specific
Araneae	Pholcidae	FM	M = exp(a + b * log(L))	-1.784	2.255	0.56	10.67	(Höfer & Ott 2009)	Inferred, web-building
Araneau	Pisauridae	FM	M = exp(a + b * log(L))	-2.108	3.017	0.67	36	(Höfer & Ott 2009)	Inferred, hunting spiders
Araneae	Salticidae	FM	M = exp(a + b * log(L))	-2.184	2.901	4.00	13.00	(Edwards 1996)	Group specific

Araneae	Sparassidae	FM	M = exp(a + b * log(L))	-2.108	3.017	0.67	36	(Höfer & Ott 2009)	Inferred, hunting spiders
Araneae	Tetrablemmidae	FM	M = exp(a + b * log(L))	-2.039	2.666	0.67	2.5	(Höfer & Ott 2009)	Inferred, oonopidae
Araneae	Tetragnathidae	FM	M = exp(a + b * log(L))	-2.615	2.574	3.50	9.00	(Edwards 1996)	Group specific
Araneae	Theridiidae	FM	M = exp(a + b * log(L))	-1.577	2.907	1.50	7.50	(Edwards 1996)	Group specific
Araneae	Theridiosomatidae	FM	M = exp(a + b * log(L))	-1.784	2.255	0.56	10.67	(Höfer & Ott 2009)	Inferred, web-building
Araneae	Thomisidae	FM	M = exp(a + b * log(L))	-1.644	2.973	1.80	8.00	(Edwards 1996)	Group specific
Araneae	Zodariidae	FM	M = exp(a + b * log(L))	-2.108	3.017	0.67	36	(Höfer & Ott 2009)	Inferred, hunting spiders
Blattodea	Blaberidae	DM	M = exp(a + b * log(L))	-3.980	2.760	2.20	14.00	(Wardhaugh 2013)	Inferred, blattodea
Blattodea	Blattellidae	DM	M = exp(a + b * log(L))	-3.980	2.760	2.20	14.00	(Wardhaugh 2013)	Inferred, blattodea
Blattodea	Blattidae	DM	M = exp(a + b * log(L))	-3.980	2.760	2.20	14.00	(Wardhaugh 2013)	Inferred, blattodea
Coleoptera	Aderidae	DM	M = exp(a + b * log(L))	-3.247	2.492	3.34	34.82	(Sample *et al.* 1993)	Inferred, coleoptera
Coleoptera	Anthicidae	DM	M = exp(a + b * log(L))	-3.247	2.492	3.34	34.82	(Sample *et al.* 1993)	Inferred, coleoptera
Coleoptera	Anthribidae	DM	M = exp(a + b * log(L))	-3.247	2.492	3.34	34.82	(Sample *et al.* 1993)	Inferred, coleoptera
Coleoptera	Carabidae	DM	M = a * L^b	0.0237	2.7054	2.88	24	(Lang, Krooss & Stumpf	Group specific
Coleoptera	Chrysomelidae	DM	M = exp(a + b * log(L))	-2.427	2.171	3.34	7.84	(Sample *et al.* 1993)	Group specific
Coleoptera	Corylophidae	DM	M = exp(a + b * log(L))	-3.247	2.492	3.34	34.82	(Sample *et al.* 1993)	Inferred, coleoptera
Coleoptera	Colydiidae	DM	M = exp(a + b * log(L))	-3.247	2.492	3.34	34.82	(Sample *et al.* 1993)	Inferred, coleoptera
Coleoptera	Discolomidae	DM	M = exp(a + b * log(L))	-3.247	2.492	3.34	34.82	(Sample *et al.* 1993)	Inferred, coleoptera
Coleoptera	Hydraenidae	DM	M = exp(a + b * log(L))	-3.247	2.492	3.34	34.82	(Sample *et al.* 1993)	Inferred, coleoptera
Coleoptera	Lagrioidinae	DM	M = exp(a + b * log(L))	-3.247	2.492	3.34	34.82	(Sample *et al.* 1993)	Inferred, coleoptera
Coleoptera	Pselaphidae	DM	M = exp(a + b * log(L))	-3.247	2.492	3.34	34.82	(Sample *et al.* 1993)	Inferred, coleoptera
Coleoptera	Scolytidae	DM	M = exp(a + b * log(L))	-3.247	2.492	3.34	34.82	(Sample *et al.* 1993)	Inferred, coleoptera
Coleoptera	Curculionidae	DM	M = exp(a + b * log(L))	-3.247	2.492	3.34	34.82	(Sample *et al.* 1993)	Inferred, coleoptera
Coleoptera	Elateridae	DM	M = a * L^b	0.0138	2.595	1.65	10.3	(Gruner 2003)	Inferred, slender beetles
Coleoptera	Nitidulidae	DM	M = exp(a + b * log(L))	-3.247	2.492	3.34	34.82	(Sample *et al.* 1993)	Inferred, coleoptera
Coleoptera	Phalacridae	DM	M = exp(a + b * log(L))	-3.247	2.492	3.34	34.82	(Sample *et al.* 1993)	Inferred, coleoptera
Coleoptera	Ptiliidae	DM	M = exp(a + b * log(L))	-3.247	2.492	3.34	34.82	(Sample *et al.* 1993)	Inferred, coleoptera
Coleoptera	Scarabaeidae	DM	M = exp(a + b * log(L))	-2.448	2.494	4.24	24.79	(Sample *et al.* 1993)	Group specific
Coleoptera	Scydmaenidae	DM	M = exp(a + b * log(L))	-3.247	2.492	3.34	34.82	(Sample *et al.* 1993)	Inferred, coleoptera
Coleoptera	Silvanidae	DM	M = a * L^b	0.0138	2.595	1.65	10.3	(Gruner 2003)	Inferred, slender beetles
Coleoptera	Staphylinidae	DM	M = a * L^b	0.0134	2.26	2.2	13.6	(Lang, Krooss & Stumpf 1997)	Group specific
Coleoptera	Tenebrionidae	DM	M = exp(a + b * log(L))	-0.043	1.2	5.65	13.39	(Sample *et al.* 1993)	Group specific
Dermaptera	Anisolabididae	DM	M = exp(a + b * log(L))	-3.628	2.494	2.13	54.51	(Sample *et al.* 1993)	Inferred, all insect taxa
Dermaptera	Labiduridae	DM	M = exp(a + b * log(L))	-3.628	2.494	2.13	54.51	(Sample *et al.* 1993)	Inferred, all insect taxa
Dermaptera	Labiidae	DM	M = exp(a + b * log(L))	-3.628	2.494	2.13	54.51	(Sample *et al.* 1993)	Inferred, all insect taxa

Dermaptera	Spongiphoridae	DM	M = exp(a + b * log(L))	-3.628	2.494	2.13	54.51	(Sample *et al.* 1993)	Inferred, all insect taxa
Dermaptera	Uniden	DM	M = exp(a + b * log(L))	-3.628	2.494	2.13	54.51	(Sample *et al.* 1993)	Inferred, all insect taxa
Diplura	Campodeidae	DM	M = a * (L)^b	0.034	2.191	0.9	17.6	(Gruner 2003)	Inferred, general arthropod
Diplura	Japygidae	DM	M = a * (L)^b	0.034	2.191	0.9	17.6	(Gruner 2003)	Inferred, general arthropod
Diplura	Stratiopmydae	DM	M = a * (L)^b	0.034	2.191	0.9	17.6	(Gruner 2003)	Inferred, general arthropod
Diplura	Uniden	DM	M = a * (L)^b	0.034	2.191	0.9	17.6	(Gruner 2003)	Inferred, general arthropod
Diptera	Adults	DM	M = a * (L)^b	0.0153	2.573	1.75	8.6	(Gruner 2003)	Original, diptera adult
Diptera	Asteiidae	DM	M = a * (L)^b	0.0153	2.573	1.75	8.6	(Gruner 2003)	Original, diptera adult
Diptera	Bibionidae	DM	M = a * (L)^b	0.035	2.173	0.9	17.6	(Gruner 2003)	Inferred, all insect taxa
Diptera	Calliphoridae	DM	M = a * (L)^b	0.0153	2.573	1.75	8.6	(Gruner 2003)	Original, diptera adult
Diptera	Cecidomyiidae	DM	M = a * (L)^b	0.035	2.173	0.9	17.6	(Gruner 2003)	Inferred, all insect taxa
Diptera	Ceratopogonidae	DM	M = a * (L)^b	0.0153	2.573	1.75	8.6	(Gruner 2003)	Original, diptera adult
Diptera	Chironomidae	DM	M = a * (L)^b	0.0153	2.573	1.75	8.6	(Gruner 2003)	Original, diptera adult
Diptera	Chloropidae	DM	M = a * (L)^b	0.0153	2.573	1.75	8.6	(Gruner 2003)	Original, diptera adult
Diptera	Clusiidae	DM	M = a * (L)^b	0.0153	2.573	1.75	8.6	(Gruner 2003)	Original, diptera adult
Diptera	Culicidae	DM	M = a * (L)^b	0.0153	2.573	1.75	8.6	(Gruner 2003)	Original, diptera adult
Diptera	Deuterophlebiidae	DM	M = a * (L)^b	0.0153	2.573	1.75	8.6	(Gruner 2003)	Original, diptera adult
Diptera	Dolichopodidae	DM	M = a * (L)^b	0.0153	2.573	1.75	8.6	(Gruner 2003)	Original, diptera adult
Diptera	Drosophilidae	DM	M = a * (L)^b	0.0153	2.573	1.75	8.6	(Gruner 2003)	Original, diptera adult
Diptera	Lauxaniidae	DM	M = a * (L)^b	0.0153	2.573	1.75	8.6	(Gruner 2003)	Original, diptera adult
Diptera	Muscidae	DM	M = a * (L)^b	0.0153	2.573	1.75	8.6	(Gruner 2003)	Original, diptera adult
Diptera	Mycetophylidae	DM	M = a * (L)^b	0.0153	2.573	1.75	8.6	(Gruner 2003)	Original, diptera adult
Diptera	Opomyzidae	DM	M = a * (L)^b	0.0153	2.573	1.75	8.6	(Gruner 2003)	Original, diptera adult
Diptera	Phoridae	DM	M = a * (L)^b	0.0153	2.573	1.75	8.6	(Gruner 2003)	Original, diptera adult
Diptera	Piophilidae	DM	M = a * (L)^b	0.0153	2.573	1.75	8.6	(Gruner 2003)	Original, diptera adult
Diptera	Psychodidae	DM	M = a * (L)^b	0.0153	2.573	1.75	8.6	(Gruner 2003)	Original, diptera adult
Diptera	Sciaridae	DM	M = a * (L)^b	0.0153	2.573	1.75	8.6	(Gruner 2003)	Original, diptera adult
Diptera	Simuliidae	DM	M = a * (L)^b	0.0153	2.573	1.75	8.6	(Gruner 2003)	Original, diptera adult
Diptera	Sphaeroceridae	DM	M = a * (L)^b	0.0153	2.573	1.75	8.6	(Gruner 2003)	Original, diptera adult
Diptera	Pipunculidae	DM	M = a * (L)^b	0.0153	2.573	1.75	8.6	(Gruner 2003)	Original, diptera adult
Diptera	Scatopsidae	DM	M = a * (L)^b	0.0153	2.573	1.75	8.6	(Gruner 2003)	Original, diptera adult
Diptera	Tipulidae	DM	M = a * (L)^b	0.0153	2.573	1.75	8.6	(Gruner 2003)	Original, diptera adult
Diptera	Uniden	DM	M = a * (L)^b	0.0153	2.573	1.75	8.6	(Gruner 2003)	Original, diptera adult
Ephemeroptera	Baetidae	DM	M = a * (L)^b	0.035	2.173	0.9	17.6	(Gruner 2003)	Inferred, all insect taxa
Chilopoda	All	DM	M = exp(a + b * log(L))	-4.049	2.18	4	47	(Gowing & Recher 1984)	Inferred, chilopoda

Geophilomorpha	Dignathodontidae	DM	M = exp(a + b * log(L))	-4.049	2.18	4	47	(Gowing & Recher 1984)	Inferred, chilopoda
Geophilomorpha	Geophilidae	DM	M = exp(a + b * log(L))	-4.049	2.18	4	47	(Gowing & Recher 1984)	Inferred, chilopoda
Geophilomorpha	Mecistocephalidae	DM	M = exp(a + b * log(L))	-4.049	2.18	4	47	(Gowing & Recher 1984)	Inferred, chilopoda
Diplopoda	All	DM	M = exp(a + b * log(L))	-4.591	2.543	11.0	47.0	(Gowing & Recher 1984)	Inferred, diplopoda
Glomerida	Glomeridae	DM	M = exp(a + b * log(L))	-4.591	2.543	11.0	47.0	(Gowing & Recher 1984)	Inferred, diplopoda
Hemiptera	Aleyrodidae	DM	M = exp(a + b * log(L))	-2.823	2.225	2.13	13.25	(Sample *et al.* 1993)	Inferred, homoptera
Hemiptera	Alydidae	DM	M = exp(a + b * log(L))	-4.784	3.075	3.2	40.23	(Sample *et al.* 1993)	Original, hemiptera
Hemiptera	Anthocoridae	DM	M = exp(a + b * log(L))	-4.784	3.075	3.2	40.23	(Sample *et al.* 1993)	Original, hemiptera
Hemiptera	Aphididae	DM	M = exp(a + b * log(L))	-2.823	2.225	2.13	13.25	(Sample *et al.* 1993)	Inferred, homoptera
Hemiptera	Aradidae	DM	M = exp(a + b * log(L))	-4.784	3.075	3.2	40.23	(Sample *et al.* 1993)	Original, hemiptera
Hemiptera	Ceratocombidae	DM	M = exp(a + b * log(L))	-4.784	3.075	3.2	40.23	(Sample *et al.* 1993)	Original, hemiptera
Hemiptera	Cicadellidae	DM	M = exp(a + b * log(L))	-3.735	2.561	2.13	13.25	(Sample *et al.* 1993)	Group specific
Hemiptera	Cixiidae	DM	M = exp(a + b * log(L))	-4.784	3.075	3.2	40.23	(Sample *et al.* 1993)	Inferred, hemiptera
Hemiptera	Coreidae	DM	M = exp(a + b * log(L))	-4.784	3.075	3.2	40.23	(Sample *et al.* 1993)	Inferred, hemiptera
Hemiptera	Cydnidae	DM	M = exp(a + b * log(L))	-4.784	3.075	3.2	40.23	(Sample *et al.* 1993)	Inferred, hemiptera
Hemiptera	Delphacidae	DM	M = exp(a + b * log(L))	-2.823	2.225	2.13	13.25	(Sample *et al.* 1993)	Inferred, homoptera
Hemiptera	Derbidae	DM	M = exp(a + b * log(L))	-2.823	2.225	2.13	13.25	(Sample *et al.* 1993)	Inferred, homoptera
Hemiptera	Dictyopharidae	DM	M = exp(a + b * log(L))	-2.823	2.225	2.13	13.25	(Sample *et al.* 1993)	Inferred, homoptera
Hemiptera	Dipsocoridae	DM	M = exp(a + b * log(L))	-4.784	3.075	3.2	40.23	(Sample *et al.* 1993)	Inferred, hemiptera
Hemiptera	Eriosomatidae	DM	M = exp(a + b * log(L))	-2.823	2.225	2.13	13.25	(Sample *et al.* 1993)	Inferred, homoptera
Hemiptera	Flatidae	DM	M = exp(a + b * log(L))	-2.823	2.225	2.13	13.25	(Sample *et al.* 1993)	Inferred, homoptera
Hemiptera	Geocoridae	DM	M = exp(a + b * log(L))	-4.784	3.075	3.2	40.23	(Sample *et al.* 1993)	Inferred, hemiptera
Hemiptera	Hydrometridae	DM	M = exp(a + b * log(L))	-4.784	3.075	3.2	40.23	(Sample *et al.* 1993)	Inferred, hemiptera
Hemiptera	Largidae	DM	M = exp(a + b * log(L))	-4.784	3.075	3.2	40.23	(Sample *et al.* 1993)	Inferred, hemiptera
Hemiptera	Lophopidae	DM	M = exp(a + b * log(L))	-2.823	2.225	2.13	13.25	(Sample *et al.* 1993)	Inferred, homoptera
Hemiptera	Lygaeidae	DM	M = exp(a + b * log(L))	-4.784	3.075	3.2	40.23	(Sample *et al.* 1993)	Inferred, hemiptera
Hemiptera	Meenoplidae	DM	M = exp(a + b * log(L))	-2.823	2.225	2.13	13.25	(Sample *et al.* 1993)	Inferred, homoptera
Hemiptera	Miridae	DM	M = exp(a + b * log(L))	-4.784	3.075	3.2	40.23	(Sample *et al.* 1993)	Inferred, hemiptera
Hemiptera	Nabidae	DM	M = exp(a + b * log(L))	-4.784	3.075	3.2	40.23	(Sample *et al.* 1993)	Inferred, hemiptera
Hemiptera	Pentatomidae	DM	M = exp(a + b * log(L))	-4.197	3.053	6.35	16.73	(Sample *et al.* 1993)	Group specific
Hemiptera	Pseudococcidae	DM	M = exp(a + b * log(L))	-2.823	2.225	2.13	13.25	(Sample *et al.* 1993)	Inferred, homoptera
Hemiptera	Reduviidae	DM	M = exp(a + b * log(L))	-4.784	3.075	3.2	40.23	(Sample *et al.* 1993)	Inferred, hemiptera
Hemiptera	Ricaniidae	DM	M = exp(a + b * log(L))	-2.823	2.225	2.13	13.25	(Sample *et al.* 1993)	Inferred, homoptera
Hemiptera	Schizopteridae	DM	M = exp(a + b * log(L))	-4.784	3.075	3.2	40.23	(Sample *et al.* 1993)	Inferred, hemiptera
Hemiptera	Tingidae	DM	M = exp(a + b * log(L))	-4.784	3.075	3.2	40.23	(Sample *et al.* 1993)	Inferred, hemiptera

Hemiptera	Tropiduchidae	DM	M = exp(a + b * log(L))	-2.823	2.225	2.13	13.25	(Sample *et al.* 1993)	Inferred, homoptera
Hemiptera	Uniden	DM	M = exp(a + b * log(L))	-4.784	3.075	3.2	40.23	(Sample *et al.* 1993)	Inferred, hemiptera
Hymenoptera	Aphelinidae	DM	M = exp(a + b * log(L))	-3.336	2.104	1	12	(Gowing & Recher 1984)	Inferred, hym. Excl formicidae
Hymenoptera	Bethylidae	DM	M = exp(a + b * log(L))	-3.336	2.104	1	12	(Gowing & Recher 1984)	Inferred, hym. Excl formicidae
Hymenoptera	Braconidae	DM	M = exp(a + b * log(L))	-3.336	2.104	1	12	(Gowing & Recher 1984)	Inferred, hym. Excl formicidae
Hymenoptera	Ceraphronidae	DM	M = exp(a + b * log(L))	-3.336	2.104	1	12	(Gowing & Recher 1984)	Inferred, hym. Excl formicidae
Hymenoptera	Chalcididae	DM	M = exp(a + b * log(L))	-3.336	2.104	1	12	(Gowing & Recher 1984)	Inferred, hym. Excl formicidae
Hymenoptera	Cynipidae	DM	M = exp(a + b * log(L))	-3.336	2.104	1	12	(Gowing & Recher 1984)	Inferred, hym. Excl formicidae
Hymenoptera	Diapriidae	DM	M = exp(a + b * log(L))	-3.336	2.104	1	12	(Gowing & Recher 1984)	Inferred, hym. Excl formicidae
Hymenoptera	Dryinidae	DM	M = exp(a + b * log(L))	-3.336	2.104	1	12	(Gowing & Recher 1984)	Inferred, hym. Excl formicidae
Hymenoptera	Dryniidae	DM	M = exp(a + b * log(L))	-3.336	2.104	1	12	(Gowing & Recher 1984)	Inferred, hym. Excl formicidae
Hymenoptera	Encyrtidae	DM	M = exp(a + b * log(L))	-3.336	2.104	1	12	(Gowing & Recher 1984)	Inferred, hym. Excl formicidae
Hymenoptera	Eucoilidae	DM	M = exp(a + b * log(L))	-3.336	2.104	1	12	(Gowing & Recher 1984)	Inferred, hym. Excl formicidae
Hymenoptera	Eulophidae	DM	M = exp(a + b * log(L))	-3.336	2.104	1	12	(Gowing & Recher 1984)	Inferred, hym. Excl formicidae
Hymenoptera	Figitidae	DM	M = exp(a + b * log(L))	-3.336	2.104	1	12	(Gowing & Recher 1984)	Inferred, hym. Excl formicidae
Hymenoptera	Formicidae	DM	M = exp(a + b * log(L))	-3.996	2.489	2	18	(Gowing & Recher 1984)	Group specific
Hymenoptera	Ichneumonidae	DM	M = exp(a + b * log(L))	-3.336	2.104	1	12	(Gowing & Recher 1984)	Inferred, hym. Excl formicidae
Hymenoptera	Mymaridae	DM	M = exp(a + b * log(L))	-3.336	2.104	1	12	(Gowing & Recher 1984)	Inferred, hym. Excl formicidae
Hymenoptera	Mymarommatidae	DM	M = exp(a + b * log(L))	-3.336	2.104	1	12	(Gowing & Recher 1984)	Inferred, hym. Excl formicidae
Hymenoptera	Platygastridae	DM	M = exp(a + b * log(L))	-3.336	2.104	1	12	(Gowing & Recher 1984)	Inferred, hym. Excl formicidae
Hymenoptera	Scelionidae	DM	M = exp(a + b * log(L))	-3.336	2.104	1	12	(Gowing & Recher 1984)	Inferred, hym. Excl formicidae
Hymenoptera	Sphecidae	DM	M = exp(a + b * log(L))	-3.336	2.104	1	12	(Gowing & Recher 1984)	Inferred, hym. Excl formicidae
Hymenoptera	Tiphiidae	DM	M = exp(a + b * log(L))	-3.336	2.104	1	12	(Gowing & Recher 1984)	Inferred, hym. Excl formicidae
Hymenoptera	Trichogrammatidae	DM	M = exp(a + b * log(L))	-3.336	2.104	1	12	(Gowing & Recher 1984)	Inferred, hym. Excl formicidae
Hymenoptera	Vespidae	DM	M = exp(a + b * log(L))	-3.336	2.104	1	12	(Gowing & Recher 1984)	Inferred, hym. Excl formicidae
Isopoda	All	DM	M = exp(a + b * log(L))	-4.81	3.44	2.7	8	(Wardhaugh 2013)	Original, isopoda
Isopoda	Oniscidae	DM	M = exp(a + b * log(L))	-4.81	3.44	2.7	8	(Wardhaugh 2013)	Original, isopoda
Isopoda	Philosciidae	DM	M = exp(a + b * log(L))	-4.81	3.44	2.7	8	(Wardhaugh 2013)	Original, isopoda
Isopoda	Armadillidae	DM	M = exp(a + b * log(L))	-4.81	3.44	2.7	8	(Wardhaugh 2013)	Original, isopoda
Isopoda	Termitidae	DM	M = exp(a + b * log(L))	-4.81	3.44	2.7	8	(Wardhaugh 2013)	Original, isopoda
Isoptera	Rhinotermitidae	DM	M = e^a * L^b	-5.802	3.177	3.30	5.60	(Johnson & Strong 2000)	Inferred, isoptera
Isoptera	Termitidae	DM	M = e^a * L^b	-5.802	3.177	3.30	5.60	(Johnson & Strong 2000)	Inferred, isoptera
Lepidoptera	Acanthopteroctetidae	DM	M = exp(a + b * log(L))	-5.036	3.122	2.76	40.73	(Sample *et al.* 1993)	Inferred, lepidoptera
Lepidoptera	Acanthopteroctetidae	DM	M = exp(a + b * log(L))	-5.036	3.122	2.76	40.73	(Sample *et al.* 1993)	Inferred, lepidoptera
Lepidoptera	Gelechiidae	DM	M = exp(a + b * log(L))	-5.036	3.122	2.76	40.73	(Sample *et al.* 1993)	Inferred, lepidoptera

Lepidoptera	Geometridae	DM	M = exp(a + b * log(L))	-5.036	3.122	2.76	40.73	(Sample *et al.* 1993)	Inferred, lepidoptera
Lepidoptera	Gracillariidae	DM	M = exp(a + b * log(L))	-5.036	3.122	2.76	40.73	(Sample *et al.* 1993)	Inferred, lepidoptera
Lepidoptera	Noctuidae	DM	M = exp(a + b * log(L))	-5.036	3.122	2.76	40.73	(Sample *et al.* 1993)	Inferred, lepidoptera
Lepidoptera	Pyralidae	DM	M = exp(a + b * log(L))	-5.036	3.122	2.76	40.73	(Sample *et al.* 1993)	Inferred, lepidoptera
Lepidoptera	Thyrididae	DM	M = exp(a + b * log(L))	-5.036	3.122	2.76	40.73	(Sample *et al.* 1993)	Inferred, lepidoptera
Lepidoptera	Tineidae	DM	M = exp(a + b * log(L))	-5.036	3.122	2.76	40.73	(Sample *et al.* 1993)	Inferred, lepidoptera
Lepidoptera	Tortricidae	DM	M = exp(a + b * log(L))	-5.036	3.122	2.76	40.73	(Sample *et al.* 1993)	Inferred, lepidoptera
Lepidoptera	Zygaenidae	DM	M = exp(a + b * log(L))	-5.036	3.122	2.76	40.73	(Sample *et al.* 1993)	Inferred, lepidoptera
Lepidoptera	Uniden	DM	M = exp(a + b * log(L))	-5.036	3.122	2.76	40.73	(Sample *et al.* 1993)	Inferred, lepidoptera
Lithobiomorpha	Henicopidae	DM	M = exp(a + b * log(L))	-4.049	2.18	4	47	(Gowing & Recher 1984)	Inferred, chilopoda
Mantodea	Mantidae	DM	M = exp(a + b * log(L))	-6.340	3.010	6.00	66.00	(Wardhaugh 2013)	Group specific
Neuroptera	Chrysopidae	DM	M = exp(a + b * log(L))	-4.483	2.570	3.45	54.51	(Sample *et al.* 1993)	Inferred, neuroptera
Opiliones	All	FM	M = exp(a + b * log(L))	-0.899	2.984	0.57	6.9	(Höfer & Ott 2009)	Inferred, opiliones
Orthoptera	Acrididae	DM	M = exp(a + b * log(L))	-3.17	2.61	2.3	33	(Wardhaugh 2013)	Inferred, orthoptera
Orthoptera	Gryllidae	DM	M = exp(a + b * log(L))	-3.17	2.61	2.3	33	(Wardhaugh 2013)	Inferred, orthoptera
Orthoptera	Tetrigidae	DM	M = exp(a + b * log(L))	-3.17	2.61	2.3	33	(Wardhaugh 2013)	Inferred, orthoptera
Orthoptera	Gryllacrididae	DM	M = exp(a + b * log(L))	-3.17	2.61	2.3	33	(Wardhaugh 2013)	Inferred, orthoptera
Orthoptera	Tettigoniidae	DM	M = exp(a + b * log(L))	-3.17	2.61	2.3	33	(Wardhaugh 2013)	Inferred, orthoptera
Orthoptera	Tridactylidae	DM	M = exp(a + b * log(L))	-3.17	2.61	2.3	33	(Wardhaugh 2013)	Inferred, orthoptera
Polydesmida	Paradoxosomatidae	DM	M = exp(a + b * log(L))	-4.591	2.543	11.0	47.0	(Gowing & Recher 1984)	Inferred, diplopoda
Polydesmida	Platyrhacidae	DM	M = exp(a + b * log(L))	-4.591	2.543	11.0	47.0	(Gowing & Recher 1984)	Inferred, diplopoda
Polydesmida	Cryptodesmidae	DM	M = exp(a + b * log(L))	-4.591	2.543	11.0	47.0	(Gowing & Recher 1984)	Inferred, diplopoda
Polydesmida	Dalodesmidae	DM	M = exp(a + b * log(L))	-4.591	2.543	11.0	47.0	(Gowing & Recher 1984)	Inferred, diplopoda
Polydesmida	Haplodesmidae	DM	M = exp(a + b * log(L))	-4.591	2.543	11.0	47.0	(Gowing & Recher 1984)	Inferred, diplopoda
Polydesmida	Opisotretidae	DM	M = exp(a + b * log(L))	-4.591	2.543	11.0	47.0	(Gowing & Recher 1984)	Inferred, diplopoda
Polydesmida	Pyrgodesmidae	DM	M = exp(a + b * log(L))	-4.591	2.543	11.0	47.0	(Gowing & Recher 1984)	Inferred, diplopoda
Polyxenida	Polyxenidae	DM	M = exp(a + b * log(L))	-4.591	2.543	11.0	47.0	(Gowing & Recher 1984)	Inferred, diplopoda
Pseudoscorpionida	All	FM	M = exp(a + b * log(L))	-1.892	2.515	0.86	2.10	(Höfer & Ott 2009)	Group specific
Psocoptera	Uniden	DM	M = a * (L)^b	0.014	3.115	1.50	3.15	(Gruner 2003)	Inferred, psocoptera
Psocoptera	Psoquillidae	DM	M = a * (L)^b	0.014	3.115	1.50	3.15	(Gruner 2003)	Inferred, psocoptera
Psocoptera	Pachytroctidae	DM	M = a * (L)^b	0.014	3.115	1.50	3.15	(Gruner 2003)	Inferred, psocoptera
Psocoptera	Mesopsocidae	DM	M = a * (L)^b	0.014	3.115	1.50	3.15	(Gruner 2003)	Inferred, psocoptera
Psocoptera	Liposcelidae	DM	M = a * (L)^b	0.014	3.115	1.50	3.15	(Gruner 2003)	Inferred, psocoptera
Psocoptera	Ectopsocidae	DM	M = a * (L)^b	0.014	3.115	1.50	3.15	(Gruner 2003)	Inferred, psocoptera
Psocoptera	Epipsocidae	DM	M = a * (L)^b	0.014	3.115	1.50	3.15	(Gruner 2003)	Inferred, psocoptera

Psocoptera	Elipsocidae	DM	M = a * (L)^b	0.014	3.115	1.50	3.15	(Gruner 2003)	Inferred, psocoptera
Psocoptera	Hemipsocidae	DM	M = a * (L)^b	0.014	3.115	1.50	3.15	(Gruner 2003)	Inferred, psocoptera
Psocoptera	Lepidopsocidae	DM	M = a * (L)^b	0.014	3.115	1.50	3.15	(Gruner 2003)	Inferred, psocoptera
Psocoptera	Psyllipsocidae	DM	M = a * (L)^b	0.014	3.115	1.50	3.15	(Gruner 2003)	Inferred, psocoptera
Schizomida	Protoschizomidae	FM	M = exp(a + b * log(L))	-2.108	3.017	0.67	36	(Höfer & Ott 2009)	Inferred, hunting spiders
Scolopendromorpha	Cryptopidae	DM	M = exp(a + b * log(L))	-4.049	2.18	4	47	(Gowing & Recher 1984)	Inferred, chilopoda
Symphyla	Scutegerillidae	DM	M = a * (L)^b	0.035	2.173	0.9	17.6	(Gruner 2003)	Inferred, all insect taxa
Thysanoptera	Aeolothripidae	DM	M = a * (L)^b	0.035	2.173	0.9	17.6	(Gruner 2003)	Inferred, all insect taxa
Thysanoptera	Phlaeothripidae	DM	M = a * (L)^b	0.035	2.173	0.9	17.6	(Gruner 2003)	Inferred, all insect taxa
Thysanoptera	Thripidae	DM	M = a * (L)^b	0.035	2.173	0.9	17.6	(Gruner 2003)	Inferred, all insect taxa
Thysanoptera	Merothripidae	DM	M = a * (L)^b	0.035	2.173	0.9	17.6	(Gruner 2003)	Inferred, all insect taxa
Schizomida	Hubbardiidae	FM	M = exp(a + b * log(L))	-2.108	3.017	0.67	36	(Höfer & Ott 2009)	Inferred, hunting spiders

Table S 3.4: Dry-to-FM conversion from the literature for transformation of dry body masses (DM) (from length-DM 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 Tab. 1)	FM = exp(a+b * log(DM))	0.6111	1.0213	(Mercer *et al.* 2001)	Insecta

Table S 3.5: Soil data (soil depths: 1=0-10 cm; 2=10-30). (baseline; 52 plots; no controls)

PlotID	Sand1	Sand2	Silt1	Silt2	Clay1	Clay2	pH1	pH2	C1	C2	N1	N2	CN1	CN2
1	0.289	0.283	0.433	0.431	0.278	0.286	4.470	4.380	0.018	0.016	0.004	0.004	0.042	0.044
2	0.332	0.292	0.406	0.417	0.262	0.292	4.610	4.420	0.023	0.019	0.003	0.004	0.066	0.044
3	0.353	0.339	0.373	0.322	0.274	0.339	4.470	4.400	0.020	0.012	0.004	0.003	0.048	0.035
4	0.269	0.295	0.410	0.437	0.320	0.268	4.400	4.220	0.024	0.012	0.005	0.005	0.052	0.027
5	0.348	0.276	0.450	0.444	0.202	0.279	4.410	4.380	0.018	0.008	0.004	0.004	0.046	0.023
6	0.373	0.398	0.350	0.270	0.277	0.332	4.260	4.190	0.017	0.011	0.004	0.004	0.043	0.030
7	0.332	0.321	0.332	0.369	0.336	0.310	4.370	4.430	0.020	0.017	0.004	0.004	0.051	0.041
8	0.338	0.355	0.372	0.285	0.290	0.360	4.080	4.260	0.012	0.010	0.004	0.004	0.034	0.027
9	0.393	0.304	0.307	0.354	0.300	0.342	5.020	4.960	0.021	0.012	0.004	0.004	0.050	0.031
10	0.276	0.260	0.332	0.383	0.392	0.358	4.210	4.130	0.019	0.014	0.004	0.004	0.047	0.036
11	0.243	0.224	0.419	0.410	0.338	0.366	4.680	4.380	0.017	0.012	0.004	0.004	0.043	0.028
12	0.352	0.349	0.451	0.475	0.197	0.177	4.500	4.330	0.024	0.018	0.004	0.004	0.055	0.044
13	0.111	0.086	0.543	0.539	0.347	0.375	4.380	4.490	0.022	0.015	0.005	0.004	0.048	0.037
14	0.351	0.327	0.345	0.376	0.304	0.297	4.680	4.550	0.010	0.008	0.004	0.004	0.029	0.021
15	0.244	0.213	0.478	0.451	0.279	0.336	4.260	4.290	0.037	0.009	0.005	0.004	0.078	0.021
16	0.279	0.278	0.468	0.439	0.253	0.283	4.210	4.250	0.019	0.007	0.004	0.004	0.050	0.019
17	0.247	0.250	0.441	0.415	0.312	0.334	4.490	4.560	0.026	0.012	0.006	0.004	0.045	0.027
18	0.254	0.252	0.431	0.349	0.315	0.399	4.300	4.310	0.016	0.011	0.004	0.004	0.037	0.027
19	0.080	0.086	0.548	0.470	0.372	0.444	4.410	4.320	0.039	0.023	0.005	0.004	0.072	0.061
20	0.235	0.186	0.470	0.523	0.294	0.291	4.560	4.670	0.027	0.021	0.004	0.004	0.065	0.052
21	0.186	0.161	0.425	0.426	0.389	0.413	4.280	4.270	0.016	0.013	0.004	0.003	0.047	0.037
22	0.095	0.075	0.438	0.365	0.467	0.561	4.580	4.430	0.018	0.014	0.003	0.004	0.054	0.036
23	0.139	0.154	0.530	0.443	0.331	0.403	4.400	4.130	0.024	0.014	0.004	0.003	0.057	0.041
24	0.533	0.593	0.230	0.187	0.237	0.219	4.610	4.380	0.021	0.014	0.003	0.004	0.062	0.037
25	0.195	0.195	0.431	0.400	0.374	0.405	4.070	4.250	0.012	0.004	0.004	0.003	0.031	0.012
26	0.259	0.245	0.364	0.397	0.377	0.359	5.280	4.250	0.023	0.014	0.004	0.003	0.062	0.042
27	0.154	0.130	0.409	0.459	0.437	0.411	4.610	4.560	0.026	0.019	0.004	0.004	0.060	0.047
28	0.413	0.398	0.321	0.329	0.266	0.273	4.510	4.290	0.025	0.016	0.004	0.004	0.059	0.041
29	0.600	0.632	0.181	0.151	0.219	0.218	4.590	4.550	0.014	0.011	0.004	0.004	0.037	0.030
30	0.225	0.225	0.354	0.314	0.421	0.461	4.750	4.660	0.023	0.011	0.004	0.004	0.061	0.025
31	0.393	0.382	0.443	0.441	0.163	0.177	4.620	4.500	0.024	0.017	0.004	0.004	0.055	0.042
32	0.133	0.117	0.579	0.629	0.288	0.254	4.040	4.220	0.027	0.017	0.004	0.004	0.061	0.044
33	0.383	0.350	0.336	0.314	0.281	0.336	4.370	4.360	0.022	0.013	0.003	0.003	0.064	0.038
34	0.458	0.418	0.332	0.365	0.210	0.217	4.530	4.370	0.016	0.007	0.003	0.004	0.048	0.020
35	0.354	0.317	0.424	0.374	0.222	0.309	4.220	4.310	0.031	0.016	0.004	0.004	0.071	0.038
36	0.599	0.614	0.264	0.232	0.137	0.154	4.310	4.280	0.018	0.014	0.004	0.004	0.047	0.039
37	0.503	0.497	0.223	0.254	0.274	0.249	4.270	4.400	0.021	0.012	0.005	0.004	0.045	0.031
38	0.353	0.465	0.422	0.297	0.226	0.239	4.330	4.390	0.026	0.019	0.005	0.004	0.056	0.047
39	0.372	0.386	0.405	0.357	0.222	0.258	4.550	4.490	0.017	0.012	0.004	0.004	0.042	0.031
40	0.046	0.036	0.423	0.441	0.531	0.523	3.970	4.100	0.022	0.016	0.004	0.005	0.052	0.034
41	0.412	0.356	0.324	0.342	0.264	0.301	4.440	4.320	0.017	0.009	0.005	0.003	0.033	0.026
42	0.394	0.410	0.375	0.365	0.231	0.225	4.460	4.470	0.017	0.013	0.005	0.005	0.033	0.027
43	0.456	0.352	0.379	0.442	0.165	0.207	4.780	4.430	0.028	0.017	0.006	0.005	0.048	0.034
44	0.307	0.341	0.438	0.413	0.256	0.246	4.560	4.340	0.020	0.013	0.006	0.005	0.036	0.026
45	0.213	0.181	0.444	0.447	0.344	0.372	4.360	4.330	0.035	0.020	0.006	0.005	0.056	0.036
46	0.099	0.086	0.465	0.444	0.436	0.469	4.460	4.270	0.025	0.023	0.005	0.005	0.050	0.042
47	0.280	0.247	0.392	0.389	0.329	0.365	4.590	4.600	0.022	0.015	0.004	0.004	0.063	0.036
48	0.285	0.231	0.364	0.387	0.351	0.383	4.400	4.350	0.018	0.010	0.004	0.004	0.045	0.023
49	0.305	0.343	0.497	0.439	0.198	0.217	4.500	4.470	0.015	0.009	0.005	0.005	0.032	0.019
50	0.125	0.146	0.507	0.521	0.368	0.333	4.090	4.130	0.033	0.018	0.006	0.005	0.053	0.034
51	0.275	0.309	0.527	0.447	0.199	0.244	4.430	4.440	0.025	0.016	0.006	0.005	0.045	0.032
52	0.323	0.356	0.473	0.421	0.204	0.224	4.240	4.470	0.020	0.012	0.006	0.005	0.034	0.025

Table S 3.6: Abiotic data (baseline; 52 plots; no controls)

PlotID	PC axis 1	PC axis 2	PC axis 3	Slope	Bare soil (logit-transf.)	Gap fraction (logit-transf.)	Altitude	Bulk Density
1	-0.008	0.017	-0.023	12.2	0.426	-7.600	61.187	1.096
2	-0.044	0.151	-0.165	12.6	-1.072	-7.824	46.909	1.013
3	0.064	0.002	-0.089	3.8	-2.143	-7.264	40.508	1.029
4	-0.048	0.018	0.096	7.6	-1.696	-7.824	55.266	0.927
5	0.079	-0.085	0.075	5.0	-1.696	-7.130	54.217	1.180
6	0.109	-0.062	-0.034	9.8	-2.376	-6.375	44.756	0.991
7	0.002	0.048	-0.108	1.8	-3.664	-5.681	37.585	1.024
8	0.122	-0.187	0.006	4.3	-1.355	-7.824	62.622	1.165
9	0.121	0.058	-0.151	14.6	-1.355	-7.600	50.671	1.127
10	-0.019	-0.119	-0.075	7.6	-0.824	-7.418	57.198	1.147
11	0.002	-0.100	-0.006	0.4	0.426	-7.824	57.346	1.023
12	-0.031	0.204	0.036	8.7	-4.185	-5.127	53.014	0.935
13	-0.158	-0.122	0.021	9.2	-1.072	-6.570	53.488	1.239
14	0.187	-0.186	0.029	7.8	-1.551	-7.824	51.453	1.330
15	NA	NA	NA	6.7	-4.185	NA	64.824	0.972
16	0.028	-0.117	0.091	5.7	-2.844	-6.375	54.111	1.024
17	-0.041	-0.028	0.126	0.5	-2.512	-6.724	54.584	1.261
18	0.011	-0.150	0.066	3.2	-2.376	-6.907	51.891	1.039
19	-0.350	0.144	-0.207	2.4	-2.143	-5.806	48.205	1.054
20	-0.164	0.202	-0.140	0.6	-2.143	-6.724	42.325	0.911
21	-0.048	-0.219	-0.135	1.3	-1.072	-7.130	64.646	1.297
22	-0.109	-0.254	-0.273	20.8	-2.143	-6.907	44.184	1.232
23	-0.132	-0.125	-0.109	20.9	-2.143	-8.111	53.527	1.288
24	0.208	0.195	-0.210	6.8	-2.376	-7.600	53.576	1.043
25	0.046	-0.361	0.115	2.4	-1.696	-6.318	45.676	1.060
26	NA	NA	NA	1.8	NA	-6.375	44.704	1.101
27	NA	NA	NA	1.0	NA	-6.436	45.110	1.020
28	0.046	0.135	-0.124	16.0	-2.143	-7.418	67.125	1.039
29	0.348	0.076	-0.081	5.0	-2.376	-6.811	47.803	1.199
30	0.001	-0.114	-0.203	1.2	-1.072	-6.644	62.541	1.199
31	0.045	0.171	-0.009	9.4	-1.355	-7.012	52.121	1.284
32	-0.233	0.016	0.051	1.0	-2.844	-6.811	52.459	1.030
33	0.055	0.041	-0.213	3.8	-1.355	-7.418	60.492	1.011
34	0.192	-0.004	0.016	2.1	-3.317	-6.375	44.696	0.976
35	-0.054	0.117	-0.078	0.3	-2.376	-6.907	44.409	1.201
36	0.243	0.193	-0.035	2.4	-0.385	-7.600	47.186	1.058
37	0.183	0.049	-0.032	0.2	-1.355	-7.824	45.073	1.190
38	-0.007	0.236	-0.048	0.2	-4.185	-6.644	38.856	0.891
39	0.118	0.007	0.019	1.9	-2.844	-6.375	43.305	1.144
40	-0.257	-0.235	-0.060	2.0	-4.185	-6.501	52.591	0.972
41	0.143	-0.087	0.094	4.2	-2.143	-7.418	54.482	1.205
42	0.106	0.033	0.205	5.8	-2.844	-6.318	46.566	1.151
43	-0.004	0.284	0.205	6.8	-1.355	-8.111	52.190	0.910
44	0.019	0.014	0.251	5.0	-2.844	-5.334	45.754	1.139
45	-0.244	0.165	0.150	0.4	-5.293	-6.436	42.781	0.793
46	-0.261	-0.032	-0.010	13.0	-1.355	-7.418	47.151	1.107
47	-0.029	0.033	-0.175	3.7	-2.844	-5.422	51.193	1.019
48	0.022	-0.164	0.025	0.9	-0.824	-7.824	46.168	1.236
49	0.093	-0.098	0.295	4.7	-0.824	-6.436	42.980	1.429
50	-0.286	0.048	0.227	1.3	-5.293	-5.445	47.903	0.931
51	-0.085	0.154	0.256	1.2	-5.293	-7.264	46.758	0.883
52	0.018	0.039	0.335	2.9	-1.072	-6.907	54.421	1.053

Table S 3.7: 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, SR = species richness, AB = abundance, FR = family richness, BM = body mass, LL inv. = leaf-litter invertebrates, HL inv. = herb-layer invertebrates.

Response	Fixed effects	Estimate	Std. Error	t-value	p-value		R2
PCaxis1	TD	-0.0552	0.034	-1.643	0.104		0.043
	PS	-0.013	0.014	-0.874	0.384		
	TD: PS	0.006	0.006	0.973	0.333		
PCaxis 2	TD	0.038	0.032	1.184	0.239		0.141
	PS	0.050	0.014	3.631	<0.001	***	
	TD: PS	-0.008	0.006	-1.343	0.183		
PCaxis 3	TD	0.102	0.031	3.229	0.002	**	0.162
	PS	0.038	0.013	2.808	0.006	**	
	TD: PS	-0.023	0.006	-4.034	<0.001	***	
Slope	TD	-3.457	1.172	-2.951	0.004	**	0.102
	PS	-1.414	0.504	-2.808	0.006	**	
	TD: PS	0.738	0.212	3.475	<0.001	***	
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 SR (nb)	TD	-0.156	0.065	-2.408	0.016	*	0.075
	PS	-0.065	0.028	-2.351	0.019	*	
	TD: PS	0.031	0.011	2.727	0.006	**	
Plant AB	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 SR	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 AB	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 BM	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. FM	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. AB	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. BM	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	
HL inv. SR	TD	0.202	0.123	1.644	0.100	0.071
	PS	0.055	0.055	1.001	0.317	
	TD: PS	-0.023	0.022	-1.010	0.312	
HL inv. AB	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. BM	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	

Table S 3.8: Biotic data (baseline; 52 plots; no controls). SR = species richness, AB = abundance, BM = biomass, FR = family richness, LL/HL inv. = leaf-litter/herb-layer invertebrates

PlotID	Plant SR	Plant AB	Bird SR	Bird AB	Bird BM [g]	LL inv. FR	LL inv. AB	LL inv. BM [mg]	HL inv. FR	HL inv. AB	HL inv. BM [mg]
1	14	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	21	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	16	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	21	718	4	14	289.06	13	39	37.00	22	50	116.08
17	19	603	6	14	810.48	12	23	48.73	16	48	473.72
18	24	872	7	19	1115.99	8	9	110.47	11	47	346.00
19	21	642	9	14	582.17	12	38	45.80	15	35	258.98
20	21	330	5	7	252.04	6	23	11.58	19	44	201.39
21	22	595	4	8	353.96	14	33	68.23	20	49	205.17
22	21	646	3	8	202.69	5	6	8.21	6	9	74.77
23	20	632	6	18	789.38	8	11	5.73	18	35	119.64
24	13	525	4	12	360.60	8	14	5.02	9	20	331.77
25	18	384	1	3	29.04	13	37	91.60	6	8	21.23
28	19	438	5	15	570.60	12	19	45.60	19	29	36.28
29	23	507	6	13	565.84	10	20	33.78	5	10	88.11
30	13	734	4	12	296.83	4	4	12.84	15	38	165.46
31	14	474	7	10	317.63	13	27	31.21	4	9	118.56
32	21	492	2	4	56.84	12	46	21.70	10	31	147.92
33	15	594	5	8	467.71	4	9	2.15	6	25	102.52
34	13	1092	7	25	701.73	6	29	34.44	12	39	805.17
35	20	851	3	4	118.86	3	35	35.09	14	53	233.24
36	19	414	4	5	223.50	6	14	10.69	4	13	101.92
37	22	304	11	21	1244.57	6	7	0.76	6	13	193.15
38	8	120	7	18	542.43	15	42	53.03	12	18	268.28
39	11	399	4	14	224.08	6	9	25.17	11	17	57.79
40	18	340	5	13	342.32	8	20	17.41	9	22	512.67
41	17	514	2	4	74.96	14	83	94.65	15	27	39.08
42	16	379	2	3	27.46	9	23	11.30	23	68	685.27
43	17	268	2	6	50.18	3	4	1.18	7	13	106.69
44	16	254	6	15	330.03	11	112	78.22	9	19	289.24
45	15	230	7	32	676.98	16	83	149.17	27	54	746.31
46	12	223	3	6	128.98	26	224	180.06	5	36	159.10
47	14	369	1	1	27.80	14	25	9.33	6	16	610.80
48	26	682	3	6	140.92	3	5	2.47	5	6	30.08
49	19	455	3	6	261.76	3	7	5.05	13	23	145.71
50	5	359	3	7	221.96	17	69	49.84	22	46	302.90
51	6	347	5	15	420.08	16	63	90.36	19	39	78.98
52	19	548	4	8	156.66	1	3	0.61	6	13	63.74

Table S 3.9: List of plant species (baseline; 52 plots; no controls)

Species	Family	Total abundance	Dominance (number of plots present on)
Adiantum latifolium Lam.	Pteridaceae	228	32
Ageratum conyzoides (L.) L.	Compositae	380	16
Ageratum spec.	Compositae	1	1
Alternanthera sessilis (L.) R.Br. ex DC.	Amaranthaceae	57	4
Asplenium normale D. Don	Aspleniaceae	91	17
cf. *Asplenium* spec.	Aspleniaceae	3	2
Asystasia gangetica (L.) T.Anderson	Acanthaceae	4470	49
Bauhinia semibifida Roxb.	Leguminosae	1	1
Blechnum orientale L.	Blechnaceae	8	2
Breynia cernua (Poir.) Müll.Arg.	Phyllanthaceae	7	4
Centotheca lappacea (L.) Desv.	Poaceae	1390	42
Centrosema pubescens Benth.	Leguminosae	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	2171	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	1256	41
Cyperus diffusus Vahl	Cyperaceae	156	28
Cyrtococcum patens (L.) A.Camus	Poaceae	1251	38
Cyrtococcum spec. (L.)	Poaceae	17	2
Dicranopteris linearis (Burm. f.) Underw.	Gleicheniaceae	9	1
Dioscorea alata L.	Dioscoreaceae	3	2
Elaeis guineensis Jacq.	Arecaceae	122	30
fern spec. 01		1	1
cf. *Ficus* spec.	Moraceae	1	1
Ficus cf. *variegata* Blume	Moraceae	19	7
grass spec.	Poaceae	4	1
grass spec. 01	Poaceae	250	5
grass spec. 02	Poaceae	2	1
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	82	23
Mallotus peltatus (Geiseler) Müll.Arg.	Euphorbiaceae	5	1
Melastoma malabathricum L.	Melastomataceae	66	23
Merremia spec.	Convolvulaceae	7	2
Merremia umbellata (L.) Hallier f.	Convolvulaceae	71	5
Microlepia speluncae (L.) T. Moore	Dennstaedtiaceae	76	22

Mikania micrantha (L.) Willd.	Compositae	81	17
Mimosa cf. *pudica* L.	Leguminosae	13	4
Nephrolepis cf. *acutifolia* (Desv.) Christ	Nephrolepidaceae	1975	42
Oplismenus compositus (L.) P.Beauv.	Poaceae	38	2
Ottochloa nodosa (Kunth) Dandy	Poaceae	938	10
Ottochloa spec. 1 (Kunth) Dandy	Poaceae	684	37
Oxalis barrelieri L.	Oxalidaceae	6	1
Panicum cf. *laxum* Sw.	Poaceae	1294	29
Paspalum cf. *conjugatum* P.J.Bergius	Poaceae	1393	49
Paspalum spec.	Poaceae	18	6
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	8	4
Pteris cf. *armata* C. Presl	Pteridaceae	50	4
Pteris ensiformis Burm. f.	Pteridaceae	1	1
Pueraria phaseoloides (Roxb.) Benth.	Leguminosae	5	2
Salvia occidentalis Sw.	Lamiaceae	3	1
Schizostachyum sp.	Poaceae	1	1
Scleria levis Retz.	Cyperaceae	264	36
Scleria spec.	Cyperaceae	1	1
seedling spec. 1		1	1
Selaginella willdenowii (Desv. ex Poir.) Baker	Selaginellaceae	81	14
Solanum jamaicense Mill.	Solanaceae	12	6
Spermacoce alata Aubl.	Rubiaceae	1598	32
Stenochlaena palustris (Burm. f.) Bedd.	Blechnaceae	14	2
Strombosia javanica Thwaites	Olacaceae	11	1
Taenitis blechnoides (Willd.) Sw.	Pteridaceae	434	23
Tectaria vasta (Blume) Copel.	Tectariaceae	21	6
Urceola brachysepala Hook.f.	Apocynaceae	29	3
Urceola spec.	Apocynaceae	72	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. 12		1	1
woody spec. 13		2	1
woody spec. 14		1	1

Table S 3.10: List of bird species recorded within a 75 m radius around the centre of each plot (baseline; 52 plots; no controls)

Species	Family	Total abundance	Total biomass [g]	Dominance (number of plots present on)	IUCN status
Amaurornis phoenicurus	Rallidae	10	1440.00	5	LC
Celeus brachyurus	Picidae	1	85.94	1	LC
Centropus sinensis	Cuculidae	1	280.70	1	LC
Chalcophaps indica	Columbidae	9	1228.86	7	LC
Dicaeum trigonostigma	Dicaeidae	16	113.60	13	LC
Eurystomus orientalis	Coraciidae	2	286.04	2	LC
Geopelia striata	Columbidae	8	452.80	6	LC
Halcyon smyrnensis	Alcedinidae	33	2924.80	22	LC
Megalaima	Ramphastidae	2	88.98	2	LC
Merops viridis	Meropidae	3	34.80	1	LC
Orthotomus ruficeps	Sylviidae	61	429.30	27	LC
Orthotomus sericeus	Sylviidae	21	216.00	14	LC
Prinia familiaris	Cisticolidae	241	1810.16	48	LC
Pycnonotus aurigaster	Pycnonotidae	31	1019.59	14	LC
Pycnonotus goiavier	Pycnonotidae	191	4698.20	38	LC
Pycnonotus plumosus	Pycnonotidae	14	453.05	7	LC
Rhipidura javanica	Rhipiduridae	2	25.00	2	LC
Spilornis cheela	Accipitridae	1	597.74	1	LC
Stigmatopelia chinensis	Columbidae	8	1272.00	6	LC
Todiramphus chloris	Alcedinidae	14	859.17	10	LC
Treron vernans	Columbidae	3	396.00	3	LC

IUCN status: LC = least concern

Table S 3.11: List of families of leaf-litter invertebrates recorded on the plots (baseline; 52 plots; no controls)

Family	Order	Total abundance (of individuals in this family)	Total biomass [mg]	Dominance (number of plots present on)
Aphididae	Hemiptera	1	0.06	1
Araneidae	Araneae	3	7.66	3
Armadillidae	Isopoda	3	29.15	1
Blaberidae	Blattodea	10	19.14	7
Blattellidae	Blattodea	7	18.11	5
Blattidae	Blattodea	8	7.08	7
Campodeidae	Diplura	1	0.34	1
Carabidae	Coleoptera	7	9.22	5
Chrysomelidae	Coleoptera	2	13.02	2
Cicadellidae	Hemiptera	1	1.24	1
Colydiidae	Coleoptera	2	0.33	2
Corinnidae	Araneae	17	79.22	14
Cryptodesmidae	Polydesmida	1	0.70	1
Cryptopidae	Scolopendromorpha	4	13.23	2
Ctenidae	Araneae	2	15.84	2
Cydnidae	Hemiptera	8	3.42	2
Dalodesmidae	Polydesmida	3	6.40	1
Delphacidae	Hemiptera	2	0.47	2

Dignathodontidae	Geophilomorpha	1	0.25	1
Dipsocoridae	Hemiptera	22	2.66	10
Drosophilidae	Diplura	1	0.50	1
Dryinidae	Hymenoptera	1	0.40	1
Elateridae	Coleoptera	2	0.08	2
Epipsocidae	Psocoptera	2	0.08	1
Formicidae	Hymenoptera	1291	562.23	50
Geophilidae	Geophilomorpha	16	207.48	10
Glomeridae	Glomerida	4	11.06	3
Gnaphosidae	Araneae	36	16.40	24
Gryllidae	Orthoptera	6	25.86	6
Henicopidae	Lithobiomorpha	16	18.57	6
Hubbardiidae	Schizomida	1	9.90	1
Hydraenidae	Coleoptera	2	0.26	1
Japygidae	Diplura	9	13.70	5
Labiduridae	Dermaptera	1	4.35	1
Labiidae	Dermaptera	7	26.39	7
Largidae	Hemiptera	6	2.39	4
Linyphiidae	Araneae	28	9.91	18
Liposcelidae	Psocoptera	1	0.24	1
Lycosidae	Araneae	44	126.11	23
Lygaeidae	Hemiptera	6	1.32	4
Mantidae	Mantodea	3	0.71	3
Mesopsocidae	Psocoptera	1	0.05	1
Miridae	Hemiptera	2	0.35	2
Myrmeleontidae	Neuroptera	1	2.00	1
Mysmenidae	Araneae	30	2.91	16
Neobisiidae	Pseudoscorpion	1	0.29	1
Nitidulidae	Coleoptera	2	1.69	2
Olpiidae	Pseudoscorpion	1	0.35	1
Oniscidae	Isopoda	1	0.18	1
Oonopidae	Araneae	34	12.79	15
Opisotretidae	Polydesmida	6	4.81	4
Oxyopidae	Araneae	7	36.46	7
Pachytroctidae	Psocoptera	1	0.07	1
Paradoxosomatidae	Polydesmida	1	0.54	1
Phalacridae	Coleoptera	36	8.67	3
Phalangodidae	Opiliones	4	7.15	2
Philosciidae	Isopoda	44	115.33	17
Phlaeothripidae	Thysanoptera	7	1.39	6
Pholcidae	Araneae	1	0.21	1
Platyrhacidae	Polydesmida	1	22.35	1
Polyxenidae	Polyxenida	5	0.59	5
Protoschizomidae	Schizomida	1	0.84	1
Pseudococcidae	Hemiptera	1	0.39	1
Psoquillidae	Psocoptera	3	0.96	3
Ptiliidae	Coleoptera	1	0.03	1
Pyrgodesmidae	Polydesmida	70	62.15	20
Reduviidae	Hemiptera	8	227.19	6
Rhinotermitidae	Isoptera	3	1.11	2
Salticidae	Araneae	24	59.81	18
Schizopteridae	Hemiptera	6	0.18	5
Scolytinae	Coleoptera	3	0.74	3
Scutigerellidae	Symphyla	4	1.49	4
Scydmaenidae	Coleoptera	3	0.08	1
Sironidae	Opiliones	1	14.35	1
Spongiphoridae	Dermaptera	22	84.49	2
Staphylinidae	Coleoptera	113	24.53	20

Stratiomydae	Diplura	1	4.54	1
Tenebrionidae	Coleoptera	13	56.57	9
Termitidae	Isoptera	10	8.93	1
Tetrablemmidae	Araneae	10	1.50	6
Tetrigidae	Orthoptera	4	14.90	4
Tettigoniidae	Orthoptera	1	3.11	1
Theridiidae	Araneae	45	43.31	23
Theridiosomatidae	Araneae	19	4.36	13
Thomisidae	Araneae	13	39.57	10
Tingidae	Hemiptera	3	0.30	2
Tridactylidae	Orthoptera	1	2.54	1

Table S 3.12: List of families of herb-layer invertebrates recorded on the plots (baseline; 52 plots; no controls)

Family	Order	Total abundance (of individuals in this family)	Total biomass [mg]	Dominance (number of plots present on)
Acanthopteroctetidae	Lepidoptera	1	6.09	1
Acrididae	Orthoptera	58	6282.27	24
Aderidae	Coleoptera	4	2.30	4
Anthocoridae	Hemiptera	10	1.57	2
Anthribidae	Coleoptera	2	0.58	1
Aphelinidae	Hymenoptera	1	0.06	1
Aphididae	Hemiptera	14	0.81	5
Aradidae	Hemiptera	1	1.46	1
Araneidae	Araneae	12	70.62	9
Asteiidae	Diptera	22	3.30	9
Baetidae	Ephemeroptera	3	4.52	3
Bibionidae	Diptera	1	11.80	1
Blaberidae	Blattodea	1	0.77	1
Blattellidae	Blattodea	15	178.96	15
Blattidae	Blattodea	1	5.42	1
Braconidae	Hymenoptera	8	2.94	8
Calliphoridae	Diptera	2	1.19	1
Carabidae	Coleoptera	1	4.04	1
Cecidomyiidae	Diptera	9	0.27	6
Ceraphronidae	Hymenoptera	5	0.10	4
Ceratopogonidae	Diptera	11	2.01	8
Chironomidae	Diptera	2	0.44	1
Chloropidae	Diptera	8	0.75	6
Chrysomelidae	Coleoptera	4	30.50	4
Cicadellidae	Hemiptera	96	123.60	26
Clusiidae	Diptera	1	0.55	1
Coreidae	Hemiptera	1	41.75	1
Culicidae	Diptera	26	21.68	20
Curculionidae	Coleoptera	1	0.50	1
Delphacidae	Hemiptera	53	71.70	21
Derbidae	Hemiptera	3	5.25	3
Diapriidae	Hymenoptera	3	0.46	3
Dolichopodidae	Diptera	1	1.27	1

Drosophilidae	Diptera	1	0.69	1
Encyrtidae	Hymenoptera	1	0.04	1
Eulophidae	Hymenoptera	12	1.86	9
Figitidae	Hymenoptera	1	0.06	1
Flatidae	Hemiptera	4	3.72	3
Formicidae	Hymenoptera	91	68.48	34
Geocoridae	Hemiptera	2	1.53	2
Geometridae	Lepidoptera	6	5.79	5
Gryllidae	Orthoptera	499	3064.30	51
Henicopidae	Lithobiomorpha	1	0.21	1
Ichneumonidae	Hymenoptera	16	5.72	12
Lauxaniiidae	Diptera	5	2.72	4
Linyphiidae	Araneae	2	3.95	2
Lophopidae	Hemiptera	1	0.68	1
Lycosidae	Araneae	46	461.74	26
Mantidae	Mantodea	8	298.35	7
Meenoplidae	Hemiptera	2	2.18	2
Miridae	Hemiptera	30	5.29	18
Muscidae	Diptera	3	0.61	3
Mycetophilidae	Diptera	1	0.80	1
Mymaridae	Hymenoptera	2	0.06	2
Mysmenidae	Araneae	1	0.08	1
Nabidae	Hemiptera	2	1.06	2
Noctuidae	Lepidoptera	2	1.25	2
Opomyzidae	Diptera	3	0.61	3
Oxyopidae	Araneae	79	829.09	30
Phalacridae	Coleoptera	1	0.30	1
Phlaeothripidae	Thysanoptera	6	0.55	3
Phoridae	Diptera	2	0.10	2
Piophilidae	Diptera	3	0.21	3
Pipunculidae	Diptera	2	2.92	1
Pisauridae	Araneae	1	91.93	1
Platygastridae	Hymenoptera	2	0.05	2
Pseudococcidae	Hemiptera	1	0.02	1
Psychodidae	Diptera	4	0.13	4
Pyralidae	Lepidoptera	1	8.15	1
Pyrgodesmidae	Polydesmida	5	9.02	4
Reduviidae	Hemiptera	5	34.31	5
Salticidae	Araneae	23	92.96	15
Scatopsidae	Diptera	1	0.06	1
Scelionidae	Hymenoptera	25	3.62	12
Sciaridae	Diptera	19	0.98	10
Sphaeroceridae	Diptera	5	0.76	4
Staphylinidae	Coleoptera	4	3.11	4
Tetrigidae	Orthoptera	36	1010.79	22
Tettigoniidae	Orthoptera	19	703.32	11
Theridiidae	Araneae	28	91.57	21
Theridiosomatidae	Araneae	8	1.14	7
Thomisidae	Araneae	22	76.50	14
Thyrididae	Lepidoptera	4	21.64	4
Tineidae	Lepidoptera	8	5.17	6
Tingidae	Hemiptera	1	0.06	1
Tiphiidae	Hymenoptera	2	4.76	1
Tipulidae	Diptera	23	25.59	14
Tortricidae	Lepidoptera	1	0.32	1
Trichodectidae	Phthiraptera	1	0.01	1
Trichogrammatidae	Hymenoptera	1	0.00	1
Tridactylidae	Orthoptera	2	13.35	2

Tropiduchidae	Hemiptera	10	44.55	6
Vespidae	Hymenoptera	3	20.14	2
Zygaenidae	Lepidoptera	1	8.82	1

Table S 3.13: Biotic data (first year; 56 plots). SR = species richness, AB = abundance, BM = biomass, FR = family richness, LL/HL inv. = leaf-litter/herb-layer invertebrates

PlotID	Bird SR	Bird AB	Bird BM	LL inv. FR	LL inv. AB	LL inv. BM	HL inv. FR	HL inv. AB	HL inv. BM
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	2132.6	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	641.1	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	1723.4	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	298.2	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	115.4	3	3	0.72	12	16	22.44
31	2	6	76.2	4	9	6.35	12	17	1393.20
32	4	9	176.61	7	13	12.55	17	42	1087.27
33	4	8	716.7	4	9	18.57	20	81	384.49
34	3	6	221.24	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	305.3	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	222.7	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	169.8	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	131.8	8	43	29.74	14	21	42.52
56	4	10	812.85	16	77	40.40	15	26	106.60

Table S 3.14: List of bird species recorded within a 75 m radius around the centre of each plot one year after establishment (first year; 56 plots)

Species	Family	Total abundance	Total biomass [g]	Dominance (number of plots present on)	IUCN status
Centropus sinensis	Cuculidae	1	280.70	1	LC
Chalcophaps indica	Columbidae	10	955.78	7	LC
Coturnix chinesis	Phasanianidae	1	40.41	1	LC
Dicaeum trigonostigma	Dicaeidae	20	127.80	16	LC
Geopelia striata	Columbidae	41	1811.20	18	LC
Halcyon smyrnensis	Alcedinidae	19	1736.60	13	LC
Lanius schach	Laniidae	2	103.02	2	LC
Lonchura punctulata	Estrildidae	7	40.80	3	LC
Orthotomus atrogularis	Sylviidae	1	7.68	1	LC
Orthotomus ruficeps	Sylviidae	45	210.60	20	LC
Orthotomus sericeus	Sylviidae	1	10.80	1	LC
Prinia familiaris	Cisticolidae	252	1539.12	50	LC
Pycnonotus aurigaster	Pycnonotidae	6	221.65	3	LC
Pycnonotus goiavier	Pycnonotidae	198	4281.20	45	LC
Pycnonotus plumosus	Pycnonotidae	6	174.25	4	LC
Rhipidura javanica	Rhipiduridae	5	62.50	4	LC
Spilornis cheela	Accipitridae	8	4781.92	6	LC
Spizaetus cirrhatus	Accipitridae	1	1475.12	1	LC
Stigmatopelia chinensis	Columbidae	64	8904.00	28	LC
Todiramphus chloris	Alcedinidae	61	3634.95	32	LC

IUCN status: LC = least concern

Table S 3.15: List of families of leaf-litter invertebrates recorded on the plots one year after establishment (first year; 56 plots)

Family	Order	Total abundance (of individuals in this family)	Total biomass [mg]	Dominance (number of plots present on)
Acrididae	Orthoptera	2	233.96	1
Aderidae	Coleoptera	10	2.10	5
Aeolothripidae	Thysanoptera	2	0.27	2

Anisolabididae	Dermaptera	3	76.89	1
Aphididae	Hemiptera	4	0.60	3
Araneidae	Araneae	7	25.20	7
Blaberidae	Blattodea	9	3.59	6
Blattellidae	Blattodea	12	15.18	10
Blattidae	Blattodea	2	0.66	2
Carabidae	Coleoptera	19	6.86	12
Ceratocombidae	Hemiptera	1	0.01	1
Chrysomelidae	Coleoptera	15	1.98	2
Cicadellidae	Hemiptera	4	1.41	3
Corinnidae	Araneae	15	64.10	14
Corylophidae	Coleoptera	6	1.23	5
Cryptodesmidae	Polydesmida	2	2.10	2
Ctenidae	Araneae	4	16.92	3
Curculionidae	Coleoptera	1	1.62	1
Cydnidae	Hemiptera	11	3.33	6
Dignathodontidae	Geophilomorpha	1	0.25	1
Dipsocoridae	Hemiptera	14	1.40	9
Discolomidae	Coleoptera	1	0.39	1
Dryinidae	Hymenoptera	1	0.30	1
Ectopsocidae	Psocoptera	12	0.49	3
Elateridae	Coleoptera	3	0.25	2
Formicidae	Hymenoptera	1551	1163.63	53
Gelechiidae	Lepidoptera	1	0.58	1
Geophilidae	Geophilomorpha	1	12.15	1
Gnaphosidae	Araneae	4	3.25	4
Gracillariidae	Lepidoptera	3	0.97	3
Gryllidae	Orthoptera	16	27.30	12
Haplodesmidae	Polydesmida	6	1.65	4
Hemipsocidae	Psocoptera	3	0.09	1
Heteroceridae	Coleoptera	1	4.89	1
Japygidae	Diplura	10	10.84	7
Lagrioidinae	Coleoptera	1	0.26	1
Linyphiidae	Araneae	64	20.29	23
Liposcelidae	Psocoptera	3	0.05	1
Lycosidae	Araneae	58	225.67	28
Mecistocephalidae	Geophilomorpha	3	39.98	3
Nabidae	Hemiptera	15	27.77	10
Neobisiidae	Pseudoscorpion	1	0.24	1
Nitidulidae	Coleoptera	4	0.55	2
Oonopidae	Araneae	13	4.11	8
Oxyopidae	Araneae	11	23.57	10
Pachytroctidae	Psocoptera	3	0.14	2
Pentatomidae	Hemiptera	5	543.95	4
Phalacridae	Coleoptera	18	1.38	12
Philosciidae	Isopoda	10	20.44	9
Phlaeothripidae	Thysanoptera	9	2.45	6
Polyxenidae	Polyxenida	12	4.52	7
Pselaphidae	Coleoptera	7	1.48	7
Ptiliidae	Coleoptera	1	0.03	1
Pyralidae	Lepidoptera	1	1.82	1
Pyrgodesmidae	Polydesmida	65	63.11	20
Reduviidae	Hemiptera	2	63.06	2
Salticidae	Araneae	22	85.07	16
Scarabaeidae	Coleoptera	1	8.66	1
Scelionidae	Hymenoptera	2	0.10	2
Schizopteridae	Hemiptera	7	0.16	5
Scolytinae	Coleoptera	1	0.11	1

Scutigerellidae	Symphyla	11	4.73	8
Scydmaenidae	Coleoptera	4	0.69	3
Silvanidae	Coleoptera	10	1.64	8
Sparassidae	Araneae	3	1.56	3
Staphylinidae	Coleoptera	34	7.27	17
Termitidae	Isopoda	1	1.48	1
Tetrablemmidae	Araneae	2	0.51	2
Tetragnathidae	Araneae	8	21.82	6
Tetrigidae	Orthoptera	3	37.38	2
Theridiidae	Araneae	39	31.61	23
Theridiosomatidae	Araneae	1	0.17	1
Thomisidae	Araneae	12	22.65	8
Zodariidae	Araneae	5	19.51	5

Table S 3.16: List of families of herb-layer invertebrates recorded on the plots one year after establishment (first year; 56 plots)

Family	Order	Total abundance (of individuals in this family)	Total biomass [mg]	Dominance (number of plots present on)
Acrididae	Orthoptera	100	10985.43	38
Aderidae	Coleoptera	4	3.45	4
Aeolothripidae	Thysanoptera	7	0.25	7
Aleyrodidae	Hemiptera	23	1.80	14
Alydidae	Hemiptera	2	56.01	1
Anapidae	Araneae	3	4.51	3
Anthicidae	Coleoptera	1	1.10	1
Aphelinidae	Hymenoptera	2	0.14	1
Aphididae	Hemiptera	38	3.32	21
Aradidae	Hemiptera	1	0.44	1
Araneidae	Araneae	2	4.00	2
Asteiidae	Diptera	5	0.55	3
Baetidae	Ephemeroptera	1	1.86	1
Bethylidae	Hymenoptera	3	1.86	3
Blaberidae	Blattodea	9	32.00	8
Blattellidae	Blattodea	7	8.19	5
Blattidae	Blattodea	8	177.08	8
Braconidae	Hymenoptera	32	15.95	17
Carabidae	Coleoptera	2	4.17	2
Cecidomyiidae	Diptera	72	3.53	34
Ceraphronidae	Hymenoptera	27	0.72	17
Ceratopogonidae	Diptera	11	0.62	6
Chalcididae	Hymenoptera	3	1.17	3
Chironomidae	Diptera	1	0.06	1
Chloropidae	Diptera	2	0.29	2
Chrysomelidae	Coleoptera	3	4.45	3
Chrysopidae	Neuroptera	1	6.05	1
Cicadellidae	Hemiptera	146	196.70	40
Cixiidae	Hemiptera	14	3.91	10
Clubionidae	Araneae	1	7.74	1
Corinnidae	Araneae	7	7.45	7
Ctenidae	Araneae	1	10.97	1

Culicidae	Diptera	5	1.21	5
Cynipidae	Hymenoptera	2	0.25	1
Deinopidae	Araneae	1	22.25	1
Delphacidae	Hemiptera	23	12.66	18
Deuterophlebiidae	Diptera	1	0.01	1
Dictyopharidae	Hemiptera	2	20.33	2
Dolichopodidae	Diptera	6	0.55	5
Dysderidae	Araneae	1	5.79	1
Ectopsocidae	Psocoptera	1	0.02	1
Elipsocidae	Psocoptera	2	0.08	2
Encyrtidae	Hymenoptera	18	0.53	16
Eriosomatidae	Hemiptera	3	0.21	3
Eucoilidae	Hymenoptera	2	0.08	2
Eulophidae	Hymenoptera	22	2.75	17
Formicidae	Hymenoptera	255	213.86	52
Gelechiidae	Lepidoptera	3	2.06	3
Gnaphosidae	Araneae	2	5.18	2
Gracillariidae	Lepidoptera	12	3.57	11
Gryllacrididae	Orthoptera	4	325.74	3
Gryllidae	Orthoptera	764	7354.87	54
Hydrometridae	Hemiptera	2	17.94	2
Ichneumonidae	Hymenoptera	1	2.02	1
Lepidopsocidae	Psocoptera	3	0.69	3
Linyphiidae	Araneae	17	30.45	16
Liposcelidae	Psocoptera	6	0.02	3
Lycosidae	Araneae	85	1273.62	36
Mantidae	Mantodea	14	527.72	12
Merothripidae	Thysanoptera	2	0.14	2
Miridae	Hemiptera	50	11.17	16
Miturgidae	Araneae	1	2.26	1
Muscidae	Diptera	3	1.31	3
Mycetophilidae	Diptera	1	0.14	1
Mymaridae	Hymenoptera	59	1.26	27
Mymarommatidae	Hymenoptera	3	0.04	3
Nabidae	Hemiptera	27	88.67	13
Noctuidae	Lepidoptera	4	4.19	3
Ochyroceratidae	Araneae	1	0.90	1
Oxyopidae	Araneae	91	574.37	38
Pachytroctidae	Psocoptera	4	0.15	4
Pentatomidae	Hemiptera	1	117.74	1
Phalacridae	Coleoptera	2	0.60	2
Phasmatidae	Phasmatodea	1	1220.85	1
Philodromidae	Araneae	1	30.76	1
Phlaeothripidae	Thysanoptera	11	1.39	6
Pholcidae	Araneae	1	2.31	1
Platygastridae	Hymenoptera	1	0.03	1
Polyxenidae	Polyxenida	2	0.64	2
Psychodidae	Diptera	1	0.03	1
Psyllipsocidae	Psocoptera	2	1.91	2
Pyralidae	Lepidoptera	1	1.50	1
Reduviidae	Hemiptera	5	606.11	4
Ricaniidae	Hemiptera	1	0.26	1
Salticidae	Araneae	36	140.86	25
Scelionidae	Hymenoptera	89	10.69	37
Schizopteridae	Hemiptera	6	0.52	6
Sciaridae	Diptera	3	0.04	3
Simuliidae	Diptera	4	0.18	4
Sparassidae	Araneae	4	22.34	4

Sphecidae	Hymenoptera	1	13.89	1
Staphylinidae	Coleoptera	3	1.67	3
Termitidae	Isoptera	1	2.67	1
Tetragnathidae	Araneae	1	1.46	1
Tetrigidae	Orthoptera	37	978.99	23
Tettigoniidae	Orthoptera	20	2320.63	16
Theridiidae	Araneae	8	3.24	7
Theridiosomatidae	Araneae	75	24.19	34
Thomisidae	Araneae	8	22.93	6
Thripidae	Thysanoptera	22	1.28	13
Tingidae	Hemiptera	3	0.20	3
Tipulidae	Diptera	5	2.75	5
Trichogrammatidae	Hymenoptera	15	0.18	13
Tridactylidae	Orthoptera	6	39.30	5
Tropiduchidae	Hemiptera	2	2.23	2

Table S 3.17: Species/family numbers, beta diversity and Simpson index for plants, birds and leaf litter invertebrates in forest, oil palm and the experimental site.

		Forest	Oil palm	Experiment
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 Simpson index	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 Simpson index (±SD)	0.65 ± 0.06	0.47 ± 0.26	0.52 ± 0.23

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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.

Miriam Teuscher

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