Rubber plantations in the Indo-Burma biodiversity hotspot: habitat loss, biodiversity and economics

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Contents

Abstract

Natural rubber is in high demand for the manufacture of tyres, and rubber plantations are expanding globally. Southeast Asia is the epicentre of rubber cultivation, where deforestation to make way for rubber has been occurring for decades. This process has caused substantial biodiversity loss and carbon emissions. Expansion has recently shifted northwards into mainland Southeast Asia (the Indo-Burma biodiversity hotspot) due to the development of hardier rubber varieties that can survive longer dry seasons and cooler climates. The northward shift has been exacerbated by replacement of rubber with oil palm further south. Profitability and extent of rubber are comparable to oil palm, but rubber has received far less attention and scrutiny from civil society. Future demand for natural rubber is predicted to require 4.3 – 8.5 million ha of additional plantation area by 2024, relative to a 2010 baseline. Profits accruing from logging and conversion of forest to rubber in Cambodia are shown to be very high. The carbon prices that would be needed for a REDD+ program in Indo-Burma to match costs of forest conservation where rubber is a threat, are \$30 – 51 tCO_2^{-1}. These prices are far higher than those currently paid on carbon markets or through carbon funds, highlighting the importance of supply-chain initiatives, environmental governance and full valuation of ecosystem services for defending forests from conversion to rubber. Agroforestry methods for cultivating rubber in Thailand were found to produce yields comparable to monocultural methods, while providing modest benefits for bird and butterfly diversity. Agroforests did not support any species of conservation concern, and contiguous forests are irreplaceable for the conservation of forest biodiversity. Functional diversity of birds was found not to differ between rubber agroforests and monocultures, and species that feed primarily on nectar and fruit were extremely scarce in both types of rubber plantation.

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Chapter 1

Introduction

1.1 The biodiversity crisis and tropical forests

Global biodiversity indicators paint a grim picture: 322 vertebrate species have gone extinct since 1500, 67% of monitored invertebrate populations are in decline (Dirzo *et al.* 2014), populations of more than 1,600 terrestrial vertebrate species reduced by 21–51% from 1970 to 2012 (WWF 2016), and there is strong evidence that a sixth anthropogenically-induced mass extinction event is underway (Ceballos *et al.* 2015). Each year, ~52 species of amphibians, birds and mammals have their IUCN Red List categorisation moved closer to extinction, only partially slowed by conservation efforts (Hoffmann *et al.* 2010).

Loss and degradation of habitat, particularly through agricultural expansion, are the key drivers of species decline (Green *et al.* 2005, Baillie *et al.* 2010, Böhm *et al.* 2013, WWF 2016). Additional threats include direct exploitation for consumption or trade, pollution, introduced species and diseases, and climate change, often working in synergy (Brook *et al.* 2008, WWF 2016). These losses are having major effects on ecosystem processes and function, comparable to the effects of ozone or nutrient pollution (Hooper *et al.* 2012).

All drivers of biodiversity loss are fundamentally underpinned by overconsumption of natural resources by people. Overall, human consumption of ecosystem goods and services has been exceeding the rate of regeneration since the 1980s, causing an "ecological overshoot" situation (Wackernagel *et al.* 2002, Kitzes *et al.* 2008). Humans appropriate at least 25% of global net primary productivity (Haberl *et al.* 2007, Krausmann *et al.* 2013), and of all ice-free land, 30 – 40% is used for agriculture and 75% is modified by humans (Vitousek *et al.* 1997, Foley *et al.* 2005, Ellis and Ramankutty 2008, Ramankutty *et al.* 2008, Ellis *et al.* 2010), while net forest cover declined by 1.5 million km^2 between 2000 and 2012 (Hansen *et al.* 2013). Analysis of progress towards the "Aichi Targets" (agreed at the Convention on Biological Diversity in 2010) based on 55 indicators, suggests that trends in biodiversity loss are unlikely to have improved by 2020 (Tittensor *et al.* 2014).

The state of natural capital is also declining (86% of all indicators assessed) while delivery of benefits is increasing, indicating unsustainable use; this suggests that although human wellbeing is increasing in the near term as a result of unsustainable use of natural capital, this trend is unlikely to continue in the longer term (Shepherd *et al.* 2016). Land-use change is estimated to have reduced the value of ecosystem services by $4.3 – 20.2 trillion per year between 1997 and 2011 (Costanza *et al.* 2014), with an estimated $6.3 trillion per year of ecosystem service value lost annually through impaired ecosystem function resulting from land degradation (poor management of natural capital; Sutton *et al.* 2016).

Tropical forests contain more than 50% of the earth's known species, directly provide more than 1 billion people with food, timber, medicines and ecosystem services, and regulate climate, exchanging more water and carbon with the atmosphere than any other biome (Lewis *et al.* 2015). They take diverse forms, from lowland evergreen forests with multiple strata and towering emergent trees more than 90 m in height (Carnegie Airborne Observatory 2017) to open grassland-savannahs (Parr *et al.* 2014). Between 2000 and 2012, 32% (~0.7 million km^2) of all global forest loss occurred in tropical rainforests and, despite a reduced deforestation rate of rainforests in Brazil, this was more than offset by increased annual rates of loss in other places, including dry tropical forests in South America and Indonesia (Hansen *et al.* 2013). Agricultural expansion is the key driver of tropical deforestation: 27% of the tropical forest biome has been replaced with agriculture (Ramankutty *et al.* 2008) and 78% of new agricultural land came at the expense of tropical forest from 1980 to 2000 (Gibbs *et al.* 2010). Mining of geological resources and fossil fuels is also causing forest loss, and additional pervasive pollution (Asner *et al.* 2013, Edwards *et al.* 2014, Abood *et al.* 2015, Alvarez-Berríos and Mitchell Aide 2015). Degradation is estimated to affect 30% of forests globally (International Sustainability Unit 2015), leading to carbon emissions (Berenguer *et al.* 2014) and affecting biodiversity (Edwards, Larsen, *et al.* 2011, Gibson *et al.* 2011, Barlow *et al.* 2016). Key drivers of degradation are selective logging, fire, fragmentation and edge effects (Lewis *et al.* 2015). In addition, apparently intact forests are increasingly de-faunated by hunting or trapping for direct consumption or trade, resulting in "empty forests" that have altered ecological functioning and processes (Redford 1992, Lewis *et al.* 2015).

1.2 Climate change

Anthropogenic emissions of carbon dioxide and other greenhouse gases are driving changes to the global climate system, causing warming and acidification of the oceans, declines in sea ice, sea level rise, changes in the frequency and magnitude of extreme weather events, and alterations to temperature and rainfall patterns (Stern 2007). Climate change is already affecting biodiversity through range shifts, changes to phenology, species invasions, alterations to ecological communities and, in marine systems, ocean acidification (Walther *et al.* 2002, Parmesan and Yohe 2003, Thomas *et al.* 2004). Human welfare, particularly of the poor, is also put at risk through changes to water availability, food production and exposure to extreme weather events (Stern 2007).

Forests are involved in fundamental climate processes, regulating water and carbon exchange with the atmosphere (Bonan 2008), with tropical forests playing a particularly important role (Lewis *et al.* 2015), but human activity undermines delivery of these fundamental ecosystem services. Carbon emissions from forestry and non-agricultural land uses (FOLU) account for ~11% of annual global emissions (mostly from forest fires, peat fires and peat decay; IPCC 2014). Forests absorbed around 60% of all fossil fuel carbon emissions from 1990 to 2007, and although deforestation of tropical forests produced the equivalent of ~40% of fossil fuel emissions, more than half of this was offset by regeneration of degraded forests, and regrowth on abandoned agricultural land in the tropics (Pan *et al.* 2011). The net effect of forest carbon uptake and emissions from deforestation is that tropical forests are nearly carbon neutral (Pan *et al.* 2011). Agriculture contributes a further 13% of carbon emissions annually (IPCC 2014) and, including all greenhouses gases (CO_2, CH_4 and NO_2), deforestation and agriculture together account for 36% of all emissions, 60% of which occurs in tropical countries (DeFries and Rosenzweig 2010).

Agricultural land expanded by ~3% per year from 1985 – 2005, with a net redistribution away from temperate areas towards the tropics (Foley *et al.* 2011). The only large areas of land suitable for agriculture that remain unconverted are tropical forests and woodlands (DeFries and Rosenzweig 2010). Forest clearance for agriculture in the tropics represents a poor trade-off between carbon emissions and productivity: deforestation increased agricultural area by 2.5% from 2000 to 2005, but generated 39% of all CO_2 emissions by tropical countries (DeFries and Rosenzweig 2010, West *et al.* 2010). Each ton of crop yield produced in the tropics results in around 3 tonnes of carbon emissions (~11 tonnes CO_2), whereas crops grown in temperate regions emit only 1 tonne (West *et al.* 2010). Despite these costs, expansion of agricultural area has contributed far less to agricultural production than intensification of existing land in developing countries (DeFries and Rosenzweig 2010, Foley *et al.* 2011). Together, this makes the conservation of forests, and the interactions between forests and agriculture, key for tackling global climate change.

1.3 Carbon finance as a tool for forest conservation

Economic drivers strongly influence the rates of deforestation (Foley *et al.* 2011), while ecosystem goods and services (“natural capital”) are under-priced in markets relative to their shadow prices (i.e. the estimated price in the absence of a real market for a good or service), giving little reason to economise on their use (Dasgupta 2008). This results in unrealistic estimates of the importance of natural capital for national incomes, and makes the accurate valuation of ecosystem services vitally important (Dasgupta 2008). Valuation of ecosystem services does not necessarily mean they should be commodified or privatised, as they are best considered public goods or common-pool resources; instead, non-market institutions are likely needed to ensure that ecosystem service values are properly accounted for (Costanza *et al.* 2014). In the case of forests, modelling has showed that without climate change mitigation strategies that place value on terrestrial carbon stocks, large areas of forest will be cleared during the 21st century in both temperate and tropical environments (Thomson *et al.* 2010) and, although the commodification of carbon in forests could risk costs for biodiversity and forest dependent people if non-carbon benefits are not taken into consideration, existing markets already commodify extractive forest products without internalising these costs (Turnhout *et al.* 2017).

The concept of payments for the carbon sequestration and storage services provided by forests was first formalised in the United Nations Framework Convention on Climate Change (UNFCCC) negotiations in 2001, by including afforestation and reforestation as part of the Clean Development Mechanism (CDM) developed under the 1997 Kyoto Protocol. Avoided deforestation (Reduced Emissions from Deforestation; RED) was added into UNFCCC negotiations in 2005 under pressure from the Coalition of Rainforest Nations, with degradation added in 2007 (REDD), but these were not included in the CDM. The concept developed into REDD+ in 2008 as the additional co-benefits of forest protection for biodiversity, people, and other ecosystem services became increasingly recognised. The Warsaw Framework, produced in 2013, outlined guidance for national scale REDD+ activities (monitoring, reporting, verification of emissions reductions, and safeguards), and REDD+ was finally fully integrated into climate negotiations with the 2016 Paris Agreement.

REDD+ has generated a far greater commitment of funding, and interest, than any other idea for protecting tropical forests (Angelsen *et al.* 2012), and a range of REDD+ activities have developed alongside the UNFCCC negotiations, from small-scale demonstration projects to preparatory and readiness activities by tropical forest nations. Nearly $10 billion had been committed to national scale REDD+ programmes even before the Paris Agreement, and $6 billion had been disbursed; however, at least five times more funding is estimated to be needed to cover the results-based finance (Silva-Chávez *et al.* 2015, Wolosin *et al.* 2016). Public funding has been channelled through UNREDD, the World Bank's Forest Carbon Partnership Facility (FCPF), and multi- and bilateral agreements between national governments, while private funding of REDD+ projects through voluntary carbon markets are the only place where REDD+ credits can currently be traded (Angelsen *et al.* 2009, Turnhout *et al.* 2017). Assuming a carbon price of $5 tCO_2^{-1} (the price used by the FCPF), and assuming that all finance pledged for REDD+ so far is used to pay for verified emissions reductions (rather than preparatory activities), only about 50% of the estimated supply of carbon credits will be paid for (Turnhout *et al.* 2017). Ninety percent of REDD+ funding so far has come from public money, but private sector finance and input will also be needed to fulfil the aims of REDD+ (Graham and Silva-Chávez 2016). The inclusion of REDD+ credits on compliance markets, as is planned in 2018 for California's state-drive carbon market (which serves its cap-and-trade scheme), may generate additional funding (Turnhout *et al.* 2017).

Large-scale agriculture is a key driver of deforestation that tends to prioritise short-term economic gain (Geist and Lambin 2002, Boucher and Elias 2013). Multiple studies have found that funds available through REDD+ will be insufficient to fully compensate the forgone profits (opportunity costs) of avoided deforestation for large-scale agriculture (e.g. Kremen *et al.* 2000, Edwards, Fisher, *et al.* 2011, Fisher, Edwards, *et al.* 2011, Fisher, Lewis, *et al.* 2011). As these costs vary in space, together with carbon stocks and biodiversity value, conservation planning that incorporates cost-effectiveness is likely to increase efficiency of conservation efforts (Naidoo and Ricketts 2006, Naidoo *et al.* 2006), including REDD+. There are now region specific analyses of cost-effectiveness of REDD+ strategies and locations, that can inform policy-making (Gilroy *et al.* 2014, Graham *et al.* 2016, 2017), but gaps in knowledge remain.

REDD+ may pose risks to biodiversity by focussing forest conservation efforts on high-carbon forests, displacing damaging activity to lower-carbon but high conservation value habitats (Miles and Kapos 2008, Harrison and Paoli 2012), particularly for tropical grassy biomes (Parr *et al.* 2014). In Indonesia there is evidence for spatial congruence between REDD+ projects and biodiversity benefits, but this is driven by conservation focussed NGOs utilising REDD+ as a tool, rather than spatial congruence between carbon density and biodiverse areas; indeed, if REDD+ is optimised for cost-effectiveness in Indonesia by targeting the most carbon-rich forests, maximum species richness may not necessarily be protected (Murray *et al.* 2015), although threatened mammals may be (Venter, Meijaard, *et al.* 2009). At the global level there is substantial congruence between carbon density and biodiversity conservation value, but there are notable exceptions, and relationships can be highly scale-dependent, for example in very fragmented high-carbon ecosystems that contain endangered species (Strassburg *et al.* 2010). Considering costs, the most cost-effective locations may not align with maximum biodiversity benefits (Venter, Laurance, *et al.* 2009, Siikamäki and Newbold 2012), but inclusion of biodiversity in decision making could substantially improve co-benefits while compromising less than 10% of carbon stock (Venter, Laurance, *et al.* 2009). The long-term success of REDD+ may actually depend on biodiversity value: continued ecosystem function of forests is required for long-term carbon sequestration services by forests, which may be compromised through biodiversity loss, such as through seed dispersal of carbon-dense tree species by large mammals and birds (Brodie and Gibbs 2009, Díaz *et al.* 2009, Hinsley *et al.* 2014).

In addition, the importance of co-benefits to REDD+ activities so far is evident in the numerous certification schemes for biodiversity and sustainable development; 81% of all REDD+ projects with buyers had a co-benefit certification, such as Climate, Community and Biodiversity Standards, Forest Stewardship Council or the Rainforest Alliance, and many were already conservation projects (Merger *et al.* 2011, Murray *et al.* 2015, Turnhout *et al.* 2017). At the UNFCCC level, safeguards (no net harm; different to co-benefits which are considered additional positive externalities; Phelps *et al.* 2012) for biodiversity and people are built into the Warsaw Framework for national REDD+ development, and countries are also encouraged to include co-benefits in national scale planning, although performance-based payments specifically for co-benefits may be unlikely (Turnhout *et al.* 2017). The potential for biodiversity co-benefits of REDD+ are, therefore, neither automatic nor guaranteed, and may require additional policies, incentives or strategies (Gardner *et al.* 2012, Phelps *et al.* 2012).

1.4 Biodiversity in tropical agricultural landscapes

It is often stated that food production will need to double by 2050 to meet the consumption demands of a growing human population, but this statistic is often misused (Tomlinson 2013). There is currently sufficient food production for the entire human population, and hunger and malnutrition are caused by lack of food access, distribution problems, and wastage (Godfray *et al.* 2010, Foley *et al.* 2011, Tscharntke *et al.* 2012, Tomlinson 2013, Kremen 2015). However, existing demand for food is likely to be compounded by diet changes and increasing consumption by those who can afford it, the use of land to grow bioenergy crops, and growing demand for non-food agricultural commodities (Godfray *et al.* 2010, Foley *et al.* 2011). Only 62% of all crop production is used directly for human food; 35% is used for animal feed and 3% for industrial products, seeds and bioenergy, and the proportion of food to non-food crops varies substantially among regions (Foley *et al.* 2011). It has thus been argued that future increased demand could be met by closing yield gaps, reducing waste, and shifting more of production to direct human consumption, rather than raising animals, but that this increase in production must come from increased productivity on existing land rather than agricultural expansion (DeFries and Rosenzweig 2010, Godfray *et al.* 2010, Foley *et al.* 2011).

There is vigorous debate about the best approaches to conserving biodiversity in landscapes that contain agriculture. The "land-sharing" approach suggests that wildlife-friendly farming methods can help minimise biodiversity loss in agricultural landscapes, for example by retaining small areas of natural habitat and reducing the effects of chemical inputs on non-target taxa (Green *et al.* 2005). This idea is particularly prevalent in Europe, where most ecosystems have already been transformed by agriculture, and declines in farmland birds through intensification have led to substantial subsidies for wildlife-friendly farming practices (Donald *et al.* 2002, Green *et al.* 2005). However, reduced-intensity farming could increase the total area of land needed for a particular level of production, resulting in expansion of farmland onto natural habitats that support species unable to persist in agricultural landscapes, generating net losses for biodiversity (Green *et al.* 2005). Alternatively, in the "land-sparing" approach, yields on existing farmland are increased, potentially freeing up farmland for restoration or reducing pressure for conversion of natural habitat (Green *et al.* 2005).

The most rigorous protocol for comparing the biodiversity benefits of land-sparing and land-sharing compares the abundances of individual species across sites that vary in yields (Green *et al.* 2005); application of this method in Ghana and India found that land-sparing benefitted more species (Phalan *et al.* 2011). Numerous other studies have applied similar methods in a range of contexts, but there are a range of issues with the land-sparing land-sharing paradigm, and associated debate (Kremen 2015). The extremes of both the land-sparing and land-sharing scenarios have poor outcomes for biodiversity: in the former, large reserves become isolated in a completely inhospitable matrix, and in the latter, tiny isolated fragments of natural habitat are surrounded by wildlife-friendly agriculture (Kremen 2015). Moreover, the debate suggests that an either-or choice can be made, which doesn't exist in reality (Fischer *et al.* 2011, Kremen 2015).

Biodiversity and yields can both be high in some systems and, as well known in agricultural habitats in Europe, some globally threatened open-habitat species are dependent on low-intensity agriculture in the developing world, which are often overlooked in the focus on forest dependent species in the tropics (Fischer *et al.* 2011, Wright *et al.* 2012). In addition, many areas are unsuitable for conventional intensification: these tend to already be cultivated using complex agro-ecological systems under a land-sharing approach (Fischer *et al.* 2011). Food security for the rural poor comes from local scale production, and 75% of chronically hungry people are smallholder farmers who produce 50 – 70% of the world's food; these farmers often face yield gaps, but conventional intensification tends to be inappropriate due to the costs of inputs, and is more suitable for commodity crops that do not feed the hungry (DeFries and Rosenzweig 2010, Kremen 2015). Conventional intensification also has its own negative effects on biodiversity, ecosystems and human health, including water degradation, increased energy use and pollution (Foley *et al.* 2011).

In addition, the relationship between agricultural yield and land-sparing is not simple, and is strongly influenced by markets and governmental policies – specifically, strong environmental governance (DeFries and Rosenzweig 2010, Kremen 2015). Increased yields can lead to increased encroachment onto forested land at the local level due to rebound effects, or "Jevons paradox" (Rudel *et al.* 2009, Angelsen 2010, Lambin and Meyfroidt 2011, Phelps *et al.* 2013, Ceddia *et al.* 2014). Evidence for land sparing taking place as the result of agricultural intensification is mixed, and depends on the crops in question. Analysis across 124 countries showed that increased yields led to area decreases for the same crop types, but other crops still expanded, and although forest was spared it was unclear whether this was consolidated or resulted in forest fragments within the agricultural landscape (Ewers *et al.* 2009). These findings were corroborated by global-scale modelling, which found that although land sparing has taken place following the Green Revolution, as predicted by the Borlaug hypothesis (Borlaug 2007), the amount of land spared was much less than predicted, and was affected by elasticity of demand for agricultural products, spatial proximity of yield increases to forest margins, and labour intensiveness of the crops in question (Stevenson *et al.* 2013). Intensification of crops with relatively fixed demand, that are consumed locally, and are grown in well-established agricultural areas away from forest margins, is likely to spare forest; in contrast, intensification of globally traded cash crops with elastic demand, grown close to the forest frontier, is likely to increase forest clearance (Stevenson *et al.* 2013, Kremen 2015). International trade in agricultural commodities and wood products also means that avoided deforestation can be displaced among nations, meaning efforts to reduce deforestation at the global scale must be closely linked to global trade (Meyfroidt *et al.* 2010). In this latter case, supply chain interventions such as agricultural sustainability standards and zero-deforestation commitments that link into global trade can be successful (Nepstad *et al.* 2014, Tayleur *et al.* 2016).

The land-sparing debate can also become irrelevant in some landscapes, for example where forest has already been widely cleared and agricultural activities are well established, but can be highly relevant in others, such as in the design of Brazil's forest set-aside policies (Kremen 2015) or wildlife-friendly plantation landscapes (Edwards *et al.* 2010). Future deforestation will likely be driven by large-scale agricultural production, as in the Southern Amazon and Southeast Asia, as in many cases land tenure is clearer and the risk of social conflicts is lower, which creates an opportunity for land-use planning and application of land-sparing or -sharing principles; in contrast, small farmers are unlikely to be able to move, and landscape-scale planning of small farm expansion may be less feasible (DeFries and Rosenzweig 2010, Meyfroidt *et al.* 2014). It is also important to remember that land sparing does not equate to nature sparing: benefits for biodiversity depend on specific policies and actions, such as establishment of protected areas (Kremen 2015), and the capacity to protect forests is low in many developing countries, whereas land-sharing is a well-understood concept (Fischer *et al.* 2011).

An alternative "both-and" framing of the debate has been proposed, which focuses research on how the matrix between areas of natural habitat can support species persistence in reserves and promote dispersal, and how biodiversity and livelihoods can be reconciled (Kremen 2015). This approach is supported by findings that conservation outcomes in protected tropical forests are strongly and directly linked to changes in surrounding habitats (Laurance *et al.* 2012), and the broad recognition that both large, high-quality areas of natural habitat, and connectivity between these areas, are necessary for biodiversity conservation (Hodgson *et al.* 2011).

Research is also needed that directly assesses the biodiversity outcomes of specific management techniques, rather than assessing broad-scale patterns, as low yields do not equate to biodiversity benefits (Kremen 2015), such as assessing the effect of epiphyte removal in oil palm (Prescott *et al.* 2016) or structure of cacao agroforests (Clough *et al.* 2011), while also considering the socio-economics of management. For example, farmers may prefer a particular farming method despite yield or income losses (Steffan-Dewenter *et al.* 2007, Plumb *et al.* 2012).

An additional important point for tropical agricultural systems is the relative role of ecosystem services provided by on-farm biodiversity for small low-input farms. Alongside the negative environmental consequences of conventional intensification, yield increases seem to be slowing: yields increased by 56% from 1965 to 1985, but only by 20% from 1985 to 2005 (Foley *et al.* 2011). Opportunities for harnessing the ecosystem-service benefits of on-farm biodiversity through “agroecological intensification” strategies are now being identified, which aim to regenerate long-term ecosystem properties such as water storage, soil health and resistance to pest and diseases (Lin 2011, Kremen 2015), for example by increasing pollinator diversity to improve yields (Garibaldi *et al.* 2016). Agroecological intensification methods tend to be knowledge, management and labour intensive, and thus appropriate for smaller scale farms (Kremen 2015), although techniques such as crop diversification can also provide net benefits on larger scale farms in developed countries (Davis *et al.* 2012). Diversified agricultural systems do less environmental harm than intensified ones, but can result in some yield gaps despite increased provision of ecosystem services, meaning more research into agroecological intensification methods is urgently needed (Lin 2011, Kremen and Miles 2012).

Agroforestry, a broad term encompassing any practice that integrates trees or other large woody perennial plants with other crops in a farming system, is one method that has received research attention for its perceived role as a biodiversity-friendly production system (Schroth *et al.* 2004). Agroforests can be a useful tool for biodiversity conservation outside of protected areas, whether by directly acting as wildlife habitat, forming corridors or permeable matrices between forest fragments, maintaining habitat heterogeneity at plot and landscape levels, or by alleviating extractive pressure on forest reserves by providing forest resources (Bhagwat *et al.* 2008).

1.5 The study system: natural rubber (*Hevea brasiliensis*) in Indo-Burma

The research in this thesis focusses on the expansion and production of natural rubber (*Hevea brasiliensis*), and its impacts on forests and biodiversity in the Indo-Burma biodiversity hotspot. This hotspot covers Laos, Cambodia, Vietnam, most of Myanmar and Thailand, and parts of Southwest China, including Xishuangbanna and Hainan Island (Myers *et al.* 2000). This region is commonly termed "mainland Southeast Asia" in other research disciplines, and the two terms are used interchangeably in the thesis. Indo-Burma has received far less conservation research attention than other parts of Southeast Asia, particularly Sundaland (Giam and Wilcove 2012), but research specific to this region is vital given differences in biogeography, climate and socio-economic context.

Rubber is a major cash crop in Southeast Asia, rivalling oil palm in profitability (Clough *et al.* 2016) and extent, and its expansion is now a major driver of deforestation in Indo-Burma (Chapter 2). Expansion is also now occurring in tropical Africa (Ordway *et al.* 2017), highlighting its global importance as a driver of land use change. In extent, impact and threat posed to forests and biodiversity, it is comparable to other major global cash crops, but has received less attention in the conservation literature, and far less public scrutiny (Chapter 2). Rubber had, until recently, slipped under the radar of commodity-targetted sustainability efforts, such as those for oil palm, cocoa, or paper pulp (Tayleur *et al.* 2016), but two initiatives emerged while this research was underway: the Sustainable Natural Rubber Initiative, established by the International Rubber Study Group in 2014 (IRSG 2014), and the first business commitment to "deforestation-free rubber" by Michelin in 2016 (Michelin 2016).

Within Indo-Burma, Cambodia, a hotspot of deforestation and rubber expansion, is used as a case-study to investigate economic trade-offs between forest protection, and logging and conversion to large-scale monocultural rubber plantations. Southern Thailand, the world's biggest producer of natural rubber, is then used as a case-study to investigate the biodiversity benefits of rubber agroforestry in smallholder plantations.

1.6 Research aims and structure

The research conducted for this thesis was conducted in an attempt to provide policy-relevant evidence for use in efforts to prevent deforestation for rubber and develop sustainability standards. More broadly, it is hoped that the research contributes to understanding the scale of economic incentives for deforestation in Indo-Burma, and sheds more light on trade-offs between biodiversity and yields in tropical agro-ecosystems. All chapters have been prepared as manuscripts for submission to scientific journals, and are in various stages of the publication process. Each chapter has its own set of references, supplementary material, and supplementary references, and there is necessarily some repetition of methods.

The first piece of research in this thesis (chapter 2) is a review, that brings together existing knowledge of the biodiversity impacts of rubber on tropical biodiversity, and estimates the scale of future rubber expansion needed to meet global demand. This chapter has already been published and was the second most accessed paper published by *Conservation Letters* in 2015 (Warren-Thomas *et al.* 2015).

Chapter 3 focusses on carbon finance as a tool to protect forests in Cambodia from conversion to rubber plantations. Despite an accumulation of knowledge about other economic drivers of deforestation in Southeast Asia (Wilcove *et al.* 2013), the magnitude of economic incentives to log and convert forest to rubber in Cambodia, or the wider region, are not well understood. This chapter is currently in review at *Nature Communications*.

Chapter 4 shifts focus onto the biodiversity value of rubber plantations in Thailand, and investigates whether the value of rubber plantations could be improved for birds, reptiles and butterflies by using agroforestry techniques. This chapter has been prepared for submission to *Journal of Applied Ecology*.

Chapter 5 investigates the functional diversity of birds in rubber monocultures and agroforests in Thailand, and discusses implications for ecosystem functioning and services. This chapter has been prepared for submission to *Biological Conservation*.

The final chapter summarises the findings of the entire thesis, and makes some recommendations for future research.

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Chapter 2

Increasing demand for natural rubber necessitates a robust sustainability initiative to mitigate impacts on tropical biodiversity

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2.1 Abstract

Strong international demand for natural rubber is driving expansion of industrial-scale and smallholder monoculture plantations, with >2 million ha established during the last decade. Mainland Southeast Asia and Southwest China represent the epicentre of rapid rubber expansion; here we review impacts on forest ecosystems and biodiversity. We estimate that 4.3 – 8.5 million ha of additional rubber plantations are required to meet projected demand by 2024, threatening significant areas of Asian forest, including many protected areas. Uncertainties concern the potential for yield intensification of existing cultivation to mitigate demand for new rubber area, versus potential displacement of rubber by more profitable oil palm. Our review of available studies indicates that conversion of forests or swidden agriculture to monoculture rubber negatively impacts bird, bat and invertebrate biodiversity. However, rubber agroforests in some areas of Southeast Asia support a subset of forest biodiversity in landscapes that retain little natural forest. Work is urgently needed to: improve understanding of whether land-sparing or land-sharing rubber cultivation will best serve biodiversity conservation, investigate the potential to accommodate biodiversity within existing rubber-dominated landscapes while maintaining yields, and ensure rigorous biodiversity and social standards via the development of a sustainability initiative.

2.2 Introduction

Tropical forest loss is increasing (Hansen et al. 2013), primarily due to agricultural expansion (Gibbs et al. 2010; Foley et al. 2011). Continued agricultural expansion and intensification are predicted, driven by rising demand (Laurance et al. 2014). Concern over expansion of agro-industrial tree plantations in the tropics, including oil palm (Fitzherbert et al. 2008; Koh & Wilcove 2008) and paper-pulp (Wilcove et al. 2013), led to a series of sustainability labels developed to reduce negative biodiversity, ecosystem service and social outcomes (Edwards & Laurance 2012; Edwards et al. 2012). Here, we focus on another rapidly expanding plantation crop: natural rubber, *Hevea brasiliensis.* There is growing concern that rubber cultivation is negatively impacting livelihoods, soils and ecosystem services (Ziegler et al. 2009b; Fox & Castella 2013; Xu et al. 2013). Here, we estimate potential future rubber extent, and collate evidence for biodiversity impacts of rubber cultivation from across Southeast Asia, to inform emerging sustainability labelling efforts by the rubber industry and focus further research on this rapidly expanding crop.

The distribution of rubber across Southeast Asia (Figure 1) coincides with four biodiversity hotspots: Sundaland (Malay Peninsula, Borneo, Sumatra, Java, and Bali), Indo-Burma (Laos, Cambodia, Vietnam, most of Myanmar and Thailand, and parts of Southwest China, including Xishuangbanna and Hainan Island), Wallacea (Indonesian islands east of Bali and Borneo but west of New Guinea, plus Timor Leste) and the Philippines (Myers et al. 2000), supporting large numbers of endemic and highly threatened species (Sodhi et al. 2004). Rubber cultivation occurs within multiple biogeographic realms and ecoregions, including subtropical montane rainforests and coniferous forests in Southwest China, moist and dry evergreen and deciduous forests in Indo-Burma, and tropical and sub-tropical moist lowland forests in Sundaland, Wallacea and the Philippines (Olson et al. 2001). Cultivation practices vary from large-industrial or smallholder monocultural plantations, to various methods of rubber agroforestry (Fox & Castella 2013).

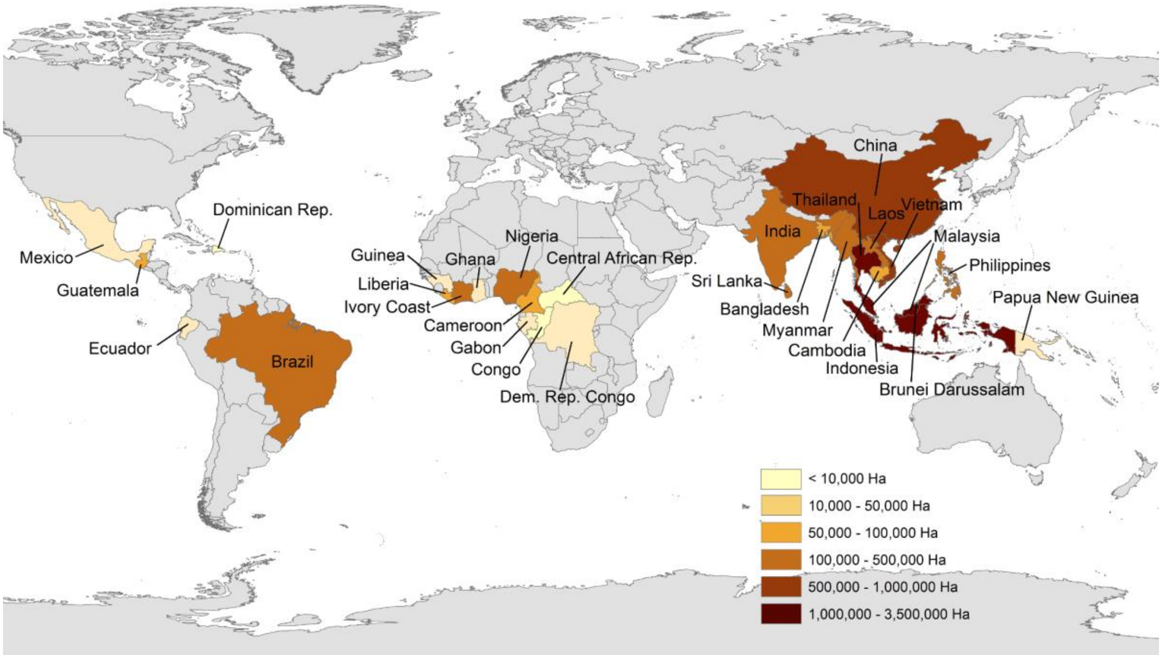

FIGURE 1

Rubber extent in all rubber producing countries, excluding Bolivia for which data were unavailable. Data sources listed in Table S2.

Global demand for natural rubber has increased rapidly in the past decade, driven particularly by China's economic emergence (Figure S1; FAO 2013). Natural rubber is preferred for many products, with 70% of global consumption used in tyres (Clay 2004). Rising demand, partly driven by the increased cost of crude oil used for synthetic alternatives (Figure 2), has caused price volatility, peaking in 2011 at US$6.26 kg^{-1} on the Singapore Commodity Exchange and with a longer-term increase from US$1.1 kg^{-1} in 2003 to US$2.8 kg^{-1} in 2013 (Figure 2). By 2012, rubber covered an area equivalent to 71% of oil palm extent within Southeast Asia (including Southwest China) and 57% of oil palm globally (FAO 2013). It is the most rapidly expanding tree crop within mainland Southeast Asia (Cambodia, Laos, Myanmar, Thailand, Vietnam, and Yunnan, Southwest China; Fox et al. 2012).

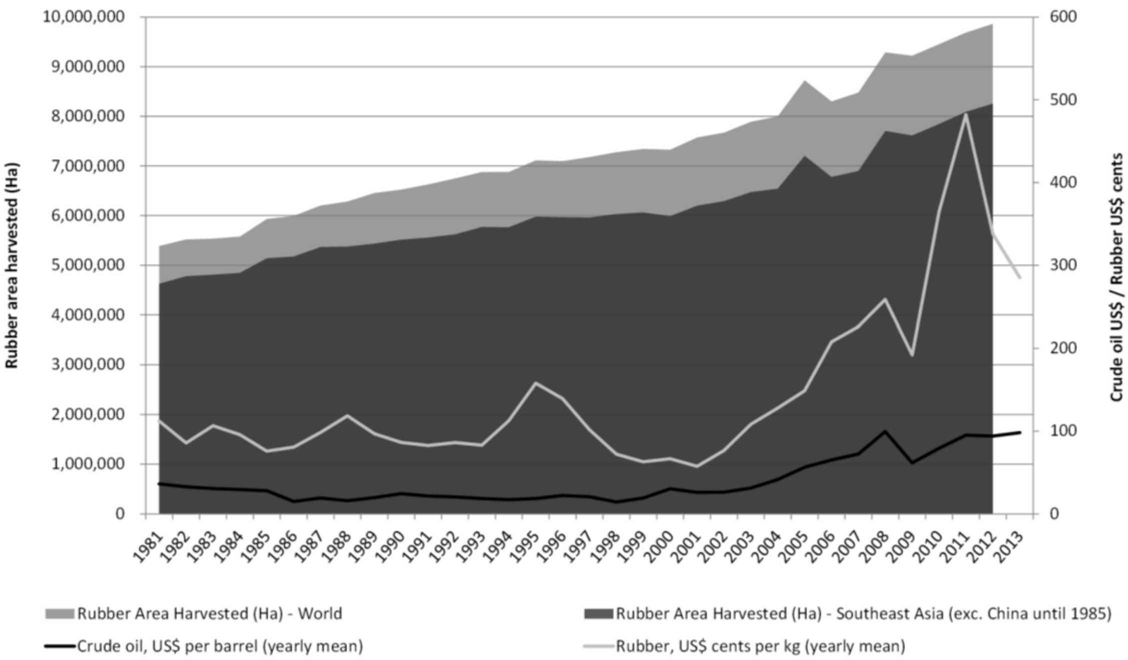

FIGURE 2

Trends in harvested area of rubber and price of rubber and crude oil, 1981 – 2013. Rubber area data sourced from FAOSTAT Online Statistical Service (FAO, 2013). Data do not include Laos (no data available) and data for China are only included from 1985 onwards. Price data for crude oil in US$ per barrel sourced from IMF Primary Commodity Prices database (IMF 2013) and for natural rubber in US$ per kg from the World Bank Global Economic Monitor Databank on commodities, defined as "Rubber (Asia), RSS3 grade, Singapore Commodity Exchange Ltd (SICOM) nearby contract beginning 2004; during 2000 to 2003, Singapore RSS1; previously Malaysia RSS1" (The World Bank 2013).

Concern over rubber expansion has been building, initially focussing on rapid planting in Xishuangbanna, since the early 2000s (Guo et al. 2002; Fox & Vogler 2005; Ziegler et al. 2009b; Xu et al. 2013), then widening to mainland Southeast Asia (Li & Fox 2012; Fox & Castella 2013). In montane regions of mainland Southeast Asia (MMSEA; defined as areas >300m asl), plantations on steep slopes detrimentally affect soil erosion, landslide risk and water quality (Li et al. 2007; Ziegler et al. 2009a), with ecosystem service provision across 35,000 ha of Xishuangbanna (Menglun township) reduced by an estimated 28% over 18 years following rubber establishment, a loss valued at US$11.4 million (Hu et al. 2008). Conversion of swidden (or shifting) agriculture and forest to rubber can result in substantial carbon emissions (Li et al. 2008), although carbon outcomes can be highly variable (Ziegler et al. 2012; Yuen et al. 2013).

Conversion to rubber can increase evapo-transpiration by 15-18% relative to native vegetation (Tan et al. 2011). While native vegetation takes up sub-surface water after rainfall, rubber depletes deep-soil moisture during the dry season, with potential to reduce groundwater and streamflow (Guardiola-Claramonte et al. 2008; Kobayashi et al. 2014). These impacts may be compounded by reduced fog interception relative to complex natural canopies, which provides a major dry season water input in

Xishuangbanna (Xu et al. 2013). Basin-scale modelling showed conversion to rubber could reduce annual water discharge by 29% (Guardiola-Claramonte et al. 2010) and, although unproven, low stream flow and well desiccation have been attributed to rubber plantations in Xishuangbanna (Qiu 2009).

Although establishment of rubber plantations has substantially increased smallholder income in Southwest China and Northern Thailand (Liu et al. 2006; Fox et al. 2013) there are concerns that replacing swidden agriculture with industrial-scale rubber plantations in mainland Southeast Asia could disadvantage rural communities (Baird 2010; Ziegler et al. 2011; Fox & Castella 2013). Reports of evictions, coercion, increased poverty, decreased food security and poor labour conditions associated with rubber plantations have recently emerged from Laos, Cambodia and Myanmar (OHCHR 2007; Baird 2010; Woods 2011; Global Witness 2013). Despite concern over possible biodiversity declines following conversion to rubber (e.g. Ziegler et al. 2009b), emerging evidence of biodiversity impacts has not been collated and synthesised previously, despite a rubber extent comparable to that of oil palm.

In this paper we summarise the history of rubber expansion and land-use change, contrasting the contexts across Southeast Asia, particularly between insular (Sabah, Sarawak, Indonesia) and mainland areas. We project the likely scale of expansion required for expected future rubber demand, and quantitatively review evidence on the responses of biodiversity to rubber cultivation in differing bio-geographic contexts. We finish by highlighting research needed to help meet demand at minimum environmental cost, and to build a robust rubber sustainability initiative.

2.3 Land use change for rubber cultivation – a brief history

Southeast Asia (including parts of Southwest China) is the epicentre of rubber cultivation, containing 84% of total global area in 2012 (Figure 1, Table S1). Rubber was first planted in state-run plantations in Malaysia, Indonesia, and southern areas of Thailand, Vietnam, Cambodia and Myanmar, and subsequently adopted into smallholder agroforestry systems 10° either side of the equator (Clay 2004). 'Traditional' rubber varieties required ≈2000 sunshine hours yr^{-1}, mean annual temperatures of 28±2°C, and annual rainfall of 2000-4000mm (Priyadarshan et al. 2005). From the 1950s, development of high-yielding clonal varieties in China, which tolerate long dry seasons, less sunshine and temperatures as low as -1°C (Priyadarshan et al. 2005), facilitated a wave of rubber monoculture expansion to 22°N (Clay 2004; Li & Fox 2012) and to higher altitudes (Nguyen 2013; >900 m asl, returns are minimal or non-existent, Yi et al. 2013). Expansion was compounded by replacement of rubber with oil palm across Malaysia and Indonesia (Gunarso et al. 2013), coupled with the ability of rubber to grow on a wide range of soil types (Priyadarshan et al. 2005; Usha Nair et al. 2010; Priyadarshan 2011; Li et al. 2012), including low-fertility areas unsuitable for more profitable crops such as cacao, coffee, or oil palm.

Subsequent expansion has been rapid: globally, land area under rubber has grown 1.8-fold over the past three decades, from 5.5 to 9.9 million ha from 1983 to 2012 (Figure 2). The mean expansion rate of 107,608 (±21,269 SE) ha yr^{-1} in harvested area during the first two decades more than doubled to 219,188 (±111,440 SE) ha yr^{-1} in the last decade (Figure 2). Official data on rubber area at the national level (FAO 2013) can be unreliable (Table S1) resulting in attempts to directly assess rubber area using remote sensing. In mainland Southeast Asia, 2.1 million ha of rubber has been detected, with around 550,000 ha established within four years preceding Li and Fox's study (2012). In Bungo District, Jambi, Indonesia, where primary forests are almost non-existent, analysis of land-use change showed a net increase in rubber despite expansion of oil palm onto former rubber plantations (Feintrenie & Levang 2009; Ekadinata & Vincent 2011). In contrast, rubber area in Peninsula Malaysia declined with conversion to oil palm (Abdullah & Hezri 2008).

Smallholders tend 85-93% of the rubber area in Thailand and Malaysia (in plantations, Figure 3a), and in Indonesia (in agroforests, Figure 3b), but elsewhere in mainland Southeast Asia, agribusiness dominates production (50-77%; Fox & Castella 2013) with heavy investment in monocultural plantations (Li & Fox 2012). Rubber is also cultivated in the Philippines, mostly on the island of Mindanao (BAS 2013), and commonly in monocultures, with a small amount of agroforestry (Mercado et al. 2010).

2.4 Growing demand and future expansion

Demand for natural rubber is strong: global consumption in 2010 was 10,700,000 t, centred on the Asia-Pacific region (70%; IRSG 2013). Predictions suggest strong near-term demand, underpinned by growth in global rubber consumption (3.5% per annum) and the tyre market (5.3% per annum; Pakiam 2013). Li and Fox (2012) report data from a 2009 study by the International Rubber Study Group (IRSG) predicting annual consumption of 13,000,000 t by 2018, an increase of 3,100,000 t from 2010. More recently, IRSG estimated annual consumption of 17,000,000 t by 2023 (Rubberworld 2014), or 19,100,000 t by 2025 (Rusmana 2013); the mean (18,050,000 t by 2024) represents an increase of 7,350,000 t (≈40%) from 2010. The governments of Laos (Baird 2010), Cambodia (Vannarin & Lewis 2013), Malaysia (ETP 2013), Myanmar (Woods 2011) and Vietnam (Li & Fox 2012) intend to increase the area under cultivation, while there is also potential to intensify low yielding rubber, chiefly managed by smallholders, across Malaysia and Indonesia (Table S2, Figure S2).

2.4.1 How much land is required to meet demand by 2018 and 2024?

From these estimates of rubber demand by 2018 and 2024, we quantify potential expansion in plantation area. We explore four scenarios for Southeast Asia:

1a, Basic:

retention of existing rubber cultivation at current yields without intensification or further displacement, with future demand met by expansion at yields of modern plantations in mainland Southeast Asia (0.915 to 1.452 t ha^{-1} yr^{-1}, Supplementary Note 1).

1b, Basic + displacement:

as 1a but with displacement of existing rubber cultivation by oil palm in Sabah, Sarawak and Indonesia, considering two scenarios of oil palm expansion from the Roundtable on Sustainable Palm Oil (RSPO): business-as-usual (BAU: 3,350,000 ha additional oil palm for 2010-2018), or a moratorium on peat and high biomass forest conversion (2,600,000 ha; Harris et al. 2013), with 34% of oil palm expansion predicted to displace rubber (Supplementary Note 1). Rubber demand not met by remaining production (Supplementary Note 1, Table S7) is met by expansion in mainland Southeast Asia, as in 1a.

2a, Intensified:

some future demand is met by intensification of existing smallholder rubber cultivation in peninsula Malaysia, Sabah, Sarawak and Indonesia (plus a small 38,000 ha area of low-yielding estate cultivation on peninsula Malaysia), under scenarios derived from: likely maximum achievable yields, existing rubber area, and existing yields (Supplementary Note 1, Tables S4-S6). Due to uncertainty in likely uptake of intensified production, we consider intensification of 75% by area as an upper bound, but 25-50% more plausible (Supplementary Note 1). Residual future demand is met by expansion, as in 1a.

2b, Intensified + displacement:

as 2a, but also with displacement of some existing rubber production in Sabah, Sarawak and Indonesia by oil palm as in 1b. Residual future demand is met by expansion, as in 1a.

Anticipating intensification of 25 - 50% of low-yielding area in Indonesia and Malaysia, with no displacement by oil palm, we estimate that 1,394,707 - 3,017,838 ha of rubber expansion would be required to meet predicted 2018 demand (Table 1). Under the BAU scenario of oil palm expansion, this increases to 1,919,123 - 3,850,027 ha, making the threat from rubber expansion similar to that predicted for oil palm (2,600,000 - 3,350,000 ha) over the same period (Table S7). By 2024, with 25-50% intensification, we estimate 4,321,704 - 7,662,647 ha of expansion without oil palm displacement, and 4,846,120 - 8,494,836 ha under BAU oil palm expansion. Under a moratorium on peat/high biomass forest conversion, expansion estimates for oil palm lie between these figures (Table 1).

Scenarios	Scenario of new oil palm expansion	Area existing rubber in Sabah, Sarawak and Indonesia displaced by oil palm by 2018	Scenario of intensification in Indonesia/ Malaysia[*]	Area of monocultural plantation required to meet predicted demand[†] (ha), under scenarios of upper and lower monoculture yields in mainland Southeast Asia[‡]			
		ha	%	Demand: 13,800,000 t yr^{-1} by 2018 (3.1 million t increase from 2010)		Demand: 18,050,000 t yr^{-1} by 2024 (7.35 million t increase from 2010)	
				Yield: 0.915 t ha^{-1} yr^{-1}	Yield: 1.452 t ha^{-1} yr^{-1}	Yield: 0.915 t ha^{-1} yr^{-1}	Yield: 1.452 t ha^{-1} yr^{-1}
1a	**Not considered**	0 ha	**0**	3,387,978	2,134,986	8,032,787	5,061,983
2a			**25**	3,017,838	1,764,846	7,662,647	4,691,844
2a			**50**	2,647,699	1,394,707	7,292,507	4,321,704
2a			**75**	2,148,339	895,347	6,793,148	3,822,345
1b	**Peat/high biomass moratorium**	884,000 ha[ʃ]	**0**	4,057,405	2,556,836	8,702,213	5,483,833
2b			**25**	3,687,265	2,186,696	8,332,074	5,113,693
2b			**50**	3,317,125	1,816,556	7,961,934	4,743,553
2b			**75**	2,817,766	1,317,197	7,462,575	4,244,194
1b	**Business-as-usual**[¶]	1,139,000 ha	**0**	4,220,167	2,659,403	8,864,975	5,586,400
2b			**25**	3,850,027	2,289,263	8,494,836	5,216,260
2b			**50**	3,479,887	1,919,123	8,124,696	4,846,120
2b			**75**	2,980,528	1,419,764	7,625,337	4,346,761

TABLE 1

Estimated area of new monocultural rubber plantations required on mainland Southeast Asia to meet demand predicted for 2018 and 2024, considering a) upper and lower bounds of potential rubber yield achieved in new monocultural rubber plantations, b) extent of intensification of existing rubber production by smallholders in Malaysia and Indonesia (including a small 38,000 ha area of low-yielding estate rubber on peninsula Malaysia), and c) displacement of smallholder rubber production by oil palm in Sabah, Sarawak and Indonesia. Scenario numbers follow those in main text. Shaded cells represent most likely intensification scenarios.

[*] Intensifying to a yield of 1.494 t ha^{-1} yr^{-1} in Malaysia, or to 1.310 t ha^{-1} yr^{-1} in Indonesia (Table S6)

[†] Minimum and maximum yields of current plantations on mainland Southeast Asia, based on tapped area adjusted for initial unproductive years during the 25-year planation cycle (Supplementary Note 1, Table S3)

[‡] Demand estimates from IRSG as reported in Li & Fox (2012), Rusmana (2013) and Rubberworld (2014)

[ʃ] Area and production estimates from Table S7; this is area of displaced rubber cultivation, which is converted to production and then to area of new plantations, and added to total predicted rubber area for each intensification and demand scenario.

[¶] Harris et al. (2013) predict a greater area of oil palm expansion in this scenario, where plantations continue to be established using business-as-usual practices

2.5 Biodiversity and rubber cultivation

Natural forest has been recently converted to rubber plantations in mainland Southeast Asia (Li et al. 2007; Li & Fox 2012; Supplementary Note 2), and to rubber agroforests and plantations in Indonesia (Ekadinata & Vincent 2011). In Vietnam, 79% of rubber plantations established in the Central Highlands by 2012 were on former natural forest (92,000 ha; Phuc & Nghi 2014), and in Xishuangbanna, low-altitude areas highest in plant biodiversity are most profitable for rubber (Yi et al., 2013). Within MMSEA, 14% of young and mature rubber plantations were established onto Global Land Cover classes representing natural tree cover (Li & Fox 2012, Supplementary Note 2). This has included de-gazettement of protected areas in China (Guo et al. 2002), Laos (Baird 2010) and Cambodia (Open Development Cambodia 2014). For example, more than 70% of the 75,000 ha Snoul Wildlife Sanctuary, Cambodia, mostly comprising lowland evergreen forest, was cleared for rubber during 2009-2013 (Boyle & Titthara 2013).

Natural habitat conversion to rubber is set to continue: regional scale simulations for MMSEA predict conversion of 4.25 million ha to rubber and other deciduous broadleaved plantations by 2050, mostly replacing evergreen broadleaf forest and forest-field mosaics (Fox et al. 2012). In Cambodia, the majority of areas allocated to rubber are forested (Dararath et al. 2011; Open Development Cambodia 2014), including within the largest contiguous lowland dry evergreen and semi-evergreen forest remaining in mainland Southeast Asia (McKenney et al. 2004) and globally significant dry deciduous forests (Tordoff et al. 2005). Such areas support an assemblage of Critically Endangered and Endangered waterbirds, ungulates and primates, likely to decline on clearance and fragmentation of currently contiguous forests (Tordoff et al. 2005).

Although no studies have quantified the loss of large ungulates, primates, apex predators or waterbirds following forest conversion to rubber in Southeast Asia, population persistence is unlikely within highly managed, active rubber landscapes. Danielsen and Heegaard (1995) reported lower primate richness and abundance in plantations relative to primary forest, with macaques and gibbons absent, and a substantial reduction in the abundance of tree shrews and squirrels. We found eight studies assessing impacts on smaller taxa in Southeast Asia. Synthesising across these, we find that conversion of primary or secondary forest to rubber monoculture decreases the species richness of birds, bats and carabid beetles by 19-76% (Figure 3c, 1-7; Danielsen & Heegaard 1995; Aratrakorn et al. 2006; Peh et al. 2006; Meng et al. 2011; Phommexay et al. 2011; Li et al. 2013). Conversion also changes species composition, with forest specialists replaced by disturbance-tolerant, widespread species (Nájera & Simonetti 2010). In lowland Thailand, 15 of 16 threatened bird species were restricted to forest, whereas species composition in rubber was similar to oil palm, representing a replacement of forest specialists (particularly frugivores and insectivores) with widespread generalists, usually of smaller body size (Aratrakorn et al. 2006). Similarly, on Hainan Island, 29 of 53 bird species in secondary semi-deciduous forest were absent from mature monoculture rubber, especially obligate frugivores, whereas 19 of 43 species in rubber were absent from forest (Li et al. 2013). This pattern is similar for carabid beetles in China (Meng et al. 2011), and bats in Indonesia (Danielsen & Heegaard 1995) and Thailand (Phommexay et al. 2011), where 13 species were restricted to forest, and insectivorous bats showed twenty-fold lower activity in rubber (355 individuals from 24 species in forest, versus 16 individuals from eight species in plantations) attributed to lower insect biomass.

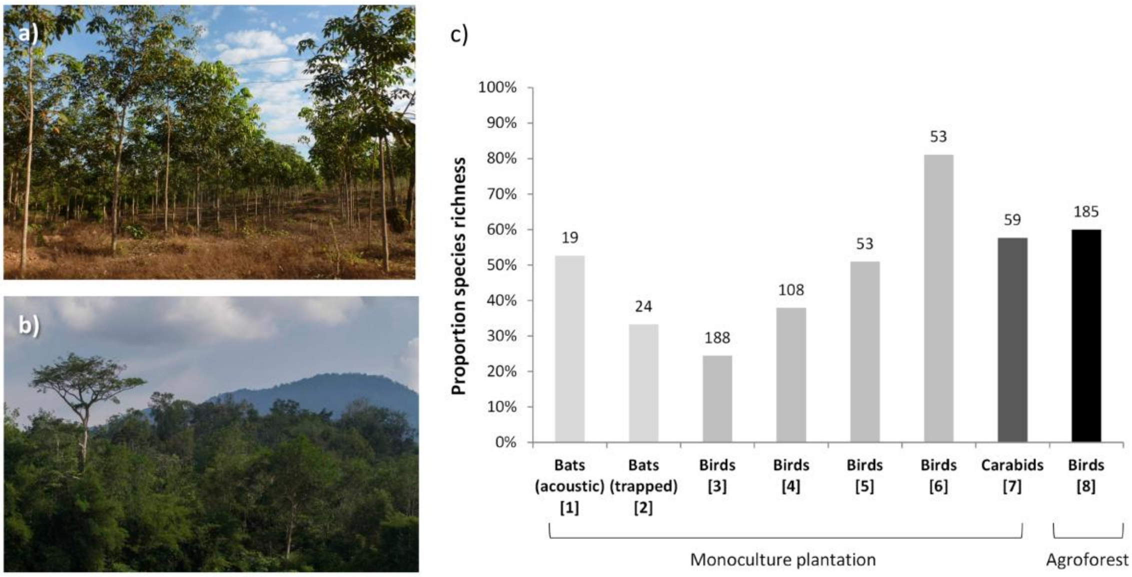

FIGURE 3

(a) Newly established immature rubber plantation, Kratie, Cambodia. Intensively managed monoculture rubber has a simple structure comprising a closed canopy kept clear of understorey growth. (b) Rubber agroforestry, Lubuk Beringin village, Jambi, Indonesia. Smallholder rubber agroforests are low-intensity multi-cropping systems that contain natural colonising vegetation, making them more structurally complex. (c) Species richness of mature monoculture rubber plantations as a percentage of that found in natural forests (lowland primary rainforest [1-5], semi-deciduous monsoon forest [6] or primary and secondary forest [7]) and of rubber agroforest compared to primary lowland rainforest [8]. Study locations: [1,2] southern Thailand (Phommexay et al. 2011), [3] peninsular Malaysia (Peh et al. 2006), [4] southern Thailand (Aratrakorn et al. 2006), [5] Sumatra, Indonesia (Danielsen & Heegaard 1995), [6] Hainan Island, China (Li et al. 2013), [7] Yunnan, China (Meng et al. 2011) and [8] Sumatra, Indonesia (Thiollay 1995). Numbers at top of bars represent species richness of natural forest for each study. Photo credits: (a) Eleanor Warren-Thomas; and (b) Tri Saputro for Center for International Forestry Research (CIFOR), photograph licensed under a Creative Commons Attribution-NonCommercial-NoDerivs License 2.0

While assessing impacts of primary forest conversion to rubber is relatively straightforward, more complex patterns of land-use change present a challenge in assessing biodiversity impacts. In mainland Southeast Asia, over half the current rubber plantation extent was established on mosaics of natural vegetation (grassland, shrubland and forest) and cropland, including former swidden (Supplementary Note 2; Li et al. 2007; Li & Fox 2012), while in Indonesia conversion of low-intensity rubber agroforest (Figure 3b) to monocultural plantations is an emerging trend (Feintrenie & Levang

2009; Ekadinata & Vincent 2011). Moreover, rubber plantation establishment on swidden or agroforest may displace these into frontier forests, particularly where migrants or outside companies establish plantations (e.g. China; Li et al. 2007), representing leakage of biodiversity impacts beyond plantation boundaries.

The biodiversity value of swidden in Southeast Asia is poorly known, and no direct comparisons between swidden and rubber have been made (but see Rerkasem et al. (2009) for loss of exceptional agrobiodiversity after swidden conversion to rubber). The reduction in species richness of 19% following conversion of secondary forest to rubber monoculture on Hainan (Li et al. 2013), suggests secondary forest fallows in swidden landscapes might also retain higher biodiversity value than rubber monocultures.

Although there are negatives for species richness and composition of creating rubber agroforest on primary or secondary forest (Figure 3c, [8]; Thiollay 1995), agroforest harbours greater biological value than monoculture rubber, supporting more forest specialist bird and plant species (Beukema et al. 2007), with increased bird diversity in plantations that have greater complexity in habitat structure (Aratrakorn et al. 2006; Nájera & Simonetti 2010). In some lowland areas of Indonesia, rubber agroforests are the only remaining forest-like habitats, supporting a subset of forest species not found in expanding monocultures (Beukema et al. 2007; Feintrenie & Levang 2009; Ekadinata & Vincent 2011).

There are also indications of substantial impacts on freshwater taxa. In Laos, local people reported dramatic declines in fish, crabs, shrimps, shellfish, turtles and streambank vegetation, attributed to run-off from rubber plantations (pesticide, herbicide and sediment), with fishermen reporting skin reactions from standing in streams (Baird 2010). In Xishuangbanna, fertiliser run-off from rubber plantations has caused waterway eutrophication, declines in filtering services by aquatic vegetation, and contamination of well water (Xu et al., 2013), while benthic macroinvertebrate diversity declines with increased intensity of rubber cultivation (Zhao et al 2014). Together, these findings show that rubber expansion could substantially exacerbate the extinction crisis in Southeast Asia.

2.6 Critical directions

The recent rubber boom has been compared to that of oil palm (Fox et al. 2012) with potentially catastrophic biodiversity impacts. Net area under rubber is increasing in Borneo and Sumatra, despite oil palm replacing some rubber area, alongside the novel expansion of monocultures in mainland Southeast Asia. Some have suggested policies to support and promote monoculture cultivation by smallholders in this novel expansion (Fox & Castella 2013). Others promote low-intensity agroforestry (Yi et al. 2013), which could provide farmers with diverse income sources while reducing ecological impacts within cultivated areas; although this could reduce yield and thus increase hunger for land. We therefore highlight two critical areas for further work:

2.6.1 Research to support meeting rubber demand while minimising biodiversity loss

Meeting global rubber demand while minimising biodiversity and ecosystem service losses requires understanding contrasts in species assemblage among production systems of differing yield (agroforests, monocultures) and when replacing different land uses (e.g. swidden, natural forest).

Research is needed to:

a) Quantify biodiversity value of swidden landscapes relative to rubber; considering monocultural rubber plantations in mainland Southeast Asia, and both agroforests and monocultures in Sabah, Sarawak, Indonesia and the Philippines. Knowledge about impacts on aquatic ecosystems is scarce, and also necessitates urgent research, particularly where local populations depend upon freshwater fisheries (Baird 2010).

b) Evaluate relative benefits for forest biodiversity (Phalan et al. 2011) and carbon storage (Gilroy et al. 2014) of low-intensity agroforest rubber (possibly including high-yielding varieties) over a wider area of mainland Southeast Asia (land-sharing), and intensive high-yielding monocultures combined with protected natural habitats (land-sparing). Within monocultures, assess whether retention of connected and protected forest patches on a fine scale offers greater resilience for biodiversity, versus intensified plantations with protection of larger forest blocks elsewhere in a landscape. In Brazil, forest species utilise rubber monocultures up to 2km from the edge of large forest fragments (140–625 ha; Flesher & Laufer 2013), but in Bornean oil palm plantations, smaller forest patches (0.7–87 ha) are species-poor, and protecting larger forest blocks would protect more bird biodiversity (Edwards et al. 2010).

c) Use spatially explicit conservation planning to investigate least damaging locations for rubber development, as conducted for oil palm (Venter et al. 2013). Modelling predicted yields of agroforests, smallholder plantations and large-scale commercial plantations, the costs of expansion onto different land-use types, and a range of conservation scenarios (land-sharing vs sparing, carbon protection, biodiversity conservation; e.g., Koh & Ghazoul 2010) will inform trade-offs between production, profit, and wildlife conservation.

d) Investigate whether biodiversity value within plantations can be improved without negatively affecting yield (e.g. as for coffee and cacao; Tscharntke et al. 2011). Although there has been little success in enhancing the biodiversity value of oil palm (Fitzherbert et al. 2008), given the apparently higher biodiversity value of agroforests with dense semi-natural understorey vegetation (Figure 3b), compared with rubber monoculture (Figure 3a; Beukema et al. 2007; Nájera & Simonetti 2010), we need to understand whether structural complexity can be improved within monoculture rubber without reducing yield. Similarly, we need to identify and quantify any pest control benefits of wildlife within plantations, and investigate whether landscape configuration of forest and cultivation impacts yield (Edwards et al. 2014).

2.6.2 The urgent need for a robust sustainability initiative

A sustainability standard for rubber cultivation, the Sustainable Natural Rubber Initiative (SNR-i; IRSG 2014) is only just emerging, leaving rubber expansion to be driven by market forces, farmer choice, and governmental policy. Negative environmental consequences of rubber cultivation are known within MMSEA, but whether expansion-focussed policies will be modified is unclear; although in Xishuangbanna there are recent plans to revert relatively unproductive rubber areas to forest (Ives 2013). While RSPO certification encourages oil palm expansion onto non-forest lands, including rubber (Koh & Wilcove 2008), rubber can currently expand without limitations to market access on recently deforested land or steep slopes, including those originally intended for oil palm, but which cannot be RSPO certified (Lim 2011).

There are many criticisms of current certification schemes: certified products are not fully sold, there are issues with compliance and integrating smallholders, and assessments of biologically important locations are questionable and potentially corruptible (e.g., Schouten & Glasbergen 2011; Edwards & Laurance 2012). Notwithstanding the complexities of developing an effective certification label, there are reasons to be optimistic that certification requirements may strengthen to prevent conservation losses and gain market traction. In the cases of oil palm, paper-pulp, and cattle, consumer pressure has resulted in major corporations only purchasing certified products; further, 400 of the world's largest corporations have stated that by 2020 their supply chains will be deforestation free (Preston 2010).

A potential concern may be the contribution of China, as the world's largest consumer of rubber, to driving sustainable rubber cultivation, given low interest in RSPO-certified oil palm thus far (Laurance et al. 2010). However, where large international companies or distributors commit to sourcing sustainable commodities, strong pressure can be exerted on producers (e.g. Nestlé and Unilever actions on oil palm). Major tyre producers, for instance, Bridgestone (Japan), Michelin (France), Goodyear Tire and Rubber Company (USA) and Continental AG (Germany) are based in economies with a stronger interest in sustainable sourcing, but supply tyres to the Chinese market (e.g., Bridgestone 2013). Moreover, without such a standard, there is little hope for change.

The SNR-i launched its pilot phase in January 2015, with participating entities (small/large growers, processors, traders, and downstream rubber users) offering compliance with Voluntary Guidelines and Criteria (IRSG 2014). Criterion 3 refers to forest sustainability, requiring establishment of plantations only on land "officially identified as suitable for rubber plantations or agricultural purposes" and "respect for legally protected areas and protected species habitats", ensuring that "new natural rubber plantations are not established within protected areas". We assert that environmental impact assessments must be compulsory for new plantations under this criterion, and high conservation value and high carbon stock forests identified during the assessment process must be directly protected from conversion to rubber cultivation. Although Criterion 5 addresses respect of human and labour rights through avoidance of child and forced labour, the standard must also place strong emphasis on free prior and informed consent for local people involved in plantation establishment. The standard should also contain measures to support existing agroforestry producers in accessing sustainability-focussed rubber markets.

In conclusion, the speed and scale of the new rubber boom means environmental and social considerations have so far been sidelined, with a spate of protected area de-gazettement and evictions of marginalised local peoples. The current focal regions for rubber production in Sundaland, and its rapid expansion in Indo-Burma, make this an urgent issue of global conservation importance. We urge that scientists fully engage with the development of the SNR-i to ensure relevance to biodiversity conservation, with prevention of further rubber development in key natural forests the minimum prerequisite for continued access to lucrative western and brand-label markets. Business-as-usual practice carries with it a significant danger that rubber development could destroy Indo-Burma's remaining wildernesses, and with it, the last hopes of regaining mammal populations that just a century ago were only rivalled by those in East Africa (Tordoff et al. 2005).

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2.10 Online supplementary material

This online supplementary information includes (in sequence as referred to in main text):

FIGURE S1: Top five importers of rubber 2000 – 2011

TABLE S1: Data sources on rubber extent in Southeast Asia.

TABLE S2: Harvested area, annual production and yield of rubber producing countries in 2011

FIGURE S2: Yield (tonnes ha-1) of rubber producing countries relative to mean global yield

SUPPLEMENTARY NOTE 1: Predicted expansion of rubber cultivation area in response to increased demand, smallholder intensification and conversion of rubber plantations to oil palm.

TABLE S3: Yield of rubber producing countries in mainland Southeast Asia; data from ANRPC (2014) for 2011. No data are available for Laos.

TABLE S4: Yield estimates of existing smallholder and estate rubber production in Malaysia and Indonesia, from governmental statistics and on-farm studies.

TABLE S5: Smallholder and plantation production figures used in subsequent analysis for Malaysia & Indonesia - selected figures from Table S4

TABLE S6: Intensification scenarios: we explore intensification of both smallholder and estate rubber area in Malaysia (insular and peninsula) and smallholder rubber area in Indonesia, by estimating the production increase generated by intensifying of 25%, 50% or 75% of existing rubber area to the maximum likely yields for each location.

TABLE S7: Oil palm expansion and displacement of rubber agroforest and plantations in insular Malaysia and Indonesia.

TABLE S8: Predicted area of new monocultural rubber plantations required on mainland Southeast Asia to meet predicted demand by 2018 and 2024, considering a) upper and lower bounds of potential rubber yield achieved in new monocultural rubber plantations, b) extent of intensification of existing rubber production by smallholders in Malaysia and Indonesia, and b) displacement of smallholder rubber production by oil palm in insular Malaysia and Indonesia.

SUPPLEMENTARY NOTE 2: Rubber expansion in Montane Mainland Southeast Asia (MMSEA)

FIGURE S1

Top five importers of rubber 2000 – 2011. Data include imports of "rubber, natural dry" and "rubber, natural" as defined by the FAO (FAO 2013).

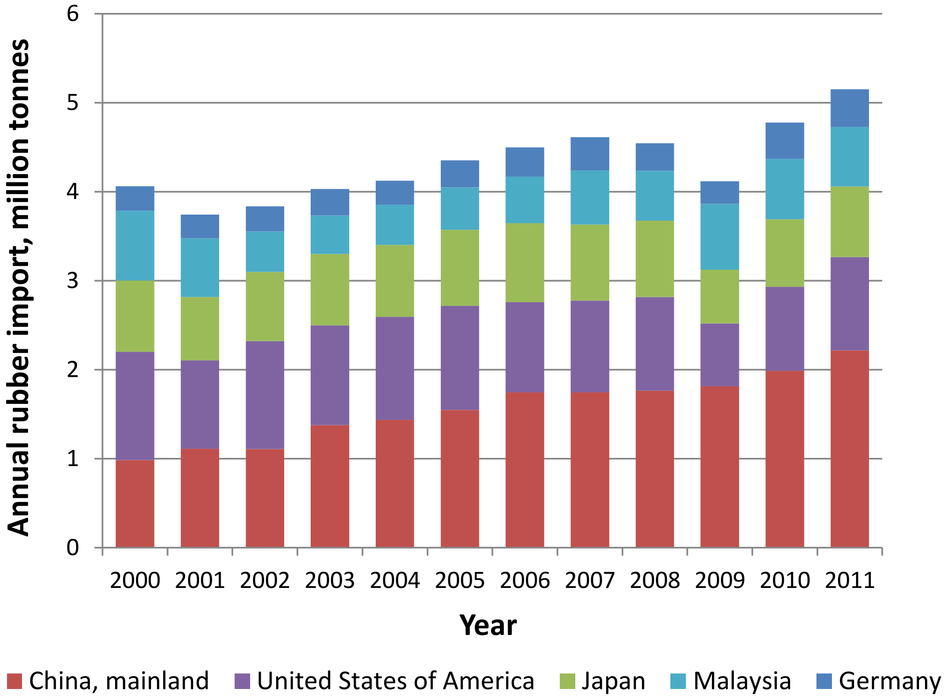


TABLE S1

Data sources for rubber extent in Southeast Asia. Data for the area covered by rubber plantations in Southeast Asia vary among reported sources, and recent increases may not be represented in officially reported data until new plantations have reached productive age (typically five years; Clay 2004). The Malaysian government successfully lobbied for rubber plantations to be classified as 'forest' by the FAO (Clay 2004), which results in two sources of FAO data on rubber area: FAOSTAT Online Statistical Service crop production data (FAO 2013) and the FAO Forest Resources Assessment (FRA 2010). Discrepancies arise in reporting between these two data sources: for example, the Philippines report 8,000 ha of rubber plantation in the FRA, but 161,565 ha of rubber area harvested, while Thailand reports 540,500 ha greater rubber extent in the FRA relative to harvested area. Two further national level sources of data comprise: the bulletin of the Association of Natural Rubber Producing Countries (ANRPC) that publish monthly production and extent data based on self-reported data (ANRPC 2010), and Li and Fox (2012) who collected sub-national statistics from governmental and non-governmental sources on rubber tree extent for China, Myanmar, Laos, Thailand, Vietnam and Cambodia. Both of these sources show discrepancies with FAO data. Figures marked * are those considered most reliable for each country (for justification, see footnotes) and hence were used to generate Figure 2 in the main article.

Country	Rubber Extent (ha)				
	Productive		**Planted**		
	FAO 2012 (Harvested)¶	**ANRPC December 2010 (Tapped)†**	**FRA 2010 (Planted)‡**	**ANRPC December 2010 (Total)†**	**Li and Fox, 2012§**
Cambodia	36,051	45,000	69,000*	143,400	110,000
Indonesia	3,484,100*	2,773,000	-	3,445,000	-
Laos	-	-	-	-	131,454*
Thailand	2,050,500	1,900,000	2,591,000*	2,761,000	2,156,059
Malaysia	1,200,000	655,000	1,132,000*	1,029,000	-
Myanmar	200,000	-	-	-	380,282*
Philippines	176,244*	60,400	8,000	129,500	-
China	600,000*	566,000	-	1,002,000	400,000
Vietnam	505,804	445,000	630,000*	715,000	550,800

¶ 'Area Harvested (ha)' reported for 2012 in crop production statistics (FAO 2013).

† ANRPC Monthly Bulletin published in December 2010 as reported by governments on 16th December 2010 (ANRPC 2010).

‡ Area (ha) listed as 'Rubber Plantations' in 2010 in the UN FAO Forest Resources Assessment (FRA 2010).

§ Sub-national statistical sources (governmental, industry, media reports) compiled by Li and Fox (Li & Fox 2012) with full list of references.

* Data from the FAO Forest Resources Assessment (FRA 2010) on total rubber plantation area is considered the most reliable, as FAO 'Area Harvested' data (FAO, 2013) are likely to omit recently established plantations. In Indonesia, Laos, Myanmar and China, these data are not available, and in the Philippines there is a large discrepancy with other data sources, so other data sources were selected in these countries. Data for Indonesia were based on FAO (2013), which closely corresponds to ANRPC (2010) data. Data for Laos were taken from Li

and Fox (2012) as the only available data, originally from a governmental source. Data for Myanmar were taken from Li and Fox (2012) as this was sourced from an industry group conference, in preference to the FAO Area Harvested data (FAO, 2013), which omitted recently established plantations. Data from China were taken from FAO Area Harvested data (FAO, 2013), given the lack of FRA (2010) data and discrepancy between Li and Fox (2012) and ANRPC (2010) data. Data for the Philippines were based on FAO Area Harvested (FAO, 2013) given the large discrepancy between the FRA (2010) data and all other sources.

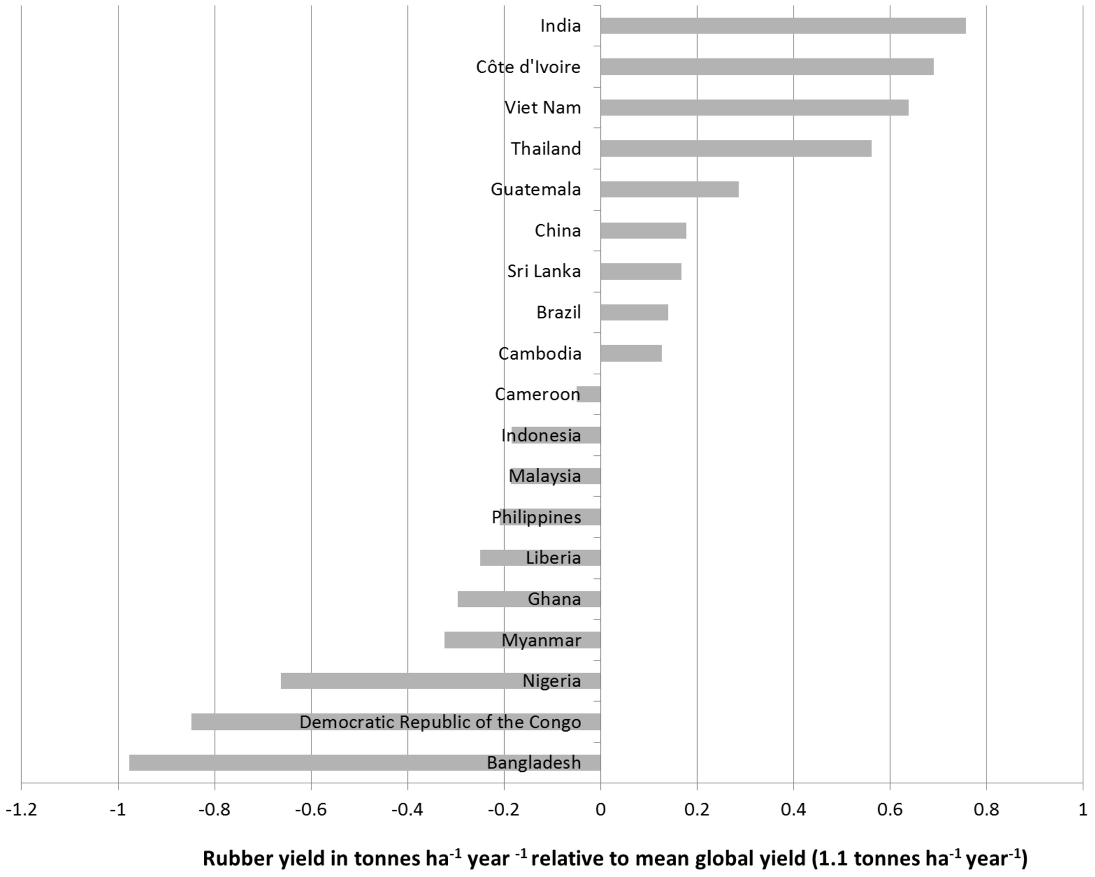
TABLE S2

Harvested area, annual production and yield of rubber producing countries in 2011 (FAO 2013).

Country	Area harvested (ha)	Annual production (tonnes)	Annual production (tonnes ha^{-1})
Bangladesh	59,054	5,997	0.102
Democratic Republic of the Congo	50,000	11,500	0.230
Nigeria	345,000	143,500	0.416
Myanmar	198,364	149,627	0.754
Ghana	25,800	20,185	0.782
Liberia	76,000	63,000	0.829
Philippines	161,565	140,500	0.870
Malaysia	1,117,392	996,673	0.892
Indonesia	3,456,100	3,088,400	0.894
Cameroon	54,000	55,500	1.028
Cambodia	36,051	43,471	1.206
Brazil	134,947	164,498	1.219
Sri Lanka	127,000	158,198	1.246
China	597,770	750,852	1.256
Guatemala	75,825	103,435	1.364
Thailand	2,042,502	3,348,897	1.640
Vietnam	459,947	789,635	1.717
Côte d'Ivoire	135,000	238,717	1.768
India	485,665	891,344	1.835

FIGURE S2

Yield (tonnes ha^{-1} year^{-1}) of rubber producing countries relative to mean global yield, as calculated from FAO Area Harvested and Annual Production data (Table S1), for countries with >25,000 ha of rubber extent (FAO 2013). Rubber producing countries with <25,000 ha excluded from this figure analysis are: Bolivia, Brunei, Central African Republic, Congo, Dominican Republic, Gabon, Guinea, Ecuador, Mexico, and Papua New Guinea.



SUPPLEMENTARY NOTE 1

Predicted expansion of rubber cultivation area in response to increased demand, smallholder intensification and conversion of rubber plantations to oil palm

Predictions of future rubber demand

We utilise estimates of future rubber demand published by the International Rubber Study Group (IRSG). Li and Fox (2012) report data from a 2009 IRSG report that predicts rubber demand will reach 13.8 million tonnes by 2018, an increase of 3.1 million tonnes from 2010 levels (10.7 million tonnes). More recent estimates from IRSG have suggested that consumption could reach 19.1 million tonnes by 2025 (Rusmana 2013), or 12.4 million tons by 2015 and 17.0 million tons by 2023 (Rubberworld 2014). We take the mean average of these two figures to estimate 18.5 million tons by 2024, implying an increase of 7.35 million tonnes from 2010 levels.

We use the estimates of additional rubber demand by 2018 (3.1 million tonnes) and 2024 (7.35 million tonnes) as a basis to explore future scenarios of rubber expansion in Southeast Asia, considering: i) the likely yield of new plantations that will be established in mainland Southeast Asia, ii) the potential for offsetting this expansion by meeting some additional demand through intensification of existing rubber cultivation in Malaysia and Indonesia and iii) the potential for oil palm expansion in Indonesia and insular Malaysia to replace existing rubber plantations, with displacement increasing the extent of new rubber production required on mainland Southeast Asia in order to meet future demand.

i) Likely yield of new plantations in mainland Southeast Asia

The clearest source of data on rubber production, planted and tapped area, and yield in Southeast Asia are the self-reported statistics published by the Association of Natural Rubber Producing Countries (ANRPC 2014). Although similar data on the national harvested area of rubber and annual production are available from the FAO, a comparison of these data with ANRPC shows that the former are likely in some cases to reflect planted rather than tapped area (Table S1).

To predict the yield of new plantations on mainland Southeast Asia, we use data on rubber area and production for Cambodia, China, Thailand and Vietnam, to calculate mean yield in tonnes per hectare of productive plantation, at the national level. We have not used yield estimates derived from production relative to total planted area, due to the large extent of newly planted but as-yet unproductive plantations in countries such as Cambodia, that make yield calculated relative to planted area unrealistically low (Table S3). However, yield estimates solely based on tapped area over-estimate national yields at steady state management (i.e. not during a phase of rapid plantation expansion and establishment) due to rotational clearance and replanting of over-mature plantations post economic optimum, such that under cyclical plantation management a proportion of rubber area is unproductive while rubber trees mature and begin producing latex. In monocultural plantations, rubber trees are planted on a 25 year cycle, with saplings taking around six years to become productive, and production declining after around 19 years (Hansen & Top 2006; Hing & Thun 2009). Trees are then cleared and replanted with new saplings, beginning a new 25 year production cycle. We therefore adjust the total tapped area by a factor of 1.24 (1+6/25 = 1.24), hereafter referred to as "adjusted tapped area".

Yields calculated directly from actual tapped area and production ranged from 1.135 t ha^{-1} yr^{-1} (Cambodia) to 1.800 t ha^{-1} yr^{-1} (Thailand) (Table S3). These data are corroborated by on-farm data, suggesting that the estimates for productive areas are reliable: latex productivity of tapped plantation area in Vietnam varied from 1.29 t ha^{-1} yr^{-1} from years 1-10 at 630m asl, to 2.01 t ha^{-1} yr^{-1} during years 11-20 at 110 m asl (Nguyen 2013). In Cambodia, mean reported yields over productive years 7 – 25 vary from 1.28 t ha^{-1} yr^{-1} (ACI, 2005) to 1.74 t ha^{-1} yr^{-1} (Hansen & Top 2006), and in Laos, models predict yields of 1.0 – 1.3 t ha $^{-1}$ yr^{-1} over a 35 year cultivation cycle (Manivong & Cramb 2008).

Yield calculated relative to adjusted tapped area ranged from 0.915 t ha^{-1} yr^{-1} (Cambodia) to 1.452 t ha^{-1} yr^{-1} (Thailand) for new plantations on mainland Southeast Asia. We use these latter figures as the minimum and maximum likely average yields of new rubber area established on mainland Southeast Asia. We anticipate that many new plantations will be established in upland or marginal environments, and will tend to have lower average yields (Manivong & Cramb 2008; Nguyen 2013). We also note that low-intensity rubber agroforestry has been suggested as a more sustainable cultivation method over monocultures in China (Yi et al. 2013) and also in South Asia (Nath et al. 2013), potentially reducing mean yields of new rubber area. We therefore suggest that the mean yield of new plantations is likely to lie between these two estimates.

TABLE S3

Yield of rubber producing countries in mainland Southeast Asia. Data from ANRPC (2014) for 2011. No data are available for Laos.

	Cambodia	**China**	**Thailand**	**Vietnam**
Planted area (ha)	213,100	1,070,000	2,760,000	834,200
Tapped area (ha)	45,200	619,000	1,985,000	471,900
Adjusted tapped area (adjusted for management cycle) (ha)	56,048	767,560	2,461,400	585,156
Production of natural rubber (t)	51,300	727,000	3,573,000	811,600
Average annual yield per cultivated area (t ha^{-1} yr^{-1})	0.241	0.679	1.295	0.973
Average annual yield per tapped area (t ha^{-1} yr^{-1})	1.135	1.174	1.8	1.72
Average annual yield per adjusted tapped area (t ha^{-1} yr^{-1})	0.915	0.947	1.452	1.387

ii) Intensification of rubber production in Malaysia and Indonesia

Yield estimates for existing smallholder and estate rubber production in Malaysia and Indonesia

Malaysia and Indonesia contain a large extent of existing rubber cultivation that could potentially be intensified, partially meeting future increased demand for natural rubber production and offsetting the requirement for new plantation area in mainland Southeast Asia. Here we explore current yield estimates for existing rubber cultivation in Malaysia and Indonesia, in preparation for considering possible production increases. Such increases could be achieved by intensifying proportions of the rubber area to the maximum likely yields for the area – we consider this in the next section. Smallholder rubber may be expected to yield less than estate grown rubber, due to lower availability of capital for high-cost inputs such as fertiliser, yield stimulating chemicals or pesticides, and may represent the greatest opportunity for intensification, although there may also be opportunities for increased production within estates on Peninsula Malaysia.

As smallholder cultivation practices differ between Malaysia and Indonesia, we treat the two countries separately in our intensification scenarios. Although approximately 93% of rubber is produced by smallholders in Malaysia (Department of Statistics Malaysia 2011; Fox & Castella 2013), smallholder cultivation uses clonal rubber monocultures, following governmental rubber support schemes that have reached the vast majority of smallholders (Penot 2010)**.** By contrast, in Indonesia approximately 85% of total rubber area is produced by smallholders, with 84% of the smallholder rubber area cultivated within agroforests (Joshi et al. 2003; Fox & Castella 2013; BPS-Statistics Indonesia 2014). Here, governmental support schemes promoting clonal rubber monocultures reached only 15% of smallholders during the 1980s and 1990s, affecting around 350,000 ha of smallholder area, with many smallholders unable to fund replacement of trees as productivity declined (Penot 2004). As this is a small proportion of total smallholder area, there are no recent data available on the area of rubber still in monocultural production by smallholders in Indonesia, and there is the possibility that the initial clonal plantations have by now declined in production, we do not consider this subset of smallholder area separately from agroforests.

Estimates of current yields in Malaysia and Indonesia were available from the ANRPC, national governmental statistics, and from on-farm studies (Table S4). Data on planted area (tapped area data unavailable) and production of both smallholder and estate rubber are produced by the Indonesian and Malaysian governments; these are similar to those data submitted to the ANRPC, and we consider them to be a reliable source. Using these sources (yield based on planted area), we estimate the current average yields of smallholder rubber to be: 0.805 t ha^{-1} yr^{-1} in Indonesia, 1.241 t ha^{-1} yr^{-1} in Peninsula Malaysia, and 0.227 t ha^{-1} yr^{-1} in insular Malaysia (Table S5).

Expressing yield relative to tapped area adjusted for management cycle (adjustment factor of x1.24, see above) provides a yield estimate for Indonesia (0.870 t ha^{-1} yr^{-1}) close to the yield calculated relative to total cultivated area (0.872 t ha^{-1} yr^{-1}). This suggests that the maximum possible rubber area is likely to be in production without a substantial part of the planted area lying abandoned or long-term fallow, although theoretically some methods of rubber agroforestry (*sisipan*) allow continuous tapping, potentially increasing the proportion of rubber area that can be productive at any one time. However, in Malaysia (pooling insular and peninsula data), the yield estimated relative to adjusted tapped area (1.204 t ha^{-1} yr^{-1}) is greater than the yield calculated relative to total cultivated area (0.951 t ha^{-1} yr^{-1}), suggesting that there may be a larger extent of unproductive and potentially abandoned plantation in Malaysia.

Potential mechanisms for intensification of smallholder rubber in Indonesia and Malaysia

Although the Malaysian government continues to promote improvements in rubber productivity by smallholders through the provision of high yielding planting material (ETP 2013), we anticipate that yield increases on Peninsula Malaysia will be relatively modest, as most productive smallholders already cultivate monocultural rubber using modern clonal varieties (Penot 2004), and yields already compare favourably to estate-grown rubber (Table S4). In contrast, yields of smallholder rubber on insular Malaysia (Sabah and Sarawak) are low, indicating either that large areas of cultivation are currently unproductive, or that the cultivation system is exceptionally low-yielding. It is here that we may expect increases in production within Malaysia could be achieved, either through regeneration of defunct plantations to new monocultural plantations, or through improvement of rubber agroforest yields.

The situation in Indonesia is different, where a range of rubber agroforestry methods dominate smallholder production. Rubber agroforestry in Indonesia can be characterised into two systems: *sisipan* in which rubber trees are individually replaced as they decline in productivity, generating a continuous cover stand of rubber trees with mixed ages, and *ladang* shifting agriculture, in which rubber trees are planted on fallow land as part of a shifting cultivation system, and are completely cleared and replaced after production declines, generating small stands of uniform age in a complex matrix of other land uses (Joshi et al. 2003). The *sisipan* method is favoured for continuing cultivation of existing multi-age agroforests, rather than conversion to the *ladang* system, as it avoids the gap in income generation during tree establishment phase of monocultural methods (Lehébel-Péron et al. 2011).

Improvements of yield in rubber agroforest could be achieved through introduction of high-yielding clonal rubber into rubber agroforests, but the high risk of pest damage to expensive seedlings means that farmers are reluctant to do this, preferring to adopt a monoculture-type intensive system when using expensive planting material (Joshi et al. 2003). Farmers could also convert rubber agroforest to rubber monoculture, which some farmers have done in Indonesia, but this switch is not viable for the majority of resource-poor farmers, due to the high costs of planting material and the required five to seven years without income while rubber trees mature (Joshi et al. 2002). This is supported by economic analysis of alternative rubber cultivation systems (monoculture, different agroforestry systems) showing that the economic return to labour inputs in rubber agroforests are similar to that of rubber monocultures, and that although the economic return per land area is higher within monoculture, this can only be sustained for 25-30 years before substantial new investment is needed to replant the trees (Lehébel-Péron et al. 2011). Alternatively, the density of rubber trees (using local varieties) planted within *sisipan* systems could be increased, although under present market conditions, other crops become more profitable once rubber trees become >20 years old, such as the bean *Parkia speciosa*, encouraging maintenance of a diversity of crops within the agroforest (Lehébel-Péron et al. 2011). Farmers may also wish to maintain a diversity of income sources that have stronger links to stable local markets, rather than variable global commodity markets, through recent experience with strong market shocks (Lehébel-Péron et al. 2011).

Thus farmers in Indonesia are unlikely to be able to fund replacement of trees after the first 25-year plantation cycle (Penot 2004). Moreover, multiple-crop agroforests are a lower risk investment than monocultures, remaining attractive for many farmers despite lower returns (Feintrenie & Levang 2009). Meanwhile, there are also calls for REDD+ and market-based mechanisms to support rubber agroforestry systems across Southeast Asia for ecosystem services benefits (Feintrenie & Levang 2009; Fox et al. 2013; Yi et al. 2013).

For these reasons, we suggest that yield increases of rubber agroforests in Indonesia are likely to remain limited in the near term, and scenarios of intensification over a smaller percentage of current rubber area (e.g. 25-50%) are more plausible than higher scenarios (e.g. 75% of existing rubber area intensified).

We use yield and production estimates from Table S5 to estimate production increases under scenarios of smallholder rubber intensification, in Table S6

Potential maximum yield of intensified rubber production in Indonesia and Malaysia

Indonesia

National-level planted area data show that in Indonesia, estate-grown rubber yields around 33% more per ha (1.202 t ha^{-1} yr^{-1}) than smallholder-grown rubber (0.805 t ha^{-1} yr^{-1}). One on-farm study of a 50 year *ladang* agroforestry cycle appears to show much greater yields for smallholder agroforest: annual yield of dry rubber from an 'average' mature rubber agroforest in Sumatra, planted with 200 productive trees per hectare, was estimated as 0.93 t ha^{-1} yr^{-1} in years 11-14, 1.488 t ha^{-1} yr^{-1} for years 15-20, 1.86 t ha^{-1} yr^{-1} in years 21-40, and 1.488 t ha^{-1} yr^{-1} in years 40-49, generating a mean annual yield of 1.622 t ha^{-1} yr^{-1} over 40 years of productive life (Lehébel-Péron et al. 2011). However, the origin of these figures is not clear in the study, and we therefore treat them with caution. The national level yield figures fall within the range of on-farm yield estimates for estate and rubber production, and therefore appear reliable, but we use the maximum reported yield from an on-farm study of estate-grown rubber in Indonesia as the maximum that is likely to be attainable through intensification of smallholder rubber in Indonesia, via replanting of agroforest area with monoculture rubber: the maximum predicted yield after intensification is therefore taken to be 1.310 t ha^{-1} yr^{-1} (Table S4).

Malaysia

In Malaysia, national-level yield estimates based on planted area are only 8.5% greater for estate grown rubber (1.063 t ha^{-1} yr^{-1}), than for smallholders (0.980 t ha^{-1} yr^{-1}). However, when looking at sub-national data from 2010 on the planted area and production within peninsula Malaysia specifically (Department of Statistics Malaysia 2011), we find that estate yields (1.129 t ha^{-1} yr^{-1}) are actually lower than smallholder yields (1.241 t ha^{-1} yr^{-1}), with a mean for peninsula Malaysia of 1.233 t ha^{-1} yr^{-1}. We therefore include the estate rubber area in peninsula Malaysia (49,861 ha) in our intensification scenarios. We also find that mean yields on peninsula Malaysia are much higher than the national average (i.e. pooling across insular regions also). Although no sub-national production data are published for Sabah or Sarawak, 939,241 t of rubber were produced on the peninsula, leaving 56,969 t of national production outstanding that must be generated by insular Malaysia over 251,481 ha of planted area, generating a low yield of 0.227 t ha^{-1} yr^{-1} (Table S4).

Together, this suggests that the majority of rubber planted on peninsula Malaysia, both by smallholders and in estates, is already being tapped at levels near the likely maximum, while on Sabah and Sarawak, either large areas are unproductive, or smallholder cultivation in these areas generates substantially lower yields than on peninsula Malaysia, potentially in very low intensity agroforestry. We therefore suggest that yield increases over the planted rubber area on peninsula Malaysia are likely to be modest, whereas across the 251,481 ha of planted rubber on Sabah and Sarawak more substantial increases would be possible. When predicting potential intensification across Malaysia, we estimate the increased production that might be possible from both estates and smallholder plantations, because smallholder monocultures yield more than estates on Peninsula Malaysia.

The highest reliable yield figure for any rubber production system in Malaysia is generated from ANRPC data on the tapped area and production of rubber at the national level. We take this to represent the maximum achievable yield of intensified smallholder or estate rubber in Malaysia: 1.494 t ha^{-1} yr^{-1} (Table S4).

TABLE S4

Yield estimates of existing smallholder and estate rubber production in Malaysia and Indonesia, from governmental statistics and on-farm studies.

	Production (t yr^{-1})	Area (ha)	Yield (t ha^{-1} yr^{-1})
Indonesia, National			
All production			
ANRPC, 2011†	3,013,000		
ANRPC, 2011, planted		3,456,000	
ANRPC, 2011, planted, calculated yield			0.872
ANRPC, 2011, tapped		2,792,000	
ANRPC, 2011, tapped, calculated yield			1.079
ANRPC, 2011, adjusted tapped		3,462,080	
ANRPC, 2011, adjusted tapped, calculated yield			0.87
FAO, 2011¶	3,088,400		
FAO, 2011, area harvested		3,456,100	
FAO, 2011, calculated yield			0.894
BPS-Statistics Indonesia, 2011≠	2,990,200		
BPS-Statistics Indonesia, 2011, planted		3,456,100	
BPS-Statistics Indonesia, 2011, calculated yield			0.865
Smallholder production			
BPS-Statistics Indonesia, 2011	2,359,800		
BPS-Statistics Indonesia, 2011, planted		2,931,800	
BPS-Statistics Indonesia, 2011, planted, calculated yield			0.805
Lehébel-Péron et al. 2011			1.622*
Penot, 1995 in Joshi et al. 2003			0.59
Estate production			
BPS-Statistics Indonesia, 2011	630,400		
BPS-Statistics Indonesia, 2011, planted		524,300	
BPS-Statistics Indonesia, 2011, planted, calculated yield			1.202
Penot, 1995 in Joshi et al. 2003, private estate			1.065
Penot, 1995 in Joshi et al. 2003, government estate			1.31
Malaysia, National			
All production			
ANRPC, 2011	996,200		
ANRPC, 2011, planted		1,048,000	
ANRPC, 2011, planted, calculated yield			0.951
ANRPC, 2011, tapped		667,000	
ANRPC, 2011, tapped, calculated yield			1.494
ANRPC, 2011, adjusted tapped		827,080	
ANRPC, 2011, adjusted tapped, calculated yield			1.204
FAO, 2011	996,673		
FAO, 2011, area harvested		1,117,392	
FAO, 2011, area harvested, calculated yield			0.892
Department of Statistics Malaysia, 2011	996,210		
Department of Statistics Malaysia, 2011, planted		1,012,588	
Department of Statistics Malaysia, 2011, planted, calculated yield			0.984
Smallholder production			
Department of Statistics Malaysia, 2011	943,194		
Department of Statistics Malaysia, 2011, planted		962,727	
Department of Statistics Malaysia, 2011, planted, calculated yield			0.98
Estate production			
Department of Statistics Malaysia, 2011	53,016		

	Production (t yr^{-1})	Area (ha)	Yield (t ha^{-1} yr^{-1})
Department of Statistics Malaysia, 2011, planted		49,861	
Department of Statistics Malaysia, 2011, planted, calculated yield			1.063
Malaysia, Peninsula only (data only available until 2010)			
All production			
Department of Statistics Malaysia, 2010	939,241		
Department of Statistics Malaysia, 2010, planted		761,500	
Department of Statistics Malaysia, 2010, planted, calculated yield			1.233
Smallholder production			
Department of Statistics Malaysia, 2010	882,904		
Department of Statistics Malaysia, 2010, planted		711,634	
Department of Statistics Malaysia, 2010, planted, calculated yield			1.241
Estate production			
Department of Statistics Malaysia, 2010	56,337		
Department of Statistics Malaysia, 2010, planted		49,886	
Department of Statistics Malaysia, 2010, planted, calculated yield			1.129
Malaysia, Sabah & Sarawak			
All production			
Department of Statistics Malaysia, 2010, calculated from above	56,969		
Department of Statistics Malaysia, 2010, planted		251,481	
Department of Statistics Malaysia, 2010, planted, calculated yield			0.227
Smallholder production			
Department of Statistics Malaysia, 2010, calculated from above	56,969		
Department of Statistics Malaysia, 2010, planted		251,481	
Department of Statistics Malaysia, 2010, planted, calculated yield			0.227
Estate production			
Department of Statistics Malaysia, 2010	0		
Department of Statistics Malaysia, 2010, planted		0	
Department of Statistics Malaysia, 2010, planted, calculated yield			0

† (ANRPC 2014)

¶ (FAO 2013)

‡ (BPS-Statistics Indonesia 2014)

∫ (Department of Statistics Malaysia 2011)

TABLE S5

Smallholder and estate production figures used in subsequent analysis for Malaysia & Indonesia – selected figures from Table S4.

	Total area of planted rubber (ha)	**Total area rubber held by smallholders (ha)**	**Smallholder production (t yr^{-1})**	**Existing smallholder yield (t ha^{-1} yr^{-1})**	**Total area rubber in estates (ha)**	**Estate production (t yr^{-1})**	**Rubber estate yield (t ha^{-1} yr^{-1})**	**Production total (t yr^{-1})**
Malaysia (Department of Statistics Malaysia, 2014)	1,012,588	962,727	943,194	0.98	49,861	53,016	1.063	996,210
Malaysia (peninsula)* (Department of Statistics Malaysia, 2014)	761,500	711,634	882,904	1.241	49,886*	56,337	1.129	939,241
Malaysia (insular)* (Department of Statistics Malaysia, 2014)	251,481	251,481	56,969	0.227	-	-	-	56,969
Indonesia (BPS-Indonesia, 2014)	3,456,100	2,931,800	2,359,800	0.805	524,300	630,400	1.202	2,990,200
TOTAL: Insular Malaysia & Indonesia†	3,707,581	3,183,281	2,416,769		524,300		630,400	3,047,169
TOTAL: All Malaysia & Indonesia	4,468,688	3,894,527	3,302,994		574,161		683,416	3,986,410

* data from 2010, when rubber production from plantations was lower than in 2011, causing the apparent discrepancy between estate rubber production at the national level, and at the peninsula level, even though all estate rubber is reported as being on Peninsula Malaysia (Department of Statistics Malaysia, 2014).

† used for oil palm expansion estimates, as no expansion is predicted on peninsula Malaysia (Harris et al., 2013)

TABLE S6

Intensification scenarios: we explore intensification of both smallholder and estate rubber area in Malaysia (insular and peninsula) and smallholder rubber area in Indonesia, by estimating the production increase generated by intensifying of 25%, 50% or 75% of existing rubber area to the maximum likely yields for each location.

		Area intensified (ha)*		**Existing yield (t ha^{-1} yr^{-1})†**		**Potential maximum yield (t ha^{-1} yr^{-1})‡**		**Potential increase in production (t yr^{-1})**		
Region	**% area intensified**	**Estate**	**Smallhold**	**Estate**	**Smallhold**	**Estate**	**Smallhold**	**Estate**	**Smallhold**	**TOTAL**
Peninsula Malaysia	0%	0	0	1.129	1.241	1.494	1.494	0	0	0
	25%	12,472	177,909	1.129	1.241	1.494	1.494	4,552	45,011	0
	50%	24,943	355,817	1.129	1.241	1.494	1.494	9,104	90,022	0
	75%	37,415	533,726	1.129	1.241	1.494	1.494	13,656	135,033	49,563
Insular Malaysia	0%	n/a	0	n/a	0.227	n/a	1.494	n/a	0	0
	25%	n/a	62,870	n/a	0.227	n/a	1.494	n/a	79,657	0
	50%	n/a	125,741	n/a	0.227	n/a	1.494	n/a	159,313	0
	75%	n/a	188,611	n/a	0.227	n/a	1.494	n/a	238,970	79,657
Indonesia	0%	n/a	0	n/a	0.805	n/a	1.31	n/a	0	0
	25%	n/a	732,950	n/a	0.805	n/a	1.31	n/a	370,140	370,140
	50%	n/a	1,465,900	n/a	0.805	n/a	1.31	n/a	740,280	740,280
	75%	n/a	2,198,850	n/a	0.805	n/a	1.31	n/a	1,110,419	1,110,419
All Malaysia and Indonesia	0%							**0**	**0**	**0**
	25%							**4,552**	**494,807**	**370,140**
	50%							**9,104**	**989,614**	**740,280**
	75%							**13,656**	**1,484,422**	**1,239,639**

*	extent of estate and smallholder rubber area from Table S5
†	existing yield of estate and smallholder rubber from Table S5
‡	maximum yield reported from Malaysia, tapped area yield at national level, as discussed in main text
§	maximum yield reported from state-run rubber plantation in Indonesia, as discussed in main text

iii) Displacement of rubber production in Indonesia and insular Malaysia by expansion of oil palm

We estimate the potential displacement of rubber cultivation by oil palm expansion in Indonesia and insular Malaysia using analysis by the Roundtable on Sustainable Palm Oil (RSPO), who considered oil palm expansion in the coming decade under two modes: a moratorium on expansion on peat and high biomass forest, or business as usual expansion (Harris et al. 2013). From this study we extracted oil palm expansion figures from 2010 to 2018, to match the timescale of the rubber demand predictions considered. We estimated the proportion of this expansion that would occur on existing rubber cultivation, using historical rates of land use change for oil palm.

Data on past land use changes for oil palm in Malaysia and Indonesia are generally of low quality, with unclear definitions of land use (Wicke et al. 2011), but remote sensing analysis showed that between 1990-2010 approximately 34% of new oil palm area in Indonesia (Sumatra, Kalimantan and Papua) and Malaysia (Peninsula, Sabah and Sarawak) was established on mixed tree crop agroforests or tree plantations of unspecified crops (Gunarso et al. 2013).

Actual rates of future rubber conversion may be lower than this, given that: 1) classification of bare soil conversion to oil palm could mask a higher rate of agroforest/plantation or forest conversion over the period 1990-2010, increasing uncertainty in estimates of former land use (Gunarso et al. 2013, Supplementary Material), 2) analysis of national level statistics suggest that 41-45% oil palm expansion in Indonesia and Malaysia between 1990-2005 occurred on former cropland, including rubber plantations, (Koh & Wilcove 2008), which is corroborated by 3) a lower percentage of oil palm has been established on agroforest/plantation in the past five years relative to historical rates in all areas except peninsula Malaysia, while the percentage established on former forest has increased, suggesting that the availability of cropland for conversion to oil palm is decreasing (Gunarso et al. 2013, Supplementary Material). The alternative view is that pressure to reduce forest conversion to oil palm and to restore formerly converted peat forests (Harris et al. 2013), may point to a future trend reverting back to conversion of non-natural forest land uses to oil palm.

We assume that the entirety of these agroforests and plantations converted to oil palm comprised rubber, given the dominance of rubber cultivation as an agroforest and plantation crop in these regions (Joshi et al. 2003), although the exact proportion of rubber within these categories was not detailed (Gunarso et al. 2013, Supplementary Material).

We use this estimate as the best information currently available and assume that a similar proportion of oil palm expansion over the coming decade will be established onto rubber (Table S7). Of the oil palm expansion predicted under RSPO scenarios for 2018, we assume 34% will occur onto rubber area within smallholder cultivation (and estate cultivation in the case of Peninsula Malaysia). Displaced area is converted to displaced production using estimates of current yield (as used for the intensification scenarios), and the area of new, high-yielding plantations required to meet this displaced production is then calculated using the upper and lower estimates of yield for Southeast Asia (Table S7).

TABLE S7

Oil palm expansion (under RSPO scenarios for 2010 - 2018) and displacement of rubber agroforest and plantations in insular Malaysia and Indonesia.

	Business as usual			**Peat/high biomass moratorium**		
	Insular Malaysia	**Indonesia**	**TOTAL**	**Insular Malaysia**	**Indonesia**	**TOTAL**
Oil palm expansion predicted by 2018 (ha)*	1,030,000	2,320,000	3,350,000	700,000	1,900,000	2,600,000
Agroforest/plantation replaced by oil palm †	350,200	788,800	1,139,000	238,000	646,000	884,000
% replaced area in smallholder cultivation‡	100%	85%		100%	85%	
Area of replaced smallholder rubber (ha)	350,200	670,480	1,020,680	238,000	549,100	787,100
Area of replaced estate rubber (ha)	-	118,320	118,320	-	96,900	96,900
Displaced production of replaced smallholder rubber (t) §	79,495	539,736	619,232	54,026	442,026	496,052
Displaced production of replaced estate rubber (t) §	-	142,221	142,221	-	116,474	116,474
TOTAL rubber production displaced by oil palm (t)	79,495	681,957	761,452	54,026	558,499	612,525
Area of new plantations required, if planted at 0.915 t ha^{-1}¶	86,880	745,308	**832,188**	59,045	610,382	**669,427**
Area of new plantations required, if planted at 1.452 t ha^{-1}¶	54,749	469,667	**524,416**	37,208	384,641	**421,849**

Emboldened figures used in scenarios in Table S8.

* Predictions of oil palm expansion taken from Harris et al. (2013)

† 34% of oil palm establishment for the period 1990-2010 in Indonesia and Malaysia occurred on former agroforests/plantations (Gunarso et al, 2013) – we assume all of this area comprised rubber plantations.

‡ Data from Table S4 showing proportion of cultivation in smallholdings/estates

§ Yield data from Table S4

¶ Predicted future yields of new plantations on mainland Southeast Asia based on tapped area (adjusted for management cycle) from Table S3

TABLE S8

Predicted area of new monocultural rubber plantations required on mainland Southeast Asia to meet predicted additional demand for natural rubber by 2018 and 2024, considering a) upper and lower bounds of potential rubber yield achieved in new monocultural rubber plantations in Southeast Asia, b) extent of intensification of existing rubber production by smallholders in Malaysia and Indonesia, and c) displacement of smallholder rubber production by oil palm in insular Malaysia and Indonesia.

Scenarios of oil palm expansion	**Predicted area of rubber displaced by oil palm by 2018**	**Scenarios of intensification in Indonesia/ Malaysia***	**Area of monocultural plantation required to meet predicted demand‡ (ha), under scenarios of upper and lower monoculture yields in mainland Southeast Asia†**			
	ha	**%**	**Demand: 13,800,000 t yr^{-1} by 2018 (3.1 million t increase from 2010)**		**Demand: 18,050,000 t yr^{-1} by 2024 (7.35 million t increase from 2010)**	
			Yield: 0.915 t ha^{-1} yr^{-1}	**Yield: 1.452 t ha^{-1} yr^{-1}**	**Yield: 0.915 t ha^{-1} yr^{-1}**	**Yield: 1.452 t ha^{-1} yr^{-1}**
Not considered	0 ha	**0**	3,387,978	2,134,986	8,032,787	5,061,983
		25	3,017,838	1,764,846	7,662,647	4,691,844
		50	2,647,699	1,394,707	7,292,507	4,321,704
		75	2,148,339	895,347	6,793,148	3,822,345
Peat/high biomass moratorium	884,000 ha∫	**0**	4,057,405	2,556,836	8,702,213	5,483,833
		25	3,687,265	2,186,696	8,332,074	5,113,693
		50	3,317,125	1,816,556	7,961,934	4,743,553
		75	2,817,766	1,317,197	7,462,575	4,244,194
Business-as-usual¶	1,139,000 ha	**0**	4,220,167	2,659,403	8,864,975	5,586,400
		25	3,850,027	2,289,263	8,494,836	5,216,260
		50	3,479,887	1,919,123	8,124,696	4,846,120
		75	2,980,528	1,419,764	7,625,337	4,346,761

* Intensifying to a yield of 1.494 t ha^{-1} yr^{-1} in Malaysia, or to 1.310 t ha^{-1} yr^{-1} in Indonesia (Table S6)

† Minimum and maximum yields of current plantations on mainland Southeast Asia, based on adjusted tapped area (Table S3)

‡ Demand estimates from IRSG as reported in Li & Fox (2012), Rusmana (2013) and Rubberworld (2014)

∫ Area and production estimates from Table S7; area here is area of rubber cultivation, which is converted to production and then to area of new plantations, and added to total predicted rubber area for each intensification and demand scenario.

¶ Harris et al. (2013) predict a greater area of oil palm expansion in this scenario, where plantations continue to be established using business-as-usual practices

SUPPLEMENTARY NOTE 2: Rubber expansion in MMSEA

A recent remote sensing assessment of rubber expansion across montane mainland Southeast Asia (MMSEA), which comprises parts of China, Cambodia, Laos, Thailand and Vietnam, detected 555,000 ha of newly established plantations <4 years old, mostly in Yunnan, Southwest China (71%), northern Laos, eastern Myanmar, northeast Thailand and northern Vietnam, and 1.57 million ha of mature plantations ≥ 4 years old (Li & Fox 2012). The Global Land Cover 2000 dataset (Bartholomé & Belward 2005) used to establish former land use does not cover Southwest China. Of the young plantations <4 years old for which former land use was known (29% of the 555,000 ha detected), tree cover (broadleaved evergreen, broadleaved deciduous and dry dipterocarp, including both degraded and open forest, 22,100 ha, 14%), natural vegetation-cropland mosaics (105,000 ha, 66%) and cultivated areas (33,000 ha, 20%) were replaced with rubber. For plantations >4 years old, former land use was identified for 63% of the 1.57 million ha detected, as fewer plantations were located in China. For these mature plantations; rubber replaced broadleaf evergreen forest, broadleaf deciduous and dry dipterocarp forest (141,000 ha, 14%), natural vegetation-cropland mosaics (556,000 ha, 56%) and cropland (298,000 ha, 30%; Li & Fox 2012). Thus, patterns of landuse transition have been broadly similar between recent expansion and earlier, now mature, plantations; with 70-80% of plantation area established either onto natural tree cover, or onto mosaics of natural vegetation and cropland over both periods. This corroborates other studies in MMSEA that identify replacement of broadleaf primary and secondary rain forest in Southwest China (Li et al. 2007; Xu et al. 2013), shrubs and grasses (Fox et al. 2012) and traditional swidden agriculture (Ziegler et al. 2009; Fox et al. 2013; Xu et al. 2013) with rubber.

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Chapter 3

Protecting tropical forests from the rapid expansion of rubber using carbon payments

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3.1 Abstract

Expansion of *Hevea brasiliensis* rubber plantations is a resurgent driver of deforestation, carbon emissions and biodiversity loss in Southeast Asia, particularly on the mainland. Southeast Asian rubber extent is massive, equivalent to 67% of oil palm, with rapid further expansion predicted. Results-based carbon finance could dis-incentivise forest conversion to rubber, but efficacy will be limited unless payments match, or at least approach, the costs of avoided deforestation. These include opportunity costs (timber and rubber profits), plus carbon finance scheme setup and implementation costs. Using comprehensive Cambodian forest data, and exploring scenarios of selective logging and conversion, we find that carbon prices of \$30-\$51 tCO_2^{-1} are needed to breakeven against costs; higher than those currently paid on carbon markets or through carbon funds. To defend forests from rubber, either carbon prices must be increased, or other strategies are needed, such as corporate zero-deforestation pledges or governmental commitment to forest protection.

3.2 Introduction

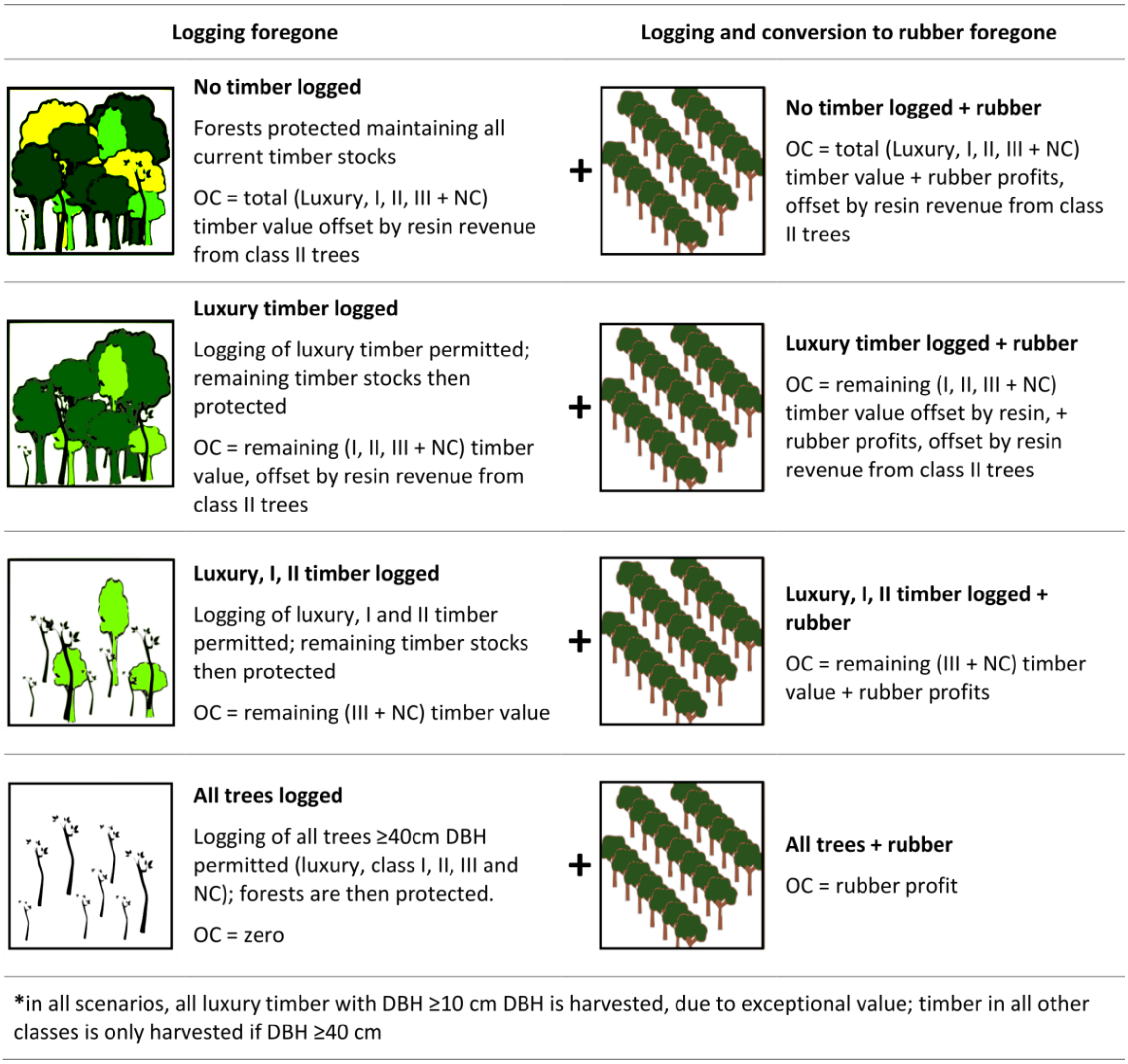
Forest is being converted to *Hevea brasiliensis* rubber plantations across Southeast Asia, resulting in the loss of forest carbon stocks and substantial declines in biodiversity (Ahrends et al. 2015, Warren-Thomas et al. 2015, Blagodatsky et al. 2016). Eighty-five per cent of global rubber area occurs in Southeast Asia, where expansion has driven northwards into Cambodia, China, Laos, Myanmar and Vietnam (hereafter termed mainland Southeast Asia, but also known as the Indo-Burma biodiversity hotspot), replacing forest and traditional swidden cultivation (Ahrends et al. 2015, Warren-Thomas et al. 2015). Despite its massive extent (8.6 million ha in Southeast Asia in 2014, equivalent to 67% of oil palm extent; FAO 2014), and comparable negative consequences for biodiversity and ecosystem services (Clough et al. 2016), conversion of forest to rubber monoculture has not faced the same public scrutiny as oil palm. Here, we analyse carbon outcomes and opportunity costs of forgoing forest conversion to rubber, including profits from timber extraction, and ask whether permitting selective logging could reduce these opportunity costs to improve the likelihood of success for forest carbon finance.

Where climatic conditions are suitable for both oil palm and rubber, they can generate similar profits per unit land area, but oil palm provides better returns if labour supply is restricted (Clough et al. 2016). However, rubber can tolerate a wider range of climatic conditions and soil types, permitting its expansion into mainland Southeast Asia (Warren-Thomas et al. 2015), although reduced yields and tree mortality are reported from many northern parts of its range (Ahrends et al. 2015). Recent expansion of rubber has mostly occurred in areas unsuitable for oil palm (Ahrends et al. 2015, Pirker et al. 2016).

Demand for natural rubber continues to grow, predominantly driven by the tyre industry, and plantations are predicted to expand by 4.3–8.5 million ha within a decade (Warren-Thomas et al. 2015). This expansion not only threatens forest carbon stocks, but also has serious implications for biodiversity conservation. The forests of mainland Southeast Asia are globally unique ecosystems, supporting numerous threatened and endemic animal, bird, invertebrate and plant species (Tordoff et al. 2005, CEPF 2012, WWF 2016), including exceptionally valuable luxury timbers (e.g. rosewoods, *Dalbergia* spp.).

Rubber prices are currently relatively low (Supplementary Figure 1), offering a lull in expansion, and an opportunity to develop strategies for future planting that minimise negative outcomes for climate and forests. Stemming rubber expansion onto biodiversity-rich forest could reduce carbon emissions and achieve conservation gains simultaneously, making efficient use of limited funds (Miles and Kapos 2008, Venter et al. 2009). However, the effectiveness of any forest carbon finance scheme will depend on the number of carbon credits generated, the perceived costs of conserving forest, and the price offered for carbon credits.

We analysed the carbon outcomes and opportunity costs of forgoing forest conversion to rubber, including profits from timber extraction, and asked whether permitting selective logging could reduce opportunity costs, and improve the likelihood of success for forest carbon finance. We modelled scenarios of protecting either intact forest ("No timber logged"), or forest degraded by permitting selective logging (felling only trees ≥40cm DBH at three intensity levels, depending on timber royalty/value classes: (1) "Luxury logged"; (2) "Luxury, I, II logged"; (3) "All trees logged"), from subsequent conversion to rubber (Figure 1; Supplementary Note 1). We calculated rubber profits based on typical monocultural plantation systems, containing high-yielding clonal varieties of rubber planted at densities of 400 – 550 stems ha^{-1} (Priyadarshan 2011). Such systems are ubiquitous across mainland Southeast Asia, within both smallholdings and larger estates (Phommexay et al. 2011, Shigematsu et al. 2013, Yi, Cannon, et al. 2014, Ahrends et al. 2015). We also included the economic value of dipterocarp tree resin collection as an economic benefit of forests retaining class I and II timber species (all resin species are class II). For each scenario we estimated the breakeven carbon price (\$ tCO_2^{-1}) that would match the opportunity costs of forgoing further logging and conversion to rubber, plus the setup and implementation costs of a carbon finance scheme. We used substantial inventory data of 20,281 trees (DBH ≥10 cm; Supplementary Table 1) from six forest landscapes in Cambodia (Supplementary Figure 2). These span two forest types in zones climatically suitable for rubber (Ahrends et al. 2015): 'dense' evergreen and semi-evergreen (35-55 m height) and 'open' deciduous/mixed-deciduous forests (25–35 m; WCS 2015). They include the largest remaining contiguous lowland evergreen forest in mainland Southeast Asia (McKenney et al. 2004) and globally significant extents of open forest (Wohlfart et al. 2014).



Logging foregone	Logging and conversion to rubber foregone
No timber logged Forests protected maintaining all current timber stocks OC = total (Luxury, I, II, III + NC) timber value offset by resin revenue from class II trees	**No timber logged + rubber** OC = total (Luxury, I, II, III + NC) timber value + rubber profits, offset by resin revenue from class II trees
Luxury timber logged Logging of luxury timber permitted; remaining timber stocks then protected OC = remaining (I, II, III + NC) timber value, offset by resin revenue from class II trees	**Luxury timber logged + rubber** OC = remaining (I, II, III + NC) timber value offset by resin, + rubber profits, offset by resin revenue from class II trees
Luxury, I, II timber logged Logging of luxury, I and II timber permitted; remaining timber stocks then protected OC = remaining (III + NC) timber value	**Luxury, I, II timber logged + rubber** OC = remaining (III + NC) timber value + rubber profits
All trees logged Logging of all trees ≥40cm DBH permitted (luxury, class I, II, III and NC); forests are then protected. OC = zero	**All trees + rubber** OC = rubber profit

*in all scenarios, all luxury timber with DBH ≥10 cm DBH is harvested, due to exceptional value; timber in all other classes is only harvested if DBH ≥40 cm

FIGURE 1 - SCENARIOS OF INTERVENTION TO PROTECT FOREST FROM CONVERSION TO RUBBER

Schematic shows scenarios of intervention to protect remaining forest in: initial state ("No timber logged"); after selective logging ("Luxury timber logged" or "Luxury, I, II timber logged") and after all trees (≥40 cm DBH) have been logged ("All trees logged"). Tree species were assigned to one of four royalty classes: luxury, I, II, III, or non-classified (NC; Supplementary Table 2) based on a governmental list (FA 2004); harvest of luxury timber considers all stems ≥10 cm DBH, for other classes stems ≥40 cm DBH. All resin trees are classified as class II. The left column considers opportunity costs (OC) of only offsetting logging, in situations where conversion to rubber is prohibited; the right column considers scenarios where potential for conversion to rubber generates additional opportunity costs of forest protection.

We find that the carbon prices needed to fully match the costs of protecting intact or selectively logged forests in mainland Southeast Asia from conversion to rubber are higher than those currently paid on carbon markets (~\$5–13 tCO_2^{-1}) or through carbon funds (~\$5 tCO_2^{-1}). Prices for dense forests would need to reach \$29.86–\$37.48 tCO_2^{-1}, and for open forests, \$30.93–\$51.11 tCO_2^{-1}. Under current conditions, protecting forests from conversion to rubber under a forest carbon finance scheme would likely entail substantial net costs. However, the breakeven carbon prices are close to, or below, the predicted social cost of carbon (at least \$36 tCO_2^{-1}). Carbon prices might rise to meet opportunity costs in the near term, but market feedbacks could mean that commodity prices, and therefore costs of foregone conversion, also rise in the future. To prevent emissions of forest carbon and the loss of irreplaceable biodiversity due to the expansion of rubber, additional strategies will be needed beyond forest carbon finance. These might include a rubber sustainability initiative, zero-deforestation pledges from major rubber consuming companies, and government commitment to forest conservation coupled with improved forest governance and effective land-use planning.

3.3 Methods

[NB – Nature Communications manuscripts are formatted with methods placed after the introduction, results and discussion. For this thesis version of the manuscript, the structure has been reorganised such that methods follow the introduction, hence appearing repetitive of the final introductory paragraph]

3.3.1 Study region

We used data from Cambodia as a case study for lowland areas of mainland Southeast Asia, and for the Indo-Burma biodiversity hotspot, that covers Laos, Cambodia, Vietnam, most of Myanmar and Thailand, and parts of Southwest China, including Xishuangbanna and Hainan Island (Myers *et al.* 2000). Ten million ha of forest covered 55% of Cambodia in 2010 (FAO 2010), but the country now has the world's fifth highest deforestation rate (Hansen *et al.* 2013). Cambodian forests range from fully deciduous to almost completely evergreen (Tani *et al.* 2007, Theilade *et al.* 2011) but can be categorised into two broad groups: 'dense forest' comprises evergreen and semi-evergreen stands, with tree heights reaching 35 – 55 m; 'open forest' comprises areas of dry deciduous dipterocarp and mixed-deciduous forests, with tree heights reaching 25 – 35 m (WCS 2015). Swamp and hill evergreen forest types found in some periodically inundated or mountainous areas (Tani *et al.* 2007, Theilade *et al.* 2011) were not considered in this study.

The expansion of rubber is strongly promoted by the Cambodian government; rubber area increased by 175% between 2009 and 2013, to 328,800 ha (MAFF 2015). Cashew, cassava and sugar also expanded rapidly (Supplementary Methods). Timber is logged both illegally, and legally under licenses for infrastructure projects and industrial-scale plantations (ELCs), including of rubber (Stibig *et al.* 2007, Üllenberg 2009, Saing *et al.* 2012, Global Witness 2013, EIA 2014, Forest Trends 2015, Milne 2015). Illegal logging of high-value timber is common, involving a range of actors (Blaser *et al.* 2011) (Supplementary Note 1). Smallholders seeking agricultural land for subsistence or cash crops, firewood and timber also drive deforestation (WCS 2015).

Opportunities for using forest carbon finance to protect forests in mainland Southeast Asia are being actively explored. Cambodia, alongside Vietnam and Lao PDR, is being supported by the UN-REDD (Reducing Emissions from Deforestation and Forest Degradation) program (GCP 2015), and has begun the REDD+ Readiness process with assistance from the World Bank's Forest Carbon Partnership Facility (FCPC) and UN-REDD, in anticipation of developing a national-level program (GCP 2015). A number of pilot REDD+ demonstration projects are underway, seeking funding from voluntary carbon markets (LEAF 2013).

3.3.2 Approach to modelling opportunity costs and carbon breakeven prices

Opportunity costs were defined as forgone direct profits from logging, the net present value (NPV) of rubber in large plantations or of other cash-crop agriculture (cassava, cashew, and sugarcane, in large plantations or smallholdings), and cash income from collecting dipterocarp tree resin, which is forgone once dipterocarp trees are felled (Supplementary Methods). This traditional livelihood activity directly conflicts with logging, because resin-producing species also have valuable timber (Evans *et al.* 2003, Hansen and Neth 2006, Theilade and Schmidt 2011), being listed as class II species (Supplementary Table 2). Total opportunity cost was thus based on forgone profits from logging and/or rubber, offset by lost resin revenue where class I and II trees are logged out. We do not estimate other non-timber forest product benefits (Supplementary Methods).

We did not distinguish between legal and illegal activities, as we wished to understand the underlying economic drivers of forest conversion, while acknowledging that when designing actual incentive mechanisms there may be good reasons for treating legal revenue streams differently from illegal ones, so as to avoid indirectly rewarding illegal behaviour. However, timber revenue was calculated as a farm-gate price and we did not consider legal downstream benefits that accrue to the wider economy, nor those benefits of doubtful legality that accrue mainly to non-local actors, including agro-industrial companies and elite logging 'tycoons' (Üllenberg 2009), such as the sale of high value timber on the international market (Supplementary Table 9, although export of logs and most sawn timber is illegal; Supplementary Note 1). These exclusions are likely to lead to an under-estimate of opportunity cost, but are appropriate given the absence of any robust data on these benefits, and the need for any forest carbon finance scheme to operate transparently and legally. Hence, our calculations provide a minimum estimate of the economic challenge that a forest carbon finance scheme may face in influencing land use decisions.

To calculate carbon breakeven prices, we incorporated the following parameters: timber profit (assuming a single offtake; \$ ha^{-1}), forest carbon stock (tC ha^{-1}), post-deforestation land-use carbon stock (tC ha^{-1}), 25-year discounted resin revenue (10% discount rate; \$ ha^{-1}) and 25-year NPV of rubber or cash crops (10% discount rate, \$ ha^{-1}). All input costs and prices were adjusted to 2013 US\$ before analysis; all output values are thus in 2013 US\$.

When calculating each parameter, to account for both uncertainties within, and variance between, data sources, values were resampled for each of 10,000 model iterations from either a normal distribution defined by the mean and standard error of the mean (SE; used to resample timber volume, carbon stock values and agricultural farm gate prices, for which the distribution of values was known), or a uniform distribution bounded by minimum and maximum estimates (used to resample agricultural yields, agricultural input costs, timber prices and timber extraction costs, for which the underlying distribution of parameter values was unknown; Supplementary Table 10).

All parameter values were resampled independently at each iteration, with the exception of timber volume (m^3 ha^{-1}) and carbon stock (tC ha^{-1}). For these, a single forest inventory was randomly selected for each model iteration, in order to capture geographic variation without bias from relative inventory extent (Supplementary Table 1), and thereby avoiding the need for weighting. For each forest inventory, the mean and SE of timber volume, carbon stock and stem density (Supplementary Table 2) were calculated per tree species, and thus each royalty class. Where trees of smaller size classes were sampled from subplots nested within main plots (Supplementary Table 1), standardised values (ha^{-1}) still allowed mean and SE to be calculated per royalty and size class and, as the numbers of subplots and main plots were equal within each such inventory (Supplementary Table 1), no weightings were required. From the selected inventory, timber volumes and carbon stocks were simultaneously sampled from the same point in their distribution relative to the mean, as values of timber volume and carbon stock were likely to be correlated.

Stem-specific timber volume and carbon stock estimates (derived separately from DBH) were negatively skewed across all forest inventories. To address this, timber and carbon densities per plot were square-root transformed before calculating the mean and SE for each forest inventory, reducing the influence of infrequent plots with exceptionally high timber and carbon density. Timber and carbon values resampled from the resulting normal distribution were back-transformed before use in the model. Carbon stocks and wood volumes are presented in results as the unweighted mean and 95% confidence interval across all 10,000 iterations.

Agricultural yields, costs and farm-gate prices for all crops were sampled independently for each iteration, but the position within the distribution for each parameter was held constant across each crop type for each iteration. Resin production and prices were also sampled independently for each iteration.

Opportunity costs of logging and rubber (or other cash-crops; offset by lost resin revenue; \$ ha^{-1}) and breakeven carbon prices needed to offset the opportunity costs, plus setup and implementation costs (based on emitted forest carbon offset by post-deforestation land-use carbon stocks; \$ tCO_2^{-1}) were then generated for each scenario. Results are presented as the median and interquartile range across 10,000 model iterations. Indicative real-world carbon prices (Supplementary Table 5) are shown in relation to breakeven carbon prices.

3.3.3 Timber profits

Forest inventories (Supplementary Figure 2) were used to estimate timber volumes. Five inventories used fixed sampling areas (3.1 - 60 ha total per landscape; Supplementary Table 1) while inventory F05 used variable radius plots (Lambrick *et al.* 2014). Within forest types, sites had similar relative distributions of size classes for all trees (Supplementary Figure 4, Supplementary Table 11) and within royalty classes (Supplementary Figure 9). In each, all trees ≥10 cm DBH were measured and identified to species level; nomenclature was standardised across datasets following The Plant List Version 1.1 (2013) (The Plant List. Version 1.1. 2013). Vines were not recorded. Tree species were assigned to one of five royalty (value) classes: luxury, I, II, III, or non-classified (NC; Supplementary Table 2) based on a government list of timber species (FA 2004). The 14 luxury timber species included Burmese Rosewood (*Dalbergia oliveri,* commonly called *D. bariensis* in Cambodia (Hartvig *et al.* 2015), IUCN EN, CITES Appendix II), Siamese Rosewood (*D. cochinchinensis,* VU, CITES Appendix II) and Burmese Padauk (*Pterocarpus macrocarpus,* unassessed). All Dipterocarp species were class I or II and included popular timber species (e.g. *Dipterocarpus alatus*, EN and *Anisoptera scaphula*, CR); other popular timber species in class I were *Sindora siamensis*, LC, and *Heritiera* (*Tarrietia*) *javanica,* unassessed (Blaser *et al.* 2011)).

Logging revenues depend on the minimum tree size commercially harvested, which may differ according to royalty class. Luxury species are exceptionally valuable and even small amounts are harvested (EIA 2012); we therefore assumed all luxury trees ≥10 cm DBH would be logged. For class I and II species, we assumed a minimum harvestable DBH of 40 cm, but also explored the effect of reducing minimum harvestable DBH to 30cm (Supplementary Note 1; Supplementary Table 3). Class III trees (that are used for local construction or fuelwood) and non-classified timbers (assumed to be only useful as fuelwood) ≥40 cm DBH were initially assumed to have market value (Supplementary Table 9). However, extraction of class III and non-classified timbers was found to incur a net cost in open forest (-\$57, \$-456 to -\$21 ha^{-1}) and in dense forest (-\$1,336, -\$2,096 to -\$850 ha^{-1}), despite assuming relatively low timber extraction costs, that involved selective logging activity by local people in Cambodia in a 'business-as-usual' scenario with no formal logging concessions, inventories, management plan, or demarcation of logging areas. Costs included: wage labour, food, motorbike fuel, ox-cart transportation to the roadside/village and chainsaw maintenance, but excluded the capital cost of the chainsaw. If class III and non-classified classes were to be extracted, this would likely be for firewood or construction locally (with extraction costs subsumed within non-market subsistence livelihood activities), or through destructive clearance during land preparation for agriculture (already considered in establishment costs for scenarios of agricultural conversion; Supplementary Table 12). Therefore, maximum potential timber profit accrued solely from logging luxury, class I and class II timber, and we assumed that the opportunity cost of protecting forests from further logging after the "Luxury, I, II timber logged" scenarios was reduced to zero (Figure 3, Supplementary Table 3).

The timber profit remaining in the forest (R_x; \$ ha^{-1}) in each logging scenario x, representing the opportunity cost of intervening at that point to protect timber remaining within the forest from further logging, was calculated as shown in equation (1):

$$R_x = \sum_{a=1}^{5} V_a * (p_a - C) \quad \textbf{(1)}$$

Where V_a is the timber volume (m^3 ha^{-1}) of timber royalty class *a* (five classes; Supplementary Table 2), estimated using Cambodian government standard timber equations (Supplementary Table 13) reduced by 20% to account for wastage (Putz *et al.* 2008), p_a is the timber price (\$ m^{-3}) for that royalty class (Tables S8 and S14), and C the cost (\$ m^{-3}) of extraction to the roadside or village (Supplementary Table 15). Timber prices were estimated at the local (roadside or village) level in the absence of formal timber markets.

3.3.4 Forest carbon stocks

As for timber volume, forest inventories (Supplementary Table 1) were used to estimate forest carbon stocks for all stems ≥10 cm DBH, per royalty class, per forest plot, quantifying above-ground biomass (AGB) and below-ground biomass (BGB) (WCS 2015). AGB per plot and per royalty class (t ha^{-1}) was calculated using the Chave D Moist forest equation, using DBH only (Chave *et al.* 2005), verified via destructive sampling for a REDD+ pilot project in Cambodia (WCS 2015). Species-specific wood density was used where possible (Chave *et al.* 2009, Zanne *et al.* 2009); other species were assigned the mean wood density for the genus within the same region or, if no values were available for the genus, the mean wood density of all tree species across all inventories. BGB was estimated as 24% of AGB per plot (Cairns *et al.* 1997). AGB and BGB were summed, and multiplied by 0.5 to give estimated carbon content (tC ha^{-1}) (Chave *et al.* 2005). Deadwood and soil organic carbon pools were not estimated; deadwood accounts for only 3% of emissions reductions from avoided deforestation, and soil organic carbon stocks are assumed not to change when land use conversion is to perennial crops according to the Intergovernmental Panel on Climate Change (IPCC) tier 1 carbon outcome calculation methods, and the carbon accounting methodology used for the REDD+ pilot project in Cambodia (WCS 2015).

3.3.5 Post-deforestation land-use carbon stocks

We estimated the AGB and BGB carbon stocks of post-deforestation land-use classes which may partially offset forest carbon emissions. Time-averaged carbon stocks (taCs) were estimated for each crop type, which give the mean C stock over a plantation cycle from planting to harvesting (Gibbs *et al.* 2008, Blagodatsky *et al.* 2016). This approach allows carbon stock estimates to be scaled up from a single plot to the landscape level comparison of land uses with different rotation lengths, accommodates clearance and carbon release at the end of the crop rotation, and better reflects the net carbon outcomes and long term climate impact of a transition from one steady-state land use to another than a time series of carbon fluxes (Cowie *et al.* 2007, Yang *et al.* 2016). The taCs approach is consistent with the IPCC Good Practice Guidelines (IPCC 2003) and the carbon accounting methodology used for the REDD+ pilot project in Cambodia (WCS 2015).

The carbon stock estimate for rubber (52.5 tC ha^{-1}) was based on multiple estimates of taCs calculated either as the carbon stock in the median year of the plantation cycle using logistic or Gompertz models of growth, or 50% of the carbon stock in the final year of the plantation cycle assuming a linear biomass increase (Blagodatsky *et al.* 2016). Time-averaged carbon stocks of other crops (cashew 22.3 tC ha^{-1}, sugarcane 6.8 tC ha^{-1}, cassava 2.5 tC ha^{-1}) were estimated as 50% of the carbon stock accumulated at the maximum rotation length (Supplementary Table 7). As for forests, soil carbon stocks were not considered, although there is strong evidence for soil carbon reductions when forest is converted to rubber (Blagodatsky *et al.* 2016) or other tree cash crops (van Straaten *et al.* 2015).

3.3.6 Resin revenue

The potential revenue generated by resin collection over a 25-year period (*D;* $ ha^{-1}; years 0 – 24 inclusive) was calculated following equation (2):

$$D = \sum_{\mathrm{n}=0}^{24} \frac{[(t * i) * y] * p_R}{(1+r)^n} \quad (2)$$

where t is resin tree stem density ha^{-1} (from forest inventories), i the likely proportion of non-starter, or exhausted trees that do not yield, y the resin yield (litres stem^{-1} yr^{-1}) and p_R the resin price ($ litre^{-1}; Supplementary Table 16). Resin revenue is discounted over a 25-year timeframe n relative to the present (year 0) using a discount rate r of 10%. All trees ≥30 cm DBH can potentially be tapped, with no identified relationship between resin yield and DBH; labour costs were not included in calculation of resin profits, as resin tends to be collected only when there are few or no alternative wage options (Evans *et al.* 2003).

3.3.7 Agricultural net present value

We estimated likely farm-gate profits for rubber and other cash crops using region-specific data (Supplementary Tables 6 and 12). The 25-year discounted net present value (NPV, $ ha^{-1}; P_b) of each potential crop (b; rubber, cashew, cassava, sugar) was calculated as shown in equation (3):

$$P_b = \sum_{\mathrm{n}=0}^{24} \frac{(y_b * p_b) - C_b}{(1+r)^n} \quad (3)$$

where y_b is the year-specific yield (t ha^{-1} yr^{-1}), p_b the price (\$ t^{-1}) and C_b the cost of production (\$ ha^{-1} yr^{-1}). Profits are discounted over a 25-year timeframe n using a discount rate r of 10%.

A comparison of the spatial distribution of historically suitable environmental space for rubber (Ahrends *et al.* 2015) and the spatial distribution of deciduous dipterocarp forest (DDF (Wohlfart *et al.* 2014); which shares many characteristics with our open forest category, although often in fine-grained mosaic with mixed deciduous and other forest types) shows most DDF lies outside the optimal zones for rubber cultivation. Reduced rubber yields were predicted (though the magnitude of reduction was not defined) in areas of drought risk, defined as <60 mm rainfall month^{-1} for >5 months year^{-1}, and/or <1200 mm rainfall year^{-1} and/or <20 mm rainfall during the driest quarter (Ahrends *et al.* 2015). This drought risk definition overlaps with the bioclimatic limits of DDF (1000 – 1500 mm rainfall year^{-1} with a defined dry season) (Wohlfart *et al.* 2014). Although rubber yield reductions due to drought have not been quantified, reduced dry season growth can delay the onset of tapping from the sixth to the tenth year after planting (Carr 2012). We therefore delayed the onset of tapping in the plantation cycle in open forest scenarios (Supplementary Table 12).

To accommodate change in annual yield across a 25-year production cycle, model iteration-specific yield curves were simulated separately for each crop (Supplementary Figure 10, Supplementary Table 12), using a single iteration-specific randomly-generated yield index (proportionate between minimum and maximum values, uniform distribution). Crop-specific production costs were sampled from a uniform distribution between the minimum and maximum values available in the literature (Supplementary Table 12) and crop-specific farm-gate prices were used (Supplementary Table 6 and 12).

3.3.8 Breakeven carbon prices, including opportunity costs, setup and implementation costs

The breakeven carbon price (E_{xb}; \$ tCO$_2^{-1}$) required to offset the opportunity cost of forest conservation ($(R_x - D) + P_b$) and cover the costs of REDD+ project setup (one-off) and implementation (discounted over 25 years; G; \$ ha^{-1}) for each scenario of logging (x) and crop (b, including the option of no crop) was calculated as shown in equation (4):

$$E_{xb} = \frac{[(R_x - D) + P_b] + G}{3.67 * Z_x} \tag{4}$$

where Z_x is the residual carbon stock (tC ha^{-1}) of all trees ≥10 cm DBH remaining in each logging scenario (x) and 3.67 the conversion factor from tC to tCO$_2$ (Fisher *et al.* 2011). Carbon stocks of post-deforestation land-uses were subtracted from Z_x when exploring the impact of incorporating these stocks on carbon breakeven prices. Estimated PES project setup (\$4.95 ha^{-1}) and implementation costs (\$9.47–\$13.09 ha^{-1} yr^{-1}) were obtained from a multi-year spending history and projected management expenditure budget for a pilot REDD+ project in Cambodia (Wildlife

Conservation Society, unpublished data). These costs fell well within annual management and implementation cost estimates in existing literature, that range from \$0.87–\$20.01 ha^{-1} (Gilroy *et al.* 2014). Annual implementation costs were discounted and summed across a 25-year timescale.

Finally, sensitivity analyses explored the impacts on carbon breakeven price of: increasing or decreasing timber, resin and agricultural commodity prices (Supplementary Figure 6), non-availability of resin markets (Supplementary Table 8), reducing the threshold of commercially viable stem diameter on timber profits (Supplementary Table 3), and alternative discount rates of 5%, 8% and 15% as applied to agricultural NPV and resin revenue (Supplementary Figures 7-8).

3.3.9 Leakage

The costs of controlling for leakage of avoided deforestation for rubber, or forest degradation through selective logging, were not included in analyses. Ultimately, the need for land for rubber expansion will only be mitigated through reduction in global demand for natural rubber, which is reliant upon 1) global markets and demand for products such as vehicle and aircraft tyres, 2) development of alternatives to natural rubber, or 3) improvements in recycling methods. Similarly, demand for timber, within and beyond mainland Southeast Asia, would need to be met from well-managed sources before leakage of forest degradation or conversion could be effectively controlled. However, a robust rubber sustainability initiative, or corporate zero deforestation commitments, may displace rubber plantations to sites where land use conversion entails negligible net carbon emissions. We have therefore not attempted to incorporate the cost of controlling leakage in this analysis.

3.3.10 Data availability

A summary of the agricultural data used for this study are shown in Supplementary Table 12, with data sources detailed in Supplementary Table 6. Original forest inventory data are not publicly available, and were made available for sole use in this study with permission of the Forestry Administration of the Royal Government of Cambodia, Wildlife Conservation Society Cambodia Program, Wildlife Conservation Society Global Conservation Program, Permian Global in collaboration with Ecometrica and Birdlife Cambodia, and the study co-authors (D.P. Bebber, P. Chhang, F.H. Lambrick, I. Theilade). Derived data supporting the findings of this study, and all R scripts used to resample data and run the models, are available from the corresponding author on reasonable request.

3.4 Results

3.4.1 Timber volume and carbon stocks

Harvestable wood volume of all tree species, assuming a minimum harvestable DBH of 40 cm (≥10 cm for luxury timber; Supplementary Note 1), was 49.4 ± 0.5 m^3 ha^{-1} in dense forest, but just 13.6 ± 0.3 m^3 ha^{-1} in open forest (mean ± SE; Table 1). Timber of royalty classes I and II accounted for 54% of volume in dense forest and 69% in open forest. Luxury timber was rare, contributing only 1.1 ± 0.0 m^3 ha^{-1} in dense forest (2%) and 1.3 ± 0.1 m^3 ha^{-1} in open forest (10%).

Forest type	Timber royalty class	Carbon stock ≥40 cm DBH (tC ha^{-1})	Carbon stock ≥30 cm DBH (tC ha^{-1})	Wood volume ≥40 cm DBH (m^3 ha^{-1})	Wood volume ≥30 cm DBH (m^3 ha^{-1})
Dense	Luxury	2.2 ± 0.0		1.1 ± 0.3	
	I	30.8 ± 0.4	35.0 ± 0.4	16.9 ± 0.2	19.2 ± 0.3
	II	12.1 ± 0.3	14.6 ± 0.3	9.8 ± 0.2	12.1 ± 0.2
	III	3.5 ± 0.1	5.3 ± 0.1	2.4 ± 0.1	3.4 ± 0.1
	Non-classified	39.0 ± 0.4	53.5 ± 0.5	19.3 ± 0.2	26.2 ± 0.2
Open	Luxury	1.8 ± 0.1		1.3 ± 0.1	
	I	20.5 ± 0.5	29.5 ± 0.1	6.6 ± 0.1	14.7 ± 0.3
	II	4.6 ± 0.1	9.1 ± 0.0	2.7 ± 0.1	7.0 ± 0.1
	III	0.5 ± 0.0	1.2 ± 0.4	0.3 ± 0.0	1.5 ± 0.0
	Non-classified	8.0 ± 0.3	12.6 ± 0.1	2.7 ± 0.1	8.0 ± 0.2

Table 1 – Mean carbon stock and wood volume held in harvestable stems of each timber royalty class in dense and open forests

Mean carbon stock and wood volume are shown with the 95% confidence interval of the mean.

Mean forest carbon stocks, measured as combined above-ground and below-ground biomass (AGB and BGB) of all stems ≥10 cm DBH, were 194 ± 1.2 tC ha^{-1} in dense forest (123—284 tC ha^{-1} among individual landscapes) and 104 ± 0.8 tC ha^{-1} in open forest (60—157 tC ha^{-1} among landscapes; Table 1, Supplementary Figure 3). Lower carbon stocks in open forest reflected both a greater proportion of smaller stems (Supplementary Figure 4) and lower stem density (mean across inventories 213—311 ha^{-1} in open; 415—589 ha^{-1} in dense; Supplementary Table 2), despite similar wood density (weighted mean 0.713 g cm^{-3} in open; 0.630 g cm^{-3} in dense).

Forest carbon stock changed minimally following selective logging of luxury timber ("Luxury logged" scenario), reducing by 1% in dense forest and 2% in open. Additional logging of classes I and II ("Luxury, I, II logged") reduced carbon stocks by 20% in dense forest (to 175 ± 1.1 tC ha^{-1}) and 26%

in open forest (to 78 ± 0.7 tC ha^{-1}; Table 1; Figure 2). Even the removal of all trees ≥40 cm DBH ("All trees logged"), left 60% (dense) and 66% (open) of original carbon stock. Therefore, substantial forest carbon is retained before conversion to rubber, even after logging of valuable timber or removing all large trees.

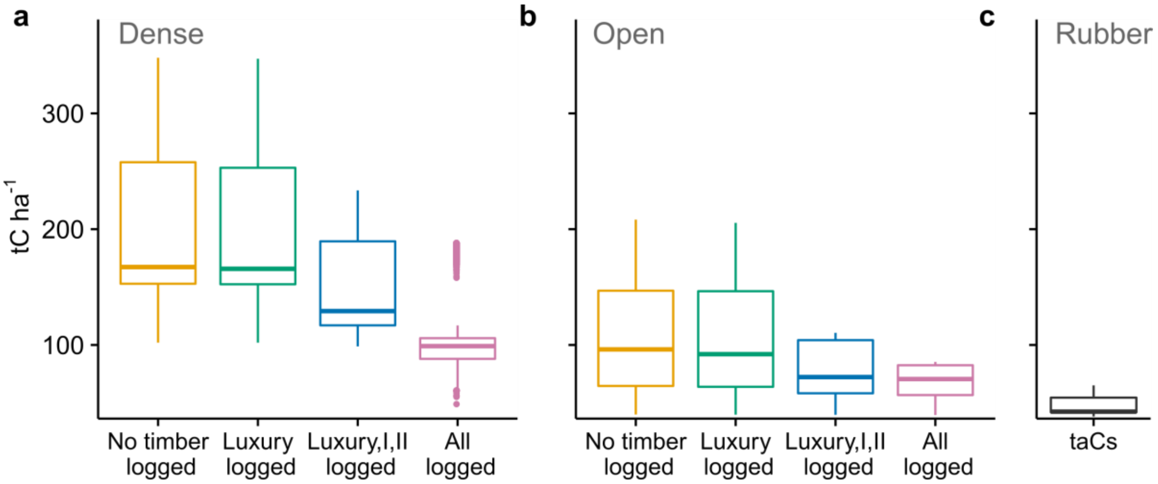


FIGURE 2 – EFFECTS OF SELECTIVE LOGGING ON DENSE AND OPEN FOREST CARBON STOCKS

Carbon stock (tC ha^{-1}) of a) dense and b) open forest in initial state ('No timber logged') and under scenarios of selective or complete logging (following Figure 1), and c) time-averaged carbon stocks (taCs) of rubber plantations in Southeast Asia (Blagodatsky *et al.* 2016). Central bar shows median, box shows upper and lower quartiles, whiskers extend to 1.5x the inter-quartile range, and outliers are presented as dots.

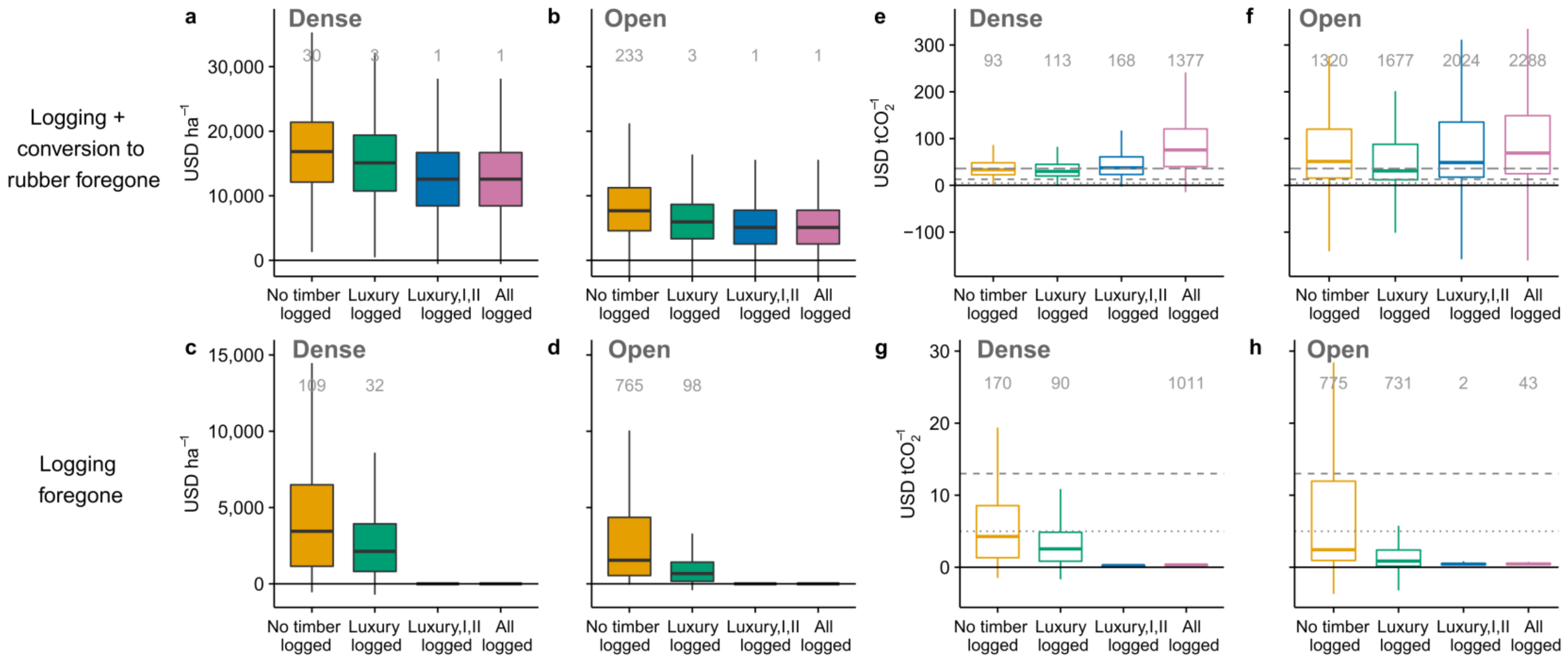
Rubber plantations are considered forest cover in FAO Forest Resources Assessments (FAO 2010), while the USAID LEAF Atlas maps rubber-dominated landscapes as forest (such as Southern Thailand), but protected open forests in Eastern Cambodia as non-forest (Petrova *et al.* 2012). However, we find that even assuming high post-deforestation time-averaged carbon stocks (taCs) for rubber of 52.5 tC ha^{-1} (from Cambodia, Thailand and Indonesia (Blagodatsky *et al.* 2016), likely greater than will be achieved in seasonal open forest environments), conversion of intact forest to rubber would still generate net losses of 141.5 ± 1.2 tC ha^{-1} in dense forest and 51.5 ± 0.8 tC ha^{-1} in open forest (Figure 2). Even conversion of degraded logged open forest would generate net emissions, as well as biodiversity loss. Additionally, although we do not account for changes in soil organic carbon (SOC) because the Intergovernmental Panel on Climate Change (IPCC) tier 1 carbon outcome calculation method assumes no SOC change with conversion to perennial tree crops, conversion of lowland forest to rubber plantations does generate SOC emissions (van Straaten *et al.* 2015) which, if included, would increase net emissions.

3.4.2 Logging and conversion to rubber

Total opportunity costs of intervening to protect intact forest ("No timber logged + rubber" scenario), calculated as the profit from a single offtake of all commercial timber (Supplementary Table 3) plus the 25-year net present value (NPV; 10% discount rate) from subsequent rubber plantations (Supplementary Table 4), were \$16,841 (median, interquartile range \$12,118-\$21,397) ha^{-1} in dense forest and \$7,674 (\$4,581-\$11,250) ha^{-1} in open forest (Figure 3). Intervening after removal of luxury timber ("Luxury timber logged + rubber" scenario) reduced opportunity costs of logging by 38% in dense forest and 56% in open; however, total opportunity costs (including rubber) were only reduced to \$15,097 (\$10,738-\$19,390) ha^{-1} and \$5,956 (\$3,341-\$8,663) ha^{-1}, respectively. After all valuable timber had been logged out ("Luxury, I, II, logged" or "All trees logged"), the opportunity cost of rubber alone was \$12,570 (\$8,436-\$16,698) ha^{-1} in dense forest, and \$5,089 (\$2,532-\$7,764) ha^{-1} in open forest. The substantially lower NPV of rubber in open forest arises from the delay of tapping from six years to ten years after planting, due to slower tree growth in drier conditions. Using a discount rate of 8% to allow comparison, our estimate of rubber NPV in dense forest areas (\$16,533 ha^{-1}, \$11,403-\$21,732 ha^{-1}) is similar to estimates from lowland Xishuangbanna, China (~\$19,800 ha^{-1}, 25-year NPV, 8% discount rate; Yi, Cannon, *et al.* 2014).

Figure 3 – Opportunity costs and breakeven carbon prices needed to protect forests from logging and conversion to rubber

Opportunity costs (a – d) include forgone profits from logging alone, or logging and rubber, offset by resin revenue except where resin trees (all class II) are logged out (in the "Luxury, I, II logged" and "All timber logged" scenarios). Breakeven carbon prices (e – h) are the prices needed to offset combined opportunity costs and carbon finance scheme setup and implementation costs. Costs are shown separately for dense and open forests. Time-averaged post-deforestation land-use carbon stocks partially offset forest carbon losses. Scenarios (of permitted selective logging, with and without potential for conversion to rubber) follow Figure 1; boxplot format as Figure 2. Grey lines on breakeven carbon price panels (e – h) represent indicative global carbon prices: dotted = \$5 tCO_2^{-1} (voluntary market forest carbon sales and non-market carbon fund prices), short dash = \$13 tCO_2^{-1} (compliance market prices) and long dash = \$36 tCO_2^{-1} (social cost of carbon, not shown on "Logging foregone" plots; see Supplementary Table 5). Outliers (more than 1.5x the interquartile range) are not displayed to improve the clarity of the figure; the value shown above each box-whisker gives the *n* outliers excluded out of 10,000 modelled results.



High opportunity costs translated into high breakeven carbon prices, far greater than indicative carbon prices currently paid in voluntary carbon market sales and carbon funds (\$5 tCO_2^{-1}) or compliance market sales (\$13 tCO_2^{-1}), although for dense forests, breakeven prices were below the estimated social cost of carbon (\$36 tCO_2^{-1}; Supplementary Table 5). Protecting intact forest ("No timber logged + rubber") required \$33.43 (median, interquartile range \$22.65-\$48.20) tCO_2^{-1} for dense forest and \$51.11 (\$15.59-\$120.19) tCO_2^{-1} for open forest (Figure 3). Removal of luxury timber reduced breakeven prices to \$29.86 (\$20.02-\$44.96) tCO_2^{-1} in dense forest and \$30.93 (\$11.95-\$87.78) tCO_2^{-1} in open forest, bringing the latter below the estimated social cost. This was because luxury timber comprised only a small proportion of forest carbon (Table 1), but a large proportion of timber value (Supplementary Table 3), so that logging opportunity costs were substantially reduced while forest carbon stocks remained mostly intact.

Although further logging of all valuable timber ("Luxury, I, II logged + rubber") reduced the opportunity costs of logging to zero, breakeven prices in this scenario were actually higher than the intact forest scenario for dense forest (\$37.48, \$23.28-\$60.90 tCO_2^{-1}), and reduced only slightly in open forest (\$48.83, \$17.56-\$135.18 tCO_2^{-1}). This was due to the large proportion of forest carbon held in class I and II species (Table 1); removing large trees of these timber classes substantially depleted residual carbon stocks while reducing logging opportunity costs. With fewer carbon credits a greater breakeven price was needed to offset the opportunity cost of rubber. In a few model iterations, conversion of heavily degraded open forest to rubber generated net carbon gains, producing negative carbon prices. This effect is further shown in Figure 4; although substantial variation in carbon prices is linked to opportunity costs, in both forest types carbon breakeven prices decrease as forest carbon stock increases.

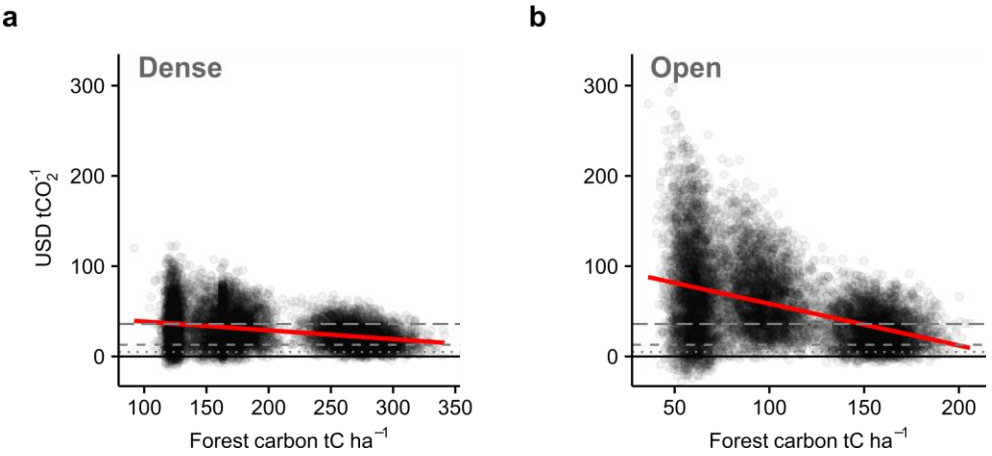


FIGURE 4 – EFFECT OF FOREST CARBON STOCK ON BREAKEVEN CARBON PRICES IN DENSE AND OPEN FORESTS

The response of breakeven carbon price to forest carbon stock under the "No timber logged" scenario is shown for a) dense and b) open forests. Each dot represents the outcome of one model iteration. Grey dashed lines indicate real-world carbon prices, following Figure 3. Red lines represent a linear model relating forest carbon to breakeven carbon price (with grey shaded *SE* too narrow to be visible).

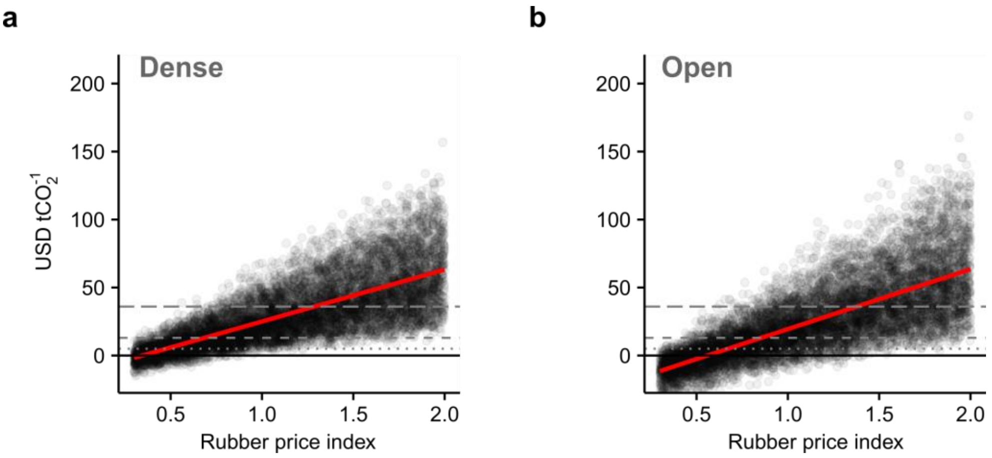


FIGURE 5 – EFFECT OF RUBBER PRICE ON BREAKEVEN CARBON PRICES IN DENSE AND OPEN FORESTS

The response of breakeven carbon price to rubber prices under the "No timber logged" scenario is shown for a) dense and b) open forests. Each dot represents the outcome of one model iteration. Grey dashed lines indicate real-world carbon prices, following Figure 3. Red lines represent a linear model relating breakeven carbon price to rubber price index (with grey shaded SE, too narrow to be visible), where an index value of 1.0 is the ten-year mean rubber price (2003 – 2012).

3.4.3 Sensitivity analysis

Farm gate prices for rubber strongly influenced carbon breakeven prices in both dense and open forest (Figure 5). To make our results robust to short-term price volatility (Supplementary Figure 1), we used a 10-year mean price (2003–2012; \$2,595 ± 200 t^{-1}). However, even using the relatively low 2014 rubber price (\$1,644 ± 200 t^{-1}, indexed at ~0.6 relative to the 10-year mean in Figure 5), breakeven prices in the "No timber logged + rubber" scenario only reduced to \$19.09 (\$11.52-\$27.82) tCO_2^{-1} in dense forest, and \$16.08 (\$0.14-\$60.65) tCO_2^{-1} in open forest, still higher than carbon market prices, although well below the estimated social cost.

As future market changes could influence the relative profitability of alternative crops, we also considered the NPV of other major cash crops in Cambodia: cassava, cashew and sugarcane. Oil palm was not assessed as much of mainland Southeast Asia is marginal or unsuitable for its cultivation (Pirker *et al.* 2016); however, 25-year oil palm NPV in Malaysia was estimated to be \$11,240 ha^{-1} (Fisher *et al.* 2011). Estimates of cassava NPV exceeded that of rubber (\$14,597, \$10,133-\$19,124 ha^{-1}), but other crops were less profitable (Supplementary Table 4). We note that cassava yields and prices could be lower than our estimates, due to the potential for nutrient depletion with repeated cultivation and lack of access to markets, which we have not accounted for (Supplementary Table 6). Although all three crops store less carbon than rubber (Supplementary Table 7), cassava and cashew still generated high breakeven carbon prices in the "No timber logged" scenarios: for cassava \$27.02 (\$19.59-\$36.66) tCO_2^{-1} in dense forest and \$49.76 (\$31.54-\$76.14) tCO_2^{-1} in open forest, and for cashew \$21.98 (\$15.29-\$30.31) tCO_2^{-1} and \$47.21 (\$25.59-\$75.52) tCO_2^{-1}, respectively (Supplementary Figure 5). Breakeven prices were affected by crop price, as for rubber (Supplementary Figure 6), but omitting potential revenues from dipterocarp resin harvest (Supplementary Table 8), and changing resin prices (Supplementary Figure 6), had negligible effects on breakeven prices.

Predicted NPVs of all crops were highly sensitive to changes in discount rate. Rubber NPV increased to ~\$25,800 ha^{-1} with a 5% discount rate in dense forest (giving a breakeven carbon price of \$60.04, \$41.20-\$88.06 tCO_2^{-1} assuming protection of an intact forest) and \$14,700 ha^{-1} in open forest (\$108.68, \$43.43-\$255.92 tCO_2^{-1}). A 15% discount rate reduced rubber NPV to ~\$6,200 ha^{-1} in dense forest (\$20.62, \$13.60-\$29.41 tCO_2^{-1}) and \$1,100 ha^{-1} in open forest (\$20.12, \$3.47-\$62.34 tCO_2^{-1}; Supplementary Table 4 and Figures 7-8). We use 10% for our main analysis to allow comparability with other studies, but the choice of discount rate introduces substantial variation in our estimates of opportunity cost. Discount rates of 5% are commonly used in social investments (Johnston and Cornelis van Kooten 2015), but discount rates of 8% have been recommended for cost-benefit analysis in Asia (Yi, Cannon, *et al.* 2014); we therefore present the full range of NPV results in Supplementary Table 4.

3.4.4 Logging without conversion to rubber

If the threat of forest conversion to rubber could be removed, our analysis shows that carbon prices close to those currently paid on voluntary markets and carbon funds (\$5 tCO_2^{-1}) could meet the opportunity costs of logging in mainland Southeast Asia. This could be achieved through government zoning, market exclusion of "deforestation rubber" via development of a robust sustainability initiative (Tayleur *et al.* 2016), or further corporate zero deforestation commitments such as that announced by Michelin (2016). In this case, opportunity costs of forgoing logging ("No timber logged") were less than a quarter (\$3,443, \$1,151-\$6,490 ha^{-1}) in dense forest and around a fifth (\$1,534, \$563-\$4,356 ha^{-1}) in open forest (Figure 3, Supplementary Table 3) of the costs of forgoing both logging and rubber in the "No timber logged" scenario. Consequently, if forest conversion is prevented by other means, the median breakeven carbon price of protecting intact dense forest from any logging was only \$4.27 (\$1.33-\$8.56) tCO_2^{-1}, and \$2.43 (\$0.95-\$11.95) tCO_2^{-1} in open (Figure 3).

Changes in timber price influenced breakeven carbon prices in logging-only scenarios (Supplementary Figure 6). Likewise, reducing the minimum threshold for timber harvest to 30 cm DBH increased breakeven carbon prices of intact forest to \$5.23 (\$2.23-\$9.61) tCO_2^{-1} in dense forest and \$6.26 (\$3.52-\$16.22) tCO_2^{-1} in open forest, with the opportunity cost of logging in open forests more than doubling to \$3,373 (\$1,214-\$6,346) ha^{-1}, owing to the high density of class I and II stems 30-40 cm DBH in open forest (Supplementary Table 3).

3.5 Discussion

Our findings show that forest conversion to rubber can currently generate far more revenue than a carbon finance scheme so that, under current market conditions, avoiding deforestation requires recognition of environmental, social or other ecosystem service benefits of forests, and a willingness to accept apparent economic costs. However, for dense forests, mean breakeven prices were close to estimates of the social cost of carbon, which is a measure of future damage costs resulting from an emission of a tonne of CO_2 today, and indicates the carbon price, or tax, needed to fully internalise the costs of climate change (Hope and Hope 2013). When considering relatively low rubber prices, breakeven carbon prices for both forest types were substantially below the social cost. We used a conservative value of \$36 tCO_2^{-1}, based on World Bank and US government estimates (Supplementary Table 5). However, a review of studies in 2012 gave a mean estimate of \$177 tCO_2^{-1} (SD \$293 tCO_2^{-1}) (Tol 2011) while subsequent analyses produced estimates of \$103 tCO_2^{-1} (Hope and Hope 2013) or \$220 tCO_2 (Moore and Diaz 2015). Considering these much greater predicted values for the social cost of carbon, preventing forest conversion to rubber becomes a highly cost-effective action to reduce emissions, even for intact open forests.

There are indications that carbon market prices could be raised much closer to the social cost of carbon in some sectors to meet climate change targets: for instance, if recent proposals to set a price floor of €20-30 (~$23-34) tCO_2^{-1} on the EU Emissions Trading Scheme come to fruition, a new global benchmark could be set (Dinguirard 2016, Szabo 2016). Recent research investigating the incentives required to decarbonise the energy sector to meet the Paris Agreement targets (i.e., limiting global temperature rise to below 2°C) similarly found the need to introduce carbon prices to the industry and power sectors of all countries, with prices of \$20 tCO_2^{-1} by 2020 and \$120 tCO_2^{-1} by 2030 in OECD countries, \$10-\$90 tCO_2^{-1} in major emerging economies, and \$5-\$30 tCO_2^{-1} elsewhere (OECD/IEA 2017). Then, carbon finance for dense forests could be nearly as lucrative as conversion to rubber in the near-term while, in the longer-term, prices could be high enough to defend even open forests from conversion on a cost-benefit analysis basis, notwithstanding the risk of unintended market feedbacks arising from restricted supply (see below) (Lim *et al.* 2017). We also note that even if full opportunity costs of conservation are not met, smaller financial incentives to conserve forest may be an attractive option if there is existing social or political pressure to conserve, or where non-market values are recognised.

Open forests tend to be drier with poorer sandier soils (Sawada *et al.* 2007) and thus may have lower agricultural potential. We incorporated the effect of delayed maturation of rubber under drier open forest conditions, but robust data on rubber yields in such conditions are notably lacking (Carr 2012). Poorer growth could also result in lower rubber carbon stocks (Ahrends *et al.* 2015, Blagodatsky *et al.* 2016), reducing the breakeven price needed to match rubber profits in open forest areas, and improving the prospects for protection using carbon finance. Robust data on the relative yield and carbon stocks of rubber plantations established on former open or dense forests are, therefore, urgently required (Blagodatsky *et al.* 2016). However, where land concessions prove unfavourable for rubber, the high potential NPV of cassava, known to grow successfully in less favourable environments, at least in the short term (Supplementary Table 6), reinforces the importance of other mechanisms to curb forest conversion.

We have used a non-spatial approach to estimate breakeven carbon prices for dense and open forest in mainland Southeast Asia. We show that rubber NPV is likely substantially lower in open than in dense forest areas, and were able to incorporate geographic variability in timber and carbon stocks, which influenced breakeven carbon prices. Additional spatial variation in rubber NPV and carbon breakeven prices will be generated by distance to markets, regional farm gate prices, yields (affected by soil type and quality, topography, elevation, water availability, planting material, etc.), and labour costs, amongst others. However, spatially-explicit data on potential rubber NPV are not currently available for most of mainland Southeast Asia, including Cambodia, not least because recently established plantations are not yet productive. This precluded meaningful marginal cost curve analyses to quantify the additional area of rubber expansion that could potentially be avoided for incremental increases in carbon price. Such spatial analysis has been conducted locally for Xishuangbanna, a hotspot of rubber expansion in Southwest China, where field data from existing plantations show that NPV decreases with greater elevation, particularly above 900 m asl (Yi, Cannon, *et al.* 2014, Yi, Wong, *et al.* 2014). Once context-specific rubber yield, price and cost data become available, marginal cost analyses may be possible for mainland Southeast Asia. Nevertheless, if carbon finance focuses on the cheapest avoided emissions first, making each additional tonne of carbon more expensive than the last, initial efforts to protect forests from rubber might only require prices at the low end of our presented range. However, if forests have good potential for conversion to rubber but are also priorities for conservation using carbon finance, due to high carbon densities and or biodiversity value, costs may be much higher.

While we have assessed the likelihood of success for carbon finance schemes in tackling forest conversion to rubber under current conditions, and considered a range of potential price changes, rubber prices may rise in the future if rubber production is constrained relative to demand due to restriction of planting in forested areas (Lim *et al.* 2017). The design of any initiative attempting to prevent forest conversion to rubber would therefore need to account for potential market feedbacks generated through conservation activities, which could otherwise generate net negative outcomes for carbon emissions and biodiversity (Lim *et al.* 2017). Ultimately, the demand for natural rubber might only be mitigated through further development of synthetic alternatives (although these are currently petroleum based and may represent a worse outcome for carbon emissions), or though improvements in methods for recycling natural rubber.

In contrast to mainland Southeast Asia's dense forests, forests of insular Southeast Asia have substantially higher timber volumes (84.9 ± 9.0 SE m^3 ha^{-1}, 50 – 60cm DBH; Edwards *et al.* 2011), which translate into higher timber profits ($5,563 ± 757 SE ha^{-1} in dense forest; Edwards *et al.* 2011), and require higher carbon prices to match the opportunity costs of logging (e.g. $22–28 tCO_2^{-1}; Fisher *et al.* 2011). However, the presence of high-value luxury timbers (Milne 2015) poses a distinct problem for timber valuation in mainland Southeast Asia. Timber prices, particularly for luxury species, increase up the supply chain (Supplementary Table 9) and the Cambodian timber trade is highly opaque, involving informal payment systems and considerable illegality (Forest Trends 2015, Milne 2015). Such issues are found across mainland Southeast Asia. Although using local-level timber prices was appropriate due to the lack of formal timber markets, this underestimates total opportunity costs accruing to hidden but powerful actors, especially those selling timber illegally on international markets. These additional opportunity costs may play out through pressure on governmental decision makers, particularly those involved in land allocation. Thus, forest conservation efforts based on climate change or biodiversity outcomes cannot, in this context, be divorced from social demands for governance and accountability (Forest Trends 2015).

In the context of current carbon finance markets and funds, policy initiatives are urgently needed if we are to stem emissions of forest carbon, and the loss of irreplaceable biodiversity, caused by rubber expansion onto forest in mainland Southeast Asia. These include: 1) a rubber sustainability initiative that restricts market access for deforestation rubber and/or offers a price premium for non-deforestation rubber, 2) zero-deforestation pledges from major corporate rubber consumers, and 3) governmental commitment to forest conservation that couples improved forest governance with effective land-use planning. Such support, together with measures to tackle threats from other cash crops, could unlock the potential for carbon markets to help protect the unique forests of mainland Southeast Asia from logging.

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3.8 Online supplementary material

Note: *Nature Communications* is formatted such that methods are placed after the introduction, results and discussion, and the supplementary online material follows this structure, with supplementary material for the methods placed after supplementary material for the rest of the text. For this thesis version of the manuscript, the main text material has been reorganised so that the methods are given between the introduction and the results, following the order of all other chapters, but the supplementary material for the methods remains in a separate section. Material is ordered as figures, tables, then text, following *Nature Communications* formatting requirements.

This online supplementary information includes:

Supplementary material for introduction, results and discussion:

SUPPLEMENTARY TABLE 4: Median and interquartile range of agricultural 25-year Net Present Value

SUPPLEMENTARY TABLE 5: Real world carbon prices

SUPPLEMENTARY TABLE 6: Data sources for agricultural net present value calculation

SUPPLEMENTARY TABLE 7: Post-deforestation land-use carbon stock estimates

SUPPLEMENTARY TABLE 8: Value of dipterocarp resin collection and influence on breakeven carbon prices

SUPPLEMENTARY TABLE 9: Price estimates for timber royalty classes at various selling points in Cambodia

SUPPLEMENTARY NOTE 1: Background to forest management and logging in Cambodia

Supplementary material for methods

SUPPLEMENTARY FIGURE 10: Rubber yield curve simulation example

SUPPLEMENTARY TABLE 10: Resampling input parameters

SUPPLEMENTARY TABLE 11: Proportion of luxury stems ≥60cm DBH compared between pairs of landscapes by Chi-squared two-sampled proportions test; there were no significant differences

SUPPLEMENTARY TABLE 12: Input parameters for agricultural net present value calculation

SUPPLEMENTARY TABLE 13: Harvestable timber volume equations for evergreen, mixed and deciduous forests

SUPPLEMENTARY TABLE 14: Timber species named in roadside/village price estimates

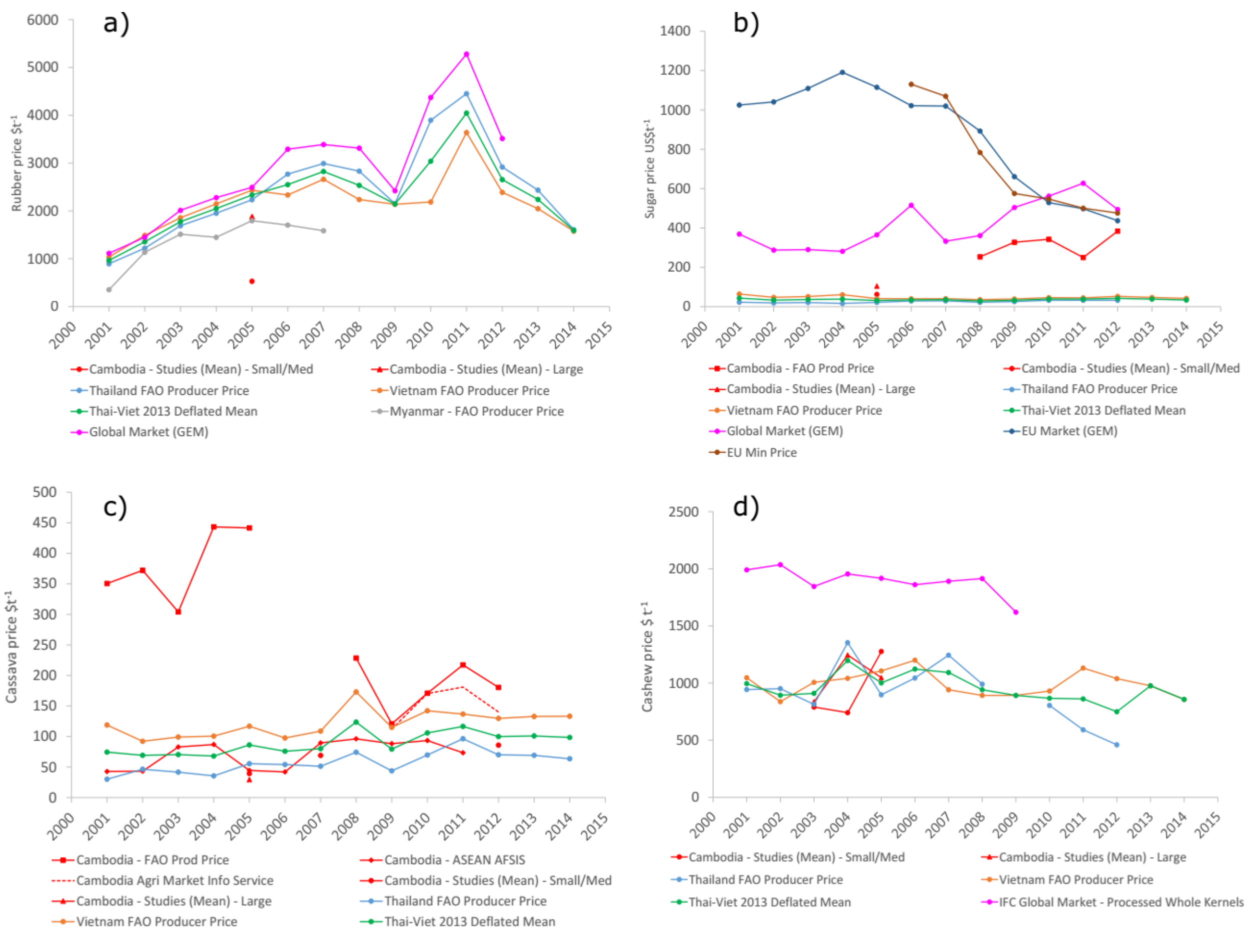
SUPPLEMENTARY TABLE 15: Timber extraction cost estimates

SUPPLEMENTARY TABLE 16: Dipterocarpus spp. resin revenue estimation parameters

SUPPLEMENTARY METHODS: Modelling opportunity costs and carbon breakeven prices

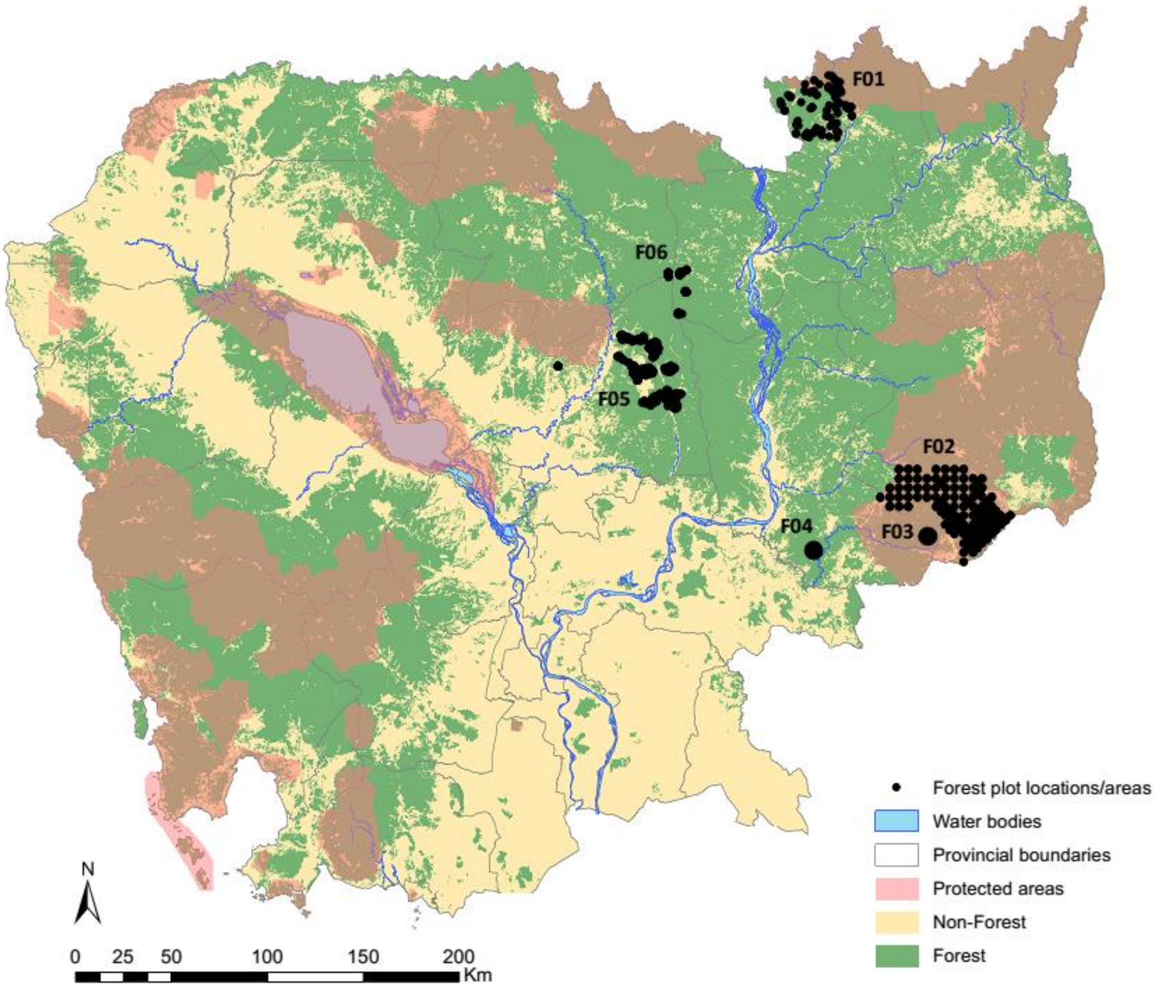
SUPPLEMENTARY FIGURE 1: Producer price comparison among data sources

Panels show comparison of producer prices from different data sources for: a) rubber, b) sugar, c) cassava and d) cashew. Prices shown are nominal dollars adjusted to US$ 2013 dollars using a consumer price index (CPI) averaged across Thailand, Vietnam and Cambodia.



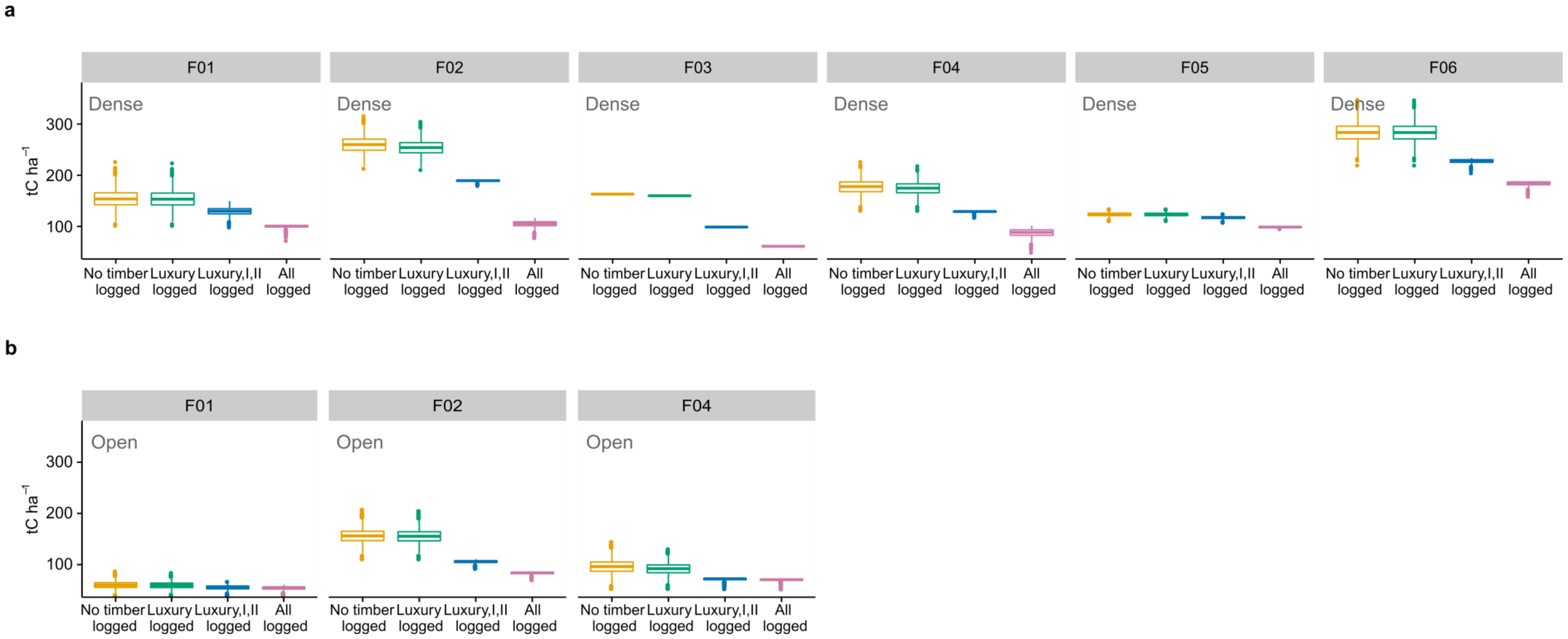
Supplementary Figure 2: Map of forest inventory locations

Forest inventories were obtained from six landscapes (F01 – F06) in Cambodia (Supplementary Table 1); dense forest was sampled in each landscape, and open forest in three landscapes. Two landscapes are managed for biodiversity conservation (F01 and F02), two are partly managed by communities (F04 and F05) and two are not under formal management (F03 and F06). Some selective logging had taken place in all landscapes prior to data collection, as has occurred across most of the region (Supplementary Note 1). F03 is represented by a single marker as the inventory comprised a single 60 ha plot, and F04 is represented by a single marker as individual plot locations were not available. Dense forest was sampled at all locations, and open forest at F01, F02 and F04. Data sources: F01 (Permian Global in collaboration with Ecometrica and Birdlife Cambodia, unpublished data, 2009); F02 & F03 (Wildlife Conservation Society/Forestry Administration, unpublished data, 2011); F04 (CDRI, unpublished data, 2006, Hansen and Neth 2006); F05 (Lambrick *et al.* 2014); F06 (Theilade *et al.* 2011, with the late J.F. Maxwell).



SUPPLEMENTARY FIGURE 3: Forest carbon stock of dense and open forest in each of six Cambodian forest landscapes

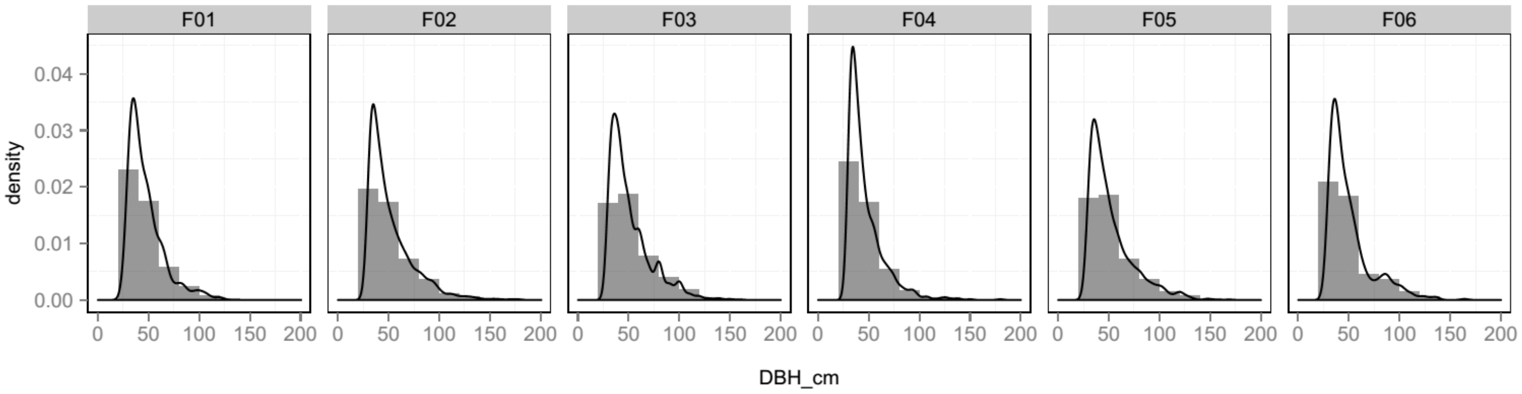
The between-landscape variation in carbon stock (tC ha^{-1}), shown for a) dense forest and b) open forest, reflects differences in annual rainfall, dry season length, and species composition and structure (Sawada *et al.* 2007, WCS 2015), but may also reflect exploitation history.



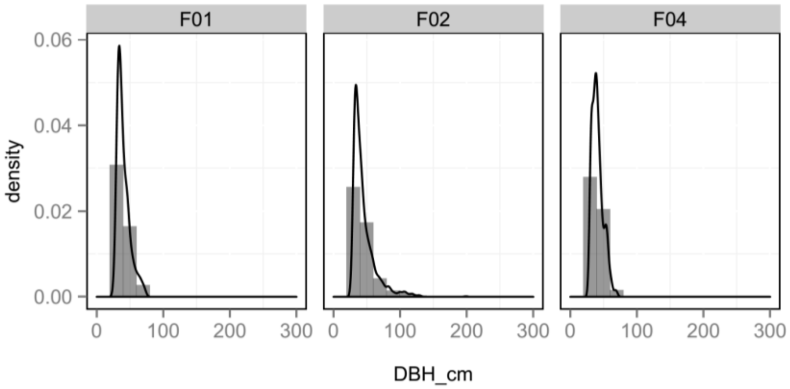
SUPPLEMENTARY FIGURE 4: Frequency distribution of stem diameters for each forest inventory

Data only includes stems ≥30cm in a) dense forest and b) open forest. Bars show the relative frequency of trees within DBH size categories, while curves represent a smoothed density distribution. Frequency distribution of tree sizes is similar across dense forest landscapes, while in open forest landscapes. Although open forest in landscapes F02 and F01, and dense forest in landscape F02 appeared to have a greater proportion of larger luxury class stems (≥60cm DBH) than other landscapes, the differences were not significant (Supplementary Figure 9; Supplementary Table 11).

a) Dense forest

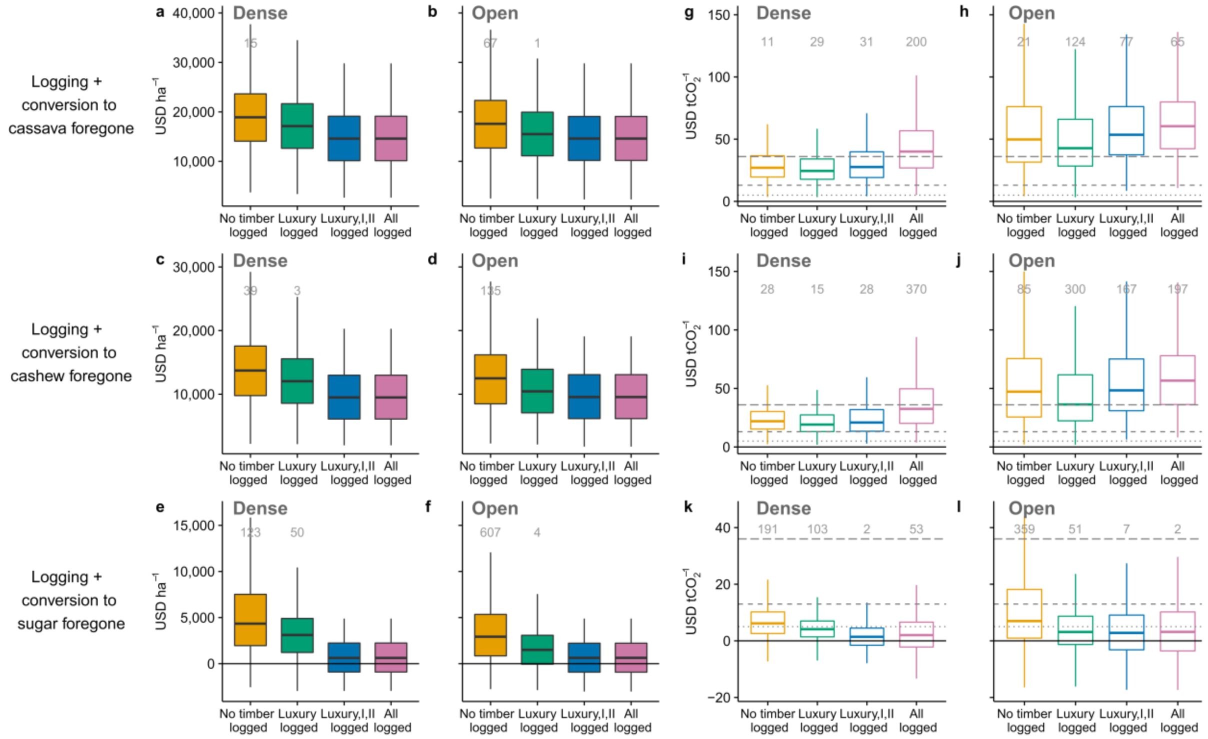


b) Open forest



SUPPLEMENTARY FIGURE 5: Opportunity costs and breakeven carbon prices needed to protect forests from logging and conversion to cassava, cashew and sugar

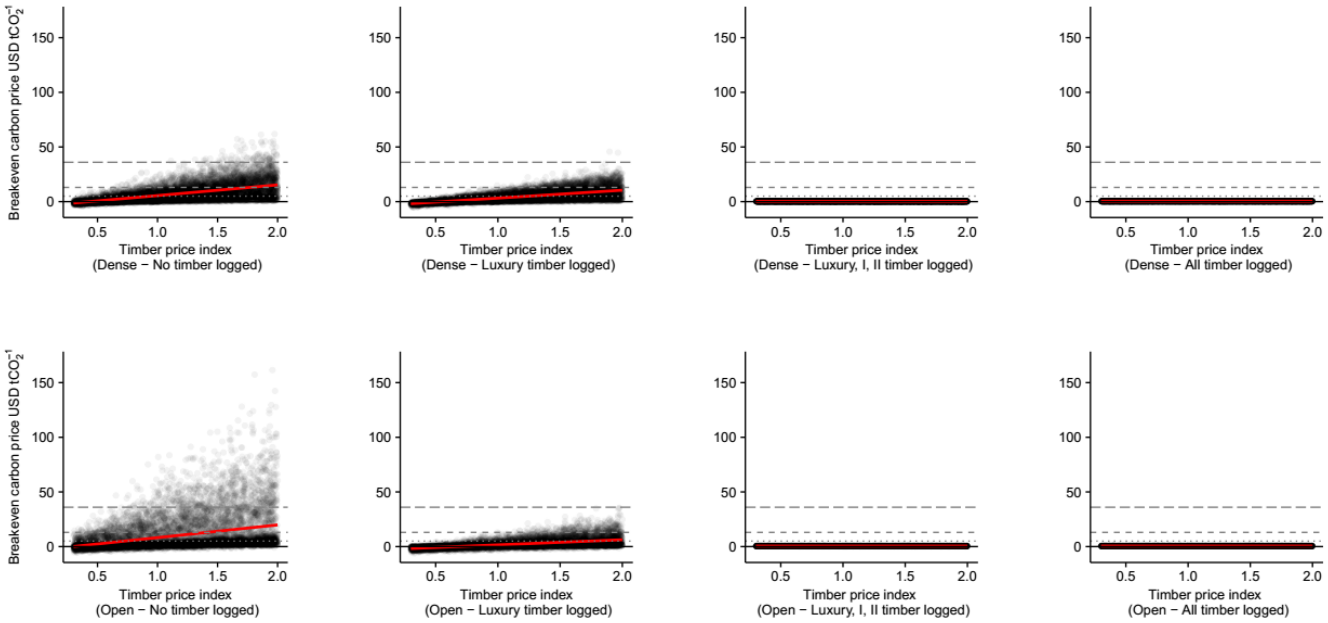
Opportunity costs (a – f) are based on the forgone profits from logging (for luxury class timber, trees ≥10 cm DBH, other classes of timber, trees ≥40 cm DBH) and agriculture (cassava, cashew or sugar, 25 year NPV, 10% discount rate), offset by lost revenue from resin collection with the logging of resin trees (timber royalty class II), which are logged in the "Luxury, I, II logged" and "All logged" scenarios. Breakeven carbon prices (g – l) are the prices needed to offset opportunity costs, REDD+ setup costs and implementation costs. Costs are shown separately for dense and open forests. Time-averaged post-deforestation land use carbon stocks partially offset forest carbon losses. Grey lines in the BCP panels represent real world carbon prices (Supplementary Table 10): dotted = \$5 tCO_2^{-1} (indicative of voluntary market forest carbon sales and non-market carbon fund prices), short dash = \$13 tCO_2^{-1} (indicative of compliance market prices) and long dash = \$36 tCO_2^{-1} (indicative of the social cost of carbon). Outliers (more than 1.5x the interquartile range) are not displayed to improve the clarity of the figure; the value shown above each box-whisker gives the n outliers excluded out of 10,000 modelled results.



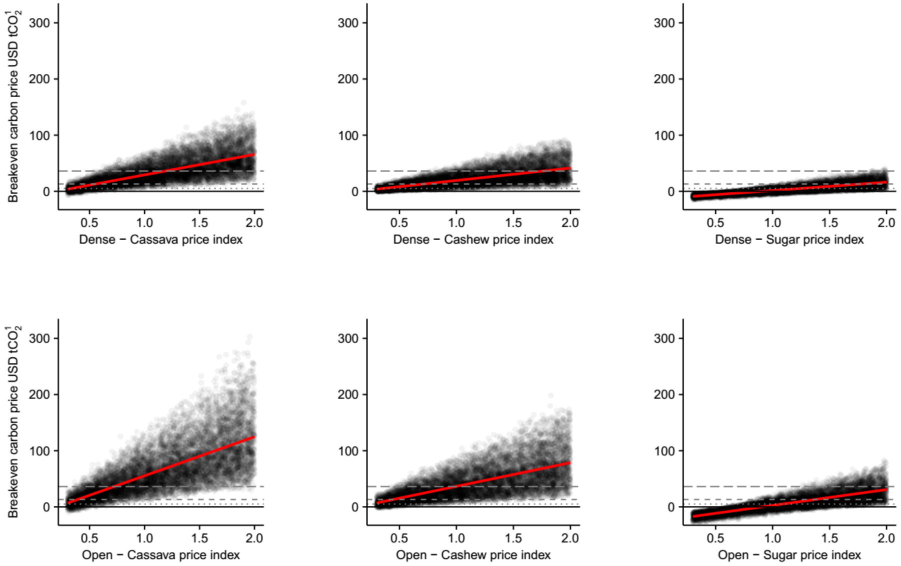
SUPPLEMENTARY FIGURE 6: Sensitivity analysis assessing the effect of commodity prices on breakeven carbon prices

Sensitivity analyses explored the impacts of increasing and decreasing a) timber, b) agricultural and c) resin prices on carbon breakeven price, using a price index randomly drawn from a uniform distribution between 0.3 and 2.0 (i.e. from less than a third, to two times the mean price), following Gilroy et al (2014). This index range encompassed all annual producer farm gate price fluctuations for natural rubber 2000 – 2014 inclusive. For each input variable examined (timber, agricultural or resin price), carbon equilibrium prices are shown in relation to the price index. For agricultural price sensitivity analysis, we only show sensitivity of carbon breakeven prices under the "No timber logged" scenario for each crop. Increases in timber and agricultural prices could have a strong effect on the opportunity costs of conservation. In contrast, resin prices would need to increase by more than two times their current value in order to reduce carbon equilibrium prices. Grey lines on the panels represent real world carbon prices (Supplementary Table 10): dotted = \$5 tCO_2^{-1} (indicative of voluntary market forest carbon sales and non-market carbon fund prices), short dash = \$13 tCO_2^{-1} (indicative of compliance market prices) and long dash = \$36 tCO_2^{-1} (indicative of the social cost of carbon).

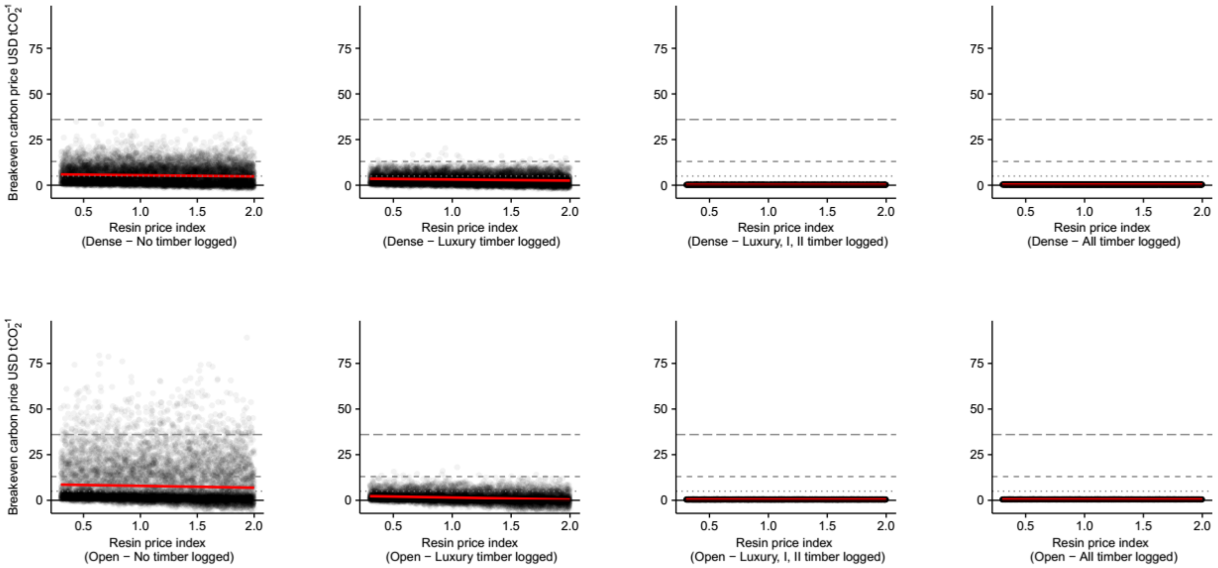
a) Timber prices – "Logging only"



b) Agricultural prices – “No timber logged”

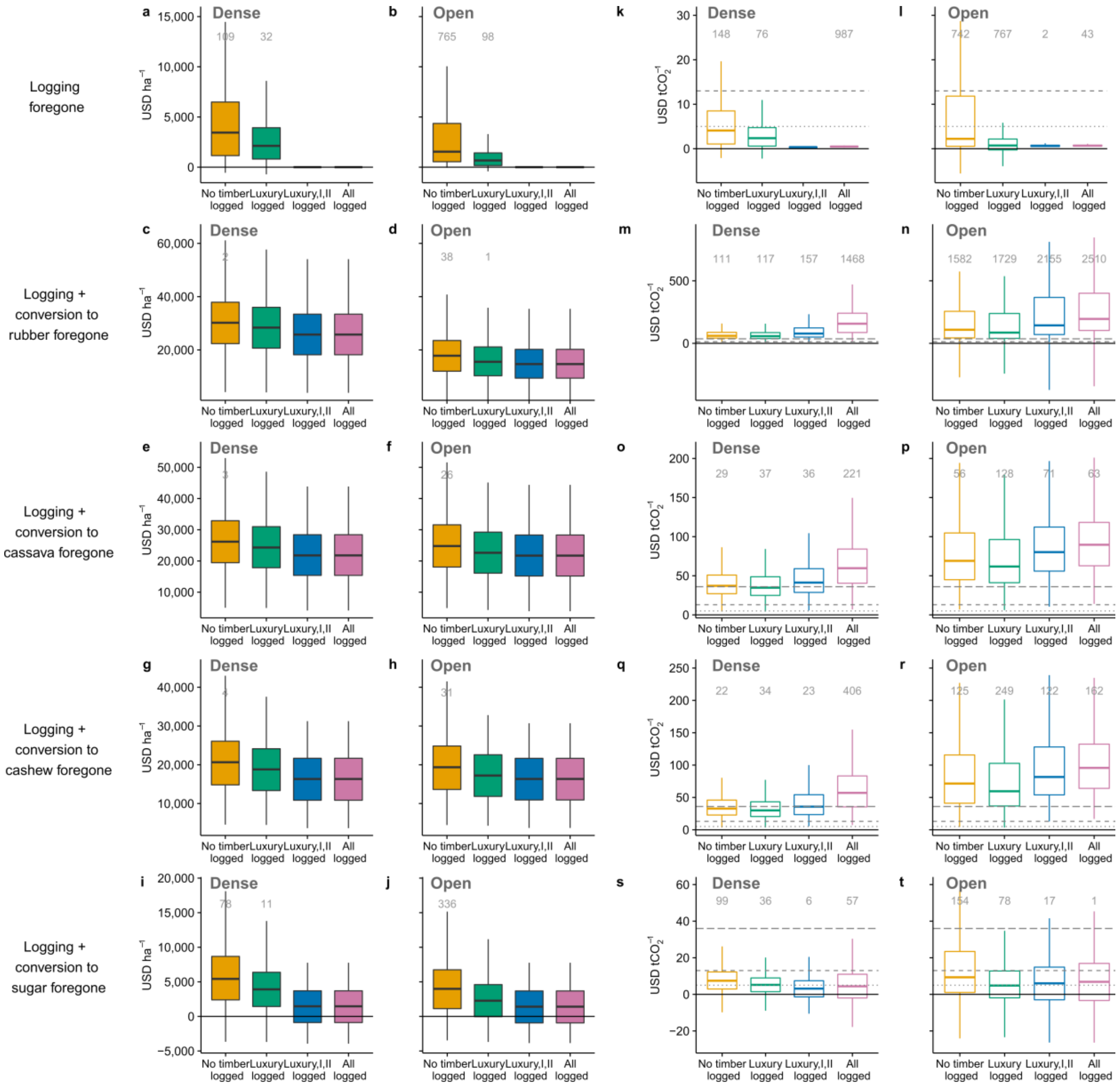


c) Resin prices - "Logging only"



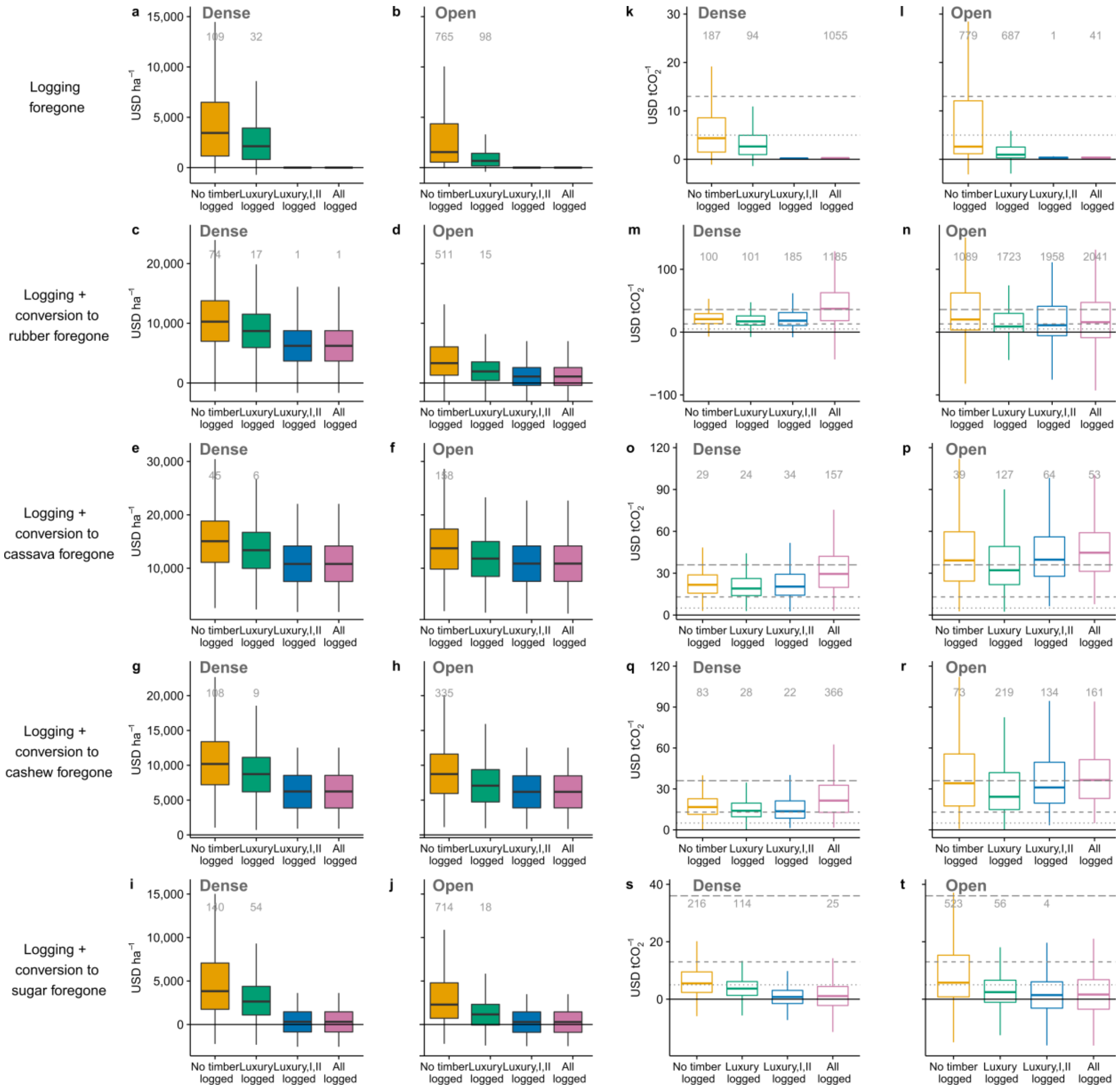
SUPPLEMENTARY FIGURE 7: Consequence of an alternative 5% discount rate on opportunity costs and breakeven carbon prices needed to protect forests from logging and conversion to rubber and other cash crops

Opportunity costs (OC; a – j) include forgone profits from logging (for luxury class timber, trees ≥10 cm DBH, other classes of timber, trees ≥40 cm DBH), and/or conversion to agriculture, offset by resin revenue, except where resin trees (class II) are logged out (in the "luxury, I, II logged" and "all timber logged" scenarios). Breakeven carbon prices (BCP; k – t) are the prices needed to offset opportunity costs, REDD+ setup costs and implementation costs. Costs are shown separately for dense and open forests. Time-averaged post-deforestation land use carbon stocks partially offset forest carbon losses. Grey lines on BCP panels represent real world carbon prices: dotted = \$5 tCO_2^{-1} (indicative of voluntary market forest carbon sales and non-market carbon fund prices), short dash = \$13 tCO_2^{-1} (indicative of compliance market prices) and long dash = \$36 tCO_2^{-1} (indicative of the social cost of carbon). Outliers (more than 1.5x the interquartile range) are not displayed to improve the clarity of the figure; the value shown above each box-whisker gives the n outliers excluded out of 10,000 modelled results.



Supplementary Figure 8: Consequence of an alternative 15% discount rate on opportunity costs and breakeven carbon prices needed to protect forests from logging and conversion to rubber and other cash crops

Opportunity costs (OC; a – j) include forgone profits from logging (for luxury class timber, trees ≥10 cm DBH, other classes of timber, trees ≥40 cm DBH), and/or conversion to agriculture, offset by resin revenue, except where resin trees (class II) are logged out (in the "luxury, I, II logged" and "all timber logged" scenarios). Breakeven carbon prices (BCP; k – t) are the prices needed to offset opportunity costs, REDD+ setup costs and implementation costs. Costs are shown separately for dense and open forests. Time-averaged post-deforestation land use carbon stocks partially offset forest carbon losses. Grey lines on BCP panels represent real world carbon prices: dotted = $5 tCO$_2^{-1}$ (indicative of voluntary market forest carbon sales and non-market carbon fund prices), short dash = $13 tCO$_2^{-1}$ (indicative of compliance market prices) and long dash = $36 tCO$_2^{-1}$ (indicative of the social cost of carbon). Outliers (more than 1.5x the interquartile range) are not displayed to improve the clarity of the figure; the value shown above each box-whisker gives the n outliers excluded out of 10,000 modelled results.

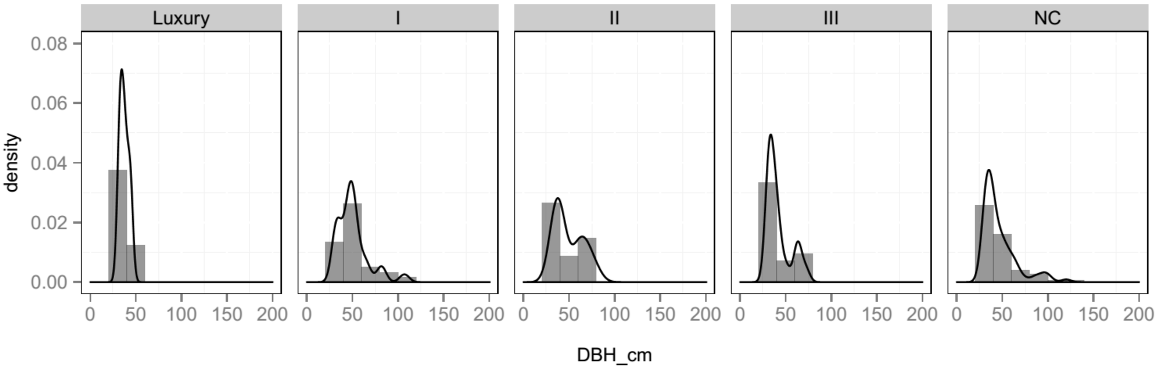


SUPPLEMENTARY FIGURE 9: Frequency distribution of stem diameters for each timber royalty class within each forest inventory

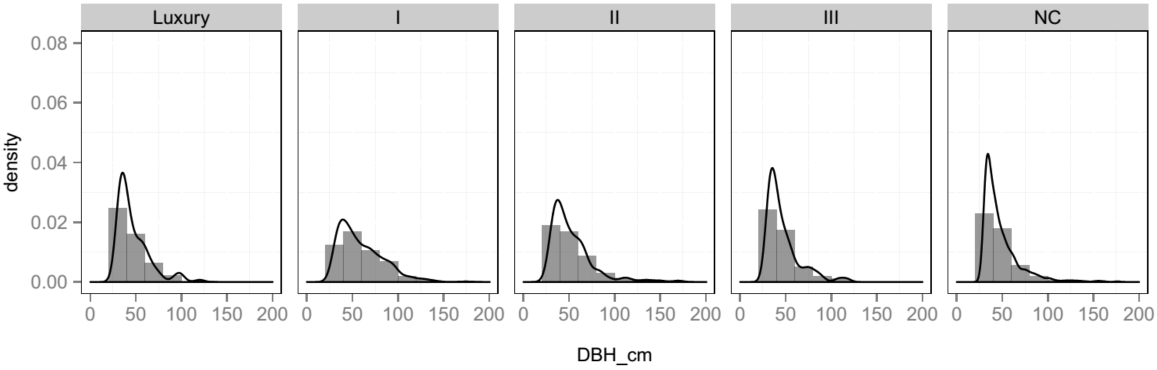
Data only includes stems ≥30cm in dense forest (a, i – vi) and open forest (b, i – iii). Bars show the relative frequency of trees within DBH size categories, while curves represent a smoothed density distribution. Frequency distribution of tree sizes is remarkably similar across all forest landscapes.

a) Dense forest

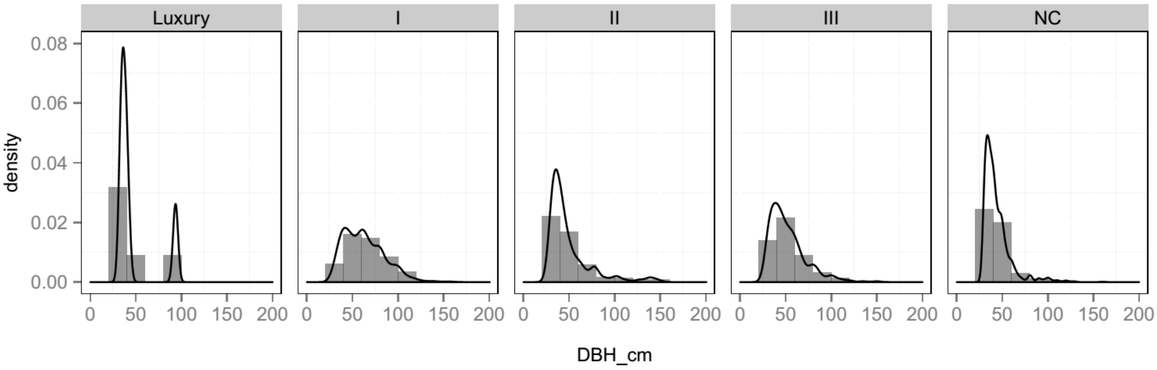
i. F01



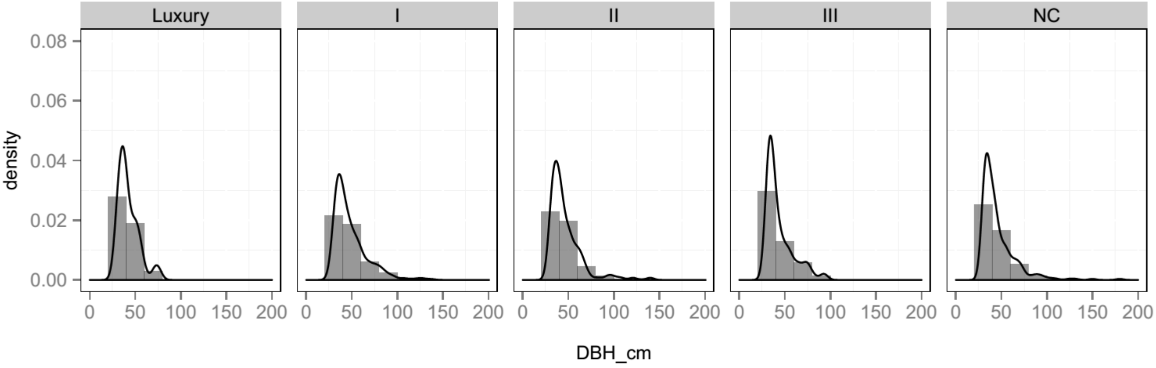
ii. F02



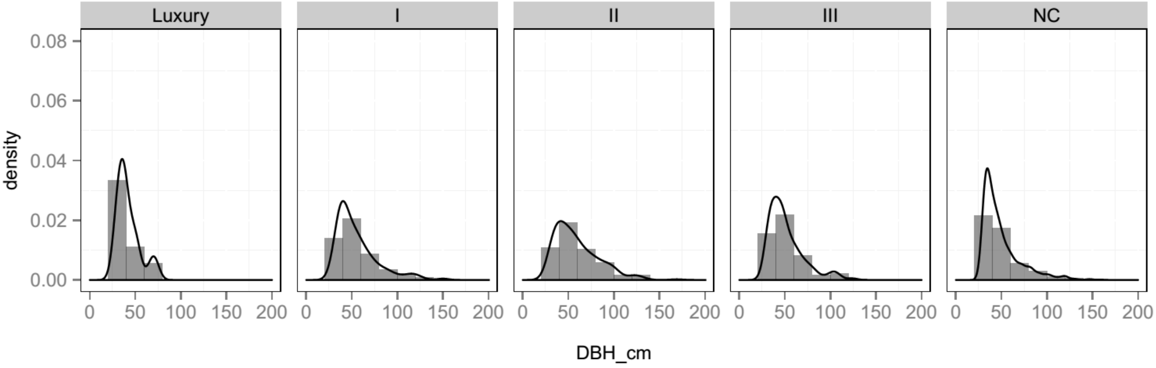
iii. F03



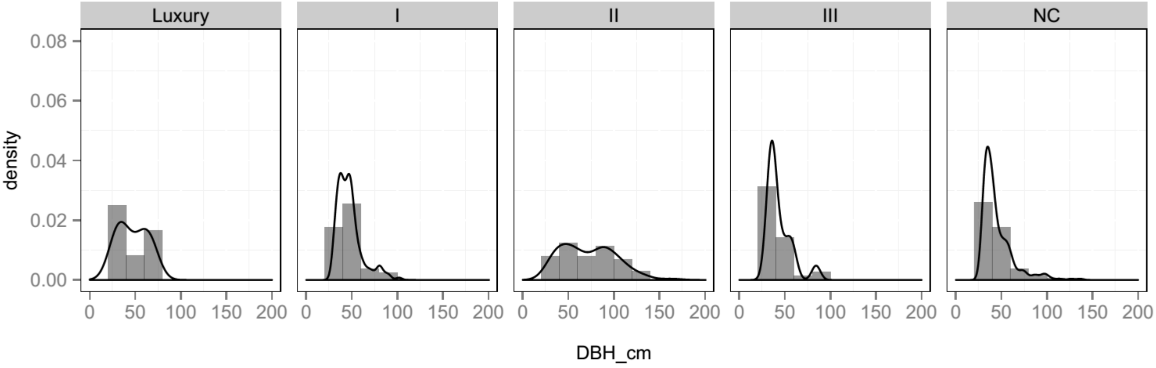
iv. F04



v. F05

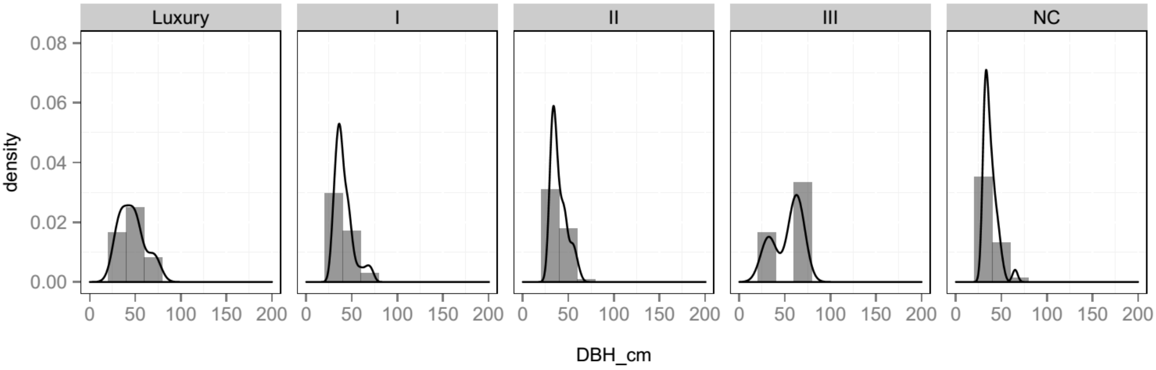


vi. F06

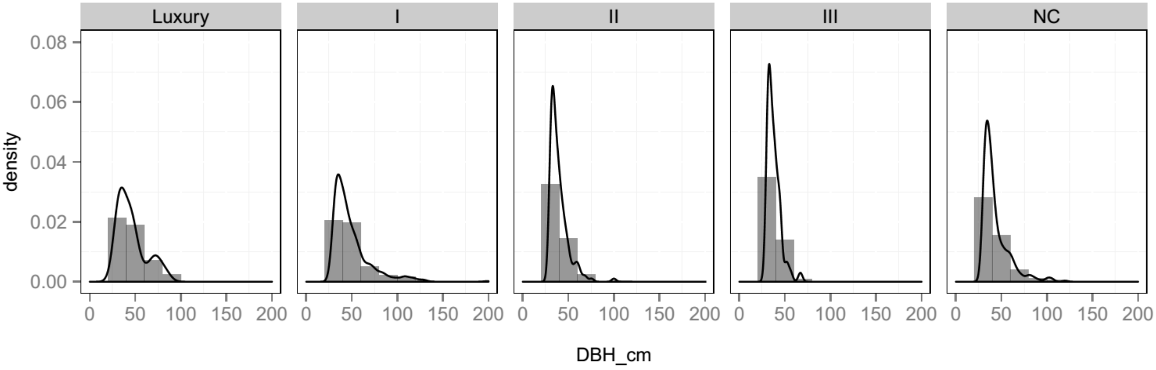


b) Open forest

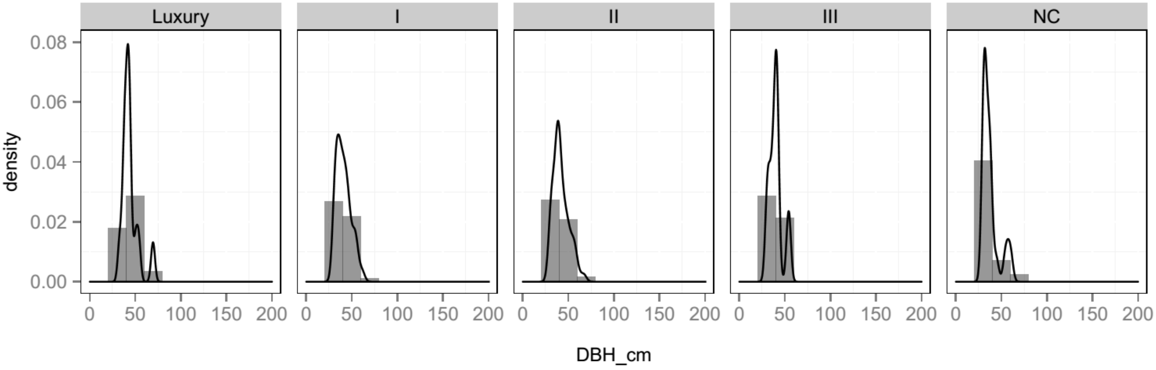
i. F01



ii. F02



iii. F04



SUPPLEMENTARY TABLE 1: Tree inventories used to parameterise carbon and timber models

Inventories were originally collected for forest structure, carbon stock measurement and forest composition studies. Five inventories used a fixed sampling area (3.1 - 60 ha total per landscape) while F05 used variable radius plots. Where data were available for trees 5 ≤ 10cm DBH, these were omitted from analysis, standardising to a minimum DBH of 10cm across all datasets. Data sources: F01 (Permian Global in collaboration with Ecometrica and Birdlife Cambodia), F02 and F03 (Wildlife Conservation Society/Forestry Administration, unpublished data, 2011), F04 (CDRI, unpublished data, 2006), F05 (Lambrick et al. 2014), F06 (Theilade et al. 2011, with the late J.F. Maxwell). Approx. coverage indicates the maximum distance between plots within each dataset.

Forest category	Source	Forest type	n trees >10 cm DBH	n trees >30 cm DBH	Tree size (DBH, cm)	n plots	Plot dimensions (m)	Plot area (ha)	Total area sampled (ha)	Approx. coverage (km)
Dense	F01	Semi-Evergreen	457	188	5 - 20	31	Radius = 5.64	0.01	0.31	38
					>20	31	Radius = 17.84	0.1	3.1	
	F02	Evergreen/Semi-Evergreen	4594	2289	5 – 15	63	3x subplots; radius = 5	0.024	1.48	60
					15 – 30	63	3x subplots; radius = 15	0.212	13.36	
					>30	63	3x subplots; radius = 20	0.377	23.75	
	F03	Evergreen	3246	2784	5 - 15	24 (pooled to 1)	10 x 25	0.025	0.6	n/a
					15 - 30	24 (pooled to 1)	10 x 50	0.05	1.2	
					>30	1	1000 x 600	60	60	
	F04	Evergreen/Semi-Evergreen	3038	894	5 – 10	24	25 x 50	0.125	3	n/a
					10 – 30	24	50 x 50	0.25	6	
					>30	24	50 x 100	0.5	12	
	F05	Evergreen, Semi-Evergreen + Deciduous	3013	1349	>10	361	n/a - variable radius	n/a	n/a	48
	F06	Evergreen, Riverine, Lagostroemia	2512	576	>10	100	10 x 50	0.05	5	83
Total			**16860**	**8080**		**585**			**129.8**	**260**
Open	F01	Deciduous	373	128	5 – 20	36	Radius = 5.64	0.01	0.36	29
					>20	36	Radius = 17.84	0.1	3.6	
	F02	Deciduous/Semi-Evergreen matrix	2366	1193	5 – 15	41	Radius = 5	0.024	0.97	60
					15 - 30	41	Radius = 15	0.212	8.69	
					>30	41	Radius = 20	0.377	15.46	
	F04	Deciduous	682	195	5 – 10	15	25 x 25	0.0625	0.94	n/a
					10 – 30	15	25 x 50	0.125	1.88	
					>30	15	50 x 50	0.25	3.75	
Total			**3421**	**1516**		**92**			**35.65**	**260**
		Grand Total	**20281**	**9596**		**667**			**165.45**	**260**

SUPPLEMENTARY TABLE 2: Commercial timber species and royalty classes in Cambodia.

[NB – this is submitted as a separate document to Nature Communications, so has its own short reference list]

Timber royalty classes published by the Forestry Administration of Cambodia (2), with IUCN threat category (3). Royalty classes determine the royalty payment that should be paid to the Royal Government of Cambodia when felling trees (4) and reflect commercial value (5). Luxury class timber commands the highest commercial value (see Supplementary Table 8) and royalty payment, followed in descending order by I, II, III and non-classified (NC) species. When assigning tree species from forest inventories to timber royalty classes, both Khmer and scientific species names in inventories were checked against the timber royalty class list; trees without species names and species recorded in forest inventories not listed on the FA timber royalty class list (2) were classed as NC, except where specified in notes a - f. Species listed on the royalty class list but not recorded in any of the forest inventories are listed here for reference. Nomenculature in column "Scientific name" follows The Plant List (6). Scientific names as recorded in the forest inventories or the timber royalty class list (1) are also shown, in column "Recorded scientific name". Mean density (and 95% confidence interval) of stems ≥10 cm DBH in dense and open forest were calculated from plot-level data for each inventory. Inventory names have been anonymised (D1 – D6; O1 – O3) in the interest of data confidentiality and security for sites containing high value timber. Note column refers to the following footnotes:

* References for resin species (5,7-11)
** This inventory was completed over a single large area, and a single stem density for the total area is given, rather than a mean and CI

Notes:
(a) *Dalbergia bariensis* is a synonym of *D. oliveri* but is commonly referred to as *D. bariensis* in Cambodia (1); all *Dalbergia* species are listed on CITES Appendix II
(b) *Lagerstroemia macrocarpa* was not named in the list of timber royalties (2), but was reported with the same common name as *Lagerstroemia* sp and is thus grouped as class I, as it is likely to be treated the same way.
(c) *Anisoptera costata* is not specifically named in the list of timber royalties (2), but both *A. costata* and *A. scaphula* are given the same common, and *A. costata* is named elsewhere as a class II industrial timber species (12), so they are likely to be treated in the same way.
(d) *Hopea* sp. was reported from two datasets with the same common name as other *Hopea* species, and is thus grouped together with them as class II as they are likely to be treated the same way.
(e) *Shorea farinosa* was not named in the list of timber royalties (2) but was reported with the same common name as *Shorea* sp. in four of the forest inventories, so is likely to be treated the same way.
(f) *Vatica odorata* was not named in the list of timber royalties (2) but was reported with the same common name as *Vatica astrotricha* in four of the forest inventories, so is likely to be treated the same way.
(g) *Artocarpus rigidus* is not specifically named in the list of timber royalties (2) but was reported with the same common name as *A. integer* in four of the forest inventories, so is

likely to be treated the same way.

References

(1) Hartvig, I., Czako, M., Kjær, E. D., Nielsen, L. R. & Theilade, I. The use of DNA barcoding in identification and conservation of rosewood (Dalbergia spp.). PLoS One 10, (2015); **(2)** FA. Forest Systems Research and Modelling Handbook Regional Volume Table. Appendix 1 - List of Species and Respective Species Groups. (Kingdom of Cambodia, Forestry Administration; Indufor Oy; Foret Ressources Management; Societe Generale de Surveillance, 2004).; **(3)** IUCN. The IUCN Red List of Threatened Species. Version 2014.3. (2014). at http://www.iucnredlist.org; **(4)** Kim, S., Phat, N., Koike, M. & Hayashi, H. Estimating actual and potential government revenues from timber harvesting in Cambodia. For. Policy Econ. 8, 625–635 (2006); **(5)** Hansen, K. K. & Neth, T. Natural forest benefits and economic analysis of natural forest conversion in Cambodia. Working Paper 33. (Cambodia Development Resource Institute, 2006); **(6)** The Plant List. Version 1.1. (2013). at http://www.theplantlist.org; (7) Appanah, S., Turnbull, J. M. & Research, C. I. F. A Review of Dipterocarps: Taxonomy, Ecology, and Silviculture. (Center for International Forestry Research, 1998); **(8)** Baird, I. G. & Dearden, P. Biodiversity conservation and resource tenure regimes: A case study from Northeast Cambodia. Environ. Manage. 32, 541–550 (2003); **(9)** Conservation International. Prey Lang Forest Landscape. A Biodiversity Assessment for Forestry Administration by Conservation International & Winrock International. (Conservation International; Winrock International, 2015); **(10)** Evans, T. D., Piseth, H., Phaktra, P. & Mary, H. A study of resin-tapping and livelihoods in Southern Mondulkiri, Cambodia, with implications for conservation and forest management. (Wildlife Conservation Society, 2003); **(11)** Huljus, J. & Jell, B. Cambodia. Review of strategic forest management plans prepared by concession companies operating in Cambodia. Part II. Final report. (GFA Terra Systems, 2005); **(12)** Sok Tha, M. & Aare Olsen, J. Cambodia Tree Seed Project / Danida. National Priority Tree Species Workshop, Phnom Penh, 15 - 16 August 2000. (Cambodia Tree Seed Centre, Department of Forestry and Wildlife, Ministry of Agriculture, Forestry and Fisheries, 2001).

Note	Scientific name	Local name	Recorded scientific name	Royalty class	IUCN	Family	*Resin species	Wood density	Mean (± CI) stem density: dense forest (DBH ≥10 cm; ha-1)					Mean (± CI) stem density: open forest (DBH ≥10 cm; ha-1)			
									D1	D2	D3	D4	D5**	D6	O1	O2	O3
	Afzelia xylocarpa	Beng	*Pahudia cochinchinen*	Luxury	EN	Leguminosae		0.605	0.2 ± 0.39	3.66 ± 1.55	-	-	2.5	-	-	2.67 ± 1.9	-
	Albizia lebbeck	Chreis	*Albizzia lebbek*	Luxury	-	Leguminosae		0.599	-	-	4.83 ± 8.79	-	-	0.5 ± 0.54	-	-	0.28 ± 0.28
a	***Dalbergia oliveri***	Neang Noun	*Dalbergia oliveri*	Luxury	EN	Leguminosae		0.731	0.2 ± 0.39	-	0.34 ± 0.68	-	-	0.08 ± 0.16	-	-	0.28 ± 0.28
a	***Dalbergia bariensis***	Neang Noun	*Dalbergia bariensis*	Luxury	EN	Leguminosae		0.731	0.6 ± 1.18	5.14 ± 3.69	-	-	0.02	-	-	1.6 ± 0.67	-
a	***Dalbergia cochinchinensis***	Krornhoung	*Dalbergia conchinchi*	Luxury	VU	Leguminosae		0.88	-	-	0.69 ± 1.35	-	-	-	-	-	-
	Dasymaschalon lomentaceum	Choeung Chab	*Lasymachal lamenta*	Luxury	-	Annonaceae		0.618	-	0.35 ± 0.44	-	-	-	1 ± 1.8	-	0.12 ± 0.12	-
	Diospyros bejaudii	Angkot Khmau	*Diospyros bejaudi*	Luxury	-	Ebenaceae		0.796	-	-	-	5.5 ± 3.44	4.23	6.33 ± 3.16	-	-	-

Note	Scientific name	Local name	Recorded scientific name	Royalty class	IUCN	Family	*Resin species	Wood density	Mean (± CI) stem density: dense forest (DBH ≥10 cm; ha-1)					Mean (± CI) stem density: open forest (DBH ≥10 cm; ha-1)			
									D1	D2	D3	D4	D5**	D6	O1	O2	O3
	Diospyros helferi	Tror Ying	*Diospyros helferi*	Luxury	-	Ebenaceae		0.72	0.8 ± 1.24	-	-	-	-	-	-	-	-
	Diospyros sp.	Chhoeu Khmav /Neang Khmav	*Diospyros sp.*	Luxury	-	Ebenaceae		0.675	8 ± 3.15	-	-	-	-	-	-	-	-
	Fagraea fragrans	Tatrav	*Fagraeafra sp.*	Luxury	-	Gentianaceae		0.688	0.8 ± 1.24	0.04 ± 0.08	-	-	-	-	-	-	-
	Melanorrhoea lac cifera	Kroel	*Melanorrho laccifera*	Luxury	-	Anacardiaceae		0.715	-	-	-	0.1 ± 0.13	0.05	1.58 ± 1.75	8.53 ± 4.15	-	-
	Pterocarpus macrocarpus/ pedatus	Thnong Sor	*Pterocarpu cambodatus*	Luxury	-	Leguminosae		0.712	0.2 ± 0.39	-	1.03 ± 1.13	0.39 ± 0.48	-	0.58 ± 0.8	3.2 ± 1.75	-	6.94 ± 3.98
	Senna garrettiana	Haisanh/Ngays ang/Chansar	*Cassia garretiana*	Luxury	-	Leguminosae		0.618	-	-	-	-	-	-	-	-	-
	Senna siamea	Angkanh	*Cassia siamea*	Luxury	-	Leguminosae		0.663	-	-	-	-	-	-	-	-	-
	Dysoxylum loureirii	Houn Dan/ Moreaspreouph nom	*Disoxylon joureiri*	Luxury	-	Meliaceae		0.618	-	-	-	-	-	-	-	-	-
	Artocarpus sp.	Som Por	*Artocarpus sempervir*	I	-	Moraceae		0.477	-	-	-	0.2 ± 0.39	-	0.17 ± 0.33	0.27 ± 0.27	-	-
	Ceriops decandra	Sme	*Ceriops roxburghiana*	I	NT	Rhizophoraceae		0.77	-	-	-	-	-	-	-	-	-
	Chukrasia tabularis	Vor Yong	*Chukrsia tabularis*	I	LC	Meliaceae		0.548	-	-	-	-	-	-	-	-	-
	Crudia chrysantha	Sdey	*Crudia chrysantha*	I	-	Leguminosae		0.672	-	-	-	-	-	-	-	-	-
	Dialium cochinchinense	Krorlanh	*Dialium cochinchinen*	I	NT	Leguminosae		0.94	0.2 ± 0.39	-	-	0.56 ± 0.45	-	1.58 ± 1.51	0.53 ± 0.53	-	-
	Hopea ferrea	Koki Thmor	*Hopea ferrea*	I	EN	Dipterocarpaceae		0.89	0.2 ± 0.39	-	-	0.05 ± 0.1	-	-	-	-	-
	Hopea helferi	Koki Dek	*Hopea helferi*	I	CR	Dipterocarpaceae		0.88	-	-	3.45 ± 3.12	-	-	-	-	-	-
	Hopea odorata	Koki Mosau	*Hopea odorata*	I	VU	Dipterocarpaceae		0.635	2.6 ± 2.2	-	1.03 ± 1.49	-	-	0.75 ± 0.74	-	-	-
	Hopea recopei	Popel	*Hopea recopei*	I	EN	Dipterocarpaceae		0.749	-	-	1.38 ± 1.61	-	-	-	-	-	5 ± 2.99
	Intsia bijuga	Phkai Proek	*Afzelia bijuga*	I	VU	Leguminosae		0.72	-	-	-	-	-	-	-	-	-
b	***Lagerstroemia cochinchinensis***	Sralao	*Lagerstroemia cochinchinensis*	I	-	Leguminosae		0.618	43.4 ± 16.46	-	-	-	-	-	-	-	-
	Lagerstroemia sp.	Srorlao	*Lagerstroe sp.*	I	-	Lythraceae		0.596	-	43.61 ± 13.37	-	2.68 ± 2.15	17.92	-	-	21.8 ± 4.9	-
	Litsea vang	Beloy	*Litsea veng*	I	-	Lauraceae		0.452	-	-	-	0.36 ± 0.49	1.72	0.17 ± 0.33	-	-	-
	Manilkara hexandra	Kes	*Manilkara/manico hexandra/alexandr*	I	-	Sapotaceae		1.06	-	-	-	-	-	-	-	-	-
	Mesua ferrea	Bosneak	*Mesua ferrea*	I	-	Calophyllaceae		0.92	-	-	-	-	-	-	-	-	-
	Peltophorum dasyrrhachis	Treal	*Peltophoru dasyrach*	I	-	Leguminosae		0.553	2.4 ± 2.75	4.6 ± 3.47	-	-	-	-	-	0.26 ± 0.2	-
	Peltophorum	Trorsek /	*Peltophoru ferrugin*	I	-	Leguminosae		0.562	-	-	-	-	-	-	-	-	-

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									D1	D2	D3	D4	D5**	D6	O1	O2	O3
	ferrugineum	Tramkang															
	Pentacme suavis	Raing Phnom	*Pentacme suavis*	I	-	Dipterocarpaceae		0.618	-	-	-	-	-	-	-	-	-
	Shorea obtusa	Phcek	*Shorea obtusa*	I	LC	Dipterocarpaceae		0.85	-	-	2.07 ± 2.46	0.58 ± 0.7	-	0.5 ± 0.83	29.07 ± 14.34	22.14 ± 9.17	9.17 ± 3.87
	Sindora siamensis	Krorkors	*Sindora cochinchinen*	I	LC	Leguminosae		0.716	-	-	-	-	-	-	1.87 ± 1.16	0.68 ± 0.28	-
	Stereospermum chelonoides sp.1	Angkat Tmaat	*Stereosper chelon*	I	-	Bigoniaceae		0.618	-	-	-	-	-	-	-	-	-
	Tarrietia javanica	Doncherm	*Tarrietia javanica*	I	-	Sterculiaceae		0.618	-	0.08 ± 0.12	-	3.61 ± 2.61	1.2	1.33 ± 1.41	-	-	-
	Tectona grandis	Meysak	*Tectona grandis*	I	-	Verbenacae		0.619	-	-	-	-	-	-	-	-	-
	Terminalia tomentosa	Chhlik	*Terminalia tomentosa*	I	-	Combretaceae		0.606	-	-	-	-	-	-	-	-	-
	Vitex sp.	Phnel/Popoul	*Vitex sp.*	I	-	Lamiaceae		0.604	-	6.44 ± 3.04	-	4.52 ± 2.82	12.23	15.25 ± 6.26	0.27 ± 0.27	2.72 ± 1.41	-
	Xylia xylocarpa	Sokrom	*Yylia dolabriformis*	I	-	Leguminosae		0.72	9 ± 5.12	8.37 ± 5.18	1.72 ± 1.4	1.53 ± 2.17	0.67	2.17 ± 2.27	4.8 ± 1.84	16.43 ± 3.35	0.28 ± 0.28
	Adina cordifolia	Khvao	*Adina cordifolia*	II	-	Rubiaceae		0.59	-	-	-	-	-	-	-	-	-
c	***Anisoptera costata***	Phdeak	*Anisoptera costata*	II	EN	Dipterocarpaceae		0.553	11.4 ± 3.31	0.04 ± 0.08	-	8.76 ± 3.46	1.17	1.67 ± 1.33	-	-	-
	Anisoptera scaphula	Phdeak	*Anisoptera glabra*	II	CR	Dipterocarpaceae		0.44	-	-	-	-	-	-	-	-	-
	Dacrycarpus imbricatus	Srol Sar	*Poducarpus cupressin*	II	LC	Podocarpaceae		0.413	-	-	-	-	-	0.08 ± 0.16	-	-	-
	Dacrydium elatum	Srol Kraham	*Dacrydium elatum*	II	LC	Podocarpaceae		0.485	-	-	-	-	-	-	-	-	-
	Dehaasia cuneata	Atith/Neang Phor Ek	*Hassia cuneata*	II	-	Lauraceae		0.565	5.8 ± 2.38	-	-	2.13 ± 1.32	11.25	8.83 ± 4.68	-	-	-
	Dipterocarpus alatus	Chhoeteal Mosau	*Dipterocarpus alatus*	II	EN	Dipterocarpaceae	Yes*	0.599	2.2 ± 1.57	-	1.72 ± 2.76	8.08 ± 2.73	4.78	5.5 ± 3.66	-	-	-
	Dipterocarpus costatus	Chhoeteal Bangkouy/Neangdeng	*Dipterocarpus costat*	II	EN	Dipterocarpaceae	Yes*	0.755	11 ± 2.92	-	-	-	-	0.17 ± 0.33	-	-	-
	Dipterocarpus dyeri	Chhoeteal Chhngar	*Dipterocarpus dyori*	II	CR	Dipterocarpaceae		0.64	-	7.73 ± 5.41	-	-	-	0.33 ± 0.65	-	1.35 ± 1.03	-
	Dipterocarpus intricatus	Trach	*Dipterocarpus intric*	II	LC	Dipterocarpaceae	Yes*	0.64	-	1.96 ± 3.08	2.07 ± 2.26	0.61 ± 0.84	0.05	0.83 ± 0.91	1.07 ± 0.73	4.64 ± 2.05	1.67 ± 1.16
	Dipterocarpus obtusifolius	Tbeng	*Dipterocar obtusi*	II	LC	Dipterocarpaceae		0.65	-	0.07 ± 0.15	0.69 ± 1.35	-	-	0.17 ± 0.33	70.13 ± 23.76	1.08 ± 1.08	54.44 ± 14.65
	Dipterocarpus tuberculatus	Khlong	*Dipterocarpus tuberc*	II	LC	Dipterocarpaceae	Yes*	0.72	-	0.04 ± 0.08	-	1.52 ± 1.72	-	0.17 ± 0.33	26.67 ± 18.58	25.82 ± 6.36	23.61 ± 12.86
	Dipterocarpus turbinatus	Chhoeteal Breng	*Dipterocarpus jourdalnii*	II	CR	Dipterocarpaceae	Yes*	0.619	0.4 ± 0.78	-	-	-	-	-	-	-	-

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									D1	**D2**	**D3**	**D4**	**D5****	**D6**	**O1**	**O2**	**O3**
	Hopea pierrei	Koki Khasac	*Hopea pierrei*	II	EN	Dipterocarpaceae		0.812	-	-	-	-	-	0.83 ± 1.63	-	-	-
d	***Hopea sp.***	Koki	*Hopea sp*	II	-	Dipterocarpaceae		0.618	-	1.58 ± 1.19	-	0.04 ± 0.09	0.23	-	-	-	-
	Madhuca elliptica	Srakom	*Payena elliptica*	II	-	Sapotaceae		0.697	-	-	9.66 ± 12.25	-	-	-	-	-	-
	Pinus latteri	Sral	*Pinus merkusii*	II	NT	Pinaceae		0.547	-	-	-	-	-	-	-	-	-
e	***Shorea farinosa***	Lombor	*Shorea farinosa*	II	-	Dipterocarpaceae		0.707	-	0.6 ± 1.18	-	0.15 ± 0.2	0.15	0.25 ± 0.36	-	-	-
	Shorea hypochra	Koki Phnong\ Kamnhan	*Shorea hypochra*	II	CR	Dipterocarpaceae		0.615	1.4 ± 1.28	-	-	-	-	-	-	-	-
	Shorea sp.	Lumbor	*Shorea sp.*	II	-	Dipterocarpaceae		0.571	-	-	-	-	-	-	-	-	-
	Shorea thorelli	Kchov/ Kamleng	*Shorea thorelli*	II	CR	Dipterocarpaceae		0.571	-	-	-	-	0.07	-	-	-	-
	Shorea vulgaris	Chorchong	*Shorea vulgaris*	II	-	Dipterocarpaceae		0.571	-	1.08 ± 1.58	-	-	14.8	5.25 ± 4.93	-	-	-
	Toona sureni	Chham Chha	*Toona febrifuga*	II	-	Meliaceae		0.399	-	-	-	-	-	-	-	-	-
	unknown	Totim Prey		II				0.618	-	-	-	-	-	-	-	-	-
	Vatica astrotricha	Chrasmas	*Vatica astrotricha*	II	-	Dipterocarpaceae		0.677	-	12.25 ± 12.42	-	-	29.12	-	-	1.04 ± 1.04	-
f	***Vatica odorata***	Chramas	*Vatica odorata*	II	-	Dipterocarpaceae		0.571	26.6 ± 7.43	-	1.03 ± 1.49	90.28 ± 15.2	-	18.92 ± 11.75	-	-	-
	Vatica philastreana	Trorlat	*Vatica philastreana*	II	-	Dipterocarpaceae		0.705	-	-	7.24 ± 14.19	-	-	0.5 ± 0.72	0.53 ± 0.36	-	-
	Aglaia spectabilis	Bag Kheou	*Aglasia gigantea*	III	LC	Meliaceae		0.575	-	-	-	-	-	-	-	-	-
	Albizia myriophylla	Kray Sar	*Albizzia thorelli*	III	-	Leguminosae		0.545	-	-	-	3.55 ± 2.15	1.67	7.67 ± 4.66	-	-	-
	Aquilaria crassna	Chan Krasna	*Aquilaria crasna*	III	CR	Thymelaeaceae		0.347	-	-	-	-	-	-	-	-	-
g	***Artocarpus rigidus***	Khnorprei	*Artocarpus rigidus*	III	-	Moraceae		0.79	-	0.16 ± 0.24	0.69 ± 0.94	-	0.03	1.75 ± 1.21	-	-	-
	Artocarpus integer	Khnor Prey	*Artocarpus intergrif*	III	-	Moraceae		0.551	-	-	-	-	-	-	-	-	-
	Bruguiera gymnorhiza	Kong Kangnhy	*Rhizophpra conjugata*	III	LC	Rhizophoraceae		0.71	-	-	-	-	-	-	-	-	-
	Calophyllum sp.	Phaong	*Callophyll sp*	III	-	Clusiaceae		0.55	-	-	-	1.03 ± 1.68	0.02	1.33 ± 0.93	2.13 ± 2.13	-	-
	Carallia brachiata	Tra Meng	*Carallia lucida*	III	-	Rhizophoraceae		0.713	2 ± 1.53	-	-	0.61 ± 0.75	2.77	2.25 ± 1.36	0.27 ± 0.27	-	-
	Careya arborea	Kanndol	*Careya sphaerica*	III	-	Lecythidaceae		0.731	0.4 ± 0.55	0.58 ± 0.43	3.45 ± 6.76	-	0.12	0.33 ± 0.51	6.13 ± 3.82	2.89 ± 0.66	0.28 ± 0.28
	Cinnamomum litseifolium	Chek Tum	*Cinnamomum litsaef o*	III	VU	Lauraceae		0.479	-	-	-	-	-	-	-	-	-
	Cratoxylum formosum	Lo Ngieng	*Cratoxylon prunifoli*	III	-	Clusiaceae		0.744	15.6 ± 6.95	7.05 ± 5.54	-	-	0.02	12.92 ± 14.08	1.6 ± 0.86	5.47 ± 2.72	-
	Crypteronia sp.	Trorp Tom	*Crypteroni sp.*	III	-	Crypteroniaceae		0.602	-	-	-	-	-	-	-	-	-

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	Eugenia sp.	Pring/ Krorb Bek	*Eugenia sp.*	III	-	Myrtaceae		0.697	2 ± 1.53	4.58 ± 2.64	-	-	7.77	-	-	4.1 ± 1.23	-
	Garcinia celebica	Prous	*Garcinia ferrea*	III	-	Clusiaceae		0.76	-	-	-	-	-	-	-	-	-
	Garcinia schomburgkiana	Trormoung	*Garcinia schomburghi*	III	-	Clusiaceae		0.727	-	1.71 ± 1.03	-	-	-	-	-	0.23 ± 0.23	-
	Homallium sp.	Ateang/ Roteang	*Homalium annamensis*	III	-	Saliaceae		0.676	-	-	-	-	-	-	-	-	-
	Hydnocarpus anthelminthicus	Krorbao	*Hydnocarpu anthelmi*	III	-	Achariaceae		0.634	-	-	-	0.2 ± 0.39	10.85	-	-	-	-
	Kayea eugeniifolia	Kreas	*Kayea eugenicefolia*	III	-	Calophyllaceae		0.682	-	-	-	-	-	-	-	-	-
	Knema corticosa	Sma Krabey	*Knema corticosa*	III	LC	Myristicaceae		0.499	-	0.15 ± 0.21	3.45 ± 6.76	-	0.03	3.08 ± 3.17	1.6 ± 1.16	0.82 ± 0.4	-
	Magnifera indica	Svay Prey	*Mangifera indica*	III	-	Anacardiaceae		0.561	-	0.75 ± 1.47	-	-	-	-	-	-	-
	Melaleuca leucadendra	Smach	*Melaleuca leucadendr*	III	-	Myrtaceae		0.645	-	0.08 ± 0.12	-	-	0.83	3.08 ± 3.6	0.53 ± 0.53	-	-
	Parinari anamensis	Thlok	*Parinarium annamensi*	III	-	Chrysobalanaceae		0.624	4.2 ± 2.03	0.44 ± 0.34	2.76 ± 2.73	11.24 ± 6.69	-	12.17 ± 12.13	1.6 ± 1.16	-	1.39 ± 0.9
	Rhizophora mucronata	Kong Kangchhmol	*Rhizophora mucronata*	III	LC	Rhizophoraceae		0.821	-	-	-	0.08 ± 0.16	-	0.17 ± 0.33	-	-	-
	Sandoricum koetjape	Kompeng Reach	*Sandoricum indicum*	III	-	Meliaceae		0.415	0.4 ± 0.55	0.13 ± 0.14	1.72 ± 1.96	0.08 ± 0.09	11.5	0.42 ± 0.47	-	-	-
	Sarcocephalus cordatus	Kdol	*Sarcocepha cordat*	III	-	Rubiaceae		0.618	-	-	-	-	-	-	-	-	-
	Sterculia campanulata	Chan Toum Peang	*Pterocymbi/ sterc cmpanulatumcapan*	III	-	Malvaceae		0.28	-	-	-	-	-	-	-	-	-
	Stereospermum chelonoides sp2	Chorng Uor Thmat	*Stereosper mum chenlo*	III	-	Bigoniaceae		0.618	-	-	-	-	-	-	-	-	-
	Swintonia pierrei	Svay Cham Reang	*Switonia pierri*	III	-	Anacardiaceae		0.732	-	-	-	-	-	-	-	-	-
	Terminalia cambodiana	Taour	*Terminalia cambodiana*	III	-	Combretaceae		0.513	-	-	-	-	-	1.17 ± 2.29	-	-	-
	Terminalia chebula sp1	Taour	*Terminalia chebula*	III	-	Combretaceae		0.618	-	-	-	-	-	-	-	-	-
	Terminalia mucronata	Pram Domleng	*Terminalia mucronata*	III	-	Combretaceae		0.606	-	-	-	-	-	-	-	-	-
	Tetrameles nudiflora	Sam Pong	*Tetrameles nudiflora*	III	LC	Datiscaceae		0.618	-	2.87 ± 2.78	-	-	6.38	0.42 ± 0.67	-	-	-
	unknown	Bay Pou Vaing		III				0.618	5.8 ± 6.38	251.1 ± 34.24	83.79 ± 52.01	205.01 ± 33.17	210	90.08 ± 25.31	32.8 ± 6.46	111.47 ± 15.47	8.61 ± 4.05
	Acacia caesia	Thmeas	*Acacia intsii*	NC		Mimosaceae		0.8	-	0.04 ± 0.08	-	-	-	-	-	0.23 ± 0.16	-
	Acacia farnesiana	Sambour Meas	*Acacia famesiana*	NC	-	Mimosaceae		0.8	-	-	-	-	-	-	-	-	-
	Acacia harmandiana	-	*Acacia harmandiana*	NC	-	Mimosaceae		0.606	0.6 ± 0.87	-	-	-	-	-	-	-	-

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	Acalypha siamensis	Ter Prey	*Acacia harmandiana*	NC	-	Mimosaceae		0.618	-	11.29 ± 11.06	-	-	-	-	-	-	-
	Acronychia pedunculata	-	*Acronychia pedunculata*	NC	-	Rutaceae		0.3	3 ± 1.96	-	-	-	-	-	-	-	-
	Aglaia lawii	-	*Aglaia lawii*	NC	LC	Meliaceae		0.618	2 ± 1.62	-	-	1.26 ± 1.63	-	-	-	-	-
	Aglaia odorata	Tror Yorng	*Aglaia odorata*	NC	NT	Meliaceae		0.661	-	-	-	-	44.87	-	-	-	-
	Aglaia edulis	Bangkow	*Aglaia edulis*	NC	NT	Meliaceae		0.618	-	-	-	-	-	1 ± 1.96	-	-	-
	Albizia lebbekoides	Chamriek	*Albizzia lebekkoides*	NC	-	Leguminosae		0.545	-	-	-	-	-	-	-	-	-
	Alchornea rugosa	-	*Alchornea rugosa*	NC	-	Euphorbiaceae		0.595	0.2 ± 0.39	-	-	-	-	-	-	-	-
	Alstonia scholaris	Po Peal Kheir	*Alstonia scholaris*	NC	LC	Apocynaceae		0.618	0.4 ± 0.55	-	1.03 ± 1.13	-	-	-	-	-	-
	Anacardium occidentale	Svay Chanti	*Anacadium occidental*	NC	-	Anacardiaceae		0.468	-	-	-	-	-	-	-	-	-
	Ancistrocladus tectorius	Khannma	*Ancistrocladus harmandii*	NC	-	Ancistrocladaceae		0.618	-	-	-	-	-	-	-	-	-
	Anogeissus acuminata	Soury	*Anogeissus acumenata*	NC	-	Combretaceae		0.88	-	-	-	-	0.07	0.42 ± 0.47	-	-	-
	Antidesma cochinchinense	Dang Keap Kdam	*Antidesma cochinchinensis*	NC	-	Phyllanthaceae		0.401	0.2 ± 0.39	0.07 ± 0.15	-	-	-	-	-	1.39 ± 1.11	-
	Antidesma ghaesembilla	Dang Keab Kdam	*Antidesma ghaesembilla*	NC	-	Phyllanthaceae		0.618	1.4 ± 1.15	-	3.79 ± 6.77	-	-	0.83 ± 1.63	-	-	-
	Antidesma montanum	-	*Antidesma montanum*	NC	-	Phyllanthaceae		0.61	4.6 ± 2.99	-	-	-	-	-	-	-	-
	Antidesma sp.	-	*Antidesma sp.*	NC	-	Phyllanthaceae		0.618	5 ± 3.27	-	-	-	-	-	-	-	-
	Antidesma japonicum	-	*Antidesma japonicum*	NC	-	Phyllanthaceae		0.618	-	-	-	0.31 ± 0.62	-	0.5 ± 0.72	-	-	-
	Aphanamixis polystachya	-	*Aphanamixis polystachya*	NC	LC	Meliaceae		0.633	2 ± 1.42	-	-	-	-	-	-	-	-
	Aporosa octandra	-	*Aporosa octandra*	NC	-	Phyllanthaceae		0.618	0.2 ± 0.39	-	-	-	-	-	-	-	-
	Aporosa planchoniana	-	*Aporosa planchoniana*	NC	-	Phyllanthaceae		0.618	-	-	15.52 ± 15.97	-	-	-	-	-	-
	Aporosa sp.	Krong	*Aporosa sp.*	NC	-	Phyllanthaceae		0.37	-	-	-	-	-	-	-	-	-
	Aporosa tetrapleura	-	*Aporosa tetrapleura*	NC	-	Phyllanthaceae		0.37	0.2 ± 0.39	-	-	-	-	-	-	-	-
	Archidendron clypearia	-	*Archidendron clypearia*	NC	-	Leguminosae		0.618	0.6 ± 0.87	-	-	-	-	-	-	-	-
	Ardisia helferiana	Chhom Pou Prey	*Ardisia helferiana*	NC	-	Primulaceae		0.6	-	-	-	-	-	-	-	-	-
	Artocarpus chama	-	*Artocarpus chama*	NC	-	Moraceae		0.618	0.4 ± 0.55	-	-	-	-	-	-	-	-

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	Artocarpus heterophyllus	-	*Artocarpus heterophyllus*	NC	-	Moraceae		0.618	-	-	-	0.05 ± 0.1	-	-	-	-	-
	Artocarpus nitidus	-	*Artocarpus nitidus*	NC	-	Moraceae		0.484	0.6 ± 0.67	-	-	-	-	-	-	-	-
	Atalantia citroides	Kroch Prey	*Atlantia citroides*	NC	-	Rutaceae		0.618	-	2.22 ± 2.3	-	-	-	0.17 ± 0.33	-	-	-
	Avicennia officinalis	Ko Mouy	*Avicennia officanalis*	NC	-	Acanthaceae		0.609	-	-	-	-	-	-	-	-	-
	Azadirachta indica	Sdav	*Alzadirachta indica*	NC	-	Meliaceae		0.64	-	0.07 ± 0.15	0.34 ± 0.68	-	-	-	1.33 ± 0.75	1.04 ± 1.04	1.11 ± 0.77
	Baccaurea ramiflora	Phnheav	*Baccaurea ramiflora*	NC	-	Phyllanthaceae		0.624	2.8 ± 1.76	2.97 ± 4.58	3.45 ± 6.76	-	16.67	1 ± 0.97	-	-	-
	Balakata baccata	-	*Balakata baccata*	NC	-	Euphorbiaceae		0.618	2.2 ± 2.29	-	-	-	-	-	-	-	-
	Barringtonia acutangula	Raing Toek	*Baringtoni acutangula*	NC	-	Lecythidaceae		0.525	0.6 ± 0.67	-	-	-	-	-	-	-	0.28 ± 0.28
	Bauhinia acumianta	Choeung Ko	*Bauhinia acuminata*	NC	LC	Leguminosae		0.648	-	0.15 ± 0.29	-	-	-	-	-	0.18 ± 0.13	-
	Bauhinia variegata	-	*Bauhinia variegata*	NC	LC	Leguminosae		0.618	0.2 ± 0.39	-	0.34 ± 0.68	-	-	0.33 ± 0.65	-	-	-
	Bauhinia pulla	Kleng Por	*Bauhinia pulla*	NC	-	Leguminosae		0.648	-	-	-	-	-	-	-	-	-
	Bombax anceps	Roka	*Bombax mataricum*	NC	-	Malvaceae		0.413	0.2 ± 0.39	-	-	0.04 ± 0.05	0.05	0.58 ± 0.73	1.6 ± 1.09	-	-
	Bouea oppositifolia	Mak Prang	*Bouea burmanica*	NC	-	Anacardiaceae		0.745	-	-	13.45 ± 18.15	-	-	-	-	-	-
	Breonia chinensis	-	*Breonia chinensis*	NC	-	Rubiaceae		0.606	-	-	-	-	-	4.33 ± 5.32	-	-	-
	Breynia vitis-idaea	Phnek Preap	*Breynia rhamnoides*	NC	-	Phyllanthaceae		0.618	-	-	-	-	-	-	-	-	-
	Bridelia retusa	Thmenh Trey	*Euphorbiac bridelia cambodiana*	NC	-	Phyllanthaceae		0.716	0.6 ± 0.67	-	-	-	-	-	-	-	-
	Bruguiera sexan gula	Pluoung	*Bruguiera sexangula*	NC	LC	Rhizophoraceae		0.74	-	-	-	-	-	-	-	-	-
	Buchanania glabra	-	*Buchanania glabra*	NC	-	Anacardiaceae		0.34	1.8 ± 1.77	-	-	-	-	-	-	-	-
	Buchanania siamensis	-	*Buchanania siamensis*	NC	-	Anacardiaceae		0.754	-	-	-	-	-	-	-	-	0.83 ± 0.61
	Butea monosperma	Chhar	*Butea frondosa*	NC	-	Leguminosae		0.33	-	-	-	-	-	-	-	-	0.56 ± 0.39
	Calophyllum calaba	Khting	*Calophyllu saigonen*	NC	-	Clusiaceae		0.55	2.8 ± 1.58	-	-	-	-	-	-	-	-
	Calophyllum polyanthum	-	*Calophyllum polyanthum*	NC	-	Clusiaceae		0.618	0.6 ± 0.67	-	-	-	-	-	-	-	-
	Calophyllum thorelii	-	*Calophyllum thorelii*	NC	-	Clusiaceae		0.618	1.4 ± 1.39	-	-	-	-	-	-	-	-

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									D1	**D2**	**D3**	**D4**	**D5****	**D6**	**O1**	**O2**	**O3**
	Cananga latifolia	Chhker Srerng	*Cnanga latifolia*	NC	-	Annonaceae		0.28	1.8 ± 1.59	-	1.72 ± 3.38	-	-	-	-	0.18 ± 0.13	-
	Canarium pimela	Kana	*Canarium pimela*	NC	-	Burseraceae		0.545	-	-	-	-	-	-	-	-	-
	Capparis sepiaria	Kanchoeu Bey Dach	*Capparis micrantha*	NC	-	Capparaceae		0.618	-	-	-	0.26 ± 0.52	-	0.17 ± 0.33	-	-	-
	Cardiospermum halicacabum	Ambeng Bek	*Cardiospermum halicacabum*	NC	-	Sapindaceae		0.618	-	-	-	-	-	-	-	-	-
	Carissa spinarum	Proum	*Carissia cochinchinensis*	NC	-	Apocynaceae		0.618	-	-	-	-	-	-	-	-	-
	Casearia graveolens	-	*Casearia graveolens*	NC	-	Saliaceae		0.618	-	-	0.69 ± 0.94	-	-	-	-	-	-
	Cassia javanica	Bo Proeuk	*Cassia javanica*	NC	-	Leguminosae		0.545	-	-	-	-	-	-	-	-	-
	Castanopsis sp.			NC	-	Fagaceae		0.606	1.4 ± 1.28	-	-	-	-	-	-	-	-
	Catunaregam tomentosa	Rovieng	*Randia tomantosa*	NC	-	Rubiaceae		0.688	-	0.04 ± 0.08	-	-	-	-	-	0.12 ± 0.12	-
	Cephalanthus angustifolius			NC	-	Rubiaceae		0.618	-	-	0.69 ± 0.94	-	-	-	-	-	-
	Chaetocarpus castanocarpus			NC	-	Peraceae		0.618	9 ± 4.4	-	-	0.69 ± 0.94	-	-	-	-	-
	Chisocheton cumingianus			NC	-	Meliaceae		0.75	13.2 ± 5.85	-	-	-	-	-	-	-	-
	Cinnamomum cambodianum	Tep Phirou	*Cinnamomum cambodianum*	NC	-	Lauraceae		0.479	-	-	-	0.66 ± 1.11	-	1.17 ± 1.73	-	-	-
	Cinnamomum camphora			NC	-	Lauraceae		0.618	-	-	-	0.05 ± 0.1	-	-	-	-	-
	Cinnamomum cassia	Sambour Loveng	*Cinnamomum cassia*	NC	-	Lauraceae		0.479	-	-	-	-	-	-	-	-	-
	Cinnamomum iners			NC	-	Lauraceae		0.504	2 ± 2.12	-	-	-	-	-	-	-	-
	Cinnamomum polyadelphum			NC	-	Lauraceae		0.618	0.2 ± 0.39	-	-	0.16 ± 0.31	-	-	-	-	-
	Cleistanthus sp.	Speou Tek	*Euphorbiac cleistanthus sp*	NC	-	Phyllanthaceae		0.551	-	-	-	0.52 ± 1.01	-	-	-	-	-
	Cleistanthus tomentosus	Neang Sar	*Cleistantu eburneus*	NC	-	Phyllanthaceae		0.551	6.6 ± 3.7	-	-	-	-	-	-	-	-
	Colona auriculata	Preal	*Colombia auriculata*	NC	-	Malvaceae		0.359	-	-	-	-	-	-	-	-	-
	Combretum quadrangulare	Sang Ke	*Combretum quadrangulare*	NC	-	Combretaceae		0.8	1.8 ± 1.77	-	7.24 ± 13.51	-	-	-	-	1.04 ± 0.48	-
	Crateva nurvala	Tounlorp	*Crataeva nurvala*	NC	-	Capparaceae		0.34	-	-	-	-	-	-	-	-	-
	Croton joufra			NC	-	Euphorbiaceae		0.479	-	0.04 ± 0.08	-	0.48 ± 0.93	-	0.5 ± 0.72	-	-	-
	Croton thorelii			NC	-	Euphorbiaceae		0.552	1 ± 1.02	-	-	-	-	-	-	-	-
	Cynometra	Ampil Toeuk	*Cynometra*	NC	-	Leguminosae		0.787	-	-	-	-	-	-	-	-	-

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									D1	D2	D3	D4	D5**	D6	O1	O2	O3
	ramiflora	Prey	*ramiflora*														
	Dalbergia nigrescens	Snuol	*Dalbergia nigrescens*	NC	-	Leguminosae		0.618	0.6 ± 0.87	-	-	-	-	-	-	-	-
	Desmodium renifolium			NC	-	Fabaceae		0.618	-	0.99 ± 1.02	-	-	-	0.17 ± 0.33	-	-	-
	Dillenia indica			NC	-	Dilleniaceae		0.618	0.4 ± 0.55	-	-	-	-	-	-	-	-
	Dillenia ovata	Plor	*Dilleniace dillenia ovata*	NC	VU	Dilleniaceae		0.622	0.4 ± 0.55	-	-	-	-	0.33 ± 0.45	1.6 ± 0.86	-	0.56 ± 0.56
	Dillenia parviflora			NC	-	Dilleniaceae		0.618	0.4 ± 0.55	-	-	-	-	-	-	-	-
	Dillenia sp.			NC	-	Dilleniaceae		0.618	-	-	-	0.74 ± 0.93	0.02	0.5 ± 0.83	-	-	-
	Dimocarpus longan	Mean Prey	*Euphoria cambodiana*	NC	-	Sapindaceae		0.7	5.8 ± 2.45	0.22 ± 0.44	-	27.22 ± 6.62	34.32	9.42 ± 7.26	-	-	-
	Dioscorea hispida	Kdurch	*Dioscorea hispida*	NC	-	Dioscoreaceae		0.618	-	-	-	26.58 ± 6.42	-	0.92 ± 1.8	-	-	-
	Diospyros buxifolia	Chang Nang	*Diosyros boxifolia*	NC	-	Ebenaceae		0.775	-	-	-	0.73 ± 1.43	-	-	-	-	-
	Diospyros chevalieri	Dongkor	*Diospyros chevalieri*	NC	-	Ebenaceae		0.675	-	-	-	-	-	-	-	-	-
	Diospyros crumenata			NC	EN	Ebenaceae		0.622	11.6 ± 5.26	-	14.14 ± 27.71	0.03 ± 0.05	-	-	-	-	-
	Diospyros filipendula			NC	-	Ebenaceae		0.675	6.6 ± 2.73	-	-	-	-	-	-	-	-
	Diospyros hasseltii			NC	-	Ebenaceae		0.618	0.4 ± 0.55	-	0.34 ± 0.68	-	-	0.17 ± 0.33	-	-	-
	Diospyros mollis	Mak Kloeu	*Diospyros mollis*	NC	-	Ebenaceae		0.675	-	-	-	-	-	-	-	-	-
	Diospyros nitida	Chhoe Phloeung	*Diospyros nitida*	NC	-	Ebenaceae		0.675	-	-	-	2.92 ± 2.33	-	-	-	-	-
	Diospyros sylvatica	Kchas	*Diospyros sylvatica*	NC	-	Ebenaceae		0.675	3.8 ± 2.41	0.87 ± 1.41	2.07 ± 4.06	-	11.77	5.83 ± 5.42	-	-	-
	Diospyros undulata			NC	-	Ebenaceae		0.553	5.8 ± 3.21	-	-	-	-	-	-	-	-
	Diospyros venosa			NC	-	Ebenaceae		0.618	3.2 ± 2.6	-	-	-	-	-	-	-	-
	Diploknema sp.	Knay Morn	*Diploknema sp*	NC	-	Sapotaceae		0.765	-	-	-	-	-	-	-	-	-
	Dracaena angustifolia			NC	-	Ruscaceae		0.618	0.2 ± 0.39	-	-	-	-	-	-	-	-
	Dracaena elliptica			NC	-	Ruscaceae		0.618	0.6 ± 0.67	-	-	-	-	-	-	-	-
	Dracaena sp.	Angre Dek	*Dracaena sp*	NC	-	Asparageaceae		0.42	-	-	-	-	-	-	-	-	-
	Drypetes cambodica			NC	-	Putranjavaceae		0.618	1 ± 1.02	-	-	-	-	-	-	-	-

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									D1	D2	D3	D4	D5**	D6	O1	O2	O3
	Elaeis guineensis	Thnot Preng	*Elaeis guineensis*	NC	-	Arecaceae		0.618	-	-	-	-	-	-	-	-	-
	Elaeocarpus floribundus			NC	-	Elaeocarpaceae		0.618	3.6 ± 2.64	-	-	-	-	-	-	-	-
	Elaeocarpus hygrophilus			NC	-	Elaeocarpaceae		0.618	1.4 ± 1.15	-	7.93 ± 13.53	-	-	-	-	-	-
	Elaeocarpus sp.			NC	-	Elaeocarpaceae		0.486	1.2 ± 1.22	-	-	-	-	-	-	-	-
	Elaeocarpus stipularis			NC	-	Elaeocarpaceae		0.618	3.8 ± 2.34	-	-	-	-	-	-	-	-
	Ellipanthus tomentosus			NC	-	Connaraceae		0.618	0.2 ± 0.39	-	0.69 ± 0.94	-	-	-	-	-	-
	Eugenia albiflora			NC	-	Myrtaceae		0.618	7 ± 3.31	-	-	-	-	-	-	-	-
	Eugenia chanlos			NC	-	Myrtaceae		0.618	1 ± 1.61	-	-	-	-	-	-	-	-
	Eugenia cinerea			NC	-	Myrtaceae		0.618	0.6 ± 0.67	-	-	-	-	-	-	-	-
	Eugenia formosa			NC	-	Myrtaceae		0.618	2 ± 2.05	-	-	-	-	-	-	-	-
	Eugenia grandis			NC	-	Myrtaceae		0.618	13.2 ± 4.1	-	-	-	-	-	-	-	-
	Eugenia grata			NC	-	Myrtaceae		0.618	0.4 ± 0.78	-	-	-	-	-	-	-	-
	Eugenia laosensis			NC	-	Myrtaceae		0.618	0.8 ± 0.95	-	-	-	-	-	-	-	-
	Eugenia polyantha			NC	-	Myrtaceae		0.618	1.8 ± 1.48	-	-	-	-	-	-	-	-
	Eugenia syzygioides			NC	-	Myrtaceae		0.618	11.6 ± 4.18	-	-	-	-	-	-	-	-
	Euonymus cochinchinensis			NC	LC	Celastraceae		0.618	2 ± 1.62	-	-	-	-	2.17 ± 1.83	-	-	-
	Fagraea racemosa			NC	-	Gentianaceae		0.53	4 ± 2.08	-	-	-	-	-	-	-	-
	Falconeria insigne			NC	-	Euphorbiaceae		0.618	0.4 ± 0.78	-	-	-	-	-	-	-	-
	Ficus altissima			NC	-	Moraceae		0.618	0.4 ± 0.55	-	-	-	-	-	-	-	-
	Ficus fistulosa			NC	-	Moraceae		0.618	0.2 ± 0.39	-	-	-	-	-	-	-	-
	Ficus hirta			NC	-	Moraceae		0.618	0.2 ± 0.39	-	-	-	-	-	-	-	-
	Ficus hispida			NC	-	Moraceae		0.414	-	-	0.34 ± 0.68	-	-	-	-	-	-
	Ficus microcarpa			NC	-	Moraceae		0.382	0.2 ± 0.39	-	-	-	-	-	-	-	-
	Ficus rumphii			NC	-	Moraceae		0.618	0.2 ± 0.39	-	-	-	-	-	-	-	-
	Ficus sp.	Chrey	*Moraceae ficus sp*	NC	-	Moraceae		0.414	-	-	-	0.22 ± 0.31	-	2.67 ± 2.69	-	-	-
	Ficus virens			NC	-	Moraceae		0.618	0.2 ± 0.39	-	-	-	-	-	-	-	-
	Garcinia hanburyi			NC	-	Clusiaceae		0.618	-	-	-	0.38 ± 0.75	-	-	-	-	-
	Garcinia harmandii			NC	-	Clusiaceae		0.727	0.2 ± 0.39	-	-	-	-	0.17 ± 0.33	-	-	-

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									D1	D2	D3	D4	D5**	D6	O1	O2	O3
	Garcinia loureiroi	Sandan	*Garcinia loureiri*	NC	-	Clusiaceae		0.727	-	-	-	-	-	-	-	-	-
	Garcinia merguensis			NC	-	Clusiaceae		0.727	2.8 ± 1.93	-	-	-	-	-	-	-	-
	Garcinia oliveri			NC	-	Clusiaceae		0.618	0.4 ± 0.55	-	-	3.01 ± 3.09	-	5.67 ± 3.12	1.6 ± 1.6	-	-
	Garcinia sp.			NC	-	Clusiaceae		0.618	2 ± 2.52	-	-	-	-	-	-	-	-
	Garcinia vilersiana			NC	-	Clusiaceae		0.618	2.8 ± 1.37	-	-	-	-	-	-	-	-
	Gardenia angkorensis	Dey Khla	*Gardenia ankorensis*	NC	-	Rubiaceae		0.66	-	-	-	-	-	-	-	-	-
	Gardenia cambodiana	Dorng Dav	*Gardenia cambodiana*	NC	-	Rubiaceae		0.66	-	-	-	-	-	-	-	-	-
	Gardenia philastrei	Bakdorng	*Gardenia philastrea*	NC	-	Rubiaceae		0.66	-	-	-	-	-	-	-	-	-
	Gluta laccifera			NC	-	Anacardiaceae		0.618	0.2 ± 0.39	-	-	-	-	-	-	-	-
	Helicia sp.			NC	-	Proteaceae		0.618	0.4 ± 0.55	-	-	-	-	-	-	-	-
	Heritiera javanica			NC	-	Malvaceae		0.618	5.2 ± 2.27	-	-	-	-	-	-	-	-
	Hibiscus macrophyllus			NC	-	Malvaceae		0.39	-	-	-	-	-	1.0 ± 0.97	-	-	-
	Holarrhena pubescens			NC	LC	Apocynaceae		0.375	-	-	-	-	0.83	-	-	-	-
	Homalium bhamoense	Plov Neang	*Homalium tomentosum*	NC	-	Saliaceae		0.676	-	0.53 ± 0.57	-	-	-	-	-	-	-
	Horsfeldia iria			NC	-	Myristicaceae		0.576	1.4 ± 1.15	-	-	-	-	-	-	-	-
	Hymenocardia sp.	Phnom Phnerng	*Hymenocardia riparia*	NC	-	Phyllanthaceae		0.618	-	-	-	-	-	-	-	-	-
	Irvingia malayana	Cham Bak	*Irvingiace irvingia malayna*	NC	LC	Irvingaceae		0.883	9 ± 3.02	6.44 ± 2.92	20.69 ± 14.81	6.99 ± 2.61	2.47	10.42 ± 4.43	2.4 ± 1.65	1.16 ± 0.69	4.44 ± 3.07
	Knema globularia			NC	LC	Myristicaceae		0.618	0.4 ± 0.55	-	-	3.93 ± 2.74	-	-	-	-	-
	Knema pierrei			NC	VU	Myristicaceae		0.533	1.2 ± 1.09	-	-	-	-	-	-	-	-
	Lagerstroemia anisoptera			NC	VU	Lythraceae		0.618	-	-	-	-	-	2.33 ± 3.16	-	-	-
	Lagerstroemia floribunda			NC	-	Lythraceae		0.419	-	-	-	-	-	-	-	-	0.28 ± 0.28
	Lagerstroemia macrocarpa		*Lagerstroemia macrocarpa*	NC	-	Leguminosae		0.618	0.4 ± 0.55	-	-	-	-	-	-	-	-
	Lannea coromandelica			NC	-	Anacardiaceae		0.596	0.4 ± 0.78	-	-	-	-	-	-	-	-
	Lepisanthes rubiginosa			NC	-	Sapindaceae		0.61	-	-	-	-	-	-	2.67 ± 2.67	-	-
	Lepisanthes			NC	-	Sapindaceae		0.618	0.4 ± 0.55	-	-	-	-	-	-	-	-

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									D1	**D2**	**D3**	**D4**	**D5****	**D6**	**O1**	**O2**	**O3**
	senegalensis																
	Lepisanthes tetraphylla			NC	-	Sapindaceae		0.618	0.2 ± 0.39	-	-	-	-	-	-	-	-
	Leucaena leucocephala	Sambour Tes	*Leucaena glauca*	NC	-	Leguminosae		0.52	-	-	-	-	-	-	-	-	-
	Lithocarpus elegans	Khos	*Lithocarpus eleganas*	NC	-	Fagaceae		0.799	4.6 ± 2.15	-	-	-	-	0.5 ± 0.98	-	-	-
	Lithocarpus elephantum	Krang	*Lithocarpu elephantum*	NC	-	Fagacaeae		0.673	-	-	-	0.14 ± 0.27	-	-	-	-	-
	Lithocarpus polystachyus			NC	-	Fagaceae		0.618	4.8 ± 2.17	-	-	-	-	-	-	-	-
	Lithocarpus sp.			NC	-	Fagaceae		0.618	-	-	-	-	-	1.67 ± 2.31	-	-	-
	Litsea glutinosa			NC	-	Lauraceae		0.673	-	-	-	-	-	1.17 ± 1.43	-	-	-
	Litsea malabarica			NC	-	Lauraceae		0.56	0.4 ± 0.78	-	-	-	-	-	-	-	-
	Litsea pierrei			NC	-	Lauraceae		0.618	0.4 ± 0.55	-	-	-	-	-	-	-	-
	Lophopetalum duperreanum			NC	-	Celastraceae		0.618	2.4 ± 2.18	-	-	-	-	-	-	-	-
	Lophopetalum wallichii			NC	-	Celastraceae		0.618	0.4 ± 0.55	-	-	-	-	-	-	-	-
	Macaranga denticulata			NC	-	Euphorbiaceae		0.618	-	-	-	-	-	2.67 ± 5.23	-	-	-
	Macaranga triloba			NC	-	Euphorbiaceae		0.433	0.6 ± 0.87	-	-	-	-	-	-	-	-
	Madhuca bejaudii			NC	-	Sapotaceae		0.618	-	-	6.9 ± 13.52	-	-	-	-	-	-
	Madhuca sp.			NC	-	Sapotaceae		0.681	0.6 ± 0.67	-	-	8.3 ± 3.44	-	-	-	-	-
	Mallotus paniculatus			NC	-	Euphorbiaceae		0.618	-	-	3.45 ± 6.76	-	-	-	-	-	-
	Mallotus plicatus	Chrakeng	*Coccoceras anisopodum*	NC	-	Euphorbiaceae		0.487	-	-	-	-	-	-	-	-	-
	Mangifera cochinchinensis			NC	-	Anacardiaceae		0.345	1.2 ± 1.09	-	-	-	-	0.33 ± 0.45	-	-	-
	Mangifera sp.	Svay Pongtrong /Svay Svak	*Anacardidc mangifera sp*	NC	-	Anacardiaceae		0.508	-	-	-	0.24 ± 0.28	-	-	-	-	-
	Markhamia stipulata			NC	-	Bigonieaceae		0.508	-	-	-	-	-	-	-	-	-
	Markhamia stipu lata	Dokpo	*Bignoniace markhamia pierrei*	NC	-	Bigoniaceae		0.676	0.2 ± 0.39	-	-	0.41 ± 0.81	0.02	0.5 ± 0.72	-	-	-
	Mastixia pentandra			NC	-	Cornaceae		0.676	12.2 ± 5.48	-	-	-	-	-	-	-	-
	Melodorum fruticosum			NC	-	Annonaceae		0.618	3 ± 1.88	-	-	-	-	-	-	-	-

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									D1	D2	D3	D4	D5**	D6	O1	O2	O3
	Memecylon caeruleum	Phngeas	*Memecylon floribundum*	NC	-	Melastomataceae		0.783	-	-	-	-	-	-	-	-	-
	Memecylon edule	Plong	*Melastomac memecylon edule*	NC	-	Melastomataceae		0.675	4.4 ± 3.55	-	-	-	-	-	1.07 ± 1.07	-	-
	Memecylon lilacinum			NC	-	Melastomataceae		0.618	0.8 ± 1.24	-	-	-	-	-	-	-	-
	Memecylon ovatum			NC	-	Melastomataceae		0.618	3.6 ± 2.04	-	-	-	-	-	-	-	-
	Memecylon sp.	Plong Keov	*Melastomac memecyylon sp*	NC	-	Melastomataceae		0.675	-	-	-	1.37 ± 1.75	-	-	-	-	-
	Microcos tomentosa	Po Plear	*Grewia paniculata*	NC	-	Malvaceae		0.64	1.4 ± 1.01	-	-	9.59 ± 4.18	-	-	-	-	-
	Millingtonia hortensis	Angkea Bos	*Millington hortensis*	NC	-	Bigoniaceae		0.577	-	-	-	-	-	-	-	-	-
	Mischocarpus pentapetalus			NC	-	Sapindaceae		0.618	0.4 ± 0.55	-	-	-	-	-	-	-	-
	Mitragyna diversifolia	Khtom	*Stephegyne diversifollia*	NC	-	Meliaceae		0.55	-	-	-	-	-	-	-	-	-
	Mitragyna hirsuta			NC	-	Rubiaceae		0.618	0.2 ± 0.39	-	-	-	-	-	-	-	-
	Mitrephora thorelii			NC	-	Annonaceae		0.618	0.2 ± 0.39	-	-	-	-	-	-	-	-
	Morinda citrifolia			NC	-	Rubiaceae		0.63	-	-	-	-	-	-	0.8 ± 0.58	0.41 ± 0.2	-
	Morinda tomentosa			NC	-	Rubiaceae		0.618	-	-	0.34 ± 0.68	-	-	-	-	-	-
	Mucuna pruriens	Khnhe	*Mucuna pruriens*	NC	-	Leguminosae		0.618	-	-	-	-	-	-	-	-	-
	Myristica iners			NC	LC	Myristicaceae		0.575	2.8 ± 1.67	-	-	-	-	-	-	-	-
	Nauclea officinalis			NC	-	Rubiaceae		0.618	2.4 ± 2.25	-	-	-	-	-	-	-	-
	Nauclea orientalis			NC	-	Rubiaceae		0.618	-	-	-	-	-	0.42 ± 0.82	-	-	-
	Nephelium hypoleucum			NC	-	Sapindaceae		0.491	0.8 ± 0.77	1.76 ± 1.21	-	6.97 ± 3.63	2.55	6.5 ± 4.58	-	-	-
	Nephelium melliferum			NC	-	Sapindaceae		0.762	17.6 ± 6.06	-	-	-	-	-	-	-	-
	Nephelium xerospermoides	Semorn\ Rol	*Nephealium xerosperu*	NC	-	Sapindaceae		0.762	-	-	-	-	-	-	-	-	-
	Nephelium lappa ceum			NC	LC	Sapindaceae		0.618	-	0.12 ± 0.17	-	-	-	-	-	-	-
	Nothaphoebe umbelliflora			NC	-	Lauraceae		0.71	2.4 ± 1.87	-	-	-	-	-	-	-	-
	Ochna integerrima	Angkea Sel	*Ochna harmandii*	NC	-	Ochnaceae		0.744	-	-	0.34 ± 0.68	0.67 ± 1.31	-	0.42 ± 0.82	-	-	-

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									D1	D2	D3	D4	D5**	D6	O1	O2	O3
	Ochrocarpos siamensis	Sophy	*Ochrocarpus siamensis*	NC	-	Clusiaceae		0.618	-	-	-	-	-	-	-	-	-
	Pavetta indica			NC	-	Rubiaceae		0.618	-	-	-	-	-	1.33 ± 1.52	-	-	-
	Phoebe lanceolata			NC	-	Lauraceae		0.618	2.8 ± 1.85	-	-	-	-	-	-	-	-
	Phoebe sp.			NC	-	Lauraceae		0.618	0.4 ± 0.55	-	-	-	-	-	-	-	-
	Phyllanthus amarus	Eyseiphsam Srach	*Phyllantus amarus*	NC	-	Phyllanthaceae		0.664	-	-	-	-	-	-	-	-	-
	Phyllanthus emblica	Kantout Prey	*Phyllantus emblica*	NC	-	Phyllanthaceae		0.636	0.2 ± 0.39	-	-	-	-	-	-	0.12 ± 0.12	-
	Poiarium alternifolium			NC	-	Bonnetiaceae		0.618	1.4 ± 1.7	-	-	-	-	-	-	-	-
	Polyalthia cerasoides	Kray	*Polyalthia cerasoides*	NC	-	Annonaceae		0.755	-	-	30 ± 29.17	2.95 ± 2.17	-	-	-	-	-
	Polyalthia jucunda	Sanda	*Polya jacunda*	NC	-	Annonaceae		0.57	-	-	-	-	-	-	-	-	-
	Polyalthia sp.			NC	-	Annonaceae		0.618	2.2 ± 1.84	-	-	-	-	-	-	-	-
	Prunus arborea			NC	LC	Rosaceae		0.618	0.2 ± 0.39	-	-	-	-	-	-	-	-
	Psychotria asiatica	Anntung Sor	*Psychotria revesii*	NC	-	Rubiaceae		0.45	-	-	-	-	-	-	-	-	-
	Psychotria sp.	Kloung	*Rubiaceae psychrotria sp*	NC	-	Rubiaceae		0.45	-	-	-	-	-	-	-	-	-
	Psydrax dicoccos	-	*Psydrax dicoccos*	NC	-	Rubiaceae		0.45	-	-	-	6.58 ± 2.82	-	0.08 ± 0.16	-	-	-
	Pternandra caerulescens			NC	-	Melastomataceae		0.618	4.2 ± 2.69	-	-	-	-	-	-	-	-
	Pterospermum grewiifolium			NC	-	Malvaceae		0.618	0.4 ± 0.55	-	-	-	-	-	-	-	-
	Pterospermum lanceifolium			NC	-	Malvaceae		0.618	-	-	-	-	-	2.92 ± 2.46	-	-	-
	Pterospermum littorale			NC	-	Malvaceae		0.577	5 ± 2.58	-	-	-	-	-	-	-	-
	Pterospermum macrocarpum			NC	-	Malvaceae		0.618	0.4 ± 0.55	-	-	-	-	-	-	-	-
	Pterospermum semisagittatum			NC	-	Malvaceae		0.63	-	-	-	-	-	-	0.53 ± 0.53	-	-
	Pterospermum sp.	Pang	*Sterculiac pterospermun sp*	NC	-	Malvaceae		0.521	0.2 ± 0.39	-	-	-	-	-	-	-	-
	Pterygota alata			NC	-	Sterculiaceae		0.618	-	0.13 ± 0.18	-	-	-	0.5 ± 0.49	-	-	-
	Quassia harmandiana			NC	-	Simaroubaceae		0.447	0.2 ± 0.39	-	-	0.17 ± 0.33	-	1 ± 1.65	-	-	-
	Rauwenhoffia sia mensis			NC	-	Annonaceae		0.364	-	-	-	-	-	0.17 ± 0.33	-	-	-

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									D1	D2	D3	D4	D5**	D6	O1	O2	O3
	Rhodomyrtus tomentosa	Pouch	*Rhodomyrtus tomantosa*	NC	-	Myrtaceae		0.618	-	-	-	-	-	-	-	-	-
	Sapindus rarak			NC	-	Sapindaceae		0.618	1.4 ± 2.03	-	-	-	-	-	-	-	-
	Sapium sebiferum			NC	-	Euphorbiaceae		0.618	-	-	-	0.01 ± 0.02	-	-	-	-	-
	Scaphium affine	Roung	*Sterculia lychnophora*	NC	-	Malvaceae		0.56	-	-	-	0.48 ± 0.7	-	-	-	-	-
	Schleichera oleosa	Pong Ro	*Schleicher oleosa*	NC	-	Sapindaceae		0.897	3.6 ± 2.32	1.61 ± 2.18	1.03 ± 1.49	0.27 ± 0.32	-	-	-	-	-
	Schoutenia glomerata			NC	-	Malvaceae		0.388	0.8 ± 0.95	-	-	-	-	-	-	-	-
	Schoutenia hypoleuca			NC	-	Malvaceae		0.62	-	-	-	-	-	-	-	-	0.28 ± 0.28
	Schoutenia ovata			NC	-	Tiliaceae		0.618	-	-	4.83 ± 6.85	-	-	-	-	-	-
	Scleropyrum pentandrum			NC	-	Santalaceae		0.79	-	-	0.34 ± 0.68	-	-	-	-	-	-
	Shorea guiso			NC	CR	Dipterocarpaceae		0.618	5.6 ± 2.73	-	8.28 ± 14.88	0.8 ± 0.5	-	-	-	-	-
	Shorea siamensis	Ka Chiep	*Pentapetes phoenicea*	NC	LC	Dipterocarpaceae		0.86	-	1.57 ± 1.96	5.52 ± 8.17	0.22 ± 0.27	19.22	7.67 ± 6.19	4.53 ± 4.53	19.65 ± 11.82	0.28 ± 0.28
	Sloanea sigun			NC	-	Elaeocarpaceae		0.705	0.8 ± 0.77	-	-	-	-	-	-	-	-
	Sphaerocoryne affinis	Romdoul	*Popowia aberrans*	NC	-	Annonaceae		0.618	-	-	-	-	-	-	-	-	-
	Spondias malayana			NC	-	Anacardiaceae		0.618	-	-	-	-	-	0.17 ± 0.33	-	-	-
	Spondias sp	Pon Ormbork	*Anacardiac spondias sp*	NC	-	Anacardiaceae		0.289	-	-	-	-	-	-	-	-	-
	Spondias sp	Pon Svar	*Spondias sp.*	NC	-	Anacardiaceae		0.289	-	-	-	-	-	-	-	-	-
	Sterculia foetida	Sam Rong	*Sterculia foetida*	NC	-	Malvaceae		0.448	-	-	-	-	-	-	-	-	-
	Sterculia gilva			NC	-	Malvaceae		0.289	0.4 ± 0.55	-	-	-	-	-	-	-	-
	Sterculia sp.			NC	-	Malvaceae		0.618	-	-	-	1.04 ± 1.27	3.37	-	-	-	-
	Sterculia villosa			NC	-	Malvaceae		0.373	-	-	-	-	-	0.67 ± 0.9	-	-	-
	Stereospermum cylindricum			NC	-	Bignoniaceae		0.255	0.8 ± 0.77	-	-	-	-	-	-	-	-
	Stereospermum sp.			NC	-	Bigoniaceae		0.99	-	-	-	-	-	1.92 ± 2.08	-	-	-
	Streblus asper	Snay	*Moraceae steblus asper*	NC	-	Moraceae		0.622	-	0.94 ± 1.35	0.34 ± 0.68	-	10.28	0.17 ± 0.33	-	-	-
	Strychnos nux-vomica	Sleng	*Strychnos nux-vomica*	NC	-	Loganiaceae		0.807	-	0.39 ± 0.61	0.34 ± 0.68	-	-	-	-	1.29 ± 0.53	-
	Suregada multiflora			NC	-	Euphorbiaceae		0.66	0.4 ± 0.55	-	-	0.06 ± 0.12	-	-	-	-	-

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									D1	**D2**	**D3**	**D4**	**D5****	**D6**	**O1**	**O2**	**O3**
	Swietenia macrophylla			NC	VU	Meliaceae		0.647	-	0.07 ± 0.15	-	-	-	3.75 ± 4.7	-	-	-
	Symplocos cochinchinensis			NC	-	Symplocaceae		0.49	0.2 ± 0.39	-	-	-	-	-	-	-	-
	Symplocos sp.			NC	-	Symplocaceae		0.618	0.2 ± 0.39	-	-	-	-	-	-	-	-
	Syzygium baviense			NC	-	Myrtaceae		0.733	-	-	-	-	-	-	-	-	3.33 ± 1.59
	Syzygium cumini			NC	-	Myrtaceae		0.618	-	-	-	0.27 ± 0.5	-	-	-	-	-
	Syzygium jambos	Dok Mey	*Eugenia malaccensis*	NC	-	Myrtaceae		0.65	-	-	-	-	-	-	-	-	-
	Syzygium polyanthum			NC	-	Myrtaceae		0.673	-	-	-	4.62 ± 3.12	-	-	-	-	-
	Syzygium zeylanicum			NC	-	Myrtaceae		0.558	-	-	11.03 ± 15.17	6.5 ± 4.45	-	-	-	-	-
	Terminalia bialata	Popea Khe	*Terminalia bialata*	NC	-	Combretaceae		0.606	0.4 ± 0.55	0.67 ± 1.32	-	0.23 ± 0.36	2.97	0.58 ± 0.99	1.07 ± 0.73	2.74 ± 1.42	-
	Terminalia calamansanay			NC	-	Combretaceae		0.65	0.2 ± 0.39	-	-	-	-	-	-	-	-
	Terminalia catappa	Cham Bak Baraing	*Terminalia catappa*	NC	-	Combretaceae		0.485	-	-	-	-	-	-	-	-	-
	Terminalia chebula sp2	Srormor	*Terminalia chebula*	NC	-	Combretaceae		0.618	-	-	-	-	-	-	-	-	-
	Terminalia crenata			NC	-	Combretaceae		0.618	1.8 ± 1.68	-	-	-	-	-	-	-	-
	Terminalia nigrovenulosa			NC	-	Combretaceae		0.618	-	-	-	-	-	1.75 ± 1.8	-	-	-
	Terminalia sp.			NC	-	Combretaceae		0.618	0.4 ± 0.55	-	-	0.04 ± 0.07	-	-	-	-	-
	Terminalia triptera			NC	-	Combretaceae		0.618	2.8 ± 2.09	-	-	-	-	-	-	-	-
	Terminalia nigro venulosa	Preas Phnov/Sombok Krohom	*Terminalia nigrovenulosa*	NC	-	Combretaceae		0.606	-	0.76 ± 0.6	-	0.09 ± 0.13	1.03	-	-	0.59 ± 0.31	-
	Tournefortia montana			NC	-	Boraginaceae		0.606	-	-	-	-	-	0.17 ± 0.33	-	-	-
	Tristaniopsis merguensis	Romleang	*Tristania merguensis*	NC	-	Myrtaceae		0.94	-	-	-	-	-	-	-	-	-
	unknown	Ach Sat		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Achderk		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Ambeng Chan		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Angkoch		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Angkrang Phnom		NC	-			0.618	-	-	-	-	-	-	-	-	-

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									D1	D2	D3	D4	D5**	D6	O1	O2	O3
	unknown	Aphean		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Ates		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Bak Derm		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Bakpao		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Bangkang		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Bangkeou Sva		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Bangkong Kengkong		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Batphtil		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Bor Bork		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Bror Chok		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Chang Eng Sek		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Chang Kong Romeang	*Boerhavia ripenda*	NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Cheung Krapeu		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Cheung Krorvaing		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Chhoeng Chker		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Chhoeteal Preus		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Chnok		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Chnok Trou		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Chornlos	*Erioglssum serrlata*	NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Chorntesplouk		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Chorny		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Chov		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Chungkong Phon		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Dangkeab proeus		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Dey Sampoch		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Dounkay		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Ka Youk		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Kacheal		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Kakhuch		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Kalap		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Kalkal		NC	-			0.618	-	-	-	-	-	-	-	-	-

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									D1	**D2**	**D3**	**D4**	**D5****	**D6**	**O1**	**O2**	**O3**
	unknown	Kandab Chang Et		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Kaner		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Kangsengphnom		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Kann Deang		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Katoung		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Kbal Derk		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Kbal Krorlorng		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Kbal Krorlorng		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Kdor Combrok		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Khoes Reous		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Khveng		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Kling		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Knall		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Koktmat		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Kom Pert		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Kon Khmom		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Kong Kangphnom		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Kork		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Korndork		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Korthet		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Krobao Khek		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Kroeng		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Kror Em		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Kror Mourn		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Krorchork Anderk		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Krorng Soeur		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Krorvann		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Ktith		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Lor Vea		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Lorlot		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Lort		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Lorving		NC	-			0.618	-	-	-	-	-	-	-	-	-

Note	Scientific name	Local name	Recorded scientific name	Royalty class	IUCN	Family	*Resin species	Wood density	Mean (± CI) stem density: dense forest (DBH ≥10 cm; ha-1)						Mean (± CI) stem density: open forest (DBH ≥10 cm; ha-1)		
									D1	D2	D3	D4	D5**	D6	O1	O2	O3
	unknown	Madehn		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Madehn Meas		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Mak Breing		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Mloutrayouk		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Mor Mang		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Ngok		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Nham		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Niv		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Onlok Phor Em		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Pa Ngab		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Pa Nges		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Pech Changva		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Phlang		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Phneang		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Phnerk Chma		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Phor		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Plov Sompouch		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Popoulvak		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Popuol Bay		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Poun		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Promat Khlakmom		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Promoy Vieng		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Pror Hout		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Raing		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Rom Chorng		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Romengtha Nge0Y		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Sang Ha		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Sla Kchey		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Slakrorpoul		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Sloek Lo Et		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Som Leang		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Speou Prey		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Tabort		NC	-			0.618	-	-	-	-	-	-	-	-	-

Note	Scientific name	Local name	Recorded scientific name	Royalty class	IUCN	Family	*Resin species	Wood density	Mean (± CI) stem density: dense forest (DBH ≥10 cm; ha-1)					Mean (± CI) stem density: open forest (DBH ≥10 cm; ha-1)			
									D1	**D2**	**D3**	**D4**	**D5****	**D6**	**O1**	**O2**	**O3**
	unknown	Taoniv		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Tapil		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Teng		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Tkov		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Tlerm Annderk		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Tom Poung		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Touk		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Tra Bek Chou		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Trang		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Tror Orl		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Tror Yak		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Trormoungsek	*Coelonium mutiforum*	NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Trorng		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Veay		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Voeng		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Yeam		NC	-			0.618	-	-	-	-	-	-	-	-	-
	unknown	Youk		NC	-			0.618	-	-	-	-	-	-	-	-	-
	Urena lobata	Rompeat Chrouk	*Malvaceae urena lobata*	NC	-	Malvaceae		0.618	-	-	-	-	-	-	-	-	-
	Vaccinium bracteatum			NC	-	Ericaceae		0.618	-	-	0.34 ± 0.68	-	-	-	-	-	-
	Vitex glabrata			NC	-	Lamiaceae		0.618	0.2 ± 0.39	-	0.69 ± 0.94	-	-	-	-	-	-
	Vitex negundo			NC	-	Lamiaceae		0.604	-	-	-	-	-	0.17 ± 0.33	-	-	-
	Vitex peduncularis			NC	-	Lamiaceae		0.67	0.4 ± 0.55	-	-	-	-	-	-	-	-
	Vitex pinnata	Populthmor	*Vitex pubescens*	NC	-	Lamiaceae		0.604	1.8 ± 1.38	0.13 ± 0.14	2.41 ± 2.51	2.17 ± 1.69	-	3.5 ± 1.85	0.53 ± 0.53	0.49 ± 0.28	-
	Walsera villosa			NC	-	Lamiaceae		0.618	-	-	-	0.1 ± 0.19	-	-	-	-	-
	Walsura pinnata			NC	-	Meliaceae		0.618	-	-	12.41 ± 15.43	-	-	-	-	-	-
	Walsura trichostemon			NC	-	Meliaceae		0.868	0.2 ± 0.39	-	-	-	-	-	-	-	-
	Wendlandia tinctoria			NC	-	Rubiaceae		0.618	-	-	-	-	-	0.58 ± 0.87	-	-	-
	Wrightia arborea			NC	-	Apocynaceae		0.693	-	0.12 ± 0.17	-	-	-	0.17 ± 0.33	-	-	-
	Wrightia religiosa	Sangva Pich	*Wrightiagiosa*	NC	-	Apocynaceae		0.58	-	0.82 ± 1.35	-	2.41 ± 3.36	-	-	-	-	-
	Xanthophyllum			NC	-	Polygalaceae		0.58	-	-	-	-	-	1 ± 1.16	-	-	-

Note	Scientific name	Local name	Recorded scientific name	Royalty class	IUCN	Family	*Resin species	Wood density	Mean (± CI) stem density: dense forest (DBH ≥10 cm; ha-1)						Mean (± CI) stem density: open forest (DBH ≥10 cm; ha-1)		
									D1	D2	D3	D4	D5**	D6	O1	O2	O3
	colubrinum																
	Xanthophyllum glaucum			NC	-	Polygalaceae		0.706	4.6 ± 2.35	-	-	-	-	0.5 ± 0.98	-	-	-
	Xanthophyllum sp.			NC	-	Polygalaceae		0.618	3.4 ± 1.77	-	-	-	-	-	-	-	-
	Xanthophyllum virens			NC	-	Polygalaceae		0.618	0.2 ± 0.39	-	-	-	-	-	-	-	-
	Xerospermum noronhianum			NC	-	Sapindaceae		0.618	16.2 ± 5.81	-	-	-	-	-	-	-	-
	Xylopia pierrei			NC	VU	Annonaceae		0.618	0.8 ± 0.77	-	-	-	-	-	-	-	-
	Xylopia vielana			NC	-	Meliaceae		0.618	2.2 ± 1.35	2.85 ± 2.62	-	3.2 ± 2.05	-	-	-	-	-
	Zanthoxylum rhetsum			NC	-	Rutaceae		0.536	0.2 ± 0.39	-	-	-	-	-	-	-	-
	Ziziphus cambodianus			NC	-	Rhamnaceae		0.618	0.4 ± 0.78	-	-	-	-	-	-	-	-
	unknown (all possible)							0.618	5.8 ± 6.38	251.1 ± 34.24	83.79 ± 52.01	205.01 ± 33.17	210	90.08 ± 25.31	32.8 ± 6.46	111.47 ± 15.47	8.61 ± 4.05
	TOTAL								502.40 ± 2.76	438.98 ± 3.85	415.17 ± 5.78	550.85 ± 7.04	589.73	431.83 ± 2.96	311.73 ± 2.19	291.23 ± 2.91	213.61 ± 3.49

SUPPLEMENTARY TABLE 3: Median and interquartile range of timber profits for each scenario

	Opportunity cost of protection (median, $ ha^{-1})	**Opportunity cost of protection (lower 25% quartile, $ ha^{-1})**	**Opportunity cost of protection (upper 25% quartile, $ ha^{-1})**	**% timber value removed**	**Remaining % timber profit**
Minimum harvestable DBH: 10cm for luxury, other classes 40cm					
Dense					
No timber logged	3,443	1,151	6,490	0	100.0
Luxury timber logged	2,123	810	3,931	38.3	61.7
Luxury, I, II timber logged	0	-	-	100.0	0
All timber logged	0	-	-	100.0	0
Open					
No timber logged	1,543	543	4,356	0	100.0
Luxury timber logged	671	165	1,422	56.5	43.4
Luxury, I, II timber logged	0	-	-	100.0	0
All timber logged	0	-	-	100.0	0
Minimum harvestable DBH: 10cm for luxury, other classes 30cm					
Dense					
No timber logged	4,308	1,637	7,537	0	100.0
Luxury timber logged	2,881	1,227	4,967	33.1	66.9
Luxury, I, II timber logged	0	0	0	100.0	0
All timber logged	0	0	0	100.0	0
Open					
No timber logged	3,373	1,214	6,346	0	100.0
Luxury timber logged	1,961	710	3,494	41.9	58.1
Luxury, I, II timber logged	0	0	0	100.0	0
All timber logged	0	0	0	100.0	0

SUPPLEMENTARY TABLE 4: Median and interquartile range of agricultural 25-year Net Present Value

Net present value (NPV) over 25 years, with input costs and prices in $US adjusted to 2013. NPV is shown for large, monocultural plantations of rubber and sugar, and smallholder farms of cashew and cassava

Forest type	Discount rate (%)	Crop type	25-year NPV (median, $ ha^{-1})	Lower 25% quartile ($ ha^{-1})	Upper 25% quartile ($ ha^{-1})
Dense	5	Rubber	25,774	18,191	33,423
		Cassava	21,782	15,373	28,414
		Cashew	16,328	10,847	21,680
		Sugar	1,463	-886	3,707
	8	Rubber	16,533	11,403	21,733
		Cassava	16,980	12,000	22,041
		Cashew	11,762	7,490	15,838
		Sugar	919	-856	2,784
	10	Rubber	12,571	8,436	16,698
		Cassava	14,597	10,133	19,124
		Cashew	9,491	6,099	12,989
		Sugar	619	-905	2,238
	15	Rubber	6,224	3,676	8,763
		Cassava	10,800	7,511	14,167
		Cashew	6,236	3,862	8,549
		Sugar	306	-860	1,461
Open	5	Rubber	14,697	9,414	20,219
	8		7,909	4,463	11,464
	10		5,089	2,532	7,764
	15		1,088	-403	2,591

SUPPLEMENTARY TABLE 5: Real world carbon prices

Indicative carbon prices were sought from the literature for comparison with estimated breakeven carbon prices. Three prices were selected, chosen to represent voluntary markets and carbon funds, compliance markets, and the estimated social cost of carbon, respectively.

Mean price ($ tCO2-1)	Price type	Source	Indicative price used ($ tCO_2^{-1})
1.70	All forest carbon offsets sold on the voluntary market in 2014	(Goldstein 2015)	5.00
3.70	Avoided deforestation (REDD) credits sold globally in 2014	(Goldstein 2015)	
5.00	Non-market forest carbon payments (e.g. bilateral agreements between Norway/Guyana)	(Goldstein 2015)	
5.40	All voluntary market carbon sales	(Goldstein 2015)	
12.70	All compliance market carbon sales (e.g. California's cap and trade policy)	(Goldstein 2015)	13.00
18.00	Corporate internal carbon prices	(Goldstein 2016)	
36.00	US government social cost of carbon	(Cama 2016)	36.00
40.00	World Bank social cost of carbon	(Goldstein 2016)	

SUPPLEMENTARY TABLE 6: Data sources for agricultural net present value calculation

For each parameter, price and cost estimates from different sources were adjusted to US$ 2013 using an averaged CPI for Thailand, Cambodia and Vietnam (The World Bank 2015) before calculation of means, variance or range. FAO producer prices are compared to price estimates from other sources, including GEM commodity prices, in Supplementary Figure 1. For each parameter an explanation of data treatment and value selection is given; resulting crop-specific parameter values are provided in Supplementary Table 8.

Parameter	Reference	Country	Method
Rubber – *large scale monocultural plantation crop*			
Rubber producer price (see also Supp. Fig. 1)	(FAO 2014)	Thailand/ Vietnam	Producer prices are not published for Cambodia on FAOSTAT (FAO 2014), so the mean and standard error of the mean (SE) of annual producer prices across Thailand and Vietnam (2003 – 2012 inclusive) were used to account for price volatility and regional variation in rubber prices. Compared to prices reported from ground surveys in Cambodia ($530 – 1878 t^{-1}; data from 2005 adjusted to US$ 2013; (ACI 2005, Hansen and Neth 2006, EIC 2007, Hing and Thun 2009) these values ($1355 - $4046, data from 2002 – 2012, $2333 in 2005) are relatively high; farmers, especially smallholders, may receive lower prices in Cambodia. The most recent data from 2014 gives a producer price of $1,644 t^{-1}. We do not include returns from felling the rubber trees and selling the timber at the end of the 25 year cycle as this is often used to cover the costs of replanting the next cycle (Shigematsu et al. 2013).
Rubber yield	(ACI 2005, Hansen and Neth 2006, EIC 2007)	Cambodia	Yield data for each production year of the 25-year management cycle of a large plantation were extracted from each study. Minimum and maximum yields for each year, across all studies, were used as minimum and maximum input parameters for the simulation model (n = 3). Yield estimates that appeared to use unclear units which could correspond to wet latex yield rather than dry rubber yield, were excluded from analysis. For each model iteration an annual dry rubber yield curve (t ha^{-1} yr^{-1}) over 25 years was generated as a proportion of the maximum attainable yield. For each iteration (i), a proportion ($prop_i$ range 0 to 1) was selected randomly from a uniform distribution. Then for each production year (t, range 1-25) the run-specific yield ($Y_{i,t}$) was calculated applying this proportion to the interval between reported minimum ($Ymin_t$) and maximum ($Ymax_t$) yields, following the equation: $Y_{i,t} = Ymin_t + (Ymax_t - ymin_t) * Yprop_i$. The run-specific proportion used to create the yield curve was generated independently for each crop, for each iteration. Two examples, for $prop_i = 0.25$ and 0.87, are shown in Supplementary Figure 10. For open forests, a yield penalty was applied to account for predicted slower tree growth in dry conditions by delaying the onset of tapping until 10 years after planting, rather than the usual 6 years (Carr 2012).
Rubber production cost	(ACI 2005, Hansen and Neth 2006, EIC 2007, Hing and Thun 2009)	Cambodia	Production cost data for each year of the 25-year management cycle for large monocultural plantations were extracted from each study (n = 2 referring to large plantations), standardised to USD ha^{-1} yr^{-1} in US$ 2013. Costs included: land clearance (using bulldozer or tractor, year 1 only, n = 1), land preparation (annual), planting material, annual inputs, annual labour costs. We do not include the costs of felling rubber trees at the end of the 25-year management cycle as this cost is associated with replanting and the start of the next yield production cycle. For each model iteration an annual cost curve ($ ha^{-1} yr^{-1}) over 25 years was generated as a proportion of the maximum cost. For each iteration (i), a proportion ($Cprop_i$ range 0 to 1) was selected randomly from a uniform distribution. Then for each production year (t, range 1-25) the run-specific

Parameter	Reference	Country	Method
			cost (C_{it}) was calculated applying this proportion to the interval between reported minimum ($Cmin_t$) and maximum ($Cmax_t$) costs, following the equation: $C_{i,t} = Cmin_t + (Cmax_t - Cmin_t) * Cprop_i$. The run-specific proportion used to create the cost curve was generated independently for each crop, for each iteration.
Cashew – smallholder monocultural plantation crop			
Cashew producer price (see also Supp. Fig. 1)	(FAO 2014)	Thailand/ Vietnam	Producer prices are not published for Cambodia on FAOSTAT (FAO 2014), so the mean and standard error of the mean (SE) of annual producer prices across Thailand and Vietnam for 2003 - 2012 inclusive ($861 - $1197, data from 2002 - 2012, US$ 2013) were used to account for price volatility and regional variation in cashew prices Compared to prices reported from ground surveys in Cambodia ($789 - $1047, 2003 – 2005, in US$ 2013; ACI 2005, Hansen and Neth 2006, EIC 2007), Cambodian farm gate prices are similar to producer prices in Thailand and Vietnam. Farmers are therefore likely to receive prices similar to these in Cambodia.
Cashew yield	(ACI 2005)	Cambodia	Six sets of yield data, for different management cycle lengths, were extracted from ACI (2005) for small farms, covering four provinces. Some yields seemed surprisingly high (up to 5.5 t ha^{-1}), given that average yields from a large scale plantation in Cambodia were reported to be 0.8 t ha^{-1} (Hansen and Neth 2006), and a report on the cashew industry in Cambodia states that the maximum known yields from Cambodia are 2.0 t ha^{-1}, with exceptional yields of 2.5 t ha^{-1} reported from Vietnam (IFC 2010). We therefore excluded any datasets reporting average yields >2.5 t ha^{-1} over a 25-year plantation cycle. Yield curves reported for management cycles of less than 25 years (e.g. 10 or 15 years) were extrapolated according to the proportional yield declines reported for 25-year management cycles. Minimum and maximum yields for each production year, across all six yield curves, were used as minimum and maximum input parameters for the simulation model and an iteration-specific yield curve was simulated, as for rubber. The run-specific proportion used to create yield curve was generated independently for each crop, for each iteration.
Cashew production cost	(ACI 2005)	Cambodia	Production cost data for each year of the 25-year management cycle were extracted from each of the six datasets in ACI (2005), standardised to USD ha^{-1} yr^{-1} (adjusted to 2013). Costs included: land clearance (using manual labour, year 1 only), land preparation (year 1 only), planting material, annual inputs and labour costs (including imputed family labour costs). Where management cycles reported were for less than 25 years, costs were extended to year 25 based on final year costs in each dataset. Variation in reported labour requirements among the six datasets was high (total annual labour days ranged from 25 to 267 days ha^{-1}). On inspection of the budgets, this was accounted for by a ten-fold greater number of annual labour days reported for harvesting in one smallholder budget (220 – 300 days ha^{-1}). In three other smallholder datasets, annual harvesting labour days ranged from 16 – 30 days ha^{-1}, while a maximum of 35 days ha-1 were reported from a survey of 140 smallholder cashew farmers in Ghana. We therefore considered this large estimate of labour input to be an error, and limited the maximum annual harvesting days to 35 days ha^{-1}. Minimum and maximum costs for each production year, across all six datasets, were used as minimum and maximum input parameters for the simulation model, and an iteration-specific cost curve was simulated, as for rubber. The run-specific proportion used to create the cost curve was generated independently for each crop, for each iteration.

Parameter	Reference	Country	Method
Cassava – smallholder monocultural annual crop			
Cassava producer price (see also Supp. Figure 1)	(FAO 2014)	Thailand/ Vietnam	Producer prices for raw cassava are published for Cambodia on FAOSTAT (FAO 2014), but they are much higher than any of the following price estimates for raw cassava, and therefore appear to be incorrect: producer prices for Thailand and Vietnam; farm gate prices for Cambodia reported in ACI (2005) or Hing & Thun(Hing and Thun 2009); farm gate prices provided by The Cambodian Ministry of Agriculture, Forestry and Fisheries (MAFF) to the ASEAN Food Security Information System (AFSIS 2016); or local prices reported from up to 11 local markets across Cambodia (Agricultural Marketing Information Service 2016; see Supplementary Figure 1). Farm gate prices provided by MAFF were not available for all years of interest (AFSIS 2016), so we used the mean and standard error of the mean (SE) of annual producer prices across Thailand and Vietnam for years 2003 – 2012, adjusted to US$ 2013 ($90.51 t^{-1}). This estimate is within the range of farm gate prices reported by MAFF to ASEAN ($42 – 96 t^{-1} 2001 – 2011, in US$ 2013; AFSIS 2016), and prices reported by farmers in Cambodia in 2013 (n = 15, $75.00 – $90.00 t^{-1}; SNV 2015) As for rubber, we suggest that small farmers may receive lower prices where access to markets is limited. There is also variation in price among provinces depending on the degree of harvesting, drying and transportation costs paid by the farmer versus middlemen; we base our NPV estimates on the most commonly used system in Cambodia, in which farmers sell raw cassava to traders, and traders pay harvesting, drying and transport costs (Hing and Thun 2009)
Cassava yield	(ACI 2005, Hing and Thun 2009, Sopheap et al. 2012)	Cambodia	Annual yield data (raw cassava, t ha^{-1} yr^{-1}) were extracted from each dataset. ACI (2005) provided a number of estimates for different farm sizes, while Hing & Thun (2009) and Sopheap et al (2011) reported yields for smallholder farms only. Minimum (10.5 t ha^{-1} yr^{-1}) and maximum (30.0 t ha^{-1} yr^{-1}) yields were extracted for each year across all datasets, specific to smallholder farms. The mean of these values (23.8 t ha^{-1}) is close to the mean yield reported at the national scale in Cambodia (20.49 t ha^{-1} in 2007; Sopheap et al. 2011), suggesting that these bounds are appropriate. Yields were assumed to remain constant over 25 years of repeated annual planting. This assumption is supported by data from Cambodia, that show no difference in yield between plots continuously cropped with cassava for 25 years without fertilisation and soils that had been cropped for <10 years (Sopheap et al. 2012). Supporting this, yields of 13.3 t ha^{-1} yr^{-1} are reported from fully exhausted soils in Colombia (Howeler 1991). However, cassava is potassium limited, and potassium-depleted soils can produce yields as low as 5 t ha^{-1} yr^{-1} in India, but if soils contain potassium-producing minerals, depletion does not occur even in absence of fertiliser application (Howeler 1991). Cassava is tolerant to low soil fertility conditions (Howeler 1991, Sopheap et al. 2012, Van Eijck et al. 2012). Evidence from Cambodia suggests that soil type does not affect cassava yield, although farmers self-identified areas of higher soil quality where cassava yields were increased within individual farms (Sopheap et al. 2012). We thus do not modify our yield estimates for open and dense forest areas, despite predicting that soil types may differ under each forest type. Yield curves were created for 25 consecutive years of cultivation, as for rubber and cashew, using the same proportion of maximum yield for each year. The run-specific proportion used to create yield curve was generated independently for each crop, for each iteration.
Cassava production cost	(ACI 2005, Hing and Thun 2009)	Cambodia	Annual production cost data for raw cassava were extracted from each of six datasets and standardised to USD ha^{-1} yr^{-1} units, adjusted to US$ 2013. Costs in all studies included: land clearance (using manual labour, year 1 only), land preparation (annual), planting material, annual inputs, annual labour costs (including imputed family labour costs), but did not include drying or transportation costs. Cost curves were created for 25 consecutive years, as for rubber and cashew, using the same proportion of maximum cost for each year. The run-specific proportion used to create the cost curve was generated independently for each crop, for each iteration.

Parameter	Reference	Country	Method
Sugar – large scale monocultural annual crop			
Sugar producer price (see also Supp. Figure 1)	(FAO 2014)	Thailand/ Vietnam	Producer prices are published for Cambodia on FAOSTAT (FAO 2014), but are much higher than FAOSTAT prices for Thailand and Vietnam and much higher also than Cambodian farm gate prices reported in ACI (2005). Prices were checked against global prices, and EU minimum prices, as Cambodia receives preferential pricing to export sugar to the EU through the "Everything but Arms Treaty" (Equitable Cambodia and Inclusive Development International 2013). However, Cambodia's Producer Prices were substantially lower than either of these indicators. We therefore used the mean and standard error of the mean (SE) of annual producer prices across Thailand and Vietnam for years 2003 – 2012 ($34.34 t^{-1}), but as for rubber and cassava, suggest that small farmers may often receive lower prices where access to markets is limited.
Sugar yield	(ACI 2005)	Cambodia	Annual yield data for large scale plantations from two regions of Cambodia were extracted from ACI (2005). Minimum and maximum reported yields were used as input parameters for the simulation model and were assumed to remain constant over 25 years of repeated annual planting. Yield curves were created for 25 consecutive years of cultivation, as for rubber and cashew, using the same proportion of maximum yield for each year. The run-specific proportion used to create yield curve was generated independently for each crop, for each iteration.
Sugar production cost	(ACI 2005)	Cambodia	Annual production cost data were extracted, standardised to USD ha^{-1} yr^{-1}, adjusted to US$ 2013 prices. Costs included: land clearance (using tractor or bulldozer, year 1 only), land preparation costs (annual), planting material, annual inputs, annual labour costs. Cost curves were created for 25 consecutive years, as for rubber, using the same proportion of maximum cost for each year. The run-specific proportion used to create the cost curve was generated independently for each crop, for each iteration.
Inflating US$ to 2013			
Consumer price index (CPI)	(The World Bank 2015)	Cambodia/ Thailand/ Vietnam	The World Bank Consumer Price Index (CPI) is available at the country level. For parameters obtained from multi-country studies, CPIs for Cambodia, Thailand and Vietnam were averaged and used to deflate all input costs and prices to 2013.

SUPPLEMENTARY TABLE 7: Post-deforestation land-use carbon stock estimates

Time-averaged carbon stocks (taCs) of above-ground biomass (AGB) and below-ground biomass (BGB) were estimated as either 50% of the carbon stock of a crop/plantation at the maximum rotation length (Gibbs et al. 2008), or for rubber, as the carbon stock as calculated by a regression equation at the median rotation length (Blagodatsky et al. 2016).

Land-use	taCs (tC ha-1)	Note
Rubber	52.5	Multiple estimates of taCs were generated by Blagodatsky et al in a review of studies on rubber plantation carbon dynamics (Blagodatsky et al. 2016). These estimates were either based on a division of the maximum carbon stock (at the time of clearing) by two, which assumes a linear increase in biomass during the growing cycle, or by fitting a regression model where more detailed data are available, and taking the carbon stock of the plantation as calculated by the equation at the median time in the rotation. Estimates of taCs (AGB + BGB) for 20 – 30 year monoculture rubber plantation cycles in South and Southeast Asia ranged from 40 to 65 tC ha^{-1} (Blagodatsky et al. 2016); the mean of these values (52.5 tC ha^{-1}) was used in analysis.
Cashew	22.32	Out estimate of taCs for a cashew plantation on a 10-year plantation cycle (22.32 tC ha^{-1}) were generated based on field data from Cambodia (Avtar et al. 2013). AGB of cashew plantations for each year of a 10-year plantation cycle were extracted from the data; BGB was assumed to be 24% of AGB (Cairns et al. 1997), and AGB + BGB carbon stock was assumed to be 50% of biomass. We calculated taCs to be 50% of this value (Blagodatsky et al. 2016). Where field data were not provided for a given year, the value for the next oldest year was used, generating a conservative estimate.
Cassava	2.5	Carbon stock for "annual cropland" in dry and seasonal areas of Asia reported as 5 tC ha^{-1}; time-averaged carbon stock is 50% of this value (Gibbs et al. 2008).
Sugarcane	6.75	Carbon stock for sugarcane in dry and seasonal areas of Asia reported as 13.5 tC ha^{-1}; time-averaged carbon stock is 50% of this value (Gibbs et al. 2008).

SUPPLEMENTARY TABLE 8: Value of dipterocarp resin collection and influence on breakeven carbon prices

Forest type	Median 25-year resin revenue ($ ha^{-1})	Median carbon breakeven price: "No timber logged + rubber" including resin revenue ($ tCO$_2$$^{-1}$)	Median carbon breakeven price: "No timber logged + rubber" excluding resin revenue ($ tCO$_2$$^{-1}$)
Dense	357.38	33.43	34.20
Open	234.49	51.12	52.65

SUPPLEMENTARY TABLE 9: Price estimates for timber royalty classes at various selling points in Cambodia

Minimum and maximum prices for each royalty class for the roadside/village were used as input parameters for simulations; other price points (i.e. forest, domestic or international market) were not used in the final analysis. In the absence of species-specific records from formal timber markets, all timber species in each royalty class were assumed to fetch the same price as those species from that royalty class that were explicitly named in source of prices (Supplementary Table 14). Prices shown are mean of all available data from 2007 - 2014 inclusive, except for Non-Classified timber, for which we use the price of fuelwood reported from field study in Cambodia (Blackett 2008). All prices were inflated to \$US 2013 using a CPI specific to Cambodia. All price data were based on interviews with villagers or market traders.

		Price (\$ m^{-3})						
Price point	Royalty Class	Min	Max	Mean Price	SD	SE	n¥	References
Forest	Luxury	-	-	-	-	-	-	(Grimm et al. 2007, Blackett 2008)
	I	115.4	202.0	152.6	33.1	14.8	5	
	II	116.5	116.5	116.5	-	-	1	
	III	77.7	77.7	77.7	-	-	1	
	NC	17.3	17.3	17.3	-	-	1	
Roadside/ Village	Luxury	500.0	3,129.4	1,300.5	657.4	150.8	19	(Singh 2013, Titthara 2014, WCS 2015); Hugh Wright (2010), unpublished data
	I	90.8#	290.5	151.7#	79.7	28.2	8	
	II	139.7#	290.5	251.5	58.6	26.2	5	
	III	77.7*	77.7*	77.7*	-	-	1	
	NC	17.3	17.3	17.3	-	-	1	
Domestic (national) market	Luxury	400.0	1154.6	739.3	330.2	147.7	5	(Grimm et al. 2007, Blackett 2008, Seangly 2013, Peter and Pheap 2014, Pye 2014a)
	I	346.3	692.7	517.3	122.8	46.4	7	
	II	461.8	577.3	510.6	40.3	13.4	9	
	III	77.7*	77.7*	77.7*	-	-	1	
	NC	17.3	17.3	17.3	-	-	1	
International market	Luxury	3,850.0	50,000.0	18,185.0	16,899.6	5,344.1	10	(EIA 2012a, Peter and Pheap 2014, Pye 2014b, Pye and Titthara 2014)
	I	346.3~	692.7~	517.3~	122.8~	46.4~	7	
	II	461.8~	577.3~	510.6~	40.3~	13.4~	9	
	III	77.7*	77.7*	77.7*	-	-	1	
	NC	17.3	17.3	17.3	-	-	1	

¥ n price estimates within and across all studies

Royalty class I timber is classed as more valuable than class II (FA 2004a); we thus assume the same minimum price for class I and II timber in simulation models (\$90.81)

*As for forest price

~As for domestic market price

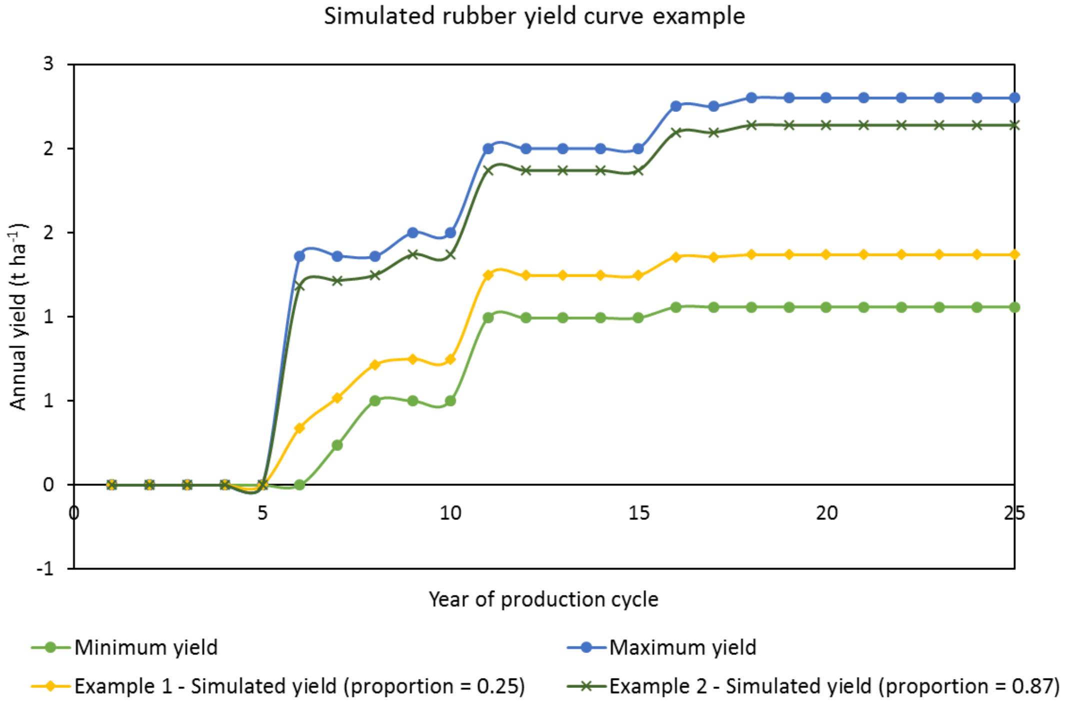
SUPPLEMENTARY NOTE 1: Background to forest management and logging in Cambodia

Forest degradation through logging has a complex history in Cambodia. Forest governance institutions were lost during the political turmoil of the Khmer Rouge era (1975 – 1980). Subsequently, nearly 70% of forested land was allocated for logging concessions in the 1990s, followed by widespread over-harvesting both within and outside concessions (Blaser *et al.* 2011). All formal logging concessions were halted in 2002, and many have since been designated as protected areas. Forested land is owned by the state and some annual logging coupes have been allocated; however, large tracts of forest have no clear management plan and illegal logging remains pervasive (Blaser *et al.* 2011, EIA 2014, Peter and Pheap 2014, Pye and Titthara 2014, Milne 2015). Allocation of forested areas for Economic Land Concessions (ELCs), which allow conversion to plantation crops, is a key driver of forest clearance in Cambodia; much of Cambodia's current timber harvest is extracted within and around ELCs (Forest Trends 2015). Much focus has been placed on the extraction of the highest-value Luxury class timber (EIA 2014), which can generate high levels of short-term income (Singh 2013). However, logging of other species (of lower royalty classes, especially classes I & II) is also pervasive (WCS 2015) and forms the bulk of timber harvested when forested land is cleared from ELCs (TWGFA *et al.* 2014).

The Forestry Administration grants transport licenses for logs ≥30cm DBH harvested from within ELCs, except for luxury timber (TWGFA *et al.* 2014). Minimum harvestable limits for all commercial tree species range from 30 – 60cm DBH (as defined by the Ministry of Agriculture, Forestry and Fisheries in Prakas 089 (2005) – a ministerial or inter-ministerial proclamation in Cambodian law), however the level of enforcement of these limits is not clear. According to Prakas 089, harvest of all luxury class timber is illegal, as is harvest of resin trees (some *Dipterocarpus* spp, all royalty class II, Supplementary Table 2) utilised by local people, unless they have given consent and been compensated. This latter group includes some of the most commercially valuable dipterocarp species. However, there is evidence for routine and widespread harvest of both luxury and resin trees (Global Witness 2015). In the 1990s commercial logging focussed on trees ≥45cm DBH (De Lopez 2003, Kao and Iida 2006), while minimum commercial harvestable DBH elsewhere in Southeast Asia is ≥40cm DBH (Fisher *et al.* 2011), and an assessment of logging in Cambodia that modelled unsustainable extraction rates assumed trees ≥40cm would be harvested (McKenney *et al.* 2004). For class I and II species, we therefore assumed a minimum harvestable DBH of 40 cm. Luxury species are exceptionally valuable and even small amounts are harvested (EIA 2012b); we therefore assumed all luxury class trees ≥10cm DBH would be harvested. Class III trees are used for local construction purposes (i.e. as timber) or as fuelwood. Non-classified trees are assumed to be only useful as fuelwood; non-classified and class III trees ≥40cm DBH were therefore assumed to have market value as fuelwood.

SUPPLEMENTARY FIGURE 10: Rubber yield curve simulation example.

For explanation of simulation, see Supplementary Table 5.



SUPPLEMENTARY TABLE 10: Resampling input parameters

For each sampling iteration, values for each parameter were sampled from either a uniform distribution between the minimum and maximum bounds, or where the shape of the distribution was known to be normal, from a normal distribution defined by the mean and standard error (SE) of the mean.

	Input parameter	Units	Bounds
Agricultural NPV	Crop input costs (annual)	USD ha^{-1} yr^{-1}	Min – Max
	Farm gate price	USD t^{-1}	Mean – SE
	Crop yield (annual)	t ha^{-1} yr^{-1}	Min – Max
Carbon stock	Forest carbon stock (square root transformed)	tC or tCO_2 ha^{-1}	Mean – SE
Timber profit	Timber volume (square root transformed)	m^3 ha^{-1}	Mean – SE
	Timber price	USD m^{-3}	Min – Max
	Extraction costs	USD m^{-3}	Min – Max

SUPPLEMENTARY TABLE 11: Proportion of luxury stems ≥60cm DBH compared between pairs of landscapes by Chi-squared two-sampled proportions test; there were no significant differences.

				F02		**F03**		**F04**		**F05**		**F06**	
	Forest type	n Luxury stems ≥30cm DBH	n Luxury stems ≥60cm DBH	x^2	p	x^2	p	x^2	p	x^2	p	x^2	p
F01	Dense	4	0	0.0690	0.79	0.0033	0.95	0.0000	1.00	0.0000	1.00	0.2344	0.63
F02	Dense	111	20	-	-	0.0000	1.00	2.1100	0.15	0.0047	0.95	0.1591	0.69
F03	Dense	11	2	-	-		-	0.4052	0.52	0.0000	1.00	0.0111	0.92
F04	Dense	34	2	-	-	-	-	-	-	0.0000	1.00	1.7647	0.18
F05	Dense	9	1	-	-	-	-	-	-	-	-	0.1563	0.69
F06	Dense	6	2	-	-	-	-	-	-	-	-	-	

				F02		F04	
	Forest type	n Luxury stems ≥30cm DBH	n Luxury stems ≥60cm DBH	x^2	p	x^2	p
F01	Open	6	1	0.0000	1.00	0.0000	1.00
F02	Open	21	4	-	-	0.2431	0.62
F04	Open	14	1	-	-	-	-

SUPPLEMENTARY TABLE 12: Input parameters for agricultural net present value calculation.

Year 1 includes land clearance costs entailed in preparing logged-over land for agriculture; $450 for large plantations (mechanised, bulldozer) or $250 for smallholders (manual labour; ACI 2005). See Supplementary Table 5 for data sources. All values in 2013 USD.

Crop	Size	Year	Annual cost (\$ ha^{-1} yr^{-1}): min	Annual cost (\$ ha^{-1} yr^{-1}): max	Farmgate price (\$ t^{-1}) mean	Farmgate price (\$ t^{-1}) SE	Annual yield – closed forest (t ha^{-1} yr^{-1}): min	Annual yield – closed forest (t ha^{-1} yr^{-1}): max	Annual yield – open forest (t ha^{-1} yr^{-1}): min	Annual yield – open forest (t ha^{-1} yr^{-1}): max
Cashew	Small-holder	1	514.06	764.61	963.48	43.75	0.00	0.00	0.00	0.00
		2	31.42	125.69	963.48	43.75	0.00	0.00	0.00	0.00
		3	27.23	173.88	963.48	43.75	0.00	1.90	0.00	1.90
		4	27.23	173.88	963.48	43.75	0.30	1.90	0.30	1.90
		5	27.23	173.88	963.48	43.75	0.30	1.90	0.30	1.90
		6	54.47	167.59	963.48	43.75	0.60	2.30	0.60	2.30
		7	54.47	167.59	963.48	43.75	0.70	2.30	0.70	2.30
		8	54.47	167.59	963.48	43.75	0.77	2.30	0.77	2.30
		9	54.47	167.59	963.48	43.75	0.77	2.30	0.77	2.30
		10	54.47	167.59	963.48	43.75	0.77	2.30	0.77	2.30
		11	54.47	173.88	963.48	43.75	0.77	3.00	0.77	3.00
		12	54.47	173.88	963.48	43.75	0.77	3.00	0.77	3.00
		13	54.47	173.88	963.48	43.75	0.77	3.00	0.77	3.00
		14	54.47	173.88	963.48	43.75	0.77	3.00	0.77	3.00
		15	54.47	173.88	963.48	43.75	0.77	3.00	0.77	3.00
		16	54.47	173.88	963.48	43.75	0.60	2.31	0.60	2.31
		17	54.47	173.88	963.48	43.75	0.60	2.31	0.60	2.31
		18	54.47	173.88	963.48	43.75	0.60	2.31	0.60	2.31
		19	54.47	173.88	963.48	43.75	0.60	2.31	0.60	2.31
		20	54.47	173.88	963.48	43.75	0.60	2.31	0.60	2.31
		21	54.47	173.88	963.48	43.75	0.60	2.31	0.60	2.31
		22	54.47	173.88	963.48	43.75	0.60	2.31	0.60	2.31
		23	54.47	173.88	963.48	43.75	0.60	2.31	0.60	2.31
		24	54.47	173.88	963.48	43.75	0.60	2.31	0.60	2.31
		25	54.47	173.88	963.48	43.75	0.60	2.31	0.60	2.31
Cassava	Small-holder	1	412.25	860.90	90.51	6.22	10.50	30.10	10.50	30.10
		2	110.29	560.00	90.51	6.22	10.50	30.10	10.50	30.10
		3	110.29	560.00	90.51	6.22	10.50	30.10	10.50	30.10
		4	110.29	560.00	90.51	6.22	10.50	30.10	10.50	30.10
		5	110.29	560.00	90.51	6.22	10.50	30.10	10.50	30.10
		6	110.29	560.00	90.51	6.22	10.50	30.10	10.50	30.10
		7	110.29	560.00	90.51	6.22	10.50	30.10	10.50	30.10
		8	110.29	560.00	90.51	6.22	10.50	30.10	10.50	30.10
		9	110.29	560.00	90.51	6.22	10.50	30.10	10.50	30.10
		10	110.29	560.00	90.51	6.22	10.50	30.10	10.50	30.10
		11	110.29	560.00	90.51	6.22	10.50	30.10	10.50	30.10
		12	110.29	560.00	90.51	6.22	10.50	30.10	10.50	30.10
		13	110.29	560.00	90.51	6.22	10.50	30.10	10.50	30.10
		14	110.29	560.00	90.51	6.22	10.50	30.10	10.50	30.10
		15	110.29	560.00	90.51	6.22	10.50	30.10	10.50	30.10
		16	110.29	560.00	90.51	6.22	10.50	30.10	10.50	30.10
		17	110.29	560.00	90.51	6.22	10.50	30.10	10.50	30.10
		18	110.29	560.00	90.51	6.22	10.50	30.10	10.50	30.10
		19	110.29	560.00	90.51	6.22	10.50	30.10	10.50	30.10
		20	110.29	560.00	90.51	6.22	10.50	30.10	10.50	30.10
		21	110.29	560.00	90.51	6.22	10.50	30.10	10.50	30.10
		22	110.29	560.00	90.51	6.22	10.50	30.10	10.50	30.10
		23	110.29	560.00	90.51	6.22	10.50	30.10	10.50	30.10
		24	110.29	560.00	90.51	6.22	10.50	30.10	10.50	30.10
		25	110.29	560.00	90.51	6.22	10.50	30.10	10.50	30.10

Crop	Size	Year	Annual cost (\$ ha^{-1} yr^{-1}): min	Annual cost (\$ ha^{-1} yr^{-1}): max	Farmgate price (\$ t^{-1}) mean	Farmgate price (\$ t^{-1}) SE	Annual yield – closed forest (t ha^{-1} yr^{-1}): min	Annual yield – closed forest (t ha^{-1} yr^{-1}): max	Annual yield – open forest (t ha^{-1} yr^{-1}): min	Annual yield – open forest (t ha^{-1} yr^{-1}): max
Sugar	Large plantation	1	1168.20	1749.82	35.74	1.30	12.00	29.50	12.00	29.50
		2	586.58	586.58	35.74	1.30	12.00	29.50	12.00	29.50
		3	586.58	586.58	35.74	1.30	12.00	29.50	12.00	29.50
		4	586.58	586.58	35.74	1.30	12.00	29.50	12.00	29.50
		5	586.58	586.58	35.74	1.30	12.00	29.50	12.00	29.50
		6	586.58	586.58	35.74	1.30	12.00	29.50	12.00	29.50
		7	586.58	586.58	35.74	1.30	12.00	29.50	12.00	29.50
		8	586.58	586.58	35.74	1.30	12.00	29.50	12.00	29.50
		9	586.58	586.58	35.74	1.30	12.00	29.50	12.00	29.50
		10	586.58	586.58	35.74	1.30	12.00	29.50	12.00	29.50
		11	586.58	586.58	35.74	1.30	12.00	29.50	12.00	29.50
		12	586.58	586.58	35.74	1.30	12.00	29.50	12.00	29.50
		13	586.58	586.58	35.74	1.30	12.00	29.50	12.00	29.50
		14	586.58	586.58	35.74	1.30	12.00	29.50	12.00	29.50
		15	586.58	586.58	35.74	1.30	12.00	29.50	12.00	29.50
		16	586.58	586.58	35.74	1.30	12.00	29.50	12.00	29.50
		17	586.58	586.58	35.74	1.30	12.00	29.50	12.00	29.50
		18	586.58	586.58	35.74	1.30	12.00	29.50	12.00	29.50
		19	586.58	586.58	35.74	1.30	12.00	29.50	12.00	29.50
		20	586.58	586.58	35.74	1.30	12.00	29.50	12.00	29.50
		21	586.58	586.58	35.74	1.30	12.00	29.50	12.00	29.50
		22	586.58	586.58	35.74	1.30	12.00	29.50	12.00	29.50
		23	586.58	586.58	35.74	1.30	12.00	29.50	12.00	29.50
		24	586.58	586.58	35.74	1.30	12.00	29.50	12.00	29.50
		25	586.58	586.58	35.74	1.30	12.00	29.50	12.00	29.50
Rubber	Large plantation	1	1141.38	1902.64	2595.56	200.27	0.00	0.00	0.00	0.00
		2	174.40	289.94	2595.56	200.27	0.00	0.00	0.00	0.00
		3	79.61	424.01	2595.56	200.27	0.00	0.00	0.00	0.00
		4	79.61	447.47	2595.56	200.27	0.00	0.00	0.00	0.00
		5	79.61	447.47	2595.56	200.27	0.00	0.00	0.00	0.00
		6	349.20	447.47	2595.56	200.27	0.00	1.36	0.00	0.00
		7	349.20	1169.80	2595.56	200.27	0.24	1.36	0.00	0.00
		8	349.20	1178.18	2595.56	200.27	0.50	1.36	0.00	0.00
		9	349.20	1178.18	2595.56	200.27	0.50	1.50	0.00	0.00
		10	349.20	1178.18	2595.56	200.27	0.50	1.50	0.00	1.36
		11	333.35	1178.18	2595.56	200.27	0.99	2.00	0.24	1.36
		12	333.35	1178.18	2595.56	200.27	0.99	2.00	0.50	1.36
		13	333.35	1178.18	2595.56	200.27	0.99	2.00	0.50	1.50
		14	333.35	1178.18	2595.56	200.27	0.99	2.00	0.50	1.50
		15	333.35	1178.18	2595.56	200.27	0.99	2.00	0.99	2.00
		16	322.30	1178.18	2595.56	200.27	1.06	2.25	0.99	2.00
		17	322.30	1178.18	2595.56	200.27	1.06	2.25	0.99	2.00
		18	322.30	1178.18	2595.56	200.27	1.06	2.30	0.99	2.00
		19	322.30	1178.18	2595.56	200.27	1.06	2.30	0.99	2.00
		20	322.30	1178.18	2595.56	200.27	1.06	2.30	1.06	2.25
		21	322.30	1178.18	2595.56	200.27	1.06	2.30	1.06	2.25
		22	322.30	1178.18	2595.56	200.27	1.06	2.30	1.06	2.30
		23	322.30	1178.18	2595.56	200.27	1.06	2.30	1.06	2.30
		24	322.30	1178.18	2595.56	200.27	1.06	2.30	1.06	2.30
		25	322.30	1178.18	2595.56	200.27	1.06	2.30	1.06	2.30

SUPPLEMENTARY TABLE 13: Harvestable timber volume equations for evergreen, mixed and deciduous forests.

Timber volume equations, that estimate harvestable volume rather than tree volume, were obtained from the Forestry Administration of the Royal Government of Cambodia (FA 2004b). For each tree, timber volume was calculated from diameter at breast height (*DBH*, in m) using the equation appropriate to size class, tree type (dipterocarp or non-dipterocarp; unknown species assumed to be non-dipterocarp) and forest type. The deciduous forest equation was used for all open forest plots; for dense forest plots the evergreen equation was used as it gave consistently lower volume estimates than mixed forest equations, thereby making estimated timber volumes conservative. Although additional equations were available that incorporate tree height (*H*, in m), forest inventories did not provide height estimates and region-specific form factors (required to estimate height from DBH data (Feldpausch *et al.* 2011)) were not available for Cambodia; therefore, DBH-only equations were used. Tree volumes (m^3) were summed per plot and per royalty class and standardised to m^3 ha^{-1}. Final harvestable timber volume was reduced by 20% to account for wastage (Putz *et al.* 2008).

Forest type	Tree type	DBH	Equation
Evergreen	Dipterocarp	<15cm	Volume (m^3) = 0.022 + 3.4 * DBH^2
	Dipterocarp	≥15 cm	Volume (m^3) = -0.0971 + 9.503 * DBH^2
	Non-Dipterocarp	<30 cm	Volume (m^3) = 0.03 + 2.8 * DBH^2
	Non-Dipterocarp	≥30 cm	Volume (m^3) = -0.331 + 6.694 * DBH^2
Mixed	Dipterocarp	<15cm	Volume (m^3) = 0.03 + 4.8 * DBH^2
	Dipterocarp	≥15 cm	Volume (m^3) = 0.00126 + 6.167 * DBH^2
	Non-Dipterocarp	<15 cm	Volume (m^3) = 0.0083 + 4.3 * DBH^2
	Non-Dipterocarp	15-30 cm	Volume (m^3) = 0.0083 + 5.3 * DBH^2
	Non-Dipterocarp	≥30 cm	Volume (m^3) = 0.0083 + 6.081 * DBH^2
Deciduous	Dipterocarp	<15cm	Volume (m^3) = 0.00849 + 4.097 * DBH^2
	Dipterocarp	≥15 cm	Volume (m^3) = -0.051 + 5.864 * DBH^2
	Non-Dipterocarp	<15 cm	Volume (m^3) = 0.03 + 3.3 * DBH^2
	Non-Dipterocarp	15-30 cm	Volume (m^3) = 0.03 + 3.55 * DBH^2
	Non-Dipterocarp	≥30 cm	Volume (m^3) = -0.413 + 7.819 * DBH^2

SUPPLEMENTARY TABLE 14: Timber species named in roadside/village price estimates

Royalty Class	Species
I	*Lagerstroemia* sp
	Hopea odorata
	Sindora siamensis
	Xylia dolabriformis
	Tarrietia javanica
II	*Anisoptera* sp
	Dipterocarpus sp
	Dipterocarpus alatus
	Dipterocarpus tuberculatus
	Dipterocarpus obtusifolius
III	Unknown*
Luxury	*Afzelia cochinchinensis*
	Dalbergia oliveri/bariensis#
	Pterocarpus pedatus
	Dalbergia cochinchinensis/D. bariensis#
NC	Unknown¥

¥ one price given for fuelwood, applied to all NC timbers (Hansen and Neth 2006)

\# *Dalbergia bariensis* is a synonym of *D. oliveri* but is commonly referred to as *D. bariensis* in Cambodia (Hartvig *et al.* 2015); *D. cochinchinesis* is listed on CITES Appendix I

* one price given for all class III timbers, at forest price point (Grimm *et al.* 2007)

These prices were applied to all species in the same royalty class as the named species i.e. all Class I species were given the same price, based on price estimates for *Lagerstroemia sp*, *Hopea odorata*, *Sindora siamensis*, *Xylia dolabriformis* and *Tarrietia javanica.*

SUPPLEMENTARY TABLE 15: Timber extraction cost estimates

Extraction cost USD m^{-3} processed wood	Notes	Reference
116.01	Cost of cutting wood in forest and ox-cart transport to village. Labour, food, fuel, chainsaw oil, 2-stroke oil, chain, chainsaw maintenance, excludes capital cost of chainsaw ($350 dollars, last 10 years), ox cart to village.	(Blackett 2008)
75.77	Cost of cutting wood in forest and ox-cart transport to village. Hired labour to cut tree, chainsaw fuel, ox cart to village.	(Grimm et al. 2007)
82.36	Cost of partial cut and transport (to village).	(Hansen and Neth 2006)

The minimum and maximum timber extraction costs from this table were used as input parameters for simulating timber costs. These costings assume selective logging activity by local people in Cambodia in a 'business-as-usual' scenario with no formal logging concessions, inventories, management plan, or demarcation of logging areas. Costs include: wage labour, food, motorbike fuel, ox-cart transportation to the roadside/village and chainsaw maintenance but exclude the capital cost of the chainsaw (around US$350; Blackett 2008). Costs in table are inflated to US$2013 using a CPI specific to Cambodia.

SUPPLEMENTARY TABLE 16: Dipterocarpus spp. resin revenue estimation parameters

Parameter	Notes	Reference
Resin yield per tree per year	23 – 40 litres yr^{-1} reported as maximum and minimum yields, across all three studies, across tree species	(Evans et al. 2003, Tola and McKenney 2003, Orwa et al. 2009)
Tree sizes tapped for resin	Trees 40 – 50 cm DBH and upwards are preferred, but trees as small as 30 cm DBH can be tapped	(Evans et al. 2003)
Non yielding trees (non-starter or exhausted)	Of 2,555 trees surveyed, 62 (2.4%) were non-starters and 146 (5.7%) were exhausted; thus only 208 (8.1%) were non-yielding	(Evans et al. 2003)
Resin price	Price in US$ litre^{-1}; mean of estimates (adjusted to 2013 US$) from 2003 – 2014 was $0.37 per litre	(Evans et al. 2003, Tola and McKenney 2003, Tola 2009) and WCS, unpublished data.

SUPPLEMENTARY METHODS: Modelling opportunity costs and carbon breakeven prices

Cash crop expansion

Cassava (163% area increase 2009 – 2013, to 421,000 ha; MAFF 2015), sugarcane (76% area increase 2009 – 2013, to 23,810 ha; MAFF 2015) and cashew (16,000 ha in 2000, 60,000 ha in 2005, no recent data available; EIC 2007) are also rapidly expanding cash crops. In Cambodia, cash-crops may be grown by smallholders (typically cassava, cashew and some rubber in farms of approximately 1-50 ha in size) or by concessionaires in large agro-industrial plantations (typically rubber or sugar).

Resin collection and other non-timber forest products

Dipterocarp resin collection is a traditional livelihood activity that generates important cash income, which directly conflicts with logging, as resin-producing species have valuable timber (Evans et al. 2003, Hansen and Neth 2006, Theilade and Schmidt 2011). Other local benefits derived from forests, including fuelwood and bushmeat (De Lopez 2003, Hansen and Neth 2006, Jiao et al. 2015), could not be estimated on a per hectare basis, as they depend on household density, extraction rates and the cost of substitute resources in local markets. However, non-market environmental income can contribute 32 – 35% of household income, of which 70% comes from forest products, excluding resin revenues (Jiao et al. 2015). As resin collection contributes only a portion of forest product income (Hansen and Neth 2006), a substantial proportion of the value of standing forests to local people is not captured in our analysis.

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Chapter 4

High-yielding rubber agroforests in Thailand provide modest benefits for biodiversity

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4.1 Abstract

Demand for natural rubber is continuing to grow, and rubber cultivation is expanding at the expense of diverse agricultural systems and natural forest. Forest conversion to monocultural rubber has a devastating effect on forest biodiversity, and complex "jungle" rubber agroforests that retain some forest biodiversity are being intensified into monocultures. In Thailand, the world's biggest rubber producer, some rubber monocultures have been inter-planted with additional species to form high-yielding agroforests, to improve farmer livelihoods in the face of market uncertainty. This study assesses the biodiversity value of these rubber agroforests relative to monocultures by surveying birds, reptiles and butterflies in 64 smallholder plots, in a nested design to capture variation in surrounding land use, and compares yield data between agroforests and monocultures. Bird richness and composition were influenced by height of the herb layer, and composition was also influenced by both non-rubber tree stem density within plots, and the amount of natural forest in the landscape. Reptile composition responded to canopy cover and the amount of open habitat in the landscape. Butterfly richness was greater in agroforests, within which richness and composition were influenced by the amount of natural forest in the landscape. Yields did not differ between the two systems. Although rubber agroforestry appears to provide some biodiversity benefits without compromising yields, potentially generating ecosystem service and livelihood benefits, conservation of contiguous natural forest areas remains of primary importance for biodiversity conservation. Biodiversity losses sustained by continued encroachment of rubber onto protected forests in Thailand and elsewhere in mainland Southeast Asia will not be mitigated by rubber agroforestry.

4.2 Introduction

Monocultural rubber plantations are expanding onto forested land in mainland Southeast Asia (also known as the Indo-Burma biodiversity hotspot) causing biodiversity loss, carbon emissions, and other environmental damage (Warren-Thomas *et al.* 2015). Conversion of highly biodiverse forest to *Hevea brasiliensis* rubber has been particularly rapid since the turn of the century, affecting even protected forests in Southwest China, Cambodia and Vietnam (Yi, Wong, *et al.* 2014, Warren-Thomas *et al.* 2015). Recent expansion of both smallholdings and agro-industrial estates has been of monocultural plantations, comprising high-yielding clonal varieties planted at densities of 400 – 550 stems ha^{-1}, managed intensively with little understorey (Phommexay *et al.* 2011, Priyadarshan 2011, Shigematsu *et al.* 2013, Yi, Cannon, *et al.* 2014). Yields range from 0.92 to 1.45 t ha^{-1} yr^{-1} (averaged over a complete ~25-year plantation cycle; Warren-Thomas *et al.* 2015). Elsewhere, particularly in Indonesia, much lower yields of only 0.4 to 0.6 t ha^{-1} yr^{-1} are achieved in complex "jungle" rubber agroforests, where biodiversity and ecosystem functioning values are high (Villamor *et al.* 2014, Drescher *et al.* 2016, Langston *et al.* 2017).

Meeting future global demand for natural rubber is likely to entail expansion of rubber area and intensification of low-yielding agroforests (Warren-Thomas *et al.* 2015). Both processes risk the loss of biodiversity and ecosystem services (Foley *et al.* 2005). Non-linear trade-offs between biodiversity/ecosystem functioning and land-use intensification and economic functions are well documented; a key challenge for sustainability is thus to find an optimal strategy, where intensification improves economic value, but severe declines in biodiversity are avoided (Clough *et al.* 2016, Teuscher *et al.* 2016). In Thailand, the world's largest rubber producer, there have been initiatives to integrate additional crops, such as fruit and timber trees, into high-yielding rubber monocultures; these agroforests provide additional profit and an economic buffer for smallholder farmers, who produce 95% of Thai rubber, when prices fall (Simien and Penot 2011). This study asks whether these rubber agroforestry systems can maintain high yields and contribute to meeting global rubber demand, while providing biodiversity co-benefits.

Although multiple studies report substantial declines in biodiversity following forest conversion to monocultural rubber (Danielsen and Heegaard 1995, Aratrakorn *et al.* 2006, Peh *et al.* 2006, Phommexay *et al.* 2011, Meng *et al.* 2012, Li *et al.* 2013), structurally diverse "jungle" rubber agroforests can harbour many species, including forest-dependent birds (Beukema *et al.* 2007), and in parts of Indonesia provide the last remaining forest-like habitats. Similarly, most lowland forest in southern Thailand, the heartland of rubber production, has already been converted to rubber monocultures. In such contexts where restoration of forest is unlikely, a land-sharing approach to rubber cultivation, where biodiversity is maintained or actively restored within a rubber-dominated landscape, such as through agroforestry, might be the only way to conserve biodiversity. However, if this entails a yield cost, additional forest may need to be cleared in other landscapes to meet demand, and reduced profits may harm farmer livelihoods. If it does not entail a yield cost, then such an approach could not only be used to improve the biodiversity value of existing plantations, but could also be used when planning areas of rubber expansion, even at large scales.

Research assessing the biodiversity value of rubber agroforestry, or measures to improve the biodiversity value of rubber monocultures is scarce. In Sumatra, Indonesia, bird species richness and the number of bird forest specialist species and species of conservation concern in "jungle" rubber agroforests was greater than in monocultural rubber, but less than in primary forest (Beukema *et al.* 2007, Prabowo *et al.* 2016), while species composition lay somewhere between forest and rubber monoculture (Prabowo *et al.* 2016). Both species richness and ecosystem functioning of leaf litter macroinvertebrates was similar in "jungle" rubber and monocultural rubber in Sumatra, although different to that of forest or oil palm (Barnes *et al.* 2014). In Brazil, where *Hevea brasiliensis* is a native species, rubber plantations containing 10 – 20 year old understorey vegetation supported a richer butterfly community that was more similar to forest fragments than to intensively managed plantations (Barbosa Cambui *et al.* 2017). Work in rubber monocultures in Southwest China showed that bird species found in rubber had wider habitat breadths than those in forest, and that the area of forest cover in the landscape was the most important factor influencing bird species richness and composition (Sreekar *et al.* 2016), while in Thailand, monocultures with a vegetated understorey had greater bird species richness than those without, but only retained species with a large relative range size, with the loss of most forest-dependent species (Aratrakorn *et al.* 2006).

The intensification and modernisation of rubber plantations in Thailand has been strongly incentivised via the Office of Rubber Replanting Aid Fund (ORRAF), and more than 85% of smallholder rubber is grown in monocultures using modern clonal planting material under specific technical guidance on planting density and chemical application; around 15% is grown using agroforestry methods, either in "jungle" type systems (<10%, but declining in popularity), or in "intensive" agroforestry systems (~5%) that combine modern clonal rubber cultivation methods with additional crops (Simien and Penot 2011). Government incentives are now encouraging more rubber farmers to plant fruit trees or oil palm (Delarue 2012), and a formal policy promoting rubber agroforestry was approved in 2014 (Stroesser 2016).

This study aimed to compare the biodiversity value of high-yielding "intensive" agroforestry systems to monocultural systems in Thailand, while also asking whether agroforestry caused a rubber yield penalty. Biodiversity responds to land use at multiple spatial scales, and is influenced by variables at both the farm and landscape levels (Perfecto *et al.* 2003, Tscharntke *et al.* 2005). We therefore conducted a field study that collected biodiversity and habitat structure data within individual agroforestry and monocultural rubber plots (smallholder farms), grouped within blocks for which land-use composition data were collected. We surveyed three taxonomic groups (birds, reptiles and fruit-feeding butterflies) and investigated the response of each group to: 1) plot type (agroforestry or monoculture), 2) habitat structural variables within each plot, and 3) land-use composition of blocks.

4.3 Methods

4.3.1 Study region

The study was conducted in southern Thailand, in Songkhla and Phattalung provinces (Supplementary Figure 1), where lowland landscapes are dominated by smallholder rubber plantations (even-aged management units, ranging from <1 ha to several ha in size). Biodiversity data were collected across both provinces, and data on rubber yields were collected from sites in Phattalung; both monocultural and agroforest plots were available in both provinces. Rubber trees are typically planted at 3 m intervals in rows 7 m apart (stem density = 476 stem ha^{-1}; Phommexay *et al.* 2011), and overall planting density of rubber trees did not differ between agroforest and monoculture (Supplementary Figure 2c and d). Agroforest plots (Figure 1b) were characterised by the systematic planting of additional commercially valuable, tree, shrub or herbaceous species, or naturally regenerated wild non-rubber trees throughout the plot. Non-rubber species were either interspersed between rubber trees within the row, or more usually in the inter-row, allowing easy access for rubber tapping. Agroforests ranged from simple systems containing one or two additional commercial plant species (Figure 1b), to complex jungle rubber systems containing multiple native tree species (Figure 1d).

Smaller areas of oil palm, fruit orchards, rice paddy, and forest fragments were also present in the landscapes. The largest forest fragments were ~320 ha of karst hilltop forest in Phattalung province and 400 ha of fragmented secondary community forest in Songkhla province; other forest patches were much smaller (~4 ha) and usually comprised heavily degraded forest and scrub. Three substantial protected forest areas in the region cover mostly upland areas (from 100 m to 1,350 m asl): Khao Ban Thad Wildlife Sanctuary (126,696 ha, partly in Phattalung, also an IBA; Birdlife International 2015), Ton Nga-Chang Wildlife Sanctuary (18,195 ha; partly in Songkhla province; Phommexay *et al.* 2011) and Khao Nam Kang National Park (212,000ha, Songkhla province; DNP 2017; map Supplementary Figure 1). Rain is usually frequent from May to December, while January to March is considered the dry season (Phommexay *et al.* 2011). Biodiversity data were collected during March - June 2016, during unusually low rainfall and high temperatures (Supplementary Figure 3) during an El Niño-Southern Oscillation event (Limsakul and Singhruck 2016).

4.3.2 Sampling sites

Environmental and biodiversity data were collected from rubber plantations in both provinces, hereafter the “biodiversity dataset” (map: Supplementary Figure 1). Sixty-four “plots” were sampled, defined as a management unit containing rubber trees of a uniform age with minimum area ≥1 ha, at least 100 m x 100 m in dimensions. Plots were categorised as either monoculture (MO; n = 25) or agroforest (AF; n = 39). Three plots classed as MO contained two or fewer non-rubber species that were patchily distributed at densities too low to be considered agroforestry; these included pineapple *Ananas comosus* plants in a small portion of the plot, a single fruit tree or scattered timber or palm stems. Mean latitude of plots in the biodiversity dataset was 7.024661°N (SD 0.281925°) and mean elevation was 82.6 m asl (range 35.0 - 137.1 m asl).

To simplify the collection of landscape composition data, plots were clustered into 23 sampling "blocks" of 600 m x 600 m, with central points of plots at least 200 m but not more than 400 m apart (Figure 2). Each block contained two or three plots, and we attempted to represent examples of both AF and MO in each block (all blocks contained AF plots, five lacked MO plots), depending on the availability of suitable plots in each area. The area and dimensions of each plot were measured by walking the boundary on foot while holding a GPS, with dimensions confirmed using a laser rangefinder. Blocks were further clustered within five "districts" (not corresponding to formal administrative districts), with individual plots <9 km apart within a district, but with districts up to 127 km apart across the entire sampling area (Supplementary Figure 1). District influenced the species richness of butterflies, but not birds or reptiles (tested using a generalised linear model with Poisson distribution and log link function), and was thus used as a random effect in species richness modelling of butterflies (Supplementary Figure 4).

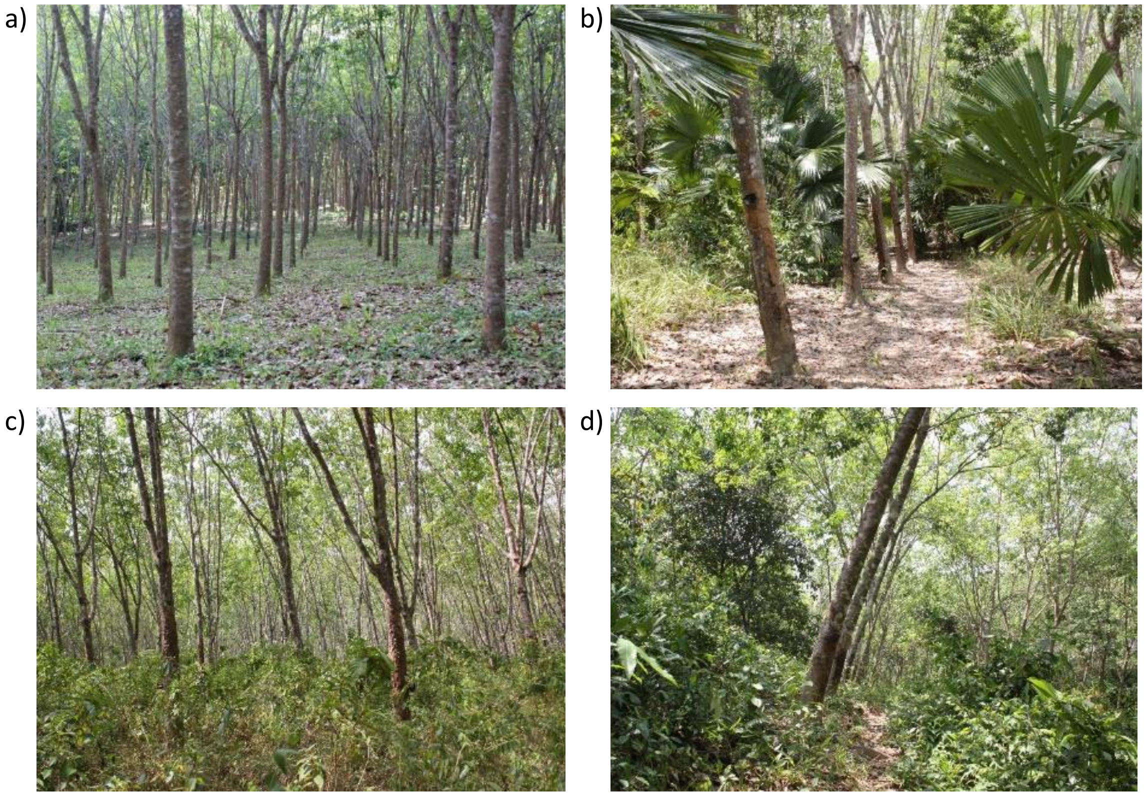

FIGURE 1 – SMALLHOLDER RUBBER FARMS IN SOUTHERN THAILAND. Panels show monoculture (a,c) and agroforest (b,d) rubber showing minimal understorey vegetation (a,b) or well developed understorey vegetation (c,d)

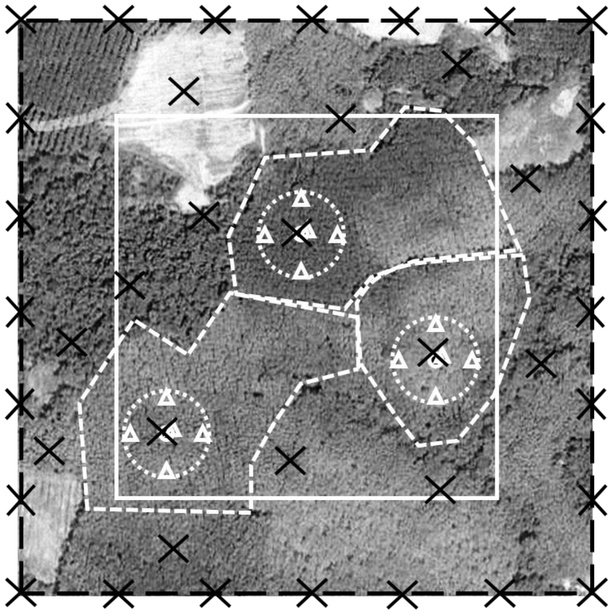

FIGURE 2 – SURVEY PLOT AND BLOCK DESIGN. Black crosses = GPS points recording land use; white circles = bird point count 50 m sampling radius; white triangles = butterfly traps and herpetofauna survey boundary; dashed white line = perimeter of plot, minimum 100 m x 100 m (1ha); solid white line shows boundary of the 400 m x 400 m square containing plot centroids; long black dashed line shows perimeter of 100 m buffer around the 400 m square, forming the 600 m x 600 m (36 ha) sampling block.

4.3.3 Biodiversity data collection

Biodiversity data were collected from two or three blocks (i.e. up to nine plots, comprising both AF and MO) each day, to control for potential weather and seasonal effects.

4.3.3.1 Bird surveys

Ten-minute point counts were conducted in the centre of each survey plot on three consecutive mornings, between 0600 and 0930, alternating the order in which points were visited each day (following (Gilroy, Woodcock, *et al.* 2014)). Fifteen-minute point counts were trialled during two weeks of pilot surveys, but were found to add no additional registrations. Birds were identified to species using sight or sound, and abundances were recorded within distance bands (A: 0 – 10m, B: 10 – 25m, C: 25 – 50m, D: 50 – 100m), along with detection method (visual, aural). Flyovers of raptors, swifts and swallows were also recorded. Digital sound recordings were made of each point count, using an Olympus LS-11 Linear Recorder. All counts were conducted by the same observer who was already familiar with bird sounds from the region. Unknown sounds were noted during the point count and were later checked against region-specific bird sound recordings (Xeno-canto Foundation 2017).

Bird species habitat associations, classified as forest interior or open habitat, were extracted from HBW Alive (del Hoyo *et al.* 2017) and conservation status was obtained from the IUCN Red List (IUCN 2016). Statistical analyses at the plot level included registrations within a 50 m radius of the point count, and included both resident and non-breeding migratory species.

4.3.3.2 Reptile surveys

Reptile Visual Encounter Surveys were conducted on four consecutive afternoons (1300 – 1800) in each plot (Crump and Scott 1994). The order of surveys was rotated, such that each plot was surveyed at least once at the beginning, middle and end of the afternoon. A 200m long "S" shaped path in the core of the survey plot, bounded by the butterfly traps (see below) was walked at a steady pace, taking 20 minutes to complete, searching 5 m either size of the path. All microhabitats were surveyed, including disturbing leaf litter, and overturning dead wood if found. All individuals were identified in the field, and no voucher specimens were taken. For each species, habitat association with forest or open habitats and conservation status was obtained (Chan-ard *et al.* 2015, IUCN 2016).

4.3.3.3 Butterfly surveys

Fruit-feeding butterflies (Nymphalidae) were sampled using non-lethal Van Someron-Rydon traps (Rydon 1964), 90 cm in height and 30 cm in circumference, constructed based on trap design #1 from (Austin and Riley 1995), utilising lampshade rings as the metal hoops. Traps were baited with approximately two tablespoons of fermented banana mixture (approximately 750 ml of ripe mashed bananas mixed with 1 teaspoon of quick action yeast, two tablespoons of sugar and 1 tablespoon of rum, left to ferment for 48 hours). Five traps were set in each plot, one at the centre and four 50 m away in cardinal directions. Traps were set on the first day and checked on each of four subsequent afternoons (1300 – 1800), replacing bait at each check and discarding old bait away from the sampling site. Without loss or damage of traps, this gave 20 trap-days per plot, but bait lost due to wind or rain (none was lost to animals), trap damage, or removal by people was noted, and the number of trap-days per plot recorded for inclusion in further analysis.

Trapped butterflies were removed, photographed (using a Canon 700D D-SLR and 105mm prime macro lens), and marked via removal of a small patch of wing scales in a unique location for each day of sampling. All individuals were released, and individuals re-trapped on subsequent sampling days were omitted from further analysis. Individuals were identified to subspecies following (Corbet and Pendlebury. 1992, Ek-Amnuay 2012) and reference collections at Prince of Songkhla University. *Mycalesis* males were identified to species level by O.B. based on unpublished taxonomic work, but identification of *Mycalesis* females requires dissection; females were therefore omitted from analysis. Of 49 plots containing *Mycalesis*, only four contained a female but no males (three AF, one MO). Conservation status was obtained for each species (IUCN 2016).

To examine whether subsequent analyses needed to control for weather effects and/or trap loss or disturbance, the effects of rainfall (ordinal, 0 – 4 recording the number of days with rainfall during sampling) and sampling trap-days (range 12 – 20, mean = 18.6 ± SD 2.2 trap days) on butterfly species richness were examined, using a generalised linear model using a Poisson distribution and log link function. Rainfall influenced species richness across all plots (Supplementary Figure 5) but the number of sampling trap-days did not (Supplementary Figure 6).

4.3.4 Land use composition per block

To provide a measure of the land-use composition of each block, land use was recorded systematically at 100 m intervals along the block perimeter, once within each sample plot and once in the management units adjacent to each sampled plot in each of four cardinal directions, giving 39 land-use data points per block; Figure 1). Where plots were adjacent (as in Figure 1), land use of the next-closest management units within the block was recorded, and where only two sample plots occurred within a block, land use was recorded in one additional management unit and its neighbours, thus 39 points were recorded for every block. Land use was recorded as one of 14 categories: rubber agroforestry (AF), monocultural rubber (MO), immature rubber (IM), bare ground (BG), scrub (SC), village, road or town (UB), natural forest (NF), fruit orchard (FO), home garden (HG), cassava (CA), oil palm (OP), rice paddy (PA), timber plantation (TI) or coconut grove (CO). Streams or rivers were also recorded with GPS points, and the total length of riparian features calculated per block using Google Earth.

The land-use points and riparian features were summarised into six explanatory variables for further analysis: the percentage of points that were rubber plantations (total of AF and MO), open habitats (total of IM, BG, CA or PA; used only in species composition analyses) and natural forest (NF); the ratio of AF to MO; the Shannon-Weiner diversity index of land uses (using point-frequency data); and riparian length.

4.3.5 Plot-level habitat structure data collection

4.3.5.1 Data collected from farmers

For each agroforestry plot sampled for biodiversity, the number of agroforestry species and names of timber, fruit species and leaf species (species where edible leaves are harvested, or where leaves are collected for non-consumptive uses e.g. roofing) were recorded by questioning the farmer. Application of herbicide and manual clearance of the understorey was observed in some MO plots during the survey period, and development and removal of the herb layer may be cyclical or episodic in both AF and MO plots. Farmers typically reported that herbicides and pesticides were not used in

AF plots. We could not validate this, but sacks of chemical fertiliser, applied to promote tree growth, were seen in some MO and AF plots. Grazing animals were occasionally observed moving through plots, but did not necessarily belong to the plot owner.

4.3.5.2 Data collected from field measurements

Habitat structure was measured in each biodiversity plot. Stem density and DBH of all tree stems ≥5 cm DBH (categorised as rubber, fruit, timber, palm or non-commercial naturally regenerated trees) was measured in two 10 m radius subplots located 50 m apart, following Barlow *et al* (2007), and pooled per plot for analysis. Understory complexity was quantified using two methods. First, the number of stems ≥1 m in height but ≤ 5cm DBH were counted within two 5 m radius subplots, with the mean small stem density (ha^{-1}) per plot calculated from pooled subplots. Second, an index of understorey density (0 – 25) recorded from the centre of each subplot as the number of 25 x 10 cm sections visible on a 2.5 m pole placed 15 m away in each of four directions (Barlow *et al.* 2007). Understorey density was measured twice along the rubber inter-row (usually kept clear for easy access by rubber tappers) and twice across rubber inter-rows at each tree subplot, and a mean value for the plot taken across all eight points. Small stem density and understorey density were moderately correlated (Pearson correlation = 0.58; Supplementary Figure 7) so only small stem density was included in models of biodiversity response. Percentage canopy cover was measured using a spherical densiometer (counting canopy gaps) at each of four cardinal points 15 m from the centre of each tree subplot, taking the mean of eight measures per plot. One observer conducted all canopy cover observations in all plots. For herbaceous vegetation, the maximum height (to 10 cm resolution) and percentage cover (estimated visually, always by the same observer) were recorded from each of four 1 m x 1 m quadrats at cardinal points around each tree subplot taking the mean (of eight measures) per plot. Herbaceous height and cover were strongly correlated (Pearson correlation = 0.68), so only herb height was included in models of biodiversity response.

All measured variables were used to compare the habitat structure of AF and MO plots and to characterise the differences between the plot type using general linear models, but variables were then further simplified for inclusion in additional analysis (Supplementary Figure 7 and accompanying text). Final habitat variables included in models of biodiversity response were: herb height (cm), canopy cover (%), small stem density (stems ha^{-1}), non-rubber tree stem density (includes timber trees, fruit trees, native trees and palms ≥5cm DBH; stems ha^{-1}), fruit tree stem density (stems ha^{-1}), and the number of agroforestry species (fruit and timber trees, and palms).

4.3.6 Rubber yield data collection

Data on rubber yields (hereafter the “yield dataset”) were collected from a separate set of agroforestry (AF, n = 47) and monoculture (MO, n = 37) rubber plots in Phattalung province. Mean latitude of sites in the yield dataset was 7.473321°N (SD 0.199305°), and mean elevation was 98.2 m asl (range 42.0 – 164.0 m asl).

Data were collected in 2016 via questionnaires conducted with farmers as part of the Heveadapt project (Stroesser 2016). Farmers were initially contacted via agroforestry networks, and focus groups were used to identify a sample of farmers that captured the full range of diversity in agroforestry methods (e.g. species planted, plot size). Two visits were made to each participating rubber farm; a first visit to complete the entire questionnaire, and a second to fill any gaps. The questionnaire collected quantitative data about the rubber farming systems, alongside other qualitative data not used in this study, and was designed for use with the Olympe decision support software (CIRAD, INRA, IRD 2007). Questionnaire topics included: agroforestry species composition and planting density; yields of rubber and agroforestry crops; investment and overhead costs; livestock; labour; farm gate prices; selling channels; income sources; farm history; and decision making processes. A general linear model was used to compare the rubber yields of AF and MO plots within the yield dataset.

Yield data were obtained from within only one province, and from a different set of rubber plots than examined in the biodiversity data set. Therefore, to ensure conclusions for the relative yield of AF and MO observed in the yield dataset sample would similarly apply to the biodiversity dataset, we compared the number of agroforestry plant species (reported by farmers in both the yield and biodiversity plots), and the stem density of timber, fruit, and rubber trees in AF plots (reported by farmers for yield plots, measured in the field for biodiversity plots) between the two datasets. All measures were similar between the biodiversity and yield datasets (general linear models and Mann-Whitney U tests; Supplementary Figures 8-9) indicating that biodiversity responses were obtained from a similar structural and compositional range of AF plots as the yield data.

4.3.7 Statistical analysis

4.3.7.1 Species richness

Sampling completeness of each taxon within each plot type (AF or MO) was calculated as the percentage of estimated species richness relative to the observed species richness based on four estimators (Jack1, Jack2, Bootstrap, and Mmean), calculated using EstimateS v9.1.0 (Colwell 2013). This was compared between plot types using Mann-Whitney U tests, with the four estimators analysed individually. For each taxon, cumulative species richness was also compared between AF and MO using sample-based rarefaction extrapolated to the largest sample size (n = 39 for AF) using the iNEXT package for R (Colwell *et al.* 2012, Chao and Colwell 2014).

For each taxon, the response of plot-level species richness to plot type, habitat structure and land-use composition was investigated using a multi-level approach. First, response to plot type (AF or MO) was investigated using hypothesis testing. Second, response to habitat structure within plots was investigated using multi-model inference (Burham and Anderson 2002), omitting plot type that was confounded by structure. Finally, response to plot type, any influential habitat structure variables, and land-use composition of the sampling block, was investigated in multi-scale models using multi-model inference.

Generalised linear mixed models (GLMMs) fitted using maximum likelihood with a Poisson distribution and log link function were used in all cases, conducted using the glmer function in lme4 package (Bates *et al.* 2015). Block was included as an intercept-only random effect in all models to account for the nested sampling design. District and rainfall index were additionally included as intercept-only random effects for butterfly models, with block nested within district, and rainfall crossed with district/block. Spatial autocorrelation in model residuals was examined using a Monte-Carlo permutation test for Moran's I with the moran.mc function in package spdep with 1000 iterations (Bivand *et al.* 2013, Bivand and Piras 2015). Model residuals were tested for overdispersion, but theta (Pearson residuals/residual degrees of freedom) was less than one in all cases (Burham and Anderson 2002).

Species richness per plot was compared between AF and MO using a GLMM, assessing support for a plot type effect by the change in Akaike Information Criterion (corrected for small sample size, AICc) relative to a null model containing only the random effects (Burnham and Anderson 2002).

Plot-level species richness response to habitat structure was investigated using multi-model inference. A global GLMM was constructed containing six variables (herb height, canopy cover, small stem density, number of agroforestry species, non-rubber tree stem density and fruit tree stem density) and a null (intercept-only) model was generated that contained only the random effects. All habitat structure variables were centred and standardised (to zero mean and 0.5 SD) so that effect sizes were on comparable scales (Grueber *et al.* 2011). The global model for each taxon was validated by checking for heteroscedasticity and normality of residuals, and residuals were checked for spatial autocorrelation using Moran's I statistic. A candidate model set, of all possible model subsets comprising four or fewer variables (ensuring at least 15 observations for each candidate variable (with n = 64 plot observations for birds, 63 for reptiles and butterflies) was generated using the dredge function in the MuMIn package (Grueber *et al.* 2011, Bartoń 2016), resulting in 57 models including the null and the global. Candidate models were ranked according to AICc and AICc weights, using the ICtab function in the bbmle package (Bolker and R Development Core Team 2017); those with a cumulative weight of 95% were averaged, using the full (zero) averaging method (Burnham and Anderson 2002, Grueber *et al.* 2011) using the model.avg function in the MuMIn package (Bartoń 2016). Candidate variables were considered to have an influence on species richness where the 95% confidence intervals of the averaged parameter estimate did not include zero (Grueber *et al.* 2011).

For each taxon, the same multi-model inference procedures were then used to investigate multi-scale models that related plot-level species richness response to plot type, plot-scale habitat structure, and block-scale land-use composition. In addition to any habitat variables found to be influential during the previous stage of analysis, the global GLMM contained five land-use variables (land-use Shannon diversity, percentage rubber points, percentage natural forest points, AF:MO ratio and length of streams/rivers), plot type, and two interaction terms (plot type and AF:MO ratio; plot type and percentage natural forest points). Block was included as a random effect.

To estimate effect sizes, investigate interactions and visualise species richness response to influential variables, species richness was predicted from the final averaged models using the predict function in the MuMIn package, holding continuous explanatory variables aside from the variable of interest at the mean, and including mean levels of the random effects (Bartoń 2016). Predictions made using the standardised variables and log link function of the final model were back transformed, to visualise predictions relative to variables in their original units. Predictions were made at points (25%, 75% and maximum of the variable of interest) and for plotting, at intervals of 0.05 standardised units of the variable of interest. The SE of predictions from the averaged model were not calculated, as tools to calculate prediction intervals for GLMMs conducted using the lme4 package (Knowles and Frederick 2016) cannot be applied to averaged models.

4.3.7.2 Species composition

The response of species composition to plot type, habitat structural and landscape variables was investigated using Redundancy Analysis (RDA). RDA was conducted using abundance data for birds and reptiles (the maximum number of individuals recorded on any one sampling day; scaled by dividing by the variance of each species to decrease the influence of highly abundant species; (Oksanen *et al.* 2017)) and presence-absence data for butterflies, because species relative abundances in fruit bait traps was unlikely to reflect relative abundances in the study area (Hughes *et al.* 1998, Lucci Freitas *et al.* 2014).

A partial RDA was run first using block as a conditional effect, to test whether plot type influenced composition when any block level effect was partialled out. A global RDA model was then created which included plot type, all habitat and all land-use variables (additionally including the percentage of open habitat points, as this was likely to influence species composition), using function rda in the vegan package (Oksanen *et al.* 2017). Block could not be used as a conditional effect when land-use variables were included in the model, because all variance explained by land use was partialled out with block. Spatial autocorrelation of the global model was examined using an adaptation of the Mantel test, which compared the mean inertia in each distance class to the pooled mean inertia of all other distance classes, using a grain size of 100 m to encompass the distances between closest neighbours (minimum distance between plot centroids was 200 m), and 9999 permutations, using the mso function in the vegan package (Wagner 2004, Oksanen *et al.* 2017). Automatic backward model selection was performed on the global model (with 9999 permutations) with a p-value threshold of 0.05 (using a "pseudo-F" test statistic, defined as the ratio of constrained and unconstrained total inertia in the RDA, each divided by their respective ranks) to drop terms from the model (Legendre *et al.* 2011, Oksanen *et al.* 2017). Significance of each term in the final model was then examined using the same method. RDA was run both with and without rare species (defined as total abundance, or sum of presences for butterflies, of less than three; Barlow *et al.* 2010); the main text figure shows the result excluding rare species. A partial RDA including Block as a conditional effect was also used to test the effect of plot type alone.

4.4 Results

4.4.1 Habitat structure of AF and MO

Agroforests were characterised by greater richness of fruit and timber tree species (Supplementary Table 1), smaller rubber basal area, greater density of timber, fruit and naturally regenerated trees and small stems, greater timber tree basal area, denser canopies, and greater understorey density than monoculture plots (Supplementary Figure 2). However, herb height was similar between AF and MO (Supplementary Figure 2). Management of understorey vegetation in both AF and MO varied among plots, ranging from bare earth (Figure 2a, 2b) to well-developed understorey vegetation in the inter-row spaces at the time of sampling (Figure 2c, 2d).

Common timber tree species in agroforestry plots included *Azadirachta indica, Dipterocarpus alatus* (IUCN EN), *Hopea odorata* (IUCN VU), and *Litsea grandis*. Another hardwood, eaglewood *Aquiliaria crassna* (IUCN CR) was cultivated for resin used in perfume. Common fruit tree species included beans *Archidendron* spp, jackfruit *Artocarpus heterophyllus*, durian *Durio* spp, mangosteen *Garcinia mangostana*, longkong *Lansium domesticum*, mango *Mangifera* spp, rambutan *Nephelium lappaceum*, stink bean *Parkia speciosa*, and gatorn *Sandoricum koetjape*. Common herbaceous fruit species were pineapple *Ananas comosus* and banana *Musa sapientum*. Palm species included *Areca catechu*, the fruits of which are used to make dye, the snake fruit palm *Salacca zalacca*, and species grown for leaf products including *Licuala paludosa* and *Livistona saribus* used for roofing and food preparation (Supplementary Table 1).

4.4.2 Rubber yields in AF vs MO

The yield dataset is considered representative of plots sampled in the biodiversity dataset, due to the similarity in rubber planting density (Supplementary Figure 8), agroforestry species richness, and stem densities of fruit and timber trees (Supplementary Figure 9). In addition, differences in elevation and latitude were minimal: mean latitude differed by 47.2 km (95% CI from Tukey's HSD test; 38.2 - 55.6 km), and mean elevation differed by only 14.1 m asl (4.3 - 24.0 m asl; Supplementary Figure 10). Rubber yields did not differ between AF and MO plots (Figure 3), as the null model was better than the model including plot type.

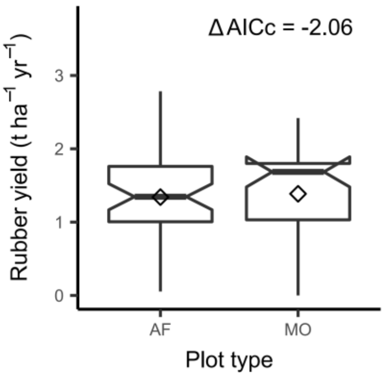

Figure 3 – Rubber yield of agroforest (AF) and monoculture (MO) plots in the yield dataset. Boxes bound 25% and 75% quartiles, lines show median, notches give approximate 95% confidence interval around median, diamonds show mean, whiskers extend to 1.5x the interquartile range, and outliers are shown as dots. ΔAICc is for a null model relative to a general linear model containing plot type; a negative AICc shows that null model had a lower AICc than the alternative model.

4.4.3 Species richness

In total, 1,204 registrations of 69 bird species, 544 individuals of 17 reptile species, and 809 individuals of 44 butterfly species (excluding females of *Mycalesis* species), were found across all plots. The mean plot-level abundances of each species are shown in Supplementary Table 2. Estimators of species richness showed that ≥74% of species were detected, and that sampling completeness did not differ between AF and MO for any taxon (Supplementary Figure 11).

4.4.3.1 Birds

AF and MO plots had similar cumulative richness of bird species across all plots (Figure 4a) and similar plot-level species richness (Figure 4d). Plot-level habitat models showed bird species richness was greater with taller herb height; herb height was therefore included in further land-use composition models (Figure 5a). There was no significant spatial autocorrelation in residuals of the global habitat structure model (Moran's *I* = -0.095, p = 0.876).

Candidate multi-scale models that contained land-use composition variables, herb height, and plot type, showed that herb height remained the only influential variable (Figure 5d). Predictions from the final averaged model showed that at the 25% quartile, 75% quartile and maximum of herb height (37 cm, 63 cm, and 98 cm respectively), mean plot-level species richness (weighted across AF and MO) was 11.8, 13.0 and 14.8 respectively (Figure 6a).

4.3.3.2 Reptiles

The cumulative species richness of reptiles did not differ between AF and MO (Figure 4b), and plot-level reptile species richness was neither influenced by plot type (Figure 4e), nor any habitat structural variables (Figure 5b). Therefore, no habitat structural variables were included in further multi-scale models. There was no significant spatial autocorrelation in model residuals (Moran's $I = 0.098$, $p = 0.061$). Averaging across candidate multi-scale land-use composition and plot type models also showed that no variables influenced reptile species richness (Figure 5e).

4.3.3.3 Butterflies

Both cumulative species richness of butterflies (Figure 4c) and plot-level richness (Figure 4f) were greater in AF than MO. Plot-level butterfly species richness was not influenced by any habitat structural variables (Figure 5c), and therefore no habitat structural variables were included in further multi-scale models. There was no significant spatial autocorrelation in the residuals of the global habitat structure model (Moran's $I = -0.056$, $p = 0.680$).

Averaging across multi-scale models containing land-use composition variables and plot type showed that, while both plot type and the percentage of natural forest points influenced species richness, the interaction between these was also influential (Figure 5f). Species richness increased with increasing percentage of natural forest points within AF plots, but natural forest extent showed no effect in MO plots (Figure 6b). Within AF plots, predicted butterfly species richness at the 25% quantile (0% natural forest), 75% quantile (7.8% natural forest), and maximum (51% natural forest) was 4.8, 5.4, and 11.2, respectively. In contrast, within MO plots, predicted butterfly species richness was 4.1, 4.1 and 4.0 respectively.

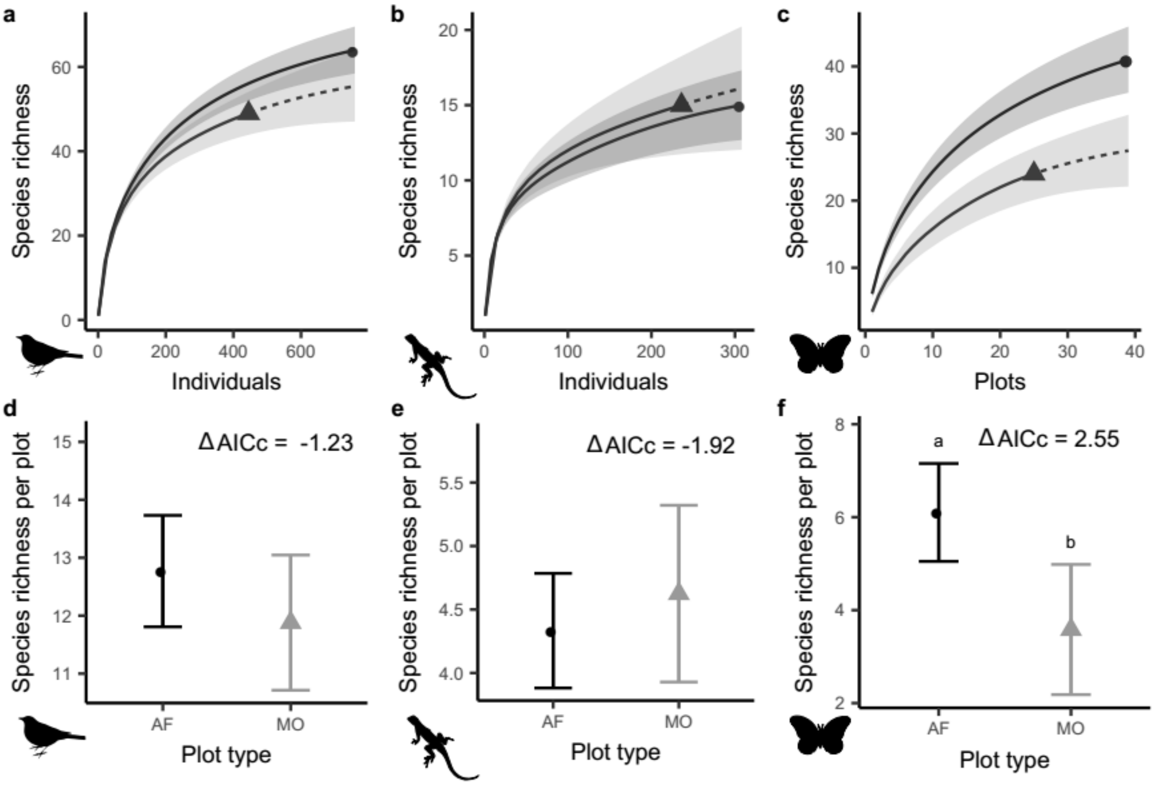

FIGURE 4 - SAMPLE-BASED RAREFACTION AND EXTRAPOLATION OF SPECIES RICHNESS, AND PLOT-LEVEL SPECIES RICHNESS, IN RUBBER AGROFOREST (AF) AND MONOCULTURE (MO). Panels show rarefaction and extrapolation across all plots (a-c) and mean and 95% CI of species richness per plot (d – f) in AF and MO. Abundance data were used for birds and reptiles, presence-absence data were used for butterflies (excluding females of *Mycalesis* spp). Circles are AF, triangles are MO. In panels a – c, dashed lines show extrapolation of MO sample (n = 25) to the same sample size as AF (n = 39), rescaled to the number of individuals for birds and reptiles, and grey shading shows 95% confidence interval. In panels d – f, symbol shows mean species richness per plot, and whiskers show 95% CI. ΔAICc is for a null model relative to a generalised linear model of response to plot type; letters indicate where plot type influences species richness. The null model had a lower AICc than the plot type model for birds and reptiles, giving a negative ΔAICc (d, e).

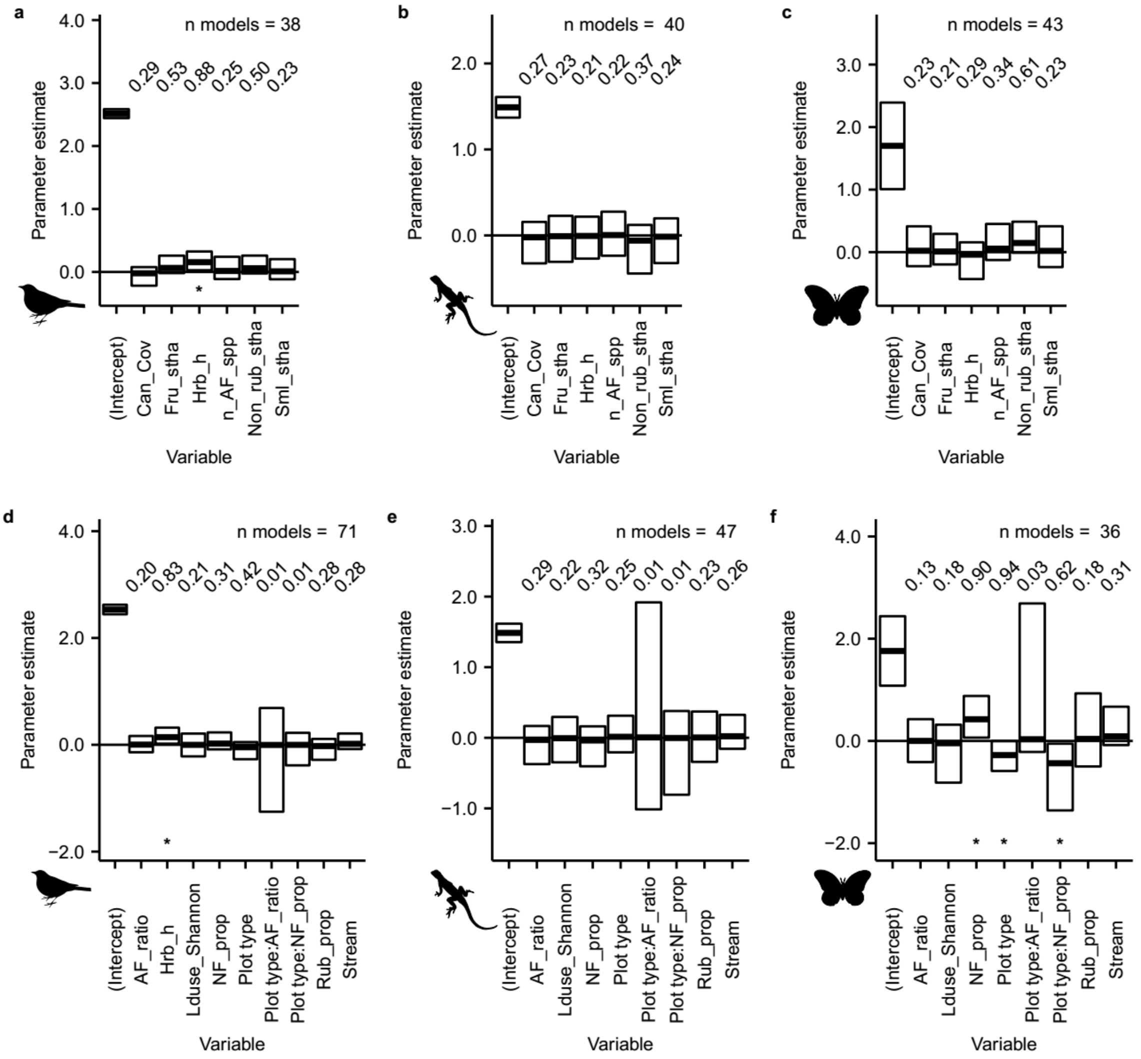

FIGURE 5 – PARAMETER ESTIMATES FOR THE AVERAGED MODEL OF SPECIES RICHNESS RESPONSE TO HABITAT STRUCTURAL VARIABLES AND TO MULTI-SCALE LAND-USE, PLOT TYPE AND HABITAT VARIABLES. Panels show species richness response to habitat variables for a) birds, b) reptiles and c) butterflies, and to plot type, land-use composition and any habitat structural variables found to be influential in the previous models for d) birds, e) reptiles and f) butterflies. In each case, full-model averaging was conducted across the 95% confidence set (sum of Akaike weights < 0.95) of all possible sub-models containing a maximum of four predictor variables. Number of models within the 95% confidence set is shown on each panel. Central line in each bar shows averaged parameter estimate (predicted change in species richness with a one-unit change of the standardised predictor variable), bar encloses lower and upper 95% CI of parameter estimate. Parameter estimates with 95% CIs that exclude zero are considered influential, and are marked with * below the bar. Relative variable importance (the proportion of models within the 95% confidence set that contain each predictor) is shown above each bar. Plot type is MO relative to AF. Habitat variables (plot level): Can_Cov = canopy cover (%); Fru_stha = stem density of fruit trees (stems ha^{-1}); Hrb_h = herb height (cm); n_AF_spp = number agroforestry species; Non_rub_stha = stem density of non-rubber trees; Sml_stha = density of small stems (stems ha^{-1}). Land-use variables (block level): AF_ratio = ratio of AF to MO; Lduse_Shannon = Shannon diversity index of land-use points; NF_prop = points in natural forest (%); Rub_prop = points in rubber plot, whether AF or MO (%); Stream = length of riparian features (m).

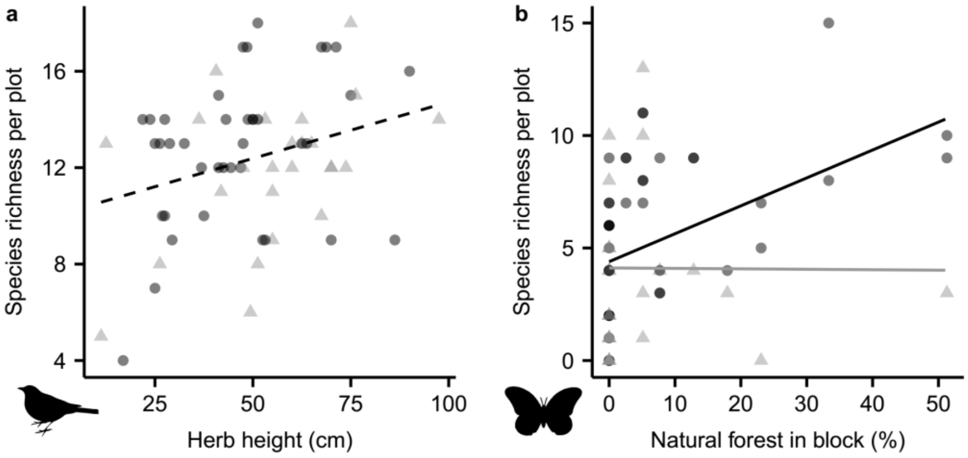

FIGURE 6 – PREDICTED VALUES OF SPECIES RICHNESS IN RESPONSE TO INFLUENTIAL VARIABLES FROM THE FINAL AVERAGED MODELS (FIGURE 5). Panels show: a) bird response to herb height (no interaction with plot type; effect in both plot types shown as dotted line) and, b) butterfly richness response to percentage natural forest in the sampling block, showing the interaction with plot type (black line = AF, grey line = MO) Original data points shown (each point represents one plot; black circles = AF, grey triangles = MO). Lines fitted to predicted species richness values (points not shown) with a linear model; CI not plotted as SE cannot be reliably computed for mixed effects models.

4.4.4 Species composition

4.4.4.1 Birds

Partial RDA (partialling out the effect of block) showed that bird species composition was not influenced by plot type, even when rare species were included (Supplementary Table 3). A Mantel test on the global RDA residuals did not show systematic spatial autocorrelation, although erratic spatial dependence was found in the dataset (at 2300 m, $p = 0.043$, 7 pairs of sites; at 8000 m, $p = 0.049$, three pairs of sites).

The best multi-scale RDA model (effect of block not partialled out) of bird composition response to land-use composition, habitat structure and plot type variables explained 16% of total inertia (pseudo-F = 1.76, $p = <0.001$), and contained: herb height, density of non-rubber trees, land-use Shannon diversity (non-significant), and the percentage of land-use points in rubber (AF and MO combined), natural forest and open habitat in the block (Figure 7a-b; Supplementary Table 4).

Although non-rubber tree stem density and percentage of natural forest points structured bird community in a similar direction, there was no correlation between the two variables (Supplementary Figure 12). Species strongly positively associated with both a greater extent of natural forest in the surrounding block and a greater density of non-rubber tree stems (a feature of AF plots) were *Merops viridis* (Blue-throated Bee-eater), *Orthotomus atrogularis* (Dark-necked Tailorbird) *Phylloscopus borealis* (Arctic Warbler), *Prionochilus maculatus* (Yellow-breasted Flowerpecker) and *Tephrodornis virgatus* (Large

Woodshrike; numbers 41, 44, 50, 54 and 66 on Figure 7b). Three species were associated with lower rubber extent in the landscape (*Arachnothera longirostra*, Little Spiderhunter; *Macronus gularis*, Pin-striped Tit Babbler and *Pellorneum ruficeps*, Puff-throated Babbler; numbers 8, 36 and 47, Figure 7b) and no species were strongly associated with greater extent of rubber.

When rare species were included in analyses, 14% of total variance was explained, plot type and small stem density became significant (although no species were strongly associated with stem density), and herb height was no longer important (Supplementary Table 5). In this case, five species became strongly associated with MO plots: *Cinnyris jugularis* (Olive-backed Sunbird), *Dicrurus leucophaeus* (Ashy Drongo, a doubleton), *Gerygone sulphurea* (Golden-bellied Gerygone), *Muscicapa dauurica* (Asian Brown Flycatcher) and *Pericrocotus divaricatus* (Ashy Minivet, an open habitat specialist; numbers 17, 24, 30, 43 and 48 on Supplementary Figure 13) and three with AF plots (*Prionochilus percussus* Crimson-breasted Flowerpecker, *Pycnonotus atriceps* Black-headed Bulbul and *Pycnonotus plumosus* Olive-winged Bulbul, numbers 55, 57 and 62; Supplementary Figure 13).

Two species of conservation concern were recorded (all as singletons), and although neither were strongly associated with any of the measured plot type, habitat or land-use variables, both were recorded within AF plots: *Eurylaimus ochromalus* Black-and-yellow Broadbill (IUCN NT) and *Megalaima mystacophanos* Red-throated Barbet (IUCN NT). All other species have IUCN LC status (Supplementary Table 2). One forest-dependent species (*Terpsiphone paradise*, Asian Paradise-flycatcher, number 67 on Figure 7b) was recorded in both AF and MO plots, and showed no strong correlation with any of the variables in the final RDA.

Rubber agroforestry thus influenced bird species composition when rare species were included in analyses, and within AF plots the density of non-rubber trees was important. Aside from the effects of rubber agroforestry, the percentage of open and forest points, as well as the overall percentage of rubber points, were important at the landscape level. Herb height was also important in plots of either type.

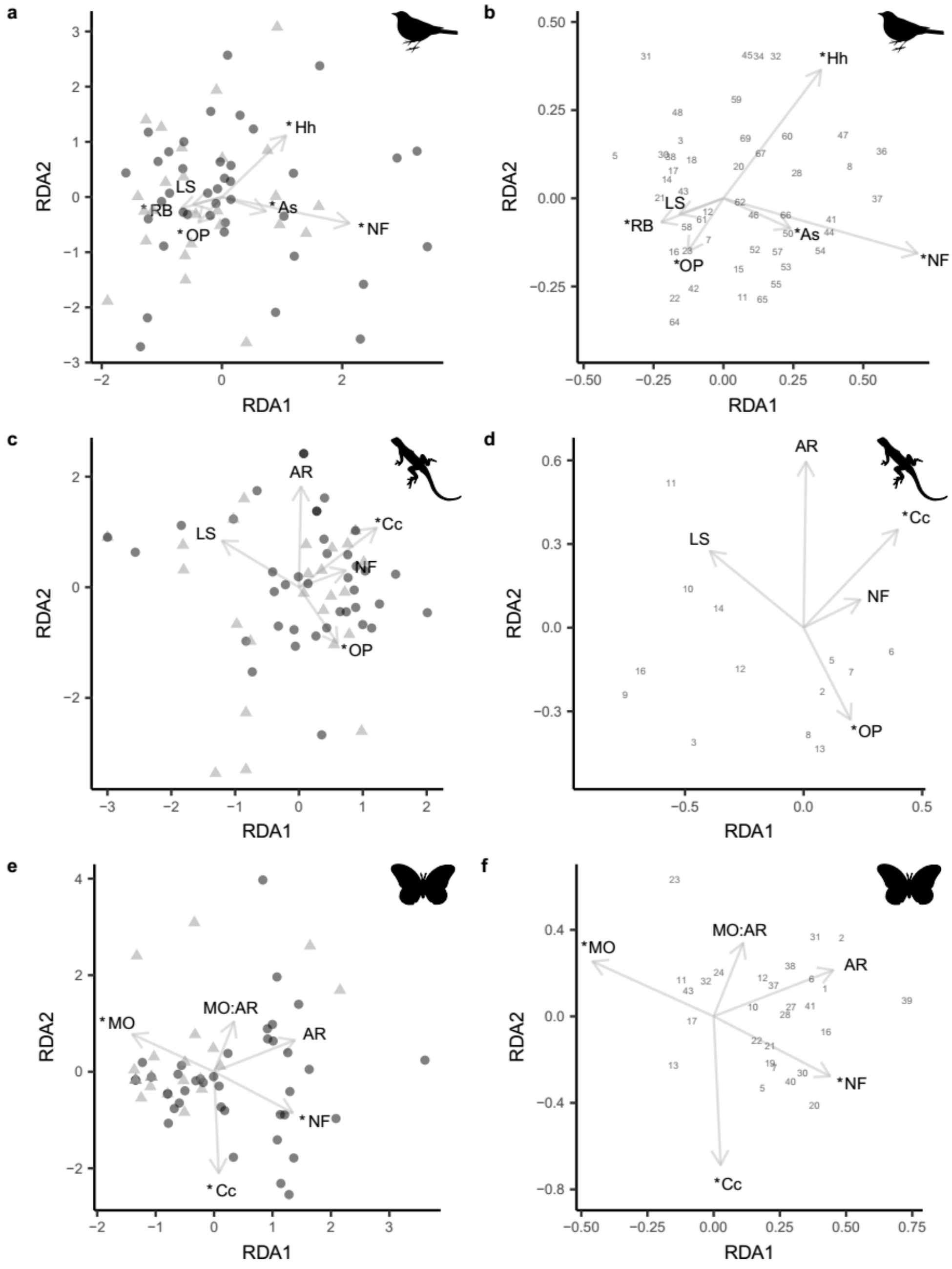

FIGURE 7 – RDA OF SPECIES COMPOSITION RESPONSE TO PLOT TYPE, PLOT-LEVEL HABITAT STRUCTURE AND SURROUNDING LANDSCAPE COMPOSITION. Panels for birds (a-b), reptiles (c-d) and butterflies (e-f), alternately show plot scores (a, c, e; AF = black circles, MO = grey triangles) or species scores (b, d, f; species numbers listed in Supplementary Table 2). Predictor variables included in the best model, defined through backwards selection, are shown as arrows; predictors that had a significant effect on species response are marked with *. Excludes rare species. Habitat variables are: AR = ratio of AF to MO in the sampling block; As = density of non-rubber trees (stems ha^{-1}); Cc = canopy cover (%); Hh = herb height (cm); LS = land-use Shannon diversity index; NF = land-use points in natural forest (%); OP = land-use points in open habitats (%); RB = land-use points in rubber (%), whether AF or MO.

4.4.4.2 Reptiles

Partial RDA showed that reptile species composition was not influenced by plot type, even when rare species were included (Supplementary Table 3). The Mantel test on the global RDA solution did not show systematic spatial autocorrelation, although spatial dependence was found at 200 m (p = 0.005, n pairs = 33), 2500 m (p = 0.011, n pairs = 11) and 3100 m (p = 0.045, n pairs = 7). The best RDA model for reptiles explained 14% of inertia (pseudo-F = 1.79, p = 0.005), and included canopy cover, and the extent of open habitat (significant effects) and land-use Shannon diversity, ratio of AF:MO in the sampling block, and the extent of natural forest (non-significant effects; Figure 7c-d; Supplementary Table 4).

Two species were positively associated with a greater extent of open habitat and a lower ratio of AF:MO in the sampling block (*Draco sumatranus,* Common Gliding Lizard and *Lygosoma bowringii*, Bowring's Supple Skink, numbers 8 and 13 Figure 7d), two were associated with less natural forest in the landscape (*Eutropis macularia*, Bronze Grass Skink and *Ptyas korros*, Indochinese Rat Snake, considered a forest species; numbers 9 and 16) and *Calotes versicolor* (Oriental Garden Lizard, number 3) was associated with lower canopy cover. The inclusion of rare species reduced explained variance to 8%, and all variables became non-significant (Supplementary Table 5, Supplementary Figure 13). Only five of the 14 species recorded have been assessed by IUCN, and have LC status, and of five species considered to be forest specialists by Chan-ard *et al* (2015), none were strongly associated any of the measured habitat or land-use variables (Supplementary Table 2).

Overall, rubber agroforestry did not appear to influence reptile composition; instead, the strongest influences on individual species related to habitat openness, including lower canopy cover associated with MO plots.

4.4.4.3 Butterflies

Partial RDA showed that butterfly species composition was not influenced by plot type, even when rare species were included (Supplementary Table 3). The Mantel test on the global RDA solution did not show systematic spatial autocorrelation, although erratic spatial dependence was found at 700 m (p = 0.042, n pairs = 7), 800 m (p = 0.007, n pairs = 16), 2300 m (p = 0.042, n pairs = 7), 2400 m (p = 0.007, n pairs = 16) and 2500 m (p = 0.017, n pairs = 11). For butterflies, 15% of total inertia in species composition was explained by the best RDA model (pseudo-F = 1.95, p = <0.001) which included canopy cover, the extent of natural forest in the block, plot type (all significant), the ratio of AF:MO in the block (non-significant), and the interaction between these latter two variables (non-significant; Figure 7e-f; Supplementary Table 4).

To explore the effect of the interaction between plot type and the ratio of AF:MO, the RDA was re-run separately for AF and MO plots (Supplementary Figure 14). This showed that the ratio of

AF:MO was only important within MO plots, with two species (*Tanaecia flora andersonii,* The Blue Count and *Tanaecia* julii, The Common Earl, numbers 37 and 39 on Supplementary Figure 14d) associated with a higher ratio of AF:MO. This also showed that the extent of natural forest only had a significant effect within AF plots (Supplementary Figure 14b). Species associated with a greater extent of natural forest points in the block included: *Euthalia teuta* (The Banded Marquis), *Mycalesis distanti-intermedia* (a Bushbrown) and *Tanaecia pelea pelea* (The Malay Viscount; numbers 20, 30 and 40 on Figure 7f). One species *Junonia atlites atlites* (The Grey Pansy, number 23 on Figure 7f) was strongly associated with lower canopy cover.

When rare species were included in analysis, the best RDA model explained 10% of total inertia; the effects of plot type and AF:MO ratio were no longer included in the model, canopy cover became non-significant, extent of natural forest was retained and the density of fruit trees became important (Supplementary Table 5). Only one species (*Charaxes moori moori*, The Malayan Yellow Nawab, a singleton) was associated with greater fruit tree density, and *Zeuxidia amethystus amethystus* (The Common Saturn, a singleton) was most strongly associated with a greater percentage of natural forest points (numbers 8 and 44 on Supplementary Figure 13f).

Overall, rubber agroforestry influenced butterfly composition; the ratio of AF:MO in the sampling block had a significant influence on composition but only within MO plots, and the percentage of natural forest points only influenced composition within AF plots.

4.5 Discussion

Future rubber demand will entail expansion and/or intensification of existing rubber plantations, which are both likely to drive the loss of biodiversity and ecosystem services. An optimal strategy between intensification and biodiversity/ecosystem functioning therefore needs to be identified. We investigated whether "intensive" rubber agroforests in Thailand retained yields while enhancing biodiversity relative to monocultures. We found that butterfly species richness was enhanced in agroforests relative to monoculture, but that both richness and composition were strongly influenced by the amount of fragmented natural forest in the surrounding landscape. Birds did not respond directly to agroforestry overall, but richness increased and composition changed with herb height irrespective of plot type. Avian composition was also influenced by the density of non-rubber trees within agroforests, and by the amount of fragmented natural forest in the landscape. In contrast to oil palm, where biodiversity gains due to understorey plant growth and increasing tree density come at a yield cost (Teuscher *et al.* 2015), and coffee where increasing shade cover decreases yield (Perfecto *et al.* 2005), rubber yields appear to be unaffected by agroforestry overall, although we were unable to directly test the effect of herb height and tree density on plot level yields. Based on these findings we suggest that "intensive" rubber agroforests can provide some biodiversity benefits that may increase ecosystem functioning and services at no yield cost, but agroforests do not support any forest dependent species or threatened species – for these, conservation of contiguous natural forest remains paramount.

4.5.1 Yields and farmer livelihoods

While we found no difference in rubber yields between AF and MO, we note that yield data were self-reported by producers. Empirical data on comparative yields in the two systems would be informative, particularly if collected alongside measurements of habitat structure variables that influence biodiversity. We suggest that because rubber is a canopy tree, and additional tree species are grown either below the rubber canopy or sharing canopy space, the relationship between rubber yields and non-rubber tree density or understorey vegetation growth may be different to that of other crops. Evidence for negative yield impacts on rubber through water and root competition with secondary crops, and positive yield impacts through weed management or erosion reduction, are currently scarce (Langenberger *et al.* 2016). The form of these relationships, and relationships between rubber yields and biodiversity benefits, warrant further direct investigation. The findings could then be used to develop guidelines for biodiversity friendly rubber agroforestry that optimise biodiversity and livelihood benefits while identifying yield costs or livelihood impacts for farmers (Perfecto *et al.* 2005). Such guidelines potentially could be incorporated into technical support for rubber farmers, such as provided by ORRAF, or in the planning or modification of existing large-scale plantations.

Aside from rubber yields, a multitude of other factors affect the sustainability of rubber agroforestry systems for farmers: yields of crops grown in the shade of rubber are lower than when unshaded, and labour constraints (rubber monocultures alone require four times the labour of oil palm per hectare) can mean that cultivation of additional crops is unfeasible (Clough *et al.* 2016, Langenberger *et al.* 2016). However, in southern Thailand, agroforestry using fruit, timber or vegetable crops not only maintains, increases and/or diversifies income, but also provides food crops that are consumed directly or shared with friends and family, providing an additional social function (Stroesser 2016). In the case of fruit crops, harvest takes place only twice a year, and timber trees require no labour inputs until felling, providing as good or better return for labour investment than monoculture, although some vegetable crops require substantial additional labour (Stroesser 2016). Moreover, in the absence of any impact on rubber yields, farmers can choose whether or not to harvest additional crops in response to prices or labour availability (Stroesser 2016). We therefore suggest that despite concerns about economic viability (Langenberger *et al.* 2016), appropriately designed agroforestry systems could provide sustainable livelihood benefits and maintain rubber yields.

4.5.2 Birds

The herb layer of rubber plantations arises through spontaneous regeneration, usually periodically removed using herbicides or manual clearance. Herbicide application to the understorey of rubber monocultures in China is known to increase runoff, soil erosion and loss of total organic carbon from sediments (Liu *et al.* 2016). We now show that the maintenance of an understorey vegetative layer could also be a simple management tool to increase bird diversity in rubber plantations, whether in AF or MO. This contrasts with findings from shade cacao in Indonesia, which found no effect of herb cover (Clough *et al.* 2009), but corroborates the outcome of studies in oil palm in Guatemala, where bird richness declined on removal of understorey vegetation (Nájera and Simonetti 2010), in Peninsula Malaysia and Sumatra where bird richness increased with the height of ground vegetation (Azhar *et al.* 2011, 2013, Teuscher *et al.* 2015), and in Thailand where bird richness was higher in oil palm and rubber monocultures containing understorey vegetation (Aratrakorn *et al.* 2006). Maintenance of the herb layer may therefore be a simple management measure that can provide multiple biodiversity and ecosystem service benefits. However, the potential effects on rubber yields of competition for water and nutrients by understorey plants (Langenberger *et al.* 2016), and the effect of different species of plants in the herb layer on both yield and birds, warrant further investigation.

The density of non-rubber tree stems in AF plots, comprising both naturally-regenerated non-commercial trees and commercially-valuable planted species, influenced bird composition in a similar way to the extent of natural forest in the block, but these variables were not correlated. We can therefore conclude that the two variables independently have similar effects on bird species composition. A similar conclusion was drawn in a study of cacao agroforestry in Sulawesi Indonesia, where distance to forest and number of shade trees had independent effects on bird richness and composition (Clough *et al.* 2009). The number of trees also had a positive effect on avian richness and abundance in oil palm plantations (Teuscher *et al.* 2015). This suggests that more complex AFs attract bird species that prefer more diverse tree stands, possibly those preferring forest fragments over agricultural areas, and may increase the permeability of rubber-dominated landscapes for species moving between forest fragments (Bhagwat *et al.* 2008).

Bird species composition in both plot types was influenced by the extent of natural forest in the surrounding block (all within forest fragments <400 ha), although richness was unaffected. This corroborates findings from rubber monocultures in Southwest China, where increased forest cover within 500 m of sample points increased species richness and altered composition (Sreekar *et al.* 2016), although a second study found that distance to large forest patches (>100 ha) influenced bird species richness, but the area of natural forest within 500 m did not (Zhang *et al.* 2017). Natural forest fragments also positively influenced bird species richness in oil palm in Colombia (Gilroy, Prescott, *et al.* 2014), Peninsula Malaysia (Azhar *et al.* 2011, 2013), and Malaysian Borneo (Koh 2008), and experimental manipulations of tree “islands” in oil palm plantations have shown benefits for birds

(Teuscher *et al.* 2016). Shaded cacao agroforests also support greater avian species richness and more forest-like bird communities in landscapes that contain more forest (Faria *et al.* 2006, 2007), and in Costa Rica small-scale forest set-asides alongside unshaded coffee supported more forest species than complex agroforest without forest fragments nearby (Chandler *et al.* 2013). Together this suggests that retaining natural forest fragments can benefit avian diversity and influence composition in rubber dominated landscapes (and thus beta diversity across the landscape (Tscharntke *et al.* 2008)), but as already found for oil palm (Edwards *et al.* 2010) fragments do not necessarily support threatened or forest dependent taxa.

Unlike the complex rubber agroforests of Indonesia, where "jungle" rubber supported twice as many species of conservation concern than rubber monocultures and oil palm combined (Prabowo *et al.* 2016), we find no evidence that high-yielding rubber agroforests support forest-dependent bird species, and scant evidence that AF supported bird species of conservation concern. With additional sampling, particularly during fruiting or flowering seasons of fruit crops, AF may be more important than shown in this study, but given that we only found singletons of such species suggests that they are not sustained within rubber AF (Barlow *et al.* 2010). Research from elsewhere in southern Thailand has already highlighted the loss of forest-dependent birds after conversion of forest to rubber monocultures (Aratrakorn *et al.* 2006), in Southwest China 50% of birds found in forest were absent from rubber monocultures (Sreekar *et al.* 2016), and complex fruit orchards in southern Thailand (likely to be more structurally diverse than AFs sampled in this study) also supported fewer bird species with differing community composition than contiguous tracts of forest (Round *et al.* 2006). Conservation of contiguous forest blocks thus remains essential for the conservation of forest and threatened birds.

4.5.3 Reptiles

Canopy cover influenced reptile composition, mostly through strong responses to low cover by some species (canopy cover range across all plots 43 – 85%), and was also influenced by the percentage of open habitat points in the landscape. This is similar to findings from Sulawesi, Indonesia, where open habitats supported different species relative to cacao agroforestry, and canopy cover and heterogeneity affected reptile composition by increasing the number of sunny patches close to shaded patches that could form suitable home ranges for individuals (Wanger *et al.* 2010).

Reptile richness and composition was overall poorly explained by the habitat and land-use variables assessed in this study. Other studies assessing reptile response to vegetation structure complexity in cacao agroforests (Deheuvels *et al.* 2014), and natural forest cover around oil palm, pasture (Gilroy, Prescott, *et al.* 2014) and cacao (Faria *et al.* 2007), have also failed to find effects. This may be because important variables were not measured: log piles, leaf litter depth, shrub cover and plot temperature influenced reptile species richness in cacao agroforests in Sulawesi, Indonesia (Wanger *et al.* 2009), leaf litter volume influenced reptile composition in unprotected forests in the Western Ghats, India (Balaji *et al.* 2014) and relative leaf litter moisture affected reptile composition in Costa Rican tree plantations (Folt and Reider 2013). The high mobility of reptile species, low detectability of some groups (particularly snakes) and the relative uniformity of leaf litter volume and thus microhabitats across all sample plots could also explain the lack of response in reptiles (Folt and Reider 2013, Deheuvels *et al.* 2014). In addition, the unusually high temperatures and low rainfall during the study period could have restricted reptiles to wetter microclimates that were not surveyed in this study, such as stream beds. Alternatively, the majority of reptile species present in the landscape may be using all habitats evenly, while forest fragments or strips in the landscape (not sampled in this study) may retain different forest-dependent species, as found in agricultural landscapes in Costa Rica (Mendenhall *et al.* 2014).

4.5.4 Butterflies

Butterfly species richness was greater in AF plots, and within these, the extent of natural forest in the surrounding block was correlated with increased butterfly richness and influenced species composition. Indeed, species richness was almost no different between AF and MO when there was no forest cover in the surrounding landscape. This corroborates work from rubber-dominated landscapes containing forest fragments (<10 ha) in the Brazilian Atlantic Forest, where the species composition of fruit-feeding butterflies in rubber plantations containing well developed inter-row vegetation (10 – 20 years old, 2 – 8 m canopy height) was similar to forest fragments, but different from both intensively managed rubber plantations (containing a herbaceous layer cleared annually) and primary forest (Barbosa Cambui *et al.* 2017). This study also concluded that the compositional similarity among forest fragments, whether surrounded by unmanaged or managed plantations, indicated that even forest-specialist butterflies were able to move through the rubber matrix to reach forest fragments (Barbosa Cambui *et al.* 2017). Given that our data were collected within AF, rather than within the forest fragments, we suggest that AF may not only provide a permeable matrix but also habitat for additional butterfly species, relative to MO, although it is unclear whether they represent "sinks" for populations that are mostly sustained within forest fragments (Gilroy and Edwards 2017). The latter seems likely given that where there was little forest in the landscape, species richness in AF was very similar to MO. Work in in oil palm has similarly shown that the amount of old-growth forest around estates increases the richness of forest-dependent butterflies within the plantation itself (Koh 2008). However, as for birds, old-growth and contiguous forest support different fruit-feeding butterfly species to secondary forest fragments meaning forest fragments within agricultural landscapes cannot replace contiguous intact forest (Veddeler *et al.* 2005, Barbosa Cambui *et al.* 2017).

Aside from the strong association between one species and low values of canopy cover, no other habitat structural variables influenced butterfly richness or composition, and thus the mechanisms for increased richness in AF relative to MO, and compositional change in AF plots in blocks with greater amounts of forest, are unclear. The response could be driven by increased availability of larval and adult food plants, or similarities in microclimate between forest fragments and AFs (affecting species presence through flight ability, thermal tolerance, or colouration; (Koh 2007)). For example, *Charaxes bernardus* uses *Litsea glutinosa* as a larval food plant (*Litsea grandis* is planted as a timber tree) and *Euthalia evelina* uses cashew *Anacardium occidentale* and *Garcinia* spp, both commonly found in rubber agroforests (Supplementary Table 1; (Ek-Amnuay 2012)). Alternatively, the common assertion from rubber farmers that pesticides were not used in AF plots could have a major impact on invertebrate diversity. The presence of rubber agroforestry may therefore complement the conservation of forest areas within rubber dominated landscapes.

4.5.6 Broader ecosystem benefits of rubber agroforestry

The provision of additional food resources in rubber agroforests (fruit, nectar, larval food plants, microhabitats) may influence functional diversity, ecosystem functioning, and provide additional ecosystem service benefits at the landscape scale, such as seed dispersal, pest control or pollination (Tscharntke *et al.* 2005, Sekercioglu 2012, Maas *et al.* 2016). The presence of mistletoe on rubber trees in China is thought to provide an additional food resource for frugivorous birds (Sreekar *et al.* 2016), and multiple fruit species in rubber AFs may thus have an effect on avian functional diversity, as frugivores are usually lost in rubber monocultures (Prabowo *et al.* 2016), potentially impacting seed dispersal (Corlett 1998, Sekercioglu 2012). Forest fragments may also play a key role in provision of ecosystem services: proximity to forest enhanced fruit set in the same rubber dominated landscapes of southern Thailand considered in this study, irrespective of forest fragment size (smallest was 360 ha; (Sritongchuay *et al.* 2016)). Within agroforests, the presence of birds and bats can provide substantial pest control services that directly affect fruit yields in cacao (Maas *et al.* 2013); whether birds provide such services in rubber agroforests or fruit orchards within the rubber-dominated landscape is currently unknown.

In addition to the biodiversity benefits of agroforestry explored in this analysis, the planting of tree species of conservation concern (IUCN VU, EN or CR) could contribute to conservation of these species (Dawson *et al.* 2013). The integration of native tree species can also increase water infiltration, improve and stabilise soil and promote vegetation species richness and quality (Liu *et al.* 2016, Langenberger 2017), providing additional ecosystem service benefits aside from enhanced biodiversity value. "Jungle" rubber provides additional ecological functions relative to monocultural rubber, including soil processes, climatic stability within plots, genetic diversity and carbon storage (Clough *et al.* 2016), but requires financial incentive to be retained in the landscape due to lower profitability (Djanibekov and Villamor 2016). The extent to which the high-yielding agroforests in this study provide these functions is yet to be established.

4.6 Conclusions

Overall, we find only modest benefits for biodiversity in "intensive" rubber agroforests relative to monocultures in southern Thailand, while yields and livelihood benefits for farmers are maintained. They may therefore represent a small win-win for farmer livelihoods and biodiversity in landscapes already dominated by rubber plantations, particularly for butterflies, and may increase provision of ecosystem services. Despite this, there is no evidence that "intensive" rubber agroforests can support forest-dependent species or those of conservation concern and, as already well documented for other crops, protection of contiguous forest blocks remains paramount for conservation of forest biodiversity. Biodiversity losses sustained by continued encroachment of rubber onto protected forests in Thailand (Aratrakorn *et al.* 2006, Round *et al.* 2006, EWT pers. obs.) and elsewhere in mainland Southeast Asia (Warren-Thomas *et al.* 2015) will not be mitigated by rubber agroforestry.

Fragments of natural forest influenced bird and butterfly diversity, suggesting that small-scale forest set-asides combined with agroforestry may benefit biodiversity in rubber dominated landscapes. This is especially important for butterflies, where biodiversity gains in agroforests seem dependent on forest fragments. However, forest fragments cannot support the same species as contiguous forest (Veddeler *et al.* 2005, Round *et al.* 2006, Edwards *et al.* 2010) and where there is a choice to be made between conserving fragments within plantation dominated landscapes or conserving contiguous tracts of forest, such as in the planning of large-scale plantations, the latter is preferable for forest dependent and threatened species, and avoids setting aside productive land that increases the footprint of agriculture, while achieving limited biodiversity gains (Edwards *et al.* 2010). We note, however, that many of the forest fragments in this study were unsuitable for cultivation in any case, whether due to topography, or because they were conserved for other reasons, such as community forestry.

Increases in non-rubber tree stem density and understorey vegetation are also likely to enhance avian diversity, and we suggest that further research on the impact of these variables on rubber yields could help develop guidelines for more biodiversity-friendly "intensive" rubber agroforests, that could even be applied to large-scale plantations.

Finally, despite these positive findings for enhancing the biodiversity value of rubber plantations without compromising yield, the prevention of forest conversion to any type of rubber cultivation system must remain paramount for conservation.

4.7 References

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4.8 Online supplementary material

This online supplementary material includes (in sequence as referred to in main text):

SUPPLEMENTARY FIGURE 1: Map of study region showing sampling blocks in the biodiversity dataset (A – E) across two districts.

SUPPLEMENTARY FIGURE 2: Habitat structure measures of rubber agroforests (AF) and monocultures (MO) biodiversity dataset plots.

SUPPLEMENTARY FIGURE 3: Monthly rainfall (sum of daily records) and maximum daily temperatures recorded at Hat Yai airport, Songkhla province, Thailand.

SUPPLEMENTARY FIGURE 4: Variation in species richness among districts

SUPPLEMENTARY FIGURE 5: Influence of rainfall on butterfly species richness.

SUPPLEMENTARY FIGURE 6: Influence of sampling trap-days on butterfly species richness.

SUPPLEMENTARY FIGURE 7: Correlation matrix of habitat structural variables across all plots using Pearson correlation, showing a) all variables and b) selected variables

SUPPLEMENTARY FIGURE 8: Rubber stem density in biodiversity and yield datasets

SUPPLEMENTARY FIGURE 9: Comparison of a) agrodiversity, b) fruit tree stem density and c) timber tree stem density of AF plots between yield and biodiversity datasets.

SUPPLEMENTARY FIGURE 10: Elevation and latitude of plots in yield and biodiversity datasets.

SUPPLEMENTARY FIGURE 11: Sampling completeness of biodiversity surveys.

SUPPLEMENTARY FIGURE 12: Correlation between proportion of natural forest in block and density of non-rubber trees in rubber plots

SUPPLEMENTARY TABLE 1: List of non-rubber plant species identified in rubber agroforests

SUPPLEMENTARY TABLE 2: Species abundances of birds, reptiles and butterflies in AF and MO, IUCN status and habitat specialisation.

SUPPLEMENTARY TABLE 3: Partial Redundancy Analysis (pRDA) assessing species composition response to plot type, after partialling out the effect of block.

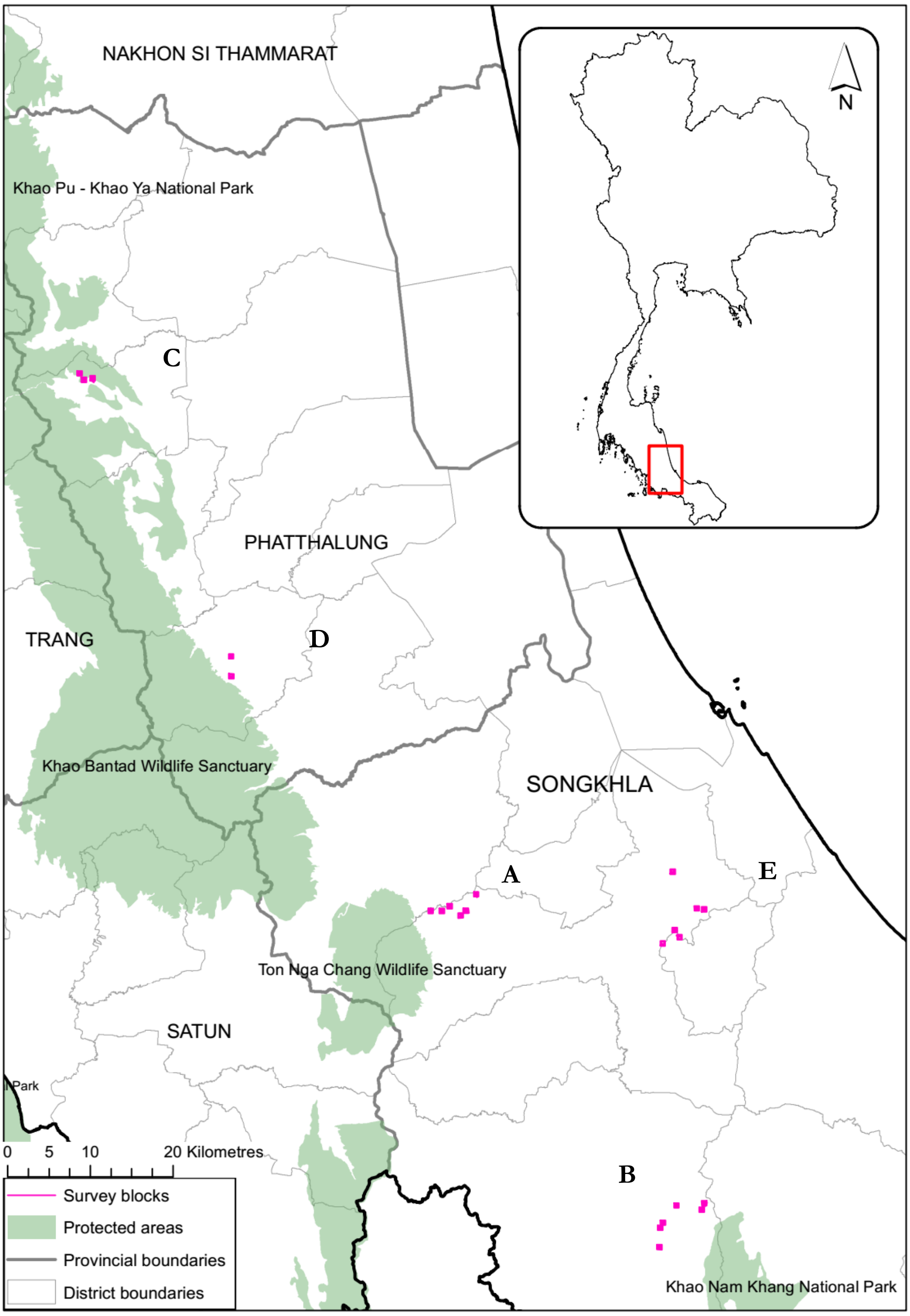
SUPPLEMENTARY TABLE 4: Results of Redundancy Analysis (RDA) of species composition response to the best model of plot type, habitat structure variables and land use composition variables, excluding rare species.

SUPPLEMENTARY FIGURE 13: RDA of species composition response to the best model of plot type, habitat structure variables and land use composition variables, including rare species.

SUPPLEMENTARY TABLE 5: Results of RDA of species composition response to the best model of plot type, habitat structure variables and land use composition variables, including rare species.

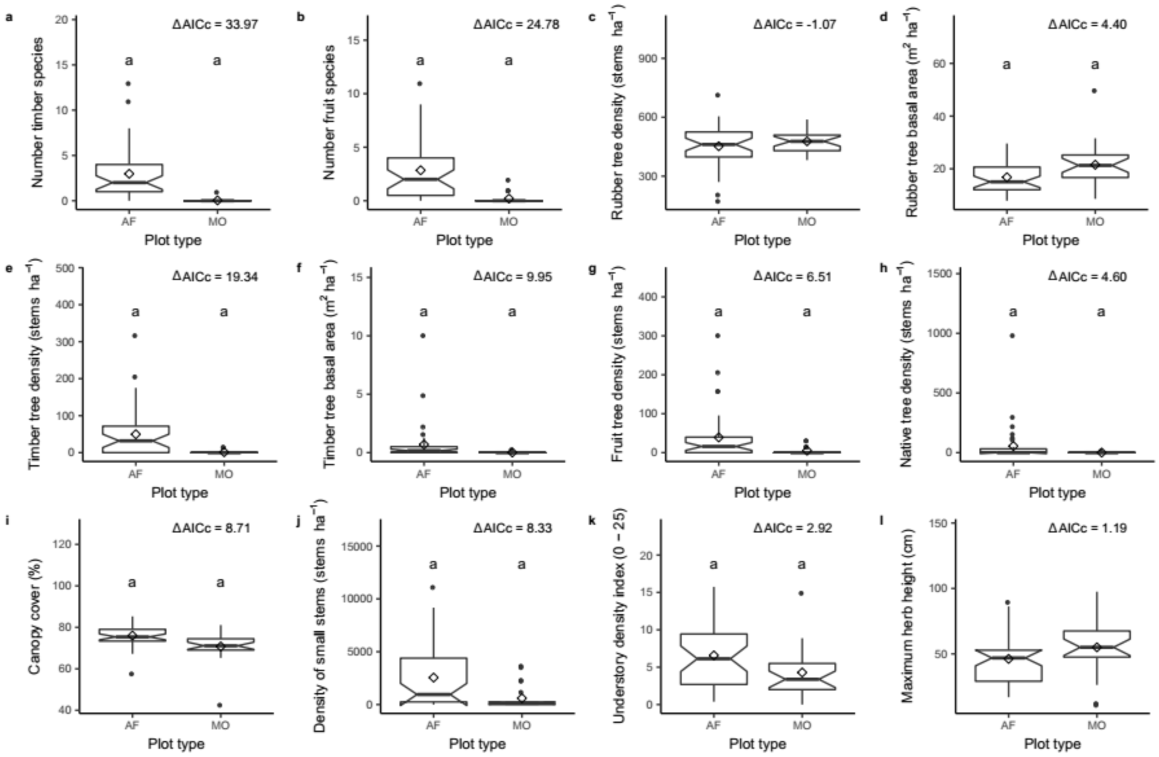
SUPPLEMENTARY FIGURE 14: RDA of butterfly species composition response within AF plots (a-b) and MO plots (c-d) to investigate interaction between plot type and AF:MO ratio in blocks.

SUPPLEMENTARY FIGURE 1: Map of study region showing sampling blocks in the biodiversity dataset (A – E) across two districts.



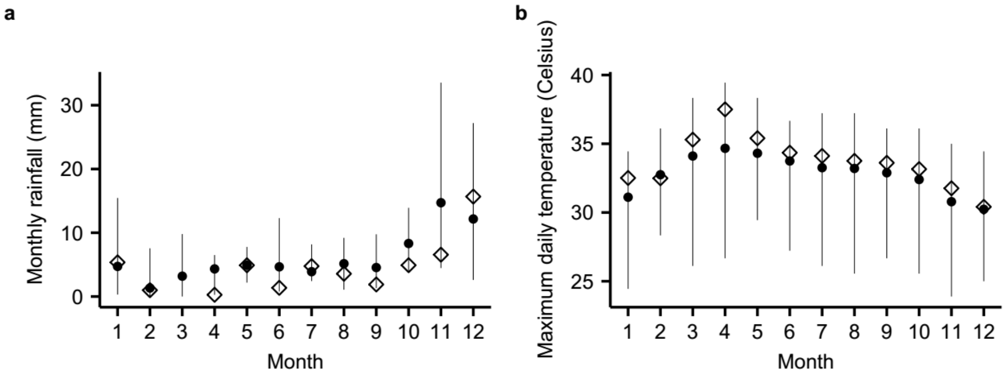
SUPPLEMENTARY FIGURE 2: Habitat structure measures of rubber agroforests (AF) and monocultures (MO) biodiversity dataset plots.

Boxes bound 25% and 75% quartiles, lines show median, notches give approximate 95% confidence interval around median, diamonds show mean, whiskers extend to 1.5x the interquartile range; outliers are shown as dots. The ΔAICc of the null model relative to a general linear model of response to plot type (AF and MO) is shown for each response variable on each panel. Where the AICc of the plot type model was more than two AICc smaller than that of the null model, the letter "a" is given above the boxplots; negative ΔAICc is given where the null model had a lower AICc than the plot type model. The following variables were square-root transformed before analysis: fruit and timber tree species richness, timber, fruit and native tree density timber tree basal area and density of small stems.



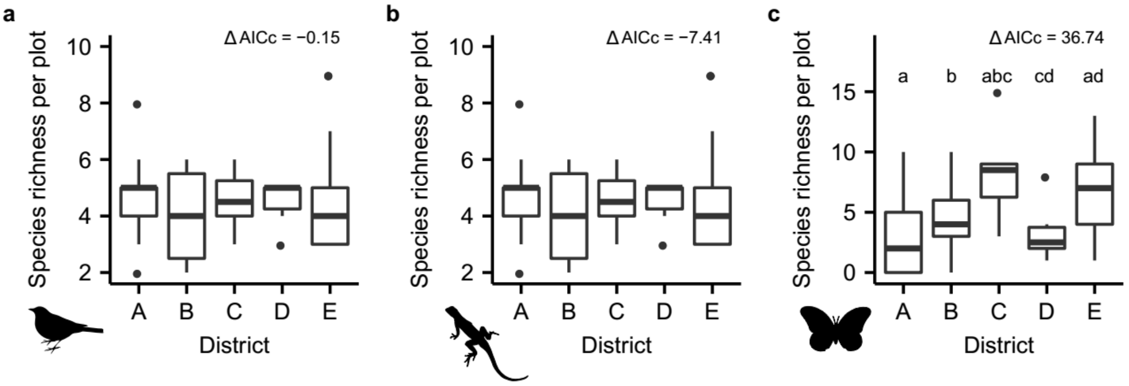
SUPPLEMENTARY FIGURE 3: Monthly rainfall (sum of daily records) and maximum daily temperatures recorded at Hat Yai airport, Songkhla province, Thailand.

Data obtained from the Global Historical Climatology Network database via Climate Data Online (NOAA 2017). Diamonds shown 2016 data (the year data for this study was collected; no data available for March), filled points show mean for each month across 2007 – 2016 inclusive, and range lines show minimum and maximum value for each month across 2007 – 2016.



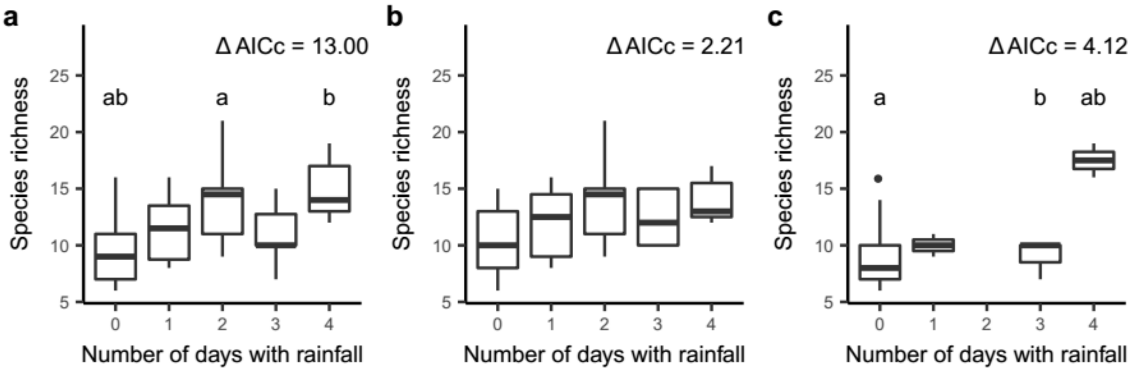
SUPPLEMENTARY FIGURE 4: Variation in species richness among districts

Panels show species richness per plot of a) birds, b) reptiles and c) butterflies, with the ΔAICc of the null model relative to a generalised linear model (Poisson distribution, log link function) comparing species richness response to district on each panel; negative ΔAICc is given where the null model had a lower AICc than the district model. A frequentist approach was then used to identify statistically significant pairwise differences ($p \leq 0.05$) between the districts, which are represented by letters above box labels, tested using Tukey's honestly significant difference. Boxplots show median (central line), upper and lower quartiles (box bounds) and 1.5x inter-quartile range (whiskers). District had an effect on species richness of butterflies, but no effect on birds or reptiles.



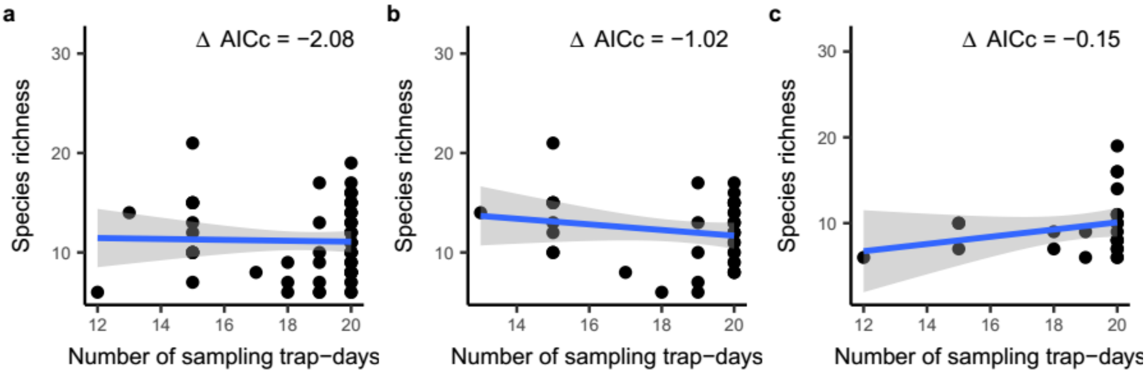
SUPPLEMENTARY FIGURE 5: Influence of rainfall on butterfly species richness.

Panels show species richness of a) all plots, b) AF plots and c) MO plots, showing the ΔAICc of the null model relative to a generalised linear model (Poisson distribution, log link function) of the response to rainfall on each panel. A frequentist approach was then used to identify statistically significant pairwise differences ($p \leq 0.05$) between the levels of rainfall, which are represented by letters above box labels, tested using Tukey's honestly significant difference. Boxplots show median (central line), upper and lower quartiles (box bounds) and 1.5x inter-quartile range (whiskers). Rainfall had an effect on species richness across all plots and in MO plots, but no effect in AF plots.



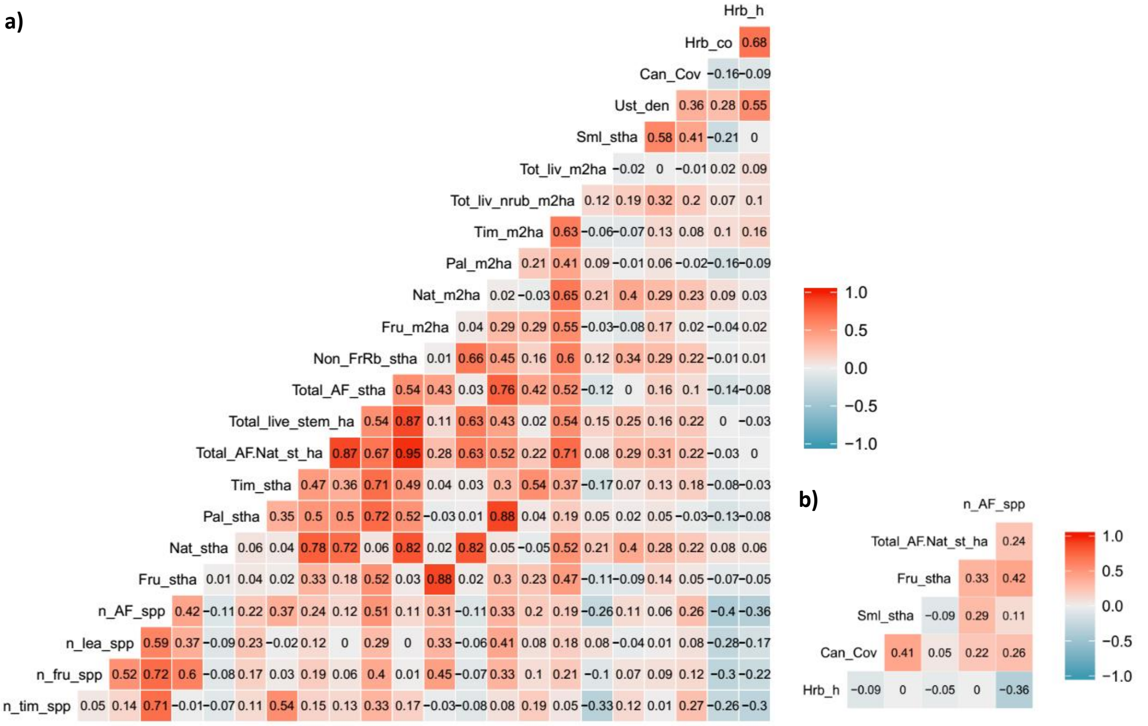
SUPPLEMENTARY FIGURE 6: Influence of sampling trap-days on butterfly species richness.

Butterfly species richness of a) all plots, b) AF plots and c) MO plots, showing the ΔAICc of the null model relative to a generalised linear model (Poisson distribution, log link function) of response to number of trap-days, with model prediction and 95% CI; negative ΔAICc is given where the null model had a lower AICc than the trap-day model. Across all plots, the null model was more strongly supported than the trap-days model, while within AF plots, and within MO plots, models relating species richness to trap-days received no support (were within two ΔAIC of the null model).



SUPPLEMENTARY FIGURE 7: Correlation matrix of habitat structural variables across all plots using Pearson correlation, showing a) all variables and b) selected variables

All habitat variables were checked for collinearity; those with a Pearson correlation ≥ 0.7, above which collinearity severely distorts model estimation (Dormann et al. 2013), were considered for exclusion from further modelling of biodiversity response. Basal area of each tree type was correlated with its respective stem density, so basal area was excluded from further modelling; stem density is more informative for management recommendations, as basal area will simply increase with time once planting density has been established. Stem density of palms, fruit trees, timber trees and native trees were then combined into a single variable: non-rubber tree stem density (ha-1). Fruit tree stem density was also included as a separate variable, as the food resource provided by fruit trees may have unique effects compared to other tree types; this did not correlate strongly with the stem density of all non-rubber trees (Pearson correlation: 0.33). The pooled number of agroforestry species was included, as this was correlated with the number of specific agroforestry species types. Understory density showed moderate correlation with small stem density (Pearson correlation 0.58) and herb height (Pearson correlation 0.55), so was omitted, and small stem density retained. Herb cover and herb height were strongly correlated (Pearson correlation 0.68), so herb cover was omitted from analysis.



a)

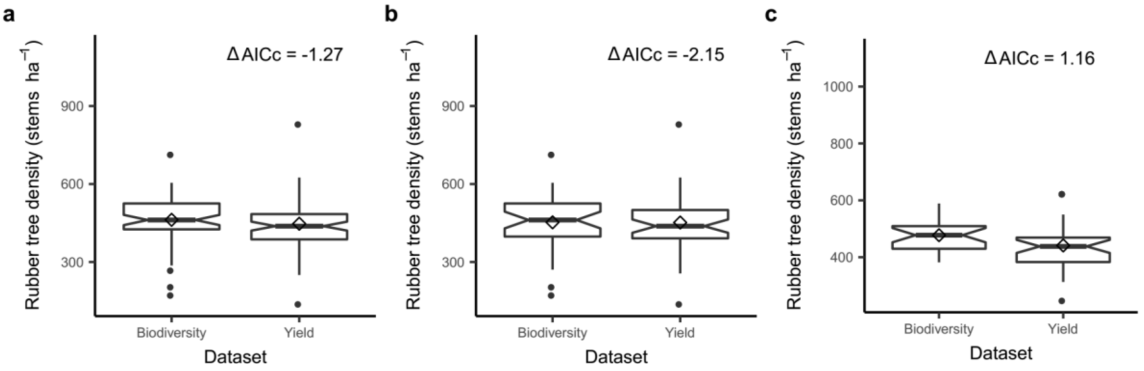
																						Hrb_h
Hrb_co																						0.68
Can_Cov																					−0.16	−0.09
Ust_den																				0.36	0.28	0.55
Sml_stha																			0.58	0.41	−0.21	0
Tot_liv_m2ha																		−0.02	0	−0.01	0.02	0.09
Tot_liv_nrub_m2ha																	0.12	0.19	0.32	0.2	0.07	0.1
Tim_m2ha																0.63	−0.06	−0.07	0.13	0.08	0.1	0.16
Pal_m2ha															0.21	0.41	0.09	−0.01	0.06	−0.02	−0.16	−0.09
Nat_m2ha														0.02	−0.03	0.65	0.21	0.4	0.29	0.23	0.09	0.03
Fru_m2ha													0.04	0.29	0.29	0.55	−0.03	−0.08	0.17	0.02	−0.04	0.02
Non_FrRb_stha												0.01	0.66	0.45	0.16	0.6	0.12	0.34	0.29	0.22	−0.01	0.01
Total_AF_stha											0.54	0.43	0.03	0.76	0.42	0.52	−0.12	0	0.16	0.1	−0.14	−0.08
Total_live_stem_ha										0.54	0.87	0.11	0.63	0.43	0.02	0.54	0.15	0.25	0.16	0.22	0	−0.03
Total_AF.Nat_st_ha									0.87	0.67	0.95	0.28	0.63	0.52	0.22	0.71	0.08	0.29	0.31	0.22	−0.03	0
Tim_stha								0.47	0.36	0.71	0.49	0.04	0.03	0.3	0.54	0.37	−0.17	0.07	0.13	0.18	−0.08	−0.03
Pal_stha							0.35	0.5	0.5	0.72	0.52	−0.03	0.01	0.88	0.04	0.19	0.05	0.02	0.05	−0.03	−0.13	−0.08
Nat_stha						0.06	0.04	0.78	0.72	0.06	0.82	0.02	0.82	0.05	−0.05	0.52	0.21	0.4	0.28	0.22	0.08	0.06
Fru_stha					0.01	0.04	0.02	0.33	0.18	0.52	0.03	0.88	0.02	0.3	0.23	0.47	−0.11	−0.09	0.14	0.05	−0.07	−0.05
n_AF_spp				0.42	−0.11	0.22	0.37	0.24	0.12	0.51	0.11	0.31	−0.11	0.33	0.2	0.19	−0.26	0.11	0.06	0.26	−0.4	−0.36
n_lea_spp			0.59	0.37	−0.09	0.23	−0.02	0.12	0	0.29	0	0.33	−0.06	0.41	0.08	0.18	0.08	−0.04	0.01	0.08	−0.28	−0.17
n_fru_spp		0.52	0.72	0.6	−0.08	0.17	0.03	0.19	0.06	0.4	0.01	0.45	−0.07	0.33	0.1	0.21	−0.1	0.07	0.09	0.12	−0.3	−0.22
n_tim_spp	0.05	0.14	0.71	−0.01	−0.07	0.11	0.54	0.15	0.13	0.33	0.17	−0.03	−0.08	0.08	0.19	0.05	−0.33	0.12	0.01	0.27	−0.26	−0.3

b)

					n_AF_spp
Total_AF.Nat_st_ha					0.24
Fru_stha				0.33	0.42
Sml_stha			−0.09	0.29	0.11
Can_Cov		0.41	0.05	0.22	0.26
Hrb_h	−0.09	0	−0.05	0	−0.36

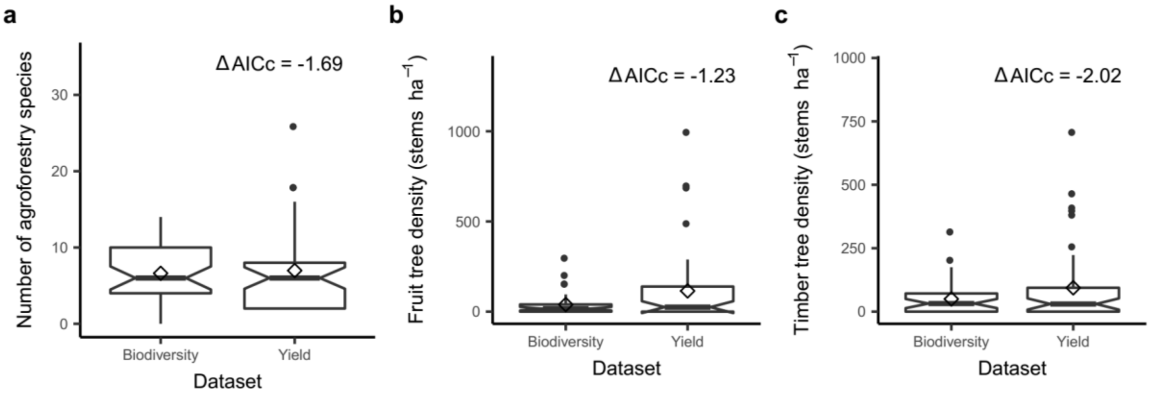
SUPPLEMENTARY FIGURE 8: Rubber stem density in biodiversity and yield datasets

Panels show rubber stem density of a) all plots, b) AF plots and c) MO plots, showing the ΔAICc of the null model relative to a general linear model contrasting plot type, AF and MO; negative ΔAICc values are given when the null model had a lower AICc than the plot type model. Boxplot format as for Supplementary Figure 4.



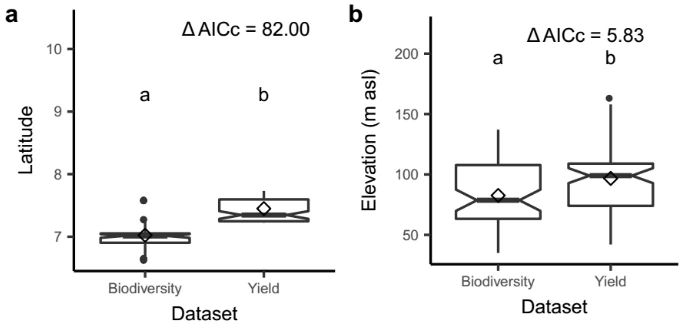
SUPPLEMENTARY FIGURE 9: Comparison of a) agrodiversity, b) fruit tree stem density and c) timber tree stem density of AF plots between yield and biodiversity datasets.

The ΔAICc of the null model, relative to a general linear model comparing each variable between the yield and biodiversity datasets, is shown on each panel. Negative ΔAICc values are given in each case, as the null model had a lower AICc than the plot type model. All variables were square-root transformed before analysis. Boxplot format as for Supplementary Figure 4.



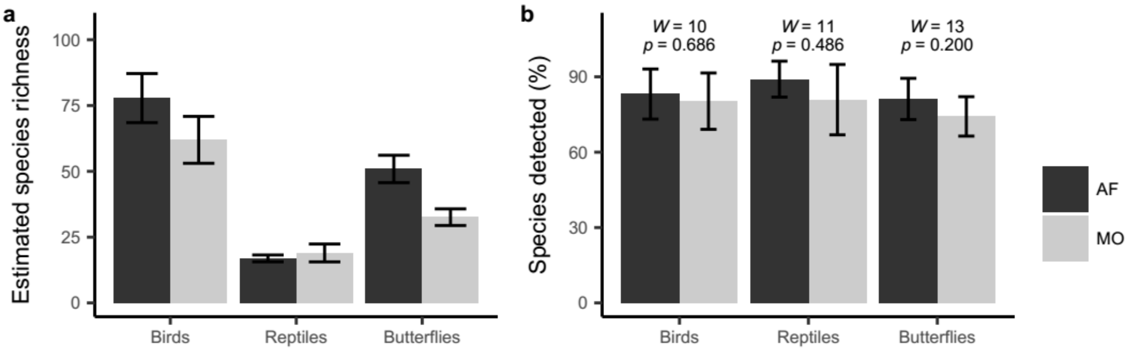
SUPPLEMENTARY FIGURE 10: Elevation and latitude of plots in yield and biodiversity datasets.

Panels show a) latitude and b) elevation of each plot, with the ΔAICc of a null model, relative to a general linear model comparing each variable between the yield and biodiversity datasets. Boxplot format as for Supplementary Figure 4.



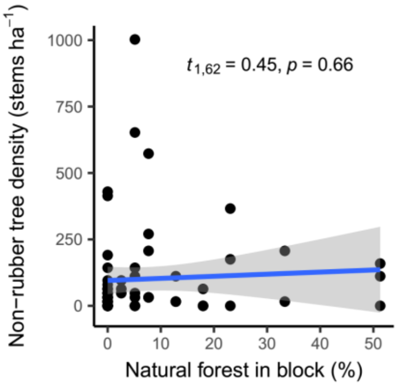
SUPPLEMENTARY FIGURE 11: Sampling completeness of biodiversity surveys.

Panels show a) estimated species richness (mean of Jack1, Jack2, Bootstrap and Mmean, error bars = 95% confidence interval of the mean) and b) percentage of mean estimated species richness observed in samples, compared between AF and MO plots using a Mann-Whitney U test for each taxon; error bars = SD around the mean.



SUPPLEMENTARY FIGURE 12: Correlation between proportion of natural forest in block and density of non-rubber trees in rubber plots

Linear model and 95% CI shown as fitted line and grey shading; result of Pearson correlation between paired measurements shown on panel.



SUPPLEMENTARY TABLE 1: List of non-rubber plant species identified in rubber agroforests

Scientific name	Common name (English)	Common name (Thai)	Type of plant	Part of plant used	Use	IUCN status
Aquilaria crassna	Agar Wood; Eagle Wood	กฤษณา	Tree	Wood	Timber/resin for perfume	CR
Azadirachta indica	Neem	สะเดา	Tree	Wood	Timber	
Casuarina equisetifolia	-	สน	Tree	Wood	Timber	
Cotylelobium lanceolatum	-	เคี่ยม	Tree	Wood	Timber	VU
Dalbergia cochinchinensis	Siamese Rosewood	พยูง	Tree	Wood	Timber	VU
Dipterocarpus alatus	Keruing; Yang	ยางนา	Tree	Wood	Timber	EN
Eugenia grandis	-	ชะเมา	Tree	Wood	Timber	
Hopea odorata	Thingan; Merawan	ตะเคียน	Tree	Wood	Timber	VU
Intsia bijuga	Borneo Teak; Moluccan Ironwood	หลุมพอ	Tree	Wood	Timber	VU
Litsea grandis	-	ทัง	Tree	Wood	Timber	
Microcos tomentosa	-	ฉับพลา	Tree	Wood	Timber	
Pterocarpus indicus	Burmese Rosewood	ประดู่	Tree	Wood	Timber	VU
Shorea roxburghii	White Meranti	พะยอม	Tree	Wood	Timber	EN
Swietenia macrophylla	Big Leaf Mahogany	มะฮอกกานี	Tree	Wood	Timber	VU
Ternstroemia wallichiana	-	ตำเสา	Tree	Wood	Timber	VU
Ananas comosus	Pineapple	สับปะรด	Herb	Fruit	Fruit	
Artocarpus heterophyllus	Jackfruit	ขนุน	Tree	Fruit	Fruit	
Bouea microphylla	-	มะปริง	Tree	Fruit	Fruit	
Citrus aurantifolia	Lime	มะนาว	Tree	Fruit	Fruit	
Cocos nucifera	Coconut	มะพร้าว	Palm	Fruit	Fruit	
Durio zibethinus	Durian	ทุเรียน	Tree	Fruit	Fruit	
Ficus sp.	-	มะเดื่อ	Tree	Fruit	Fruit	
Garcinia mangostana	Mangosteen	มังคุด	Tree	Fruit	Fruit	
Hylocereus undatus	Dragon fruit	แก้วมังกร	Tree	Fruit	Fruit	DD
Lansium domesticum	Longkong	ลองกอง	Tree	Fruit	Fruit	
Mangifera foetida	Horse Mango	มะมุด	Tree	Fruit	Fruit	LC
Mangifera indica	Mango	มะม่วง	Tree	Fruit	Fruit	DD
Musa sapientum	Banana	กล้วย	Herb	Fruit	Fruit	

Scientific name	Common name (English)	Common name (Thai)	Type of plant	Part of plant used	Use	IUCN status
Nephelium lappaceum	Rambutan	เงาะ	Tree	Fruit	Fruit	LC
Parinari anamensis	-	กะท้อนรอก	Tree	Fruit	Fruit	
Salacca zalacca	Snake fruit	สละ	Palm	Fruit	Fruit	
Sandoricum koetjape	-	กระท้อน	Tree	Fruit	Fruit	
Syzygium jambos	Wax apple	ชมพู่	Tree	Fruit	Fruit	
Tamarindus indica	Tamarind	มะขาม	Tree	Fruit	Fruit	
Anacardium occidentale	Cashew	มะม่วงหิมพานต์	Tree	Fruit + nut	Fruit, nut	
Artocarpus lacucha	Monkey fruit	มะหาด	Tree	Fruit	Cosmetics	
Areca catechu	Areca nut	หมาก	Palm	Fruit	Dye	
Bambuseae	Bamboo	ไผ่	Grass	Stem	Food, incense, others	
Thysanolaena sp.	Tiger grass	หญ้าไม้กวาด	Grass?	Stem, seed head	Brooms/brushes	
-	-	ชิง	Tree	Leaf	Cigarette paper	
Elateriospermum tapos	-	ประ	Tree	Nut	Nut	
Livistona saribus	Taraw Palm	สิเหรง	Palm	Leaf	Roof thatch	
Alpinia conchigera	-	ข่าลิง	Herb	Root	Spice	
Cinnamomum iners	Cinnamon	เชียด	Tree	Bark	Spice	
Archidendron bubalinum	-	เนียงนก	Tree	Bean	Vegetable	
Archidendron pauciflorum	-	เนียง	Tree	Bean	Vegetable	
Garcinia atroviridis	-	ส้มแขก	Tree	Fruit	Vegetable	
Garcinia cowa	-	ชะมวง	Tree	Leaf	Vegetable	
Gnetum gnemon	-	ผักเหรียง	Shrub	Leaf	Vegetable	LC
Parkia speciosa	Stink bean; Bitter bean	สะตอ	Tree	Bean	Vegetable	
Licuala paludosa	Swamp Fan Palm	กะพ้อ	Palm	Leaf	Wrapping sticky rice	

SUPPLEMENTARY TABLE 2: Species abundances of birds, reptiles and butterflies in AF and MO, IUCN status and habitat specialisation.

Bird species only include those recorded within 50m of point count location; forest interior specialist and open habitat specialist bird species categorisation based on HBW Alive (del Hoyo *et al.* 2017); reptile categorisation based on A Field Guide to the Reptiles of Thailand (Chan-ard *et al.* 2015) and habitat description on the IUCN Red List where available (IUCN 2016). ID numbers are those used in RDA plots for each taxon. Mean abundances are per plot.

* Non-breeding migratory species

IUCN Red List status based on species level taxonomic classification, not subspecies

~ Abundance of *Mycalesis* species is for males only; note that presence/absence data was used in most analyses, abundance data is given here only as background.

			AF	**MO**			
Scientific name	**Common name**	**ID no.**	**Mean abundance (± 95% CI)**	**Mean abundance (± 95% CI)**	**IUCN Status**	**Forest interior specialist**	**Open habitat specialist**
Birds			**19.46 ± 9.39**	**17.8 ± 9.54**			
Abroscopus superciliaris	Yellow-bellied Warbler	1	-	0.04 ± 0.08	LC		
Acridotheres grandis	Great Myna	2	0.03 ± 0.05	-	LC		x
Acridotheres tristis	Common Myna	3	0.08 ± 0.08	-	LC		x
Aegithina lafresnayei	Great Iora	4	0.03 ± 0.05	-	LC		
Aegithina tiphia	Common Iora	5	0.62 ± 0.22	0.52 ± 0.32	LC		
Aethopyga siparaja	Crimson Sunbird	6	0.03 ± 0.05	-	LC		
Anthreptes malacensis	Brown-throated Sunbird	7	0.18 ± 0.14	0.08 ± 0.11	LC		
Arachnothera longirostra	Little Spiderhunter	8	0.28 ± 0.19	0.20 ± 0.16	LC		
Arachnothera modesta	Grey-breasted Spiderhunter	9	0.03 ± 0.05	-	LC		
*Ardeola bacchus**	Chinese Pond Heron	10	0.03 ± 0.05	-	LC		x
Cacomantis merulinus	Plaintive Cuckoo	11	0.10 ± 0.10	-	LC		
Cacomantis sonneratii	Banded Bay Cuckoo	12	0.10 ± 0.10	-	LC		
Caprimulgus macrurus	Large-tailed Nightjar	13	0.03 ± 0.05	-	LC		
Centropus sinensis	Greater Coucal	14	0.26 ± 0.20	0.36 ± 0.25	LC		
Chalcoparia singalensis	Ruby-cheeked Sunbird	15	0.03 ± 0.05	0.08 ± 0.16	LC		
Chrysococcyx minutillus	Little Bronze Cuckoo	16	0.05 ± 0.07	0.20 ± 0.20	LC		
Cinnyris jugularis	Olive-backed Sunbird	17	1.36 ± 0.34	1.32 ± 0.42	LC		
Copsychus saularis	Oriental Magpie Robin	18	0.23 ± 0.15	0.48 ± 0.26	LC		
Corvus macrorhynchos	Large-billed Crow	19	-	0.04 ± 0.08	LC		
Cyornis tickelliae	Tickell's Blue Flycatcher	20	0.13 ± 0.13	0.08 ± 0.11	LC		x
Dendrocopos canicapillus	Grey-capped Pygmy Woodpecker	21	0.23 ± 0.15	0.36 ± 0.25	LC		x
Dicaeum cruentatum	Scarlet-backed Flowerpecker	22	0.56 ± 0.25	0.40 ± 0.25	LC		
Dicaeum trigonostigma	Orange-bellied Flowerpecker	23	1.92 ± 0.26	1.68 ± 0.27	LC		
Dicrurus leucophaeus	Ashy Drongo	24	-	0.08 ± 0.11	LC		
Eudynamys scolopaceus	Asian Koel	25	0.03 ± 0.05	0.04 ± 0.08	LC		x
Eurylaimus ochromalus	Black-and-yellow Broadbill	26	0.03 ± 0.05	-	NT		
*Ficedula elisae**	Green-backed Flycatcher	27	-	0.04 ± 0.08	LC		
*Ficedula zanthopygia**	Yellow-rumped Flycatcher	28	0.08 ± 0.08	0.04 ± 0.08	LC		
Geopelia striata	Zebra Dove	29	0.05 ± 0.07	-	LC		x
Gerygone sulphurea	Golden-bellied Gerygone	30	0.79 ± 0.15	1.04 ± 0.14	LC		
Halcyon smyrnensis	White-throated Kingfisher	31	0.41 ± 0.21	0.40 ± 0.25	LC		
Hemipus picatus	Bar-winged Flycatcher-shrike	32	0.10 ± 0.12	0.16 ± 0.24	LC		
Hypothymis azurea	Black-naped Monarch	33	0.05 ± 0.10	-	LC		
Leptocoma brasiliana	Van Hasselt's Sunbird	34	0.13 ± 0.13	0.08 ± 0.11	LC		
Loriculus galgulus	Blue-crowned Hanging Parrot	35	0.05 ± 0.07	-	LC		
Macronus gularis	Pin-striped Tit Babbler	36	0.79 ± 0.44	0.40 ± 0.32	LC		

			AF	**MO**			
Scientific name	**Common name**	**ID no.**	**Mean abundance (± 95% CI)**	**Mean abundance (± 95% CI)**	**IUCN Status**	**Forest interior specialist**	**Open habitat specialist**
Malacocincla abbotti	Abbott's Babbler	37	0.18 ± 0.14	0.04 ± 0.08	LC		
Megalaima lineata	Lineated Barbet	38	0.26 ± 0.16	0.16 ± 0.19	LC		
Megalaima mystacophanos	Red-throated Barbet	39	0.03 ± 0.05	-	NT		
*Merops philippinus**	Blue-tailed Bee-eater	40	0.03 ± 0.05	-	LC		x
Merops viridis	Blue-throated Bee-eater	41	0.08 ± 0.11	-	LC		x
Micropternus brachyurus	Rufous Woodpecker	42	0.08 ± 0.15	-	LC		
Muscicapa dauurica	Asian Brown Flycatcher	43	0.03 ± 0.05	0.20 ± 0.16	LC		
Orthotomus atrogularis	Dark-necked Tailorbird	44	0.85 ± 0.28	0.20 ± 0.16	LC		
Orthotomus sutorius	Common Tailorbird	45	1.54 ± 0.30	1.20 ± 0.49	LC		
Pachycephala cinerea	Mangrove Whistler	46	0.10 ± 0.12	0.28 ± 0.21	LC		
Pellorneum ruficeps	Puff-throated Babbler	47	1.46 ± 0.39	1.28 ± 0.47	LC		
*Pericrocotus divaricatus**	Ashy Minivet	48	0.08 ± 0.08	0.16 ± 0.15	LC		x
Phaenicophaeus tristis	Green-billed Malkoha	49	0.05 ± 0.07	-	LC		
*Phylloscopus borealis**	Arctic Warbler	50	0.21 ± 0.13	0.24 ± 0.17	LC		x
Picus puniceus	Crimson-winged Woodpecker	51	0.05 ± 0.07	-	LC		
Pitta moluccensis	Blue-winged Pitta	52	0.15 ± 0.11	0.16 ± 0.15	LC		
Prinia rufescens	Rufescent Prinia	53	1.82 ± 0.39	2.52 ± 0.57	LC		x
Prionochilus maculatus	Yellow-breasted Flowerpecker	54	0.23 ± 0.20	0.20 ± 0.16	LC		
Prionochilus percussus	Crimson-breasted Flowerpecker	55	0.08 ± 0.11	0.04 ± 0.08	LC		
Psilopogon duvaucelii	Black-eared Barbet	56	0.05 ± 0.07	-	LC		
Pycnonotus atriceps	Black-headed Bulbul	57	1.00 ± 0.31	1.00 ± 0.45	LC		
Pycnonotus blanfordi	Streak-eared Bulbul	58	0.08 ± 0.11	0.08 ± 0.16	LC		x
Pycnonotus brunneus	Asian Red-eyed Bulbul	59	0.21 ± 0.19	0.04 ± 0.08	LC		
Pycnonotus finlaysoni	Stripe-throated Bulbul	60	0.79 ± 0.27	0.80 ± 0.28	LC		
Pycnonotus goiavier	Yellow-vented Bulbul	61	0.10 ± 0.10	0.04 ± 0.08	LC		x
Pycnonotus plumosus	Olive-winged Bulbul	62	0.64 ± 0.29	0.52 ± 0.28	LC		
Sasia abnormis	Rufous Piculet	63	0.03 ± 0.05	0.04 ± 0.08	LC		
Spilopelia chinensis	Spotted Dove	64	0.03 ± 0.05	0.12 ± 0.13	LC		
Surniculus lugubris	Asian Drongo Cuckoo	65	0.05 ± 0.07	0.04 ± 0.08	LC		
Tephrodornis virgatus	Large Woodshrike	66	0.21 ± 0.40	0.04 ± 0.08	LC		
Terpsiphone paradisi	Asian Paradise-flycatcher	67	0.13 ± 0.13	0.08 ± 0.11	LC	x	
Todiramphus chloris	Collared Kingfisher	68	-	0.04 ± 0.08	LC		x
Zosterops everetti	Everett's White-eye	69	0.08 ± 0.15	0.16 ± 0.31	LC		
Reptiles			**7.90 ± 3.03**	**9.83 ± 4.43**			
Ahaetulla prasina	Asian Vine Snake	1	0.03 ± 0.05	-	LC		
Calotes emma	Emma Gray's Forest Lizard	2	1.08 ± 0.49	0.75 ± 0.49	NA	x	
Calotes versicolor	Oriental Garden Lizard	3	2.10 ± 0.50	2.88 ± 0.74	NA		
Dendrelaphis pictus	Painted Bronzeback	4	0.03 ± 0.05	0.04 ± 0.08	NA	x	
Draco blandfordii	Blandford's Gliding Lizard	5	-	0.13 ± 0.25	NA	x	
Draco maculatus	Spotted Gliding Lizard	6	0.49 ± 0.27	0.50 ± 0.29	LC		
Draco taeniopterus	Barred Flying Dragon	7	0.05 ± 0.07	0.04 ± 0.08	LC		
Draco sumatranus	Common Gliding Lizard	8	0.51 ± 0.25	0.71 ± 0.38	NA		
Eutropis macularia	Bronze Grass Skink	9	2.13 ± 0.52	2.83 ± 0.66	NA		
Eutropis multifasciata	Common Sun Skink	10	0.31 ± 0.15	0.38 ± 0.23	NA		
Hemidactylus frenatus	Common House Gecko	11	0.18 ± 0.12	0.21 ± 0.17	LC		
Hemidactylus platyurus	Flat-Tailed House Gecko	12	0.05 ± 0.07	0.08 ± 0.11	NA		
Lygosoma bowringii	Bowring's Supple Skink	13	0.79 ± 0.30	1.04 ± 0.63	NA		
Lygosoma quadrupes	Short-Limbed Supple Skink	14	0.05 ± 0.07	0.04 ± 0.08	NA	x	
Naja kaouthia	Monocled Cobra	15	-	0.04 ± 0.08	LC		
Ptyas korros	Indochinese Rat Snake	16	0.08 ± 0.08	0.17 ± 0.15	NA	x	
Takydromus sexlineatus	Asian Grass Lizard	17	0.03 ± 0.05	-	LC		x
Butterflies[#]			**15.38 ± 3.32**	**8.70 ± 4.52**			
Amathusia masina malaya	The Rusty Palmking	1	0.18 ± 0.19	0.12 ± 0.17	NA		
Ariadne ariadne pallidior	The Angled Castor	2	0.08 ± 0.11	0.12 ± 0.17	NA		
Athyma larymna siamensis	The Great Siam Sergeant	3	0.03 ± 0.05	-	NA		

			AF	**MO**			
Scientific name	**Common name**	**ID no.**	**Mean abundance (± 95% CI)**	**Mean abundance (± 95% CI)**	**IUCN Status**	**Forest interior specialist**	**Open habitat specialist**
Athyma perius perius	The Common Sergeant	4	0.03 ± 0.05	-	NA		
Charaxes athama	The Common Nawab	5	0.26 ± 0.22	0.04 ± 0.08	NA		
Charaxes bernardus crepax	The Common Tawny Rajah	6	0.08 ± 0.08	-	NA		
Charaxes hebe chersonesus	The Southern Nawab	7	0.08 ± 0.08	-	NA		
Charaxes moori moori	The Malayan Yellow Nawab	8	0.03 ± 0.05	-	NA		
Coelites epiminthia epiminthia	The Straight Banded Catseye	9	-	0.04 ± 0.08	NA		
Discophora sondaica despoliata	The Common Duffer	10	0.08 ± 0.08	-	NA		
Elymnias hypermnestra tinctoria	The Common Palmfly	11	0.13 ± 0.13	0.12 ± 0.13	NA		
Elymnias nesaea lioneli	The Tiger Palmfly	12	0.05 ± 0.07	0.04 ± 0.08	NA		
Euthalia aconthea gurda	The Mango Baron	13	0.05 ± 0.07	0.04 ± 0.08	NA		
Euthalia alpheda yamuna	The Streaked Baron	14	0.03 ± 0.05	-	NA		
Euthalia djata siamica	The Red Spot Baron	15	-	0.04 ± 0.08	LC		
Euthalia evelina compta	The Red Spot Duke	16	0.51 ± 0.33	0.04 ± 0.08	NA		
Euthalia malaccana malaccana	The Malay Red Baron	17	0.08 ± 0.11	0.08 ± 0.11	LC		
Euthalia monina monina	The Malay Baron	18	0.03 ± 0.05	0.04 ± 0.08	NA		
Euthalia recta montilis	The Red Spot Marquis	19	0.33 ± 0.35	-	NA		
Euthalia teuta	The Banded Marquis	20	0.62 ± 0.45	-	NA		
Herona marathus angustata	The Yellow Pasha	21	0.08 ± 0.08	-	NA		
Hypolimnas bolina jacintha	The Great Eggfly	22	0.36 ± 0.29	0.08 ± 0.11	NA		
Junonia atlites atlites	The Grey Pansy	23	0.03 ± 0.05	0.08 ± 0.11	NA		
Junonia iphita iphita	The Chocolate Pansy	24	0.21 ± 0.18	0.16 ± 0.19	NA		
Lebadea martha malayana	The Knight	25	0.05 ± 0.07	-	NA		
Lexias pardalis dirteana	The Common Archduke	26	0.05 ± 0.07	-	NA		
Melanitis leda leda	The Common Evening Brown	27	3.56 ± 0.94	2.04 ± 1.13	NA		
Melanitis phedima abdullae	The Dark Evening Brown	28	0.15 ± 0.21	-	NA		
Moduza procris milonia	The Common Commander	29	0.03 ± 0.05	-	NA		
Mycalesis distanti-intermedia~	Bushbrown	30	3.90 ± 1.23	2.38 ± 1.45	-		
Mycalesis mineus	The Dark Branded Bushbrown	31	0.97 ± 0.47	0.96 ± 0.70	-		
Mycalesis perseoides	The Burmese Bushbrown	32	1.08 ± 0.78	0.79 ± 0.53	-		
Mycalesis visala phamis	The Long-Branded Bushbrown	33	0.03 ± 0.05	-	-		
Neptis hylas papaja	The Common Sailor	34	-	0.04 ± 0.08	NA		
Rhinopalpa polynice eudoxia	The Wizard	35	0.05 ± 0.10	-	NA		
Tanaecia clathrata violaria	The Violet-Bordered Viscount	36	0.03 ± 0.05	-	NA		
Tanaecia flora andersonii	The Blue Count	37	0.18 ± 0.14	0.20 ± 0.25	NA		
Tanaecia iapis puseda	The Horsfield's Baron	38	0.18 ± 0.14	0.04 ± 0.08	NA		
Tanaecia julii	The Common Earl	39	1.36 ± 0.55	0.72 ± 0.67	NA		
Tanaecia pelea pelea	The Malay Viscount	40	0.23 ± 0.20	-	LC		
Telinga janardana	The Lesser Bushbrown	41	0.92 ± 0.41	0.48 ± 0.41	LC		
Ypthima baldus newboldi	The Common Fivering	42	0.03 ± 0.05	-	NA		
Ypthima nebulosa	The Malayan Fivering	43	0.05 ± 0.07	0.08 ± 0.11	NA		
Zeuxidia amethystus amethystus	The Common Saturn	44	0.03 ± 0.05	-	NA		

SUPPLEMENTARY TABLE 3: Partial Redundancy Analysis (pRDA) assessing species composition response to plot type, after partialling out the effect of block.

Variance, F and p values are reported for the whole model which contained plot type as the only environmental variable, and Block as a conditioning variable. Species abundance was scaled before analysis, so inertia is equivalent to the number of species in the ordination. Rare species are those with total abundance (or summed presence for butterflies) of less than three.

Rare species	Taxon		Df	Variance	F	Pr (>F)	Inertia	Proportion inertia explained
Excluded	Birds	**Total**					47	1
		Conditional (Block)					21.45	0.46
		Constrained					0.66	0.01
		Unconstrained					24.89	0.53
		Model (Plot type)	1	0.66	1.06	0.372		
	Reptiles	**Total**					13	1
		Conditional (Block)					7.53	0.58
		Constrained					0.05	0
		Unconstrained					5.42	0.42
		Model (Plot type)	1	0.05	0.37	0.972		
	Butterflies	**Total**					28	1
		Conditional (Block)					12.62	0.45
		Constrained					0.41	0.01
		Unconstrained					14.97	0.53
		Model (Plot type)	1	0.41	1.07	0.377		
Included	Birds	**Total**					69	1
		Conditional (Block)					29.83	0.43
		Constrained					1.02	0.01
		Unconstrained					38.15	0.55
		Model (Plot type)	1	1.02	1.07	0.352		
	Reptiles	**Total**					17	1
		Conditional (Block)					9.15	0.54
		Constrained					0.07	0
		Unconstrained					7.78	0.46
		Model (Plot type)	1	0.07	0.34	0.992		
	Butterflies	**Total**					44	1
		Conditional (Block)					18.68	0.42
		Constrained					0.63	0.01
		Unconstrained					24.69	0.56
		Model (Plot type)	1	0.63	0.99	0.481		

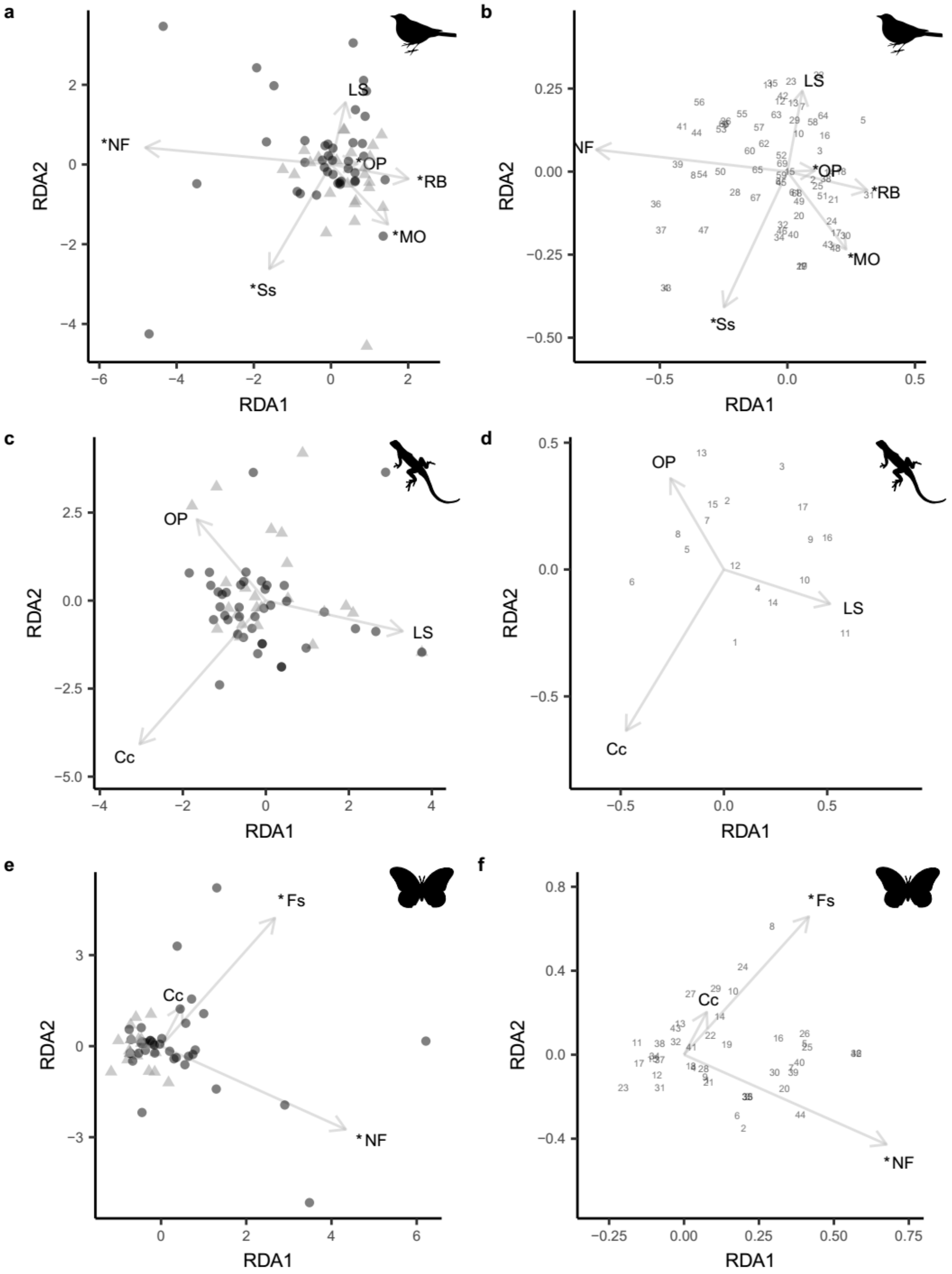
SUPPLEMENTARY TABLE 4: Results of Redundancy Analysis (RDA) of species composition response to the best model of plot type, habitat structure variables and land use composition variables, excluding rare species.

Variance, F and p values are for sequential addition of terms into the model. Variance Inflation Factor was <10 for all terms in all models, and thus terms can be considered non-collinear, and the order of inclusion in the model unimportant. Analysis excludes rare species (total abundance or sum of presences less than three). Species abundance was scaled before analysis, so inertia is equivalent to the number of species in the ordination.

Taxon		Df	Variance	Pseudo- F	Pr (>F)	Inertia	Proportion inertia explained
Birds	**Total**					47.00	1.00
	Constrained					7.35	0.16
	Unconstrained					39.65	0.84
	RDA1	1	2.23	3.20	0.000		0.05
	RDA2	1	1.52	2.19	0.000		0.03
	Model	6	7.35	1.76	<0.001		
	Residual	57	39.65				
	Herb height (cm)	1	1.04	1.49	0.022		
	Non-rubber tree stem density (stems ha^{-1})	1	1.20	1.73	0.040		
	Land use Shannon diversity	1	1.00	1.43	0.051		
	Proportion rubber (%)	1	1.47	2.11	0.003		
	Proportion natural forest (%)	1	1.43	2.06	0.000		
	Proportion open habitat (%)	1	1.22	1.75	0.004		
Reptiles	**Total**					13.00	1.00
	Constrained					1.76	0.14
	Unconstrained					11.24	0.86
	RDA1	1	1.01	5.12	0.000		0.08
	RDA2	1	0.46	2.33	0.016		0.04
	Model	5	1.76	1.79	0.005		
	Residual	57	11.24				
	Canopy cover (%)	1	0.43	2.18	0.041		
	Land use Shannon diversity	1	0.31	1.60	0.106		
	Proportion natural forest (%)	1	0.21	1.06	0.342		
	AF:MO ratio	1	0.32	1.62	0.124		
	Proportion open habitat (%)	1	0.49	2.47	0.008		
Butterflies	**Total**					28	1.00
	Constrained					4.10	0.15
	Unconstrained					23.90	0.85
	RDA1	1	1.69	4.03	0.000		
	RDA2	1	1.05	2.51	0.003		
	Model	5	4.10	1.95	<0.001		
	Residual	57	23.90				
	Plot type	1	0.80	1.91	0.009		
	Canopy cover (%)	1	0.93	2.23	0.014		
	Proportion natural forest (%)	1	0.84	1.99	0.025		
	AF:MO ratio	1	0.66	1.57	0.094		
	Plot type : AF:MO ratio	1	0.86	2.06	0.051		

SUPPLEMENTARY FIGURE 13: RDA of species composition response to the best model of plot type, habitat structure variables and land use composition variables, including rare species.

Panels show: birds (a-b), reptiles (c-d) and butterflies (e-f), with plot scores (a, c, e) and species scores (b, d, f) and the predictor variables included in the best model, defined through backwards selection. Predictors that had a significant effect on species response are marked with * (Supplementary Table 6). Includes rare species (defined as those with total abundance or sum of presences of less than three). Species numbers shown in Supplementary Table 2.



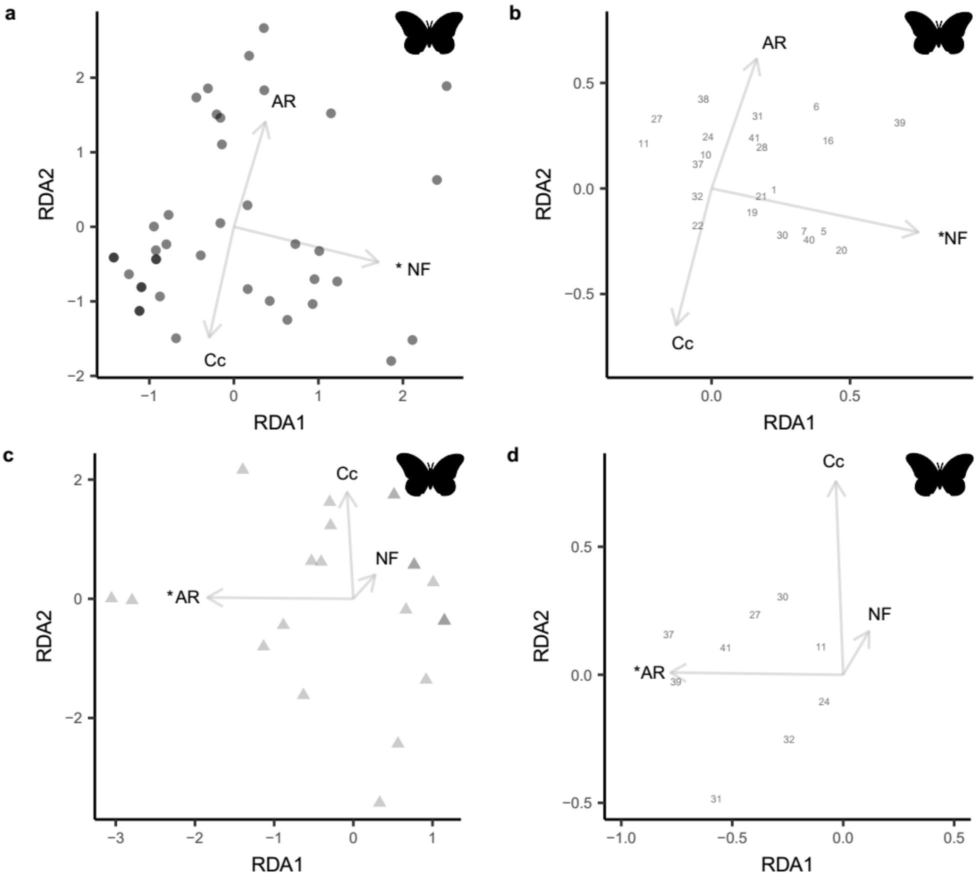
SUPPLEMENTARY TABLE 5: Results of RDA of species composition response to the best model of plot type, habitat structure variables and land use composition variables, including rare species.

Variance, F and p values are for sequential addition of terms into the model. Variance Inflation Factor was <10 for all terms in all models, and thus terms can be considered non-collinear, and the order of inclusion in the model unimportant. Analysis includes rare species (total abundance or sum of presences less than three). Species abundance was scaled before analysis, so inertia is equivalent to the number of species in the ordination.

Taxon		Df	Variance	Pseudo- F	Pr (>F)	Inertia	Proportion inertia explained
Birds	**Total**					69.00	1.00
	Constrained					9.91	0.14
	Unconstrained					59.09	0.86
	RDA1	1	3.18	3.07	0.000		
	RDA2	1	1.89	1.82	0.000		
	Model	6	9.91	1.59	0.000		
	Residual	57	59.09				
	Plot type	1	1.33	1.28	0.039		
	Small stem density (stems ha^{-1})	1	1.61	1.55	0.018		
	Land use Shannon diversity	1	1.30	1.25	0.120		
	Proportion rubber (%)	1	2.39	2.31	0.001		
	Proportion natural forest (%)	1	1.89	1.82	0.001		
	Proportion open habitat (%)	1	1.40	1.35	0.034		
Reptiles	**Total**					17.00	1.00
	Constrained					1.33	0.08
	Unconstrained					15.67	0.92
	RDA1	1	0.81	3.04	0.001		
	RDA2	1	0.44	1.66	0.123		
	Model	3	1.33	1.67	0.023		
	Residual	59	15.67				
	Canopy cover (%)	1	0.56	2.12	0.073		
	Land use Shannon diversity	1	0.34	1.28	0.227		
	Proportion open habitat (%)	1	0.43	1.60	0.074		
Butterflies	**Total**					44	1.00
	Constrained					4.516	0.10
	Unconstrained					39.484	0.90
	RDA1	1	2.18	3.26	0.002		
	RDA2	1	1.27	1.90	0.039		
	Model	3	4.52	2.25	0.001		
	Residual	59	39.48				
	Canopy cover (%)	1	1.09	1.62	0.083		
	Fruit tree stem density (stems ha^{-1})	1	1.50	2.24	0.043		
	Proportion natural forest (%)	1	1.93	2.88	0.002		

SUPPLEMENTARY FIGURE 14: RDA of butterfly species composition response within AF plots (a-b) and MO plots (c-d) to investigate interaction between plot type and AF:MO ratio in blocks.

Panels a) and c) show plots, b) and d) show species. Species numbers given in Supplementary Table 2. Excludes rare species.



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Chapter 5

Functional diversity of birds in rubber agroforest and monoculture of southern Thailand

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5.1 Abstract

Global demand for natural rubber is growing, and rubber plantations are expanding to meet demand, with increasing impacts on biodiversity and ecosystem services. Functional diversity underpins ecological functioning and the delivery of ecosystem services, which are particularly important for small-scale farmers. In Thailand, the world's biggest rubber producer, high-yielding rubber agroforests can have modest benefits for both smallholder farmer livelihoods and biodiversity relative to monocultures, but the functional diversity of species living in the two systems is unknown. This study surveyed birds in 64 rubber plots arranged in a nested sampling design in southern Thailand. Avian functional diversity measures were compared between agroforests and monocultures. Functional diversity responses to habitat structure within plots and land-use composition around plots were also assessed. Almost all bird species were small-to-medium sized and insectivorous to some degree. Very few frugivorous or nectarivorous species were recorded. The standardised effect size of functional diversity (sesFD) was greater in monocultures than in agroforests, due to the presence of open habitat and aquatic species, but all other functional diversity metrics were similar between the two plot types. Increasing herb height and the density of fruit trees positively influenced functional diversity (FD), while sesFD was negatively influenced by increasing understorey clutter and the extent of natural forest around the plot. Planting of non-rubber trees and maintenance of a herb layer within rubber plantations could be management strategies to increase functional diversity of birds, but the paucity of non-insectivorous species highlights the importance of other land uses for avian functional diversity within rubber-dominated landscapes.

5.2 Introduction

Expansion and intensification of agriculture results in biodiversity loss, reduced delivery of ecosystem services, and risks the long-term sustainability of agricultural production (Foley *et al.* 2005). Intensification using conventional methods, including chemical inputs, can result in societal costs and undermine long-term agricultural productivity, while on-farm biodiversity can provide ecosystem services that support production, including soil fertility, pollination, and pest control (Tscharntke *et al.* 2012). Trade-offs between agricultural yields and biodiversity are not necessarily linear, particularly in tropical agro-ecosystems, resulting in opportunities for biodiversity and ecosystem service gains to be made without loss of yields (Perfecto *et al.* 2005, Steffan-Dewenter *et al.* 2007, Clough *et al.* 2011, Tscharntke *et al.* 2012).

Delivery of ecosystem services results from ecological functioning, which is dependent not just on species richness or composition, but on species functional traits (Tilman *et al.* 1997, Loreau *et al.* 2001, Hooper *et al.* 2005, Cadotte *et al.* 2011, Cardinale *et al.* 2012, Tscharntke *et al.* 2012). Functional traits are measurable aspects of individuals (or species) that can affect where they live, how they interact with other individuals or species, and how they affect ecosystem functioning (Cadotte *et al.* 2011). There is now consensus that ecosystem functioning is more efficient and temporally stable in ecosystems with greater diversity of species and functional traits (Cardinale *et al.* 2012). Habitat disturbance, including land-use change, is known to result in the replacement of specialist species with generalists, which may result in reduced stability of ecosystems and reduced ecosystem functioning (Clavel *et al.* 2011). Patterns of change in the functional structure of ecological communities in response to disturbance can differ from patterns in species richness or composition, which makes the direct assessment of functional diversity responses to land-use change essential when planning conservation, restoration or agricultural management (Flynn *et al.* 2009, Mouillot *et al.* 2013, Barnes *et al.* 2014). The increased provision of ecosystem services that is expected to result from increased functional diversity (Hooper *et al.* 2005, Cardinale *et al.* 2012) is particularly important in small-scale, low-input agricultural systems that are more reliant on ecological processes to sustain agricultural production than are large-scale, heavily mechanised, agro-chemical systems (Tscharntke *et al.* 2012).

In mainland Southeast Asia, natural habitats are being replaced with rubber *Hevea brasiliensis* (Warren-Thomas *et al.* 2015), predominantly grown in intensive monocultures, with planting densities of 450 – 500 stems ha^{-1}, and routine application of pesticide and herbicide (Phommexay *et al.* 2011, Priyadarshan 2011, Shigematsu *et al.* 2013, Yi *et al.* 2014). Globally, the majority of rubber is grown by smallholders, but new large-scale monocultures are also being planted (Warren-Thomas *et al.* 2015). Intensive monocultural rubber plantations have detrimental effects on biodiversity, decreasing species richness and/or altering composition of birds (Danielsen and Heegaard 1995, Aratrakorn *et al.* 2006, Peh *et al.* 2006, Beukema *et al.* 2007, Li *et al.* 2013, Prabowo *et al.* 2016, Sreekar *et al.* 2016, Zhang *et al.* 2017), bats (Phommexay *et al.* 2011) , terrestrial mammals (Cotter *et al.* 2017), frogs (Behm *et al.* 2013), invertebrates (Meng, Martin, Liu, *et al.* 2012, Meng, Martin, Weigel, *et al.* 2012, Li *et al.* 2013, Meng *et al.* 2013, Xiao *et al.* 2014, Cotter *et al.* 2017) and plants (Beukema *et al.* 2007, Cotter *et al.* 2017) relative to forests. The expansion of rubber monocultures has also been associated with serious ecosystem service degradation via changes in hydrology, soil erosion and water pollution, as well as decreased food security (Warren-Thomas *et al.* 2015). High-yielding "intensive" rubber agroforestry, where additional crops or trees are grown between rubber trees (including fruits, vegetables or timber) is undertaken by a small proportion of farmers in Thailand, the world's largest rubber producer (Simien and Penot 2011). These agroforests maintain the high yields of monocultures (mean yield across both agroforestry and monocultures: 1.36 ± 0.21 t ha^{-1} yr^{-1}), by retaining the same planting densities and high-yielding rubber varieties as monocultures (Chapter 3), unlike the extensive low-yielding "jungle" rubber agroforests of Indonesia, which yield only 0.4 – 0.6 t ha^{-1} yr^{-1} (Villamor *et al.* 2011).

Evidence for the form of relationships between yields and biodiversity within rubber cultivation systems is beginning to accumulate. In Brazil, fruit-feeding butterfly species richness and community-composition similarity to forest fragments increased when mature inter-row vegetation was allowed to establish in rubber plantations (Barbosa Cambui *et al.* 2017), but no assessment of yield or economic viability was made. Comparisons between low-yielding "jungle" rubber and intensive monocultures in Indonesia has shown benefits for biodiversity (bird, plant, ant and oribatid mite species richness), and delivery of ecosystem services, but at the expense of yields and farmer livelihoods (Clough *et al.* 2016, Drescher *et al.* 2016, Prabowo *et al.* 2016). Most recently, evidence from the high-yielding agroforests of southern Thailand has shown that greater butterfly species richness and different community composition is supported in agroforests relative to monocultures, and that avian species composition is influenced by the density of non-rubber trees within rubber agroforests (Chapter 3). High-yielding rubber agroforests may thus represent a strategy for modestly increasing the biodiversity value of rubber plantations, while maintaining yields.

However, evidence for functional diversity responses to rubber cultivation is currently scarce. Ecological functioning as measured by energy fluxes across trophic levels of leaf-litter macroinvertebrates was lower in "jungle" and monocultural rubber than forest in Indonesia, though greater than in oil palm; in addition, ecological functioning decreased more rapidly with each species lost in "jungle" rubber than in rubber monocultures in Indonesia, driven by changes in the predator community, suggesting that each predatory species was more functionally important in "jungle" rubber than in monoculture (Barnes *et al.* 2014). Conversion of forest to rubber monocultures also affected the trophic groups and food web structures of nematode worms on Hainan Island, China (Xiao *et al.* 2014)

Direct assessments of functional diversity following forest conversion to other types of agriculture or plantations have shown declines for dung beetles (Barragán *et al.* 2011, Edwards *et al.* 2014), birds (Edwards *et al.* 2013, Almeida *et al.* 2016, Prescott *et al.* 2016), leaf-litter macroinvertebrates (Barnes *et al.* 2014) and understorey plants (Katovai *et al.* 2012). A meta-analysis of studies in North America and the Neotropics also found that functional diversity decreased with increasing intensification of land-use and, that in 31% of studies on birds and 14% of studies on mammals, the decline in functional diversity was greater than the decline in species richness (Flynn *et al.* 2009).

Forest fragments in agricultural landscapes also influence functional diversity within agro-ecosystems through spill-over (Tscharntke *et al.* 2008, Gilroy, Edwards, *et al.* 2014). As well as assessments of specific ecosystem services resulting from spill-over effects (Klein *et al.* 2003, Ricketts *et al.* 2004, Blanche *et al.* 2006, Gemmill-Herren and Ochieng' 2008, Karp *et al.* 2013, Sritongchuay *et al.* 2016), functional diversity of birds was positively influenced by the amount of fragmented natural forest in oil palm landscapes in Colombia (Prescott *et al.* 2016)

Here, we focus on avian functional diversity, because birds are functionally diverse, have a wide variety of diet types, and perform important functional roles including pollination, seed dispersal and predation (Sekercioglu 2006, Gray *et al.* 2007, Tscharntke *et al.* 2008). These functions can result in the provision of ecosystem services in landscapes containing agroforests, that benefit yields and reduce pest damage (Philpott *et al.* 2009, Sekercioglu 2012, Maas *et al.* 2016). General patterns in avian functional diversity following conversion of tropical forests to various types of agro-ecosystems (including forest remnants, agroforests and agricultural areas) are for declines in large frugivorous and insectivorous birds, while small- and medium-sized insectivores, omnivores, granivores and small frugivores fare better, particularly canopy feeding and migratory species (Tscharntke *et al.* 2008, Sekercioglu 2012). However, most research on avian functional diversity in agroforestry systems has focussed on Neotropical cacao *Theobroma cacao* and coffee *Coffea* spp. (Sekercioglu 2012), the findings of which are not necessarily applicable to other continents (Philpott *et al.* 2008), highlighting the need for region- and crop-specific studies of functional diversity in agroforestry.

No studies have yet assessed avian functional diversity in rubber plantations. In this study, we fill this knowledge gap by investigating whether avian functional diversity differed between rubber agroforests (AF) and rubber monocultures (MO) in smallholder rubber farms in southern Thailand. We assessed functional diversity based on traits relating to resource use and capture, which are known to be linked to ecosystem functioning (Flynn *et al.* 2009), namely body size (mass), diet type, foraging strata and foraging substrates. We also investigated whether plot-level habitat structural variables, land-use composition around rubber plots, and distance to the nearest contiguous forest area, affected avian functional diversity.

5.3 Methods

5.3.1 Study region

The study was conducted in southern Thailand, in Songkhla and Phattalung provinces (Supplementary Figure 1 of Chapter 3), where lowland landscapes are dominated by smallholder rubber plantations. Average rubber tree planting density was 454 ± 16.3 stems ha^{-1} (mean ± 95% CI, across AF and MO; Chapter 3). Agroforest plots contained commercially valuable, tree, shrub or herbaceous species, or naturally regenerated wild non-rubber trees, systematically planted or established throughout the plot. Agroforests ranged from simple systems containing one or two additional commercial plant species, to (rarely) complex jungle rubber systems containing multiple native tree species (Chapter 3).

Smaller areas of oil palm, fruit orchards, rice paddy, and forest fragments were also present in the landscapes. The largest forest fragments were ~320 ha of karst hilltop forest in Phattalung province and 400 ha of fragmented secondary community forest in Songkhla province; other forest patches were much smaller (~4 ha) and usually comprised heavily degraded forest and scrub. Three substantial protected forest areas in the region cover mostly upland areas (from 100 m to 1,350 m asl): Khao Ban Thad Wildlife Sanctuary (126,696 ha, partly in Phattalung, also an IBA; Birdlife International 2015), Ton Nga-Chang Wildlife Sanctuary (18,195 ha; partly in Songkhla province; Phommexay *et al.* 2011) and Khao Nam Kang National Park (212,000ha, Songkhla province; DNP 2017; map Supplementary Figure 1). Rain is usually frequent from May to December, while January to March is considered the dry season (Phommexay *et al.* 2011). Bird and habitat data were collected during March - June 2016, during unusually low rainfall and high temperatures (Chapter 3) during an El Niño-Southern Oscillation event (Limsakul and Singhruck 2016).

5.3.2 Sampling sites

Data were collected from 64 rubber "plots", defined as management units containing rubber trees of a uniform age with minimum area ≥1 ha, at least 100 m x 100 m in dimensions. Plots were categorised as either monoculture (MO; n = 25) or agroforest (AF; n = 39). Three plots classed as MO contained two or fewer non-rubber species that were patchily distributed at densities too low to be considered agroforestry; these included pineapple *Ananas comosus* plants in a small portion of the plot, a single fruit tree or scattered timber or palm stems. Mean elevation of plots was 82.6 m asl (range 35.0 - 137.1 m asl).

To simplify the collection of landscape composition data, plots were clustered into 23 sampling "blocks" of 600 m x 600 m, with central points of plots at least 200 m but not more than 400 m apart (Figure 1). Each block contained two or three plots, and we attempted to represent examples of both AF and MO in each block (all blocks contained AF plots, five lacked MO plots), depending on the number of suitable plots available in each area. The area and dimensions of each plot were measured by walking the boundary on foot while holding a GPS, with dimensions confirmed by laser rangefinder.

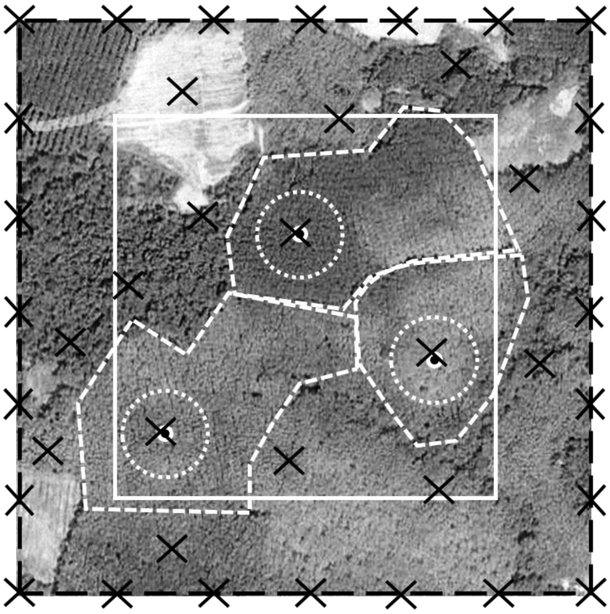

FIGURE 1 – SURVEY PLOT AND BLOCK DESIGN.

Black crosses = GPS points recording land use; white circles = bird point count centre; white dotted circles = bird point count 50 m sampling radius; dashed white line = perimeter of plot, minimum 100 m x 100 m (1 ha); solid white line shows boundary of the 400 m x 400 m square containing plot centroids; long black dashed line shows perimeter of 100 m buffer around the 400 m square, forming the 600 m x 600 m (36 ha) sampling block.

5.3.3 Bird surveys

Birds were surveyed using ten-minute point counts conducted in the centre of each survey plot on three consecutive mornings, between 0600 and 0930, alternating the order in which points were visited each day (following Gilroy, Woodcock, *et al.* 2014). The maximum abundance of each species recorded on any single morning was used in analysis. Each plot had one point count located at its centre (Figure 1). To control for potential weather and seasonal effects, two or three blocks (i.e. up to nine plots, AF and MO) were surveyed each day. Fifteen-minute point counts were trialled during two weeks of pilot surveys, but were found to add no additional registrations. Birds were identified to species using sight or sound, and abundances were recorded within distance bands (A: 0 – 10m, B: 10 – 25m, C: 25 – 50m, D: 50 – 100m), along with detection method (visual, aural). Flyovers of raptors, swifts and swallows were also recorded, but were not included in analysis. Digital sound recordings were made of each point count, using an Olympus LS-11 Linear Recorder. All counts were conducted by the same observer who was already familiar with bird sounds from the region. Unknown sounds were noted during the point count and were later checked against region-specific bird sound recordings (Xeno-canto Foundation 2017). Analyses at the plot level included registrations within a 50 m radius of the point count, and included both resident and non-breeding migratory species.

5.3.4 Land use composition and distance to contiguous forest

To provide a measure of the land-use composition of each block, land use was recorded systematically at 100 m intervals along the block perimeter, once within each sample plot and once in the management units adjacent to each sampled plot in each of the four cardinal directions, giving 39 land-use data points per block; Figure 1). Where plots were adjacent (as in Figure 1), land use of the next-closest management units within the block was recorded, and where only two sample plots occurred within a block, land use was recorded in one additional management unit and its neighbours, thus 39 points were recorded for every block (with relative frequency taken to represent area extent). Land use was recorded as one of 14 categories: rubber agroforestry (AF), monocultural rubber (MO), immature rubber (IM), bare ground (BG), scrub (SC), village, road or town (UB), natural forest (NF), fruit orchard (FO), home garden (HG), cassava (CA), oil palm (OP), rice paddy (PA), timber plantation (TI) or coconut grove (CO).

The land-use points were summarised into four explanatory variables for further analysis: the percentage of points that were rubber plantations (total of AF and MO), the percentage of points in natural forest (NF); the ratio of AF to MO; and the Shannon-Weiner diversity index of land uses (using point-frequency data). The distance (metres) between the centre of each plot, and thus each point count location, and the edge of the nearest contiguous forest area (one of the protected forest areas) was measured using Google Earth Pro 7.1.5.1557, based on cloud-free images collected between March and September 2015, on which contiguous forest stood out clearly from the rubber-dominated farmland mosaic.

5.3.5 Plot-level habitat structure data collection

For each agroforestry plot sampled, the number of agroforestry species and names of timber, fruit species and leaf species (species where edible leaves are harvested, or where leaves are collected for non-consumption e.g. roofing) were recorded by questioning the farmer. Application of herbicide and manual clearance of the understorey was observed in some MO plots during the survey period, and development and removal of the herb layer may be cyclical or episodic in both AF and MO plots. Farmers typically reported that herbicides and pesticides were not used in AF plots. We could not validate this, but sacks of chemical fertiliser, applied to promote tree growth, were seen in some MO and AF plots. Grazing animals were occasionally observed moving through plots, but did not necessarily belong to the plot owner.

Other aspects of habitat structure were directly measured in each biodiversity plot. Stem density of all trees ≥5 cm DBH (categorised as rubber, fruit, timber, palm or naturally regenerated trees) were measured in two 10 m radius subplots located 50 m apart, following Barlow *et al* (2007), and pooled per plot for analysis, giving a stem density per hectare. These data were pooled into a single explanatory variable that was included in further analysis (all non-rubber tree stems). Fruit tree stem density was considered separately, as fruit trees provide distinct food resources. Understory complexity was quantified by counting the number of stems ≥1 m in height but ≤ 5cm DBH within two 5 m radius subplots, with the mean small stem density (ha^{-1}) per plot calculated from pooled subplots. Percentage canopy cover was measured using a spherical densiometer (counting canopy gaps) at each of four cardinal points 15 m from the centre of each tree subplot, taking the mean of eight measures per plot. One observer conducted all canopy cover observations in all plots. For herbaceous vegetation, the maximum height (to 10 cm resolution) was recorded from each of four 1 m x 1 m quadrats at cardinal points around each tree subplot, taking the mean (of eight measures) per plot.

5.3.6 Functional traits

Functional trait data were gathered for each species from the *Handbook of the Birds of the World Alive* (del Hoyo *et al.* 2017) following other studies (Edwards *et al.* 2013, Gilroy *et al.* 2015, Prescott *et al.* 2016, Cosset and Edwards 2017). We considered the following traits: mass (grams, largest reported); diet (nectarivore, frugivore, insectivore, scavenger, granivore, predator, piscivore); foraging strata (open areas, forest terrestrial, forest understorey, forest midstrata, forest canopy, aquatic); and foraging substrate (soil/leaf litter, trunk/branch, foliage, aerial, sub-water-surface; Flynn *et al.* 2009, Edwards *et al.* 2013, Gilroy *et al.* 2015, Prescott *et al.* 2016, Cosset and Edwards 2017). Mass was a continuous variable, and each level within diet type, and foraging strata and substrates was binary (Supplementary Table 1) and were scored 1 when mentioned in the species account, unless qualified with the terms “sometimes”, “occasionally” or “rarely”, in which case they were scored 0.

5.3.7 Statistical analysis

5.3.7.1 Metrics of functional diversity

Continuous measures of functional diversity quantify variation in species functional traits, and improve on functional-group approaches by accounting for variation within functional groups, and by allowing the assessment of multiple traits simultaneously (Petchey *et al.* 2004, Petchey and Gaston 2006, Villéger *et al.* 2008, Mouillot *et al.* 2013). We calculated five functional diversity metrics:

1) functional diversity (FD) – a tree-based metric, calculated by using a distance matrix of functional traits to create a functional dendrogram of the entire species pool across all samples, and then calculating the total branch lengths for samples of interest (Petchey and Gaston 2002);

2) standard effect size of FD (sesFD) - FD is sensitive to species richness, so the standard effect size of FD (sesFD) was also calculated by randomising species identities (across the entire species pool) within each sample, while holding species richness and frequency constant;

3) functional evenness (FEve) - a measure of the regularity of species abundances in functional space, calculated as the shortest minimum spanning tree that links all species within a community, and which can be interpreted as the degree of occupation of niches (Villéger *et al.* 2008);

4) functional dispersion (FDis); and

5) Rao's quadratic entropy (Rao's Q) – FDis and Rao's Q can both be interpreted as a measure of variability in functional traits in a community, and are closely related, although calculated differently (Laliberté and Legendre 2010).

All analyses were calculated in R, using the packages FD and picante (Kembel *et al.* 2010, Laliberté and Legendre 2010, Laliberté *et al.* 2014, R Core Team 2017). All measures were based on a distance (dissimilarity) matrix which represented trait differences between species, calculated from the species trait matrix using extended Gower distance, which can handle continuous and binary variables (Podani and Schmera 2006, Pavoine *et al.* 2009). This was created using the gowdist function from the FD package (Laliberté and Legendre 2010, Laliberté *et al.* 2014). Values of mass were standardised (by subtracting the unweighted mean across all species, and dividing by the standard deviation) before the distance matrix was created (Laliberté and Legendre 2010).

The functional dendrogram used to calculate FD and sesFD was created using unweighted pair-group method with averaging (UPGMA) clustering; this gave the greatest co-phenetic correlation coefficient (0.78) relative to other clustering methods (complete-linkage, single-linkage, Ward's minimum variance), meaning UPGMA produced the dendrogram that most closely reflected pairwise distances between species in the distance matrix (Petchey and Gaston 2006). FD was then calculated using function pd in package picante (Kembel *et al.* 2010). FD does not account for species abundances, and rare species (defined as singletons or doubletons) could have been recorded within only one of the two plot types (agroforestry or monoculture) by chance; we therefore repeated the FD analysis omitting singleton and doubleton species (Edwards *et al.* 2013). Standardised effect size of FD (sesFD) was calculated using the "trial-swap" method (Miklós and Podani 2004); this was repeated 999 times, with the standard effect size calculated as:

(observed FD – mean randomised FD)/standard deviation randomised FD

using the ses.pd function in picante package (Kembel *et al.* 2010).

FDis (Laliberté and Legendre 2010) is calculated as the change in the abundance-weighted deviation of species trait values from the centre of functional trait space, and Rao's Q (Botta-Dukat 2005) is the abundance-weighted variance of the pair-wise distances between all species pairs, and is based on Simpson's Diversity index (Mouillot *et al.* 2013). FDis, Rao's Q and FEve are not affected by species richness, and they can be calculated when the number of traits is less than the number of species within a sample. FEve, FDis and Rao's Q (scaled by its maximal value) were all calculated using the dbFD function in the package FD (Laliberté *et al.* 2014).

Two other commonly used measures of functional diversity, functional richness (FRic) and functional divergence (FDiv; Villéger *et al.* 2008), require a greater number of species than traits for any individual sample (i.e. each plot containing a single point count in this study) and require continuous or binary traits rather than categorical variables (Schleuter *et al.* 2010). However, in our study, we had fewer species at the plot level (range: 4 – 18) than traits in our matrix (19), making FRic and FDiv inappropriate for use with our dataset.

5.3.7.2 Response of functional diversity to plot type, habitat structural variables, land-use composition variables, and distance to forest

FD and Rao's Q were compared between AF and MO at the habitat level using sample-based rarefaction, as different sample sizes were obtained in AF and MO. Rarefaction was conducted using the alpha_accum function in package BAT (Cardoso *et al.* 2017) and the rare_Rao function in package adiv (Ricotta *et al.* 2012, Pavoine 2017) respectively, using 9999 iterations. Confidence intervals are given for rarefied Rao's Q, but are not calculated by the alpha_accum function for rarefied FD. Rarefaction methods for the other functional diversity metrics (sesFD, FEve, FDis) are not currently available.

All functional diversity metrics were calculated for each plot, and were compared between AF and MO using plots as replicates. For each taxon, the response of plot-level functional diversity to plot type, habitat structure, land-use composition and distance to the nearest contiguous forest area was investigated using a multi-level approach. First, response to plot type (AF or MO) was investigated using hypothesis testing. Second, response to habitat structure within plots was investigated across all plots (irrespective of plot type) using multi-model inference (Burnham and Anderson 2002). Finally, response to plot type, any habitat structure variables found to be influential in the previous step, land-use composition of the sampling block, and distance to the nearest contiguous forest area, was investigated using multi-model inference. In both plot-scale habitat and multi-scale models, averaging was conducted over the 95% confidence set (Burnham and Anderson 2002).

Linear mixed models (LMMs) were used in all cases aside for FDis and Rao's Q, for which generalised linear mixed models (GLMMs) using a Gamma distribution (with identity and log link functions respectively) were used to ensure normality and heteroscedasticity of model residuals; these were conducted using the lmer and glmer functions in the lme4 package (Bates *et al.* 2015). Block was included as an intercept-only random effect in all models to account for the nested sampling design. Spatial autocorrelation in model residuals was examined in each case using a Monte-Carlo permutation test for Moran's I with the moran.mc function in package spdep with 1000 iterations (Bivand *et al.* 2013, Bivand and Piras 2015). Model residuals were tested for overdispersion, but theta

(Pearson residuals/residual degrees of freedom) was less than one in all cases (Burnham and Anderson 2002).

5.3.7.2.1 Plot type

Species richness per plot was compared between AF and MO using an LMM or GLMM to place functional diversity measure in context. Support for a plot type effect was assessed by the change in Akaike Information Criterion (corrected for small sample size, AICc) relative to a null model containing only block as a random effect (Burnham and Anderson 2002). A negative ΔAICc is given when the null model had a lower AICc than the plot type model.

5.3.7.2.2 Plot-level habitat structure models

Plot-level functional diversity response to habitat structure was investigated using multi-model inference. A global LMM or GLMM was constructed for each functional diversity metric, containing six plot-level explanatory habitat variables (herb height, canopy cover, small stem density, number of agroforestry species, non-rubber tree stem density and fruit tree stem density) with block as a random effect, and a null (intercept-only) model was generated that contained only block as a random effect. All habitat structure variables were centred and standardised (to zero mean and 0.5 SD) so that effect sizes were on comparable scales (Grueber *et al.* 2011). The global model for each functional diversity metric was validated by checking for heteroscedasticity and normality of residuals, and residuals were checked for spatial autocorrelation using Moran's I statistic. A set of 99 candidate models, comprising all possible model subsets with four or fewer variables (to ensure at least 15 observations for each candidate variable, from n = 64 plot observations) plus the null and the global models, was generated using the dredge function in the MuMIn package (Grueber *et al.* 2011, Bartoń 2016).

Candidate models were ranked according to AICc weights, using the ICtab function in the bbmle package (Bolker and R Development Core Team 2017); those with a cumulative weight of 95% were averaged, using the full (zero) averaging method (Burnham and Anderson 2002, Grueber *et al.* 2011) using the model.avg function in the MuMIn package (Bartoń 2016). Candidate variables were considered to have an influence on species richness where the 95% confidence intervals of the averaged parameter estimate did not include zero (Grueber *et al.* 2011). Influential habitat variables were included in further models of land-use composition effects.

5.3.7.2.3 Multi-scale habitat structure and land-use composition models

The same multi-model inference procedures were then used to investigate functional diversity response to land-use composition and distance to the nearest contiguous forest block. In addition to any plot-level habitat variables found to be influential during the previous stage of analysis, a multi-scale global LMM or GLMM was defined for each functional diversity metric that also contained four land-use variables (land-use Shannon diversity, percentage rubber points, percentage natural forest points, AF:MO ratio), plot type, distance to nearest contiguous forest area, and three interaction terms (plot type and AF:MO ratio; plot type and percentage natural forest points, plot type and distance to nearest forest).

To investigate interactions and visualise effect sizes of functional diversity response to influential variables, predictions from the final averaged models were made using the predict function in the MuMIn package which used full (zero) averaging across all models and calculated fitted functional diversity at mean levels of the random effect (Bartoń 2016). Predictions were made using the standardised variables and link function of the final model, but these were back transformed to give predictions and variables in original units. Predictions were made at intervals of 0.05 standardised units of the variable of interest. All continuous explanatory variables aside from the variable of interest were held at the mean, and the random effect of block was included. The SE of predictions from the averaged model were not calculated, as tools to calculate prediction intervals for GLMMs conducted using the lme4 package (Knowles and Frederick 2016) cannot be applied to averaged models.

5.3.8 Trait – environment relationships

To assess the relationship between individual traits and environmental variables, we used RLQ analysis (Dolédec *et al.* 1996), which summarises the multivariate structure of three tables (matrices) containing species-trait (Q) and plot-environment data (R), linked by plot-level species-abundances (L). Analysis was conducted using function rlq in package ade4 (Dray and Dufour 2007). To test the global significance of the trait-environment relationships, we then used a multivariate test based on the total inertia of the RLQ analysis where both species and sites are permuted 9999 times and compared to the observed total inertia (Dray and Legendre 2008, ter Braak *et al.* 2012); this was conducted using the function randtest.rlq in the ade4 package (Dray and Dufour 2007).

We also used another three-table approach, fourth-corner analysis, which differs from RLQ by testing for correlations between individual traits and environmental variables, followed by significance testing using permutation (Legendre *et al.* 1997, Dray and Legendre 2008, ter Braak *et al.* 2012). As for the RLQ analysis, species and sites were permuted 9999 times, and p-values were corrected for multiple comparisons (Dray *et al.* 2014), using function fourthcorner in the ade4 package (Dray and Dufour 2007).

All habitat variables, land-use composition variables, and distance to nearest forest were included in the RLQ and fourth-corner analyses as explanatory variables.

5.4 Results

Sixty-nine bird species were recorded across all rubber plots, 64 of which were recorded within AF plots (20 unique to AF) and 49 within MO plots (5 unique to MO). Twenty-two species were recorded as singletons or doubletons (i.e. "rare" species): 15 of these were found only in AF plots and five were found only in MO (the other two doubletons were found in both plot types). Thus, 70% of the species unique to AF and 100% of those unique to MO were rare species. Neither the AF-unique nor MO-unique species showed strong clustering on the functional dendrogram (Figure 1; without rarities Supplementary Figure 1).

Almost all bird species recorded were insectivorous, of which 21 species were obligate insectivores, and a further 43 were able to utilise other food types (Supplementary Table 1). Only three obligate frugivores or nectarivores were recorded (a single Blue-Crowned Hanging Parrot *Loriculus galgulus*, Crimson-Breasted Flowerpecker *Prionochilus percussus*, and Yellow-Breasted Flowerpecker *Prionochilus maculatus*), and only two granivorous species (Zebra Dove *Geopelia striata* and Spotted Dove *Spilopelia chinensis*). Only three species were obligately terrestrial, five were obligate understorey foragers and 11 foraged only in the canopy. A further eight species only use open habitats for foraging.

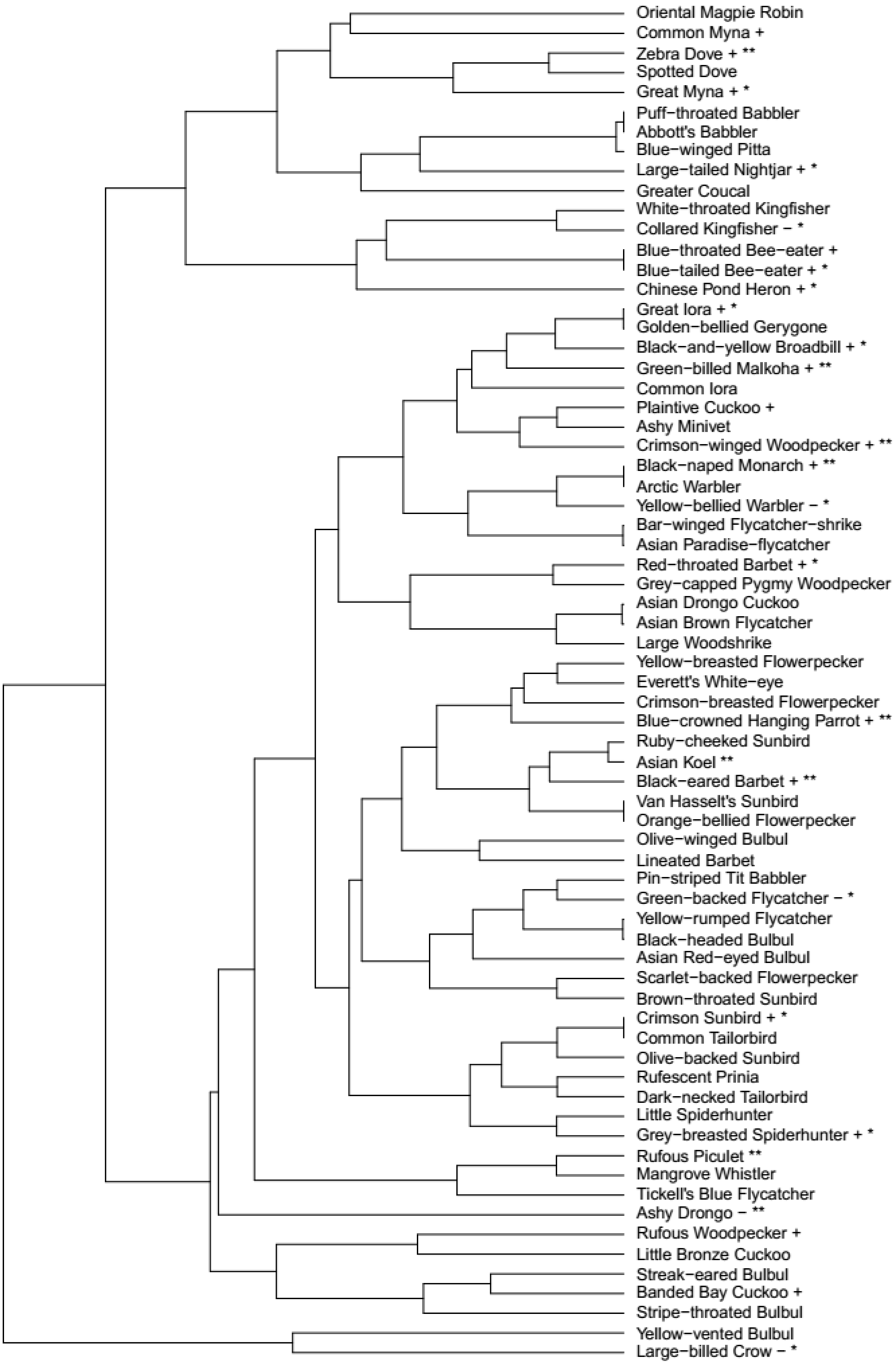

FIGURE 1 – FUNCTIONAL DENDROGRAM OF 69 BIRD SPECIES RECORDED ACROSS ALL RUBBER PLOTS, BASED ON THE TRAITS IN SUPPLEMENTARY TABLE 1. The symbol + after the species name means the species was only recorded in AF, - means species was only recorded in MO plots. A * after the name means this species was recorded as a singleton, and ** means a doubleton.

5.4.1 Effect of rubber agroforestry on functional diversity metrics

5.4.1.1 Habitat level

At the habitat level, rarefaction showed that while there was no difference in species richness between AF and MO, as confidence intervals overlapped, FD appeared to be greater in AF than MO, although the difference was minimal (Figure 2a, b). Rao's Q (a measure of functional dispersion, where lower values indicated clustering of traits; Figure 2c) was greater in MO. Thus, while functional diversity and occupation of niches was marginally greater in AF overall, dispersion of functional traits was greater in MO, and the degree of clustering was greater in AF.

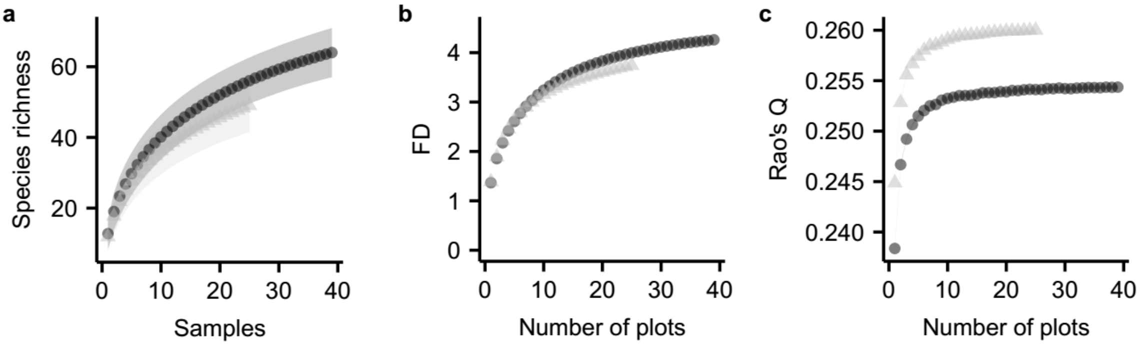

FIGURE 2 - RAREFIED HABITAT LEVEL SPECIES RICHNESS, FD AND RAO'S Q. Panels show a) species richness, b) FD and c) Rao's Q. Black circles = AF, grey triangles = MO. Confidence intervals are not calculated by the alpha_accum function (package BAT, (Cardoso et al. 2015)) used to rarefy FD, and were calculated for Rao's Q but are too small to be visible.

Dataset	Metric	AF	MO
All	Species richness	12.77 ± 0.96	11.88 ± 1.19
	FD	1.37 ± 0.08	1.37 ± 0.12
	sesFD	-0.91 ± -0.28	-0.42 ± -0.32
	FEve	0.78 ± 0.02	0.81 ± 0.02
	FDis	3.32 ± 0.09	3.36 ± 0.13
	RaoQ	0.21 ± 0.01	0.22 ± 0.02
No rarities	Species richness	12.21 ± 0.93	11.56 ± 1.18
	FD	1.32 ± 0.08	1.33 ± 0.12
	sesFD	0.04 ± 0.10	0.34 ± 0.13
	FEve	0.77 ± 0.02	0.80 ± 0.02
	FDis	3.45 ± 0.12	3.46 ± 0.17
	RaoQ	0.32 ± 0.03	0.32 ± 0.04

TABLE 1 – PLOT LEVEL SPECIES RICHNESS AND FUNCTIONAL DIVERSITY METRICS. Results show mean ± 1 SE. "No rarities" results exclude singleton and doubleton species.

5.4.1.2 Plot level

At the plot level, sesFD was greater than zero in both AF (t = 13.53, df = 38, p = <0.001) and MO (t = 10.77, df = 24, p < 0.001), meaning observed FD was greater than expected by chance in both plot types, indicating FD of species within each of AF and MO differed from the overall species pool. Plot level sesFD was greater in MO than in AF (Figure 3c, Table 1), but all other functional diversity measures were similar between plot types. When singletons and doubletons were omitted from the analyses all metrics retained the same pattern as for the full dataset (Table 1). There was no evidence of spatial autocorrelation in any of the model residuals (p > 0.380).

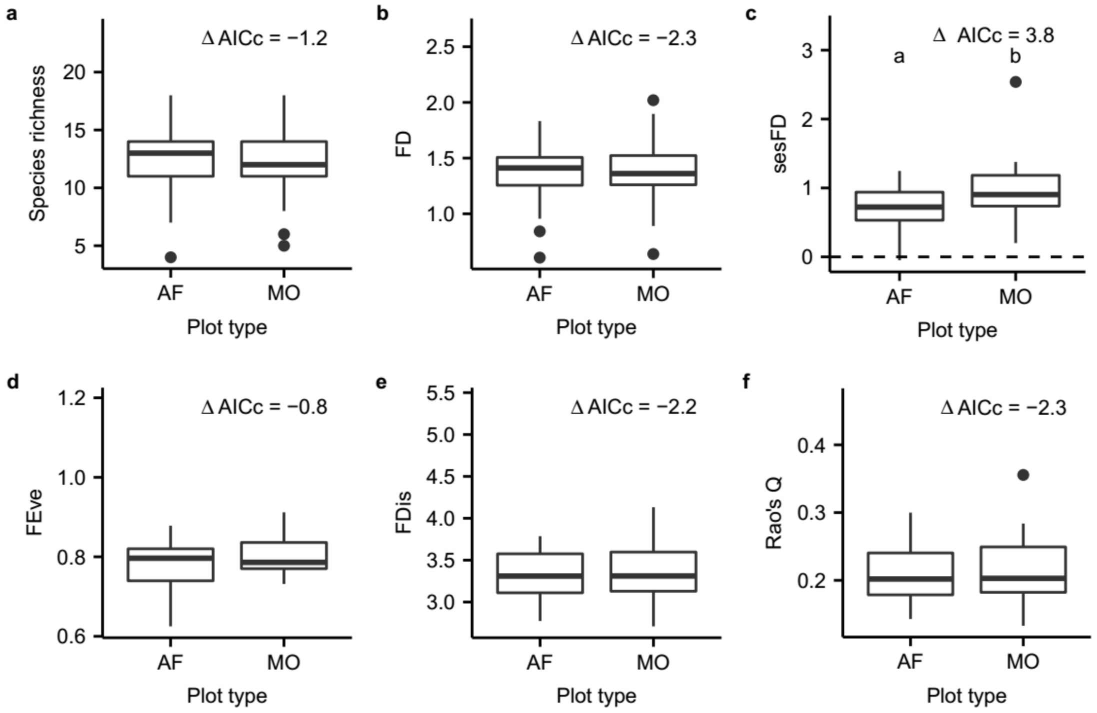

FIGURE 3 – PLOT-LEVEL SPECIES RICHNESS AND FUNCTIONAL DIVERSITY METRICS Panels show a) species richness, b) FD, c) sesFD, d) FEve, e) FDis and f) Rao's Q. Summary statistics given in Table 1. Central line in box shows median, box bounds show upper and lower quartiles, whiskers extend to 1.5x inter-quartile range, outliers shown as dots. ΔAICc is for a null model (containing block as a random effect) relative to a generalised linear model of response to plot type; a negative ΔAICc shows that the null model had a lower AICc than the alternative; different letters above the boxes indicate where plot type influences species richness.

5.4.2 Effect of plot level habitat structural variables

Averaging across the 95% confidence set of candidate models relating functional diversity metrics to habitat structure variables showed that FD was positively influenced by the density of fruit tree stems and herb height (Figure 4a), and that sesFD was negatively influenced by herb height and the density of small stems (Figure 4b). All other metrics were unaffected by any plot level habitat structure variables (Figure 4c – e).

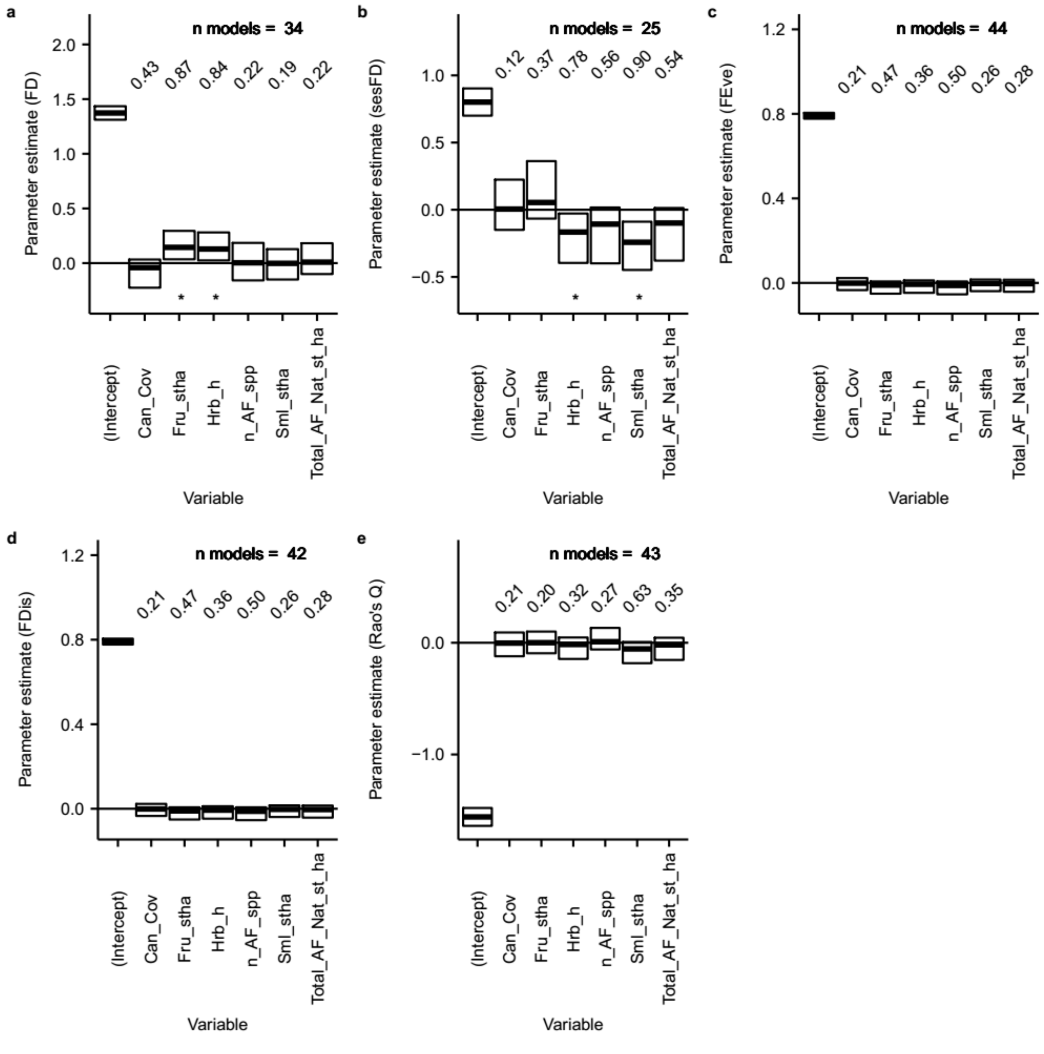

FIGURE 4 - PARAMETER ESTIMATES FOR THE AVERAGED MODELS OF FUNCTIONAL DIVERSITY METRIC RESPONSE TO HABITAT STRUCTURAL VARIABLES. Panels show: a) FD, b) sesFD, c) FEve, d) FDis and e) Rao's Q. In each case, full-model averaging was conducted across the 95% confidence set (sum of Akaike weights < 0.95) of all possible sub-models containing a maximum of four predictor variables. Number of models within the 95% confidence set is shown on each panel. Central line in each bar shows averaged parameter estimate (predicted change in species richness with a one-unit change of the standardised predictor variable), bar encloses lower and upper 95% CI of parameter estimate. Parameter estimates with 95% CIs that exclude zero are considered influential, and are marked with * below the bar. Relative variable importance (the proportion of models within the 95% confidence set that contain each predictor) is shown above each bar. Plot type

is MO relative to AF. Habitat variables (plot level): Can_Cov = canopy cover (%); Fru_stha = stem density of fruit trees (stems ha^{-1}); Hrb_h = herb height (cm); n_AF_spp = number agroforestry species; Tot_AF_Nat_st_ha = stem density of non-rubber trees; Sml_stha = density of small stems (stems ha^{-1}).

5.4.3 Effect of plot type, habitat structure, land-use composition variables and distance to contiguous forest

Averaging across the 95% confidence set of candidate multi-scale models for each functional diversity metrics (which included influential habitat variables from the previous step, together with plot type, land-use composition variables and distance to the nearest contiguous forest block) showed that FD was again positively influenced by the density of fruit tree stems and herb height, but not by any land-use variables (Figure 5a). In addition, sesFD was negatively influenced by the extent of natural forest in the sampling block, as well as the density of small stems within the plot as found in the previous step, but herb height was no longer influential (Figure 5b). The two measures of functional dispersion, FDis and Rao's Q, were both influenced by the interaction between plot type (AF or MO) and the distance to natural forest (Figure 5d-e). FEve was unaffected by any variables (Figure 5c)

Predictions from the averaged multi-scale models show the positive effect of herb height on FD across both plot types (Figure 6a), and the positive effect of fruit tree stem density on FD in both plot types (Figure 6b). The negative effect on sesFD of increasing small stem density (Figure 6c) and increasing extent of natural forest (Figure 6d) across both plot types are also clear. Plotting the interaction between plot type and distance to the nearest contiguous forest block for FDis and Rao's Q showed a negative effect of increasing distance to forest within MO plots and a positive effect of increasing distance to forest within AF plots (for both metrics), but the effect was very small (Figure 6e-f).

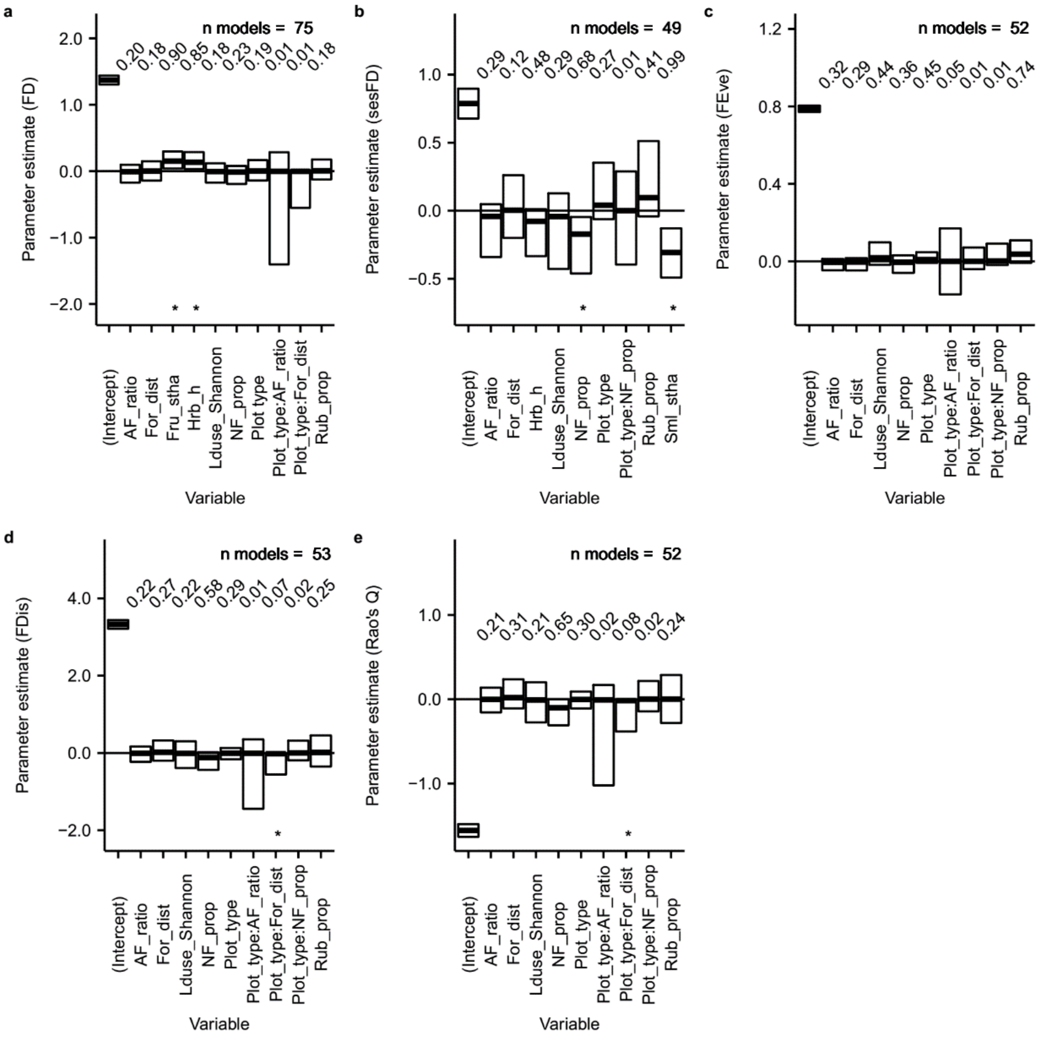

FIGURE 5 - PARAMETER ESTIMATES FOR THE AVERAGED MODELS OF FUNCTIONAL DIVERSITY METRIC RESPONSE TO INFLUENTIAL HABITAT STRUCTURAL VARIABLES, PLOT TYPE, AND LAND-USE COMPOSITION VARIABLES. Panels show: a) FD, b) sesFD, c) FEve, d) FDis and e) Rao's Q. Methods and display of parameter estimates as for Figure 4. Plot type is MO relative to AF. Habitat variables as for Figure 4. Land use variables (block level): AF_ratio = ratio of AF to MO; Lduse_Shannon = Shannon diversity index of land-use points; NF_prop = points in natural forest (%); Rub_prop = points in rubber plot, whether AF or MO (%). For_dist = distance to nearest contiguous forest block.

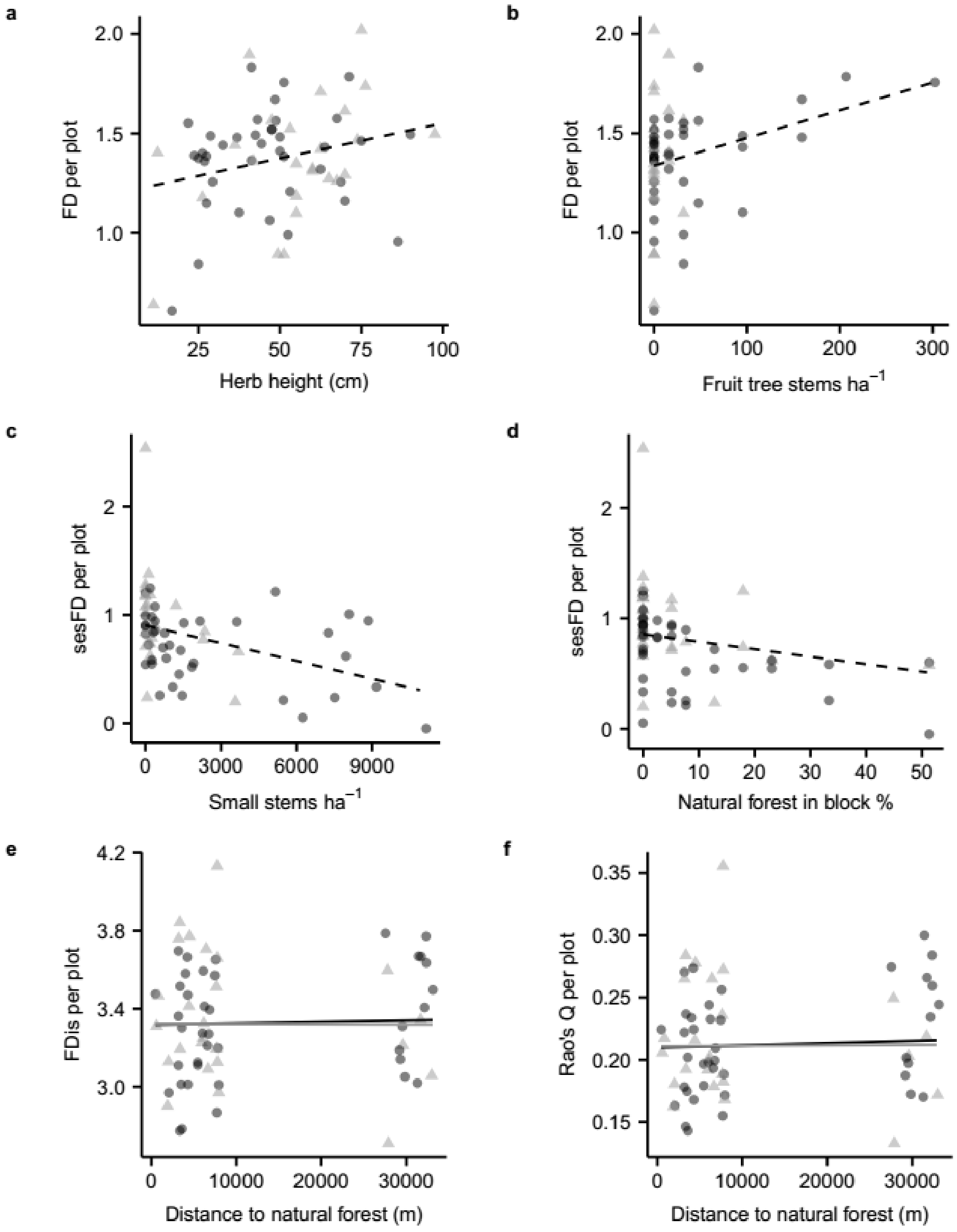

FIGURE 6 – PREDICTED VALUES OF FUNCTIONAL DIVERSITY METRIC RESPONSE TO INFLUENTIAL VARIABLES FROM THE AVERAGED MULTI-SCALE MODELS. Panels show: a) FD response to herb height, b) FD response to density of fruit trees, c) sesFD response to small stem density, d) sesFD response to percentage of land-use points in natural forest (no interaction with plot type for plots a - d; effect in both plot types shown as dotted line), e) FDis and f) Rao's Q response to distance to natural forest (showing the interaction with plot type, black line = AF, grey line = MO). Original data points shown (each point represents one plot; black circles = AF, grey triangles = MO). Lines fitted to predicted functional diversity values (points not shown) with a linear model; CI not plotted as SE cannot be reliably computed for mixed effects models.

5.4.4 Response of individual functional traits

The complete set of trait-environment relationships in the RLQ analysis were significant when sites were permuted (p = 0.007) but not when species were permuted (p = 0.436), and thus the observed relationships (Figure 7) may be no different than from a random distribution. Total inertia (explained variance) of the RLQ analysis was 35%, with 54% projected onto RLQ axis 1, and 22% on RLQ axis 2 (Figure 7). Overall correlation between environmental variables and traits was quite low for both RLQ axis 1 (0.21) and axis 2 (0.18). RLQ axis 1 preserved 74% of variance in environmental variables and 48.1% of variance in trait variables, while axis 2 preserved a further 11% of environmental variance and 20% of trait variance. Fourth-corner analysis supported the lack of confidence in the findings of the RLQ analysis, showing that none of the individual functional traits were significantly correlated with any environmental variables, including plot type (adjusted-p ≥0.54).

Plots of species in environment-trait space showed a high degree of overlap between AF and MO, with only a handful of species differing between plot types (Figure 8). These were all species that prefer open habitats, or forage in aquatic habitats: in AF, Common Myna (*Acridotheres tristis*), Chinese Pond Heron (*Ardeola bacchus*) and Collared Kingfisher (*Todiramphus chloris*; numbers 3, 10 and 31 on Figure 8b), and in MO, Large-Billed Crow (*Corvus macrorhynchos*), White-Throated Kingfisher (*Halcyon smyrnensis*) and Collared Kingfisher (*Todiramphus chloris*; numbers 19, 31 and 68 in Figure 8c).

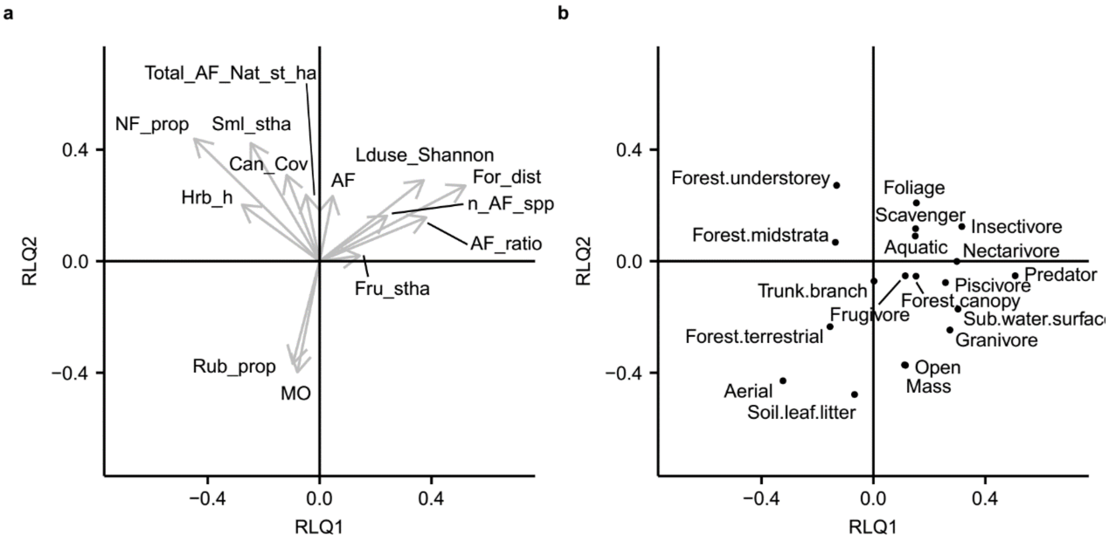

FIGURE 7 –RLQ SCORES FOR ENVIRONMENTAL VARIABLES AND FUNCTIONAL TRAITS. Panels show a) environmental variables, including plot type, habitat variables, land-use composition and distance to forest, and b) species traits. Habitat variables (plot level): Can_Cov = canopy cover (%); Fru_stha = stem density of fruit trees (stems ha^{-1}); Hrb_h = herb height (cm); n_AF_spp = number agroforestry species; Tot_AF_Nat_st_ha = stem density of non-rubber trees; Sml_stha = density of small stems (stems ha^{-1}). Land use variables (block level): AF_ratio = ratio of AF to MO; Lduse_Shannon = Shannon diversity index of land-use points; NF_prop = points in natural forest (%); Rub_prop = points in rubber plot, whether AF or MO (%). For_dist = distance to nearest contiguous forest block.

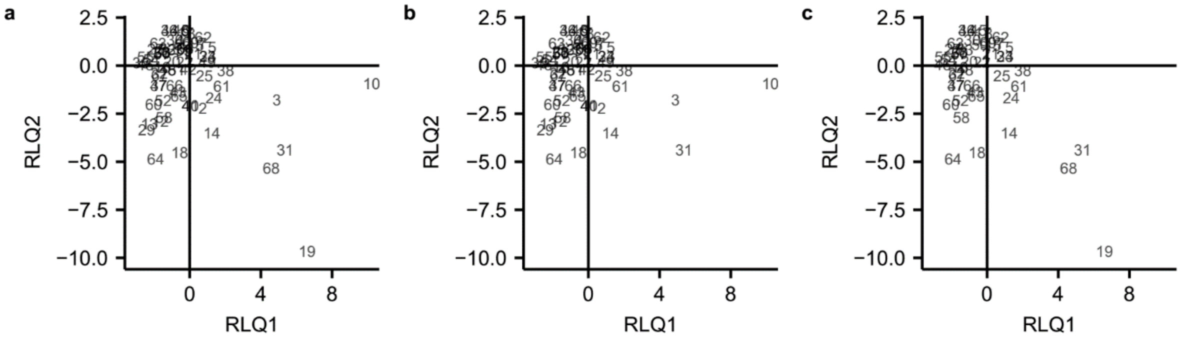

FIGURE 8 –RLQ SCORES FOR SPECIES. Panels show a) all plots, b) AF plots and c) MO plots.

5.5 Discussion

We assessed the functional diversity of birds in high-yielding "intensive" rubber agroforests (AF) and monocultures (MO) in a rubber-dominated landscape in southern Thailand, to ask whether agroforest may support greater functional diversity, and thus ecosystem functioning and services, than monocultural rubber. We found that the standardised effect size of FD was greater in MO, rather than in AF; this pattern is likely explained by the presence of species that prefer open and aquatic habitats in MO that were absent from AF, while the vast majority of species we recorded were clustered in functional trait space. Almost all of these were small-medium sized insectivorous species, either obligate insectivores, or omnivores that could feed on insects. This reflects the findings of other studies assessing avian functional diversity in agro-ecosystems containing forest fragments, agroforestry and agriculture (Tscharntke *et al.* 2008, Sekercioglu 2012). No other functional diversity metrics differed between AF and MO. Together with the absence of any significant relationships between specific traits and environmental variables, and the functional overlap shown between species in AF and MO in the RLQ analysis, this suggests that functional diversity and functional composition of birds was broadly similar across all the rubber plots we surveyed.

Beyond comparisons between AF and MO, we found that FD increased with increasing herb height and the density of fruit trees stems in the rubber plot. Species richness was also positively influenced by herb height (Chapter 3), and as FD and species richness are known to be correlated (Schleuter *et al.* 2010), this pattern may be explained by presence of additional bird species, without an independent effect on functional diversity. Maintenance of the herb layer in rubber monocultures or agroforests therefore appears to benefit for functional diversity, as well as species richness (Chapter 3, Nájera and Simonetti 2010, Azhar *et al.* 2011, 2013, Teuscher *et al.* 2015), and may thus be an easily implemented strategy for improving ecological functioning in rubber plantations. In contrast, avian species richness was not influenced by fruit tree stem density (Chapter 3) suggesting effects on functional diversity were independent of species richness. Work in Indonesia found that the total density of trees in cocoa agroforests influenced functional diversity (Clough *et al.* 2009), but the effect fruit trees was not tested separately. We did find not find that overall non-rubber tree density was influential for functional diversity, though it does influence bird species composition (Chapter 3). The majority of rubber plots contained no fruiting tree species whatsoever, so although our data were collected outside of the fruiting season, fruit trees may provide additional resources not provided by timber species that are otherwise absent from rubber plantations, such as nectar, although we collected no data on the presence of flowers. Planting of fruit trees as part of intensive rubber agroforestry systems may therefore increase the functional diversity of rubber plantations. The separate effect of fruit trees may also be due to the presence of mixed fruit orchards and home-gardens in the landscape (Round *et al.* 2006, Phommexay *et al.* 2011, Sritongchuay *et al.* 2016), which may sustain a pool of bird species adapted to capturing resources from fruit trees.

When we adjusted FD for species richness, we found that sesFD declined with increasing small stem density (a measure of understorey clutter) and the proportion of natural forest in the sampling block, suggesting that functional redundancy increased as the understorey became denser and the proportion of forest fragments in the surrounding landscape increased. This pattern may have been driven by the presence of more functionally distinct, open and aquatic habitat species that were recorded in MO plots, which may have been more likely to be found in landscapes containing less natural forest. Increased functional redundancy in landscapes containing forest fragments may mean that ecological processes linked to avian functional diversity are more temporally stable, as species losses do not necessarily result in the loss of function (Hooper *et al.* 2005).

We found very little evidence for an effect of distance to the nearest contiguous forest block on any functional diversity metric. In cacao agroforests in Indonesia, frugi- and nectarivorous birds were the only functional groups that showed decreased species richness with increasing distance to forest blocks (Clough *et al.* 2009), and in a review of multiple studies, only forest-dependent species responded to distance from forest (Tscharntke *et al.* 2008). As we recorded almost no forest-dependent species, and very few frugivores and nectarivores from these functional groups, our findings do not contradict this study. Distance to forest also had no effect on functional diversity of birds in oil palm or pasture in Colombia, but forest within the local landscape (500m radius) influenced FD, sesFD, FRic and FEve, providing evidence for a spill-over of functional diversity from forest fragments (Prescott *et al.* 2016). We found no such effects, and suggest that this may be due to difference in the quality of forest fragments and to forest types. The study in Colombia describes an “open-savanna” system with a four-month dry season to March (Prescott *et al.* 2016), whereas forests in our study system are lowland moist tropical forests with a shorter three-month dry season. Birds adapted to open, dry forests may be more likely to have traits that enable utilisation of pasture or oil palm habitats, while in our study, birds adapted to dense evergreen forest may be less likely to persist in a landscape of plantations, degraded forest and open habitats.

5.6 Conclusions

Functional diversity of birds was similar between high-yielding “intensive” rubber agroforests and rubber monocultures, but was enhanced by the height of the herb layer and the density of fruit trees, while functional redundancy was positively influenced by the increasing density of small stems in the understorey. Maintenance of understorey vegetation and the planting of fruit trees could therefore be simple management methods for enhancing avian functional diversity in rubber plantations, without negatively impacting yields or farmer livelihoods. Our finding that functional redundancy increased with the amount of natural forest in the landscape suggests that maintenance of forest fragments could help ensure long-term stability of ecological functioning in rubber-dominated landscapes. Finally, we note that frugivorous and nectarivorous birds of any body size were almost completely absent from rubber plantations. Other habitat types, such as forest fragments or fruit orchards, are likely necessary to maintain the ecological functions that these species provide, particularly seed dispersal and pollination. This may be crucial for long-term persistence of plant species at the landscape level, functional connectivity of forest fragments, and for the maintenance of pollination services that are crucial for fruit crop production in home-gardens. While these findings are based on data from complex heterogeneous landscapes, they may be particularly important in relation to large-scale agro-industrial monocultures which seem likely to substantially reduce ecological functioning at the landscape level.

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5.9 Online supplementary material

This online supplementary information includes (in sequence as referred to in main text):

SUPPLEMENTARY TABLE 1: Bird species and traits

SUPPLEMENTARY FIGURE 1: Functional dendrogram excluding singleton and doubleton species; co-phenetic correlation = 0.77.

SUPPLEMENTARY TABLE 1: Bird species and traits

Symbols following species common names indicate: species found only in AF plots (+), species found only in MO plots (-), singletons (*) and doubletons (**). Abbreviated column headings are as follows: For = Forest; terr = terrestrial; undr = understorey; mid = midstrata; can = canopy; Aqua = aquatic; Nectiv = nectarivorous; Frugiv = frugivorous; Insect = insectivorous; Scaven = scavenger; Graniv = granivorous; Predat = predator; Pisciv = piscivorous.

				Foraging strata						Foraging substrate					Diet type								
No.	**Common name**	**Scientific name**	**Body mass (g)**	**Open**	**For terr**	**For undr**	**For mid**	**For can**	**Aqua**	**Soil/ litter**	**Trunk/ branch**	**Foliage**	**Aerial**	**Sub water**	**Nectiv**	**Frugiv**	**Insect**	**Scaven**	**Graniv**	**Predat**	**Pisciv**	**Obligate insectiv**	**Obligate foraging stratum**
1	Yellow-bellied Warbler - *	*Abroscopus superciliaris*	7.0	0	0	1	1	1	0	0	0	1	1	0	0	0	1	0	0	0	0	x	
2	Great Myna + *	*Acridotheres grandis*	103.0	1	0	0	0	0	0	1	0	1	0	0	0	1	1	0	1	0	0		Open
3	Common Myna +	*Acridotheres tristis*	143.0	1	0	0	0	0	0	1	0	0	0	0	1	1	1	1	1	1	0		Open
4	Great Iora + *	*Aegithina lafresnayei*	12.0	0	0	0	1	1	0	0	0	1	0	0	0	0	1	0	0	0	0	x	
5	Common Iora	*Aegithina tiphia*	17.0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	1	0		Canopy
6	Crimson Sunbird + *	*Aethopyga siparaja*	9.0	0	0	1	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0		Understorey
7	Brown-throated Sunbird	*Anthreptes malacensis*	13.5	0	0	1	1	1	0	0	0	1	0	0	1	1	1	0	1	0	0		
8	Little Spiderhunter	*Arachnothera longirostra*	16.1	0	0	1	0	1	0	0	0	1	0	0	1	0	1	0	0	0	0		
9	Grey-breasted Spiderhunter + *	*Arachnothera modesta*	25.5	0	0	1	1	1	0	0	0	1	0	0	1	0	1	0	0	0	0		
10	Chinese Pond Heron + *	*Ardeola bacchus*	332.0	0	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	1	1		
11	Plaintive Cuckoo +	*Cacomantis merulinus*	32.0	0	0	0	0	1	0	0	1	1	0	0	0	0	1	0	0	0	0	x	Canopy
12	Banded Bay Cuckoo +	*Cacomantis sonneratii*	37.0	1	1	0	1	1	0	1	1	1	1	0	0	0	1	0	0	0	0	x	
13	Large-tailed Nightjar + *	*Caprimulgus macrurus*	90.0	1	1	1	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0	x	
14	Greater Coucal	*Centropus sinensis*	268.0	0	1	0	0	0	0	1	0	0	0	0	0	1	1	0	1	1	0		Terrestrial
15	Ruby-cheeked Sunbird	*Chalcoparia singalensis*	9.1	0	0	0	0	1	0	0	0	1	0	0	1	1	1	0	0	0	0		Canopy

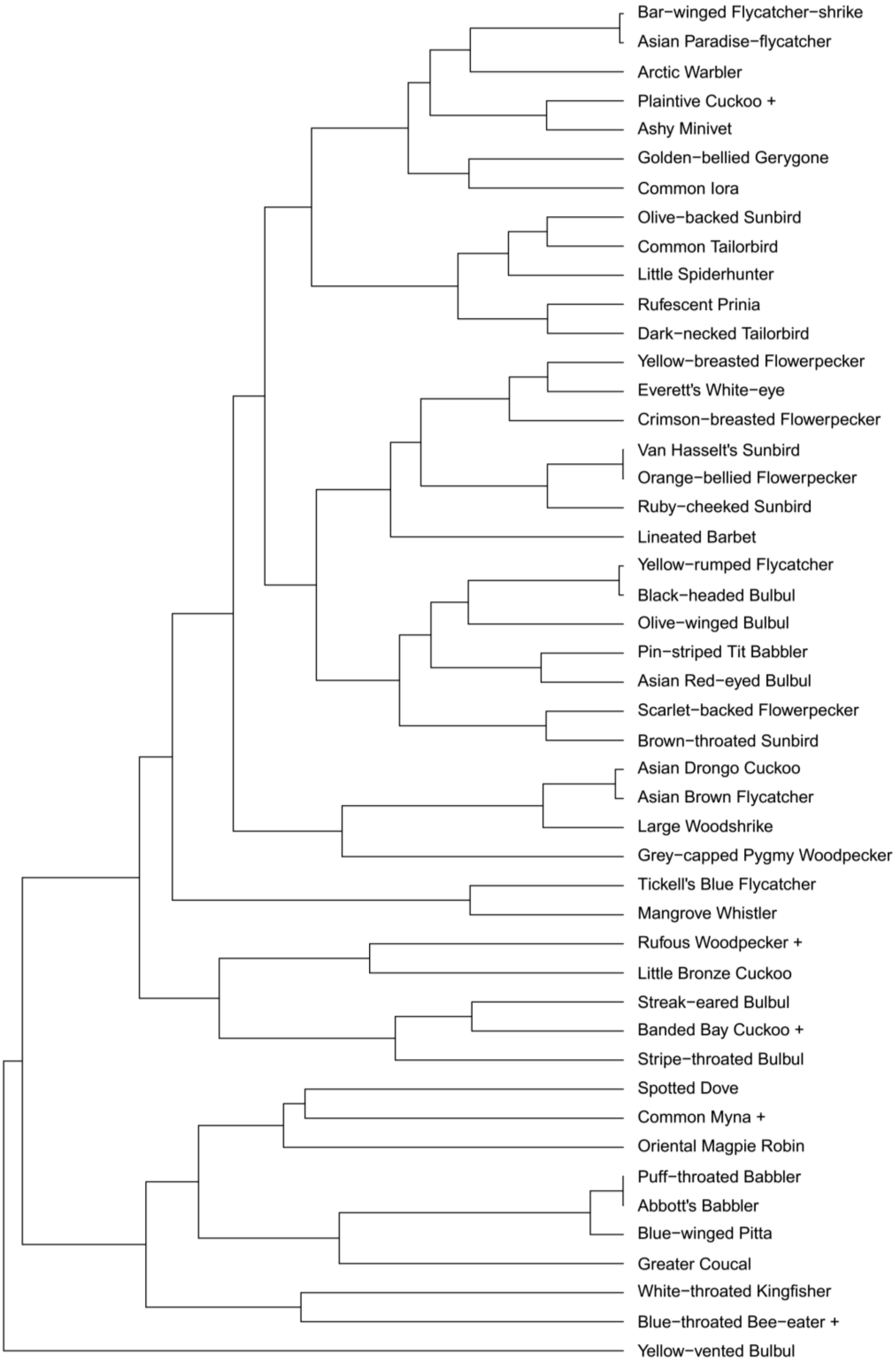
				Foraging strata						Foraging substrate					Diet type								
No.	**Common name**	**Scientific name**	**Body mass (g)**	**Open**	**For terr**	**For undr**	**For mid**	**For can**	**Aqua**	**Soil/ litter**	**Trunk/ branch**	**Foliage**	**Aerial**	**Sub water**	**Nectiv**	**Frugiv**	**Insect**	**Scaven**	**Graniv**	**Predat**	**Pisciv**	**Obligate insectiv**	**Obligate foraging stratum**
16	Little Bronze Cuckoo	*Chrysococcyx minutillus*	21.0	0	1	1	1	1	0	1	1	1	0	0	0	0	1	0	0	0	0	x	
17	Olive-backed Sunbird	*Cinnyris jugularis*	11.9	0	0	1	0	0	0	0	0	1	0	0	1	1	1	0	0	0	0		Understorey
18	Oriental Magpie Robin	*Copsychus saularis*	41.0	1	1	0	0	0	0	1	0	0	1	0	1	1	1	0	1	0	0		
19	Large-billed Crow - *	*Corvus macrorhynchos*	1000.0	1	1	0	0	1	0	1	1	1	1	0	1	1	1	1	1	1	0		
20	Tickell's Blue Flycatcher	*Cyornis tickelliae*	18.0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	1	0		
21	Grey-capped Pygmy Woodpecker	*Dendrocopos canicapillus*	32.0	0	0	1	0	1	0	0	1	1	0	0	0	1	1	0	1	0	0		
22	Scarlet-backed Flowerpecker	*Dicaeum cruentatum*	8.0	0	0	1	1	1	0	0	0	1	1	0	1	1	1	0	1	0	0		
23	Orange-bellied Flowerpecker	*Dicaeum trigonostigma*	8.7	0	0	0	0	1	0	0	0	1	0	0	1	1	1	0	1	0	0		Canopy
24	Ashy Drongo - **	*Dicrurus leucophaeus*	55.0	1	0	0	0	1	0	0	1	1	1	0	1	0	1	0	0	1	0		
25	Asian Koel **	*Eudynamys scolopaceus*	242.0	0	0	0	0	1	0	0	0	1	0	0	1	1	1	0	0	0	0		Canopy
26	Black-and-yellow Broadbill + *	*Eurylaimus ochromalus*	39.0	0	0	0	1	1	0	0	1	1	0	0	0	0	1	0	0	0	0	x	
27	Green-backed Flycatcher - *	*Ficedula elisae*	12.0	0	0	1	1	0	0	0	0	1	1	0	0	1	1	0	0	0	0		
28	Yellow-rumped Flycatcher	*Ficedula zanthopygia*	15.5	0	0	1	1	1	0	0	0	1	1	0	0	1	1	0	0	0	0		
29	Zebra Dove + **	*Geopelia striata*	72.0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	x	Open
30	Golden-bellied Gerygone	*Gerygone sulphurea*	6.0	0	0	0	1	1	0	0	0	1	0	0	0	0	1	0	0	0	0	x	
31	White-throated Kingfisher	*Halcyon smyrnensis*	110.0	1	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0	1	1		Open
32	Bar-winged Flycatcher-shrike	*Hemipus picatus*	9.5	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	x	Canopy
33	Black-naped Monarch + **	*Hypothymis azurea*	13.4	0	0	1	0	1	0	0	0	1	1	0	0	0	1	0	0	0	0	x	
34	Van Hasselt's Sunbird	*Leptocoma brasiliana*	7.5	0	0	0	0	1	0	0	0	1	0	0	1	1	1	0	1	0	0		Canopy
35	Blue-crowned Hanging Parrot + **	*Loriculus galgulus*	35.0	0	0	0	1	1	0	0	0	1	0	0	0	1	0	0	0	0	0	x	

				Foraging strata						Foraging substrate					Diet type								
No.	**Common name**	**Scientific name**	**Body mass (g)**	**Open**	**For terr**	**For undr**	**For mid**	**For can**	**Aqua**	**Soil/ litter**	**Trunk/ branch**	**Foliage**	**Aerial**	**Sub water**	**Nectiv**	**Frugiv**	**Insect**	**Scaven**	**Graniv**	**Predat**	**Pisciv**	**Obligate insectiv**	**Obligate foraging stratum**
36	Pin-striped Tit Babbler	*Macronus gularis*	14.0	0	0	1	1	0	0	0	0	1	0	0	0	1	1	0	0	0	0		
37	Abbott's Babbler	*Malacocincla abbotti*	32.0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	x	Terrestrial
38	Lineated Barbet	*Megalaima lineata*	205.0	0	0	0	1	1	0	0	0	1	0	0	1	1	1	0	0	1	0		
39	Red-throated Barbet + *	*Megalaima mystacophanos*	95.0	0	0	1	0	1	0	0	1	1	0	0	0	1	1	0	0	0	0		
40	Blue-tailed Bee-eater + *	*Merops philippinus*	43.0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1		Open
41	Blue-throated Bee-eater +	*Merops viridis*	41.0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1		Open
42	Rufous Woodpecker +	*Micropternus brachyurus*	114.0	0	0	1	1	1	0	1	1	1	0	0	1	1	1	0	0	0	0		
43	Asian Brown Flycatcher	*Muscicapa dauurica*	16.0	1	0	0	0	1	0	0	1	1	1	0	0	1	1	0	0	0	0		
44	Dark-necked Tailorbird	*Orthotomus atrogularis*	7.5	0	0	1	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	x	Understorey
45	Common Tailorbird	*Orthotomus sutorius*	10.0	0	0	1	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0		Understorey
46	Mangrove Whistler	*Pachycephala cinerea*	25.0	0	0	1	1	0	0	0	1	0	1	0	0	0	1	0	0	0	0	x	
47	Puff-throated Babbler	*Pellorneum ruficeps*	31.0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	x	Terrestrial
48	Ashy Minivet	*Pericrocotus divaricatus*	28.0	0	0	0	0	1	0	0	1	1	1	0	0	0	1	0	0	0	0		Canopy
49	Green-billed Malkoha + **	*Phaenicophaeus tristis*	115.0	0	0	0	1	1	0	0	1	1	0	0	0	0	1	0	0	1	0		
50	Arctic Warbler	*Phylloscopus borealis*	15.0	0	0	1	0	1	0	0	0	1	1	0	0	0	1	0	0	0	0	x	
51	Crimson-winged Woodpecker + **	*Picus puniceus*	96.0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	x	Canopy
52	Blue-winged Pitta	*Pitta moluccensis*	146.0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	x	Terrestrial
53	Rufescent Prinia	*Prinia rufescens*	7.0	0	0	1	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	x	Understorey
54	Yellow-breasted Flowerpecker	*Prionochilus maculatus*	11.8	0	0	0	1	1	0	0	0	1	0	0	1	1	0	0	0	0	0		
55	Crimson-breasted Flowerpecker	*Prionochilus percussus*	10.0	0	0	0	1	0	0	0	0	1	0	0	1	1	0	0	0	0	0		Midstrata

				Foraging strata						Foraging substrate					Diet type								
No.	**Common name**	**Scientific name**	**Body mass (g)**	**Open**	**For terr**	**For undr**	**For mid**	**For can**	**Aqua**	**Soil/ litter**	**Trunk/ branch**	**Foliage**	**Aerial**	**Sub water**	**Nectiv**	**Frugiv**	**Insect**	**Scaven**	**Graniv**	**Predat**	**Pisciv**	**Obligate insectiv**	**Obligate foraging stratum**
56	Black-eared Barbet + **	*Psilopogon duvaucelii*	37.0	0	0	0	0	1	0	0	0	1	0	0	0	1	1	0	0	0	0		Canopy
57	Black-headed Bulbul	*Pycnonotus atriceps*	30.0	0	0	1	1	1	0	0	0	1	1	0	0	1	1	0	0	0	0		
58	Streak-eared Bulbul	*Pycnonotus blanfordi*	36.0	1	1	0	1	1	0	1	0	1	1	0	0	1	1	0	0	0	0		
59	Asian Red-eyed Bulbul	*Pycnonotus brunneus*	37.0	0	0	1	1	0	0	0	0	1	0	0	0	1	1	0	1	0	0		
60	Stripe-throated Bulbul	*Pycnonotus finlaysoni*	32.3	1	1	1	1	0	0	1	0	1	1	0	0	1	1	0	0	0	0		
61	Yellow-vented Bulbul	*Pycnonotus goiavier*	37.0	1	0	1	0	0	0	1	1	1	1	0	1	1	1	1	1	0	0		
62	Olive-winged Bulbul	*Pycnonotus plumosus*	36.0	0	0	1	1	1	0	0	0	1	0	0	0	1	1	0	0	1	0		
63	Rufous Piculet **	*Sasia abnormis*	12.0	0	0	1	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	x	
64	Spotted Dove	*Spilopelia chinensis*	198.0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0		Open
65	Asian Drongo Cuckoo	*Surniculus lugubris*	43.6	1	0	0	0	1	0	0	1	1	1	0	0	1	1	0	0	0	0		
66	Large Woodshrike	*Tephrodornis virgatus*	46.0	1	0	1	0	1	0	0	1	1	1	0	0	1	1	0	0	0	0		
67	Asian Paradise-flycatcher	*Terpsiphone paradisi*	22.0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0		Canopy
68	Collared Kingfisher - *	*Todiramphus chloris*	100.0	1	0	0	0	0	0	1	0	0	1	1	0	0	1	0	0	1	1		Open
69	Everett's White-eye	*Zosterops everetti*	12.0	0	0	0	1	1	0	0	0	1	0	0	1	1	1	0	0	0	0		

SUPPLEMENTARY FIGURE 1: Functional dendrogram excluding singleton and doubleton species; co-phenetic correlation = 0.77.

“+” indicates species recorded in AF only.



Chapter 6

Discussion

6.1 Key findings and conclusions

The research in this thesis was conducted to provide policy-relevant evidence that could inform efforts to prevent deforestation for the expansion of rubber plantations, and support sustainability efforts focussed on rubber. This section of the thesis summarises the key findings of the research, draws together conclusions that can be taken away now, and highlights areas of research that warrant effort in future.

Before this research began, a range of analyses had mapped the recent expansion of rubber in mainland Southeast Asia, and documented negative consequences for biodiversity, ecosystem services and human wellbeing. However, this information had not been brought together to give a global perspective on the threat posed to biodiversity by rubber plantations, nor had any predictions been made about future expansion of rubber plantations globally. The synthesis of evidence for biodiversity impacts in Chapter 2 placed rubber firmly alongside oil palm as a serious driver of biodiversity loss in Southeast Asia (Chapter 2). Future rubber demand was expected to increase from 10.7 million tonnes in 2010, to 13.0 million tonnes by 2018, and 18.1 million tonnes by 2024. This additional demand was predicted to require 1.4 – 3.9 million ha of expansion by 2018, and 4.3 – 8.5 million ha by 2024, making rubber expansion a serious concern for biodiversity conservation in Southeast Asia. Comparing these predictions to the most up-to-date figures available today shows that 12.6 million tonnes of natural rubber were consumed in 2016 (IRSG 2017), and global rubber area increased by 1.7 million ha from 2010 to 2014 (FAO 2017) (data for more recent years are not yet available) indicating that demand and expansion are increasing as predicted.

In Chapter 3, it was found that rubber plantations present a powerful economic driver for deforestation in Cambodia, surprisingly far greater than predicted profits from logging, even considering illegal extraction of rare and high-value timbers. The opacity of the timber trade in Indo-Burma does mean that these estimates are conservative, and timber profits from illegal logging could be higher than predicted. The calculated breakeven carbon prices of \$30 – 51 tCO_2^{-1} needed to cover the opportunity costs of forgone forest conversion to rubber will not be offset by current prices for REDD+ credits (around \$5 tCO_2^{-1}). This information could help the spatial targeting of REDD+ activities in Indo-Burma, but also highlights the need for other conservation incentives to defend forests from rubber. Zero-deforestation commitments from tyre producers who buy natural rubber are one such strategy, as well as the usual requirements for forest protection, including strong environmental governance, social or political pressure to conserve, or proper valuation of ecosystem services in decision making. The analysis in this chapter also highlighted the very substantial carbon emissions that result from conversion of forest to rubber plantations, even considering dry and open savanna-like forest ecosystems.

In Chapter 4, rubber agroforests in southern Thailand were found to provide high rubber yields, comparable to monocultures, while providing additional livelihood benefits for farmers. However, the biodiversity benefits of agroforests were modest: butterfly species richness was greater in agroforests, but no forest-dependent or threatened bird species were found. Two within-plantation management recommendations were made to support bird diversity: the regeneration of an understorey herb layer, and increased planting of non-rubber tree stems in agroforests. At the landscape level, retention of natural forest fragments had benefits for birds and butterflies, although only within agroforests in the case of butterflies. Agroforests therefore appear to have some benefits for biodiversity within rubber-dominated landscapes, without detrimental effects on yield. Reflecting the findings of many other studies, contiguous natural forest is needed to conserve species of conservation concern, and high-yielding agroforests cannot replace these habitats.

In Chapter 5, the functional diversity of birds, which underpins ecological functioning and delivery of ecosystem services, was shown to be similar between rubber agroforests and monocultures. However, functional diversity increased with increasing herb height, and within agroforests, with increasing density of non-rubber trees. Natural forest fragment extent in the landscape and increased stem density within rubber plots both appeared to increase functional redundancy, and may contribute to long-term stability of ecological functioning. Most species recorded were small-medium insectivores or omnivores, whereas frugivores and nectarivores were notably scarce, and the ecological functions provided by these latter species are missing from rubber plots.

6.2 Further research questions

Four areas of research need on the impacts of rubber on forests and biodiversity were highlighted in Chapter 2, but only one of these is directly addressed in this thesis (biodiversity benefits of high-yielding rubber agroforests; Chapter 4). The biodiversity value of swidden landscapes relative to rubber-dominated landscapes has not yet been investigated. The relative benefits of low-intensity agroforest compared to intensified monoculture with targeted land-sparing for nature also needs further investigation, together with the benefits of "both-and" combinations of the two approaches (Kremen 2015). These topics are perhaps most relevant in Indonesia, where rubber productivity is low, agroforests provide important habitat for some forest species (Beukema *et al.* 2007) and there are opportunities to undertake landscape-scale planning of forest restoration (Buergin 2016), or in Southwest China where low-yielding rubber plantations (Ahrends *et al.* 2015) could be restored to forest or other land uses. Some work has been done to assess the importance of forest fragments of varying size for bird diversity in rubber-dominated landscapes in Southwest China: these stress the importance of forest cover and the retention of large forest fragments, although the maximum size of fragments creating within-landscape forest cover was only 76 ha, and areas were considered "large" if >100 ha (Sreekar *et al.* 2016, Zhang *et al.* 2017) – far smaller than the hundreds or thousands of forest hectares needed to support avian diversity in oil palm concessions (Edwards *et al.* 2010). Further work on this topic, particularly in agro-industrial plantation settings, would be fruitful for the development of sustainability initiatives.

Spatially-explicit planning to identify the least-damaging strategies for rubber expansion should also be conducted, as well as spatial assessment of costs and benefits of forest conversion to rubber, building on the work of Chapter 3. The interaction between rubber and other commodities should be incorporated, such as the process of rubber replacement with oil palm in Sundaland, and the differing climate envelope of rubber compared to other crops. Demand for rubber appears less elastic than for oil palm, so may be more readily tackled through supply chain initiatives and intensification than oil palm. These analyses should be conducted at the global scale to incorporate the potential for expansion in tropical Africa, and could usefully contribute to sustainability efforts by large international corporations involved in rubber trading (tyre companies) or planting (agro-industrial companies).

Additional research questions and needs have arisen during the course of this study. There is a clear need for a high-resolution global map of rubber plantation area, and monitoring of rubber expansion, given discrepancies in data reported at the national scale (Chapter 2), and the time-lag in availability of FAO data (FAO 2017). This has historically been challenging due to the similar spectral signatures of rubber plantations and other vegetation types, but methods for remote sensing of rubber are improving, making this an achievable outcome (e.g. Chen *et al.* 2012, Fan *et al.* 2015, Kou *et al.* 2015, Li *et al.* 2015).

While this study, and a number of others, have assessed the responses of biodiversity to rubber, these have mostly been conducted in regions originally covered with evergreen forest (Chapters 2 and 4). Rubber expansion onto regions formerly covered with dry deciduous dipterocarp forests (Wohlfart *et al.* 2014) is also taking place in Cambodia (Charlotte Packman, pers.comm.) and northern Thailand (Fox and Castella 2013). It is possible that species adapted to more open habitats will respond differently to forest conversion to rubber: they may be able to utilise rubber plantations more successfully than evergreen forest species, but habitat structural characteristics likely to support open habitat species may differ substantially (e.g. tree holes for cavity nesting birds, forage for grazing ungulates), warranting direct investigation.

Further research on within-plantation management to reduce harm for biodiversity and ecosystems should also be conducted. Rubber is heavily fertilised, but outcomes for yields are unclear as fertilisation is almost ubiquitous. Emissions of NO_2, a greenhouse gas that contributes to climate change, are rapidly increasing in tropical Asia, mostly due to direct emissions from the soil following fertiliser application (DeFries and Rosenzweig 2010), and over-application of fertilisers has other serious negative environmental impacts (Foley *et al.* 2011). Direct assessment of the yield benefits of chemical inputs for rubber would therefore be beneficial. In the case of large-scale agro-industrial plantations in forested landscapes, such as those in Cambodia, research assessing ways to improve the permeability of rubber plantations for forest birds and other wildlife could be useful, such as establishment of corridors to allow animal movements through rubber-dominated landscapes and improve connectivity between natural habitat patches (e.g. Nasi *et al.* 2008, Fagan *et al.* 2016). Further investigations into the relationships between rubber yields and agroforestry techniques (particularly those that require few additional labour inputs (Langenberger *et al.* 2016, Stroesser 2016)) are also needed, which could then be applied not only to small-scale farms to improve food security (Stroesser 2016), but also to large-scale plantations to improve ecosystem service and biodiversity value, and potentially additional profit.

Finally, the overall demand for rubber, both synthetic and natural, must ultimately be stabilised. Research and development of rubber recycling methods seems key to this aim, particularly in the case of tyres, and should be actively pursued by tyre manufacturers to ensure the long-term sustainability of their business activities.

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