Understanding the land use impacts of palm oil cultivation

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Abstract

Expansion of oil palm plantations drives substantial tropical deforestation, greenhouse gas emissions and biodiversity loss, but global demand for vegetable oils is increasing. I studied the consequences of recent interventions to reduce the negative environmental impacts of oil palm expansion, because their success is not well understood. I conducted fieldwork to quantify the benefits of conservation set-asides for carbon stocks in certified-sustainable oil palm plantations. Aboveground carbon stocks of forest set-asides in Sabah (Malaysian Borneo) were >1.5-fold greater than those of oil palm, and co-benefitted plant diversity, but were considerably lower than those of intact primary forest. Thus, conservation set-asides help reduce environmental impacts of oil palm agriculture, but are not a substitute for intact forest. I examined the global potential for zero-deforestation commitments to displace oil palm expansion and associated biodiversity loss into alternative natural habitats which also support unique biodiversity. Under zero-deforestation commitments, >50% of climatically-suitable locations for oil palm expansion are in tropical grassy and dry forest biomes, suggesting high potential for leakage of biodiversity loss. However, the need for further land-use change to meet rising vegetable oil demand could potentially be reduced by improving yields on current plantations, so I examined evidence for yield gaps on current plantations. Analysis of yield data from industrial plantations in Malaysia showed that factors associated with management accounted for >50% of the observed variation in yield, with only minor effects of climate (temperature and rainfall), suggesting substantial opportunities for yield improvement by improving management practices. I conclude that current interventions to reduce the negative environmental impacts of oil palm expansion are beneficial but need improving. Addressing multiple potential pathways for leakage, and supporting improved management practices to increase yields, are likely to be key improvements for reducing the environmental impacts of oil palm expansion.

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AGC Aboveground carbon (stocks)

AIC Akaike information criterion

AMI Annual moisture index

AUC Area under the curve

CI Confidence interval

CWD Coarse woody debris

DBH Diameter at breast height

ENSO El Niño Southern Oscillation

EU European Union

FFB Fresh fruit bunch(es)

GAM Generalised additive model

GAMM Generalised mixed additive model

GHG Greenhouse gas

GLMM Generalised linear mixed model

GPS Global positioning system

HCSA High carbon stocks approach

HCV High conservation value

IQR Inter-quartile range

ISPO Indonesian sustainable palm oil

LMM Linear mixed model

MAP Mean annual precipitation

MAT Mean annual temperature

ML Maximum likelihood

MPA Minimal predicted area

MSPO Malaysian sustainable palm oil

MWD Maximum water deficit

NC No convergence

NDPE No deforestation, peat or exploitation

PC Principal component

PCA Principal component analysis

PET Potential evapotranspiration

PI Prediction interval

RCP Representative concentration pathway

REML Restricted maximum likelihood

RI Random intercept

RSE Residual standard error

RSPO Roundtable on sustainable palm oil

SAR Simultaneous autoregressive (error model)

SDM Species distribution model

SE Standard error

TSS True Skill Statistic

UAV Unmanned aerial vehicle

UK United Kingdom

WGS World Geodetic System

ZDC Zero-deforestation commitment

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Declaration

I declare that this thesis is a presentation of original work and I am the sole author. This work has not previously been presented for an award at this, or any other, University. All sources are acknowledged as References.

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All chapters are reproduced in full in this thesis, with minor formatting alterations. The text was written by me, with input from co-authors as listed above. For chapter 2, I conceived the study with JKH and HK; I designed the methodology with inputs from JKH, CJM, EHW, LFB, DSC, SB, KLY, ABS and AJ; I collected the data alongside EHW, AJ and ABS collected the data; AJ and BBO led plant identification; and I analysed the data and led the writing of the manuscript. For chapter 3, I conceived the study with JKH, CLP, JML and HK; I designed the models of oil palm suitability with CJM and PJP; RvB modelled water supply and demand; CLP conducted the biome classification; RMB conducted refinements of species range maps; and I ran the oil palm suitability models, conducted the analyses and led the writing of the manuscript. For chapter 4, I conceived the study with JKH and CLP; I analysed the data and led the writing of the manuscript. For all chapters, all co-authors contributed to drafts of the manuscripts.

Chapter 1

General Introduction

1.1 Abstract

Global agricultural production has risen rapidly since the 1960s, and continues to do so in response to growing demand resulting from the rising global human population, and increasing wealth and consumption. However, most agricultural expansion is currently in the tropics, where it drives extensive land-use change, is a key source of greenhouse gas (GHG) emissions, and causes substantial biodiversity loss. Oil palm is the most productive vegetable oil crop, and has rapidly expanded globally over recent decades, currently supplying one third of global vegetable oil. Recent expansion of oil palm plantations in Southeast Asia has driven some of the highest rates of deforestation seen globally, resulting in substantial GHG emissions and biodiversity loss in a biodiversity hotspot. Oil palm agriculture represents a prime example of a highly productive agricultural system required to meet global demands, with considerable negative environmental consequences. Thus, it provides an opportunity to study how the environmental impacts of a key agricultural commodity could be reduced. In this general introduction chapter, I outline environmental issues of tropical agriculture; the environmental impacts of recent oil palm expansion, focusing on the biodiversity loss and GHG emissions; and recent interventions to reduce its environmental impacts. I also consider how climate change may affect oil palm yield and hence impact future palm oil production. These topics provide the background to the main aims of my thesis to examine the consequences of current oil palm sustainability interventions for biodiversity and carbon storage, and to examine the potential for yield improvement in existing plantations. The overall aim of my thesis is to provide new information that helps make progress in reducing the land-use impacts of oil palm agriculture.

1.2 The need for environmentally sustainable tropical agriculture

In recent decades, global agricultural expansion has shifted from temperate regions to the tropics (Hoekstra *et al.*, 2005; Meyfroidt *et al.*, 2013; Wilting *et al.*, 2017; Creutzig *et al.*, 2019), where it has disproportionately negative environmental impacts, driving substantial biodiversity loss and greenhouse gas (GHG) emissions (Myers *et al.*, 2000; Stork *et al.*, 2009; West *et al.*, 2010; Wilting *et al.*, 2017; IUCN, 2020b). Between 2000 and 2010, most cropland expansion occurred in tropical rainforest and grassy biomes in Latin America, Sub-Saharan Africa and Southeast Asia; and cropland area in many developed countries declined while imports increased (Dinerstein *et al.*, 2017; Creutzig *et al.*, 2019). Thus, the environmental impacts of high consumption in temperate regions are increasingly being displaced to the tropics (Meyfroidt *et al.*, 2013; Wilting *et al.*, 2017). However, the tropics support disproportionately high biodiversity (species richness, endemism and small-range species, among other measures) (Myers *et al.*, 2000; Stork *et al.*, 2009; IUCN, 2020b), and are thus undergoing substantial biodiversity loss from agricultural expansion (Newbold *et al.*, 2015; Tilman *et al.*, 2017), which is a key cause of the sixth 'mass extinction' event that we appear to be entering (Barnosky *et al.*, 2011; Pimm *et al.*, 2014). Expansion of agriculture in the tropics is also a key driver of global warming, because tropical habitats often have high exceptionally high carbon storage (Tubiello *et al.*, 2015; Curtis *et al.*, 2018; Santoro *et al.*, 2018a). Owing to the increasingly globalized markets for agricultural commodities, tropical deforestation is increasing with urban population growth and agricultural commodity exports, and has now become uncoupled from local population growth (Rudel *et al.*, 2009; Defries *et al.*, 2010). Thus, as global population, wealth and consumption increase over coming decades, demand for agricultural commodities is expected to increase substantially, by at least ~60% by 2050 (compared to 2005 levels), furthering the negative environmental impacts of tropical land-use change (Tilman *et al.*, 2011; Valin *et al.*, 2014; United Nations, 2015b).

Alongside the growing demand for food, demand for biofuels is currently increasing rapidly. Consequently, there is a rapidly growing demand for 'switch' crops, which can be used for either food or biofuel, such as soy and oil palm (Hasegawa *et al.*, 2018; Van Meijl *et al.*, 2018; Doelman *et al.*, 2019). Current food production is sufficient to meet the nutritional needs of a human population of 9.7 bn, as projected for 2050, if access to the global food supply is improved, and widespread replacement of animal products with plant-based alternatives occurs (which avoids feeding human-edible crops to livestock) (Cassidy *et al.*, 2013; Berners-Lee *et al.*, 2018). However, mitigation of climate change to minimise global temperature increase depends partly on increasing biofuel production in order to reduce fossil fuel consumption (Correa *et al.*, 2019; Roe *et al.*, 2019; Lane, 2020), which is likely to lead to substantial increases in crop demand (Hasegawa *et al.*, 2018; Van Meijl *et al.*, 2018; Doelman *et al.*, 2019). Thus, even with substantial shifts in dietary preference, demand for food and feed crops that can produce 'first-generation' biofuels, such as vegetable oil and bioethanol, is highly likely to increase. Between 2000 and 2010, biofuel production emerged as a novel driver of land-use change, accounting for approximately half of cropland expansion globally (Creutzig *et al.*, 2019); and global biodiesel consumption increased 32-fold between 2001 and 2016 (Chain Reaction Research, 2019). Sixty-four countries, spanning all continents, now have targets or mandates to increase biofuel consumption in place of fossil fuels, and this number is likely to increase in coming years (Lane, 2020). However, the degree of increase in global biofuel production is a critical limitation to future food crop productivity, because competition for land between crops for food and biofuel will intensify as biofuel production increases, threatening future food security (Hasegawa *et al.*, 2018; Van Meijl *et al.*, 2018; Doelman *et al.*, 2019). Like food crops, expansion of biofuel crops is also a key driver of biodiversity loss, and can result in substantial GHG emissions if replacing natural habitat (Danielsen *et al.*, 2009). Thus, there is an urgent need to understand how best to simultaneously increase agricultural production, particularly of ‘switch’ crops, while substantially improving the environmental sustainability of tropical agriculture.

Improving agricultural productivity must occur either through cropland expansion or by improving yields, yet each of these has negative environmental impacts, so the goal of increasing agricultural productivity while simultaneously improving its sustainability includes a number of trade-offs (Lipper, DeFries and Bizikova, 2020). On one hand, cropland expansion drives loss of natural habitat, directly resulting in biodiversity loss and GHG emissions (Phalan *et al.*, 2011; Carlson *et al.*, 2017). Expansion of cropland into areas of degraded habitat or fallow lands also drives biodiversity loss, by preventing habitat regeneration or restoration in these locations, and thus reducing the potential for biodiversity and carbon stock recovery in the long-term (Chazdon *et al.*, 2016; Dinerstein *et al.*, 2017, 2019). Restoration and/or regeneration are required in over half of all terrestrial ecoregions in order to protect at least 50% of their natural habitat, considered crucial for successfully conserving biodiversity (Noss *et al.*, 2012; Dinerstein *et al.*, 2017); and increasing carbon sequestration is considered essential for restricting global warming to within 1.5° C, in line with the Paris Agreement (United Nations, 2015a; Rogelj *et al.*, 2018). Thus, minimising conversion of degraded habitat and fallow lands to cropland is essential for reducing global biodiversity loss and GHG emissions. On the other hand, yield improvement is typically realised through intensification, exacerbating the environmental impacts of industrial agriculture, such as GHG emissions from nitrogen fertilisation, loss of soil fertility and pollution of water courses (among other impacts) (Zhang *et al.*, 2015; Borrelli *et al.*, 2017; FAO, 2019; Searchinger *et al.*, 2019). While recent increases in global agricultural productivity have largely occurred through yield improvements (FAO, 2020a; Lipper, DeFries and Bizikova, 2020), partly because most suitable locations for agriculture are already cultivated (Ramankutty *et al.*, 2002), this is not the case for the tropics, where recent, rapid agricultural expansion has had substantial negative environmental consequences. Thus, current global agriculture is increasing in productivity at the expense of environmental sustainability, with substantial negative consequences for tropical biodiversity. To ensure that global agriculture becomes more environmentally sustainable, we must address the sustainability of tropical land-use change, in the context of increasing demand for tropical commodities. Thus, my thesis examines how the environmental impacts of industrial oil palm agriculture can be reduced, which is a prime example of a highly productive tropical crop, used as both a food and biofuel, that has substantial negative environmental impacts.

1.3 Oil palm: a key vegetable oil crop

Oil palm *Elaeis guineensis* (Jacq.) is native to Africa (fig. 1.1) (Blach-Overgaard *et al.*, 2010; Tinker and Corley, 2015), where it is widely cultivated by smallholders, often in mixed cropping systems (Vermeulen and Goad, 2006; Tinker and Corley, 2015). Botanical evidence suggests that oil palm has been cultivated for ~5,000 years in Africa, and a jar of oil in an Egyptian tomb from 5,000 years ago may have been palm oil (Tinker and Corley, 2015). Oil palm is now cultivated throughout the humid tropics, where most lowland locations meet its bioclimatic requirements of high average temperatures and year-round rainfall (fig. 1.1) (Pirker and Mosnier, 2015; Tinker and Corley, 2015).

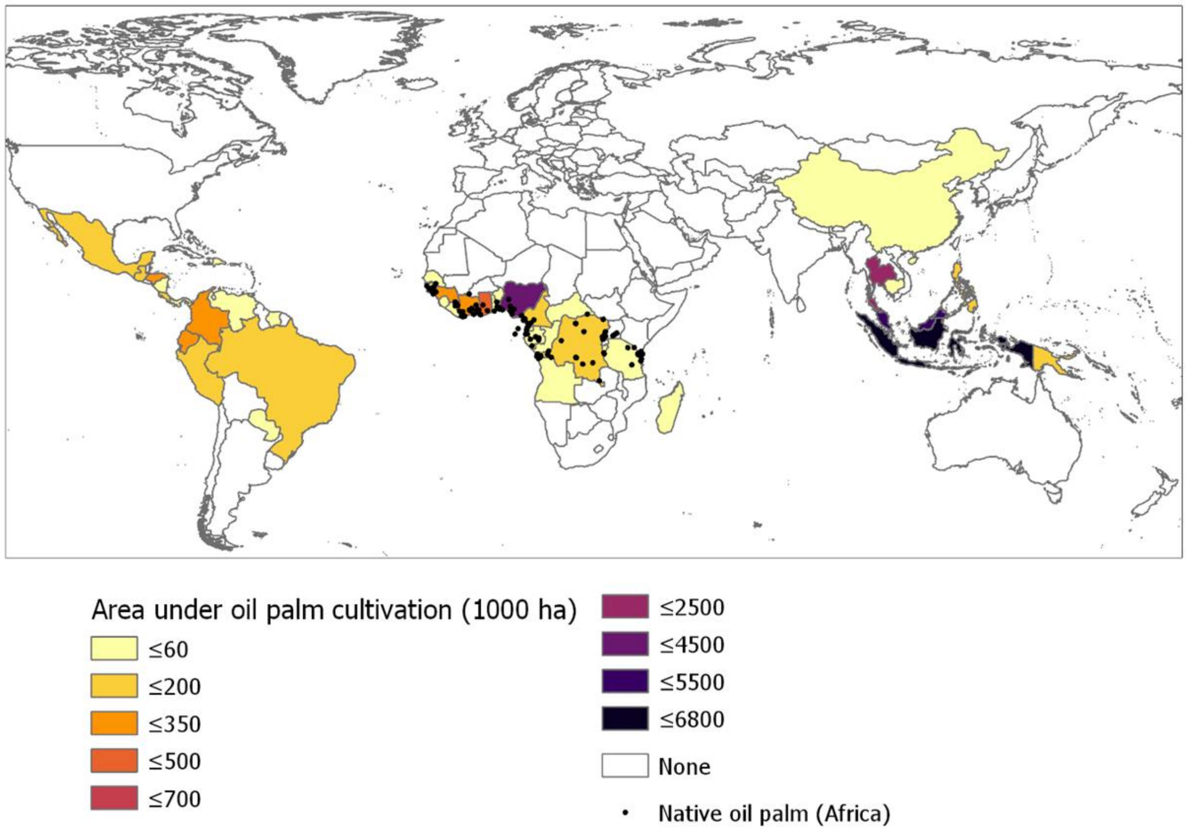


Figure 1.1. Global map of areas under oil palm cultivation in each country (colours), and distribution records of oil palm native to Africa (black points). Data on the area of oil palm cultivation are for 2018, and were obtained from (FAO, 2020c); note that country-level values include reported values and estimates, and data are incomplete. Data of the native oil palm distribution are from (Gilles *et al.*, 2016), and exclude cultivated oil palm.

The majority of global palm oil production currently takes place in commercial plantations in Southeast Asia: in 2017, Indonesia accounted for 58% of global palm oil production, and Malaysia 26% (USDA, 2020). Industrial oil palm cultivation has rapidly expanded in Indonesia and Malaysia over recent decades (fig. 1.2) (Vijay *et al.*, 2016), which has driven substantial deforestation and biodiversity loss (see section 1.4), while increasing Gross Domestic Product and the incomes of farmers, including many smallholders (Sheil *et al.*, 2009; Rist, Feintrenie and Levang, 2010; Drescher *et al.*, 2016; Purnomo *et al.*, 2020). Whilst the majority of production is by industrial or government-managed plantations in these countries, independent smallholders (family-based enterprises with less than 50 ha of land) also have a crucial role, accounting for 35-40% of the total area under oil palm cultivation in Indonesia and Malaysia, and roughly one-third of total production (Vermeulen and Goad, 2006). As all crude palm oil is extracted in industrial mills in these countries, smallholders tend either to be associated with industrial plantations, such as in 'plasma schemes' (governmental schemes in Indonesia, where industrial plantations support smallholders in establishing and cultivating oil palm, and purchase the crop at a fixed price), or to sell their fresh fruit bunches to nearby mills (Vermeulen and Goad, 2006).

However, oil palm cultivation is also rapidly expanding outside Southeast Asia, particularly in Latin America and Africa (fig. 1.1) (Vijay *et al.*, 2016; Furumo and Aide, 2017; Ordway, Asner and Lambin, 2017; Ordway *et al.*, 2019). The vast majority of oil palm-producer countries (i.e. across the tropics; see fig. 1.1) are currently expanding the area under oil palm cultivation (FAO, 2020c), and Latin America and Africa had greater relative oil palm expansion than either Indonesia or Malaysia between 2003 and 2013 (Vijay *et al.*, 2016). It is therefore highly likely that the relative importance of Latin America and Africa for global oil palm production will increase as potential locations for expansion in Southeast Asia become increasingly limited (Vijay *et al.*, 2016). Since 2001, oil palm production in Latin America has doubled, with particularly rapid increases in Colombia (currently the fourth-largest producer of palm oil) and Ecuador, partly in response to biofuel mandates (Furumo and Aide, 2017; USDA, 2020). Oil palm cultivation in Africa is already extensive: Nigeria is the fifth-largest producer of palm oil globally (USDA, 2020); and one-quarter of the total area under oil palm cultivation globally is in sub-Saharan Africa (Ordway *et al.*, 2019). Oil palm is a traditional crop in Africa, and widely cultivated by smallholders for domestic consumption (Vermeulen and Goad, 2006; Tinker and Corley, 2015), so expansion is driven by both proliferation of smallholder production and informal mills (Ordway *et al.*, 2019), and increasing industrial production, often funded by foreign investment (Feintrenie, 2014; Ordway, Asner and Lambin, 2017).

The products derived from oil palm cultivation have diverse uses (Tinker and Corley, 2015). Oil (triacylglycerols) is extracted from both the palm oil fruitlets, harvested in fresh fruit bunches (fig. 1.2), producing crude palm oil, and from the seeds within these fruitlets, producing palm kernel oil (Tinker and Corley, 2015). Most crude palm oil is used in food products and as a biofuel (Tinker and Corley, 2015); and in Africa it is consumed widely without refining, and is a key source of vitamin A (Barcelos *et al.*, 2015). Most palm kernel oil is used in non-edible industrial and agricultural products, such as detergents, plastics, surfactants, cosmetics and herbicides, although it is also used as a protein meal in animal feed (Wahid, Abdullah and Henson, 2005; Tinker and Corley, 2015; USDA, 2020).

Figure 1.2. Industrial oil palm production in Malaysia. (a) Plantation and mill; (b) recently-harvested fresh fruit bunches being prepared for milling; (c) industrial plantation, with mature oil palm in the foreground and on the left, and newly-replanted oil palm on the right; (d) fresh fruit bunch close-up. Photo credits: (a, b) Robin Hayward, (c) Emily Waddell, (d) Jiří Tůma.

Global palm oil production is greater than that of any other vegetable oil, accounting for approximately one third of total global vegetable oil production, and approximately 60% of vegetable oil exports (USDA, 2020). The yield of oil palm plantations is roughly six-fold greater than rapeseed, the next most productive vegetable oil crop (Yan, 2017), so only approximately 7% of total land area under vegetable oil crop cultivation is oil palm plantations (FAO, 2020b). Currently, India is the single largest importer of palm oil (accounting for ~19% of imports), followed by China (~14%), and the EU (~13%) (USDA, 2020). Between the 1960s and 2000s, global palm oil production increased (mostly in Indonesia and Malaysia) in response to the rapid increase in consumption of vegetable oils as a foodstuff: vegetable oil consumption doubled in developing countries and tripled in developed countries between 1963 and 2003 (Kearney, 2010; Wilcove and Koh, 2010). However, more recent increases in palm oil production have been in response to growing global demands for biofuels; and palm oil accounted for 31% of feedstock used for biofuel in 2017 (Chain Reaction Research, 2019). Given growing global demands for vegetable oils as both a foodstuff and biofuel, it is highly likely that palm oil consumption will continue to increase over coming years.

1.4 Environmental impacts of oil palm expansion

1.4.1 Environmental consequences of recent oil palm expansion in Southeast Asia

Oil palm agriculture is considered the greatest threat to the highly biodiverse flora and fauna of Southeast Asia, because it has driven extensive deforestation, fragmentation of remaining forest habitat, and pollution (Fitzherbert *et al.*, 2008; Sodhi *et al.*, 2010; Wilcove and Koh, 2010). In Insular Southeast Asia between 2000 and 2010, forest cover declined at an annual rate of 1%, faster than in any other tropical region, largely owing to the expansion of industrial oil palm plantations (Sodhi *et al.*, 2010; Miettinen, Shi and Liew, 2011; Curtis *et al.*, 2018). Consequently, the extent of anthropogenic impacts on the environment are greater in Southeast Asia than other tropical forest regions (Venter *et al.*, 2016; Austin *et al.*, 2017). Roughly half of oil palm plantations in Southeast Asia have expanded into areas that were forested in 1989 (53.8% of plantations in Indonesia, and 39.6% in Malaysia), including both primary and logged forests (Sodhi *et al.*, 2010; Vijay *et al.*, 2016). On Borneo, oil palm plantations expanded by 7.9 Mha (60-fold increase) between 1973 and 2015, three-quarters of which were planted in previously forested areas, and nearly half of which (47%) were established within five years of deforestation (i.e. the likely driver of deforestation) (Gaveau *et al.*, 2018). In Kalimantan (Indonesian Borneo, a key oil palm-producing region), 90% of oil palm expansion between 1990 and 2010 replaced forest, over half of which was old-growth forest and thus highly valuable for biodiversity and carbon storage (Gibson *et al.*, 2011; Carlson *et al.*, 2013; Asner *et al.*, 2018).

Southeast Asia supports exceptionally high biodiversity, but the recent, rapid deforestation from oil palm expansion has driven substantial biodiversity loss. The exceptionally high diversity of Southeast Asia has arisen over geological time from a series of tectonic plate collisions, which brought diverse evolutionary lineages into the region, and from historical fluctuations in sea-level in the insular landscape, causing alternating periods of inter-island migration and population isolation (Hall, 2012). Owing to high rates of endemism coupled with rapid habitat loss, the region now largely comprises the two biodiversity hotspots (regions of exceptional endemic diversity that is being rapidly lost) of Sundaland and Wallacea (Myers *et al.*, 2000; Sodhi *et al.*, 2010). Oil palm plantations support substantially lower biodiversity than rainforest, for almost all taxa studied (Fitzherbert *et al.*, 2008; Foster *et al.*, 2011; Drescher *et al.*, 2016). This biodiversity loss occurs because the florally diverse rainforest canopy and overstorey are replaced by palm monoculture, resulting in the loss of species dependent on rainforest flora (McNeely and Schroth, 2006; Bhagwat *et al.*, 2008). Oil palm monoculture also supports fewer species because it is structurally simpler than rainforest, with uniform vegetation structure, lower canopy height, sparse undergrowth, and substantial levels of human disturbance (McNeely and Schroth, 2006; Bhagwat *et al.*, 2008; Fitzherbert *et al.*, 2008). Furthermore, remnant forest patches can boost biodiversity in nearby oil palm plantations, but industrial oil palm tends to be cultivated in highly homogeneous landscapes of extensive oil palm monoculture (Koh, 2008; Azhar *et al.*, 2015). On average, only 15% of species that occur in primary forest persist in oil palm plantations; and other crops in Southeast Asia (e.g. cocoa, rubber, coffee and *Acacia* plantations) tend to support higher levels of forest biodiversity, because of greater structural complexity, retention of rainforest plant species resulting in greater overstorey and understorey diversity, and greater heterogeneity of habitats in the surrounding landscape (Bhagwat *et al.*, 2008; Fitzherbert *et al.*, 2008; Rembold *et al.*, 2017). Conversion of forest to oil palm results in declines in both species richness and abundance of most animal taxa (Foster *et al.*, 2011), with declines of ~50% in insect density and total biomass (Barnes *et al.*, 2014). Most remaining areas of forest in Southeast Asia have now been selectively logged (Gaveau *et al.*, 2016), resulting in the loss of slow-growing, canopy tree species and dependent taxa (Sodhi *et al.*, 2004; Tabarelli, Peres and Melo, 2012), and altering ecosystem processes such as the recruitment of dipterocarps, which are the dominant canopy trees in Southeast Asian rainforest (Curran *et al.*, 1999). Nevertheless, conversion of selectively-logged forest to oil palm also results in substantial biodiversity loss, because disturbed forest supports substantially greater biodiversity than oil palm in Southeast Asia (Berry *et al.*, 2010; Brühl & Eltz, 2010; Chazdon *et al.*, 2009; Dunn, 2004; Edwards *et al.*, 2014; Fitzherbert *et al.*, 2008). Preventing further conversion of logged or primary forests to oil palm is therefore considered imperative for conserving the region's biodiversity (Wilcove *et al.*, 2013).

Owing to extensive expansion into areas of rainforest, and peat soils, recent oil palm expansion in Southeast Asia has driven substantial GHG emissions of 'irrecoverable carbon' stored in these habitats (Carlson *et al.*, 2013; Pendrill *et al.*, 2019; Goldstein *et al.*, 2020). Oil palm plantations have substantially lower aboveground carbon stocks (AGC) than both old-growth and most disturbed forests in Southeast Asia (Kho and Jepsen, 2015; Asner *et al.*, 2018). Oil palm AGC ranges between 2 and 60 Mg ha^{-1}, depending on the stage of the planting cycle (oil palm is a perennial crop, replanted on a 25-30 year cycle when the palms become too tall for efficient harvesting) (Kho and Jepsen, 2015; Tinker and Corley, 2015). In contrast, the AGC of Southeast Asian forest is high in comparison to that of other tropical rainforest regions (Sullivan *et al.*, 2017), generally over 200 Mg ha^{-1} (and up to 500 Mg ha^{-1}) in intact forests, and 60-140 Mg ha^{-1} in disturbed forests (Asner *et al.*, 2018), resulting in substantial AGC losses during conversion to oil palm. Similarly, oil palm plantations support substantially lower belowground carbon stocks than rainforest, on both mineral and peat soils (Drescher *et al.*, 2016). Although oil palm has greater net primary productivity than Southeast Asian rainforest (33 Mg $ha^{-1}yr^{-1}$ for oil palm and 24 Mg $ha^{-1}yr^{-1}$ for forest), its high fruit yields (and thus harvesting of primary production) mean that inputs of organic matter to soils are substantially lower than in forest. Thus, soil organic matter and carbon content decline by approximately 50% following the conversion of forest on mineral soils to oil palm (Kotowska *et al.*, 2015; van Straaten *et al.*, 2015; Guillaume *et al.*, 2018). Moreover, recent oil palm expansion in Southeast Asia has disproportionately occurred on peatlands (Koh, Butler and Bradshaw, 2009; Miettinen, Shi and Liew, 2011), in spite of requiring drainage prior to planting, because these tend to be located in accessible lowlands (Laurance *et al.*, 2010), driving substantial GHG emissions owing to peat oxidation and loss of 'irrecoverable' belowground carbon (Koh *et al.*, 2011; Goldstein *et al.*, 2020). Over 25 years following conversion of peat to oil palm plantation in Indonesia, 420 Mg ha^{-1} of carbon stored in peat were lost, accounting for roughly two-thirds of the total GHG emissions from conversion (Hergoualc'h and Verchot, 2011). Between 1990 and 2010, 13% of oil palm expansion in Kalimantan was on peatlands, but this accounted for roughly one-third of GHG emissions from oil palm expansion (Carlson *et al.*, 2013).

Expansion of oil palm plantations has resulted in extensive fragmentation of the remaining forest in Southeast Asia (Sodhi *et al.*, 2009), driving further biodiversity loss and GHG emissions, in addition to those from habitat loss alone. Smaller fragments support fewer species, because small habitat patches contain only a fraction of the species present in the original community, particularly in tropical forests, where the majority of species are rare and beta diversity is high (Laurance *et al.*, 2018). In addition, smaller habitat patches support fewer viable populations of species of any taxon, resulting in local extinctions following fragmentation (Prugh *et al.*, 2008; Haddad *et al.*, 2015; Hanski, 2015; Laurance *et al.*, 2018). As well as the negative impacts of these 'area effects' on biodiversity, isolation of fragments increases biodiversity loss, because recolonization rates of locally-extinct species are lower in more isolated fragments and extinction rates are higher (Haddad *et al.*, 2015; Hanski, 2015). Biodiversity loss increases with time since fragmentation, due to 'extinction debts', whereby populations that are no longer viable in the fragment become functionally, and then locally extinct (Haddad *et al.*, 2015). Smaller, more isolated forest fragments in oil palm landscapes have been found to support lower richness of ants, birds, butterflies and tree seedlings, suggesting that regeneration of forest in fragments will be low (Benedick *et al.*, 2006; Brühl, Eltz, & Linsenmair, 2003; Edwards *et al.*, 2010; Stride *et al.*, 2018). In addition, oil palm acts as a barrier to the dispersal of forest butterflies, which potentially isolates populations and increases risk of extinction in small forest fragments (Scriven *et al.*, 2017). Nevertheless, larger fragments can support relatively high species richness and are therefore recommended to be prioritised for conservation within oil palm plantations (see section 1.6) (Lucey *et al.*, 2017). However, the value of forest fragments in oil palm plantations for AGC is not known, and I examine this in chapter 2.

The creation of habitat edges during fragmentation (i.e. the boundary between the forest and oil palm planted area) also has substantial impacts on biodiversity and ecosystem functioning, by generating a hotter, drier, windier and higher-light microclimate, elevating tree mortality, and favouring disturbance-tolerant species (Laurance *et al.*, 2011). In tropical forests, the largest, oldest trees (canopy and emergent trees) tend to be most negatively edge-affected (i.e. experience greatest mortality near forest edges) (Laurance *et al.*, 2000). These edge effects have substantial negative implications for forest regeneration and carbon uptake and storage, because the largest trees account for the majority of seed and seedling production, and the majority of primary productivity and AGC stocks (Laurance *et al.*, 2000). On Borneo, rainforest AGC within 100 m of forest edge are 22% lower than those of the forest interior (Ordway and Asner, 2020), highlighting indirect impacts of oil palm expansion on carbon storage of remaining forests.

In addition to driving substantial loss of GHG emissions, conversion of rainforest to oil palm plantations results in a reduction in ecosystem functions and services; and the only service which increases is goods provisioning (i.e. palm oil harvest) and associated revenue (Dislich *et al.*, 2017). Oil palm plantations have high water requirements compared to Southeast Asian rainforests, and therefore alter water cycling and increase risk of water shortage during drought periods (Manoli *et al.*, 2018). Substantial soil erosion occurs during plantation establishment and replanting (Henson, 2003), resulting in changes to the soil fungal community, including a reduction in symbiotrophs, implying loss of nutrient provisioning and an increased need for chemical fertilisation (Brinkmann *et al.*, 2019). Deforestation for oil palm expansion results in the loss of climate, soil and water regulation performed by forests, and of forest resources (including food and medicine provisioning) (Obidzinski *et al.*, 2012; Dislich *et al.*, 2017). However, oil palm expansion has increased the income of many smallholder farmers in Indonesia and Malaysia, ameliorating rural poverty (Wilcove and Koh, 2010; Drescher *et al.*, 2016; Dislich *et al.*, 2017). In Jambi, Sumatra, oil palm cultivation has also increased the access of migrant smallholders to education (Drescher *et al.*, 2016). Oil palm is more productive per unit labour than rubber, the main alternative smallholder crop, so is highly favourable for smallholders who are limited by labour (Drescher *et al.*, 2016). However, oil palm expansion in Southeast Asia often results loss of land rights or access for traditional landowners (e.g. indigenous communities), stimulating land conflicts (Koh & Wilcove, 2007; Obidzinski *et al.*, 2012).

1.4.2 Potential environmental impacts of oil palm expansion in other regions

There is currently considerable concern that increasing oil palm expansion in Africa and Latin America could drive similar biodiversity loss to that in Southeast Asia (Butler & Laurance, 2009; Vargas *et al.,* 2015; Wich *et al.*, 2014). Oil palm plantations in the Amazon support considerably lower mammal richness and abundance than primary forest, suggesting that oil palm has the potential to drive considerable loss of mammal diversity in the Amazon region, like in Southeast Asia (Yue *et al.*, 2015; Mendes-Oliveira *et al.*, 2017). There is substantial overlap between the ranges of African great apes and locations suitable for industrial oil palm cultivation, suggesting considerable potential for the range loss of great apes from oil palm expansion, as for orangutan in Southeast Asia (Wich *et al.*, 2014).

However, current rates of deforestation from oil palm expansion in Latin America and Africa are variable, suggesting that the impacts on biodiversity will depend on local context. Vijay *et al.* (2016) estimated that 31% of oil palm plantations established in 2013 had driven deforestation in South America, but only 2% and 7% in Mesoamerica and Africa respectively, compared with 45% in Southeast Asia. Furumo & Aide (2017) estimated that 80% of industrial oil palm expansion in Latin America replaced previous anthropogenic land-uses, which were mostly pastures, but also croplands and banana plantations. Expansion of oil palm on degraded pastures in Colombia does not result in a net change to ecosystem carbon storage, thereby avoiding GHG emissions from land-use change (Quezada *et al.*, 2019), and is unlikely to drive substantial biodiversity loss (Garcia-Ulloa *et al.*, 2012; Gilroy *et al.*, 2015; Ocampo-Peñuela *et al.*, 2018). However, large expanses of Latin America are suitable for oil palm cultivation, including most of the Amazon region, which would undergo considerable biodiversity loss in the face of extensive oil palm expansion (Butler & Laurance, 2009; Pirker & Mosnier, 2015). Moreover, oil palm is increasingly expanding in high forest-cover countries in Africa, such as Cameroon and Gabon (Feintrenie, 2014; Ordway, Asner and Lambin, 2017; Ordway *et al.*, 2019); and two-thirds of oil palm expansion between 2000 and 2015 in Cameroon replaced forest, although this was mostly through proliferation of low-efficiency, informal mills rather than industrial expansion (Ordway et al., 2019). Rates of deforestation from oil palm expansion in sub-Saharan Africa have historically been low, but 81% of foreign investment in countries identified as most at risk from commodity-driven deforestation is in oil palm production, suggesting considerable potential for rapid expansion of industrial oil palm, and high associated deforestation, in the region in the near future (Ordway, Asner and Lambin, 2017). Thus, industrial oil palm expansion in Latin America and Africa could result in substantial biodiversity loss, but the likely trajectories of oil palm development in the regions are unclear. It is therefore crucial to develop guidance for sustainable development of industrial oil palm cultivation in these regions. To date, the potential for oil palm to expand into grassy biomes in these regions, with consequences for biodiversity loss outside tropical rainforest, has not yet been addressed, and I examine this in chapter 3.

1.5 Impacts of climate change on oil palm agriculture

In order to improve the environmental sustainability of oil palm agriculture, it is essential to understand how it may be impacted by climate change over coming decades. Global GHG emissions currently appear to follow the Representative Concentration Pathway (RCP) 8.5 scenario, suggesting that ~4.5 °C of global warming will occur by 2100 (Schwalm, Glendon and Duffy, 2020), substantially beyond the target 1.5-2 °C limit of the Paris Agreement (United Nations, 2015a). Global warming has already occurred, and 2019 was 1.15 °C warmer than pre-industrial temperatures (1880-1990) (NOAA, 2020). Concurrent impacts of climate change on extreme rainfall patterns have also occurred, with intensification of both drought and extreme rainfall events since 1950 in many locations (Bonfils *et al.*, 2020). Climate change is expected to affect oil palm cultivation by altering both the distribution of areas suitable for growing oil palm and the yields of current oil palm-growing locations (Paterson *et al.*, 2015; Tinker and Corley, 2015; Brodie, 2016). In this section, I outline the climatic requirements of oil palm (which I also discuss in greater detail in chapter 4), followed by the potential impacts of climate change on suitable locations for oil palm cultivation, and yield of current oil palm-growing areas.

Oil palm growth and yield is optimal under high temperatures (>~22°C mean minimum temperature), high year-round rainfall (>~2000 mm per year, with >100 mm each month), and high photosynthetically-active radiation or sunshine hours (>~7 hours per day) (Tinker and Corley, 2015; Hoffmann *et al.*, 2017; FAO, 2020b). However, oil palm tolerates climate conditions outside these ranges, and is frequently cultivated in locations with low minimum temperatures or a prolonged dry season, particularly under traditional cultivation in Africa, where native oil palm grows in a wide range of climatic conditions (see fig. 1.1) (Blach-Overgaard *et al.*, 2010; Tinker and Corley, 2015). Oil palm typically tolerates temperatures between 15°C and 36-38°C, outside of which it experiences cold or heat stress, although cold tolerant varieties may withstand temperatures of 12°C (Mantel, Wösten and Verhagen, 2007; Pirker and Mosnier, 2015; Tinker and Corley, 2015). Soil moisture determines the length of the oil palm growing season, so the length and intensity of dry seasons is a key determinant of growth and yield (Mantel, Wösten and Verhagen, 2007; Pirker and Mosnier, 2015; Tinker and Corley, 2015). Much of Southeast Asia has consistently high year-round rainfall, and therefore typically higher yields than those of West and Central Africa (Tinker and Corley, 2015). The ongoing increase in global temperatures, accompanied by changes in rainfall and increased frequency of extreme climatic events, will drive substantial climatic changes in the tropics, where oil palm is currently cultivated and expanding.

Climatic changes across the tropics are expected to shift the locations that are suitable for oil palm cultivation and thus expansion, provided that oil palm expansion continues, as expected from rising demands (Corley, 2009; Van Meijl *et al.*, 2018). Areas at higher altitude and latitude than current locations suitable for oil palm cultivation are generally limited by cold, so are likely to become suitable for oil palm cultivation as global temperatures increase (Corley & Tinker 2015; Paterson *et al.* 2015, 2017). Thus, oil palm is likely to expand increasingly at higher elevation, which could drive loss of additional natural habitats, such as upland areas important for providing species with cool refugia (remaining areas of suitable habitat and temperature) under climate change (Struebig *et al.*, 2015). Across the tropics, locations of relatively high latitude, such as northern Argentina, the southern coastal states of Brazil, South Africa, Madagascar and Bangladesh, are projected to become newly suitable for oil palm cultivation under climate change, largely from increasing temperatures, potentially facilitating habitat loss of areas which are currently unsuitable for oil palm expansion (Paterson *et al.*, 2017). Conversely, some current oil palm plantations may become less climatically-suitable for oil palm and undergo decreased yields, putting these areas at risk of abandonment, which could stimulate expansion of oil palm into newly-suitable locations to compensate (Paterson *et al.* 2017). Climate change in Indonesia and Malaysia is likely to increase suitable areas for oil palm by 2070 (Paterson *et al.*, 2015); and future oil palm expansion into newly suitable areas at high elevation could reduce mammal ranges by 47-67% by 2070, considerably increasing the number of threatened mammal species on Borneo (Struebig *et al.*, 2015; Brodie, 2016). However, climate change during the 21st century is also likely to reduce the extent of highly suitable locations for oil palm (i.e. areas likely to have the highest yield) by ~10% in Indonesia and Malaysia (Paterson *et al.*, 2015), and up to 100,000 ha of oil palm plantations in the coastal lowlands of Malaysia could be inundated as a result of sea level rise (Siwar, Ahmed and Begum, 2013). Globally, the most suitable areas for oil palm cultivation are projected to decrease by 76% during the 21st century (Paterson et al., 2017), highlighting the urgent need for mitigation of climate change, alongside adaptation of oil palm cultivation, in order to avoid detrimental impacts of climate change on the oil palm industry.

However, the expected impacts of different aspects of climate change on oil palm yield of current plantations are contrasting, and the overall net expected impact is therefore unclear, although it is highly likely that current plantations will experience periods of low yield in response to extreme climatic events. The strong relationship between water availability and oil palm yield globally means that an increase in the frequency and intensity of dry periods, as projected for most tropical regions (either seasonally or following ENSO events), is highly likely to cause reductions in yield (Al-Amin *et al.*, 2010; Siwar, Ahmed and Begum, 2013). Temperature increase appears less likely to impact yield in the near future, because oil palm tolerates temperatures up to approximately 38°C, although some heat stress has been predicted for Southeast Asia in 2100 (Corley & Tinker 2015; Paterson *et al.* 2015). Nevertheless, it is likely that future heatwaves will have temperatures exceeding those previously experienced by oil palm (Barros *et al.*, 2014), so our understanding of the likely impacts of increasing temperatures on oil palm yield is poor. Increasing atmospheric carbon dioxide concentrations could drive yield increases through improved water-use efficiency and thus drought tolerance of oil palm (Tinker and Corley, 2015). However, evidence from forests suggests that changes in temperature and rainfall, and possibly the increasing frequency and intensity of fires, are driving a net decrease in vegetation growth and water use efficiency (Feeley *et al.*, 2007; Mitchard, 2018; Bauters *et al.*, 2020). Overall, we have limited understanding of how the contrasting impacts of different aspects of climate change (e.g. positive expected impacts of carbon dioxide increase, negative expected impacts of increasing drought periods) will interact to affect crop yield (Long *et al.*, 2006). It is therefore important to improve our understanding of the current importance of climate for harvested oil palm yield, which I address in chapter 4.

1.6 Recent interventions to reduce the environmental impacts of oil palm expansion

Various tools and interventions have been suggested to reduce the loss of natural habitat, biodiversity and GHG emissions from oil palm expansion (Wilcove and Koh, 2010). There are no established management practises that substantially improve biodiversity and broaden ecosystem services within the oil palm planted area (Dislich *et al.*, 2017; Fitzherbert *et al.*, 2008; Koh, 2008), so interventions to date have focused on reducing deforestation and peat conversion for the establishment of oil palm plantations, particularly in Southeast Asia (Curtis *et al.*, 2018; Koh & Wilcove, 2008; Wilcove & Koh, 2010). These interventions are largely implemented through voluntary sustainability certification, primarily by the Roundtable on Sustainable Palm Oil (RSPO), and ‘zero-deforestation commitments’ (ZDCs).

The RSPO was established in 2004 as a non-profit, industry-led voluntary certification scheme for oil palm growers (Laurance *et al.*, 2010), and has the vision of “transforming markets to make sustainable palm oil the norm” (RSPO, 2020a). The RSPO established its first Principles and Criteria for sustainable palm oil production in 2005, and began certification in 2008 (Laurance *et al.*, 2010). The 2005 Principles and Criteria required that plantation development (or replanting) had replaced neither primary forest nor habitat supporting ‘high conservation values’ (HCVs) since 2005 (RSPO, 2005). However, HCVs were not clearly defined, and initial identification of locations with HCVs was neither rigorous nor systematic (Edwards, Fisher, & Wilcove, 2012).

Thus, the 2005 RSPO Principles and Criteria left secondary and disturbed forests vulnerable to conversion (Greenpeace, 2007), in spite of their high value for carbon and biodiversity compared to oil palm plantations in Southeast Asia (Berry *et al.*, 2010; Brühl & Eltz, 2010; Chazdon *et al.*, 2009; Dunn, 2004; Edwards *et al.*, 2014; Fitzherbert *et al.*, 2008). In 2013, the Principles and Criteria were revised, to include no conversion of habitat supporting primary forest, rare, threatened, or endangered species, or HCVs, according to a more comprehensive definition (RSPO, 2013). HCVs comprised six categories of environmental and social conservation value: species diversity, landscape-level ecosystems and mosaics, ecosystems and habitats, critical ecosystem services, community needs, and cultural values (RSPO, 2013); so natural habitat was more comprehensively protected from certified oil palm expansion. Thus, certified plantations were required to 'maintain and enhance' HCV conservation set-asides within the plantations (fig. 1.3) (RSPO, 2013), which I address in detail in chapter 2. However, conservation of HCVs did not prevent deforestation under all circumstances (Senior *et al.*, 2015), which critics argued undermined the value of RSPO certification, stimulating corporations to make 'zero-deforestation commitments' independently of RSPO membership (see following paragraphs in this section, pages 30-31). Moreover, the value of HCV areas is uncertain, particularly given their fragmented nature; and I examine their value for conserving AGC in chapter 2. In 2018, the RSPO adopted a 'No Deforestation, No Peat, No Exploitation' (NDPE) policy, which requires all land to undergo a HCV-High Carbon Stock Approach (HCV-HCSA) assessment prior to conversion (RSPO, 2018), in order to designate all forest areas, and other natural habitat with HCVs, for conservation. This approach uses a decision-tree process to designate forest habitat for protection, based on the vegetation structure of rainforest in Southeast Asia, in addition to protecting habitat supporting HCVs. The HCV-HCSA protects both relatively disturbed forest vegetation ('young regenerating forest'), as well as more mature forest habitat, in order to support regeneration of degraded habitats where possible (Brown & Senior, 2014; Rosoman *et al.*, 2017). I describe this approach in more detail in chapter 3.

Figure 1.3. High Conservation Value forest patches conserved within RSPO plantations in Sabah, Malaysia. (a) Small HCV area surrounded by recently-replanted oil palm. (b) Mixed landscape of oil palm and conserved forest areas. I sampled the vegetation in these HCV sites during fieldwork presented in chapter 2. Photo credits: (a) Susannah Fleiss; (b) Robin Hayward.

There is concern that RSPO certification does not provide additionality in the reduction of negative environmental impacts of oil palm agriculture, because it does not stimulate behaviour change, but simply certifies the subset of companies that happen to have complied with the criteria (e.g. companies which planted on previously converted agricultural land) (Garrett *et al.*, 2016). The RSPO Principles and Criteria are substantially more stringent in terms of protection of natural vegetation than national policies of palm oil producer countries (Garrett *et al.*, 2016), but currently only cover 19% of global palm oil production, and roughly 12% of global oil palm plantation area (3.2 Mha of 27.1 Mha) (Harris, Goldman, & Gibbes, 2019; RSPO, 2020b). The majority of the global palm oil market is therefore outside RSPO, so most palm oil continues to drive deforestation. In Indonesia, RSPO-certified plantations were generally established in the 1980s and 1990s (i.e. prior to the formation of the RSPO), in areas of lower forest cover than non-certified plantations; and no plantation established after 2008 (i.e. when the RSPO began certification) was certified by 2017 (Carlson *et al.*, 2018). This suggests that certification has not incentivised avoidance of deforestation within plantations, but has largely been taken up by plantations with low forest cover prior to planting. Moreover, the historic failure of the RSPO to target smallholders means that RSPO certification has not yet reached some of the growers with the highest opportunity costs for avoiding deforestation (Garrett *et al.,* 2016). However, in 2019, the RSPO adopted an 'Independent Smallholder Standard' with the aim of simplifying the Principles and Criteria for application by smallholders (RSPO, 2019b), so the additionality of RSPO certification could increase over coming years given the large number of smallholder oil palm growers. There is also concern that enforcement of RSPO Principles and Criteria is weak and without independent evaluation (EIA and grassroots, 2019). In Kalimantan, Indonesia, RSPO certification has reduced deforestation within oil palm plantations, but not fire or peatland clearance; and has not reduced the rate of decline of populations of orangutans, an iconic protected species (Carlson *et al.*, 2018; Morgans *et al.*, 2018). It is therefore unclear if RSPO certification can effectively reduce natural habitat loss driven by oil palm expansion.

Over the last decade, numerous corporations have adopted 'zero-deforestation commitments' (ZDCs) across their supply chains (Haupt *et al.*, 2018), in light of the potential for RSPO-certified palm oil to drive deforestation prior to 2018 (when the RSPO adopted the NDPE policy), and the weak enforcement of the Principles and Criteria (EIA and grassroots, 2019). These ZDCs were partly adopted in response to consumer pressure (Haupt *et al.*, 2018), and are considered the strongest private instrument to reduce commodity-driven deforestation (Chain Reaction Research, 2020). In 2018, roughly two-thirds of palm oil production and one-third of oil palm land area were covered by ZDCs, which was considerably greater coverage than for other key deforestation-risk commodities (e.g. beef, soy and pulp and paper) (Haupt *et al.*, 2018), highlighting the wide reach of ZDCs and their potential to have greater impact in reducing oil palm-driven deforestation than current RSPO certification (which covers 19% of global palm oil production, see above; note that RSPO certification has included 'no-deforestation' since 2018 and is therefore a subset of the oil palm industry under ZDCs). ZDCs may incentivise oil palm growers to develop plantations in non-forest locations, but have little impact on growers outside these commitments, and thus provide limited additionality in reducing the loss of natural habitats from oil palm expansion. In chapter 3, I examine the potential for ZDCs to drive leakage of oil palm expansion and biodiversity loss into tropical grassy and dry-forest biomes, which are not comprehensively protected under current ZDCs.

In addition to the RSPO and corporate ZDCs, Indonesia and Malaysia have each developed national oil palm certification schemes, which are now mandatory for all oil palm growers in the relevant country, and therefore provide the national legal standards for oil palm cultivation. The Malaysian Sustainable Palm Oil (MSPO) and Indonesian Sustainable Palm Oil (ISPO) certification schemes were developed in response to the complexities of obtaining RSPO certification for smallholders (prior to the Independent Smallholder Standard in 2019), and in order to maintain competitiveness of Indonesian and Malaysian palm oil in global markets (Higgins and Richards, 2019). Obtaining MSPO and ISPO certification is therefore less bureaucratic than for RSPO, and more accessible for smallholders, but these schemes have received criticism for their comparatively weaker requirements for environmental protection (Higgins and Richards, 2019; Earthsight, 2020). Neither of these schemes fully protect forest or peatlands from conversion (MPOCC, 2013; Earthsight, 2020), but they provide a legal framework in which further levels of environmental protection could be incorporated, highlighting the need for robust understanding of the impacts of more stringent schemes, such as RSPO certification, to guide future improvements to wider-reaching standards for oil palm cultivation.

In 2019, the EU issued the Renewable Energy Directive II, stating it will phase palm oil out of biofuels by 2030 (excluding palm oil sustainably produced by smallholders), in order to reduce the biodiversity loss and GHG emissions driven by oil palm expansion in tropical countries. In addition, at the time of writing (in 2020), a new Environmental Bill is under consultation in the UK, which proposes requiring ‘due diligence’ of larger businesses to demonstrate that key deforestation-risk commodities (including palm oil) in their supply chains were produced following local laws to protect forests and other natural ecosystems (i.e. without illegal deforestation) (DEFRA, 2020). Thus, legislation to reduce the loss of natural habitats driven by palm oil expansion is under ongoing development in both consumer and producer nations, highlighting the importance of understanding the success of recent interventions to improve the environmental sustainability of oil palm cultivation, to help guide future developments.

1.7 Thesis aims and rationale

In this thesis, I examine how the impacts of oil palm expansion on tropical biodiversity and carbon storage can be reduced, in order to provide new information to help reduce the land-use impacts of oil palm agriculture. In chapters 2 and 3, I examine the degree to which sustainability certification helps reduce the impacts of oil palm expansion on carbon and biodiversity, both locally (chapter 2), and globally (chapter 3). From the findings in these chapters, I conclude that further expansion of oil palm plantations should be avoided where possible. To reduce the need for land-use change, and consequent biodiversity loss and greenhouse gas (GHG) emissions, oil palm production could be increased by improving the yield on current plantations. Therefore in chapter 4, I examine drivers of industrial oil palm yield in Malaysia, focusing on the role of climate, in order to understand how yield is likely to change in future, and whether there is potential to increase palm oil production without further expansion, through intensification. In chapter 5, I synthesise my findings and discuss the degree to which recent interventions to reduce the environmental impacts of oil palm expansion have been successful, and how these impacts could be further reduced. I describe the key aims of each of these chapters below.

Chapter 2: Conservation set-asides improve carbon storage and support associated plant diversity in certified sustainable oil palm plantations

In this chapter, I examine the conservation value of set-asides (mostly HCV areas) in RSPO-certified oil palm plantations for supporting AGC and associated plant diversity, using data collected during fieldwork in Sabah, Malaysian Borneo.

Key hypotheses:

(1) Forest conservation set-asides support more AGC than oil palm plantations, but less than continuous forest (primary and selectively-logged).
(2) Conservation set-asides with high AGC also support high plant diversity.
(3) Landscape-scale forest fragmentation, local topography and soil parameters are important predictors of AGC in set-asides.

Chapter 3: Zero-deforestation palm oil could threaten tropical grassy and dry forest biomes

In this chapter, I map locations of natural habitat that is climatically-suitable for oil palm expansion (both rainfed and under irrigation), in order to examine the potential for ZDCs to drive leakage of oil palm expansion (and hence biodiversity loss) from tropical rainforest to grassy and dry forest biomes.

Key hypotheses:

(1) ZDCs have the potential to drive leakage of oil palm expansion from tropical rainforest to tropical grassy and dry forest biomes, because most locations suitable for oil palm in the tropical rainforest biome would be protected under ZDCs.
(2) Irrigation could increase the total area suitable for oil palm cultivation under ZDCs, and the expected yields.
(3) ZDCs steer oil palm expansion into high-biodiversity locations within tropical grassy and dry forest biomes, whilst protecting the high-biodiversity locations within tropical rainforest.

Chapter 4: Climate has limited but varied impacts on oil palm yields in industrial plantations

In this chapter, I examine the role of climate in determining recent oil palm yield in industrial plantations in Malaysia, in order to understand yield gaps on current plantations, and how climate change might affect oil palm yield.

Key hypotheses:

(1) Climate (temperature and rainfall) is a key driver of variation in monthly oil palm yield.
(2) Monthly yield is positively related to both temperature and rainfall, with the strongest relationships at timelags corresponding to key stages of oil palm fruit development.

Chapter 2

Conservation set-asides improve carbon storage and support associated plant diversity in certified sustainable oil palm plantations

Keywords: climate mitigation; conservation set-aside; forest fragment; oil palm; sustainable agriculture; tropical forest

2.1 Highlights

- Conservation set-asides boost aboveground carbon stocks of oil palm plantations
- Set-asides co-benefit carbon and plant diversity compared to oil palm alone
- Fewer seedlings in set-asides than primary forest may reduce tree regeneration
- Management of set-asides could improve their regeneration and plant diversity

2.2 Abstract

Maintaining forest conservation set-asides is a key criterion of sustainability certification of many crops that drive tropical deforestation, but their value for carbon storage and associated biodiversity is unclear. We conducted vegetation measurements to examine the benefits of set-asides for aboveground carbon stocks (AGC) in certified oil palm plantations on Borneo, and whether their AGC is positively associated with plant diversity. The mean estimated AGC of live trees and palms ≥10 cm diameter in set-asides in certified oil palm plantations (52.8 Mg ha^{-1}) was more than 1.5-times that of oil palm (30.3 Mg ha^{-1}), with some plots supporting similar AGC to primary forest. For lowland Borneo, we estimate that the average AGC of oil palm plantations with 10% coverage of set-asides is up to 20% greater than the average AGC of oil palm plantations without set-asides, newly demonstrating carbon storage as a benefit of conservation set-asides. We found positive relationships between AGC and plant diversity, highlighting the carbon–biodiversity co-benefits of set-asides. However, set-asides had a lower density of tree seedlings than continuous primary forest, indicating potential suppression of future tree regeneration and AGC. Our findings support the application of zero-deforestation during agricultural development to conserve areas of remaining forest with high AGC and high biodiversity. We recommend management practices that boost regeneration in existing set-asides (e.g. enrichment planting), which would be most effective in larger set-asides, and could substantially increase the AGC of agricultural landscapes without removing land from production, and help conserve forest-dependent biodiversity.

2.3. Introduction

If global food demand continues to increase without substantial shifts in diet and food distribution, global crop production will need to double by 2050, causing large-scale land-use change (Ray *et al.*, 2013; Shepon *et al.*, 2018). This risks considerable environmental damage because land-use change for commodity production is the largest driver of forest loss globally, mostly occurring in the tropics (Curtis *et al.*, 2018), where forests harbour exceptional biodiversity and contribute critically to global carbon cycling (Gibson *et al.*, 2011; Baccini *et al.*, 2012). Moreover, reducing greenhouse gas (GHG) emissions from tropical agriculture and associated deforestation is fundamental to limiting climate change in line with the Paris Agreement (United Nations, 2015a; Griscom *et al.*, 2020), because global land-use accounts for nearly a quarter of recent anthropogenic GHG emissions, primarily through agriculture and deforestation (IPCC, 2019).

To reduce the environmental impacts of tropical agriculture, many corporations have made commitments to reduce deforestation in their supply chains, and 'zero-deforestation' commitments now cover two-thirds of global palm oil production (Haupt *et al.*, 2018). If successfully implemented, such commitments have the potential to considerably reduce the negative environmental impacts of oil palm agriculture, given the high GHG emissions and biodiversity loss from extensive deforestation associated with recent oil palm expansion in Southeast Asia (Wilcove *et al.*, 2013; Haupt *et al.*, 2018; Pendrill *et al.*, 2019). 'Zero-deforestation' commitments are frequently put into effect through voluntary certification schemes for sustainable commodity production, such as the Roundtable on Sustainable Palm Oil (RSPO) (Chagas *et al.*, 2018). A key criterion of many of these schemes is the maintenance of conservation set-asides of natural habitat within agricultural landscapes (Senior *et al.*, 2015; RSPO, 2018). Since its inception in 2005, RSPO certification has required natural habitat (largely primary or logged forest) with 'High Conservation Values' (HCVs) to be set-aside for conservation within oil palm concessions (RSPO, 2018). These HCV set-aside sites are identified according to their value for biodiversity, ecosystem services and local communities (Brown *et al.*, 2013; Senior *et al.*, 2015). Oil palm plantations developed before 2005, and certified subsequently, also contain HCV set-asides identified retrospectively, such as remaining areas of natural habitat with low suitability for oil palm cultivation. More recently in 2018, the RSPO strengthened their criteria for sustainability and adopted a 'no deforestation' policy, to align with 'zero-deforestation' commitments of consumer-goods corporations. These commitments require new planted areas to follow a combined HCV-High Carbon Stock Approach (HCV-HCSA) to identify forest areas for protection, based on vegetation structure (such as carbon stocks and tree density) in addition to HCVs (Rosoman *et al.*, 2017; RSPO, 2018). The HCV-HCSA includes protection of low-AGC forest, enabling regeneration of set-aside trees and aboveground carbon stocks (AGC) (Rosoman *et al.*, 2017). By protecting forest set-asides, the RSPO aims to increase the extent of forest within certified oil palm plantations, and minimize biodiversity loss and carbon emissions from land-use change (Rosoman *et al.*, 2017; RSPO, 2018). 4.2 M ha of oil palm plantations are currently RSPO-certified globally (RSPO, 2020b), so the recent requirements for set-aside conservation could have considerable implications for AGC and biodiversity. To better understand these implications, it is therefore important to examine the benefits of existing conservation set-asides in oil palm.

The benefits of maintaining conservation set-asides for ecosystem services and biodiversity are not well established (Edwards & Laurance, 2012; Senior *et al.*, 2015). Forest set-asides in Southeast Asian oil palm landscapes can support 60-70% of primary forest biodiversity and high seedling survival rates, but this depends on their size (Yeong, Reynolds and Hill, 2016; Lucey *et al.*, 2017). The fragmented nature of many set-asides (Scriven *et al.*, 2019) is likely to negatively impact their biodiversity and carbon storage capacity (Laurance *et al.*, 2011). For example, within 100 m of the forest edge, elevated tree mortality substantially reduces AGC, favouring regeneration of pioneer species with low wood density (Laurance *et al.*, 2011; Qie *et al.*, 2017; Ordway and Asner, 2020), and these negative edge-effects on AGC can extend up to 1.5 km from the forest edge (Chaplin-Kramer *et al.*, 2015). In addition to edge-effects associated with fragmentation, set-asides have frequently undergone commercial selective logging prior to plantation development, like much of the remaining forest in Southeast Asia (Flint, 1994; Gaveau *et al.*, 2016). Selective logging reduces AGC through timber extraction, and is likely to cause long-term impacts in set-asides through reduced tree regeneration, particularly under additional disturbances such as drought and increasing temperatures (Jucker *et al.*, 2018; Pillay *et al.*, 2018; Qie *et al.*, 2019). Nevertheless, recent studies based on LiDAR surveys of AGC in Malaysian Borneo found that selectively logged forests contain 60-140 Mg AGC ha^{-1}, which decreases to c. 40-100 Mg ha^{-1} at forest edges (Asner *et al.*, 2018; Ordway and Asner, 2020), suggesting that conservation set-asides of logged forest fragments could still substantially improve the AGC of plantations, given that the AGC of oil palm is c. 30 Mg ha^{-1} (Kho and Jepsen, 2015). However, the AGC of set-asides is likely to vary substantially with local context such as disturbance history (Austin *et al.*, 2017), soil and topography (Quesada *et al.*, 2012; Jucker *et al.*, 2018). It is also unclear whether set-aside AGC contributes to the conservation of biodiversity, because relationships between AGC and biodiversity in tropical forests are frequently found to be positive but are variable and scale-dependent (Deere *et al.*, 2018; Strassburg *et al.*, 2010; Sullivan *et al.*, 2017). At large spatial scales, the 'land-sharing' approach of retaining conservation set-asides within agricultural landscapes may be less effective for conserving AGC and biodiversity than the 'land-sparing' approach of conserving continuous tracts of forest, because the conservation value of continuous primary forest for biodiversity and AGC is unparalleled (Gibson *et al.*, 2011; Watson *et al.*, 2018).

In this study, we collect new field data on vegetation in forest conservation set-asides in oil palm plantations on Borneo, to establish the value of set-asides for increasing plantation AGC, and whether conservation of AGC in set-asides can have co-benefits for plant diversity. We compare plot-level AGC in set-asides with that of continuous forest (logged and primary sites) and the oil palm planted area, and compare differences in their vegetation structure, including assessing regeneration potential by examining variation in seedling density. We examine potential drivers of variation in set-aside AGC (topography, degree of fragmentation, and soil parameters), and relationships between AGC and plant diversity. We scale up our estimates of set-aside AGC to predict average AGC of oil palm plantations, and use our findings to make policy recommendations on the establishment and management of set-asides for optimizing AGC storage and conserving biodiversity.

2.4. Materials and methods

Study sites

We undertook vegetation surveys in Sabah, Malaysian Borneo, between July and November 2017, in conservation set-asides within RSPO-certified oil palm plantations (*n* = 14 sites) across Eastern Sabah, and within a single, large tract of continuous forest for comparison (*n* = 4 sites; fig. 2.1a), part of a network of forest reserves between East Sabah and the central Borneo highlands (Asner *et al.*, 2018). The majority of set-asides (12 of 14) were in oil palm plantations planted prior to the establishment of the RSPO in 2005, so were generally in locations unsuitable for planting, and had subsequently been classified for conservation under RSPO Principles and Criteria (RSPO, 2018). Whilst these set-asides were not all initially conserved specifically for AGC or biodiversity value, they provided variation in degree of forest fragmentation (from isolated fragments to sites contiguous with forest outside the plantation, such as state forest reserves; see section below “Degree of forest fragmentation in the landscape”), set-aside age (oil palm plantations aged 8-26 years since first planting), and vegetation structure representative of the likely variation in conservation set-asides designated during plantation development (e.g. under the RSPO’s 2018 ‘no deforestation’ policy (RSPO, 2018)). We sampled in fully-protected primary continuous forest (*n* = 2 sites), which has never been selectively logged. We also sampled sites in once-logged (*n* = 1 site, logged in 1988) and twice-logged (*n* = 1 site, logged in mid-1980s and 2005/6) continuous forest, to include sites spanning a range of commercial selective logging intensities likely to represent logging in set-asides prior to plantation development (Reynolds *et al.*, 2011). All sites were ≥1.5 km apart to minimise issues of spatial autocorrelation and pseudoreplication in our analyses. The dominant soil types across our sites were orthic acrisols and dystric cambisols, which are common across lowland Sabah (Land Resources Division, 1974).

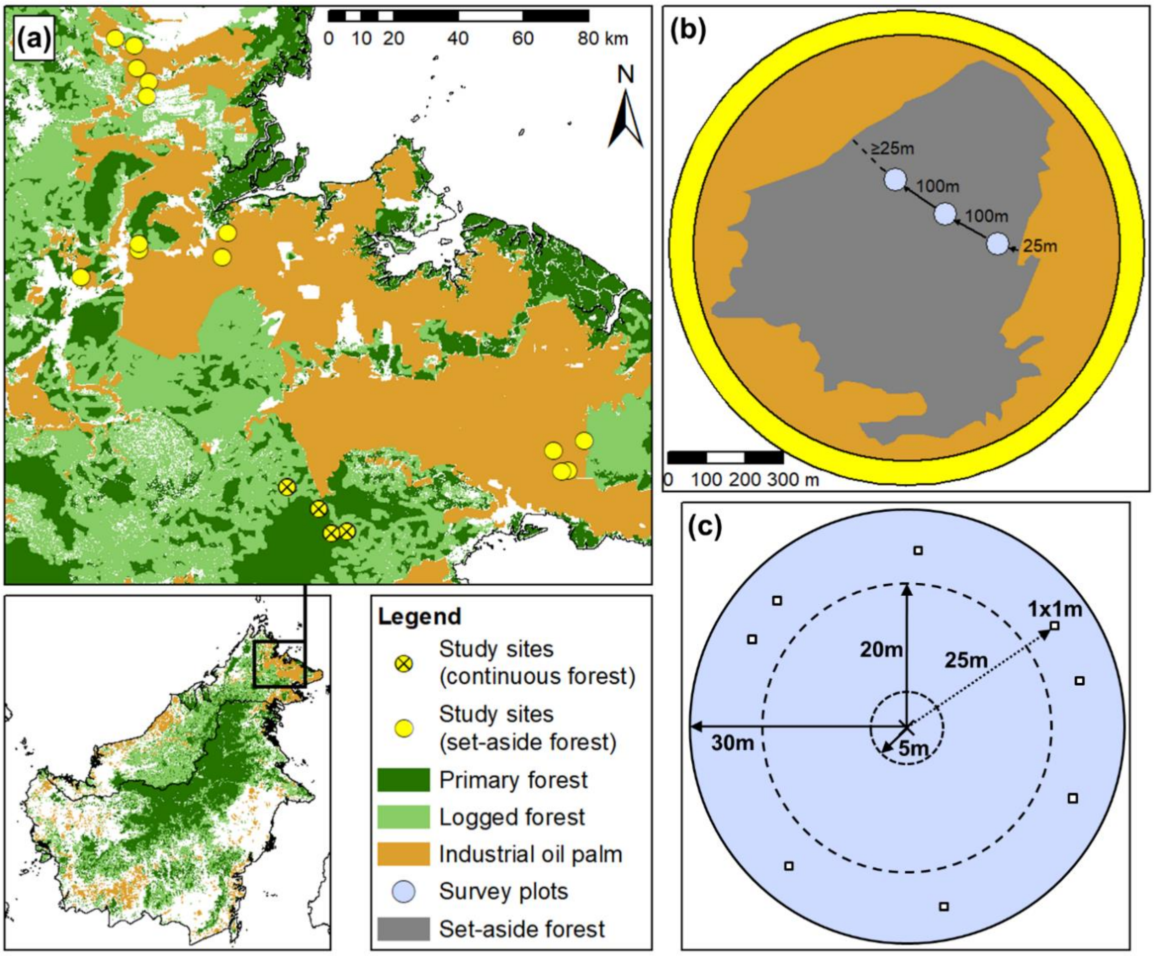


Figure 2.1. (a) Map of the sampling sites across Sabah, Malaysian Borneo (*N* = 18 sites). 14 of the sites were in set-asides in RSPO-certified oil palm plantations, and four sites were in a large tract of continuous forest (Danum Valley and Malua Forest Reserves). Forest cover and industrial oil palm plantation maps were obtained from CIFOR (Gaveau *et al.*, 2014, 2016). **(b) Transect design** (shown for a set-aside site). We placed two or three circular plots 100 m apart, with the first plot boundary 25 m from the nearest forest edge, and the boundaries of subsequent plots at least 25 m from any forest edge. **(c) Nested plot design for vegetation sampling.** In the main plot of 30 m radius, we recorded live trees and palms ≥25 cm dbh; in the subplot of 20 m radius, we recorded live trees and palms ≥10 cm and <25 cm dbh; and in the subplot of 5 m radius, we recorded live trees ≥2 cm and <10 cm dbh. We sampled seedlings (<2 cm dbh) rooted within eight 1x1 m quadrats, on random bearings 25 m from the plot centre.

Vegetation surveys

In each of the 18 sites (14 set-asides and 4 continuous sites) we estimated aboveground biomass and AGC in 2-3 circular plots (depending on set-aside size) of 30 m radius (plot size 0.28 ha; *N* = 49 plots in total). In set-asides, we placed the first plot boundary 25 m from the nearest forest edge to include edge effects, and subsequent plots 100m apart and ≥25 m from any edge (fig. 2.1b). We defined forest edge as the boundary of continuous woody vegetation over 2m height and canopy closure >20%, in line with HCSA guidelines, although boundaries between set-asides and oil palm were usually well-defined along minor plantation roads (Rosoman *et al.*, 2017). We used a nested survey design for live trees and palms (fig. 2.1c), following standard protocols (Marthews *et al.*, 2014; Phillips *et al.*, 2016). We identified live trees ≥2 cm dbh to genus, and to species when known, in the field, and identified remaining specimens and all seedlings at the herbaria at Danum Valley and Forest Research Centre, Sepilok. We also surveyed lianas and deadwood but these contributed only 6% of the variation in total AGC, so we do not include them in the main article (Supplementary Information 1.2).

Estimating tree height for tree biomass estimation

One person (AJ) estimated tree height by eye (in m; 'eye estimates') for a subset of trees ≥10 cm dbh in each plot (30.9% of stems, spanning 10-130 cm dbh), stratified by dbh, and for all palm stems, to improve the accuracy of our AGC estimates (Chave *et al.*, 2014). Eye estimates and clinometer height estimates ('tangent method') (Larjavaara and Muller-Landau, 2013) were closely correlated (r = 0.754, df = 48, p <0.001, based on 5% of stems with eye estimates), giving us confidence in our eye estimates (fig. S1.1). Both of these methods are subject to error, so we did not systematically correct eye estimates according to the clinometer estimates; thus we used the eye-estimates to predict height for all remaining stems (Larjavaara and Muller-Landau, 2013). We selected a second-order log-log model to predict remaining tree heights from the eye estimates, which had the lowest relative standard error of the four candidate models we compared using the function 'modelHD' in the BIOMASS package in R (table S1.1) (Réjou-Méchain *et al.*, 2017). We compared our field-based estimates of tree height, and resulting AGC estimates, to height and AGC estimates derived from established allometric equations, and found that the method for estimating heights did not alter our conclusions (Supplementary Information 1.1). Here, we present AGC estimates derived from field-based height estimates because these have previously been found to outperform regional and pan-tropical allometric estimates of tree height (Sullivan *et al.*, 2018).

Plant diversity and carbon stock estimation for study plots

For seedlings (<2 cm diameter), saplings (≥2 cm and <10 cm dbh) and adult trees (≥10 cm dbh), we calculated genus richness, and Fisher's alpha (based on genera; a measure of diversity robust to differences in stem density), per plot. We estimated the biomass of live tree stems ≥10 cm dbh using a pantropical allometric equation (Chave *et al.*, 2014) in the R BIOMASS package (Réjou-Méchain *et al.*, 2017), which outperforms regional models for Bornean forest (Rutishauser *et al.*, 2013). We checked all tree identifications against a database of plant taxonomy (The Plant List, 2013), and assigned wood density values at the finest taxonomic level available, from the Global Wood Density Database (Chave *et al.*, 2009; Zanne *et al.*, 2009). For trees ≥10cm dbh, we assigned wood density to 20.5% of stems by species, 78.2% by genus, 1.25% by family, and 0.032% by plot-level mean wood density (a single unidentified individual).

We used a mixed-species model to estimate palm biomass, to cover the multiple palm species in our surveys, based on dry mass fraction (which we assumed to be 0.37, the mean value for multiple species), diameter and stem height (Goodman *et al.*, 2013). We assumed a carbon content of 47.1% for all biomass (Thomas and Martin, 2012).

Estimation of oil palm AGC

Since oil palm is replanted in a regular 25-30 year cycle, we estimated time-averaged AGC stocks of oil palm (mean and 95% confidence intervals (CIs) for a 30-year planting cycle) from oil palm age-AGC functions which model carbon sequestration during oil palm growth (Carlson *et al.*, 2012, 2013). We used mean value theorem to calculate average oil palm AGC (average height of curve) for the oil palm growth curves between 0 and 30 years, providing us with mean and 95% CI estimates of time-averaged oil palm AGC for a 30-year planting cycle. We did not estimate oil palm AGC for the ages of the plantations specific to the set-asides in this study, but for unspecified industrial plantations under a 30-year planting cycle, in order to maintain general relevance of our results for the oil palm industry. To include oil palm in our statistical model comparing AGC of forest types (continuous primary, continuous logged, and set-aside) and oil palm, we simulated oil palm AGC data points following a Normal distribution with the mean and standard deviation of the time-averaged oil palm AGC (n = 15, following number of data points used to derive the oil palm growth curves in Carlson *et al.* (2013, 2012)).

Topographic measurements

To examine the influence of topography on variation in set-aside AGC, we measured slope (°) and elevation (m above sea level) in each plot. We took the maximum absolute value of four slope measurements in the cardinal directions from the plot centre as our measure of plot slope. We obtained elevation measurements from the barometric altimeter of a handheld GPS (Garmin 64s), which we had calibrated at sea level.

Degree of forest fragmentation in the landscape

To examine whether the degree of forest fragmentation surrounding plots in set-asides affected their AGC, we used UAV imagery provided by an oil palm company to determine surrounding land cover (forest or oil palm). Within a 1 km radius from the centre of each plot, we calculated total forest area (km^2) and edge index (number of 5 m-resolution grid cells containing forest–oil palm boundary, divided by total forest area; higher values signify that a greater proportion of forest is adjacent to oil palm). For each plot, we also quantified straight-line distance (m) to nearest forest–oil palm edge, and time since fragmentation (years since first adjacent oil palm establishment, obtained from the oil palm company; see fig. S1.7 for boxplots of these predictors, and scatterplots with AGC). These four variables (surrounding forest area, edge index, distance to forest, time since fragmentation) were correlated (absolute *r* values ranged 0.39-0.82; fig. S1.8), so we combined them using principal components analysis (PCA). We extracted the first principal component (PC1; which explained 68% of total variation) as a 'fragmentation index', with higher values representing greater forest fragmentation (fig. S1.9; table S1.4). We tested the impact of varying the buffer size for calculating forest area and edge index on our results (for buffers of 0.2-2 km), but it did not affect our conclusions (table S1.6).

Soil parameters

We used seven soil parameters (moisture, pH, available P, total P, total N, organic C and C:N ratio) to test the influence of soil properties and nutrients on AGC in set-asides (see fig. S1.10 for boxplots of these variables, and scatterplots with AGC). In each plot, we collected, bulked and subsampled five topsoil cores (0-20 cm depth; see Supplementary Information 1.3 for details of soil analyses, which were conducted at the Forest Research Centre, Sepilok). Because these seven parameters were correlated (fig. S1.11), we combined them by PCA and extracted the first two PCs (which explained 55% and 21% of the variation) as major gradients in soil nutrients and moisture (fig. S1.12; table S1.5).

Statistical analyses

We conducted all analyses in R version 3.6.2 (R Core Team, 2017). We compared plot-level AGC between set-asides (*n* = 37 plots), continuous forest (logged forest, *n* = 6; primary forest, *n* = 6) and oil palm (simulated data points, *n* = 15), using a Bayesian linear mixed effects model (LMM). We fitted site as a random intercept (15 simulated oil palm sites and 18 field sites) with an uninformative gamma prior for the random effect variance, using the blmer function in the R package 'blme' (Dorie, 2011). We found that model convergence was more robust under our low random effect replication using Bayesian parameter estimation than using conventional methods for parameter estimation (which was also the case for the Bayesian models described below). We expect that convergence was poor with parametric modelling because of the large variation in set-aside AGC with a relatively small sample size (37 set-aside plots). The model structure sufficiently accounted for spatial autocorrelation as the residuals were not spatially autocorrelated (Moran's I of residuals = -0.19, *p* = 0.20). We conducted post-hoc Tukey pairwise comparisons on the LMM using the glht function in the R package 'multcomp' (Hothorn, Bretz and Westfall, 2008).

We assessed differences in vegetation structure among forest types, including to obtain an indication of regeneration potential from seedlings and saplings in set-asides (from abundance, measured as stem density; and mean wood density, which indicates the likely wood density of larger trees in future, and thus the potential for AGC regeneration). We fitted three Bayesian LMMs with each of stem density, mean dbh and wood density as response variables, forest type and tree size class as fixed effects with an interaction term, and site as a random intercept with an uninformative gamma prior for its variance. We log-transformed stem density and mean dbh to remove heteroscedasticity of residuals. For models with significant main effects, we conducted post-hoc Tukey pairwise comparisons on a single categorical predictor of all pairwise combinations of forest type and size class.

To assess potential drivers of variation in AGC within set-asides, we ran generalized additive mixed models (GAMMs) using the R package 'gamm4' (Wood & Scheipl, 2017), with AGC in set-aside plots (n = 37) as the response variable, and a Gaussian family and identity link. We included the 'fragmentation index' (fragmentation PC1), two soil variables (soil PC1 and PC2) and slope as main effects; site as a random intercept; and elevation as a penalized cubic regression spline. We initially included both slope and elevation as splines, because the relationships between these and AGC can be non-linear (Jucker *et al.*, 2018), but we fitted slope as a main effect owing to insufficient variation for model computation.

To test the relationship between plant diversity and AGC, we conducted Bayesian general linear mixed effects models (GLMMs), with total AGC and size class fitted as fixed effects with an interaction term, and site as a random intercept, using the function 'bglmer' in the R package 'blme' (Dorie, 2011). We fitted the model explaining Fisher's alpha with a Gamma family and identity link, excluding four data points (three seedling and one sapling) because their Fisher's alpha values were over seven orders of magnitude greater than the other data, owing to a small number of stems of unique genera in those plots. We fitted the model explaining genus richness with a Poisson family and log link.

Extrapolating our AGC estimates to oil palm plantations

To examine the benefits of set-asides for AGC at the plantation scale, we estimated the average AGC of oil palm plantations (average carbon stocks in Mg ha^{-1} across a plantation of unspecified size) without set asides, and with set-asides (for varying set-aside coverage; 1-100% of the plantations), as well as of continuous forest sites for comparison. We define oil palm plantations as containing oil palm monoculture and set-aside forest patches (or oil palm monoculture alone), as in many industrial oil palm plantations in Southeast Asia (Wicke *et al.*, 2011; Gaveau *et al.*, 2014). We calculated total AGC mean and 95% PIs (prediction intervals) for each of the three land-use types (oil palm, set-aside and continuous forest) to determine average landscape-scale AGC (for plantations with and without set-asides, and continuous forest). We derived the 95% PIs for time-averaged oil palm AGC from the mean and 95% CIs for oil palm described above. We derived the mean and 95% PIs for set-aside and continuous forest sites from site-level estimates of set-aside AGC (*N* = 18, mean AGC of all plots at a site). We combined continuous primary and logged forest for this analysis because their plot-level AGC did not differ significantly (fig. 2.2). We estimated the average AGC of oil palm plantations with set-asides as the sum of the proportion of the plantation occupied by each land-use type (oil palm and set-aside) multiplied by the AGC (mean, lower 95% PI and upper 95% PI). We did not incorporate any effect of forest fragmentation on expected set-aside AGC (i.e. our estimates of AGC of oil palm plantations with set-asides assume that set-aside AGC is directly proportional to set-aside coverage) because we found no effect of fragmentation on set-aside AGC in this study (fig. S1.13; table S1.6). To compare the average AGC of oil palm plantations with set-asides for different values of AGC stored in set-asides, we also calculated the average AGC of oil palm plantations with set-asides for set-aside AGC of 2.5th and 97.5th percentiles of our set-aside sites (and mean oil palm AGC; for 1-100% of the plantation occupied by set-asides). It is unlikely that variation in topographic and soil parameters was sufficient to limit set-aside AGC in this study, particularly because set-asides had undergone selective logging (Quesada *et al.*, 2012; Asner *et al.*, 2018); therefore we assume that set-aside AGC could be 'improved' to the 97.5th percentile value for sites in this study.

2.5 Results

Across 49 0.28-ha plots in 18 sites, we measured 3120 live tree stems (10-140 cm dbh), 33 live palm stems (11-47.2 cm dbh), 989 saplings (2-9.8 cm dbh) and 1,076 seedlings (<2cm dbh).

Comparison of plot-level AGC between set-asides, continuous forest and oil palm

The mean plot-level AGC of live trees and palms in set-asides (52.8 Mg ha^{-1}) was more than 1.5-times the mean simulated time-averaged AGC of oil palm (30.3 Mg ha^{-1}), about half the mean AGC of continuous logged forest (101 Mg ha^{-1}), and considerably lower than that of continuous primary forest (126 Mg ha^{-1}; fig. 2.2; table S1.2). AGC of plots in set-asides was highly variable (7.8-115 Mg ha^{-1}), spanning values lower than the time-averaged AGC of oil palm to values greater than some continuous forest plots (68.4-207 Mg ha^{-1}). The variation of AGC within forest types arises from considerable variation both within and between sites (fig. S1.5).

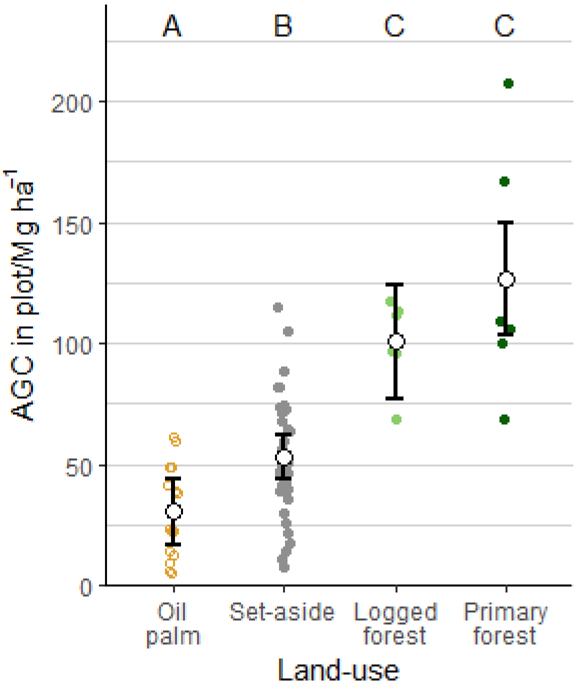


Figure 2.2. Estimated plot-level AGC by land-use type (mean ±95% CI), for all study plots (*n* = 49, closed circles), and estimated time-averaged AGC of oil palm (*n* = 15 simulated data points derived from Carlson *et al.* (2013, 2012), open circles). Estimates of AGC for field plots comprise AGC of live trees and palms ≥10 cm dbh. Model χ^2= 38.4, p <0.001 in comparison to null model (site as random intercept only). Different letters (A, B, C) denote significant difference between the land-use types at p <0.05, derived from post-hoc Tukey pairwise comparisons (table S1.2); where two land-use types have the same letter, their estimated AGC is not significantly different. See fig. S1.3 for a comparison of this model using different methods of tree height estimation; and fig. S1.4 for AGC values including deadwood and lianas.

Comparison of vegetation structure among forest types

The mean dbh of the largest tree size class (medium-large trees, ≥25 cm dbh) was significantly lower in set-asides (mean 34.7 cm) than in continuous forest (logged forest: 41.7 cm; primary forest: 48.7 cm), but there were no differences in stem density or mean wood density for size classes included in AGC estimates (small trees and medium-large trees) (fig. S1.6; table S1.3). However, mean seedling density was significantly lower in set-asides (1.63 m^{-1}) than primary continuous forest (5.83 m^{-1}).

Drivers of variation in set-aside AGC

Variation in set-aside AGC was partly explained by elevation, but we found no effect of fragmentation, soil or slope (table S1.6, fig. S1.13). Our final model included elevation alone (F = 0.14, p = 0.039) and explained 15% of variation in AGC (adjusted R^2).

Relationship between set-aside AGC and diversity

Genus richness of seedlings, saplings and adult trees were positively associated with AGC in set-asides (fig. 2.3; AGC $\chi^2 = 22.9$, $p < 0.001$). Fisher's alpha was positively associated with AGC for saplings and trees, implying that the positive relationship between diversity and AGC is independent of stem density for these size classes. In contrast, there was a weak negative association between Fisher's alpha and AGC for seedlings (fig. 2.3; size class-AGC interaction term $\chi^2 = 6.18$, $p = 0.046$).

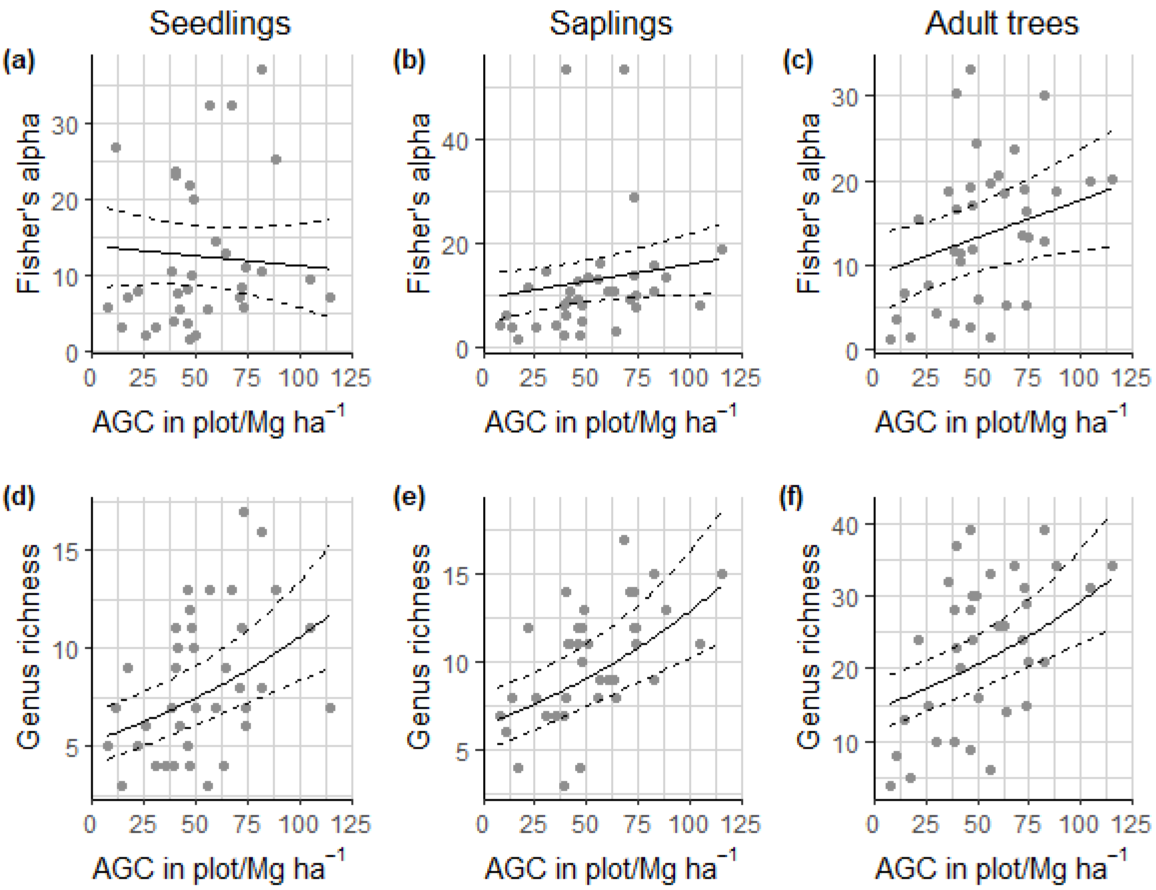


Figure 2.3. Results of Bayesian GLMMs modelling the relationship between plot-level AGC and plant diversity in set-asides, for seedlings (<2cm diameter), saplings (≥2cm and <10cm dbh) and adult trees (≥10cm dbh). (a-c) Fisher's alpha was significantly predicted by the full model (Gamma GLMM, identity link) including the AGC-size class interaction term ($\chi^2 = 6.18$, $p = 0.046$ for inclusion of the interaction term). **(d-f) Genus richness** was significantly predicted by AGC and size class (Poisson GLMM, log link; $\chi^2 = 22.9$, $p < 0.001$ for inclusion of AGC; $\chi^2 = 318.9$, $p < 0.001$ for inclusion of size class), but including the AGC-size class interaction term did not improve model fit ($\chi^2 = 0.94$, $p = 0.62$). Dashed lines denote 95% confidence intervals. Note variation in y axes.

Impact of set-asides on oil palm plantation AGC

Our estimates of average site-level AGC in set-asides (mean AGC of all plots at a site) range from 28.1 to 96.6 Mg ha^{-1}. For each additional 10% coverage of set-asides in an oil palm plantation, average plantation AGC increases by 2.34 Mg ha^{-1}, when set-aside AGC is estimated as the average site-level AGC of set-asides in this study (53.8 Mg ha^{-1}; fig. 2.4). When set-aside AGC is at the 97.5th percentile of site-level set-aside AGC (91.6 Mg ha^{-1}), each additional 10% coverage of set-asides increases average plantation AGC by 6.13 Mg ha^{-1}. Thus a plantation with 10% set-aside cover and average set-aside AGC has 7.7% greater AGC than a plantation without set-asides, and a plantation with 10% set-aside cover and 97.5th percentile set-aside AGC has 20.2% greater AGC than a plantation without set-asides.

For a plantation with existing set-asides, improving the AGC of all set-asides can substantially increase average plantation AGC, although the degree for potential improvement depends on current AGC in the set-asides (fig. 2.4). For example, in a plantation with 10% set-aside cover, increasing the set-aside AGC from mean set-aside AGC to the 97.5th percentile would increase average plantation AGC by 3.8 Mg ha^{-1} (11.6%), whereas increasing the set-aside AGC from the 2.5th percentile to the 97.5th percentile would increase average plantation AGC by 6.3 Mg ha^{-1} (20.7%).

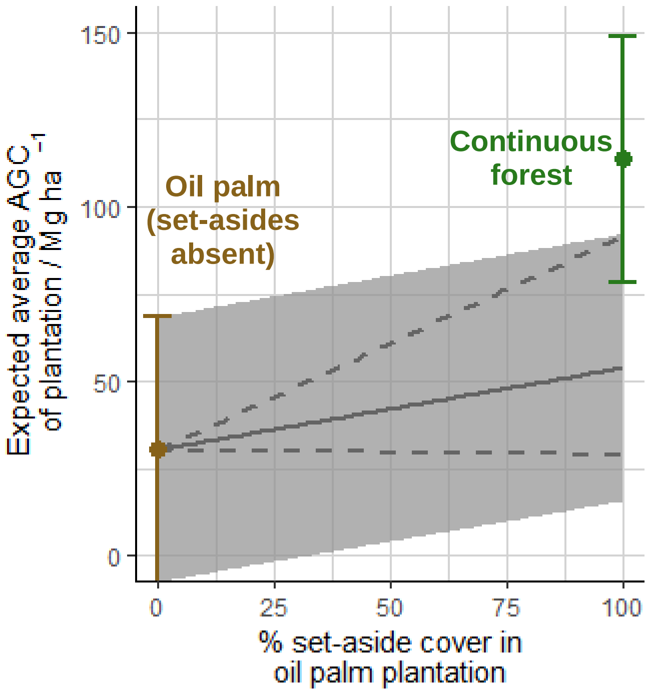


Figure 2.4. Predicted average AGC for oil palm plantations with set-asides (grey solid line and shading; mean ±95% PI), based on estimates of AGC of set-aside sites (*n* = 14). We also show the predicted average AGC (mean ±95% PI) for plantations without set-asides (i.e. oil palm monoculture only; brown point and error bars; derived from Carlson *et al.* (2013, 2012)) and in continuous forest landscapes (green point and error bars; based on estimates of AGC in continuous forest sites (*n* = 4)) for comparison. We assume that plantations comprise only oil palm and forest set-asides (when present; i.e. no water bodies, infrastructure, open areas, etc.), and that average plantation AGC increases in direct proportion to the percentage cover of set-asides. Upper and lower dashed lines are predicted AGC when the set-aside AGC is the 97.5th and 2.5th percentiles of the site-level set-aside AGC, rather than the mean (solid line).

2.6 Discussion

Value of set-asides for increasing the AGC of oil palm plantations

Mean plot-level AGC of set-asides in lowland Sabah was more than 1.5-times that of oil palm (fig. 2.2), with upper values roughly equivalent to those in continuous forest. We estimate that plantations with 10% cover of set-asides support up to ~20% more AGC than oil palm plantations without such set-asides (fig. 2.4). Globally, the 4.2 Mha of RSPO-certified plantations would support 137 Tg (137 x 10^{-12} g) AGC if they contained 10% coverage of forest set-asides similar to those in this study, which is ~10 Tg greater than the time-averaged AGC of oil palm alone for the same plantation area, assuming no set-aside coverage (127 Tg). Thus set-asides contribute substantially to carbon storage, in addition to supporting biodiversity (Lucey *et al.*, 2017), connectivity (Scriven *et al.*, 2019), and water quality (Luke *et al.*, 2017), and can therefore contribute to mitigating the GHG emissions of oil palm agriculture (Burton *et al.*, 2017). We highlight the importance of conserving the largest trees for AGC, as shown previously (Slik *et al.*, 2013), because the mean diameter of the largest tree size class in set-asides was significantly smaller than that in continuous forest, resulting in significantly lower AGC in set-asides. Positive relationships between AGC and genus richness of seedlings, saplings and adult trees in set-asides demonstrate co-benefits of conserving set-asides for high AGC and plant diversity (fig. 2.3), which we expect to hold true for other taxonomic groups (Ferreira *et al.*, 2018). The positive value of set-asides for improving AGC of oil palm plantations is likely to hold in other croplands, because oil palm has unusually high AGC for a crop (Bonini *et al.*, 2018). However, the value of set-asides for plantation-scale AGC is likely to vary between crop types; for example, negative edge effects on AGC may be stronger for perennial crops (e.g. soy) than oil palm, because of a greater contrast in vegetation structure and microclimate at edges (Laurance *et al.*, 2011), creating a more hostile environment for tree growth and recruitment.

Unparalleled value of continuous forest for AGC

Mean AGC in continuous forest plots was over double that of set-asides, highlighting the unparalleled importance of continuous forest for AGC storage (Asner *et al.*, 2018), as for biodiversity (Gibson *et al.*, 2011). Furthermore, it is likely that we under-estimated the AGC of continuous forest (Tangki and Chappell, 2008; Asner *et al.*, 2018) because our small plot size (0.28 ha) likely under-sampled the largest stems (Clark and Clark, 2000), and our continuous forest AGC values are low for the region (e.g. Asner et al., 2018), although some previous estimates are similar (Berry *et al.*, 2010, using 1 ha plots; Saner *et al.*, 2012, using 0.25 ha transects). Our continuous forest sampling design was pseudoreplicated at the spatial scale of our forest types (all continuous forest plots were spatially clustered in comparison to the spread of set-asides across Eastern Sabah), although we did not detect spatial autocorrelation in our statistical model residuals. Therefore we may have under-sampled variation for continuous forest AGC across Eastern Sabah (Ramage *et al.*, 2013). However, an improved sampling design with less clustering would not likely alter our conclusion that continuous forest has unparalleled AGC value in comparison to set-asides, because this holds true for previous estimates of continuous forest AGC in Sabah, collected using both field and LiDAR sampling (Kho and Jepsen, 2015; Asner *et al.*, 2018).

Substantial variation in set-aside AGC

AGC in plots in set-asides varied substantially (7.8-115 Mg ha^{-1}), with values ranging from less than the time-averaged AGC of oil palm (mean 30.3 Mg ha^{-1}) to greater than some continuous forest plots (68.4-207 Mg ha^{-1}). This variation in set-aside AGC is similar to existing estimates of the variation in AGC of logged (continuous and fragmented) forests across Sabah (mostly 20-120 Mg ha^{-1}; Asner *et al.*, 2018). Elevation accounted for some variation in set-aside AGC, but we were unable to explain most of the variation. The high variability of AGC in tropical primary forests is driven by multiple factors such as rainfall, soil, elevation and local plant diversity (Poorter *et al.*, 2015; Asner *et al.*, 2018), and it is likely that these also contribute to variation in the AGC of logged forest. However, we expect that variation in forest disturbance prior to or during plantation development (e.g. from commercial selective logging) is the primary driver of variation in set-aside AGC. All the set-aside sites in this study were logged at least once during plantation development, and it is highly likely that logging intensities would have varied considerably across study plots (e.g. variation in the volumes of timber extracted, and techniques used) (Putz *et al.*, 2001; Reynolds *et al.*, 2011), depending on the volume of commercial timber present, accessibility, and regulations implemented during logging operations. Negative edge effects on AGC in Sabah vary with topography and soil type, and are correlated with edge effects on other aspects of ecosystem functioning, such as foliar phosphorus content, canopy gap area, and leaf mass per area (Ordway and Asner, 2020). Given that our sample size in set-asides was relatively small (37 plots in 14 sites), variation in local disturbance and ecosystem functioning may have masked any effects of fragmentation and edge effects on set-aside AGC in this study which have been found in other studies in the region (Ordway & Asner, 2020). Much of the existing literature on forest fragmentation does not address the impacts of additional disturbances such as logging (e.g. Laurance *et al.*, 2011), even though most forests across the tropics have been selectively logged as well as fragmented (Asner *et al.*, 2009). Understanding the combined effects of multiple disturbances on the carbon storage, dynamics, biodiversity and potential for recovery of forest set-aside areas would provide insight into the potential conservation value of set-asides in the long-term, and should be a priority for future studies.

Regeneration of trees and AGC in set-asides

Set-asides had fewer seedlings than continuous primary forest, suggesting that without management intervention (see below), regeneration of trees and thus future AGC may be reduced in set-asides. The relationships between Fisher's alpha (i.e. diversity accounting for abundance) and genus richness (i.e. diversity not accounting for abundance) for seedlings with set-aside AGC were contrasting, suggesting that seedling abundance is positively correlated with set-aside AGC, driving this pattern. The reduced seedling abundance in plots with low AGC may have reduced the negative density-dependence acting on seedling recruitment, resulting in slightly higher seedling Fisher's alpha-values in set-asides with low AGC (LaManna *et al.*, 2017). This recruitment of more diverse seedlings in set-asides with low AGC could enhance AGC in these set-asides in future (Poorter *et al.*, 2015), although the relationship was weak so the effect may be minimal. Furthermore, the seedling genus richness in set-aside plots with the lowest AGC was very low (~5 genera), suggesting reduced resilience of seedlings to disturbances such as drought, which are poorly buffered in forest fragments (Ewers and Banks-Leite, 2013). Therefore, we expect that the overall reduced seedling abundance in set-asides (and particularly in those with low AGC, as suggested by the diversity relationships) will have a greater negative impact on AGC regeneration in the medium-term than any positive impact of increased seedling diversity.

Relevance of findings to current conservation policy

Within the first seven months of RSPO implementation of the HCV-HCSA, over 300,000 ha of conservation set-asides were identified within 1.6 M ha of land-holdings proposing new land clearance (RSPO, 2019a, p. 39), indicating that conservation set-asides will be an increasingly significant component of certified oil palm plantations. All the set-asides in this study were in RSPO-certified oil palm plantations, but were formed prior to the adoption of the HCV-HCSA by the RSPO (RSPO, 2018). Our set-aside site-level AGC (mean of all plots in a site; 28.1-96.6 Mg ha^{-1}) ranged from below the lower threshold for protection under the HCV-HCSA to much higher quality forest. It is therefore likely that set-asides in new plantations developed under the HCV-HCSA will span a similar or greater range of AGC than in our study sites. Thus, many set-asides designed under HCV-HCSA are likely to require management to improve their AGC and biodiversity benefits (see below).

Designing sustainable oil palm landscapes to conserve carbon

Our findings contribute new evidence to support the design of set-asides for AGC in line with the HCV-HCSA (Rosoman *et al.*, 2017; RSPO, 2018):

(a) *Maximising set-aside area where possible*. We estimate that plantations with greater cover of set-asides have higher AGC. Although we found no effect of fragmentation on set-aside AGC, fragmentation often negatively affects AGC and biodiversity, particularly in the tropics and specifically in this region (Laurance *et al.*, 2011; Lucey *et al.*, 2017; Qie *et al.*, 2017; Betts *et al.*, 2019; Ordway and Asner, 2020); thus we recommend maintaining large forest patches where possible (>200 ha 'core area', habitat at least 100 m from the forest edge, is recommended by Lucey et al. (2017)) and designing set-asides to minimise edge effects.

(b) *Prioritising forest with the highest AGC for conservation (alongside other conservation values).* We estimate that set-asides with the highest AGC (and therefore a high density of the largest trees, ≥25 cm diameter) confer over double the benefit to average plantation AGC as the same area of set-asides with average AGC, and that set-asides with higher AGC support greater plant diversity. Given the trade-off between total area of set-asides and cultivated area, prioritising high-AGC forest for conservation is preferable for minimising loss of crop area, as recommended for Gabon (Burton *et al.*, 2017).

(c) *Protecting low AGC sites.* The majority of our set-aside sites fall within the lowest AGC category of HCSA (‘Young Regenerating Forest’) (Rosoman *et al.*, 2017), considerably below the maximum AGC of set-aside sites (97 Mg ha^{-1}, corresponding to HCSA ‘Medium Density Forest’). Nonetheless, these low-AGC set-asides provide considerable opportunity for increasing plantation AGC through management for regeneration (see below).

Management of set-asides for improved carbon stocks and plant diversity

Low seedling density in set-asides highlights the potential need for management to support tree regeneration and maintain or improve set-aside AGC and plant diversity in the long-term. Forest restoration such as enrichment planting (Yeong, Reynolds and Hill, 2016) and liana cutting (Marshall *et al.*, 2016) may accelerate AGC gains in set-asides, and planting fruiting trees may attract seed dispersing birds and mammals, further enhancing forest regeneration (Meijaard *et al.*, 2005) and benefitting forest biodiversity. Focusing management on larger set-asides would likely produce greater increases in AGC and biodiversity because restoration is more likely to be successful (Crouzeilles *et al.*, 2016), and because larger sites can support greater total AGC and biodiversity.

2.7 Conclusion

Conservation set-asides in oil palm plantations can support high AGC stocks, and improve the average AGC of oil palm plantations, thereby helping to mitigate GHG emissions from oil palm agriculture. Set-aside AGC and plant diversity are positively associated, so conserving set-asides for high AGC has co-benefits for conserving high plant diversity. Our findings support the HCV-HCSA guidelines for set-aside conservation, such as prioritising conservation of locations which are large in size and/or support high AGC, as well as conserving forest areas of relatively low AGC to enable future regeneration of AGC and biodiversity. We recommend management of set-asides to improve tree and AGC regeneration, which would increase the AGC of oil palm plantations without removing land from crop production, and prevent future declines in AGC and tree diversity due to poor regeneration from the current low abundance of seedlings in set-asides.

Chapter 3

Zero-deforestation palm oil could threaten tropical grassy and dry forest biomes

3.1 Abstract

Many companies have committed to ‘zero-deforestation’ supply chains, to reduce carbon emissions and biodiversity loss from tropical commodities. We examine the potential for zero-deforestation commitments (ZDCs) to drive leakage of land-use change from tropical rainforest to lower-carbon habitats, which support distinct biodiversity, using the example of commercial oil palm, which is increasingly expanding outside the tropical rainforest biome. Tropical grassy and dry forest biomes contain >50% of climatically-suitable land (outside urban areas and cropland) for expansion of oil palm agriculture under ZDCs, equivalent to a four-fold (rainfed cultivation) to seven-fold (including irrigated cultivation) greater area than current global oil palm plantations. Within these biomes, ZDCs fail to protect areas of high vertebrate richness from expansion, although some locations are likely to have low environmental costs of conversion to oil palm. Thus, to prevent unintended consequences of ZDCs and guide oil palm expansion into locations with the least environmental impact, policies and governance for sustainable development and conservation must expand focus from rainforests to all relevant biomes.

3.2 Introduction

Agriculture has driven almost three-quarters of tropical deforestation (Hosonuma *et al.*, 2012), causing substantial biodiversity loss (Laurance, Sayer and Cassman, 2014) and greenhouse gas emissions (Pendrill *et al.*, 2019), yet continues to expand, due to the growing global population, wealth and consumption (Rudel *et al.*, 2009; Defries *et al.*, 2010). Many corporations have therefore voluntarily committed to ‘zero-deforestation’ supply chains for commodities such as palm oil and pulp and paper (Haupt *et al.*, 2018). Zero-deforestation commitments (ZDCs) protect the majority of remaining tropical rainforest from agricultural expansion (Leijten *et al.*, 2020), although their success depends on widespread uptake (Garrett *et al.*, 2019). However, expansion to meet growing demands could consequently be displaced to tropical grassy biomes (grasslands, savannas and shrublands (Lehmann and Parr, 2016)) and dry forests (closed-canopy forests with highly seasonal rainfall (Miles *et al.*, 2006)). While some highly degraded pastures in these biomes incur minimal environmental costs from conversion to agriculture (Gilroy *et al.*, 2015; Quezada *et al.*, 2019), natural grassy and dry forest habitatss often lack protection, despite supporting distinct biota and potentially high carbon stocks (Sanchez-Azofeifa *et al.*, 2005; Miles *et al.*, 2006; Ratnam *et al.*, 2011; Parr *et al.*, 2014; Aleman, Blarquez and Staver, 2016; Espírito-Santo *et al.*, 2016). Without robust guidance to identify and protect high-biodiversity areas, leakage of agricultural expansion, and consequent biodiversity loss, into these biomes under ZDCs could undermine benefits of ZDCs for rainforest biodiversity, further threatening poorly-protected biomes vulnerable to conversion, over-exploitation and climate change (Aleman *et al.*, 2016; Dinerstein *et al.*, 2017; Espírito-Santo *et al.*, 2016; Miles *et al.*, 2006; Murphy, Andersen, & Parr, 2016; Parr *et al.*, 2014; Ryan *et al.*, 2016).

Palm oil is a key deforestation-risk commodity (Vijay *et al.*, 2016), and ZDCs now cover roughly two-thirds of global palm oil production volume (Haupt *et al.*, 2018). Palm oil ZDCs are chiefly implemented through Roundtable on Sustainable Palm Oil (RSPO) certification (Haupt *et al.*, 2018), although other mechanisms are under development (e.g. near-real-time satellite monitoring (Weisse *et al.*, 2019)). RSPO certification requires oil palm expansion to follow the High Conservation Value-High Carbon Stock Approach (HCV-HCSA) (RSPO, 2018), a methodology also applied to other commodities (Rosoman *et al.*, 2017). Within agricultural concessions, the HCV-HCSA conserves: aboveground carbon stocks and woody vegetation structure ('HCS'); biodiversity, ecosystem services and social/cultural values ('HCVs'); riparian habitat; and peat soils (Rosoman *et al.*, 2017). However, the HCV-HCSA and its national-level interpretations (for country-specific application: https://hcvnetwork.org/) were largely developed in response to oil palm-driven deforestation in Southeast Asia (Vijay *et al.*, 2016), so focus on tropical rainforest, with limited guidance for other habitats and geographical regions (HCV Resource Network, 2017; Rosoman *et al.*, 2017). Tropical grassy and dry forest biomes differ in structure and function to rainforest, leading to frequent misidentification and mis-management (Miles *et al.*, 2006; Ratnam *et al.*, 2011; Parr *et al.*, 2014); and HCV-HCSA guidance is currently insufficient to prevent conversion of valuable habitat areas in these biomes during agricultural development (HCV Resource Network, 2017; Rosoman *et al.*, 2017). Commercial oil palm is expanding in Latin America and Africa, which support extensive grassy and dry forest biomes, including in dry locations under irrigation (Woittiez *et al.*, 2017), and non-forested areas (Vijay *et al.*, 2016; Furumo and Aide, 2017); indeed, the largest RSPO-certified plantation in Africa was developed entirely on savanna (Hoyle *et al.*, 2017). Thus, we urgently need to understand the potential for ZDCs to drive leakage of oil palm expansion, and consequent biodiversity loss, into biomes outside tropical rainforest.

Here, we map climatically-suitable areas for rainfed and irrigated oil palm expansion, accounting for protection under ZDCs. We find that >50% of areas climatically-suitable for oil palm expansion under ZDCs are in tropical grassy biomes and dry forests. Using ZDCs to locate new plantations fails to protect areas of high vertebrate richness from oil palm expansion within these biomes, where oil palm expansion under ZDCs could drive range reduction in 9% of threatened terrestrial vertebrate species, unless HCV-HCSA guidance is improved. Thus, we argue that to avoid unintended detrimental consequences for tropical biodiversity, policies addressing land-use change should incorporate all relevant biomes; in particular, comprehensive guidelines to identify and manage 'high conservation values' specific to tropical grassy and dry forest biomes must be developed.

3.3 Results

Potential areas for oil palm expansion under ZDCs

Globally, we estimate that 1,198 Mha of non-cultivated land (including primary vegetation, secondary vegetation, and both current and abandoned pasture, but excluding current cropland, tree plantations and urban areas), outside IUCN class I and II protected areas, are climatically-suitable for rainfed oil palm expansion in total (fig. 3.1). ZDCs protect up to 86% of this 1,198 Mha, assuming that locations ≥35 Mg ha^{-1} above-ground carbon and ≥30% canopy closure, and/or peat soils, are protected under ZDCs, in line with the HCSA (although in practice, protection depends on the local context, such as identification of additional 'HCVs'; see Methods). Thus, 167 Mha of non-cultivated, climatically-suitable land is potentially available for expansion under ZDCs, which represents a possible 6-fold expansion in global oil palm cultivation, and a potential ~4-fold global expansion in grassy and dry forest biomes alone (compared with the current planted area of 27 Mha), highlighting considerable potential for continued expansion under ZDCs.

Current criteria for ZDCs protect a considerably higher percentage of the area climatically-suitable for oil palm expansion in moist forest (93.2%) than grassy biomes (43.4%) or dry forest (53.1%) (fig. 3.2), demonstrating that ZDCs achieve their aim of protecting extensive areas of tropical moist forest from conversion to agriculture. Consequently, 95.4 Mha of the climatically-suitable 167 Mha potentially available for expansion under ZDCs is in tropical grassy and dry forest biomes, the majority (86.5%) in the Neotropics and Afrotropics (fig. 3.1). This 95.4 Mha includes both highly degraded areas and ancient habitats supporting high biodiversity. Thus, our findings emphasize the need for sustainable development guidelines for identification and protection of high-biodiversity habitats specific to these biomes and regions. Nevertheless, just under half (69.4 Mha) of the potential area for oil palm expansion under ZDCs is in highly degraded tropical moist forest (given that its aboveground carbon and canopy closure fall below the ZDC protection thresholds). Our estimates of the extent of areas suitable for expansion are sensitive to model thresholding of oil palm presence/absence, and somewhat sensitive to thresholds of habitat protection under ZDCs in line with the HCSA, but this variation does not affect our conclusion that tropical grassy and dry forest biomes, especially in the Neotropics and Afrotropics, are most vulnerable to future expansion under ZDCs (Supplementary Information 2.3).

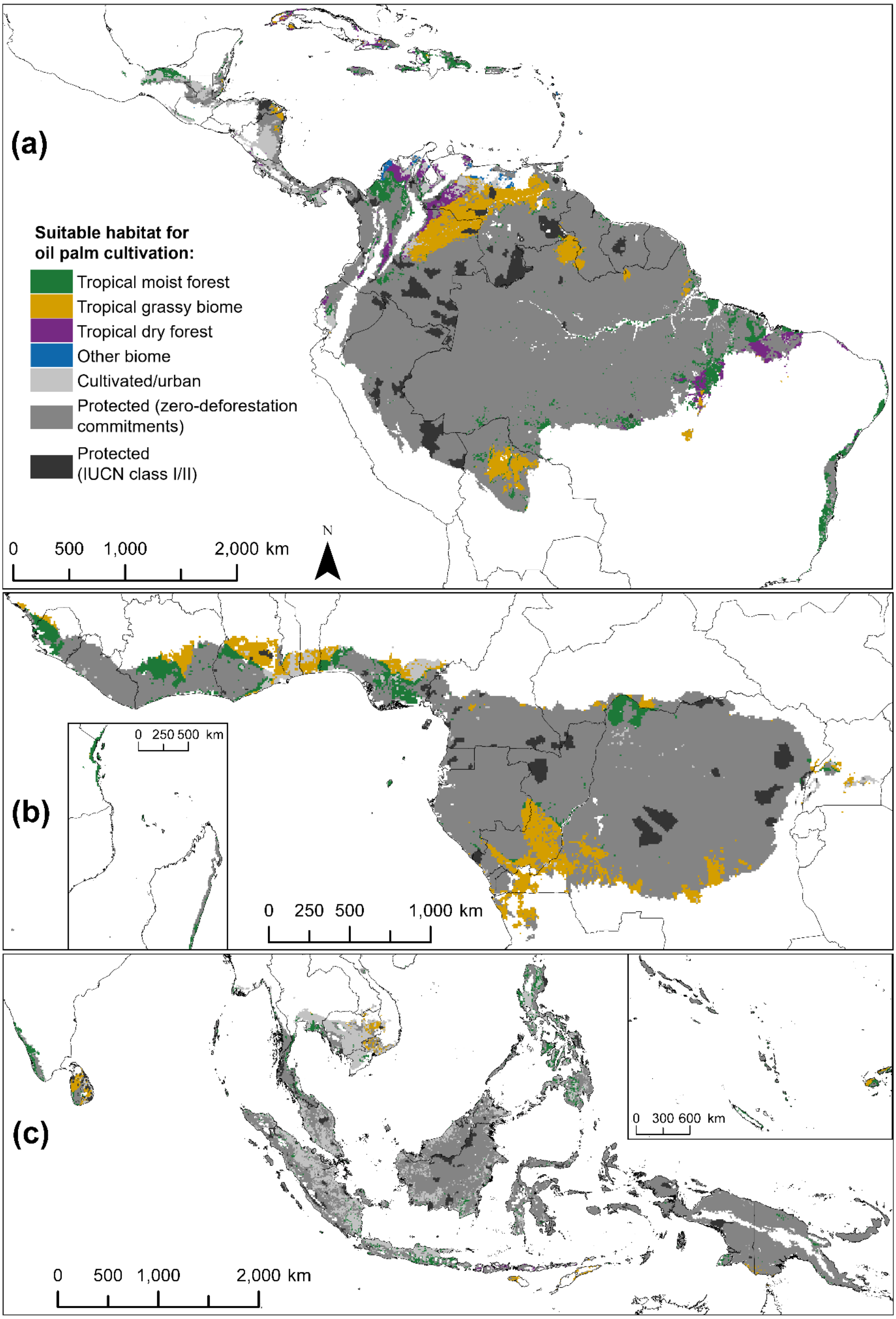


Figure 3.1. Map of climatically-suitable locations for rainfed oil palm expansion under zero-deforestation commitments (ZDCs), according to biome for (a) Neotropics, (b) tropical Africa and (c) tropical Asia and Australasia. Inset (b): East coast of Africa and in Madagascar; inset (c): South Pacific. We modelled oil palm suitability using species distribution modelling, thresholded by Minimal Predicted Area[99] (see Methods). Areas not available for expansion include: converted habitat (urban areas, cropland or tree

plantations; light grey); existing protected areas of IUCN class I and II (dark grey); and locations protected under ZDCs (≥35 Mg ha^{-1} aboveground carbon and ≥30% canopy closure, and/or peat soil, in line with the High Carbon Stock Approach; mid-grey). Thus, locations potentially available for expansion are non-cultivated land (including primary vegetation, secondary vegetation, and both current and abandoned pasture). Colours show locations of non-cultivated land which are not protected under ZDCs, and therefore potentially available for oil palm expansion, by biome; 'Other' biome refers to locations largely in Neotropical 'xeric shrublands' with relatively high rainfall. The coverage excludes permanent water bodies and mangroves. See Supplementary Information 2.3 for comparison of suitable areas under different thresholds of habitat protection and model suitability classification.

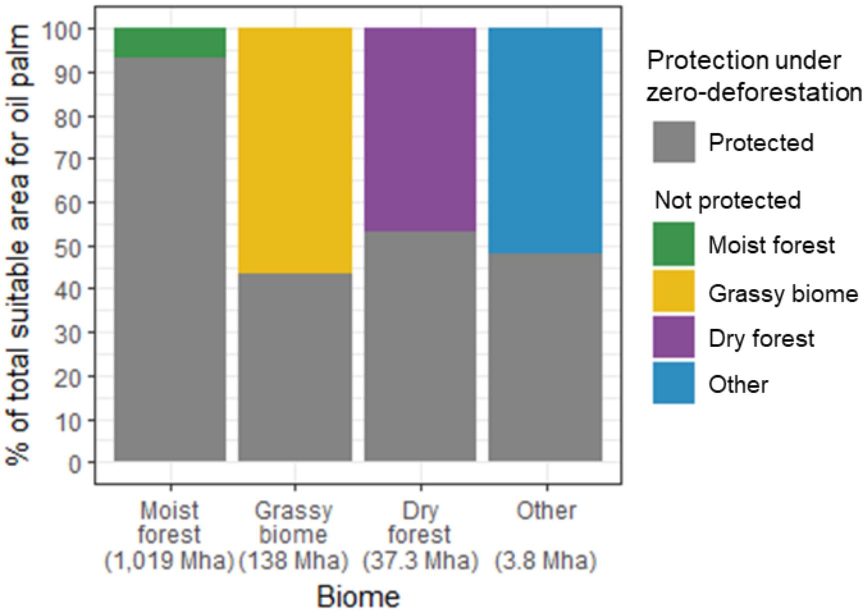


Figure 3.2. Protection of climatically-suitable areas for rainfed oil palm expansion under zero-deforestation commitments (ZDCs), according to the High Carbon Stock Approach (HCSA). Data are plotted as a percentage of the total climatically-suitable area by biome, excluding protected areas (IUCN class I and II) and urban and agricultural areas, but including primary vegetation, secondary vegetation, and both current and abandoned pasture (see fig. 3.1).

Yield in locations for potential expansion under ZDCs

Overall, 97% of locations suitable for expansion under ZDCs are likely to have low yields (~10 tha^{-1} fresh fruit bunches annually; 6.2-16.5 tha^{-1} inter-quartile range) under rainfed, high-fertiliser input cultivation, highlighting trade-offs between productivity and environmental impacts of cultivation, and suggesting that new oil palm plantations developed under ZDCs may need to be large to obtain high total oil production (fig. 3.3a; see Supplementary Information 2.1 for obtaining expected yield values from modelled climatic suitability values). This low expected yield particularly applies to climatically-suitable locations in grassy biomes (where 99.8% of all of climatically-suitable locations for expansion under ZDCs have low expected yield) and dry forests

(99.1%), but also tropical moist forests (92.2%). Assuming a conversion factor of 20% from fresh fruit bunch yield to crude palm oil production (Tinker and Corley, 2015), we expect these low-yield locations to have annual oil yields of ~2 tha^{-1}, approximately half that of existing plantations with estimated oil yields of ~4 tha^{-1}. Overall, the vast majority of suitable locations for expansion have low projected suitability, regardless of ZDCs (fig. S2.11), which could reflect that the most suitable locations for expansion (e.g. in Southeast Asia) are already converted to cropland.

Opportunities for improved yield under irrigation

Our projections of climatically-suitable areas for oil palm expansion under ZDCs presented above are based on rainfed production, but under irrigation up to 108 Mha could additionally become suitable (65% increase compared with rainfed cultivation: a potential 10-fold total increase in the current planted area; fig. 3.3b, pale colours). This is based on new monthly water availability data (see Methods), assuming that surplus available water (from freshwater lakes, rivers and renewable groundwater) irrigates the crop in dry months. Thus, irrigation could enable considerably greater oil palm expansion under ZDCs than rainfed cultivation alone, particularly in grassy biomes (up to additional 78.6 Mha or 101% increase) and dry forests (up to additional 16.4 Mha or 94% increase) in the Neotropics and Afrotropics (fig. S2.13; total suitable area increase in these biomes alone represents a 7-fold potential increase in the current planted area). Whilst we expect 97% of these areas requiring irrigation to have low yield (fig. 3.3b, pale colours), irrigation could increase yields in areas suitable for rainfed expansion, because the climatically-suitable area for expansion under ZDCs with fair or high expected yield (17.2-17.7 tha^{-1} median annual fresh fruit bunch yield under high fertiliser input) increases more than five-fold under irrigation compared with rainfed cultivation alone (fig. 3.3).

Potential for ecoregion-level habitat loss

Oil palm expansion under ZDCs could drive biodiversity loss in tropical dry forests and grassy biomes in particular, because the percentage of remaining non-cultivated land of individual ecoregions that is suitable for rainfed expansion under ZDCs is greater for tropical dry forests (median 23% of remaining ecoregion habitat) and grassy biomes (16%) than for moist forests (6%) (fig. 3.4d; fig. S2.21). Ecoregions represent unique ecosystems supporting distinct ecological assemblages, at a finer scale than biomes, so habitat loss within an ecoregion represents loss of distinctive biodiversity. Expansion under ZDCs could drive considerable biodiversity loss in a number of ecoregions with the largest suitable areas (i.e. where expansion is most likely to occur globally), because these potential expansion locations comprise a high percentage of the remaining non-cultivated area in these ecoregions (table 3.1). Thus, the biodiversity of ecoregions such as the Llanos in Colombia (~80% of non-cultivated land suitable for expansion under ZDCs), Beni savanna in northern Boliva (~70%), and Guinean savanna in West Africa (~53%), among others, appears particularly vulnerable to encroachment from oil palm expansion under ZDCs. However, these estimates of areas suitable for expansion are also likely to include some degraded pastures, which could facilitate oil palm expansion with low environmental costs (see Discussion).

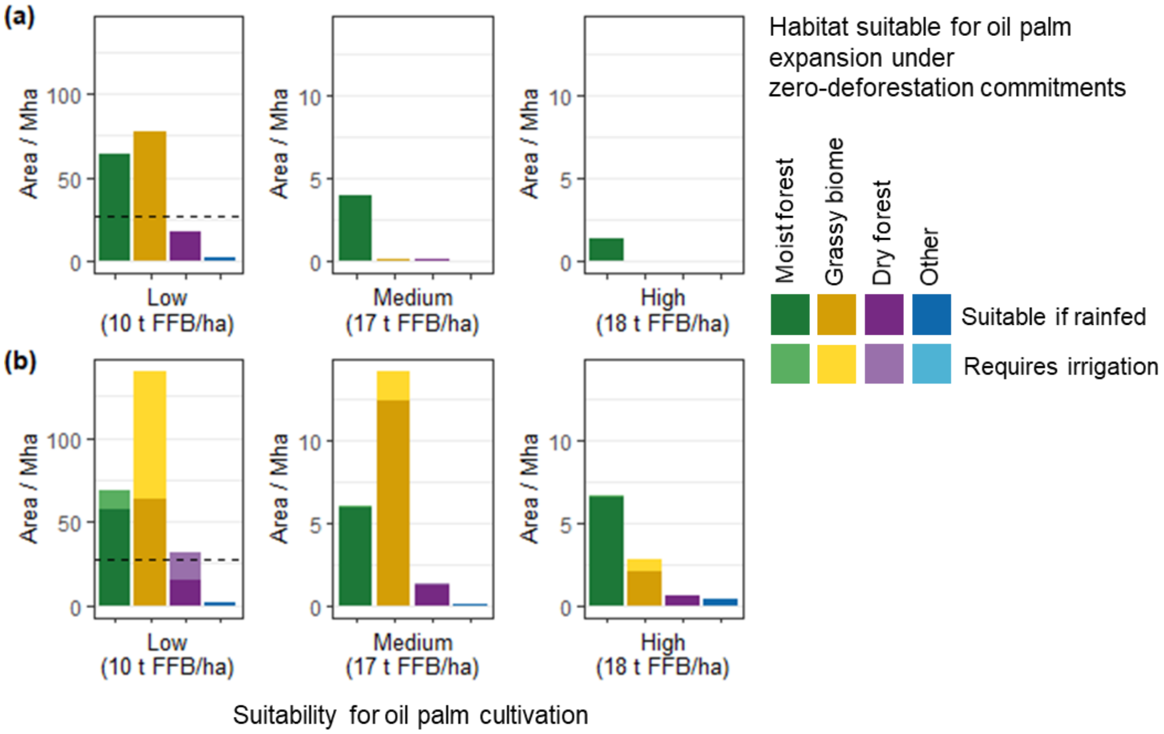


Figure 3.3. Total areas of non-cultivated land climatically-suitable for oil palm expansion under ZDCs, classified according to suitability (and expected annual fresh fruit bunch yield), by biome. (a) Under rainfed cultivation; (b) under irrigation, where dark colours represent the expected yield of locations which are also suitable if rainfed (i.e. those shown in (a)), but under irrigation; and pale colours represent locations only suitable under irrigation. We simulated the impacts of irrigation on yield by assuming that up to 100% of surplus available water (from freshwater bodies, rivers and renewable groundwater) could supplement rainfall in dry months (months where precipitation < potential evapotranspiration), in locations where surplus water was sufficient to remove a critical water deficit (see Methods; see Supplementary Information 2.4 sensitivity analysis to surplus available water). We determined the suitability classes by Minimal Predicted Area (MPA) thresholding, based on the distribution of projected suitability values at locations of oil palm mills, and extracted estimated values of oil palm yield for these classes (Supplementary Information 2.1; see Supplementary Information 2.3 and 2.4 for examination of sensitivity of findings to different thresholds for determining suitability for cultivation, and to different thresholds of habitat protection under zero-deforestation commitments). The dashed line in ‘Low Yield’ panels shows the current area of oil palm plantations globally, which is outside the axis range of the other yield classes. Note differences in y-axis values for the oil palm suitability classes.

Threats to vertebrate richness

We estimate that ZDCs successfully mitigate vertebrate (mammal, bird and amphibian) richness loss from oil palm expansion in rainforests, by protecting locations with the highest richness within the moist forest biome, and thus globally, from expansion (fig. 3.4a). However, ZDCs fail to protect locations of high vertebrate richness from expansion within tropical grassy and dry forest biomes in all continents (fig. 3.4a, fig. S2.18). In Africa, where the contrast among biomes is greatest, expansion under ZDCs in the moist forest biome would result in substantially less vertebrate richness loss if converted to oil palm (median 185 species lost per 10-km grid-cell) than expansion in locations protected by ZDCs (median 223 species),, whereas within grassy biomes, ZDCs do not effectively prevent vertebrate richness loss, because locations available for expansion under ZDCs would undergo greater richness loss (median 201 species) compared to locations protected by ZDCs (median 166 species; fig 3.4a). Thus, ZDCs could drive considerable biodiversity loss outside the tropical moist forest biome, despite successfully protecting rainforest biodiversity, highlighting the importance of comprehensive local biodiversity assessments prior to planting.

Range reduction of IUCN threatened vertebrates

Oil palm expansion under ZDCs could have negative impacts on biodiversity in all biomes by decreasing the range size of threatened vertebrates, unless areas supporting such species are consistently identified and protected (e.g. as HCVs under the HCV-HCSA, which requires protection of threatened species but is not yet well-developed outside tropical moist forest). In total, 27% (879 of 3,258 species) of threatened terrestrial vertebrate species could undergo range reduction from oil palm expansion under ZDCs, because these species' ranges overlap with potential expansion areas but they cannot persist in plantations (fig. 3.4b). This value rises to 33% of threatened species (1,071 species) that could undergo range reduction when including locations requiring irrigation (fig. S2.19). As expected, the majority of these threatened species occur in tropical moist forest (817 species; 25.1% of threatened terrestrial vertebrates), although expansion under in grassy biomes and dry forests could reduce ranges of 189 threatened vertebrate species (5.8% of all threatened vertebrates for both biomes combined, increasing to 9.4% when including locations requiring irrigation). Thus, expansion under ZDCs could have negative impacts on threatened species in all three biomes, but the threat is generally small (median overlap with areas suitable for rainfed expansion under ZDCs is 3.8% of species' total global range, spanning 0.01-100%; fig. 3.4c). Thus, there are likely opportunities for expansion without significant negative impacts on threatened species, but the consequences of range reduction will be species-specific.

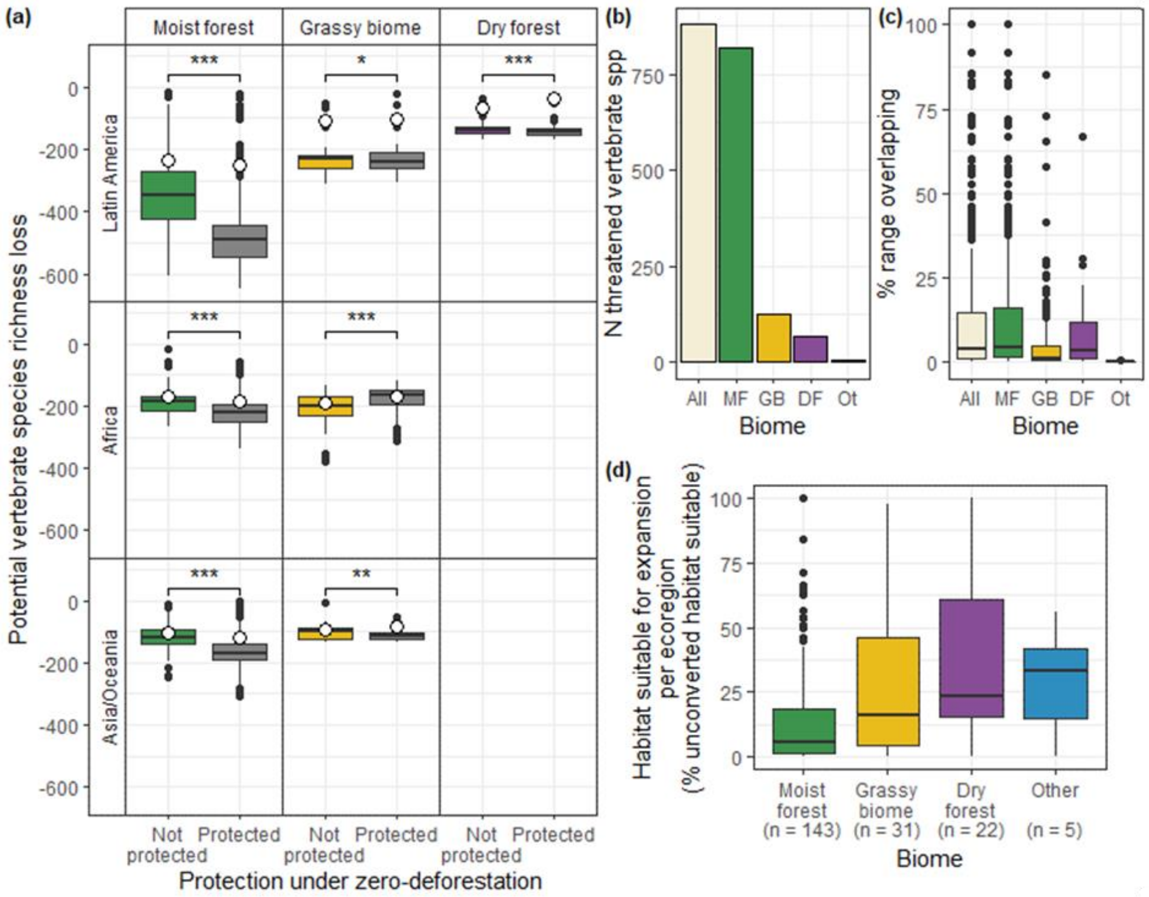


Figure 3.4. Potential biodiversity impacts of rainfed oil palm expansion under ZDCs. (a) Potential vertebrate species richness loss, from conversion of non-cultivated habitat to oil palm, by protection under ZDCs (locations of ≥35 Mg ha^{-1} and ≥30% canopy closure, and/or peat soil are protected), within each biome and continent. We estimated vertebrate ranges by refining range maps according to the habitat types suitable for each species; and calculated potential richness loss as the difference between the number of species that occur in undisturbed habitat in ~10 km grid-cells, and the number of species that can persist in plantations. Boxplots show potential richness loss for all grid-cells; white circles show the expected richness loss after accounting for spatial autocorrelation (non-spatial parameters of simultaneous autoregressive error models), and brackets denote significant differences (p <0.05) between these (* p <0.05, ** p <0.01, *** p <0.001; see table S2.7). We excluded groups with insufficient sample size (n <30) from the models, so some locations in dry forest and all 'other' biomes are not displayed. **(b) Number of threatened terrestrial vertebrate species (from a global total of N = 3,258 threatened species following refinement of range maps by potential non-cultivated habitat; see Methods) whose ranges overlap with locations that are climatically-suitable for rainfed oil palm expansion under ZDCs. (c) Percentage of threatened species' global range which overlaps with locations that are climatically-suitable for rainfed oil palm expansion under ZDCs (for n = 879 species with ranges overlapping suitable locations and which can't persist in oil palm).** For both (b) and (c), note that a species can occur in more than one biome. **(d) Boxplots of the percentage of non-cultivated land that is climatically-suitable for rainfed oil palm expansion under ZDCs in individual ecoregions.** See Supplementary Information 2.5 for sensitivity of these results to thresholds of habitat protection under ZDCs, and inclusion of locations suitable for irrigated oil palm expansion.

Table 3.1. Areas of individual ecoregions suitable for oil palm expansion under ZDCs, for the 20 ecoregions with the largest suitable area (in km^2), for suitability for (a) rainfed, and (b) both rainfed and irrigated cultivation. Rows with grey shading represent ecoregions which occur in both (a) and (b), i.e. which rank in the top 20 ecoregions with the largest suitable are for both rainfed-only and rainfed or irrigated oil palm expansion under ZDCs.

	(a) Rainfed cultivation				**(b) Irrigated and rainfed cultivation**			
	Ecoregion	**Realm**	**Biome**	**Suitable area for oil palm expansion under ZDCs: 1000 km^2 (% of total non-cultivated land)**	**Ecoregion**	**Realm**	**Biome**	**Suitable area for oil palm expansion under ZDCs: 1000 km^2 (% of total non-cultivated land)**
1	Llanos	Neotropic	Grassy biome	274 (79.7%)	Llanos	Neotropic	Grassy biome	279 (81.1%)
2	Western Congolian forest-savanna	Afrotropic	Grassy biome	109 (29.3%)	Cerrado	Neotropic	Grassy biome	245 (16.1%)
3	Guinean forest-savanna	Afrotropic	Grassy biome	93.7 (18.0%)	Guinean forest-savanna	Afrotropic	Grassy biome	132 (25.4%)
4	Beni savanna	Neotropic	Grassy biome	77.1 (70.3%)	Western Congolian forest-savanna	Afrotropic	Grassy biome	131 (35.2%)
5	Southern Congolian forest-savanna	Afrotropic	Grassy biome	59.6 (10.6%)	Southern Congolian forest-savanna	Afrotropic	Grassy biome	112 (19.8%)
6	Guianan savanna	Neotropic	Grassy biome	56.7 (53.2%)	Caatinga	Neotropic	Dry forest	82.3 (11.6%)
7	Magdalena-Urabá moist forests	Neotropic	Moist forest	45.7 (64.3%)	Beni savanna	Neotropic	Grassy biome	77.7 (70.9%)
8	Eastern Guinean forests	Afrotropic	Moist forest	44.2 (24.7%)	Mato Grosso tropical dry forests	Neotropic	Dry forest	76.2 (20.2%)
9	Tocantins/Pindare moist forests	Neotropic	Moist forest	41.3 (22.5%)	Northern Congolian Forest-Savanna	Afrotropic	Grassy biome	72.0 (10.3%)
10	Xingu-Tocantins-Araguaia moist forests	Neotropic	Moist forest	40.9 (14.9%)	Guianan savanna	Neotropic	Grassy biome	56.7 (53.2%)
11	Maranhão Babaçu forests	Neotropic	Dry forest	36.2 26.3%)	Sudd flooded grasslands	Afrotropic	Grassy biome	52.0 (27.5%)
12	Apure-Villavicencio dry forests	Neotropic	Dry forest	35.9 (64.0%)	Madeira-Tapajós moist forests	Neotropic	Moist forest	50.6 (7.1%)
13	Madeira-Tapajós moist forests	Neotropic	Moist forest	31.5 (4.4%)	Xingu-Tocantins-Araguaia moist forests	Neotropic	Moist forest	49.9 (18.2%)
14	Bahia coastal forests	Neotropic	Moist forest	30.4 (30.9%)	Sahelian Acacia savanna	Afrotropic	Grassy biome	48.5 (1.4%)

15	Mato Grosso tropical dry forests	Neotropic	Dry forest	27.6 (7.3%)	Magdalena-Urabá moist forests	Neotropic	Moist forest	45.7 (64.3%)
16	Northeast Congolian lowland forests	Afrotropic	Moist forest	26.6 (5.2%)	Eastern Guinean forests	Afrotropic	Moist forest	44.7 (25.0%)
17	Western Guinean lowland forests	Afrotropic	Moist forest	24.9 (12.3%)	East Sudanian savanna	Afrotropic	Grassy biome	43.8 (4.9%)
18	Hispaniolan moist forests	Neotropic	Moist forest	22.6 (53.5%)	Tocantins/Pindare moist forests	Neotropic	Moist forest	43.4 (23.7%)
19	Nigerian lowland forests	Afrotropic	Moist forest	19.6 (31.4%)	Maranhão Babaçu forests	Neotropic	Dry forest	42.4 (30.7%)
20	Northern Swahili coastal forests	Afrotropic	Moist forest	18.9 (14.6%)	Victoria Basin forest-savanna	Afrotropic	Grassy biome	40.5 (54.4%)

3.4 Discussion

ZDCs threaten tropical grassy and dry forest biomes

We found that the majority of non-cultivated land that is climatically-suitable for oil palm expansion under ZDCs is in tropical grassy and dry forest biomes in Latin America and Africa, which support unique ecosystems and biodiversity (Olson *et al.*, 2001; Parr *et al.*, 2014). This demonstrates the high potential for leakage of land-use change and biodiversity loss from tropical rainforest to these biomes under ZDCs, as occurred following the moratorium on soy expansion in the Brazilian Amazon (Arima *et al.*, 2011; Gibbs *et al.,* 2015). Whilst our study focuses on oil palm, tropical grassy and dry forest biomes are also suitable for other tropical commodities covered by ZDCs (e.g. soy, cattle/pasture) (Fischer *et al.*, 2012; Haupt *et al.*, 2018), so our discussion of their conservation under ZDCs is relevant to multiple commodities. In order to avoid considerable loss of biodiversity in tropical grassy and dry forest biomes as a consequence of efforts to reduce biodiversity loss in tropical rainforest, interventions addressing land-use change must address all relevant biomes, and guidelines for sustainable agricultural development specific to all these biomes must be developed.

Our results highlight that under ZDCs, oil palm expansion is likely to drive greater biodiversity loss in tropical grassy and dry forest biomes than in tropical moist forest. ZDCs steer expansion into locations with high potential vertebrate richness loss within tropical grassy and dry forest biomes, particularly in Africa; and larger proportions of their individual ecoregions are suitable for expansion, signifying greater potential for loss of individual units of biodiversity (Dinerstein *et al.*, 2017). Moreover, we have likely underestimated the potential for leakage of expansion into tropical grassy and dry forest biomes under ZDCs, although this depends on the degree of uptake of ZDCs across the oil palm sector (Garrett *et al.*, 2019). Firstly, we note that some ecoregion boundaries appear erroneous, in line with frequent mis-classification of tropical grassy biomes and dry forests (Sanchez-Azofeifa *et al.*, 2005; Miles *et al.*, 2006; Ratnam *et al.*, 2011; Parr *et al.*, 2014) which has reduced our estimate of the total area of tropical grassy and dry forest habitat suitable for oil palm expansion under ZDCs (e.g. Northeast Congolian lowland forests extend into an area of savanna; a 'finger' of savanna in southern Gabon is mispositioned and classified as moist forest in our analyses). In addition, we have not accounted for protection of areas of high biodiversity in line with the HCV-HCSA for ZDCs (HCV Resource Network, 2017), which are likely to protect more areas in tropical moist forest than in the other biomes under current guidelines (e.g. through more consistent identification of species present), because these are not well-developed outside tropical moist forest (HCV Resource Network, 2017; Rosoman *et al.*, 2017). Thus, the total area of tropical moist forest protected under these ZDC guidelines is likely to considerably exceed our estimates, further exacerbating the potential for leakage into other biomes.

We also expect that we have underestimated the impacts of expansion under ZDCs on the biodiversity of tropical grassy and dry forest biomes. We have not examined potential loss of plant or invertebrate biodiversity from expansion, but these can have high endemism and richness in grassy biomes, comparable to those of tropical rainforest in certain ecoregions (Murphy *et al.*, 2016), such as the exceptional floral diversity of the Cerrado (Klink and Machado, 2005), the second-most suitable ecoregion for expansion under ZDCs when accounting for irrigation. Additionally, woody vegetation cover is unrelated to biodiversity in grassy biomes (Veldman *et al.*, 2015), and the above-ground carbon thresholds for protection under ZDCs are too high to protect dry forests (fig. S2.8). Thus, the areas we identify as suitable for expansion under ZDCs in tropical grassy and dry forest biomes include areas of degraded habitat (where expansion could occur with low carbon emissions and reduced biodiversity loss (Gilroy *et al.*, 2015; Prescott *et al.*, 2016b, 2016a; López-Ricaurte *et al.*, 2017; Ocampo-Peñuela *et al.*, 2018; Quezada *et al.*, 2019)), as well as unique, ancient habitats which support considerably greater diversity than highly-degraded tropical moist forest (Veldman and Putz, 2011). We estimated vertebrate occurrence by assuming that habitat was intact, so we likely systematically overestimated the vertebrate richness loss from expansion under ZDCs in tropical moist forest, where no locations suitable for expansion under ZDCs are likely to be intact, in comparison to grassy biomes and dry forests, where some suitable locations are highly likely to be intact. Therefore, we expect that agricultural expansion under ZDCs could have substantial negative impacts on biodiversity in tropical grassy and dry forest biomes, further highlighting the need for robust guidance for sustainable agricultural development in these biomes.

Gaps in current guidance and key recommendations

While global conservation efforts have typically focused on rainforests, other tropical biomes are also subject to multiple threats and are less well-protected, with ~50% of tropical dry forests already converted to other land-uses (Aleman *et al.*, 2016; Dinerstein *et al.*, 2017; Espírito-Santo *et al.*, 2016; Hoekstra *et al.*, 2005; Miles *et al.*, 2006; Overbeck *et al.*, 2015; Parr *et al.*, 2014; Ryan *et al.*, 2016). In line with this, current ZDC implementation includes comprehensive guidance for sustainable agricultural development in tropical moist forests (HCV Resource Network, 2017; Rosoman *et al.*, 2017), and is highly effective in protecting the vast majority of tropical moist forest locations from conversion to oil palm (fig. 3.2), as well as effectively reducing vertebrate richness loss from conversion in this biome (fig. 3.4a). Given the exceptionally high biodiversity value and carbon storage of tropical moist forests (Gibson *et al.*, 2011; Sullivan *et al.*, 2017; Watson *et al.*, 2018), ZDCs therefore have the potential to effectively reduce biodiversity loss and carbon emissions driven by oil palm expansion globally. However, the current guidance does not currently recognise a number of fundamental differences between tropical moist forest and tropical grassy and dry forest biomes. Without modification, current guidance ("Annex 2. Grasslands in HCVs" in (HCV Resource Network, 2017)) could lead to misidentification and/or mis-management of grassy and dry forest biomes during agricultural development, threatening their biodiversity and undermining benefits of ZDCs for rainforests.

Tropical grassy and dry forest biomes are frequently misidentified as 'degraded', low-biodiversity habitat, because of superficial similarity of vegetation structure to degraded moist forest, and/or misunderstanding around ecological history (e.g. failure to recognise that grassy systems were the original habitat, and not derived) (Ratnam *et al.*, 2011; Veldman and Putz, 2011; Parr *et al.*, 2014), but they are not comprehensively defined in the ZDC guidance (HCV Resource Network, 2017; Rosoman *et al.*, 2017). Moreover, tropical grassy biomes are characterised by frequent disturbance events (e.g. fire, grazing), and can vary temporally and spatially in vegetation type and cover, often comprising a mosaic of woody and open vegetation (Ratnam *et al.*, 2011; Parr *et al.*, 2014). Without acknowledging this variation and ecological dynamism, impact assessments could fail to identify the importance of these habitats due to disturbance events or mosaic habitat structure, and plant species which are only visible seasonally or after disturbance events could be omitted from field inventories. Tropical grassy biomes can store exceptionally high below-ground carbon (as can moist forests) (Batlle-Bayer, Batjes and Bindraban, 2010), which is not currently included in the HCV-HCSA (beyond protection of peat soil). Thus, current guidance may fail to recognise and conserve the biodiversity and carbon value of these biomes during agricultural development.

Furthermore, human livelihoods and ecological functioning of grassy biomes and dry forests are often tightly linked, and unlike in tropical moist forest, human activity in grassy biomes does not always indicate habitat degradation (Sanchez-Azofeifa *et al.*, 2005; Parr *et al.*, 2014; Lehmann and Parr, 2016). Activities such as burning and grazing are fundamental disturbances for ecological functioning in grassy biomes, which in turn provide livelihoods for one fifth of the world's population (Parr *et al.*, 2014), including many of the world's poorest people (Djoudi *et al.*, 2015). If irrigation is required to boost oil palm yield in these areas, it could increase water scarcity, particularly in dry periods, potentially with substantial negative consequences for local communities and biodiversity. Whilst the HCV-HCSA requires the free, prior and informed consent of local communities for prior to development (Rosoman *et al.*, 2017), this is not guaranteed practice owing to insufficient due diligence practices (Forest Peoples Programme, 2020), so there is urgent need to incorporate local community requirements into agricultural development to aid conservation efforts (Garnett *et al.*, 2018).

To identify and protect 'high conservation values' in tropical grassy and dry forest biomes, and thereby avoid negative impacts of ZDCs for biodiversity, we recommend that the existing HCV-HCSA framework incorporates the following:

- Comprehensive definitions of different habitat types; and indicators to distinguish ancient, high-biodiversity grassy and dry forest biomes from degraded rainforest, such as fire-adapted flora in grassy biomes (and supporting the ongoing development of these indicators) (Sanchez-Azofeifa *et al.*, 2005; Ratnam *et al.*, 2011; Veldman and Putz, 2011; Veldman *et al.*, 2015; Zaloumis and Bond, 2016). Floral biodiversity surveys require expert knowledge and are key in identifying habitat intactness (Veldman *et al.*, 2015), so building this capacity in all relevant locations is crucial.
- Recognition of potential habitat dynamism and disturbance in grassy biomes: requiring identification of disturbance regimes and management which support these, recognising that some human disturbances can also drive biodiversity loss (e.g. over-grazing, use of inorganic fertilizers), and ensuring that appropriate fire and grazing of grasslands is permitted (this may require extensive discussion with local communities) (Parr *et al.*, 2014).
- Biodiversity survey design to reflect disturbance regimes (e.g. by conducting repeat plant surveys before and after disturbance events), and landscape-scale factors (e.g. large vertebrate migration routes).
- Below-ground carbon storage of natural vegetation and soils, for improved estimates of greenhouse-gas emissions from conversion to agriculture, where data are available.

- Requirements and impacts of irrigation on local hydrology, and consequences for local communities and biodiversity.

Sustainably increasing palm oil production

We found considerable potential for oil palm expansion under ZDCs, even though extensive areas are protected from expansion, suggesting that palm oil production under ZDCs can continue increasing as demand increases (Corley, 2009). However, the actual suitable area for expansion under ZDCs will likely be much lower than our estimates, because we could not account for availability of land for conversion, or exclude HCV areas (HCV Resource Network, 2017). Some additional oil palm expansion could also occur by replacing existing cropland or tree plantations (Rosoman *et al.*, 2017), which we excluded because these comprise a small proportion of recent oil palm expansion (Furumo and Aide, 2017), but this could in turn displace existing croplands to other natural habitat. Studies based in the Llanos, Colombia, have found that conversion of highly degraded pastures (not native savanna vegetation) to oil palm has limited negative impacts on biodiversity for all taxa examined, and is carbon neutral six decades after conversion (Gilroy *et al.*, 2015; Prescott *et al.*, 2016b, 2016a; López-Ricaurte *et al.*, 2017; Ocampo-Peñuela *et al.*, 2018; Quezada *et al.*, 2019). Thus, locating new oil palm plantations in degraded habitats appears key to minimizing the environmental impacts of oil palm, and examining the impacts of expansion in degraded areas in other ecosystems and biogeographic regions should be a key research priority. However, the potential avoidance of biodiversity loss and high carbon emissions from expansion in degraded habitat (Gibbs *et al.*, 2008; Ocampo-Peñuela *et al.*, 2018; Quezada *et al.*, 2019) depends on correct identification of grassy biomes and dry forests (Sanchez-Azofeifa *et al.*, 2005; Miles *et al.*, 2006; Ratnam *et al.*, 2011; Parr *et al.*, 2014), highlighting the urgent need for development of guidance to identify and protect valuable habitats within these biomes. Prioritising expansion in degraded areas prevents their regeneration, which can provide low-cost carbon capture and biodiversity benefits (Gilroy *et al.*, 2014), and would thereby hinder achieving global conservation goals (e.g. ‘Half Earth, protecting half the area of all ecoregions, and the Bonn Challenge, restoring 350 Mha of degraded habitat by 2030) (Dinerstein *et al.*, 2017; IUCN, 2020a). Moreover, targeting degraded areas must avoid the unintended consequence of incentivising active habitat degradation to facilitate expansion. Given the trade-offs of ongoing expansion with biodiversity protection and carbon storage (even when targeting expansion in highly degraded areas), and the possible limits to the area available for expansion, improving yields of existing plantations is integral to increasing production with minimal environmental impacts. Labour shortage for harvesting is a key cause of yield gaps (Murphy, 2014), and there is considerable potential to increase global productivity without further expansion or fossil fuel- or fertiliser-based inputs.

However, increasing current plantation yield does not remove economic incentives for expansion elsewhere (Villoria *et al.*, 2013); and we expect that the low yields we projected will not deter expansion under ZDCs. We projected oil yield of ~2 tha^{-1} in most locations, roughly equivalent to the maximum of other oilcrops (Fischer *et al.*, 2012), and similar to the yield of Southeast Asian smallholders in terms of fresh fruit bunches (~10 tha^{-1}) (Lee *et al.*, 2014), suggesting that oil palm would be economically viable, and preferable to cultivating other oil crops, in these locations. Moreover, in addition to irrigation, yield in these locations could be increased by implementing best management practices, and/or planting oil palm varieties which tolerate varied climatic conditions (Giam, Koh, & Wilcove, 2014; Murphy, 2014). Thus there is a strong need for both internationally-coordinated governance to reduce the negative impacts of land-use change by protecting natural habitats, and for reduction of demand growth for vegetable oils, reducing economic incentives for expansion (Koh & Lee, 2012).

3.5 Conclusion

Oil palm expansion which complies with ZDCs is most likely to take place in tropical grassy and dry forest biomes, so there is urgent need for new guidance to identify and protect biodiversity and ecological values in these biomes. Well-governed international policies which recognise and conserve all natural habitat types are thus imperative for achieving sustainable tropical agriculture.

3.6 Methods

Overview

We mapped suitability for rainfed oil palm using the species distribution model Maxent, incorporating locations of current oil palm cultivation (a global dataset of oil palm mills (World Resources Institute *et al.*, 2018)) and climate data (Fick and Hijmans, 2017). We mapped suitability for irrigated oil palm by supplementing monthly rainfall with a recent hydrological dataset of monthly surplus available freshwater (Sutanudjaja *et al.*, 2018). We quantified the areas of land suitable for oil palm cultivation (areas which have not been transformed to cropland, urban areas or tree plantations, subsequently termed ‘non-cultivated land’), whether these areas would be protected under ZDCs, and their biome type, using six global spatial datasets: land cover (Buchhorn *et al.*, 2019; Copernicus *et al.*, 2019), tree plantations (Harris *et al.*, 2019), aboveground biomass (Santoro *et al.*, 2018b, 2018a), canopy closure (Hansen *et al.*, 2013), peatlands (Gumbricht *et al.*, 2017), and terrestrial ecoregions (Dinerstein *et al.*, 2017). We compared our findings to an estimate of current global oil palm area derived from Harris *et al.* (2019). To assess the impacts of oil palm expansion on vertebrates, we estimated the potential vertebrate richness of locations we deemed to be climatically-suitable for oil palm by refining vertebrate range maps (BirdLife International and Handbook of the Birds of the World, 2016; IUCN, 2018) according to habitat types suitable for each species. We ran all models and analyses at 5' grid-cell resolution (~10 km at the Equator), the finest possible from component datasets; where data were provided at finer resolution, we aggregated them before use. We conducted all models and analyses across all tropical regions (between 23.5° N and 23.5° S) using R version 3.5.2 (R Core Team, 2017) and ArcGIS Pro version 2.2.0.

Current occurrence of oil palm cultivation

To train our species distribution models of oil palm suitability, we used a global dataset of oil palm mills, collected from major palm oil supply chains and therefore representing occurrence of industrial oil palm cultivation (World Resources Institute *et al.*, 2018) (and additionally smallholder oil palm cultivation where it is associated with industrial plantations, such as in Southeast Asia). Oil palm fresh fruit bunches require processing soon after harvest (Tinker and Corley, 2015), so mills are generally adjacent to plantations (Harris *et al.*, 2019). We excluded mills in locations likely to be irrigated (and thus cultivated under artificially-altered climatic conditions). We used a global dataset of water withdrawal for irrigation in 2014 (Sutanudjaja *et al.*, 2018) to determine locations of potential irrigation, excluding all mills within 10 km of non-zero water withdrawal for irrigation. Additionally, we excluded mills in regions described as having widespread irrigation of oil palm (Silalertruksa *et al.*, 2017). Our final dataset for the locations of cultivation of rainfed oil palm therefore comprised N = 1021 oil palm mills (occupying separate 5' grid-cells of the climate data). We assumed that each mill within a separate pixel represented one known 'presence' datapoint for oil palm cultivation.

This dataset of rainfed oil palm occurrence exhibited considerable spatial bias, reflecting spatial bias in locations of oil palm cultivation (88.4% of the mills were in Indonesia and Malaysia), but not the extent of global suitability for oil palm, which includes large areas in all tropical regions, including Latin America and Africa (Tinker and Corley, 2015; Pirker *et al.*, 2016). To reduce spatial bias, we systematically subsampled the mills to one mill per 1°-resolution grid-cell (111 km resolution at the Equator; n = 194 mills, 68.0% in Indonesia and Malaysia) (Fourcade *et al.*, 2014), and found that this considerably improved model predictive performance by reducing the dominance of the climate values at Asian mills in the overall distribution of climate values at mill locations (fig. S2.1; Supplementary Information 2.1). In comparison with models trained on the full mill dataset, models for the subsampled mills had consistently higher Boyce Index values and spatial cross-validation performance (see 'SDM evaluation' and Supplementary Information 2.1).

Climatic predictors of suitability for oil palm

We derived all climatic predictors from WorldClim version 2: global gridded climate data averaged for 1970-2000, at 5’ grid-cell resolution (Fick and Hijmans, 2017). We initially selected five climatic predictors known to correlate with oil palm growth and yield (Tinker and Corley, 2015): mean annual temperature (°C), minimum temperature of the coldest month (Tmin, °C), mean annual precipitation (mm), an annual moisture index, and maximum water deficit (MWD, mm) (see Supplementary Information 2.1 for details). Some of these predictors were inter-correlated (table S2.1), and so we ran models with two uncorrelated predictors, Tmin and MWD, which represent the most strongly limiting climatic factors for oil palm growth and yield (Tinker and Corley, 2015).

We did not include soil parameters as predictors of suitability for oil palm, because oil palm can be cultivated on the majority of tropical soil types, without substantial impacts on yield under appropriate management (Tinker and Corley, 2015), and previous estimates suggest few locations in the tropics have unsuitable soil for oil palm cultivation (Pirker *et al.*, 2016). However, we removed areas of mangrove from our projections of climatically-suitable locations for planting (see below), thereby removing areas of saline soils which limit oil palm yield (Tinker and Corley, 2015).

Running species distribution models (SDMs)

We ran SDMs of oil palm suitability using the R package *biomod2* (Thuiller *et al.*, 2016), using the SDM Maxent, because it is robust to incomplete datasets (Hernandez *et al.*, 2006; Merow *et al.*, 2013; Phillips, Anderson, & Schapire, 2006), and our oil palm mill locations do not represent all locations suitable for oil palm cultivation across the tropics. SDMs have previously been used to model climatic suitability for crops at large spatial scales (Estes *et al.*, 2013; Liu *et al.*, 2015; Singh *et al.*, 2017), and Maxent outputs have successfully projected yield when trained on high-yield locations (Estes *et al.*, 2013) such as the majority of oil palm mill locations (industrial mills supplying global traders) (World Resources Institute *et al.*, 2018). When running Maxent, we permitted linear and quadratic relationships with the two climate variables (Tinker and Corley, 2015) but otherwise maintained default settings. We projected all models across the entire tropics for the current climate.

Maxent requires randomly-sampled ‘background’ climate data to contrast with the distribution of climatic predictors at ‘presence’ (oil palm mill) locations. We randomly sampled eight sets of 50,000 background points for inclusion in models (within seven buffer distances from the presence data, spanning 200-2000 km, and additionally with no buffer), weighted by latitude to account for the variation in cell area in the unprojected climate grids, to find the optimal buffer size for model performance (VanDerWal *et al.*, 2009)). We therefore calibrated models with 16 sets of presence and background locations (2 x presence datasets, full and subsampled oil palm mills; and 8 x background datasets). We selected the optimum combination of presence and background datasets based on model evaluation metrics (VanDerWal *et al.*, 2009), and we found that an intermediate background buffer size was optimal (Supplementary Information 2.1).

We classified the continuous suitability projections (0-1) of the SDM outputs into suitable (which we further classified; see section 'Classifying expected oil palm yield') and unsuitable locations, using Minimal Predicted Area thresholding based on projected values at the oil palm mill locations (Engler, Guisan and Rechsteiner, 2004; Hirzel *et al.*, 2006) (Supplementary Information 2.1).

SDM evaluation

To examine the robustness of SDMs to spatial prediction, we conducted leave-one-out cross-validation for each model (continuous suitability output) on three spatially distinct portions of the data (Americas, Africa and Asia/Australasia), which we evaluated using the moving window Continuous Boyce Index (Hirzel *et al.*, 2006). To examine full model accuracy (i.e. where models were trained with all three spatially-distinct portions of the data), we calculated the moving window Continuous Boyce Index (Hirzel *et al.*, 2006) by testing the continuous suitability projections on a largely-independent dataset of oil palm plantations (a map of global tree plantations compiled from mixed sources, largely from remote sensing, with a small subset of oil palm plantations verified against the oil palm mills dataset used to train the models) (Harris *et al.*, 2019), with 50,000 randomly selected testing background points. We selected the single best model based on these full-model and cross-validation scores, alongside relative variable importance, for use in our analyses (Supplementary Information 2.1). Our best model included spatially-subsampled oil palm mills, and background points in a 500 km-buffer, selected primarily for its high transferability to novel locations.

To examine the sensitivity of our model outputs to the threshold used to determine oil palm suitability, we compared the performance of the best model classified into suitable and unsuitable locations at three different Minimal Predicted Area thresholds (Supplementary Information 2.1). To compare these classifications, we tested our projections for each classification on the largely-independent dataset of oil palm plantations (Harris *et al.*, 2019) (see above) using the True Skill Statistic to measure predictive accuracy (Allouche, Tsoar and Kadmon, 2006), and we compared our projections with an agro-ecological model of oil palm suitability (Pirker *et al.*, 2016). We found that the mid-range suitability classification of the three we tested (Minimal Predicted Area$_{99}$) gave high values for both of the evaluation metrics (fig. S2.5, S2.6), so we present this classification in the results in the main article.

Classifying expected oil palm yield

We classified the continuous suitability outputs of the suitable locations of the best SDM (i.e. excluding unsuitable areas) into three suitability classes for oil palm cultivation (low, medium, high), using Minimal Predicted Area thresholding (as we used for classifying suitable and unsuitable areas), where each suitability class contained one-third of the oil palm mills used to train the model (excluding any that fell below the suitability threshold; Supplementary Information 2.1). We obtained expected yield values for each of these classes from global maps of oil palm yield for the year 2010 (International Food Policy Research Institute, 2019) by comparing SDM outputs with all grid-cells where actual yield >0 tha^{-1} (Supplementary Information 2.1). For comparison, we also extracted 2010 yield values (International Food Policy Research Institute, 2019) at locations of oil palm mills (i.e. current industrial plantations) used as 'presence' locations in the SDMs.

Modelling climatically-suitable locations under irrigation

To simulate locations suitable for oil palm under irrigation, we projected our best SDM to an altered climate, and we simulated MWD under potential irrigation (Tmin was unaltered). To calculate 'irrigated' MWD, we assumed that months with sufficient surplus available water to remove a critical annual MWD were 'irrigated'. We calculated monthly surplus available water as the difference between monthly gross water demand (m^3, incorporating demand from households, industry, livestock and irrigation) and total renewable supply (m^3, incorporating unused desalinated water, renewable groundwater, and runoff from rivers, reservoirs and lakes), averaged for each month for 2005-2009 (Sutanudjaja *et al.*, 2018; Hofste *et al.*, 2019) (the most recent available data), and we converted this to mm by dividing by grid-cell area in m^2. To simulate irrigation, we assumed a critical cumulative water deficit (at which oil palm begins to suffer water stress) of 100 mm, which corresponds to empirical values of critical deficit (Tinker and Corley, 2015) and average monthly evapotranspiration (Yusop *et al.*, 2008) for oil palm, driving a ~10% decrease in yield (Carr, 2011). For locations requiring irrigation (i.e. with annual MWD >100 mm), we supplemented rainfall with surplus available water in the months with a moisture deficit (i.e. where rainfall < PET). Where monthly surplus available water was sufficient to reduce the annual MWD to <100 mm, we assumed that irrigation would be applied, because it could successfully remove the critical water deficit. Where monthly surplus available water was insufficient to reduce MWD to <100 mm, we assumed that irrigation would not be applied, and used MWD based on rainfall alone (as in the SDMs representing suitability for rainfed cultivation). We tested the sensitivity of our estimates of suitability for irrigated oil palm cultivation to the monthly surplus available water, and found that using 100% of surplus available water increases the area of non-cultivated land suitable for irrigated-only oil palm expansion by ~50% compared to using 50% of surplus available water (Supplementary Information 2.4).

Mapping non-cultivated land

We determined terrestrial non-cultivated land using Copernicus 2015 high-accuracy global land-cover data (Buchhorn *et al.*, 2019; Copernicus *et al.*, 2019), excluding all permanent water bodies (Buchhorn *et al.*, 2019; Copernicus *et al.*, 2019) and mangrove habitats (Dinerstein *et al.*, 2017). We assumed that areas of non-cultivated land represent land-cover types most likely to support native biodiversity, as many species cannot persist in cropland, tree plantations or urban areas (IUCN, 2018), and that non-cultivated land are most likely to be converted to oil palm (Vijay *et al.*, 2016). We therefore used the global land-cover map (Buchhorn *et al.*, 2019; Copernicus *et al.*, 2019) to exclude locations of cropland and urban areas, and a comprehensive database of global tree plantations (including oil palm plantations) (Harris *et al.*, 2019) to exclude locations of existing tree plantations. Our areas of non-cultivated land therefore include all primary and secondary vegetation (including undisturbed natural habitat, degraded areas and improved pasture): habitats potentially available for conversion to agriculture. Nevertheless, we acknowledge the differing biodiversity values of these habitats (intact, disturbed and improved pasture), and we address the implications of this for our findings in the Discussion (see section “ZDCs threaten tropical grassy and dry forest biomes”).

Mapping current protected areas

We used the Protected Planet World Database on Protected Areas (UNEP-WCMC and IUCN, 2020) to identify areas that are protected from conversion to industrial agriculture. We included all terrestrial protected areas of IUCN classes I and II, which are most strictly protected and therefore least likely to undergo conversion (Dudley, 2008). For a subset of protected areas without a shapefile, we estimated protected area coverage as circles centred on point coordinates, corresponding to the reported size of the protected area (km^2) (UNEP-WCMC, 2017).

Determining protection under ZDCs

During impact assessments for development of zero-deforestation oil palm plantations, HCSA guidance designates all locations with vegetation dominated by trees >30cm diameter at breast height, with >50% canopy closure and aboveground carbon of approximately >75 Mg ha^{-1} (‘low density forest’) for conservation; and all locations dominated by trees 10-30cm diameter at breast height, with 30-40% canopy closure and aboveground carbon of approximately 35-75 Mg ha^{-1} (‘young regenerating forest’) are considered ‘potential’ areas for conservation (Rosoman *et* *al.*, 2017). If areas of 'young regenerating forest' support additional conservation values identified in the 'High Conservation Value' assessment (conducted in tandem with the High Carbon Stocks Approach), or represent a significant habitat area in the landscape, they are designated for protection (Rosoman *et al.*, 2017). This vegetation stratification is based on the structure of moist forest in Southeast Asia, where oil palm has recently driven extensive deforestation (Vijay *et al.*, 2016). We therefore computed two scenarios to represent likely habitat protection under this scheme: in which all locations corresponding to (i) 'low density forest' are protected, and (ii) all 'young regenerating forest' are additionally protected. We mapped these scenarios using global datasets of canopy closure (Hansen *et al.*, 2013) and aboveground biomass ('GlobBiomass') (Santoro *et al.*, 2018b, 2018a), assuming that 50% of aboveground biomass is carbon (Chave *et al.*, 2005). For both scenarios, we included all locations with peat soils as protected from cultivation (Gumbricht *et al.*, 2017). Vegetation thresholds for determining protection are currently only developed for lowland rainforests in Southeast Asia, and thresholds in different continents and habitat types are currently under development (Rosoman *et al.*, 2017), so we applied the same thresholds of aboveground carbon and canopy closure across the tropics, regardless of continent or biome. We found that the two HCSA scenarios for habitat protection give similar patterns of relative oil palm suitability across biomes and continents; therefore we present the 'young regenerating forest' scenario (protecting of ≥35 Mg ha^{-1} and ≥30% canopy closure) in the main article, and 'low density forest' (≥75 Mg ha^{-1} and ≥50% canopy closure) in Supplementary Information 2.3-2.5.

In addition to HCSA assessments, HCVs are also identified for protection prior to oil palm development (Rosoman *et al.*, 2017). However, we did not attempt to map these additional conservation values (e.g. presence of rare species in local habitat patch, conservation of cultural values) because they cannot be captured reliably through global mapping, and require local case-by-case identification, based on on-the-ground data and stakeholder consultation. Furthermore, many of the national interpretations for HCVs were originally developed for forestry, and have not subsequently been developed for habitats other than tropical moist forest (Rayden *et al.*, 2006; Mbolo and Mimbimi Esono, 2008; Stewart and Rayden, 2008). Tropical grassy biomes are fundamentally different in biota and functioning to forests and therefore require separate criteria to identify areas with HCVs (Parr *et al.*, 2014).

Biome and biogeographic realm classification

We based our biome classification on the most recent map of Terrestrial Ecoregions of the World (Dinerstein *et al.*, 2017). We reclassified the biome assigned to 25 of 391 non-mangrove ecoregions, using ecological literature, expert knowledge of these habitats and the classification used in Murphy et al. (2016), mostly ensuring that grassland, savanna, shrubland and woodland ecoregions with a continuous grassy understorey were identified as ‘tropical grassy biome’ (Lehmann and Parr, 2016) (table S2.3). For our analyses, we then grouped ‘tropical & subtropical moist broadleaf forest’ ecoregions as tropical moist forest; ‘tropical & subtropical dry broadleaf forest’ ecoregions as tropical dry forest; we grouped ecoregions classified as ‘tropical and subtropical grasslands, savannas and shrublands’, ‘montane grasslands and shrublands’ and ‘flooded grasslands and savannahs’ as tropical grassy biomes; and we grouped ecoregions classified as ‘deserts and xeric shrublands’ and ‘tropical and subtropical coniferous forests’ as ‘other’ biomes.

We also used the map of global ecoregions (Dinerstein *et al.*, 2017) to classify locations by biogeographic realm. Because our region of interest is the tropics, we reclassified the realm of eight ecoregions in North Africa and the Arabian Peninsula, which had small suitable areas (median 161 km^2 under suitability threshold MPA_{100}) to ‘Afrotropic’ from ‘Palearctic’.

Impacts of oil palm expansion on vertebrates

Following Beyer *et al.* (2020) and Jetz, Wilcove, & Dobson (2007), we estimated potential vertebrate richness loss from oil palm expansion as the difference between current ‘potential’ richness (total number of species occurring in a grid-cell) of non-cultivated land, and richness of oil palm plantations (i.e. species which could persist in plantations). To estimate species’ occurrence, we refined global range maps for three well-documented taxa (mammals, birds and amphibians) (BirdLife International and Handbook of the Birds of the World, 2016; IUCN, 2018) according to Terrestrial Ecoregions of the World biome classification (Dinerstein *et al.*, 2017), and locations of cropland, urban areas (Buchhorn *et al.*, 2019; Copernicus *et al.*, 2019) and tree plantations (Harris *et al.*, 2019). We considered a species as ‘present’ in a given grid-cell if its original range map contained the grid-cell centre, and if the biome or transformed habitat type (cropland, urban, tree plantation) of the grid-cell was listed as suitable for the species, following matching in table S2.6. Because we assumed that locations of non-cultivated land were undisturbed, our estimates of richness prior to conversion to oil palm therefore represent maximal ‘potential’ richness for grid cells of non-cultivated land. However, the locations of non-cultivated land include both degraded and undisturbed habitat (partly depending on the biome), leading us to overestimate vertebrate richness loss from conversion to oil palm in many locations, which we address in the Discussion (see section “ZDCs threaten tropical grassy and dry forest biomes”). We considered that species remained ‘present’ in a grid-cell following conversion to oil palm if its list of suitable habitats included ‘plantation’. We also used these refined range maps to examine the overlap of locations suitable for oil palm expansion and threatened species’ ranges (vulnerable, endangered or critically endangered in the IUCN Red

List). See fig. S2.17 for maps of species richness in current land-cover, plantations, and richness loss from conversion.

Statistical models of potential richness loss

To test whether ZDCs consistently protect locations of high species richness loss across biomes and continents, we conducted spatial simultaneous autoregressive error models, comparing total vertebrate species richness loss across locations of non-cultivated land that we projected as climatically suitable for oil palm expansion. We fitted protection under ZDCs (protected or not protected), and biome (moist forest, grassy biome or dry forest) as categorical predictors in the models, with separate models for each continent (Latin America, Africa and Asia/Oceania combined) to facilitate convergence and avoid the need for a three-way interaction between protection, biome and continent in statistical analyses. Owing to limitations of computational efficiency, we spatially thinned the values of our species richness loss maps by extracting the values of every 16th grid-cell (nearest-neighbour resampling by a factor of 4), which facilitated model fit. We excluded groups (combinations of continent, biome and protection under zero-deforestation) which represented <0.33 % of the full data (n<30 after thinning) from the analysis, to enable model convergence and avoid inaccurate parameter estimation. We calculated effect sizes of each predictor, and of protection within each biome and continent, by comparing the full model to models in which each effect had been removed in turn.

Chapter 4

Climate has limited but varied impacts on oil palm yield in industrial plantations

Keywords: oil palm; sustainable intensification; climate change; Malaysia; industrial agriculture; yield improvement

4.1 Abstract

Background Vegetable oil yields need to increase to meet rising global demands with minimal conversion of natural habitat. Existing oil palm plantations present substantial opportunities for sustainable intensification, but the potential for yield improvement depends on the roles of multiple aspects of climate and management in determining yield.

Methods We determine the relative importance of climate for variation in oil palm yield during 2006-2017, in comparison to management (among-site variation), in 12 industrial plantations in Peninsular and East Malaysia (Borneo), where the climate is highly-suitable for oil palm cultivation. We quantify relationships between climate (monthly temperature and rainfall) and yield for lag times up to 36 months prior to harvest, which correspond to key stages in oil palm fruit development, for both raw and anomalised variables (without seasonal and spatial variation).

Results Over half of the explained variation in yield arose from differences among plantations (median annual fresh fruit bunch yield 16.4 – 31.6 tha^{-1}), suggesting opportunities for improved management. In contrast, climate explained <1% of variation in yield. Maximum monthly temperature during inflorescence development was the main climatic driver of yield (Spearman's Rho = 0.30), suggesting that insufficient solar radiation (a correlate of maximum temperature, generally highly important for yield) is the main climatic constraint to yield in our study sites. In addition, we found positive impacts of rainfall anomalies during key stages of fruit development (inflorescence abortion and sex determination; Spearman's Rho 0.06 and 0.08 with yield anomalies respectively), suggesting minor effects of water-limitation on yield at these sites; and a negative impact of maximum temperature anomaly during month of harvest (Spearman's Rho -0.14), suggesting possible heat stress impacts on workers.

Conclusions Our findings imply substantial yield gaps in some industrial plantations in Malaysia (possibly up to ~50%), although some differences in yield could be driven by factors such as oil palm cultivar, soil and topography. The role of climate is relatively minor, so improving management practices could improve yield considerably, enabling substantial increases in oil palm production in Malaysia without encroachment on natural habitat.

4.2 Background

The global agricultural system is currently responsible for up to one third of all greenhouse gas (GHG) emissions (Vermeulen, Campbell and Ingram, 2012) and is the single largest driver of tropical deforestation (Curtis *et al.*, 2018). Current global agriculture thus transgresses most relevant planetary boundaries, with greater use of land, phosphorus and nitrogen fertilisers, and

GHG emissions than is sustainable, leading to global environmental degradation (Conijn *et al.*, 2018). However, by 2050, the increase in global human population, wealth and consumption could result in total demand for agricultural increasing by ~60-100% compared to 2005 (Tilman *et al.*, 2011; Valin *et al.*, 2014), unless substantial changes to consumption patterns and dietary preferences occur, such as reduced consumption of animal products and reduced wastage of food (Valin *et al.*, 2014; Erb *et al.*, 2016; Berners-Lee *et al.*, 2018). Even if consumption patterns are sufficiently altered to curb the increase in food demand (Cassidy *et al.*, 2013; Berners-Lee *et al.*, 2018), demand for biofuels is rapidly increasing, and is likely to continue to do so, as a key route to reducing global GHG emissions and minimizing climate change (Correa *et al.*, 2019; Roe *et al.*, 2019; Lane, 2020). Demand for 'switch' crops such as soy and oil palm, which can be used for either food or biofuel, is rapidly increasing (Hasegawa *et al.*, 2018; Van Meijl *et al.*, 2018; Creutzig *et al.*, 2019; Doelman *et al.*, 2019), but expansion of these is a key driver of tropical deforestation, biodiversity loss and GHG emissions (Gibson *et al.*, 2011; Carlson *et al.*, 2012; Hosonuma *et al.*, 2012; Newbold *et al.*, 2015; Curtis *et al.*, 2018; Creutzig *et al.*, 2019). In order to reduce rapid declines in global biodiversity, and minimize competition for land between biofuels, agriculture and nature, cropland expansion should be avoided where possible (Van Meijl *et al.*, 2018; Doelman *et al.*, 2019; IPBES, 2019). Thus, it is imperative that agricultural systems, particularly vegetable oil crops, undergo a transformation of 'sustainable intensification', increasing production while reducing negative environmental impacts, to provide food security over coming decades, and reduce climate change and biodiversity loss (McKenzie and Williams, 2015; Conijn *et al.*, 2018; Springmann *et al.*, 2018).

Crop yield increase is a key component of sustainable intensification, because it enables production to increase without the negative environmental impacts of cropland expansion (McKenzie and Williams, 2015; Conijn *et al.*, 2018; Springmann *et al.*, 2018; Pastor *et al.*, 2019). In practice, intensification alone does not generally directly reduce cropland expansion, because expansion is driven by market growth, such as urban demand (Defries *et al.*, 2010; Byerlee, Stevenson and Villoria, 2014). Thus, improving yields of current cropland is one of a number of changes required to achieve sustainable agricultural production, which also include reduction in consumer demand and increased environmental protection (Erb *et al.*, 2016; Hunter *et al.*, 2017; Conijn *et al.*, 2018; Springmann *et al.*, 2018; IPBES, 2019). Sustainable intensification can support biodiversity protection, because 'land-sparing' (where agricultural areas have high yields with low biodiversity, and separate areas of intact natural habitat support high biodiversity), is generally preferable for total agricultural production and biodiversity protection compared with 'land-sharing' (extensive lower-intensity, higher-biodiversity agricultural systems, leaving less intact natural habitat for nature alone) (Phalan *et al.*, 2011). Furthermore, many regulating ecosystem services that underpin agricultural production (e.g. pollination, pest control, water resource and climate regulation) are largely dependent on areas of natural habitat, so minimizing natural habitat loss can also help conserve ecosystem services and so support agricultural production in the long-term (Zhang *et al.*, 2007; McKenzie and Williams, 2015).

Oil palm presents substantial opportunities for sustainable intensification of vegetable oil production, because it has substantially higher yields than other vegetable oil crops, but plantations often have high yield gaps, and recent increases in palm oil production have occurred through plantation expansion rather than intensification (Basiron, 2007; Carter *et al.*, 2007; de Vries *et al.*, 2010; Jackson *et al.*, 2019; Basri & Arif, 2009; Murphy, 2014; Woittiez *et al.*, 2017). Oil palm can be cultivated across much of the humid and semi-humid tropics (Fischer *et al.*, 2012; Pirker *et al.,* 2016), with lower long-term production costs than soy, the main alternative tropical vegetable oil crop (Yui and Yeh, 2013); and the vast majority of oil palm-producing countries are currently expanding their area of oil palm agriculture (FAO, 2020c). The yield of oil palm plantations is roughly six-fold greater than rapeseed, the next most productive vegetable oil crop (Yan, 2017). Thus, oil palm can provide substantial opportunities to minimise the total land area required to produce a given quantity of oil (Jackson *et al.*, 2019). In addition, the high yield of oil palm means that its impacts on biodiversity per tonne of oil produced tend to be lower than for alternative oil crops across the moist tropics (Beyer *et al.*, 2020), in spite of high rates of deforestation and biodiversity loss associated with oil palm expansion (Fitzherbert *et al.*, 2008; Vijay *et al.*, 2016; Curtis *et al.*, 2018).

To improve oil palm yield where possible, and maintain high productivity under expected climate change, it is essential that we understand the factors that determine oil palm yield, which primarily comprise climate and management practices (Woittiez *et al.*, 2017). Optimal climatic conditions for oil palm are high temperature and high year-round rainfall (Woittiez *et al.*, 2017), although the precise relationships between climate and yield vary according to the stage of oil palm fruit development, which begins approximately three years prior to harvest (Tinker & Corley, 2015; see table 4.1 for relationships between climate and yield identified in existing studies, according to stages of oil palm fruit development). The difference between actual crop yield and the potential yield which could be obtained if management practices were optimal is termed a yield gap (Woittiez *et al.*, 2017). Management practises to minimise yield gaps of oil palm include effective control of weeds, pests and diseases; optimal planting density; and effective frond pruning and regular fruit harvesting regimes (Woittiez *et al.*, 2017). Additionally, some environmental factors which limit yield can partially be mitigated by management, such as water and nutrient supply (which depend on rainfall and soil properties, but can be managed through irrigation or drainage, and fertilisation), and fruit set due to pollinator activity (Woittiez *et al.*, 2017). Oil palm yield also varies depending on the cultivar; currently, the most productive cultivars are clones of high-yielding individuals, which can produce ~20-30% greater yields than standard cultivars (Kushairi *et al.*, 2010), but the long crop rotation period of oil palm (25-30 years) means there are likely to be delays in planting new cultivars with improved yield (Woittiez *et al.*, 2017).

In many areas of Indonesia and Malaysia, which account for over 80% of global palm oil production, climatic conditions are near-optimal for oil palm growth (Pirker and Mosnier, 2015; Tinker and Corley, 2015; FAO, 2020b). Annual fresh fruit bunch (FFB) yields in 2011, compiled from 12 oil palm companies in Malaysia, ranged from 16.5 to 25.4 tha^{-1} (average per company) (ERE Consulting Group and RSPO, 2012), but leading plantation groups in Southeast Asia have achieved annual fresh fruit bunch (FFB) yields of c. 27 tha^{-1} (6 tha^{-1} oil yield) (Donough, Witt and Fairhurst, 2009). Yield gaps are as low as 11% in some industrial plantations, although in many instances, yield gaps are often substantial, and national-level yield growth has stagnated in recent years (Hoffmann *et al.*, 2017; Murphy, 2014; Woittiez *et al.*, 2017). Potential oil palm yield (i.e. maximum possible yield under ideal management) in these countries is largely dependent on solar radiation (Hoffmann *et al.*, 2014; Woittiez *et al.*, 2017), although some existing studies have also found that water availability is limiting (table 4.1). In order to understand the extent to which yield improvements are feasible under ongoing climate change (Barros *et al.*, 2014), it is therefore essential to understand the influence of climate and management practices on yield.

In this study, we quantify the relative importance of variation among plantations (likely to arise from variation in management) and climate for determining monthly fresh fruit bunch (FFB) yield of 83 oil palm fields across 12 industrial plantations in Malaysia, which belong to a single, large company; and we determine the relationships between climate (monthly temperature and rainfall) and yield. We test the relationships between climate and yield for timelags up to 36 months prior to harvest (see table 4.1); and we conduct analyses on both raw yield and climate values (whilst controlling for variation and autocorrelation through space and time), and on climate and yield anomalies for each month (i.e. removing spatial variation and regular seasonal cycles from all variables prior to analysis), in order to maximise the sensitivity of our analyses for revealing relationships between climate and yield. Although Malaysia (Peninsular Malaysia and Borneo) is considered broadly 'aseasonal', it is affected by both the Northeast and Southwest monsoons; and both yield and climate show regular seasonal fluctuations in Malaysia (Tang, 2019). Yield seasonality is likely primarily driven by seasonality in climatic conditions, although oil palm physiology drives alternating periods of low and high fruiting activity, and can therefore exacerbate existing seasonal cycles (Tinker and Corley, 2015). Relationships between oil palm yield and climatic variables could therefore be spurious correlations, particularly when incorporating timelags (Tinker and Corley, 2015), emphasising the importance of analysing anomalised data. We examine the robustness of the relationships between raw yield and climatic variables whilst avoiding this issue by analysing anomalised yield and climatic variables, from which we removed regular seasonal variation. Moreover, the climate anomalies allow us to detect relationships between climate and yield at additional timelags to the raw analyses, where lags of climatic variables 12 months apart are highly correlated. Thus, we address the following hypotheses:

1. Variation in yield arises from both differences among the 12 oil palm plantations, and from variation in climate.
2. Relationships between climate and yield are strongest at timelags prior to harvest which correspond to key stages of fruit development, such as sex determination, inflorescence development, and abortion (table 4.1).
3. Maximum temperature has the strongest (positive) relationship with yield (comparing rainfall, minimum temperature, maximum temperature), indicating that solar radiation is the strongest climatic constraint on yield.
4. Yield is positively related to rainfall, and this relationship is stronger at higher temperatures, when oil palm is more likely to be under drought stress.
5. The relationships between climate and yield are consistent for analyses of raw and anomalised data; and we are able to detect additional patterns (for different climatic variables and/or time-lags) by analysing the anomalised data.

Table 4.1. Summary of studies which detected effects of climate on yield, with timelags corresponding to each developmental stage of oil palm fruit development. The generalised timescale and stages of fruit development follow Tinker & Corley (2015). An inflorescence develops in the axis of each frond (leaf), and some are later aborted; oil palm is harvested as fresh fruit bunches (FFB), which comprise multiple spikelets of female inflorescences. FFB yield is a function of both fruit bunch number (i.e. how many bunches are harvested in a month), determined by sex determination and abortion; and average fruit bunch weight, determined by inflorescence development, pollination and ripening.

Months before fruit bunch ripens	Stage	Effects of climate on yield with corresponding lag time	Reference(s)
36	Frond initiated	Hypothesized: positive impact of temperature and rainfall	
33	Inflorescence initiated	Negative effect of photoperiod 33-34 months prior to harvest (Indonesia) (note that this is intercorrelated with the same effect at 9-10 months), although it is unclear whether oil palm is sufficiently sensitive to	(Legros *et al.,* 2009a)

		photoperiod to justify this effect (Tinker and Corley, 2015).	
~22-28	Sex determination	Positive effect of useful radiation (adjusted for water deficit) anomaly 24-25 months prior to harvest (Ivory Coast).	(Dufour *et al.*, 1998)
		Positive effect of drought (simulated fraction of transpirable soil water) 26-27 months prior to harvest respectively (Indonesia).	(Legros *et al.*, 2009a)
		Positive effect of drought (simulated fraction of transpirable soil water) and photoperiod combined at 29 months prior to harvest (Indonesia).	(Legros *et al.*, 2009a)
		Positive effect of monthly rainfall 20-24 months prior to harvest (Malaysia).	(Chow, 1992)
~12-19	Inflorescence development: number of spikelets and number of flowers per spikelet determined	Negative effect of water deficit anomaly 7-13 months prior to harvest (Ivory Coast).	(Dufour *et al.*, 1998)
		Positive effect of temperature anomaly 13 months prior to harvest (Malaysia).	(Shanmuganathan and Narayanan, 2012)
		Negative effect of monthly rainfall 13 months prior to harvest (Malaysia), although this was unexplained.	(Chow, 1992)
9-10	Inflorescence abortion	Negative effect of water deficit anomaly 7-13 months prior to harvest (Ivory Coast).	(Dufour *et al.*, 1998)
		Negative effect of photoperiod 9-10 months prior to harvest (Indonesia) (note that this is intercorrelated with the same effect at 33-34 months), although it is unclear whether oil palm is sufficiently sensitive to photoperiod to justify this effect (Tinker and Corley, 2015).	(Legros *et al.*, 2009a)
		Negative effect of cumulative water balance (monthly rainfall – potential evapotranspiration) 10 months prior to harvest (Indonesia)	(Legros *et al.*, 2009b)
		Positive effect of monthly rainfall 10-11 months prior to harvest (Malaysia).	

			(Chow, 1992)
5-6	Flowering (pollination required)	Negative effect of monthly rainfall, and positive effect of sunshine hours, 6 months prior to harvest: indicates impacts of climate on pollinator activity (Sabah, Malaysia).	(Hoong and Donough, 1998)
0-5	Fruit development (ripening)	Positive effect of monthly rainfall and temperature with lag of 3 and 4-5 months prior to harvest respectively (Sabah, Malaysia). Negative effect of monthly rainfall, and positive effect of sunshine hours, on oil to bunch ratio 0-1 months prior to harvest (Sabah, Malaysia).	(Puah and Sidik, 2011) (Hoong and Donough, 1998)

4.3 Methods

Study plantations

In this study, we analyse data for 12 oil palm plantations in Malaysia, which belong to a single, large industrial oil palm company. We obtained these data under confidential agreement with the oil palm company, which requires that its name is withheld. Eleven of the plantations are located in Peninsular Malaysia, spanning from the North (Kedah) to the South (Johor), and one is located in East Malaysia (Sabah) (fig. 4.1, table 4.2). The median elevation of plantations ranges 9 – 86 m above sea level (masl) (median = 39 masl; table 4.2). All plantations in this study are subject to the same company- and country-level management directives (e.g. pesticide and fertilizer application, replanting and harvesting schedules); and all oil palm varieties included in this study are therefore also likely to be related. Thus, we do not expect substantial differences in management practices among plantations if management is imposed company-wide, although some differences in yield could arise due to variation in soil type, local climate, plantation-level management (e.g. effectiveness of management; availability of workers to harvest the crop), and the specific cultivar of oil palm planted. The data associated with the study sites include date of planting of each oil palm field, but we do not have other information on cultivation or management.

Oil palm yield data

We obtained data on monthly oil palm fresh fruit bunch yield (t FFB ha^{-1}) as a time series for each of 83 oil palm 'fields' (the finest-scale level of management within a plantation; individual field size ranges 2.5 – 159 ha, median = 70.2 ha) across the 12 study plantations (data for 2 – 14 fields per plantation, median = 6 fields). The yield data were collected as the harvesting records of the oil palm fields, at the study plantations. These time-series of monthly yield data span roughly one decade (timespans per field range from 4 years 1 month to 11 years 11 months, median = 10 years 11 months), starting in July 2006 at the earliest and finishing in June 2017 at the latest (fig. S3.1). All yield data are for oil palms at least four years old, representing the regularly harvestable phases of production (Woittiez *et al.*, 2017).

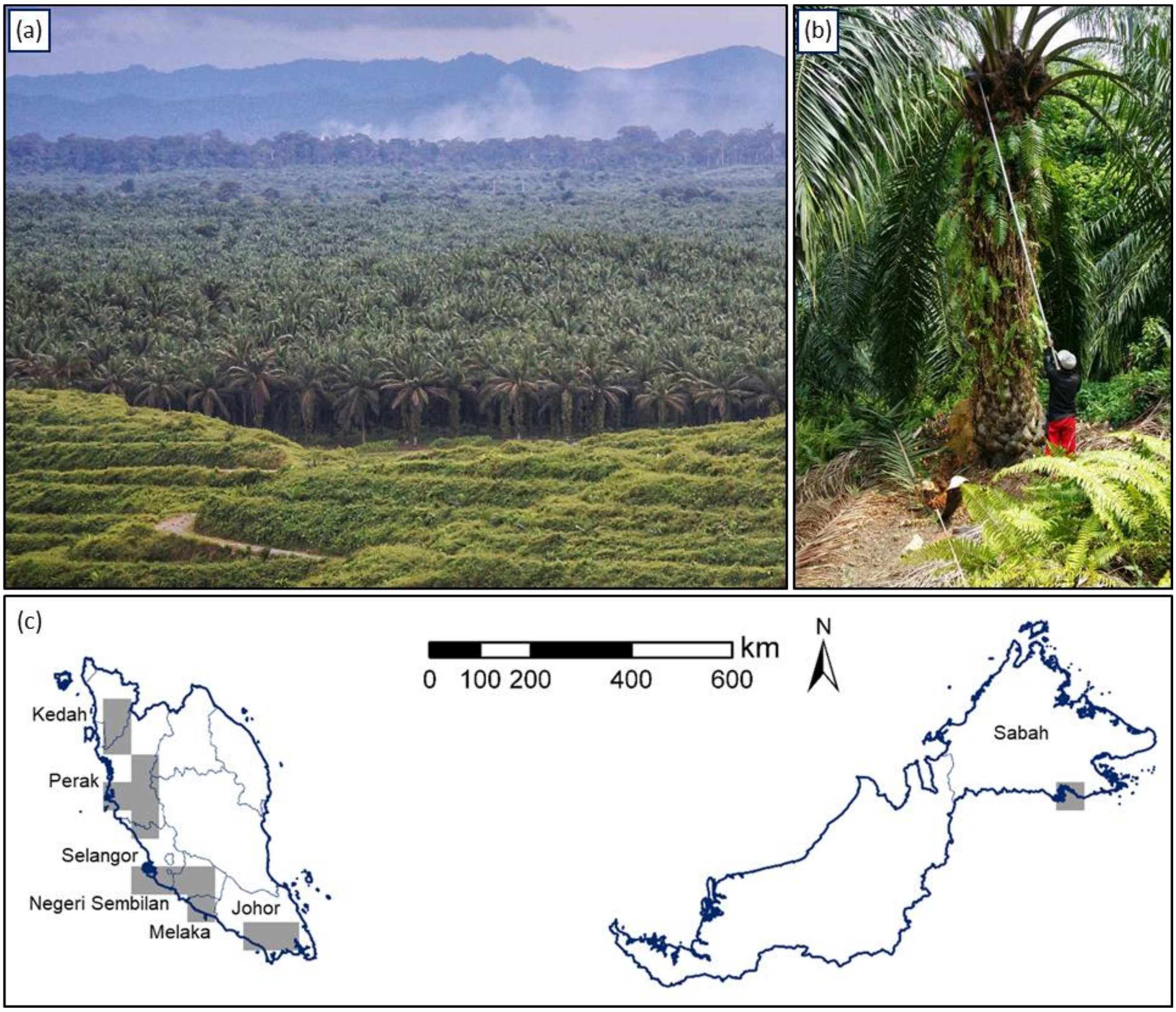


Figure 4.1. Industrial oil palm cultivation in Malaysia, and locations of plantations in this study. (a) Oil palm plantation in Sabah (photo credit Robin Hayward): terraces prepared for replanting in the foreground, mature oil palm fields in the middle ground, and remnant forest in the background. **(b) Plantation worker harvesting fresh fruit bunches (FFB) in a plantation in Sabah**, using a sickle on an extendable pole (photo credit Ahmad bin Jelling). **(c) Locations of the 83 oil palm fields (in 12 plantations) in this study**, aggregated to presence/absence in 0.5 degree (55 km)-resolution grid cells for visualisation (note that we obtained the locations as point coordinates). Grid cells for which we have data are shaded grey, and the states for which we have data are labelled. The grid cells in this map match those of the CRU TS temperature data used in this study (Harris *et al.*, 2020).

Climate data for predictors of oil palm yield

We examine monthly rainfall, minimum temperature (Tmin) and maximum temperature (Tmax) as the climatic predictors for oil palm yield in this study, because these are known to drive variation in oil palm yield, including in Southeast Asia (table 4.1). Low rainfall reduces oil palm yield by causing dry stress, and oil palm appears particularly sensitive to this during sex determination and inflorescence abortion. However, high rainfall can also have negative impacts on yield, owing to increased cloud cover, and negative impacts on pollination (table 4.1). Yield increases with temperature, because temperature both directly increases photosynthesis, and because temperature is positively correlated with solar radiation, which also directly increases photosynthesis. Thus, temperature impacts all stages of fruit development, although its effects are most apparent at certain key stages such as inflorescence development and fruit ripening (table 4.1).

We obtained monthly rainfall data (mm month^{-1}) from all of the oil palm plantations in this study, alongside the yield data. Rainfall was measured at rain gauges on the plantations, and provided at the management level of oil palm 'division' (groups of oil palm fields within a plantation, ranging 1 – 6 fields per division, median = 3 fields). The rainfall data encompass the full timespan of the yield data, and generally two decades beforehand.

We obtained monthly temperature data from the Climatic Research Unit gridded Time Series (CRU TS) version 4.04 (Harris *et al.*, 2020), which are interpolated from meteorological stations at 0.5 degree (55 km) resolution. We downloaded monthly Tmin and Tmax (°C; mean of each daily minimum and maximum temperature for a month respectively) as candidate predictors of oil palm yield.

Calculating anomalies of yield and climatic variables

We analyse raw yield data (t ha^{-1}), but to improve the sensitivity of our analyses to relationships of yield with temperature and rainfall, and to assess the reliability of the relationships we detected for the raw variables, we also calculated standardised monthly anomalies for each of the variables (yield, rainfall, Tmax and Tmin) in our analyses. Using 56 time series of oil palm yield data which spanned one decade, from July 2007 to June 2017 (i.e. data per oil palm field; excluding the 27 time series which were shorter than this), we computed anomalies for each variable (yield, rainfall, Tmax and Tmin). We calculated anomalies as the difference between each value and the mean of all values for that month for each oil palm field, scaled by the standard deviation of all values for each month and field (i.e. anomalised per time series of oil palm yield data) (see Supplementary Information 3.1 for details of anomaly calculations). The computed anomaly timeseries were therefore centred at zero and did not incorporate differences in yield mean or variation between spatial locations (oil palm fields or plantations) or months of the year (i.e. regular seasonal effect removed), enabling us to analyse relationships between 'unexpected' variation in climate and yield, given the month of the year and oil palm field.

Determining timelags of climatic predictors of oil palm yield for inclusion in models

To identify the most important candidate climatic predictors (i.e. climatic variable at a specific timelag) of oil palm yield for inclusion in our statistical models, we assessed the Spearman rank correlations between each of our candidate climatic variables (rainfall, Tmax and Tmin) and oil palm yield, for timelags of 0-36 months prior to harvest (see results section "Correlations between climatic predictors and oil palm yield at different lags prior to harvest"). We selected candidate climatic predictors with high correlations with yield relative to other timelags, at timelags which correspond to key stages of oil palm fruit development, whilst avoiding inclusion of inter-correlated predictors in the models (table 4.1, fig. 4.3; see Supplementary Information 3.2 for details). We selected Tmax and rainfall at a 14 month timelag (Spearman's Rho correlation with raw yield = 0.30 and -0.15 respectively), corresponding to oil palm inflorescence development, and rainfall at a 10 month timelag (Spearman's Rho correlation with raw yield = 0.08), corresponding to inflorescence abortion, as candidate climatic predictors of raw oil palm yield (fig. 4.3). As candidate predictors of yield anomalies, we included the anomalies of these three predictors (Tmax and rainfall at a 14 month timelag, and rainfall at a 10 month timelag), to test the robustness of their relationships with yield to the removal of regular seasonal fluctuations from the data. We also included three climatic anomaly predictors which suggested additional relationships between climate and yield: Tmax anomalies at the month of harvest (Spearman's Rho with yield anomalies = -0.14), suggesting impacts of temperature on harvesting; and rainfall and Tmin anomalies at 29 months prior to harvest (Spearman's Rho with yield anomalies = 0.08 and 0.12 respectively), corresponding to sex determination (fig. 4.3; Supplementary Information 3.2).

Modelling the impacts of spatial variation and climatic variables on oil palm yield

To quantify the degree of spatial variation in oil palm yield (among- and within plantations), and the relationships between raw climatic predictors and oil palm yield, we fitted Generalized Additive Mixed Models (GAMMs) using the 'gamm' function in the R package *mgcv* version 1.8-31 (Wood, 2011). We conducted this analysis on our full dataset (excluding two outliers; see Supplementary Information 3.1), of monthly data for 83 oil palm fields, amounting to 9,731 data points in total. To quantify among-plantation differences in oil palm yield, we fitted plantation as a random effect, and tested the importance of this for model fit, as well as the impact of additionally including a random effect for 'field within plantation'. To quantify relationships between raw climate and yield, we fitted both linear and quadratic terms for all three candidate climatic predictors of yield (Tmax at a 14 month lag, rainfall at a 14 month lag, and rainfall at a 10 month lag) in our initial full model, because yield is likely to peak at particular values of each predictor (Tinker and Corley, 2015), and exploratory analyses suggested that the relationships of these with yield were non-linear (fig. S3.7). We included an interaction term between Tmax and rainfall, with a 14 month lag, to test for changing water relations under different temperatures. In addition, we fitted smoothers to control for oil palm age and seasonality (cyclic smoothers of months of the year); and we fitted an autoregression-moving average error structure to account for temporal autocorrelation between data points from the same yield time series (i.e. in the same oil palm field). To obtain homoscedasticity and normality of residuals, we found that we needed to square-root transform the response variable (yield); we then proceeded with selection of the optimal model for GAMMs of square-root yield with a Gaussian error function and identity link. In total, we fitted 51 model permutations to find the optimal error structure (autoregression-moving average parameters and random effects of plantation/field), and 44 permutations to find the optimal fixed effects (age, seasonality, and climatic variables) (see Supplementary Information 3.3 for details of raw oil palm yield model specification and selection).

To quantify the relationships between climate and yield anomalies, we fitted Generalized Additive Models (GAMs), also using the 'gamm' function in the R package *mgcv* (Wood, 2011). We conducted this analysis on the full anomaly dataset of monthly 56 oil palm fields spanning one decade, with a total of 6,719 datapoints. These models were similar to the GAMMs of raw yield but did not include effects to account for spatial variation or seasonality, because these had been removed from the anomalised data, and only allowed for linear relationships between climatic predictors and yield anomalies (see Supplementary Information 3.4 for details of oil palm yield anomaly model specification and selection).

4.4 Results

Summary of oil palm yield in the study plantations

All of the plantations in this study had median annual yield >16 t FFB ha^{-1} and all but one had maximum annual yields >25 t FFB ha^{-1}, which are values typical of commercial plantations but probably not close to optimal yield, which is ~36 t FFB ha^{-1} in many coastal plain areas in Malaysia (although in practice, potential yield could vary substantially among the plantations in this study) (Hoffmann *et al.*, 2017; Woittiez *et al.*, 2017) (fig. 4.2; table 4.2). The highest mean annual yield of a plantation (31.6 t FFB ha^{-1}) was roughly double that of the lowest (16.4 t FFB ha^{-}

^{1}), highlighting substantial variation in yield among plantations (table 4.2, fig. 4.2). This variation among plantations accounted for the majority of spatial variation in modelled monthly yield, because median monthly yield values were generally similar among oil palm fields within each plantation (generally within ~0.3 t FFB ha^{-1} of each other; fig. S3.11), and including a random intercept for oil palm field in addition to plantation did not improve model fit (Supplementary Information 3.3). Whilst our final GAMM of raw oil palm yield included a strong effect of oil palm age (increasing sharply from four-year-old palms to a peak at 8-9 years, followed by a gradual decline; fig. S3.12), median oil palm age was generally similar across the plantations and therefore does not appear to be a major driver of the differences in yield among plantations (table 4.2).

Monthly oil palm yield varied among months of the year, and the final GAMM of raw oil palm yield included seasonal fluctuations (cyclic cubic regression spline across months of the year) for 11 of the 12 plantations (one plantation was fitted with no seasonal variation), which differed among the plantations (fig. 4.2). All fitted splines included a single peak in yield across the year, which was generally between July and September, corresponding to the observed distributions of yield values through the year for each plantation (fig. 4.2). The mean proportion of annual yield that was harvested in the peak yield month ranged 11.9 – 14.6% across all plantations, which indicates some seasonality in yield in each plantation (values above 8.33% indicate greater seasonal variation, i.e. more than one-twelfth of yield is obtained in the most productive month; table 4.2), although the degree of seasonality varies among plantations, and appears to relate partly to their location (table 4.2).

Relative importance of management and climate for explaining variation in oil palm yield

The final GAMM of raw climatic variables and oil palm yield explained almost 40% of variation in the monthly yield values (approximate R^2 of 0.384; table S3.9). Compared to the full final model, a model without any plantation terms had less than half of the variation explained (approximate R^2 = 0.18; table S3.9), highlighting that differences among oil palm plantations accounted for the majority of variation in oil palm yield. In contrast, excluding climatic predictors reduced the variation explained by less than 1%, but smoothers for seasonal fluctuations (cyclic pattern across months of the year) per plantation and for oil palm age had slightly greater importance (reduction in variation explained of ~7-9% compared to full model; table S3.9). In line with these findings, the final GAM of climate and yield anomalies explained only 9% of variation in the monthly yield anomalies (approximate R^2 of 0.09; table S3.9), of which the climate anomaly predictors accounted for 5%, highlighting that only a small fraction of 'unexpected' variation in oil palm yield (for a given month at a given oil palm field: the anomaly values) was due to 'unexpected' variation in climate. Thus, whilst we detected effects of climate on oil palm yield, the differences in yield among plantations substantially outweigh the importance of climate for determining yield. While temperature varied among months and plantations in this study, rainfall showed less variation (fig. S3.2), which may have constrained the sensitivity of our analyses of the impacts of climate on yield (although we did detect minor effects of both temperature and rainfall on yield; see sections below “Effects of temperature on oil palm yield” and “Effects of rainfall on oil palm yield, and its interaction with temperature”).

Table 4.2. Summary data for the 12 oil palm plantations included in this study, ranked by median annual yield. N fields: number of oil palm fields for which we have data; median elevation: extracted from elevation data at 30 arc-second resolution, aggregated from the Shuttle Radar Topography Mission 90 m-resolution data (Jarvis *et al.*, 2008); median annual yield: median total annual yield for all fields at a plantation, for years for which we had data for all months in an oil palm field; median palm age: median age of oil palm for all yield datapoints included in annual yield values; % yield in peak month: mean percentage of the annual yield which is harvested in the peak yield month; random intercept: random intercept fitted for the plantation, in the final GAMM of raw oil palm yield and climatic variables; monthly Tmax, Tmin and rainfall: mean and range (minimum - maximum) of all values at the timepoints of oil palm yield data for that plantation.

Plantation	**State**	**N fields**	**Median elevation (masl)**	**Median annual yield (t FFB ha^{-1})**	**Median palm age (years)**	**Maximum annual yield (t FFB ha^{-1})**	**% yield in peak month**	**Monthly Tmax (°C)**	**Monthly Tmin (°C)**	**Monthly rainfall (mm)**
1	Negeri Sembilan	5	82	16.4	8	29.6	13.8	30.6 (29.0-31.9)	22.5 (21.5-23.7)	143 (0-539)
2	Johor	3	74	18.9	9	27.2	13.6	31.2 (29.3-32.6)	23.8 (22.7-25.0)	150 (3-582)
3	Perak	10	38	20.0	10	32.7	12.4	30.0 (27.4-32.4)	23.0 (20.8-25.0)	223 (0-811)
4	Johor	2	70	20.6	9	28.3	13.2	31.0 (29.0-32.5)	23.8 (22.8-25.1)	222 (0-949)
5	Negeri Sembilan	11	40	21.1	10	24.4	13.6	31.1 (29.3-32.5)	23.3 (22.3-24.6)	135 (0-549)
6	Melaka	3	48	22.2	10	32.3	14.0	31.3 (29.9-32.7)	23.3 (22.2-24.6)	146 (0-580)
7	Kedah	5	23	22.2	11	30.5	14.6	30.8 (29.2-33.2)	22.3 (20.9-24.1)	184 (4-1070)
8	Sabah	10	24	25.3	10	43.1	11.9	30.6 (28.0-32.2)	23.1 (21.8-24.4)	166 (0-568)

9	Perak	8	86	26.2	11	32.5	13.3	28.7 (27.2-30.0)	19.9 (19.0-21.4)	144 (0-920)
10	Selangor	14	9	28.8	10	36.4	12.1	32.6 (30.7-34.2)	23.5 (22.5-24.6)	160 (0-543)
11	Perak	5	22	29.6	11	37.9	12.7	30.7 (28.5-32.5)	23.55 (22.5-25.3)	146 (0-615)
12	Selangor	7	10	31.6	9	38.2	12.1	32.4 (29.3-34.2)	23.5 (22.3-24.6)	168 (0-1338)

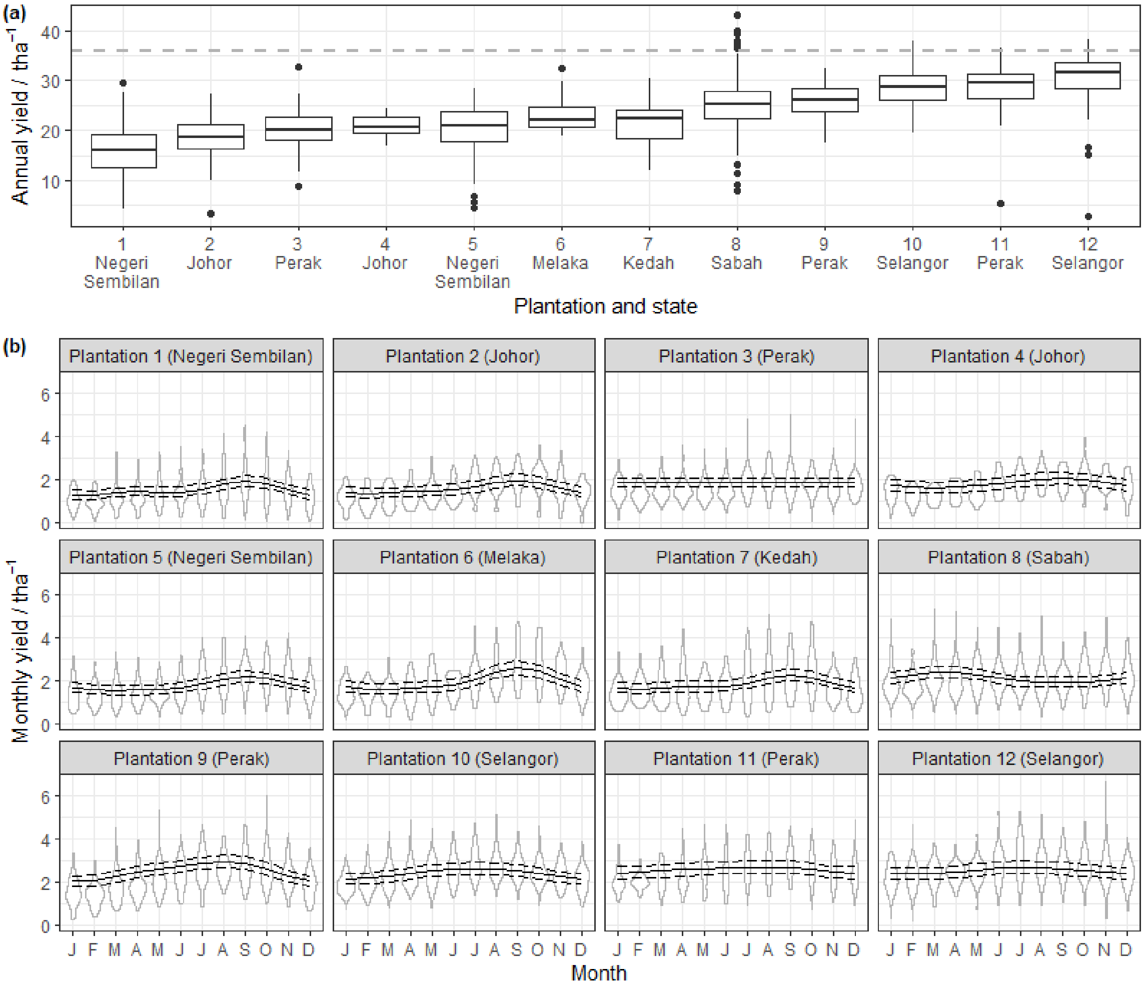
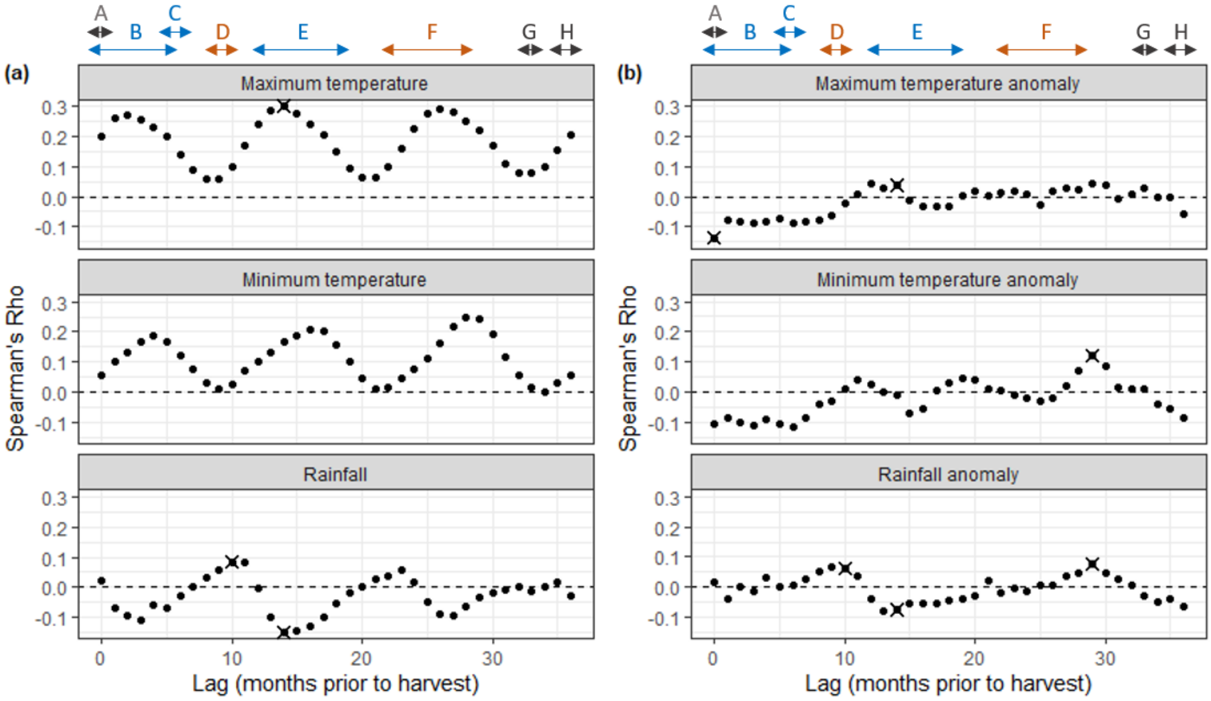


Figure 4.2. Variation in oil palm yield among study plantations, with plantations ranked by median annual yield. (a) Boxplots of annual yield for each full year of harvest in each oil palm field, by plantation. The dashed line represents the maximum potential yield in many coastal plains of Malaysia, after Hoffmann *et al.* (2014). **(b) Monthly oil palm yield in each plantation, including regular seasonal fluctuations.** Solid and dashed black lines show predicted monthly yield values from the final GAMM of raw yield and climatic variables (mean and 95% confidence intervals). The predictions incorporate both cyclic cubic regression splines of seasonality fitted across months per plantation, and random intercepts fitted for each plantation, with all other numeric predictors held at the median value, and were back-transformed from a square-root transformation for plotting purposes. Grey violin plots show distribution of actual monthly yield data for each month in each plantation.

Correlations between climatic predictors and oil palm yield at different lags prior to harvest

Raw yield was positively correlated with both Tmax (Spearman's Rho 0.05 – 0.30) and Tmin (0.0 – 0.25) for all timelags up to 36 months prior to harvest (fig. 4.3a), suggesting that increasing temperature (or an intercorrelate such as solar radiation) is a key climatic driver of yield increases at the plantations in this study. In contrast, the correlations between raw yield and rainfall vary between positive and negative values (-0.15 – 0.08), depending on the timelag (fig. 4.3a), suggesting that the plant-water relations at plantations in this study vary depending on the stage of development of the oil palm fruit. However, the correlations of all three of these raw climatic variables with yield showed substantial fluctuations around a cycle of approximately 12 months, highlighting the high degree of autocorrelation from regular seasonal fluctuations in each of the predictors (fig. S3.3), which means that interpretation of correlations at different lag times for the raw variables is not straightforward. The strongest correlation coefficients between raw climate and yield nevertheless corresponded to key stages of oil palm fruit development: a positive correlation of rainfall at lags of 10-11 months suggests that water availability reduces inflorescence abortion; a positive correlation of Tmax and negative correlation of rainfall at a 14 month timelag suggests that insufficient temperature and/or solar radiation is limiting to inflorescence development; and a positive correlation of Tmin at a timelag of 28 months suggests that temperature influences sex differentiation (the ratio of female to male inflorescences, which corresponds to number of fruit bunches produced).

All correlations between climate and yield anomalies were weaker than those for the raw variables, suggesting that the main influence of climate on yield at the plantations in this study is through regular seasonal variation. However, the calculation of anomalies could have introduced some noise into climate-yield relationships because a single anomaly value can correspond to a range of raw climate or yield values (fig. S3.9); and we used fewer data points in the anomaly analyses than the raw variables, which could have resulted in weaker relationships. The relative strength of correlations between climate and yield anomalies did not follow the same pattern as for the raw variables across the timelags of 0-36 months, owing to the removal of seasonal autocorrelation, so analyses of the anomalies allowed us to investigate effects of climate which were not detectable in the raw variables. The correlations between temperature and yield anomalies varied from weak negative to weak positive values (Tmax Spearman's Rho -0.14 – 0.04, Tmin -0.12 – 0.12), suggesting that variation in temperature does not have a consistently positive relationship with yield at all timelags (fig. 4.3b), and that this is not detectable from the raw variables owing to seasonal autocorrelation. For example, the strongest correlation of climate and yield anomalies was for Tmax at the month of harvest, suggesting that hotter temperatures reduce harvesting efficiency. Similarly, some of the strongest correlation coefficients between rainfall and yield anomalies suggest relationships which were undetectable from the raw variables, such as a positive relationship of rainfall with yield during sex determination at a timelag of 29 months, which coincides with a strong positive correlation between yield and Tmin, suggesting that sex determination is also dependent on temperature.



Stages of fruit development: affecting number of fruit bunches; affecting weight of fruit bunches

- A. Harvest
- B. Ripening
- C. Flowering; pollination
- D. Inflorescence abortion
- E. Inflorescence development: number of spikelets and number of flowers per spikelet determined
- F. Sex determination
- G. Inflorescence initiated
- H. Leaf initiated

Figure 4.3. Correlations between climatic variables and oil palm yield for timelags of 0-36 months prior to harvest, with corresponding stages of fruit development. (a) Correlations between raw climatic variables and raw oil palm yield; (b) correlations between climatic variable anomalies and yield anomalies. Crosses denote climatic predictors (i.e. climatic variables at a specific timelag) included in the models. We selected climatic predictors for inclusion in the models from their high correlations with yield relative to other timelags, at timelags which correspond to key stages of oil palm fruit development, but avoided inclusion of inter-correlated predictors in the models (see Supplementary Information 3.2 for details). Stages of fruit development are after Tinker & Corley (2015). See table 4.1 for summary of existing studies which have detected effects of climate at stages of oil palm fruit development.

Effects of temperature on oil palm yield

We found that Tmax, with a timelag of 14 months prior to harvest, was the most important climatic predictor of raw oil palm yield, based on changes to the final model R^2 when each predictor was removed (table S3.9). As temperature showed greater seasonal and spatial (among-plantation) variation than rainfall, it is unsurprising that it was more important in explaining variation in raw oil palm yield (fig. S3.2). The fitted relationship between raw yield and

Tmax was positive and quadratic, with yield increasing as Tmax increased, but at a slowing rate of increase (fig. 4.4a). With the other predictors held at median values, a 1 °C increase in Tmax from 28 °C to 29 °C drives a 9.2% increase in yield, but a 1 °C increase in Tmax from 33 °C to 34 °C drives only a 2.2% increase in yield. This positive relationship suggests that increasing Tmax, or a correlate such as solar energy, increases photosynthesis during the period of inflorescence development when the number of spikelets and number of flowers per spikelet are determined, and determines yield by affecting FFB weight (table 4.1, fig. 4.3). The curved shape of the relationship suggests that yield reaches a plateau as Tmax increases, which could indicate either that the conditions are approaching optimal, or that another climatic factor (e.g. water availability) becomes more important for yield. This positive relationship is robust to the removal of seasonal autocorrelation, because we also found a positive relationship between Tmax anomalies and yield anomalies at the same timelag (fig. S3.13). However, other climatic anomaly predictors were more important than Tmax with a lag of 14 months in explaining yield anomalies (see below), suggesting either that the primary role of Tmax with a lag of 14 months is driving seasonal variation in yield, or that its importance for yield is artificially inflated in analyses of raw variables because its seasonal fluctuations happen to correlate with yield seasonality. The seasonal fluctuations in Tmax peak in July in many plantations (fig. S3.2), which corresponds to 14 months prior to the peak in yield (generally September; fig. 4.2).

In contrast to the analyses of raw climate and yield, the most important predictors of yield anomalies were Tmin anomaly with a lag of 29 months, followed by Tmax at the month of harvest (according to effect sizes, as we were unable to compare changes to the final model R^2 when each predictor was removed; see tables S3.8, S3.9, fig. S3.13). Thus, temperature also appears to influence yield by affecting sex determination (affecting the proportion of female inflorescences and thus fruit bunch number) and harvest efficiency, which may be lower when temperatures are higher (fig. 4.3).

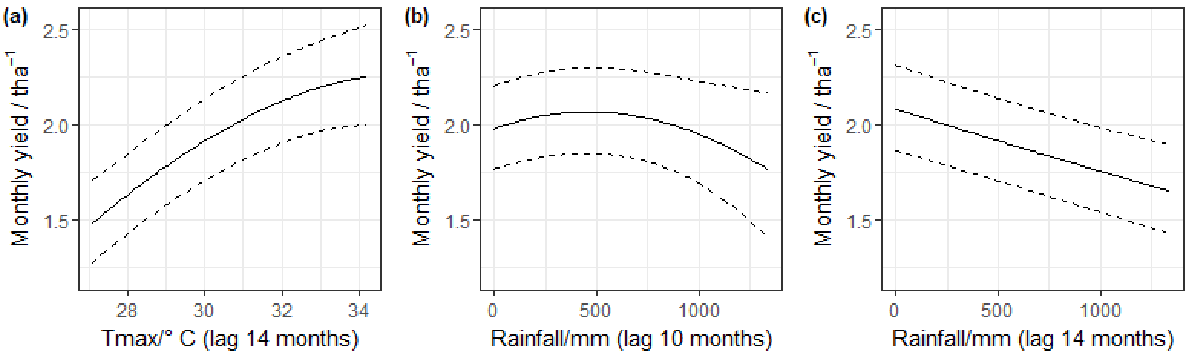


Figure 4.4. Expected yield values and 95% confidence intervals for the main effects of the three climatic predictors in the final GAMM modelling raw yield: (a) Tmax at a 14-month timelag prior to harvest; (b) rainfall at a 10-month timelag; (c) rainfall at a 14-month timelag. The yield values in these plots were predicted with all other numeric predictors in the model (the two other climatic predictors and oil palm age) held at the median value in the dataset. Yield values and 95% confidence CIs were back-transformed from the square-root scale for plotting. These were fitted with a GAMM which also included smoothers for seasonality per plantation and oil palm age (figs. 4.2, S3.12), plantation as a random intercept, and an autocorrelation-moving average error structure of order $p = 4$, $q = 4$ (table S3.5). See fig. S3.13 for the modelled relationships between climate and yield anomalies, including at these timelags.

Effects of rainfall on oil palm yield, and its interaction with temperature

We detected weak positive effects of rainfall on oil palm yield in both the raw yield and anomaly analyses, suggesting that water availability is sub-optimal at our study sites at certain key stages of oil palm fruit development. Rainfall at a timelag of 10 months prior to harvest was the second-most important climatic predictor of raw oil palm yield (table S3.9), with a weak quadratic relationship with yield. The fitted relationship between rainfall at a 10 month lag and yield predicts an optimum monthly rainfall of 460 mm, so that an increase from 0 mm to 460 mm month^{-1} in rainfall 10 months prior to harvest drives a 4.5% increase in yield, when the other predictors are at median value (fig. 4.4b). This positive effect of rainfall on yield is supported by the anomaly analyses for timelags of both 10 months prior to harvest, when fruit are aborted, and additionally for a lag of 29 months prior to harvest, when inflorescence sex is determined, which correspond to the two stages of fruit development responsible for determining total number of fruit bunches (figs. 4.3, S3.13, table 4.1).

However, the relationship between yield and rainfall at a 14 month lag prior to harvest is linear and negative, with each increase in rainfall of 500 mm month^{-1} conferring a decrease in yield of 8-9% (back-transformed from square-root yield, as fitted in the model) (fig. 4.1c). This weak negative relationship was also true for rainfall and yield anomalies at this timelag (14 months prior to harvest; fig. S3.13). Thus high rainfall, or a correlate such as cloud cover, appears to reduce the number of spikelets and/or the number of flowers which develop per spikelet (table

4.1, fig. 4.3). Given the strong positive relationship between raw yield and Tmax at this timelag, it is therefore likely that yield is limited by insufficient solar radiation at this stage, which is positively correlated with Tmax and negatively correlated with rainfall. Moreover, the interaction between rainfall and Tmax at this lag period (14 months prior to harvest) predicts the highest yield from the driest, hottest months (fig. 4.5), highlighting that insufficient temperature, or a correlate such as solar radiation, is limiting to this stage of inflorescence development, but that water availability is sufficient at this lag time. For low values of rainfall, the relationship between Tmax and yield is more curved (i.e. appears to approach a plateau) than for high values of rainfall (fig. 4.5b), which could suggest that climatic conditions are close to optimal when rainfall is low and Tmax is high. When Tmax is hotter, the negative effect of rainfall on yield is greater (steeper relationship), suggesting that high rainfall, or an intercorrelate such as cloud cover, increasingly reduces yield at higher temperatures (fig. 4.5b). However, the interaction between Tmax and rainfall anomalies 14 months prior to harvest does not follow these patterns, because the negative relationship between rainfall and yield anomalies is steepest at colder values of Tmax (fig. S3.14). Thus, the anomaly relationships suggest that negative impacts of high rainfall anomalies (or high cloud cover) on inflorescence development are less pronounced at hotter temperatures, possibly because the water requirements of oil palm are greater, and the positive impact of increased water availability from high rainfall anomalies partly offsets its negative effect on yield anomalies.

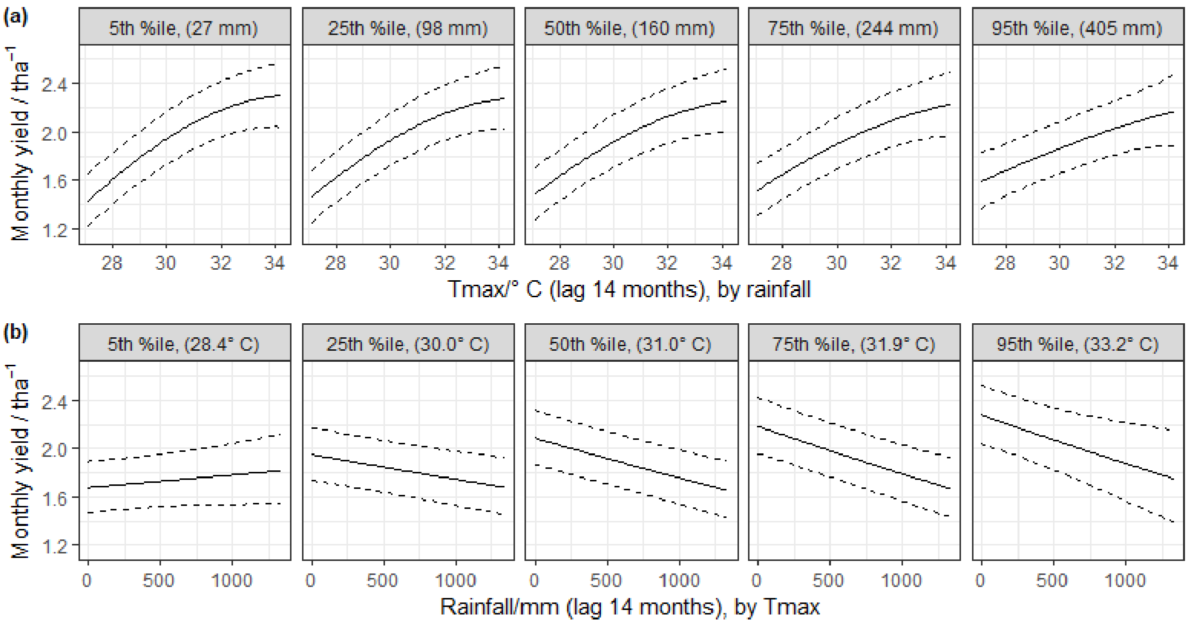


Figure 4.5. Expected yield values and 95% confidence intervals for the interaction of Tmax and rainfall at 14-month timelags prior to harvest, in the final GAMM modelling raw yield. The yield values in these plots were predicted with all other numeric predictors in the model (the two other climatic predictors and oil palm age) held at the median value in the dataset. Yield values and 95% confidence CIs were back-transformed from the square-root scale for plotting. These were fitted with a GAMM which also included smoothers for seasonality per plantation and oil palm age (fig. S3.12), plantation as a random intercept, and an autocorrelation-moving average error structure of order *p* = 4, *q* = 4 (table S3.5). See fig. S3.14 for the modelled interaction between Tmax and rainfall anomalies at this timelag.

4.5 Discussion

Oil palm yield varied substantially among the 12 industrial oil palm plantations in this study, with only minor effects of climate. Nevertheless, we detected varied impacts of both temperature and rainfall on yield at timelags corresponding to key stages of fruit development, with a greater effect of temperature than rainfall in our analyses of both raw and anomalised yield. In light of our findings, we discuss the potential drivers of differences in yield among plantations, likely impacts of climate change on yield, and the potential for sustainable intensification of industrial oil palm production in Malaysia.

Variation in oil palm yield among plantations

We found that the majority of variation in yield that we could explain was due to differences among plantations. We expect that management is the main driver of this among-plantation variation, even though the plantations in this study were all owned by a single company, because previous studies have identified management as the main determinant of differences in yield among plantations and/or fields, rather than soil type or other environmental factors (Euler *et al.*, 2016; Hoffmann *et al.*, 2017). Frequency of harvesting is a key determinant of yield, because overly long harvesting intervals reduce the total ripe fruit harvested by allowing some to rot (Donough, Witt and Fairhurst, 2009; Cock *et al.*, 2016; Euler *et al.*, 2016). Yield gaps in Malaysia are largely attributed to labour shortages preventing optimal harvest cycles, and Sarawak (East Malaysia) has reported 15% yield losses owing to rotting of unharvested fruits (Murphy, 2014). We therefore expect that variation in labour availability and the harvest frequency is probably the main driver of variation in yield among plantations in this study. Nevertheless, some degree of among-plantation variation could also arise through a number of environmental factors, and how effectively they are managed (Woittiez *et al.*, 2017). These factors include:

i. Presence and abundance of pests and pathogens of oil palm, such as the pathogenic fungus *Ganoderma,* which causes basal stem rot and mortality of all infected palms, and the rhinoceros beetle *Oryctes rhinoceros*, which are both prevalent in Malaysia (Barcelos *et al.*, 2015; Murphy, 2014).

ii. Soil type, nutrient contents, permeability and water-holding capacity (among other properties) (Tinker and Corley, 2015; Woittiez *et al.*, 2017). The dominant soil types across much of Malaysia are acrisols and ferralsols (Hengl *et al.*, 2017; ISRIC, 2017), which are highly weathered soils with low nutrient contents, and require careful management for optimal yields, such as cover crop establishment, mulching with empty fruit bunches, and fertilisation (Pirker and Mosnier, 2015).

iii. Local topography, because steep slopes increase surface run-off, reducing water availability and increasing soil erosion and fertiliser loss (Woittiez *et al.*, 2017).

iv. Pollination efficiency, and thus variation in fruit set, which is low in some areas of Southeast Asia (Teo, 2015).

In this study, we neither had access to data for these four potential sources of variation in yield, nor to data relating to the labour capacity and harvesting schedules of our study plantations. We therefore suggest that investigating the roles of labour availability, harvesting schedules and these other potential drivers of yield should be a key priority for future research.

Importance of climatic variation for oil palm yield in Malaysia

We identified a number of impacts of climate on oil palm yield, at timelags corresponding to key stages of fruit development, although the effects of climate on yield were negligible in comparison to among-plantation variation (likely due to management). Existing literature suggests that solar radiation is the most important climatic variable for oil palm yield in

Southeast Asia (Hoffmann *et al.*, 2014; Woittiez *et al.*, 2017), and our finding that maximum temperature was the most important climatic variable for raw oil palm yield is in line with this, because maximum temperature is correlated with solar radiation (Harris *et al.*, 2020; Tinker & Corley, 2015). Similarly, we found negative relationships between rainfall (raw and/or anomalies) and yield at timelags corresponding to determination of the number of FFB produced (sex determination and inflorescence abortion), previously identified as sensitive to water availability in Southeast Asia (Dufour *et al.*, 1998; Legros *et al.*, 2009a,b). Thus our findings support previous research suggesting that water stress reduces photosynthesis and thus the carbohydrates available for fruit development, triggering a high ratio of male inflorescences initiation and/or high abortion rates, possibly with selective abortion of female inflorescences (Tinker and Corley, 2015). We also found a positive effect of Tmin anomaly during sex determination, which is a probable correlate of 'useful radiation' previously identified as having a positive effect at this developmental stage (Dufour *et al*., 1998; see table 4.1), representing increasing capacity for photosynthesis.

However, we also identified some effects of climate on yield which we are not explained in existing literature. We found that anomalised Tmax at month of harvest was the strongest climatic predictor of yield anomalies, which we did not expect, because oil palm fruit continue ripening until the point of harvest, and ripening is positively affected by temperature and solar radiation (Hoong & Donough, 1998; Tinker & Corley, 2015; see table 4.1). Harvesting of FFB, which generally weigh 15-20 kg, is reliant on manual labour (fig. 4.1; Donough *et al.*, 2009; Murphy, 2014). We therefore expect that this negative relationship between Tmax and yield anomalies at month of harvest is a result of reduced efficiency of workers performing the harvest under hotter temperatures, further highlighting limitations to oil palm yield from difficulties of harvesting (Murphy, 2014). In addition, we are not aware of an explanation for the negative relationship between rainfall and yield during inflorescence development, although it has previously been identified for oil palm yield in Malaysia (Chow, 1992). The contrast between the direction of this relationship and those between yield and rainfall during sex determination and abortion highlights contrasting responses of oil palm to water availability depending on the stage of fruit development, and suggests that during inflorescence development, yield is more dependent on solar radiation than water availability. Oil palm stomatal conductance depends on air humidity, which is positively related to rainfall, and stomatal closure occurs even under conditions of high soil moisture when air is dry (Henson & Harun, 2005; Tinker & Corley, 2015). We thus surmise that air humidity at our study sites was generally high, and therefore less limiting to inflorescence development than insufficient solar radiation, resulting in a weak negative relationship between rainfall and yield during inflorescence development, owing to increased cloud cover and decreased solar radiation.

Overall, the relative importance of different lag times of climate for yield anomalies was in-line with previous research findings, suggesting that (i) management (worker efficiency) at the stage of harvest is highly important for yield (although we have not come across the specific negative effect of Tmax for yield during harvest in existing literature); (ii) developmental stages that determine number of FFB are highly important for yield (sex determination and inflorescence abortion; fig. 4.3); and (iii) climate during developmental stages affecting FFB weight is important for yield (inflorescence development), but less so than climate during determination of FFB number (Donough, Witt and Fairhurst, 2009; Tinker and Corley, 2015). In contrast, our analyses of raw yield suggested that climate during inflorescence development and determination of FFB weight was more important than climate during stages affecting FFB number, which contradicts previous findings that the majority of FFB yield variation is determined by FFB number; and that yield seasonality is largely driven by variation in FFB number (Donough, Witt and Fairhurst, 2009; Tinker and Corley, 2015). This suggests either that the importance of Tmax with a timelag of 14 months is artificially inflated in our analyses of raw yield, because its seasonal peak coincides with 14 months prior to the seasonal peak in yield; or that Tmax primarily drives the seasonality at our study sites, owing to high year-round rainfall but stronger seasonal variation in temperature, in contrast to patterns in locations with more seasonal rainfall (Tinker and Corley, 2015).

Expected changes to yield in Malaysia under climate change

Climate change is expected to drive substantial temperature increase in Southeast Asia, with increases in extreme wet precipitation events and drought events associated with the El Niño Southern Oscillation (ENSO) (Barros *et al.*, 2014; Cai *et al.*, 2014; Tangang *et al.*, 2017). These changes are likely to have multiple impacts on oil palm cultivation, growth and yield (Paterson *et al.*, 2015; Tinker & Corley, 2015).

Under a rapid economic growth scenario with mid-century reductions in fossil fuel consumption, mean temperature in Southeast Asia is predicted to increase by 3.5°C at the end of this century (Barros *et al.*, 2014). Our finding that raw yield is positively related to Tmax suggests that increasing temperatures will benefit yield, although our study only encompasses a limited range of Tmax (~27-34°C), well below the heat stress threshold of ~38°C (Tinker and Corley, 2015). Paterson *et al.* (2015) estimated that a substantial area of western Peninsular Malaysia would exceed the oil palm heat stress threshold by 2100, although this will not be exceeded in central, eastern and southern Peninsular Malaysia, nor in Malaysian Borneo. Thus the impacts of future temperature increase on oil palm yield in Malaysia do not seem substantial, but future projected temperatures (particularly during heat waves) will be considerably greater than those currently experienced by oil palm in Southeast Asia (Barros *et al.*, 2014), so it is possible that negative impacts have been overlooked. For example, we found that the strongest relationship between yield anomalies and climate anomalies was a negative relationship with Tmax at the month of harvest. This suggests that high temperatures reduce harvesting efficiency, possibly owing to more difficult conditions for workers, because harvesting is reliant on manual labour to harvest the FFB, which generally weigh 15-20 kg (fig. 4.1; Donough *et al.*, 2009; Murphy, 2014). Although we did not identify a negative impact of temperature on yield per se, this relationship suggests that increasing temperatures, and particularly extreme high temperatures during heatwaves, could have severe negative consequences for the oil palm industry, through reduced worker efficiency and increased risk of heat stress in workers.

Although annual precipitation has increased in eastern Peninsular Malaysia during 1971-2010 (Mayowa *et al.*, 2015), mean annual precipitation is projected to undergo minimal change in Southeast Asia over the coming century, but uncertainty around precipitation projections is high (Barros *et al.*, 2014). We did not find conclusive evidence that oil palm has higher water requirements at hotter temperatures for the climatic range in this study (fig. 4.5), suggesting that oil palm in Malaysia is therefore unlikely to experience substantially greater drought stress on average under future climate change than currently. However, we found negative relationships between rainfall and yield relating to sex determination and inflorescence abortion, and water requirements of oil palm are likely to be greater at hotter temperatures (Tinker and Corley, 2015), although we did not find conclusive evidence for an interaction between these in this study, suggesting that future increases in temperatures could result in yield reductions through increased proportion of male inflorescences and increased inflorescence abortion. Nevertheless, increasing atmospheric carbon dioxide concentration is projected to increase oil palm water-use efficiency, so overall impacts of climate change on plant-water relations and oil palm yield are unclear (Wang *et al.*, 2012; Tinker and Corley, 2015).

Whilst changes to average annual (and quarterly) rainfall in Malaysia are expected to be negligible, the patterns of extreme rainfall events are likely to change, with consequences for oil palm yield, although we did not address the impacts of rainfall extremes on yield in this study. Both extreme wet precipitation events and ENSO droughts are expected to increase in Malaysia over the coming century, although uncertainty around these estimates is high (e.g. Spinoni *et al.* (2020) project decreases in drought in SE Asia by 2080) (Barros *et al.*, 2014; Cai *et al.*, 2014; Tangang *et al.*, 2017). Previous studies have identified water deficit as a key driver of yield (table 4.1), and oil palm yield is typically lower in regions with a regular dry season, through impacts of drought stress on inflorescence abortion and sex determination (Tinker and Corley, 2015). Low rainfall and high temperatures associated with ENSO droughts have caused reductions in annual oil palm yield in Malaysia (Oettli, Behera and Yamagata, 2018), although we did not detect conclusive evidence of greater water stress under higher temperatures in this study. Thus the increasing intensity of ENSO events and associated droughts is likely to cause periods of low oil palm yield in Malaysia, corresponding with ENSO cycles every ~2-7 years (Caliman and Southworth, 1998; Tangang *et al.*, 2017). Similarly, the projected increase in frequency and intensity of extreme heavy rainfall events in Malaysia is likely to drive concurrent periods of low oil palm yield over the coming century. Flooding substantially limits the potential for harvesting, resulting in yield reductions (Murphy, 2014); severe waterlogging has direct negative impacts on yield by causing palm mortality (Abram *et al.*, 2014); and heavy rainfall has negative impacts on pollinator populations and fruit set (Hoong and Donough, 1998). In addition to changes in temperature and rainfall, multiple factors associated with climate change are likely to impact oil palm yield, which are likely to interact, making inferences about future oil palm yield highly uncertain. Increasing carbon dioxide concentrations could support high future productivity through increased photosynthetic efficiency (Ibrahim *et al.*, 2010), but in natural forests, tree growth and water use efficiency have decreased due to the negative impacts of fire and drought outweighing any benefits of increasing carbon dioxide concentrations (Feeley *et al.*, 2007; Mitchard, 2018; Bauters *et al.*, 2020). Many coastal plantations in Malaysia are at increasing risk of inundation and/or salinification from sea level rise (Siwar, Ahmed and Begum, 2013). Climate change is also likely to increase impacts of oil palm pests and diseases, because increasing stress of palms is likely to increase their vulnerability to infection (Paterson, Sariah, & Lima, 2013). Thus, the net impacts of climate change on oil palm production are highly uncertain, and our detected effect of a negative impact of temperature during harvest may suggest that negative impacts of climate change on workers could outweigh any increases in productivity from rising temperatures and carbon dioxide concentrations.

Current yield gaps

We found that differences in yield among plantations were the primary source of variation in oil palm yield, likely caused by differences in management, suggesting that improving management could result in substantial yield improvements in many plantations. Hoffmann *et al.* (2014) estimated that the potential annual FFB yield of coastal areas was generally 36 t FFB ha^{-1}, which is over double the lowest plantation annual yield in this study, and suggests that only ~60% of the potential yield is achieved in the majority of plantations in this study, and possibly as low as 50% in the least-productive plantation. However, estimated potential yield varies substantially across Malaysia (9 – 48 t FFB ha^{-1}) (Hoffmann *et al.*, 2014), so it is possible that the actual yield gap in the plantations in this study is considerably lower (or higher). The plantations in this study are owned and managed by a single, large-scale company, and we surmise that lack of labour availability and other management constraints may be greater in smaller-scale plantations, suggesting that many plantations in Malaysia achieve less than ~60% of their potential yield. This is in line with previous estimates of 44-63% of potential yield achieved for the whole of Malaysia (depending on potential yield estimation) (Fischer *et al.*, 2014), but greater than 67-89%, estimated for four plantations in Malaysia and Indonesia (Hoffmann *et al.*, 2017). Overall, yield gaps for oil palm in Malaysia appear substantial, and in combination with relatively weak expected impacts of climate change on average oil palm yield, suggest that there is considerable potential to improve oil palm yield in Malaysia in existing plantations.

Potential for sustainable intensification of oil palm in Malaysia

To increase crop production whilst reducing the environmental impacts of agriculture, it is essential that targets for both of these are set and addressed simultaneously (Cunningham *et al.*, 2013; Hunter *et al.*, 2017). Whilst there is substantial theoretical potential for higher productivity of Malaysian oil palm, the degree to which this is possible in practice, and whether it would be sustainable, are less clear.

Closing the current substantial yield gaps in Malaysia appears to depend largely on improving harvesting frequency, and thus either procuring more labourers for harvesting, or mechanising the process (Kushairi *et al.*, 2018; Kushairi, Singh, & Ong-Abdullah, 2017; Murphy, 2014). Currently, the majority of oil palm workers in Malaysia are migrant labourers from Indonesia, but recent economic changes in Indonesia, including expansion of oil palm plantations, are reducing incentives for migration; and Malaysian policies to restrict the number of migrant labourers granted visas further reduce overall worker availability (Murphy, 2014). Tools for harvesting from young- and intermediate-aged palms (up to 5 m height) have recently been developed, but efficient mechanisation of harvesting older, taller palms (requiring 10-13 m working height) is more challenging (Shuib, Khalid and Deraman, 2011). Moreover, extensive rollout of new technologies would be expensive and require additional natural resources for machinery production and energy provision. Development of oil palm varieties with altered architecture, such as dwarfism or long fruit stalks, could also help improve harvesting efficiency, although oil palm breeding and replanting cycles are relatively slow (replanting every ~25 years), so this does not provide a short-term solution (Kushairi *et al.*, 2017; Murphy, 2014; Woittiez *et al.*, 2017).

If yield of existing plantations in Malaysia were increased substantially, rising demands for vegetable oils could be met with less need for further encroachment of natural habitat (Byerlee, Stevenson and Villoria, 2014). In theory, such yield improvements could help conserve Southeast Asian rainforest, which has recently undergone extensive habitat loss (Wilcove *et al.*, 2013), as well as natural habitats in other regions which are currently expanding oil palm production, such as West Africa and South and Central America (Greenpeace, 2012; Castiblanco, Etter and Aide, 2013; Vijay *et al.*, 2016). However, improving crop yields can lead to greater incentives for expansion, owing to higher returns from land-use change (Byerlee, Stevenson and Villoria, 2014;

Carrasco *et al.*, 2014); and if markets are elastic (i.e. respond to changes in demand) then increasing productivity does not reduce pressure for land-use change (Hertel, 2012). Villoria, Golub, Byerlee, & Stevenson (2013) found that increasing the productivity of oil palm in Malaysia and Indonesia most effectively saves forest, both in Southeast Asia and globally, when alongside increased productivity of other crops, owing to reduced food prices and lower returns for oil palm producers. Given that global demand for vegetable oils is increasing, and prices are forecast to remain relatively stable over coming years (OECD and FAO, 2019), effective governance and incentives to preserve natural habitat are essential for reducing land-use change driven by oil palm expansion, alongside improving productivity. Certification schemes such as the Roundtable on Sustainable Palm Oil (RSPO) could therefore play a substantial role in simultaneously reducing natural habitat loss, by implementing recent 'zero-deforestation' commitments alongside supporting best management practices to close yield gaps (Haupt *et al.*, 2018; RSPO, 2018). Whilst RSPO certification has been voluntary to date, and thus has the potential to drive leakage of deforestation (Heilmayr, Carlson and Benedict, 2020), several sub-national jurisdictions, including the East Malaysian state of Sabah, are currently developing implementation of a 'jurisdictional' approach for state-wide certification (RSPO, 2019c), which should increase overall uptake of the scheme and thus the potential for reducing habitat loss (Byerlee, Stevenson and Villoria, 2014).

If harvesting is done manually, increasing its frequency to improve oil palm productivity incurs no substantial environmental costs, but other management aspects of maintaining and/or improving productivity increase the environmental footprint associated with oil palm production. Over time, soil is increasingly degraded in oil palm plantations, decreasing in carbon content (Guillaume *et al.*, 2016), and replanting results in substantial soil biodiversity loss (Ashton-Butt *et al.*, 2019). In addition, use of chemical fertilisers for oil palm is widespread, which are a key source of global GHG emissions (Tian *et al.*, 2020) and soil degradation (Osman, 2014). There is therefore a strong need for the development of more sustainable soil management techniques in oil palm, such as mulching with empty fruit bunches, which can improve yield and soil organic carbon (Tao *et al.*, 2017).

4.6 Conclusions

We found that variation in oil palm yield in industrial plantations in Malaysia is largely due to differences between plantations, which we attribute to differences in management, likely reflecting availability of workers for harvesting. Weak impacts of climate on yield suggest that productivity is greater at higher temperatures, and has varied responses to rainfall depending on the stage of fruit development.

Our findings suggest that yield gaps in industrial oil palm plantations in Malaysia are substantial, highlighting the considerable potential for increased palm oil production in current plantations. We expect that the yield gaps are largely driven by limited availability of labourers for harvesting fresh fruit bunches, highlighting the need for improving the socio-economic conditions and incentives for working in the industry, which would enable yield improvements with no additional environmental costs, and/or mechanising harvesting. The relationships that we detected between yield and climate were weak and do not suggest substantial impacts of climate change on oil palm yield in Malaysia, although future projected climatic conditions are outside the range of those in this study. We therefore conclude that oil palm production in Malaysia can increase substantially without additional land-use change, and high average yields (improved from current yields where feasible) should be supported in future decades, although strong regulation of land management and incentives to minimize deforestation are necessary to prevent additional expansion.

Chapter 5

General discussion

5.1 Abstract

In this general discussion, I summarise my thesis findings in relation to the specific chapter aims and the overall thesis aim of understanding how to reduce the land use impacts of oil palm cultivation on carbon and biodiversity. I synthesize the findings from the data chapters and discuss the degree to which recent interventions to reduce the environmental impacts of oil palm expansion have been successful. I conclude that sustainability certification and voluntary zero-deforestation commitments are helpful in reducing environmental impacts but currently insufficient, and that the future success of these sustainability criteria depend on addressing a number of pathways for leakage of environmental impacts. I discuss where oil palm expansion could take place with minimal negative environmental impacts, concluding that avoiding expansion where possible is preferable for minimising carbon emissions and biodiversity loss. I discuss how oil palm production could sustainably meet future needs, concluding that exploring alternative management practises for oil palm is critical to ensuring future sustainable production under high global demands for vegetable oils, alongside strong governance and regulation of practises such as expansion, and efforts to reduce global palm oil demand.

5.2 Summary of thesis findings

In this thesis, I examined the degree to which sustainability certification helps reduce the impacts of oil palm expansion on carbon and biodiversity. I conducted fieldwork in Sabah, Malaysian Borneo, to quantify the value of conservation set-asides in certified oil palm plantations for aboveground carbon stocks (AGC) and associated plant diversity. I found that conservation set-asides boost AGC and plant diversity of oil palm plantations, but do not replace the conservation value of continuous primary forest. I then examined the global potential for zero-deforestation commitments (ZDCs) to drive leakage of oil palm expansion, and associated biodiversity loss, from tropical rainforest into tropical grassy and dry forest biomes. I found that the majority of locations of natural habitat that I projected to be climatically-suitable for oil palm expansion under ZDCs are in tropical grassy and dry forest biomes, where ZDCs could steer oil palm expansion into locations that would result in high vertebrate richness loss. I concluded that there is considerable potential for leakage of natural habitat and biodiversity loss under ZDCs, and an urgent need for improved guidance to protect grassy and dry forest biomes. To reduce the need for land-use change, and consequent biodiversity loss and greenhouse gas (GHG) emissions, oil palm production could be increased by improving the yield of current plantations. I therefore examined the role of climate in determining oil palm yield in industrial plantations in Malaysia. I found that climate has a minor role in explaining variation in yield compared to between-plantation variation, indicating that differences in management were the main cause of yield variation. I concluded that there is substantial scope to improve yield in current oil palm plantations, even in relatively high-yield locations, through improvements in management practices. I outline the findings of each of these three chapters in more detail below.

Chapter 2: Conservation set-asides improve carbon storage and support associated plant diversity in certified sustainable oil palm plantations

Main objectives:

(1) Quantify the value of conservation set-asides in Roundtable on Sustainable Palm Oil (RSPO)-certified oil palm plantations for conserving aboveground carbon stocks (AGC), in comparison to both the oil palm crop and continuous forest (selectively logged and primary).

(2) Compare vegetation structure between conservation set-asides and continuous forest, to understand the drivers of differences in AGC, and the potential for regeneration in set-asides, using seedling density as an indicator of regeneration potential.

(3) Examine how landscape-scale forest fragmentation, local topography, and soil parameters influence set-aside AGC.

(4) Examine whether conserving AGC in set-asides has co-benefits for diversity of trees, saplings and seedlings.

(5) Scale-up AGC estimates to predict the average AGC of oil palm plantations with different coverage of set-asides.

In this chapter, I concluded that maintaining conservation set-asides within oil palm plantations benefits AGC, because I found that set-asides supported more than 1.5-times the AGC of oil palm plantations on average. I also concluded that conserving AGC in set-asides has co-benefits for plant diversity, because the plant diversity of set-asides was positively related to their AGC. However, I found that average set-aside AGC was less than half that of continuous forest, owing to reduced numbers of the largest trees in set-asides, highlighting the unparalleled conservation value of continuous forest. I found that there was considerable variation in the AGC of plots in set-asides (7.8–115 Mg ha^{-1} in live trees and palms), ranging from below that of oil palm to equivalent to some continuous forest plots. Landscape-scale fragmentation did not explain this variation in set-aside AGC, suggesting that disturbances that I was unable to account for (such as site-specific history of selective logging) were important for explaining set-aside AGC; and that the AGC of some set-aside plots could be considerably improved. In addition, I found that the density of seedlings in set-asides was substantially lower than that of continuous forest, suggesting that the potential for ongoing tree regeneration in set-asides is low. I therefore concluded that conservation set-asides in oil palm plantations could benefit from management such as enrichment planting, to boost regeneration and thus support future AGC and biodiversity.

Chapter 3: Zero-deforestation palm oil could threaten tropical grassy and dry forest biomes

Main objectives:

(1) Map locations of natural habitat that are climatically-suitable for oil palm expansion (both rainfed and under irrigation), in order to assess the potential for zero-deforestation commitments (ZDCs) to drive leakage of oil palm expansion from tropical rainforest to grassy and dry forest biomes.

(2) Compare the proportion of non-agricultural land remaining in individual ecoregions that could potentially be converted to oil palm in tropical rainforest, grassy and dry forest biomes under ZDCs.

(3) Examine the likely yield of oil palm in these grassy and dry forest biome locations, in comparison to current plantations, and assess the potential role of irrigation in improving yields.

(4) Examine the impacts of oil palm expansion under ZDCs on biodiversity:

    a. assess the potential for loss of unique ecosystems and biological communities;

    b. examine whether ZDCs protect locations of high species richness;

    c. quantify the potential for reduction of vertebrate ranges in each biome.

In this chapter, I concluded that there is considerable potential for ZDCs to drive leakage of oil palm expansion from tropical rainforest to other biomes, because the majority of natural habitat that is climatically-suitable for oil palm expansion is in grassy and dry forest biomes, owing to extensive protection of remaining tropical rainforest by ZDCs. Whereas ZDCs protect locations with high vertebrate richness from conversion in the tropical rainforest biome, the opposite is true for tropical grassy and dry forest biomes, where ZDCs steer oil palm expansion into areas of high vertebrate richness. Moreover, in tropical dry forest and grassy biomes, there is high potential for expansion under ZDCs to drive loss of unique ecological communities, because high proportions of the remaining habitat of individual ecoregions are suitable for expansion. Thus, I concluded that there is considerable potential for oil palm expansion to drive biodiversity loss under ZDCs, mostly in tropical grassy and dry forest biomes. In addition, I found that irrigation could improve yields in many locations in dry forest and grassy biomes, which could increase the risk of water scarcity. Thus, by shifting oil palm agriculture away from the wettest locations in the tropics, an unintended consequence of ZDCs is that they could cause environmental issues not typically associated with oil palm agriculture currently. However, I found that the potential for reductions in vertebrate ranges from oil palm expansion was generally small, which suggests that some oil palm expansion could occur without substantial negative impacts on biodiversity. Overall, I concluded that there is an urgent need for improved guidance on sustainability criteria for oil palm cultivation specific to tropical grassy and dry forest biomes, in order to avoid substantial negative environmental consequences of ZDCs.

Chapter 4: Climate has limited but varied impacts on oil palm yields in industrial plantations

Main objectives:

(1) Quantify the relative importance of climate (temperature and rainfall) and management (between-plantation variation) for oil palm yields in industrial plantations in Malaysia.

(2) Quantify the relationships between climatic variables (temperature and rainfall) and yield during oil palm fruit development (up to 36 months prior to harvest), in order to understand how climate affects yield, and the potential impacts of future climate change on yield.

(3) Examine relationships between climate and yield anomalies (values normalised per month and location, to remove seasonal and spatial variation), in order to test the robustness of my findings and improve the sensitivity of my analyses.

In this chapter, I concluded that management is the main driver of variation in yield in industrial plantations in Malaysia, because I found that the role of climate in explaining variation in yield was negligible in comparison with between-plantation variation. I therefore concluded that there is considerable potential to improve yields on current oil palm plantations, which would increase oil palm production without further land-use change. I found that maximum monthly temperature was the most important climatic driver of increased yield, suggesting that impacts of future climate warming may not have negative consequences on yield, although the impacts of warming outside the temperature range of my data are unclear. However, I also found positive relationships between rainfall and yield for key periods of oil palm fruit development (inflorescence abortion and sex determination), which suggested that the expected increase in drought periods in Southeast Asia are likely to cause periodic reductions in yield.

5.3 Have recent interventions to reduce the negative impacts of oil palm expansion been successful?

In chapters 2 and 3, I examined the success of recent interventions to improve the environmental sustainability of oil palm agriculture. Over the last 15 years, sustainability certification of palm oil, principally by the Roundtable on Sustainable Palm Oil (RSPO), has been developed to reduce the GHG emissions and biodiversity loss from oil palm expansion; and 19%

of palm oil is now RSPO-certified (RSPO, 2005, 2013, 2018, 2020b). However, RSPO certification only recently adopted ‘no deforestation’ commitments into its Principles & Criteria in 2018, and the enforcement of RSPO guidelines is currently poor (RSPO, 2018; EIA and grassroots, 2019). Many corporations have voluntarily committed to ‘zero-deforestation’ in their palm oil supply chains, which now cover two-thirds of global palm oil production and one-third of plantation area, and are primarily implemented through RSPO certification (Haupt *et al.*, 2018). Therefore, the degree to which certification and ZDCs can reduce the negative environmental impacts of oil palm cultivation is of key importance for improving its sustainability.

In both chapters 2 and 3, I found positive effects of RSPO certification and ZDCs for reducing the biodiversity loss and GHG emissions associated with expansion of oil palm plantations in tropical rainforest. In chapter 2, I found that certification can help improve the AGC and plant diversity within oil palm plantations, due to the conservation of set-asides of rainforest. In chapter 3, I found that ZDCs would protect the vast majority of tropical rainforest from oil palm expansion, preventing loss of biodiversity and GHG emissions in this biome. Within the tropical rainforest biome, I found that ZDCs protect the locations of highest vertebrate richness, and so my results suggest that sustainability certification and ZDCs could help reduce the ongoing loss of global biodiversity and GHG emissions associated with tropical deforestation (Curtis *et al.*, 2018; Gibbs *et al.*, 2010; Hoekstra *et al.*, 2005; Pendrill *et al.*, 2019).

However, I also identified some issues with certification and ZDCs. In chapter 3, I found that there is considerable potential for ZDCs (of which RSPO certification is currently the principal means of implementation) to drive leakage of oil palm expansion into tropical grassy and dry forest biomes, because of the current focus of habitat protection on tropical rainforest, at the expense of other biomes. If oil palm expansion drives habitat loss in these biomes, locations with high carbon stocks (particularly when accounting for both aboveground and belowground carbon) and unique biodiversity could be lost, with potentially substantial consequences for local people (Grace *et al.*, 2006; Miles *et al.*, 2006; Batlle-Bayer, Batjes and Bindraban, 2010; Lehmann and Parr, 2016). Thus, ongoing oil palm expansion into grassy and dry forest biomes as a consequence of ZDCs could undermine the benefits of ZDCs for protecting rainforest biodiversity and carbon stocks, because ZDCs would displace biodiversity loss between biomes rather than reduce it globally. My results highlight the urgent need for guidance to identify and protect ‘high conservation values’ in tropical grassy and dry forest biomes, in addition to the existing guidance for tropical rainforests, in order to steer oil palm expansion into locations with minimal negative environmental impacts in these biomes.

Moreover, the extensive protection of tropical moist forests by ZDCs and RSPO certification, which I identified in chapter 3, could result in some companies becoming disincentivized to commit to ZDCs or RSPO certification, in order to continue oil palm expansion in rainforest locations, where the most suitable conditions for oil palm cultivation are located (see chapter 3). Without high uptake of ZDCs across the oil palm sector, accompanied by strong governance and enforcement, there is considerable potential for leakage to undermine potential benefits of ZDCs and certification (Garrett *et al*., 2019), because the net global deforestation from oil palm would not decrease, but be carried out by a subset of companies. Previous studies have identified that both industrial plantations and smallholders that expand on non-forest land are most likely to become certified (Carlson *et al.*, 2018; Slingerland, 2018), suggesting that the impact of RSPO certification in reducing deforestation is limited. Nevertheless, the proportion of oil palm expansion in Indonesia that occurs at the expense of forests is decreasing, so ZDCs and certification could help accelerate this current trend (Austin *et al.,* 2017). Given that RSPO certification and ZDCs are a relatively recent intervention to reduce the environmental impacts of oil palm expansion, assessing the extent to which these are having a net positive impact should be a key priority for ongoing research. To reduce the potential for between-company leakage, policy measures should be put in place to enforce ZDCs and certification, and increase the proportion of the oil palm sector covered by such commitments. Pressure from consumers to reduce the biodiversity loss associated with oil palm expansion can stimulate sustainable sourcing policies of companies, potentially banning imports of oil palm grown at the expense of forests (and ideally other natural habitats), and boosting the market for sustainable palm oil. Localities that produce oil palm could ban conversion of natural habitats, in order to prevent between-company leakage within each locality; and the jurisdictional approach for certification currently under pilot by the RSPO is an example of a potential intervention which could thus minimize between-company leakage within sub-national jurisdictions (RSPO, 2019c). However, national and international coordination of stringent habitat protection policies is essential to avoid stimulating a ‘race to the bottom’, where expansion at the expense of natural habitats leaks into least-regulated localities.

If the potential for leakage of oil palm expansion between biomes and between corporations were successfully minimized, my findings that ZDCs and RSPO certification protect extensive areas of tropical rainforest appear positive, particularly given that I found that even highly disturbed forest conservation set-asides are valuable for AGC and plant diversity (chapter 2). However, in chapter 2, I also found that the potential for regeneration of trees and AGC in conservation set-asides is uncertain, because the density of seedlings in set-asides was substantially lower than in continuous forest, suggesting that the conservation value of patches of forest within RSPO-certified plantations could decline over time. This finding is in line with previous studies identifying reduced regeneration and recruitment in fragmented forests in Borneo, suggesting that small forest patches have extinction debts that are likely to result in future reductions in tree diversity and changes in community composition (Stride *et al.*, 2018, 2019). Thus, the future conservation value of set-asides for AGC and tree diversity is uncertain, as found for fragmented forest patches in other tropical forest landscapes (Benítez-Malvido and Martínez-Ramos, 2003). However, I estimated that improving forest regeneration and set-aside AGC could substantially boost the AGC of oil palm plantations, with co-benefits for plant diversity, and probably for other forest taxa (Labrière *et al.*, 2016; Deere *et al.*, 2018). Thus, understanding how to ensure successful regeneration in set-aside patches of natural habitat within agricultural landscapes should be a key priority for future research, particularly in light of the need to minimize cropland removed from production (Hertel, 2011) whilst boosting carbon uptake by natural ecosystems where possible (Dinerstein et al., 2020).

Overall, I conclude that ZDCs and RSPO certification can help reduce the environmental impacts of oil palm expansion, but that they are currently insufficient to drive a net global reduction in GHG emissions and biodiversity loss associated with oil palm expansion. Without coordinated national and international interventions to regulate oil palm expansion, steering expansion into locations with minimal environmental impacts in all biomes, there is considerable potential for leakage of expansion between biomes, oil palm companies, and locations with different levels of regulation. In this thesis, I have addressed the environmental impacts of oil palm expansion, but there are many tropical agricultural commodities that drive deforestation, including soy, beef, maize, cocoa, rubber, pulp and paper, timber, sugar cane, coffee and cotton (Ahrends *et al.*, 2015; Trase, 2018; Pendrill *et al.*, 2019; Jayathilake *et al.*, 2020). Most of these other key drivers of deforestation can also be cultivated across the tropics, including in locations in grassy and dry forest biomes (Fischer *et al.*, 2002; Leijten et al., 2020), so coordinated regulation to prevent leakage of expansion from one crop to another is also essential to minimize biodiversity loss and GHG emissions globally. Whilst certification and ZDCs have helped set out preliminary measures to reduce oil palm-driven deforestation, these interventions will need to be substantially strengthened in order to have an overall positive impact and avoid leakage effects.

5.4 Where could industrial oil palm expand with minimal negative environmental impacts?

If regulations were to protect all locations of ‘high conservation value’ successfully (including rare and/or diverse species, natural habitats, and ecosystems; locations critical for ecosystem services; and locations of importance for local communities) (Senior *et al.*, 2015), a key question is where can oil palm plantations expand? The two typically-cited locations for sustainable cropland expansion are existing croplands (i.e. replacing other crops) and degraded natural habitats (e.g. Rosoman *et al.*, 2017). However, there are issues with both of these, which I outline below.

If industrial oil palm were to replace areas of existing cropland, there would be high potential for leakage of the displaced crops to other locations, which could result in net loss of natural habitats, biodiversity and GHG emissions. Currently, this is particularly likely because ZDCs cover a greater proportion of the oil palm sector than other key deforestation-risk commodities (Haupt *et al.*, 2018), highlighting the need for strong national and international regulation of land-use to avoid between-crop leakage. Whilst oil palm has considerably higher yield than other oil crops (Basiron, 2007), so can theoretically facilitate vegetable oil production with lower environmental costs (Beyer *et al.*, 2020), replacement of other cropping systems with oil palm monoculture could lead to loss of diverse cropping systems and food sovereignty, potentially jeopardising the food security of local communities (Rosset, 2011; Pingali, 2012).

Corley (2009) estimated that there is sufficient area of derived savanna (anthropogenic grassland with low biodiversity value) and fallow land across the tropics to enable oil palm expansion without loss of valuable natural habitats, even under scenarios of high future consumption. Research in Colombia has found that oil palm expansion on degraded pastures has limited or no negative impacts on faunal diversity and carbon, although bird occupancy of plantations is influenced by the configuration of surrounding natural habitat (e.g. mosaic forest) (Gilroy *et al.*, 2015; Prescott *et al.*, 2016b, 2016a; Quezada *et al.*, 2019). Thus, given the large extent of pasturage in the Neotropics (FAO, 2020b), there appear to be substantial opportunities for the expansion of oil palm with minimal environmental costs. Oil palm expansion in degraded pastures could also provide economic benefits, such as employment and income generation, provided that workers' rights are respected (Boron *et al.*, 2016), although targeting expansion on degraded habitats could stimulate land conflict, because degradation has occurred due to past human activity, and local communities are therefore likely to have stakes in degraded areas (Corley, 2009; Lehmann and Parr, 2016). However, as I discuss in chapter 3, the success of oil palm expansion with low environmental impacts depends on correct identification of higher-biodiversity ecosystems, but current guidance for sustainable oil palm expansion is insufficient to distinguish high-biodiversity, old-growth grassy biomes, where oil palm expansion would drive considerable biodiversity loss (López-Ricaurte *et al.*, 2017), and low-biodiversity, derived savannas (Veldman and Putz, 2011; Parr *et al.*, 2014). Thus, without improved guidance, supporting oil palm expansion into grasslands is risks driving considerable tropical biodiversity loss. Recommending oil palm expansion into degraded habitats more generally could also result in the loss of irreplaceable ecosystems, because tropical dry forests have undergone such extensive degradation that there is no remaining 'primary' habitat (Dinerstein *et al.*, 2017; Hoekstra *et al.*, 2005; Miles *et al.*, 2006), further highlighting the need for appropriate guidance for sustainable development of oil palm plantations, specific to the relevant habitat. In general, expansion of oil palm into degraded habitats and fallow land would prevent regeneration of these habitats, which is crucial for halting biodiversity loss in many ecoregions (Dinerstein *et al.*, 2017), and could risk incentivizing habitat degradation to obtain permissions for conversion to oil palm. Natural regeneration of highly degraded habitats can provide substantial carbon sequestration and biodiversity benefits at low cost (Gilroy *et al.*, 2014; Chazdon *et al.*, 2016), so oil palm expansion at the expense of regeneration would incur long-term carbon and biodiversity costs. There is also a risk that expansion of oil palm plantations in degraded habitats would drive leakage of other commodities, particularly cattle grazing (given that degraded pastures are cited as a potential location for sustainable oil palm expansion), into other natural habitats, thereby failing to reduce net natural habitat and biodiversity loss (Garcia-Ulloa *et al.*, 2012; Gilroy *et al.*, 2015).

Thus, I conclude that oil palm expansion should be targeted on degraded lands, and avoided elsewhere, provided that guidance to correctly distinguish low-biodiversity areas from higher-biodiversity savannas and dry forests is in place. To reduce biodiversity loss and GHG emissions, expansion should be minimised where possible, in order to allow regeneration of habitats that are currently degraded. This would require strong, coordinated governance, across multiple regions and for all land-use types, in order to avoid leakage effects.

5.5 Future oil palm production within planetary boundaries

Demand for vegetable oils as a foodstuff, biofuel and for other uses is increasing, and is expected to continue to do so over coming decades (Corley, 2009; Doelman *et al.*, 2019; Pastor *et al.*, 2019; Searchinger *et al.*, 2019). Given its high yield compared to other vegetable oil crops (Basiron, 2007), oil palm cultivation is highly profitable across much of the tropics (Carrasco *et al.*, 2014; Koh & Wilcove, 2007). Global oil palm production will therefore continue to increase in response to growing demand over coming decades (Corley, 2009; Carrasco *et al.*, 2014). In this section, I discuss how oil palm production could increase sustainably, including under expected climate change.

To meet increasing demand for vegetable oil, global palm oil production could either increase by improving the yield of existing plantations (intensification) or by expanding the area of oil palm cultivation. In the previous sections of this discussion, I have concluded that oil palm expansion should be avoided where possible, to minimize further biodiversity loss and GHG emissions. This is in line with the general paradigm that land sparing (retaining extensive areas of natural habitat) is preferable to land sharing for conserving forest biodiversity (Phalan *et al.*, 2011). Thus, to reduce the competition for land between crops and nature conservation (Smith *et al.*, 2010), crop yield gaps should be minimized (Hunter *et al.*, 2017; Searchinger *et al.*, 2019). However, most of the increase in global palm oil production to date has occurred through expansion of plantations, rather than yield improvements, and there are substantial yield gaps in oil palm cultivation globally, including in industrial plantations (Carter *et al.*, 2007; Basri & Arif, 2009), as I found in chapter 4. Nearly 10% of plantation area in Malaysia consists of oil palm stands over 25 years of age, with consequently reduced yield and high costs of harvesting (Basri & Arif, 2009). Widespread replanting of old oil palm stands would help improve yields (albeit with an initial period of reduced yields from very young palms) without further loss of natural habitat, particularly if improved cultivars were used as the new planting material (Kushairi *et al.*, 2010). Other costs of oil palm production, including fertiliser and labour costs, have been increasing over recent decades, disincentivizing oil palm growers from intensifying production (Basri & Arif, 2009). However, intensifying production by increasing harvesting frequency would substantially increase yields, such as by increasing labour supply or mechanising harvesting, although this would increase plantation management costs (Murphy, 2014). Increased harvesting would likely have some trade-offs for biodiversity and ecosystem functioning, such as by decreasing organic matter inputs to soils (Kotowska *et al.*, 2015; van Straaten *et al.*, 2015; Guillaume *et al.*, 2018), but alternative management practises, such as mulching with empty fruit bunches, could offset this (Tao *et al.*, 2017). In contrast, intensification by increasing chemical fertiliser inputs is likely to have severe negative impacts on soils, GHG emissions and aquatic ecosystems (Conijn *et al.*, 2018; MacDonald *et al.* 2011; Zhang et al., 2015). Thus, there is an urgent need to develop and encourage management practises which support biodiversity, ecosystem functioning and services in plantations, while also supporting high yields (i.e. win-win land-sparing, or sustainable intensification). Overall, there appear to be limited incentives for oil palm growers to intensify production, because of high intensification costs, and because the high yield of oil palm provides high financial returns even when yield gaps are substantial. Thus, to intensify oil palm production, incentives to reduce yield gaps may be necessary, such as increased premium prices for oil palm produced from plantations with low yield gaps. To develop such incentives, there would need to be substantial endorsement from consumers and oil palm buyers, to provide financial incentives to increase sustainable palm oil intensification. Moreover, intensifying oil palm production on existing plantations would not necessarily reduce the financial incentives to continue oil palm expansion (Villoria *et al.*, 2013), again highlighting the need for strong regulation of expansion to improve the sustainability of oil palm agriculture.

Currently, industrial oil palm plantations support very low biodiversity (Fitzherbert *et al.*, 2008; Foster *et al.*, 2011; Barnes *et al.*, 2014; Drescher *et al.*, 2016); and in chapter 2, I demonstrated that conservation set-asides within plantations can help improve AGC and plant diversity in plantations. While the land sparing–land sharing paradigm suggests that there is a strong trade-off between agricultural productivity and biodiversity value of the planted area (Phalan *et al.*, 2011), there is increasing evidence that diversifying crop systems generally improves both yield and biodiversity and ecosystem functioning, although some trade-offs exist in particular contexts (Tamburini *et al.*, 2020). If there are some trade-offs between biodiversity and ecosystem functioning of the oil palm planted area and yield, I expect that both yield and biodiversity could nevertheless increase in many plantations from current levels, because plantations are managed as monocultures with little biodiversity (Fitzherbert *et al.*, 2008; Foster *et al.*, 2011; Barnes *et al.*, 2014; Drescher *et al.*, 2016), yet have substantial yield gaps, largely owing to insufficient harvesting (Murphy, 2014). There is currently limited application of practices to improve the biodiversity of the planted area (i.e. land sharing), but there are ongoing efforts to develop such practises, which could have multiple benefits for biodiversity and ecosystem services, including improved carbon storage, increased organic matter inputs to soils, reduced soil erosion, increased diversity of food and timber products, and improved income stability of smallholder farmers (Bhagwat and Willis, 2009; De Beenhouwer, Aerts and Honnay, 2013; Budiadi *et al.*, 2019). A recent experiment planting patches of timber and fruit trees among oil palms in Sumatra has found that the ‘tree islands’ of oil palm agroforestry improve structural complexity, with likely positive impacts for biodiversity, and also boost oil palm yields, suggesting that there could be substantial potential for boosting the biodiversity of plantations without reductions in yield (Gérard *et al.*, 2017; Zemp *et al.*, 2019; Tamburini *et al.*, 2020). Crop modelling suggests that intercropping of oil palm with cocoa would improve groundwater replenishment and total productivity in comparison to oil palm monoculture, with greater labour efficiency, and improved income security for growers as revenue is not solely dependent on palm oil price (Khasanah *et al.*, 2020). Diversifying the oil palm monoculture would reduce the financial impacts of oil palm pest and disease outbreaks, which are expected to increase over coming years (Paterson *et al.*, 2013), while also reducing the likelihood of outbreaks (Ratnadass *et al.*, 2012). It is also highly likely that incorporating native forest trees in the oil palm planted area would improve its permeability to forest species, facilitating their dispersal and thus improving the connectivity of adjacent forest patches (Bhagwat *et al.*, 2008). Thus, there appears to be substantial potential to diversify plantations, with multiple benefits for environmental sustainability and potential positive impacts on yield. Ongoing development of management practises to increase biodiversity and ecosystem functioning within the oil palm planted area, and their impacts on yield, should be a key research priority.

Over coming decades, climate change will have increasing impacts on oil palm productivity, although the net effects of combined changes in climate are uncertain, as I outlined in chapter 1, and the direct response of oil palm yield to heat stress is unclear, as I found in chapter 4. However, my findings in chapter 4 suggest that increasing drought across many tropical regions is likely to have negative impacts on yield (Barros *et al.*, 2014). In chapter 3, I found that irrigation could be important for improving oil palm yields in partially water-limited locations, where oil palm is likely to expand under ZDCs. Therefore, it appears highly likely that irrigation will become increasingly important for oil palm production over coming years; and it is already widely used in Thailand, South India, and parts of Latin America (do Amaral Teles *et al.*, 2016; Rao, 2013; Silalertruksa *et al.*, 2017). However, irrigation is the primary cause of freshwater consumption globally (Wada *et al.*, 2011), including unsustainable groundwater depletion (Dalin *et al.*, 2017); and many regions face water-scarcity (Wada *et al.*, 2011). Oil palm would require irrigation during periods of low rainfall, coinciding with peak water scarcity (see chapter 3), so regulation of oil palm irrigation is imperative for ensuring that it is sustainable. This would require incorporation of irrigation into environmental impact assessments prior to planting, with particular focus on ensuring the water needs of local communities are not jeopardized, as I discuss in chapter 3. In particular, if oil palm expands into degraded pasture areas such as in the Neotropics, which are typically drier than moist forest regions, and projected to have increasing droughts in future (Barros *et al.*, 2014), irrigation may become increasingly important for maintaining productivity under climate change. There are technologies to improve the sustainability of water withdrawal for irrigation, such as inter-basin water transfers, and to prevent negative impacts of irrigation on soil (such as salinization and waterlogging) and pollution of freshwater courses, but these all incur high costs (Liu *et al*., 2017; Wichelns & Oster, 2006). Given that irrigation is likely to play a key role in food security of many semi-arid regions over coming decades (Liu *et al.*, 2017), water withdrawal for irrigation may be most sustainably used on staple crops, rather than oil palm. The development of national and international protocols for water withdrawal for all crops should be a high priority for improving both food security and agricultural sustainability.

Global demand for food, and particularly for vegetable oils, has risen rapidly over recent decades, and is expected to continue to do so without interventions to reduce consumption (Koh and Lee, 2012; Valin *et al.*, 2014; McKenzie and Williams, 2015; Berners-Lee *et al.*, 2018). However, reducing consumption is critical to ensuring that the global food system can remain within planetary boundaries by 2050 (Cassidy *et al.*, 2013; Bajželj *et al.*, 2014; Berners-Lee *et al.*, 2018). Similarly, reducing consumption of palm oil directly reduces the incentive for oil palm expansion, and consequent biodiversity loss and GHG emissions from land-use change (Koh and Lee, 2012). I conclude that oil palm expansion should be avoided wherever possible (sections 5.3 and 5.4), but improving the yield of existing plantations would not necessarily reduce incentives to continue oil palm expansion (Villoria *et al.*, 2013), so measures to reduce consumption of palm oil, focused on regions of high per-capita oil consumption, are imperative for ensuring future sustainability. This would require shifting consumer and corporate perspectives towards long-term sustainability at the expense of some individual consumption and corporate profits, and could be part of wider changes towards more sustainable diets.

5.6 Conclusions

Zero-deforestation commitments and sustainability certification to reduce the environmental impacts of oil palm expansion are helping to conserve AGC and biodiversity in some contexts, and could therefore inform the development of similar commitments for other tropical commodities, but are currently insufficient to drive a net reduction in the habitat and biodiversity loss from oil palm expansion globally. Crucially, there are a number of pathways for leakage of oil palm expansion and natural habitat loss (between biomes, companies, localities, and commodities), which require strong, coordinated regulation, and are crucial for the validity of certified-sustainable palm oil. In light of the high potential for leakage, and the importance of regeneration of degraded natural habitat for future biodiversity and AGC, avoiding further oil palm expansion is preferable where possible. Thus, the future sustainability of oil palm agriculture requires improving oil palm yield in existing plantations, alongside regulation to steer oil palm expansion into the least-valuable areas for conservation, as well as a reduction in the growing demand for vegetable oils. Within plantations, conservation set-asides should be managed and monitored to ensure successful habitat regeneration and thus long-term benefits for biodiversity and carbon storage; and practises to enhance the biodiversity and ecosystem functioning of the planted area should be applied where possible, particularly when such practises do not present a trade-off with yield. Palm oil sustainability certification and zero-deforestation commitments have developed rapidly, in recent years; and through further coordinated efforts of industry, governments and consumers, the detrimental environmental impacts of oil palm could be substantially reduced over coming decades.

Appendix 1

Conservation set-asides improve carbon storage and support associated plant diversity in certified sustainable oil palm plantations: Supplementary information

Supplementary Information 1.1. Comparison of methods to estimate tree height

To examine potential error introduced by field-derived estimates of tree height (log-log model used to estimate tree height for all stems without an eye estimate of height, from relationship of eye estimates to dbh), and implications for AGC stock values, we compared the field-based estimates of tree height to estimates of tree height using established allometric equations. We estimated the height of all tree stems (i) using a climatic model, based on dbh and a bioclimatic variable representing environmental stress (Chave *et al.*, 2014); and (ii) using a regional model for Southeast Asia, based on dbh (Feldpausch *et al.* 2012), in addition to (iii) the field-derived estimates of tree height using a second-order log-log model (selected because it had the lowest relative standard error of four candidate models relating field-estimated height to dbh; table S1.1). In comparison to the log-log model based on field data, we found that the established allometric models for tree height (climatic and regional) estimated greater tree height values at lower dbh values and considerably lower height values at greater dbh values, in line with existing comparisons of models of tree height for lowland dipterocarp forest in Sabah (fig. S1.2; see plot IDs 49 and 63 in fig. S2 of Sullivan *et al.* (2018a)) (Sullivan *et al.*, 2018a, 2018b). This resulted in slightly higher estimations of AGC in set-asides from allometric models (mean set-aside AGC = 69.1 Mgha^{-1} for climatic height model; 68.4 Mgha^{-1} for regional height model) than the log-log model (mean set-aside AGC = 52.8 Mgha^{-1}), because of the relatively high density of smaller trees in set-asides, although correlation between total plot-level AGC for different methods of tree height estimation was high (*r* = 0.964-0.993; fig. S1.3).

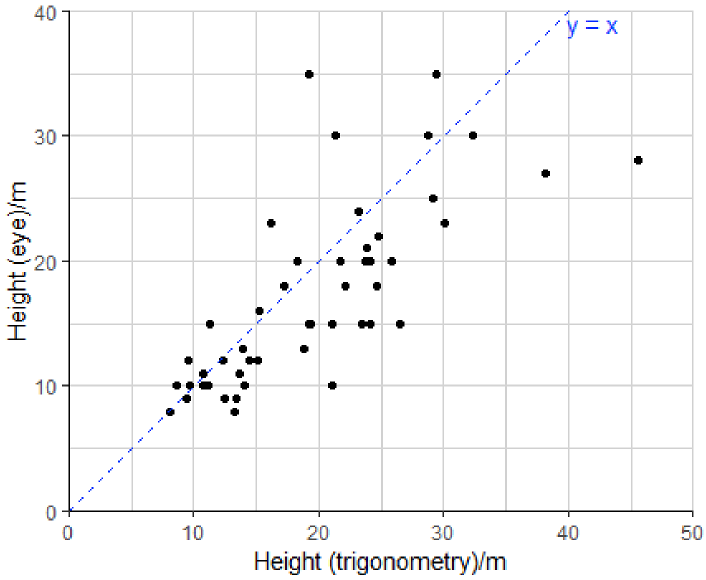


Figure S1.1. Scatterplot of tree height estimates by trigonometry ('tangent method') and by eye (*N* = 50). The dotted line represents equal values for both estimations. The Pearson product-moment correlation of the two estimates is high (*r* = 0.754, *df* = 48, *p* <0.001).

Table S1.1. Candidate models predicting tree height estimated by eye (H) from diameter (DBH), and their residual standard error (RSE). All models and metrics were computed and evaluated using the modelHD function in R package BIOMASS (Réjou-Méchain *et al.*, 2017)**.** We selected the second order log-log model as the top model because it has the lowest relative standard error (RSE). The log-log models include the Baskerville correction to remove bias from back-transformation (Baskerville, 1972).

Model	**Formula**	**RSE**
First order log-log	$\ln(H) = 0.543 + 0.694*\ln(DBH)$	5.55
Second order log-log	$\ln(H) = 2.34 - 0.427*\ln(DBH) + 0.170*\ln(DBH)^2$	5.38
Weibull	$H = 6621*(1-\exp(-(DBH/855931)^{0.796}))$	5.44
Michaelis-Menten	$H = (147*DBH) / (203 + DBH)$	5.55

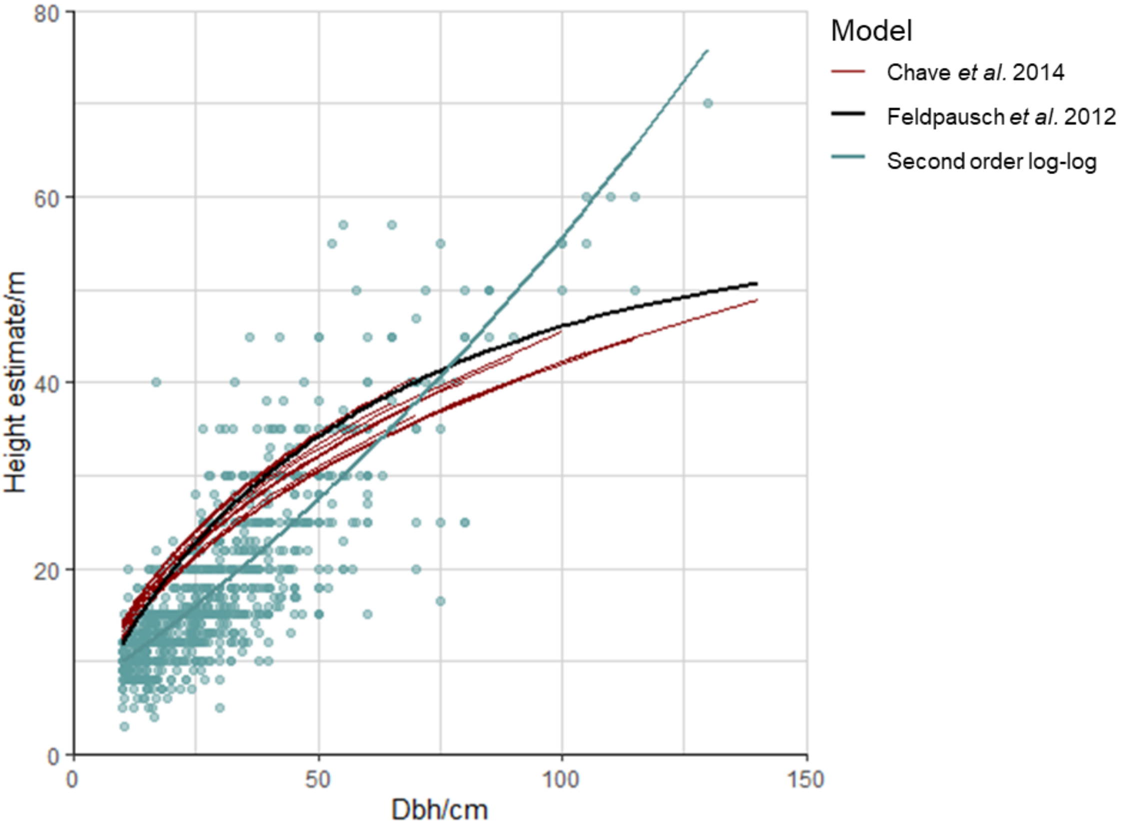


Figure S1.2. Models estimating tree height from dbh. Points show tree height estimated by eye in the field (n = 964, 30.9% of all stems), from which the best dbh-height model was a second order log-log model (table S1.1), which we used to predict the height of all remaining stems (shown in blue). For comparison, we show tree height estimated using a climatic model, equation (6) in Chave *et al.* (2014), based on dbh and a measure of environmental stress at study site coordinates (E, where sites in this study have values of E between -0.17 and -0.034; the variation in the height predictions from this model arises from differences in E between study sites) (shown in red). We also show tree height estimated from dbh using a regional model for Southeast Asia, developed by Feldpausch *et al.* (2012) (shown in black).

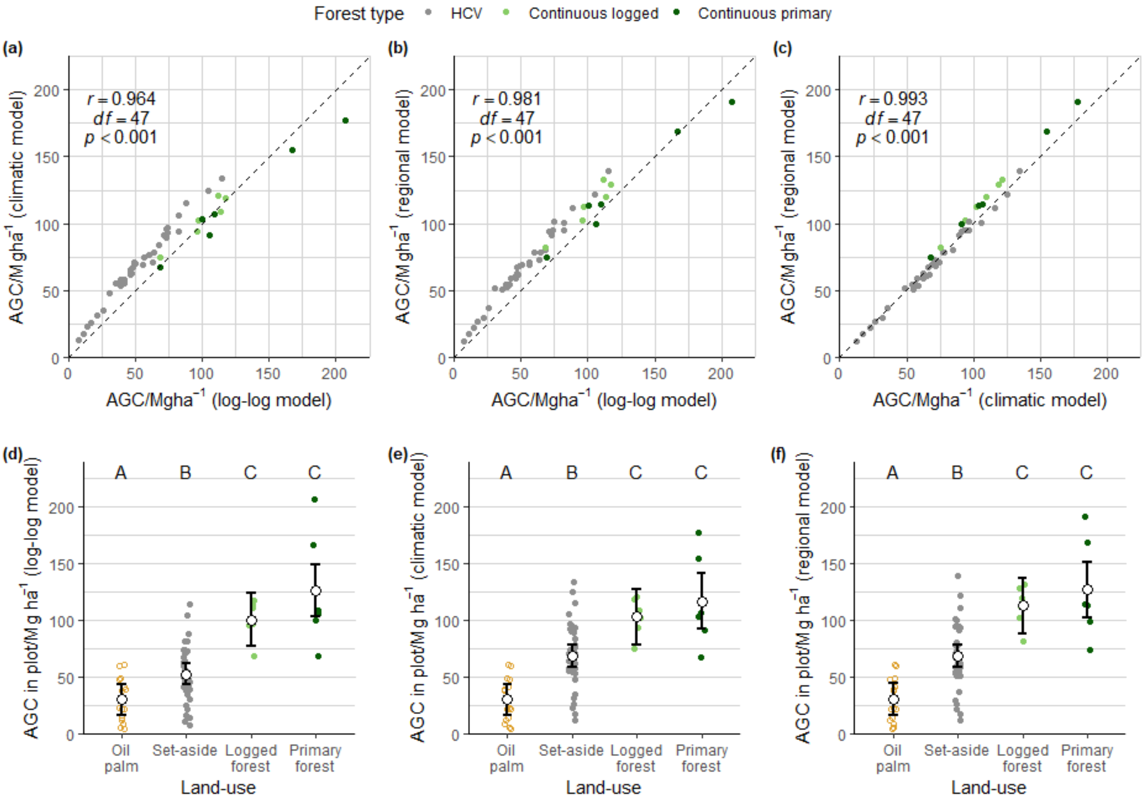


Figure S1.3. Comparison of different methods for estimating tree height (second order log-log model derived from field estimates of tree height by eye, climatic model (Chave *et al.*, 2014) **and Southeast Asian regional model** (Feldpausch *et al.*, 2012)**). (a, b, c) Scatterplots for pairwise comparison of total estimated AGC at each plot using different methods of estimating tree height.** Plots are labelled with pairwise correlations (Pearson product's moment correlation coefficient). Dashed line is y = x. **(d, e, f) Estimated plot-level AGC by land-use type (mean ±95% CI), for all study plots (*n* = 49, closed circles), and estimated time-averaged AGC of oil palm (*n* = 15 simulated data points derived from Carlson *et al.* (2013, 2012), open circles).** Estimates of AGC for field plots comprise AGC of live trees and palms ≥10 cm dbh. Note that (d) is identical to fig. 2.2 in the main article. Different letters (A, B, C) denote significant difference between the land-use types at *p* <0.05, derived from post-hoc Tukey pairwise comparisons (table S1.2); where two land-use types have the same letter, their estimated AGC is not significantly different.

Supplementary Information 1.2. Carbon stocks of deadwood and lianas

In addition to live trees and palms, we surveyed coarse woody debris (CWD, deadwood ≥10 cm diameter) and lianas ≥2 cm dbh and estimated their AGC. These data are not presented in the main text because they contributed only 6.3% of the variation in total AGC (AGC summed for live trees and palms, CWD and lianas) (estimated as the marginal R-squared of a linear mixed-effects model with CWD and liana AGC as a predictor, total AGC as the response, and site as a random effect). Inclusion of CWD and liana AGC in our comparison of AGC in oil palm, set-asides and continuous forest types does not affect our conclusions that set-asides support higher AGC than oil palm, and lower AGC than continuous forest (fig. S1.4; table S1.2).

We surveyed CWD in line with the nested subplot design for live trees and palms (fig. 2.1 main article): in the main plot of 30 m radius, we recorded CWD ≥25 cm diameter; and in the subplot of 20 m radius, we recorded CWD ≥10 cm and <25 cm diameter, following the protocol of Pfeifer *et al.*, (2015), including estimating the height of all standing deadwood by eye (as for living trees). We measured liana dbh of individuals ≥2 cm dbh that entered crowns of live trees recorded in the 20 m and 30 m subplots (i.e. ≥10 cm dbh) following a standard protocol (Gerwing *et al.*, 2006).

We estimated biomass of CWD by multiplying volume and wood density for each item of CWD. We calculated the volume of each piece of CWD as a frustrum of a cone, after estimating the end diameter of standing and hanging CWD using a taper function (Chambers *et al.*, 2000), and we assigned wood density values by state of decay on a five-point scale from Pfeifer *et al.*, (2015). We estimated dead palm biomass in the same way as living palm biomass because palm wood density fluctuates during the first two years of decomposition (Barbosa *et al.*, 2017) (see main article). We estimated liana biomass using a pantropical allometric equation based on dbh (Schnitzer, DeWalt and Chave, 2006). As for live trees and palms, we assumed a carbon content of 47.1% for CWD and liana biomass (Thomas and Martin, 2012).

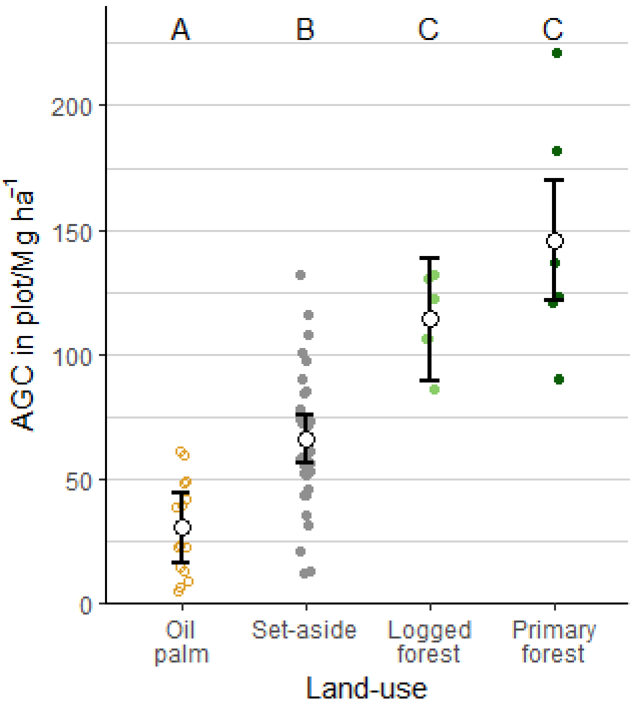


Figure S1.4. Estimated total plot-level AGC by land-use type (mean ±95% CI), for all study plots (*n* = 49, closed circles), and estimated time-averaged AGC of oil palm (*n* = 15 simulated data points derived from Carlson et al. (2013, 2012), open circles). Estimates of AGC for field plots comprise AGC of live trees, palms, CWD and lianas. Different letters (A, B, C) denote significant difference between the land-use types at *p* <0.05, derived from post-hoc Tukey pairwise comparisons (table S1.2); where two land-use types have the same letter, their estimated AGC is not significantly different.

Supplementary Information 1.3. Methods for soil analysis

We collected five topsoil cores in each plot (0-20 cm depth; one core at the plot centre, and four cores 15 m from the centre, in each cardinal direction). We weighed the soil samples before drying (at 50° C) until the weight stabilised; and we calculated gravimetric soil moisture content as the difference between wet and dry weight, divided by the dry weight (from which we calculated the mean of all samples in a plot). After drying, we bulked and thoroughly mixed all five samples for each plot, which we subsampled for analysis at plot level. All soil chemical analyses were conducted at the Forest Research Centre, Sepilok, Sabah. Prior to chemical analysis, we removed stones and root material was removed from the samples, and passed the soil was passed through a 2-mm sieve. We measured pH with a combination of glass-calomel electrode in a 1:2:5 ratio of soil to deionised water. We used water to extract available P, while total P was extracted using the sulphuric acid-hydrogen peroxide procedure described in Allen (1989); and we measured P contents in the extracts and digests using the molybdenum-blue method (Anderson and Ingram, 1993) and read these at 880nm on a spectrophotometer. We further ground the samples through a 0.425-mm sieve for carbon and nitrogen analyses. We measured organic C using the Walkley-Black method, determined total N by dry combustion at 900° C. We calculated the C:N ratio as organic C divided by total N.

Supplementary Information 1.4. Supplementary material for comparison of plot-level AGC between set-asides, continuous forest and oil palm

Table S1.2. Results of post-hoc Tukey pairwise comparisons, following Bayesian linear mixed-effects models of differences in AGC between land-use types. *z*-values and associated *p*-values for pairwise comparison of live tree and palm AGC between land-use types, for tree heights estimated using (a) second-order log-log model from field data, as presented in the main article, (b) climatic model (Chave *et al.*, 2014), (c) regional model for Southeast Asia (Feldpausch *et al.*, 2012); and for (d) total AGC (including lianas and CWD, as well as live trees and palms) with tree heights estimated using the second-order log-log model. The final linear mixed-effects models included land-use type as fixed term and site as random intercept term. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

(a) Log-log model (from field estimates)	**Oil palm**	**Set-aside**	**Logged forest**	**Primary forest**
Oil palm		*z* = 2.75, *p* = 0.028*	*z* = 5.23, *p* <0.001***	*z* = 7.15, *p* <0.001***
Set-aside			*z* = 3.82, *p* <0.001***	*z* = 5.88, *p* <0.001***
Logged forest				*z* = 1.57, *p* = 0.384
Primary forest				

(b) Climatic model	**Oil palm**	**Set-aside**	**Logged forest**	**Primary forest**
Oil palm		*z* = 4.60, *p* <0.001***	*z* = 5.18, *p* <0.001***	*z* = 6.15, *p* <0.001***
Set-aside			*z* = 2.59, *p* = 0.0444*	*z* = 3.62, *p* = 0.0015**
Logged forest				*z* = 0.783, *p* = 0.855
Primary forest				

(c) Regional model	**Oil palm**	**Set-aside**	**Logged forest**	**Primary forest**
Oil palm		*z* = 4.43, *p* <0.001***	*z* = 5.80, *p* <0.001***	*z* = 6.79, *p* <0.001***
Set-aside			*z* = 3.35, *p* = 0.0047**	*z* = 4.40, *p* <0.001***
Logged forest				*z* = 0.804, *p* = 0.845
Primary forest				

(d) Total AGC (including lianas and CWD)	**Oil palm**	**Set-aside**	**Logged forest**	**Primary forest**
Oil palm		*z* = 4.25, *p* <0.001***	*z* = 5.99, *p* <0.001***	*z* = 8.25, *p* <0.001***
Set-aside			*z* = 3.66, *p* = 0.0013**	*z* = 6.08, *p* <0.001***
Logged forest				*z* = 1.84, *p* = 0.243
Primary forest				

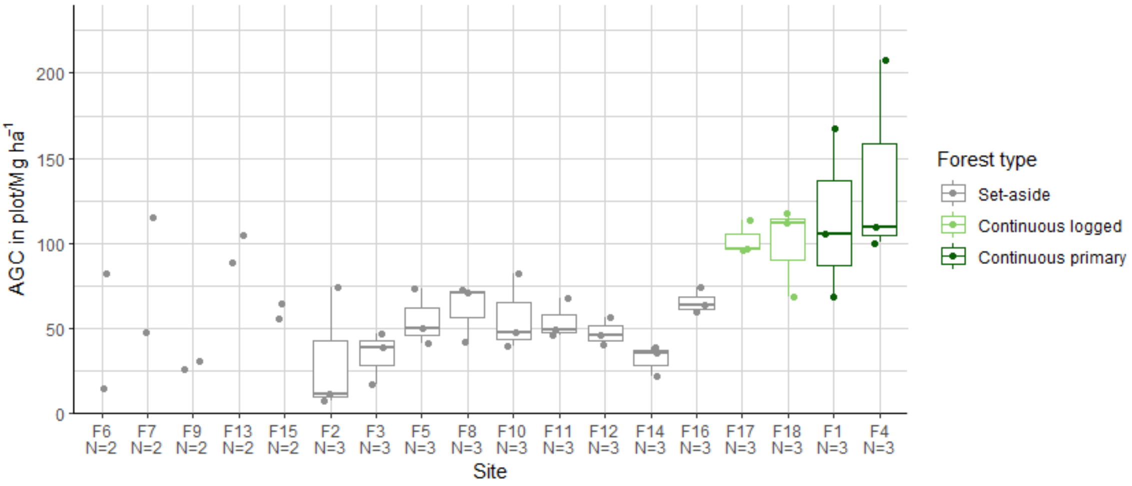


Figure S1.5. Site-level variation in estimated AGC of all study plots. Site codes (Fx) are followed by number of plots in each site on the x axis labels; set-aside sites with only two plots are on the left. Boxplot central bars show the median; lower and upper hinges show the first and third quartiles respectively, and whiskers extend to the maximum and minimum values.

Supplementary Information 1.5. Supplementary material for comparison of vegetation structure among forest types

Table S1.3. Results of post-hoc Tukey pairwise comparisons, following linear mixed-effects models of differences in vegetation structure between forest types. Forest type significantly predicted log-transformed mean dbh (final model fixed effects were forest type and size class with interaction term; χ^2 = 654.5, p <0.001) and log-transformed stem density (final model fixed effects were forest type and size class with interaction term; χ^2 = 564.5, p <0.001) but not mean wood density (final model fixed effect was size class; χ^2= 41.2, p <0.001). For stem density we conducted the log-transformation on n+1 stems ha^{-1} to include a single zero value. We conducted post-hoc Tukey pairwise comparisons for the models in which forest type was significant only (mean dbh and stem density), on models fitted with a single categorical predictor formed from combining levels of forest type and size class.

		Mean dbh (cm)		
		Set-aside	**Logged forest**	**Primary forest**
Saplings	**Set-aside**		z = -2.02, p = 0.498	z = 0.943, p = 0.989
	Logged forest			z = 2.26, p = 0.339
	Primary forest			
Medium trees	**Set-aside**		z = -0.670, p = 0.999	z = 0.485, p = 1.00
	Logged forest			z = 0.879, p = 0.993
	Primary forest			
Large trees	**Set-aside**		z = 4.12, p = 0.0012 **	z = 7.61, p <0.001 ***
	Logged forest			z = 2.66, p = 0.143
	Primary forest			

		Stem density (n ha^{-1})		
		Set-aside	**Logged forest**	**Primary forest**
Seedlings	**Set-aside**		z = 2.15, p = 0.536	z = 4.52, p <0.001 ***
	Logged forest			z = 1.80, p = 0.748
	Primary forest			
Saplings	**Set-aside**		z = 0.840, p = 0.999	z = 0.767, p = 0.999
	Logged forest			z = 0.056, p = 1.00
	Primary forest			

Medium trees	**Set-aside**		*z* = -0.820, *p* = 0.999	*z* = -2.16, *p* = 0.530
	Logged forest			*z* = -1.02, *p* = 0.996
	Primary forest			
Large trees	**Set-aside**		*z* = 1.93, *p* = 0.700	*z* = 0.667, *p* = 0.999
	Logged forest			*z* = -0.958, *p* = 0.998
	Primary forest			

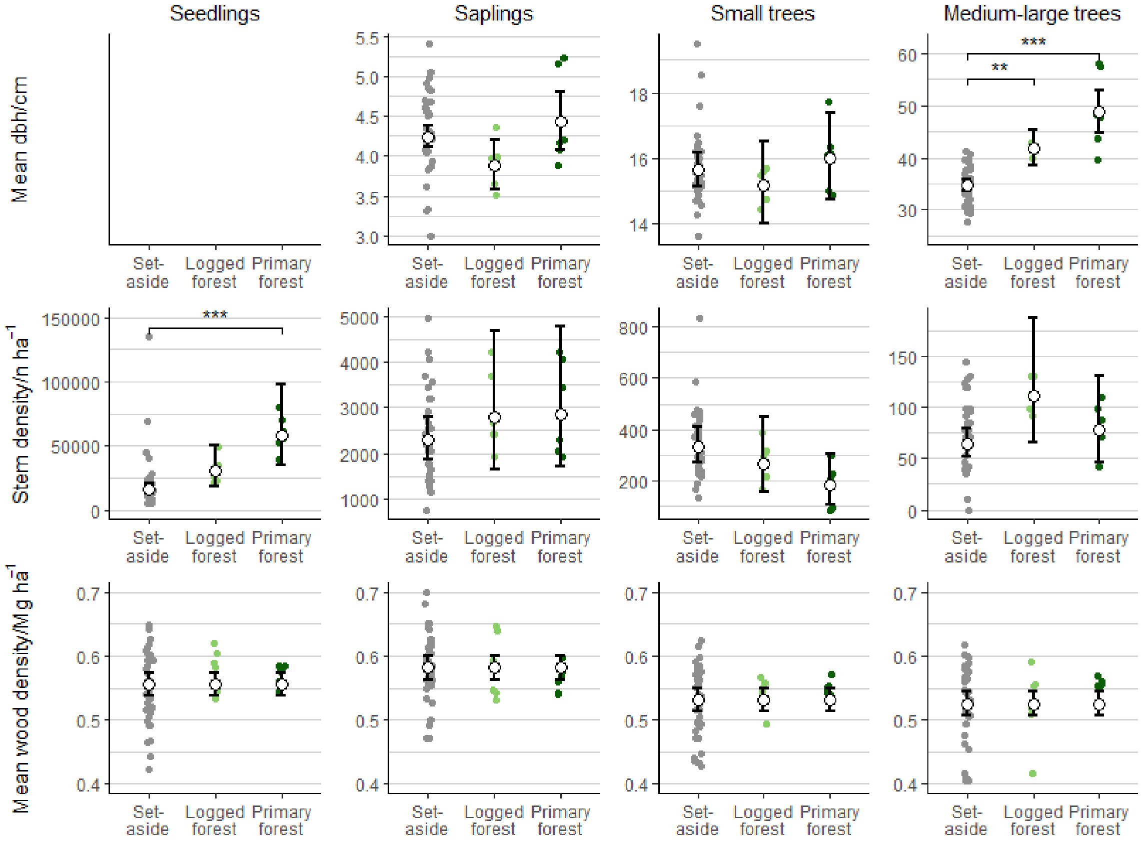


Figure S1.6. Comparison of mean dbh, stem density and mean wood density between forest types (set-asides, continuous logged forest and continuous primary forest), for seedlings (<2 cm dbh), saplings (≥2 cm and <10 cm dbh), small trees (≥10 cm and <25 cm dbh) and medium-large trees (≥25 cm dbh), for all study plots (*N* = 49). Forest type significantly predicted log-transformed mean dbh (final model fixed effects were forest type and size class with interaction term; χ^2 = 654.5, *p* <0.001) and log-transformed stem density (final model fixed effects were forest type and size class with interaction term; χ^2 = 564.5, *p* <0.001) but not mean wood density (final model fixed effect was size class; χ^2= 41.2, *p* <0.001). We have back-transformed model predictions for plotting, when variables were log-transformed in the LMEs. Note differences in y axes among size classes for mean dbh and stem density plots. Significance bars denote results of post-hoc Tukey pairwise comparisons (table S1.3). ** *p* <0.01; *** *p* <0.001

Supplementary Information 1.6. Supplementary material for analysis of the drivers of variation in set-aside AGC

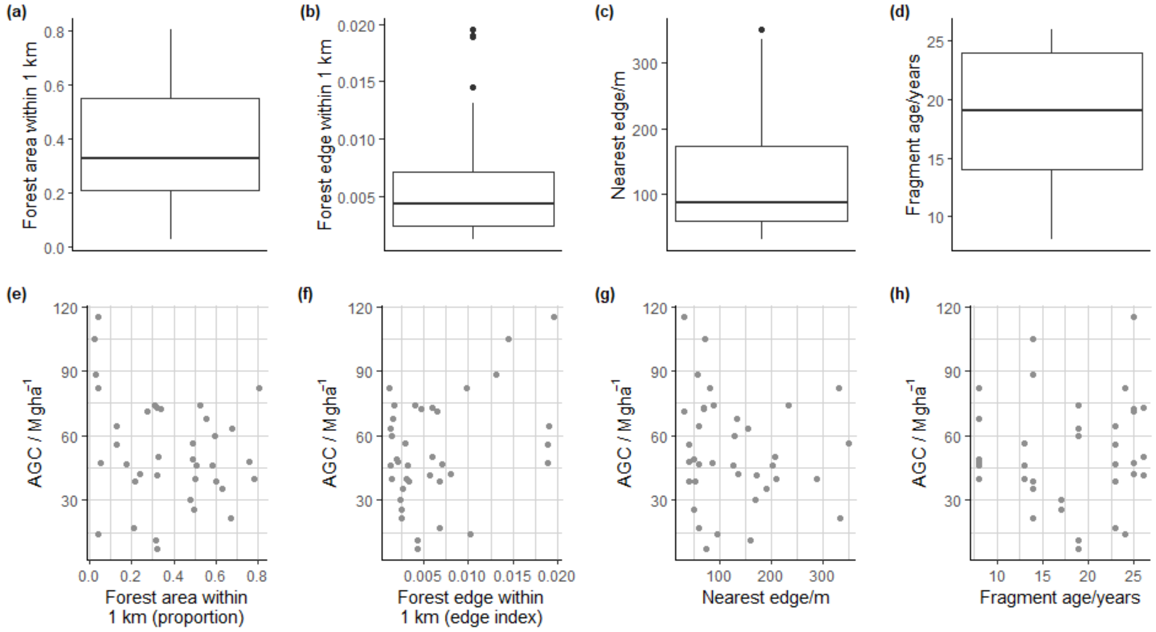


Figure S1.7. Predictors for assessing the effects of degree of forest fragmentation on AGC in set-asides: (a-d) boxplots of values for all plots in set-asides; (e-h) scatterplots with AGC in live trees and palms for all plots in set-asides. Forest area and forest edge index are shown for buffer sizes of 1 km from the plot centre (although we ran models with a range of buffer sizes), and total forest area is expressed as a proportion. These four predictors were intercorrelated so we combined them in a principal components analysis (figs. S1.8, S1.9; table S1.4). Boxplot central bars show the median; lower and upper hinges show the first and third quartiles respectively, and whiskers extend to the maximum and minimum values within 1.5*IQR of the hinges; outliers greater than 1.5*IQR from the hinges are plotted as individual points.

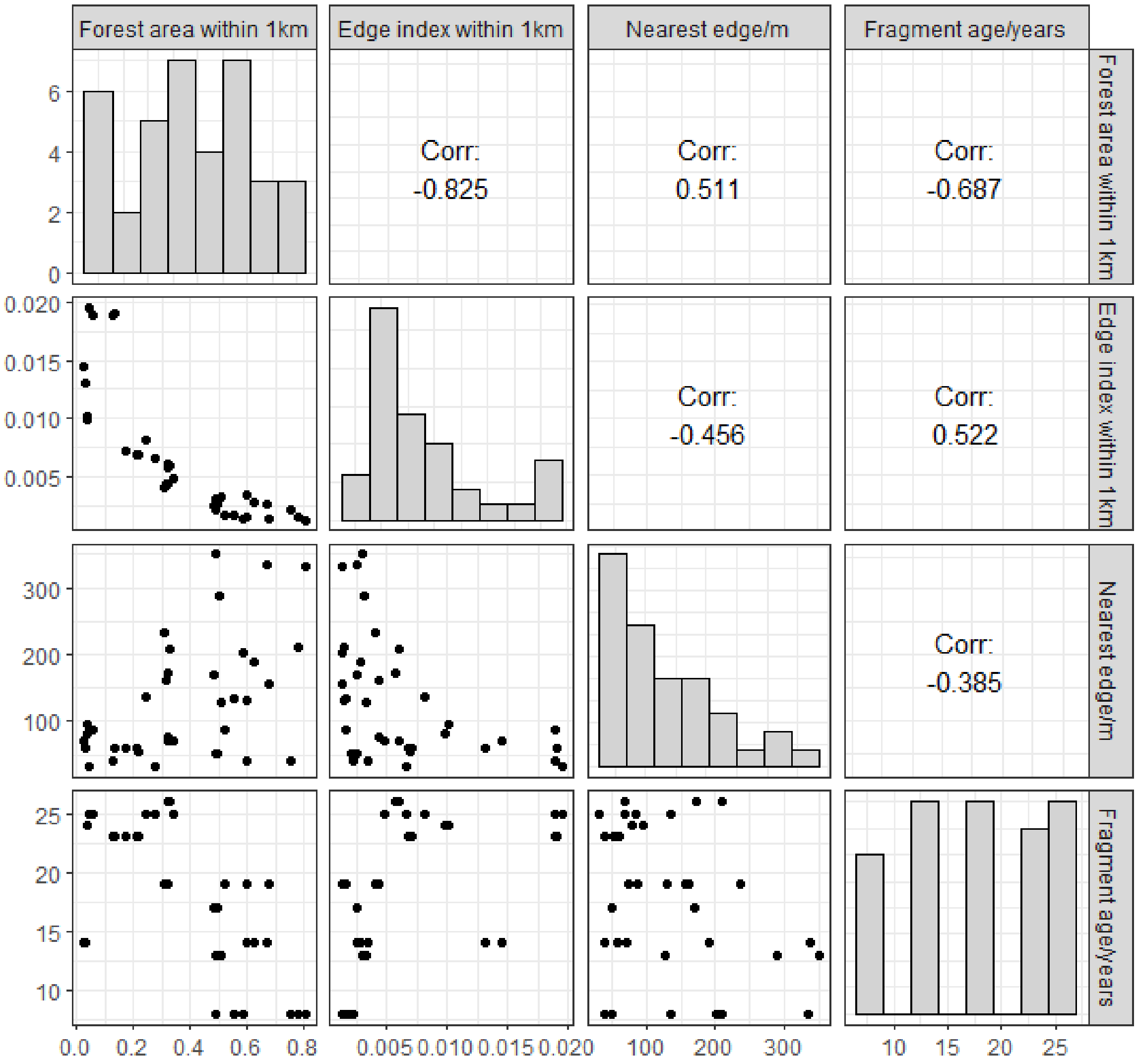


Figure S1.8. Pairwise scatterplots and Pearson correlation coefficients of predictors for assessing the effects of degree of forest fragmentation on AGC in set-asides. We calculated forest area as the proportion of landscape within 1 km buffer which is forest; and forest edge index as the number of 5 m-resolution grid cells containing forest–oil palm boundary, divided by total forest area; greater values indicate more edge, i.e. a greater proportion of the forest is adjacent to oil palm. Owing to high intercorrelation between these predictors (note that whilst we would expect forest area, edge index and distance to nearest edge to be intercorrelated, fragment age was negatively correlated with forest area owing to the field sites available for sampling), we combined them using principal components analysis and extracted the first principle component as a 'fragmentation index' (fig. S1.9).

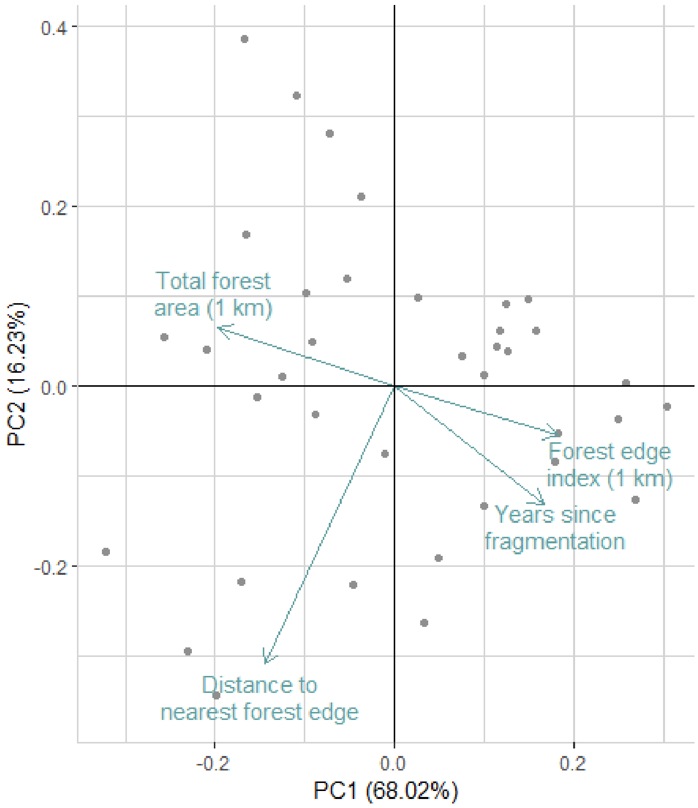


Figure S1.9. Scatterplot of PC1 and PC2 (scaled to sum of squares = 1) for the PCA of landscape characteristics for set-asides, with correlations of component variables. We conducted this PCA using buffer sizes of 0.2 - 2 km for forest area and forest edge index; the ordination for buffer sizes of 1 km are shown in this plot. We use PC1 as a ‘fragmentation index’, where higher values represent a greater degree of forest fragmentation (table S1.4).

Table S1.4. PCAs of the effects of degree of forest fragmentation (where we extracted PC1 as a fragmentation index). We conducted this analysis for a range of buffer sizes for total forest area and edge index, to demonstrate that varying the buffer size does not affect the results and hence our conclusions.

Buffer size (m)	**Proportion of variance explained by PC1**	**Correlation of PC1 and components**			
		Total forest area in buffer	**Edge index in buffer**	**Nearest edge**	**Years since fragmentation**
200	0.693	-0.566	0.565	-0.517	0.306
500	0.698	-0.562	0.543	-0.483	0.395
1000	0.680	-0.567	0.527	-0.415	0.479
1500	0.653	-0.560	0.524	-0.384	0.513
2000	0.635	-0.565	0.519	-0.362	0.529

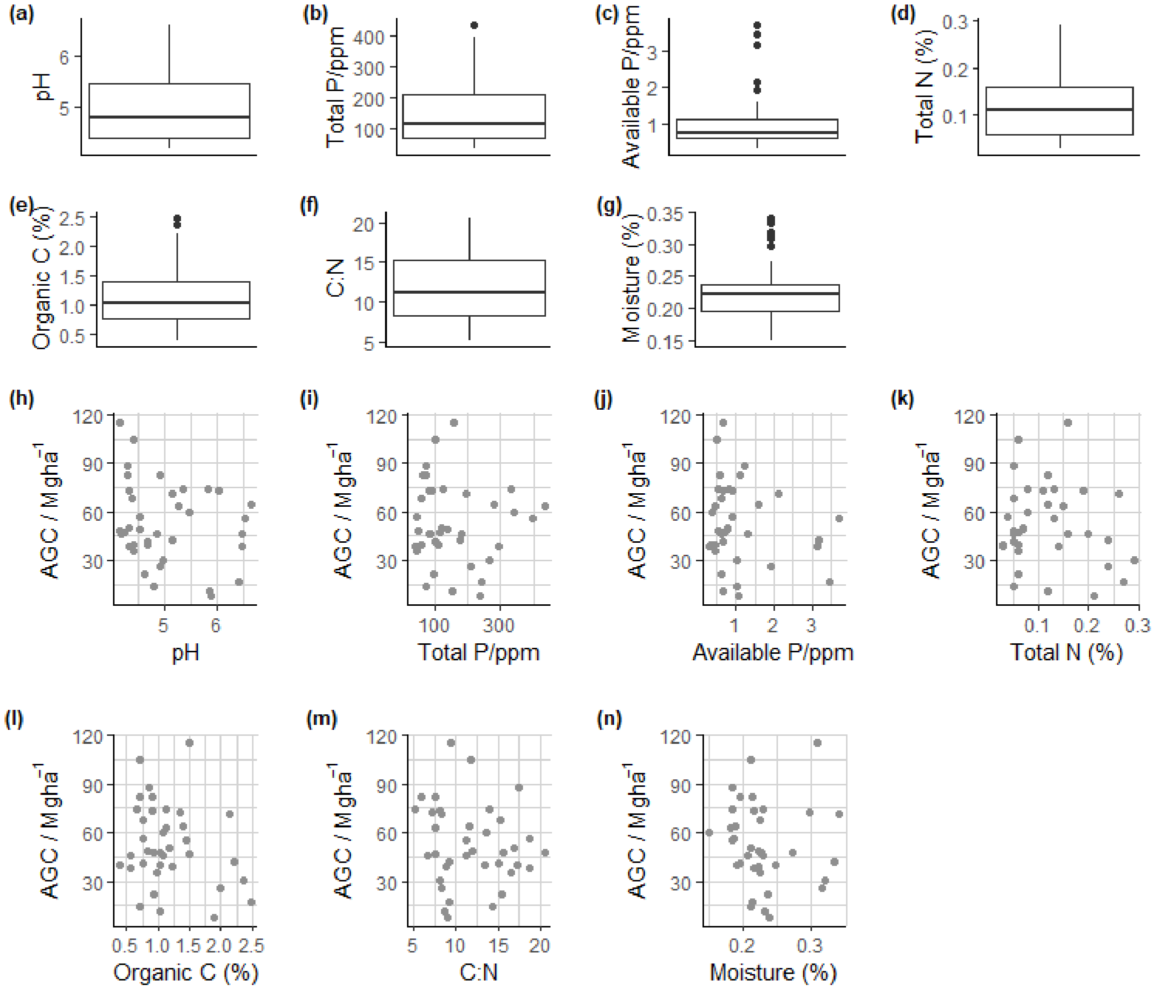


Figure S1.10. Predictors for assessing the effects of soil parameters on AGC in set-asides: (a-d) boxplots of values for all plots in set-asides; (e-h) scatterplots with AGC in live trees and palms for all plots in set-asides. These seven predictors were intercorrelated so we combined them in a principal components analysis (figs. S1.11, S1.12; table S1.5). Boxplot central bars show the median; lower and upper hinges show the first and third quartiles respectively, and whiskers extend to the maximum and minimum values within 1.5*IQR of the hinges; outliers greater than 1.5*IQR from the hinges are plotted as individual points.

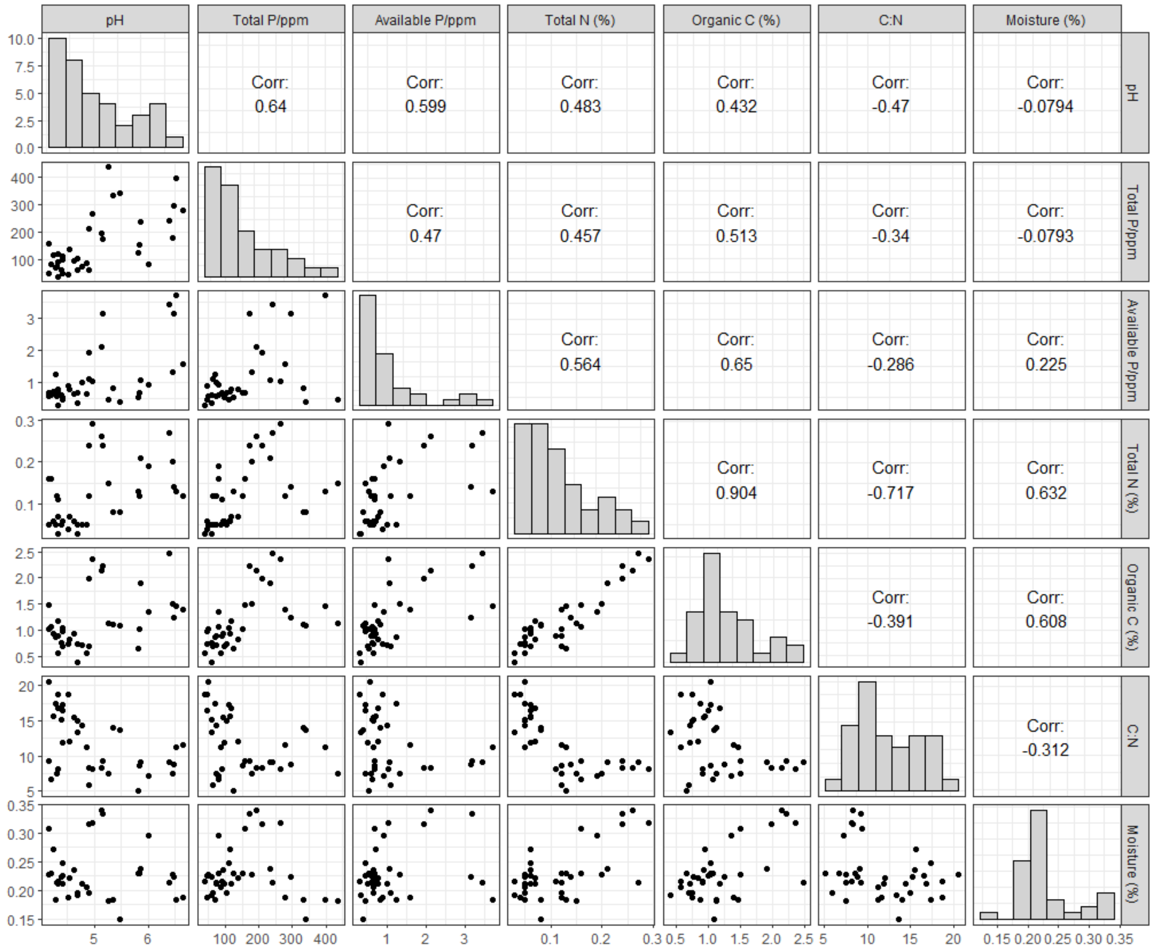


Figure S1.11. Pairwise scatterplots and Pearson correlation coefficients of predictors for assessing the effects of soil parameters on AGC in set-asides. Owing to intercorrelation between these predictors, we combined them using principal components analysis and extracted the first and second principle components as major gradients in soil nutrients and moisture (fig. S1.12).

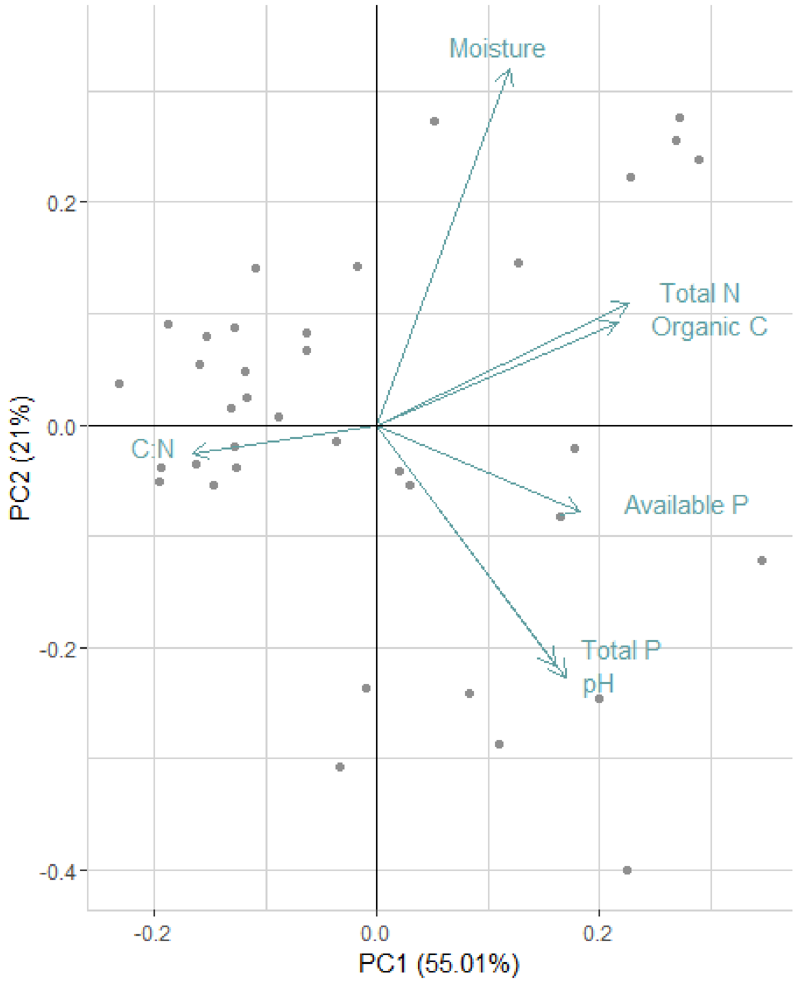


Figure S1.12. Scatterplot of PC1 and PC2 (scaled to sum of squares = 1) for the PCA of soil parameters of plots in set-asides, with correlations of component variables. We use PC1 and PC2 as major gradients in soil nutrients and moisture (table S1.5).

Table S1.5. Correlation of individual soil parameters and soil PC1 and PC2.

Principle component (PC)	**Correlation of PC and components**						
	pH	**Total P**	**Available P**	**Total N**	**Organic C**	**C:N**	**Moisture**
PC1 (explained 55% variance)	0.355	0.335	0.382	0.476	0.453	-0.346	0.251
PC2 (explained 21% variance)	-0.475	-0.453	-0.164	0.229	0.193	-0.053	0.671

Table S1.6. Results of GAMMs of drivers of variation in set-aside AGC. We compared the impact of using 5 different buffer sizes for calculating the fragmentation index, and removed all non-significant terms to derive the final model (which does not include fragmentation). All variables were scaled for model computation. All models included site as a random effect. * $p < 0.05$

Full model, 200 m buffer size used for calculating fragmentation index

Adjusted $R^2 = 0.151$; log likelihood (LMM) = -153.5 (df = 8)

Fixed effects	**Estimate**	**Standard error**	***t*-value**	***P* (>|*t*|)**
Fragmentation index (200 m)	7.29	4.40	1.66	0.108
Soil PC1	-5.06	4.46	-1.13	0.267
Soil PC2	3.09	4.15	0.75	0.461
Slope	-1.37	4.31	-0.32	0.754
Smoother		**Effective d.f.**	***F***	***p***
Elevation		0.768	0.096	0.102

Full model, 500 m buffer size used for calculating fragmentation index

Adjusted $R^2 = 0.112$; log likelihood (LMM) = -167.2 (df = 8)

Fixed effects	**Estimate**	**Standard error**	***t*-value**	***P* (>|*t*|)**
Fragmentation index (500 m)	8.43	4.41	1.91	0.416
Soil PC1	-5.07	4.56	-1.11	0.275
Soil PC2	3.22	4.12	0.781	0.441
Slope	-0.538	4.36	-0.12	0.90
Smoother		**Effective d.f.**	***F***	***p***
Elevation		1.05	0.123	0.0531

Full model, 1000 m buffer size used for calculating fragmentation index

Adjusted $R^2 = 0.118$; log likelihood (LMM) = -167.5 (df = 8)

Fixed effects	**Estimate**	**Standard error**	***t*-value**	***P* (>|*t*|)**
Fragmentation index (1000 m)	6.58	4.30	1.53	0.136
Soil PC1	-5.07	4.56	-1.11	0.275
Soil PC2	3.22	4.12	0.781	0.441
Slope	-0.538	4.36	-0.12	0.90
Smoother		**Effective d.f.**	***F***	***p***
Elevation		1.05	0.123	0.0531

Full model, 1500 m buffer size used for calculating fragmentation index

Adjusted R^2 = 0.104; log likelihood (LMM) = -167.9 (df = 8)

Fixed effects	**Estimate**	**Standard error**	***t*-value**	***P* (>|*t*|)**
Fragmentation index (1500 m)	4.91	4.31	1.14	0.264
Soil PC1	-4.10	4.57	-0.90	0.376
Soil PC2	3.53	4.23	0.84	0.410
Slope	-0.80	4.42	-0.18	0.858
Smoother		**Effective d.f.**	***F***	***p***
Elevation		1.16	0.135	0.043 *

Full model, 2000 m buffer size used for calculating fragmentation index

Adjusted R^2 = 0.099; log likelihood (LMM) = -168.1 (df = 8)

Fixed effects	**Estimate**	**Standard error**	***t*-value**	***P* (>|*t*|)**
Fragmentation index (2000 m)	4.20	4.32	0.97	0.338
Soil PC1	-3.70	4.56	-0.81	0.423
Soil PC2	3.58	4.28	0.84	0.409
Slope	-0.89	4.45	-0.20	0.843
Smoother		**Effective d.f.**	***F***	***p***
Elevation		1.21	0.139	0.042 *

Final model (non-significant terms removed at *p* >0.05)

Adjusted R^2 = 0.15; log likelihood (LMM) = -169.2 (df = 4)

Fixed effects	**Estimate**	**Standard error**	***t*-value**	***P* (>|*t*|)**
-	-	-	-	-
Smoother		**Effective d.f.**	***F***	***p***
Elevation		1.25	0.14	0.0385 *

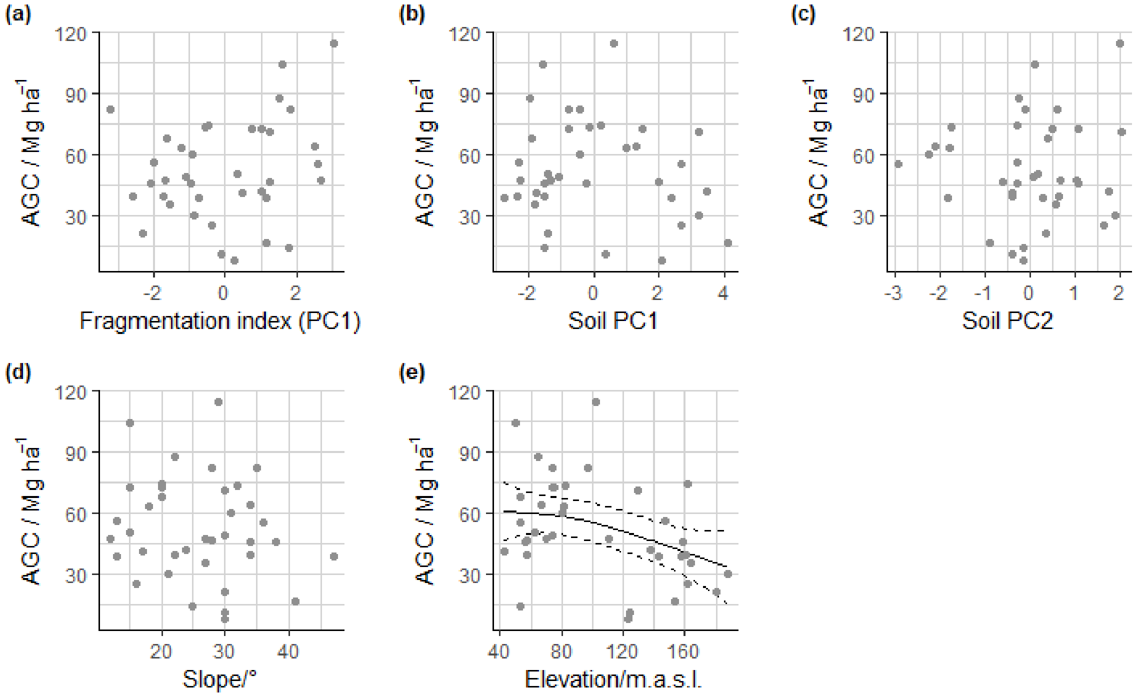


Figure S1.13. GAMM results testing drivers of variation in live tree and palm AGC in plots in set-asides. (a, b, c, d) Fixed effects (fragmentation index, soil PCs and slope). **(e)** Elevation smoother fitted with a penalized cubic spline. Live tree and palm AGC estimates (solid lines) ± 95% CIs (dashed lines) are shown for elevation, which was the only term included in the final model as the other variables were not significant (table S1.6).

Appendix 2

Zero-deforestation palm oil could threaten tropical grassy and dry forest biomes: Supplementary Information

Overview

This document provides the supplementary information for the methods and results presented in chapter 3 ‘Zero-deforestation palm oil could threaten tropical grassy and dry forest biomes’. In Supplementary Information 2.1, we present methodological details of modelling oil palm suitability (selection of predictors, model evaluation, selection and thresholding of oil palm suitability models, and deriving estimates of oil palm yield from model outputs), to support the main text Methods (it is expected that the main text Methods would be read prior to this document). In Supplementary Information 2.2, we present methodological details of biome classification and a comparison of biome vegetation structure, also to support the main text Methods. In Supplementary Information 2.3 and 2.4, we present sensitivity analyses of our rainfed and irrigated oil palm suitability projections respectively, to the choice of oil palm suitability threshold, and to the choice of thresholds of woody vegetation structure determining protection under zero-deforestation commitments. These sections thus explore uncertainties around our results of suitable areas for oil palm expansion under zero-deforestation commitments that are presented in the main article. In Supplementary Information 2.5, we present sensitivity analyses of the results of the potential impacts of zero-deforestation oil palm expansion on biodiversity (ecoregion-level suitability for expansion and impacts on vertebrates) presented in the main article, to suitability for irrigated oil palm (as opposed to rainfed, which is presented in the main article) and to the choice of thresholds of woody vegetation structure determining protection under zero-deforestation commitments.

Supplementary Information 2.1: additional methodological details for oil palm suitability models

Selection of climatic predictors of oil palm suitability

We selected five climatic predictors known to correlate with oil palm growth and yield (Tinker and Corley, 2015): mean annual temperature (MAT, °C), minimum temperature of the coldest month (Tmin, °C), mean annual precipitation (MAP, mm), an annual moisture index (AMI), and maximum water deficit (MWD, mm). We downloaded three of these (MAT, Tmin and MAP) from WorldClim, calculated AMI as the ratio of mean annual precipitation to mean annual potential evapotranspiration (PET, calculated according to the Hargreaves Equation (Hargreaves and Allen, 2003; Zomer *et al.*, 2008), and we calculated MWD as the greatest cumulative deficit in mean monthly rainfall, where a deficit is a month with rainfall < monthly PET, representing the length and severity of dry season (Platts *et al.*, 2010). Some of these predictors were inter-correlated (table S2.1), so we ran models with two uncorrelated predictors, Tmin and MWD, which represent the most strongly limiting climatic factors for oil palm growth and yield (Tinker and Corley, 2015).

Table S1. Inter-correlation of the five climatic predictors, calculated using Spearman's Rho, with *r* > 0.7 (shown in bold) indicating high inter-correlation. The inter-correlation shown are for the dataset used in the final model (see below), but were similar across all datasets used in model calibration.

	MAT	**Tmin**	**MAP**	**MWD**	**AMI**
MAT	1				
Tmin	**0.862**	1			
MAP	0.164	0.394	1		
MWD	0.038	-0.230	**-0.811**	1	
AMI	0.0857	0.352	**0.972**	**-0.812**	1

Evaluation of oil palm suitability models

To obtain a measure of model transferability, indicating model accuracy during spatial prediction, we calculated the moving-window Continuous Boyce Index (Hirzel *et al.*, 2006) for cross-validation, using the function *ecospat.boyce* in the R package 'ecospat' version 3, by training each model on two out of three spatially distinct portions of the data (Americas, Africa and Asia/Australasia), and testing it on the remaining portion. As rainfall and temperature distributions differ between these continents (see fig. S2.1 for distribution of climate values at oil palm mills in each continent), this provides a test of model performance when predicted to novel climatic environments from the training data.

For evaluation of the full models, we compared our model predictions to a largely-independent dataset of oil palm plantations in 23 countries (Harris, Goldman and Gibbes, 2019). We rasterised these polygons of oil palm plantations to the resolution of our model outputs (5') before converting to points, and removed potentially irrigated locations in using the same methods as for the training data of oil palm mills (we excluded all locations within 10km of non-zero water withdrawal for irrigation (Sutanudjaja *et al.*, 2018) and in regions with widespread irrigation of oil palm (Silalertruksa *et al.*, 2017); see Methods for oil palm presence locations in main article). To assess unclassified (i.e. continuous model outputs) full model performance, we calculated the moving window Continuous Boyce Index (Hirzel *et al.*, 2006) as for the cross-validation, testing our continuous suitability predictions against these oil palm plantations (Harris, Goldman and Gibbes, 2019) and 50,000 randomly selected background points. The Continuous Boyce Index represents the correlation between the ratio of predicted to expected presence points (for a given suitability value or bin, the ratio of presences predicted by the model to the number of points expected to have the suitability value given chance alone, i.e.

based on the relative area of habitat that has the suitability value of interest) and the projected suitability values (Hirzel *et al.*, 2006). For low projected suitability values, a good model has a low ratio of predicted to expected presence points; and for high projected suitability values, a good model has a high ratio of predicted to expected presence points; and so the relationship between these provides a measure of model performance. The Continuous Boyce Index can have values ranging from -1 to 1 (where negative values indicate an incorrect model, that tends to predict absences in locations of testing presence data; 0 indicates a model similar to chance alone; and positive values indicate a good model, that predicts presences in locations of testing presence data), and is highly correlated with metrics for evaluating species distribution models that incorporate both presence and absence data, such as Area Under the Curve (AUC) of false-positive to true-positive ratios (Hirzel *et al.*, 2006).

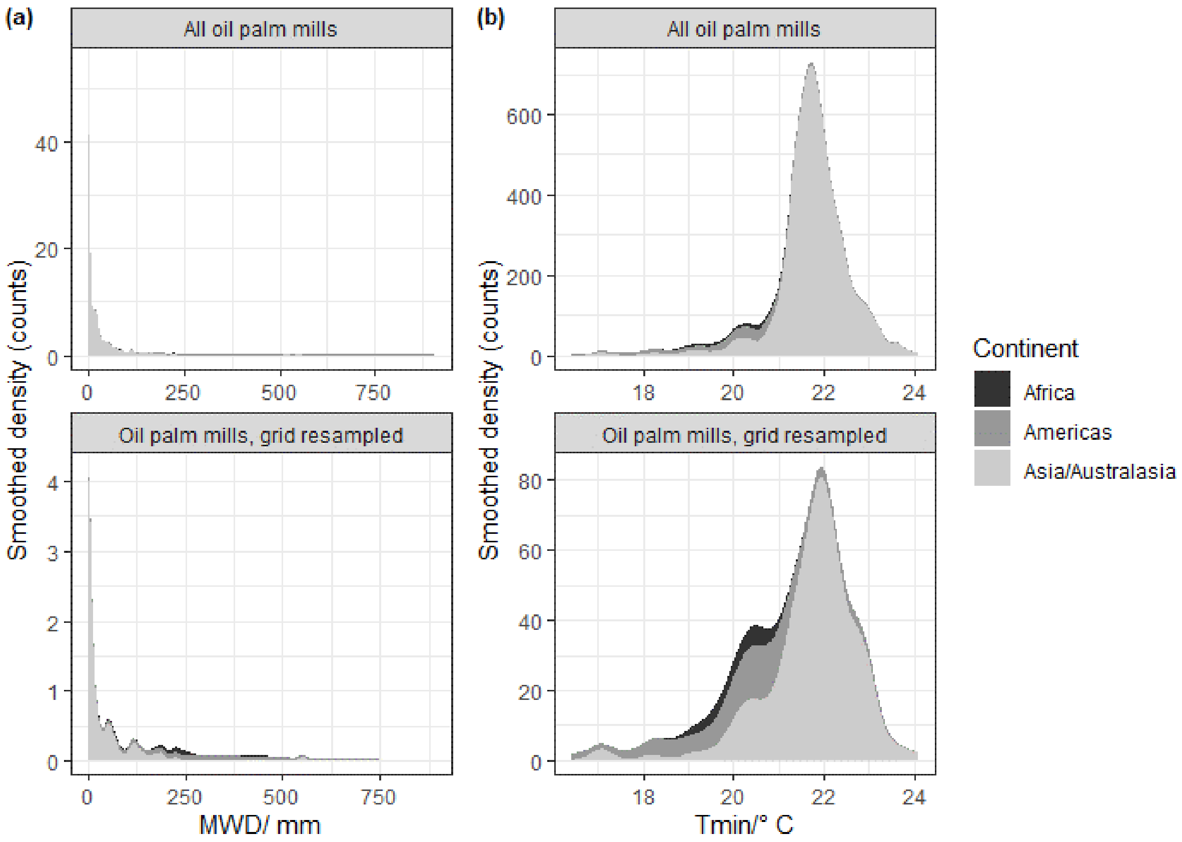


Figure S2.1. Distribution of temperature and rainfall values for (a) full oil palm mill dataset and (b) systematically resampled oil palm mill dataset (reducing spatial autocorrelation by resampling at a coarse grid-cell resolution of 1°, or ~111 km at the Equator). Climate values at oil palm mill locations in Asia/Australasia dominate the overall distribution, owing to the high number of mills in Indonesia and Malaysia. Grid resampling reduces this, which leads to better model predictive power for (see below).

Selection of best model

We selected the top model using the following criteria: high full model performance (high continuous Boyce Index score); high transferability to new environments (consistently high continuous Boyce Index scores when trained and tested on spatially distinct portions of the data); and relatively high importance of both climatic predictors (to avoid domination of the model by a single predictor) (VanDerWal *et al.*, 2009).

We found that all models accurately predicted suitability for oil palm (full-model continuous Boyce Index 0.762-0.914 when tested with largely-independent oil palm plantation locations (Harris, Goldman and Gibbes, 2019)), but that models tended to vary in their transferability (cross-validation Boyce Index 0.004-0.919) and relative variable importance (fig. S2.2). Models with correction for spatial autocorrelation (by grid resampling the training data) had higher transferability (cross-validation continuous Boyce Index) than models without the correction, and higher full model accuracy (full model continuous Boyce Index). Of the models with correction for spatial autocorrelation, smaller background buffer sizes conferred greater transferability, with the highest transferability for the model with 500 km background buffer size, and smaller background buffer sizes also conferred greater full model performance (fig. S2.2). We therefore selected the model with 500 km background buffer size and correction for spatial autocorrelation as the best model, which has a high full-model score (continuous Boyce Index, 0.900), the highest transferability (continuous Boyce Index 0.546-0.892 for cross-validation), and is not dominated by a single climatic predictor (fig. S2.2).

Whilst the lowest cross-validation continuous Boyce Index score for our selected best model is relatively low (0.546), we expect this score to represent a conservative estimate of full model transferability, because the most highly-scoring cross-validations for this model were trained on data which spanned a range of climate space close to that of the full model (fig. S2.3; also see fig. S2.1 for differences in distributions of climate values at mill locations in each continent). We therefore expect the full model to have transferability similar to its higher cross-validation scores (0.846, 0.892).

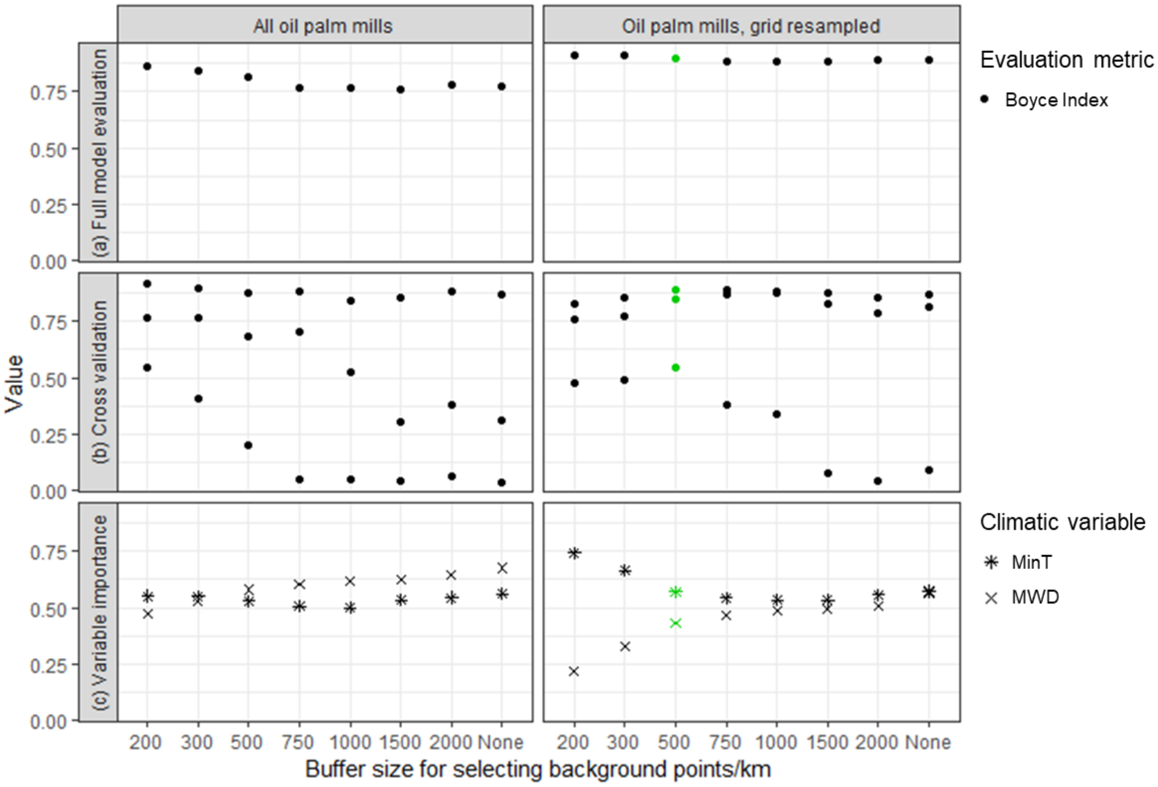


Figure S2.2. Evaluation scores for metrics assessing prediction accuracy of full oil palm suitability models, for varying background point selection method: for models using full oil palm mills dataset, and correcting for spatial autocorrelation by resampling at a coarse grid-cell resolution (1°, or ~111 km at the Equator). (a) Full model evaluation (continuous Boyce Index), where all models were trained on oil palm mills (World Resources Institute *et al.*, 2018), and tested on global plantations data (Harris, Goldman and Gibbes, 2019) (see Methods in main text) using the continuous Boyce Index, where 1 indicates a perfect score (the distribution of predicted presences follows that of the testing presences) (Hirzel *et al.*, 2006). **(b) Continental cross-validation scores (continuous Boyce Index),** where each model was trained on data for two continents only and tested on data for the third withheld continent. Consistent high scores indicate transferability of a model into new environments. **(c) Variable importance for the two climatic predictors used to train the model** (Tmin: minimum temperature of the coldest month, in °C; MWD: maximum water deficit, in mm). The best model is displayed in green, which we selected because of its high full model accuracy, transferability (cross-validation scores), and variable importance not dominated by a single predictor.

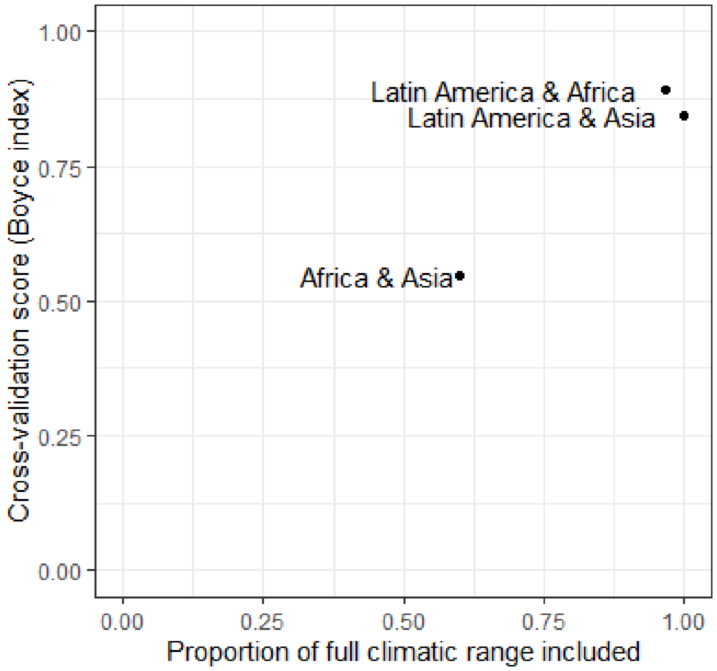


Figure S2.3. Cross-validation continuous Boyce index scores, in comparison to the proportion of the full climatic range of training data encompassed by each subset, for each cross-validation run of the best model. Labels correspond to the continents which were used to train each run (Latin America, Africa and Asia/Australasia); the remaining continent was used for testing. The cross-validation runs which most accurately predicted suitability for oil palm (continuous Boyce index) are those which were trained on data spanning a high proportion of the climatic range occupied by the full training data, suggesting that the full model (trained on the full climatic range) has high transferability. We calculated climatic range as the minimum convex polygon for scaled climatic variables (Tmin and MWD).

Thresholding of oil palm suitability models

We used Minimal Predicted Area thresholding (Engler, Guisan and Rechsteiner, 2004; Hirzel *et al.*, 2006) to classify the continuous suitability projections of our best model (0-1), based on the distribution of continuous projected suitability values at oil palm mill (i.e. ‘presence’) locations used to train the model (table S2.2, fig. S2.4). To test the sensitivity of our projected climatically suitable area to the threshold used to determine suitability, we used three Minimal Predicted Area thresholds to classify our best model. We classified locations as ‘suitable’ where the predicted suitability value was greater than the minimum predicted suitability for a given percentile of the oil palm mills used to train the model (thresholds for suitability ranged 0.018 – 0.152; fig. S2.4), and all other locations as ‘unsuitable’. Additionally, we classified the suitable locations into three classes of expected productivity, with equal percentiles of predicted values at the oil palm mill locations used to train the models (table S2.2).

We compared the performance of the three different classifications of our best model using the True Skill Statistic (TSS) (Allouche, Tsoar and Kadmon, 2006) and the Jaccard coefficient, to compare our predicted suitable area to that of an agro-ecological model of suitability for oil palm. We calculated TSS using oil palm plantations that are largely-independent of the oil palm mills dataset used to train the models (a map of global tree plantations compiled from mixed sources, largely from remote sensing, with a small subset of oil palm plantations verified against the oil palm mills dataset used to train the models) (Harris, Goldman and Gibbes, 2019) as testing presence locations, and randomly sampled points outside these plantations as testing pseudo-absence points, in equal number to the testing presence locations. We calculated the Jaccard coefficient for comparison of our classified model with an agro-ecological model of suitability for oil palm cultivation, in which suitability for oil palm cultivation was determined by expert knowledge of suitable ranges of a large number biophysical variables for cultivation (Pirker *et al.*, 2016). This model incorporated many more biophysical variables for oil palm suitability than we could examine (because intercorrelation of variables did not present issues for the methodology), so thus provided a suitability model for comparison with our results that was based on highly contrasting methods. Because the suitability predictions of the agro-ecological model (Pirker *et al.*, 2016) were available at a resolution of 25.3' (~47 km at the Equator), we aggregated our binary suitability predictions to this resolution before conducting the calculations.

We found that TSS is highest for the model classified using MPA_{95} (i.e. with the smallest total predicted area), whereas the Jaccard coefficient is highest for the model classified using MPA_{100} (i.e. with the largest total predicted area) (fig. S2.5, fig. S2.6). Because TSS incorporates both sensitivity and specificity, and all three of our final model classifications have high sensitivity (0.996-1.00), the TSS scores of our final model classifications are penalized by their specificity (0.613-0.798). However, our randomly sampled pseudo-absence points used to test the model could be suitable for oil palm cultivation in practice, but not planted with oil palm for a variety of reasons. Our TSS scores are therefore likely to underestimate the performance of our models. Nevertheless, our model thresholded at MPA_{100} appears to overestimate the area suitable for oil palm cultivation in comparison to the agro-ecological model (fig. S2.6c). We therefore present figures in the main text using the model thresholded at MPA_{99}, at which the two validation measures (TSS and Jaccard coefficient) are most closely equalised, and present uncertainty of results from model thresholding in Supplementary Information 2.3 and 2.4.

Table S2.2. Percentiles of predicted values at presence locations used to classify the continuous best model outputs (0-1) into suitable and unsuitable locations, with three classes of expected productivity, according to Minimal Predicted Area thresholding.

Minimal Predicted Area threshold for suitability	**Relative area predicted as suitable**	**Unsuitable**	**Suitable: expected productivity**		
			Low	**Medium**	**High**
MPA$_{95}$	Smallest	≤P_{95}	>P_{95} and ≤$P_{63.3}$	>$P_{63.3}$ and ≤$P_{31.7}$	>$P_{31.7}$
MPA$_{99}$	Medium	≤P_{99}	>P_{99} and ≤P_{66}	>P_{66} and ≤P_{33}	>P_{33}
MPA$_{100}$	Largest	≤P_{100} (minimum)	>P_{100} and ≤$P_{66.7}$	>$P_{66.7}$ and ≤$P_{33.3}$	>$P_{33.3}$

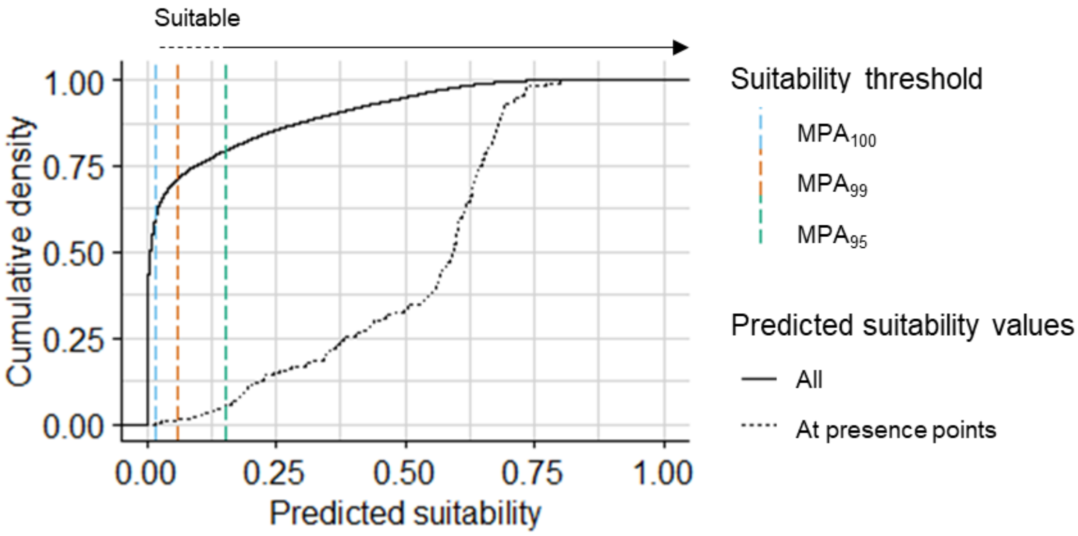


Figure S2.4. Cumulative density of continuous predicted suitability values of the best model, at presence points (oil palm mills) used to train the model (dotted line), and for all grid cells in the tropics (solid line); with the three MPA thresholds used to classify the output into suitable/unsuitable. Cumulative density refers to number of oil palm mills for the presence points used to train the model; and to number of grid cells (in WGS 1984 unprojected coordinate system) for all predicted values.

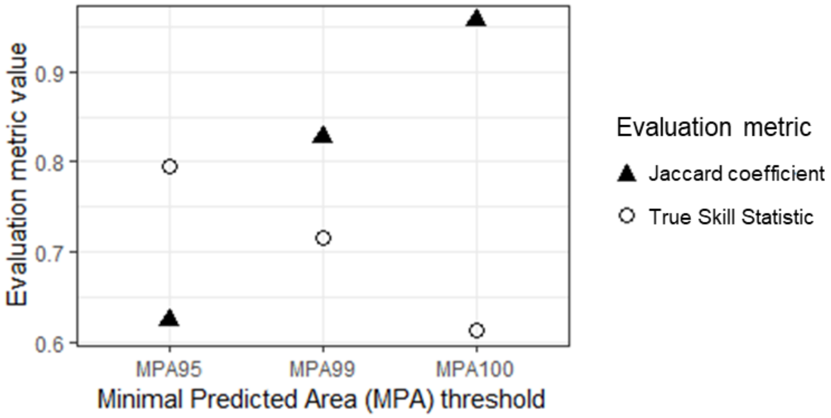


Figure S2.5. Evaluation metrics to compare three Minimal Predicted Area thresholds for classifying the continuous suitability predictions of the best model into suitable and unsuitable locations for oil palm cultivation. We calculated TSS using largely-independent oil palm plantations (Harris, Goldman and Gibbes, 2019) as testing presence locations, and random pseudo-absence points. We calculated the Jaccard coefficient for comparison of our classified model with an agro-ecological model (Pirker *et al.*, 2016).

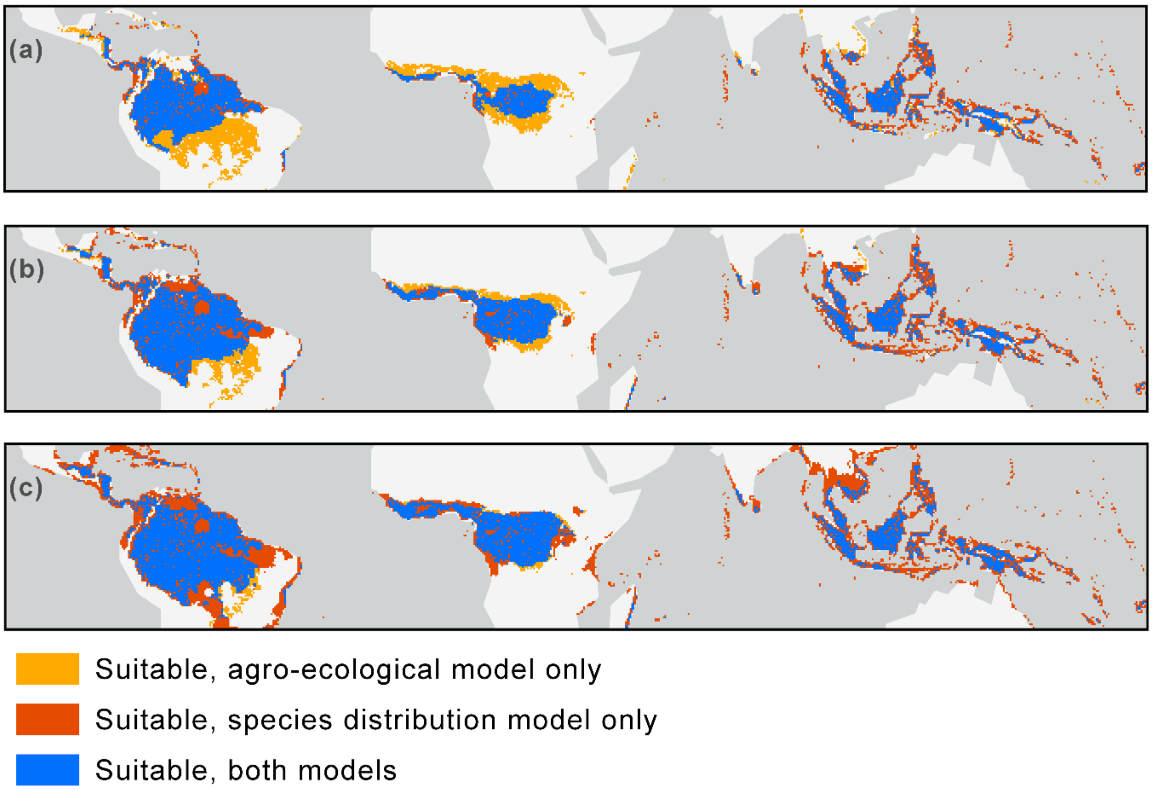


Figure S2.6. Comparison of areas predicted as suitable for oil palm cultivation, between an agro-ecological model and the species distribution model presented in this manuscript. (a) For the species distribution model thresholded at MPA_{95}; (b) for the species distribution model thresholded at MPA_{99}; (c) for the species distribution model thresholded at MPA_{100}. See (Pirker *et al.*, 2016) for details of the agro-ecological model.

Estimating oil palm yield from projected suitability values

Our oil palm suitability projections represented expected suitability for oil palm cultivation, from which we were able to derive values of expected oil palm yield for each of the three suitable classes for oil palm cultivation (low, medium and high; see table S2.2). We overlaid our maps of the three suitability classes with maps of estimated oil palm yield for the year 2010 (International Food Policy Research Institute, 2019), which were produced by spatial allocation of reported crop production statistics from global administrative units. We compared our SDM outputs with all grid-cells of oil palm yield, where actual yield >0 tha^{-1} (i.e. production was occurring; fig. S2.7).

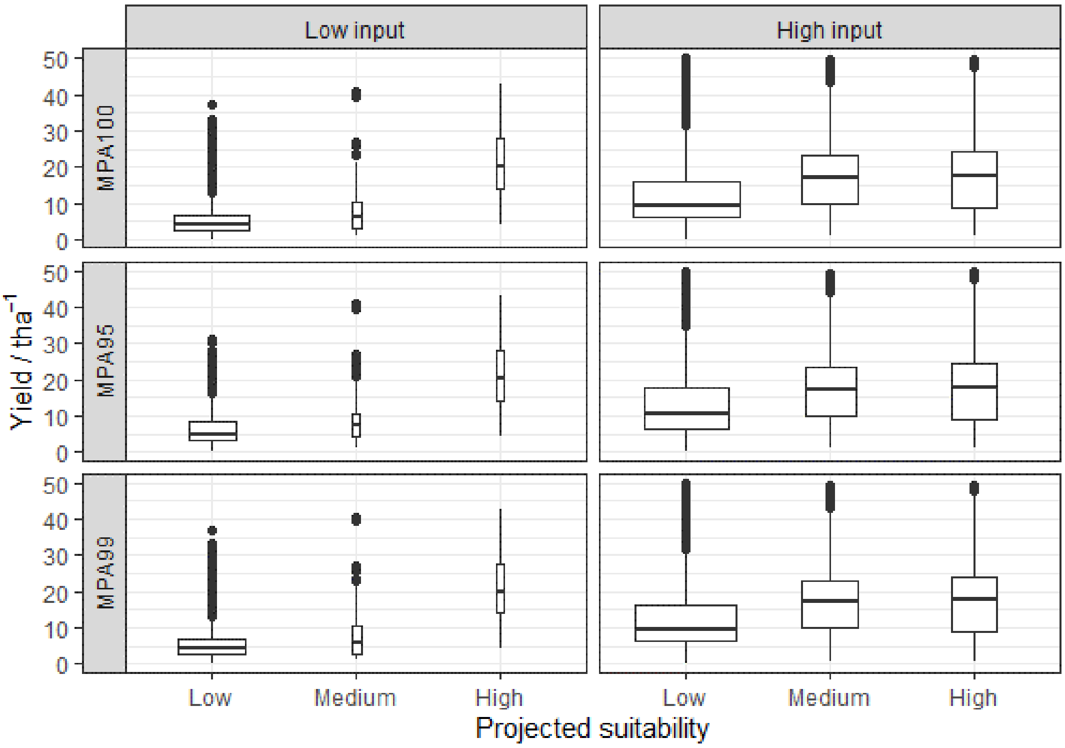


Figure S2.7. Oil palm yield values for each projected suitability class, shown for low and high fertiliser input cultivation and for each of the three thresholds used to classify the best model (MPA95, MPA99, MPA100; see table S2.2). Boxplots of global rainfed oil palm annual yield data are from (International Food Policy Research Institute, 2019). Note that results for MPA$_{99}$ are reported in the main article. Central bars show the median, lower and upper hinges show the first and third quartiles respectively, whiskers extend to the maximum and minimum values within 1.5*inter-quartile range, outliers are plotted individually, and boxplot width relates to sample size within each group (proportional to the square-root of the within-group sample size). N = 103,163 5-arc minute grid cells for all groups; smallest n = 71 for low input, high expected productivity, all model thresholds; largest n = 21,429 for high input, low expected productivity, MPA$_{100}$. We excluded all grid-cells with outlying yield >50 tha^{-1} (n = 576) as these appear to be overestimates (Tinker and Corley, 2015).

Supplementary Information 2.2: biome classification and woody vegetation structure

To ensure that grassland, savanna, shrubland and woodland ecoregions with a continuous grassy understorey were identified as ‘tropical grassy biome’ (Lehmann and Parr, 2016), we reclassified 25 of 391 non-mangrove ecoregions which occur in the tropics in Terrestrial Ecoregions of the World (Dinerstein *et al.*, 2017) (table S2.3). These changes were based on expert knowledge and the classification used in Murphy *et al.* 2016 (Murphy, Andersen and Parr, 2016).

We compared the woody vegetation structure (canopy closure and aboveground carbon stocks, both used to determine thresholds of habitat protection under the High Carbon Stock Approach for zero-deforestation commitments across the four biomes in our analyses (tropical moist forest, tropical grassy biome, tropical dry forest biome, and other), and found that the vast majority of tropical grassy and dry forest habitat falls below protection thresholds for aboveground carbon stocks (fig. S2.8).

Table S2.3. Biome classification for the 25 tropical ecoregions which we reclassified from the original Terrestrial Ecoregions of the World dataset (Dinerstein *et al.*, 2017), based on our knowledge of these habitats, and of the classification used in a previous study(Murphy, Andersen and Parr, 2016). We retained the original classification for all other ecoregions. In the main text, we refer to ‘tropical & subtropical moist broadleaf forests’ as ‘tropical moist forests’, ‘tropical & subtropical dry broadleaf forests’ as ‘dry forests’, ‘tropical & subtropical grasslands, savannas & shrublands’ as ‘tropical grassy biomes’, and remaining biome types as ‘other’. ECO_ID refers to the unique identifier assigned each ecoregion in the original dataset.

Ecoregion name	ECO_ID	Biogeographic realm	Original biome	Reclassified biome
Mato Grosso tropical dry forests	481	Neotropic	Tropical & Subtropical Moist Broadleaf Forests	Tropical & Subtropical Dry Broadleaf Forests
Bahamian pineyards	552	Neotropic	Tropical & Subtropical Coniferous Forests	Tropical & Subtropical Grasslands, Savannas & Shrublands
Central Deccan Plateau dry deciduous forests	290	Indomalayan	Tropical & Subtropical Dry Broadleaf Forests	Tropical & Subtropical Grasslands, Savannas & Shrublands
Central Indochina dry forests	291	Indomalayan	Tropical & Subtropical Dry Broadleaf Forests	Tropical & Subtropical Grasslands, Savannas & Shrublands
Chhota-Nagpur dry deciduous forests	292	Indomalayan	Tropical & Subtropical Dry Broadleaf Forests	Tropical & Subtropical Grasslands, Savannas & Shrublands
Chiquitano dry forests	529	Neotropic	Tropical & Subtropical Dry Broadleaf Forests	Tropical & Subtropical Grasslands, Savannas & Shrublands

Cuban pine forests	554	Neotropic	Tropical & Subtropical Coniferous Forests	Tropical & Subtropical Grasslands, Savannas & Shrublands
Hispaniolan pine forests	555	Neotropic	Tropical & Subtropical Coniferous Forests	Tropical & Subtropical Grasslands, Savannas & Shrublands
Irrawaddy dry forests	294	Indomalayan	Tropical & Subtropical Dry Broadleaf Forests	Tropical & Subtropical Grasslands, Savannas & Shrublands
Khathiar-Gir dry deciduous forests	295	Indomalayan	Tropical & Subtropical Dry Broadleaf Forests	Tropical & Subtropical Grasslands, Savannas & Shrublands
Luzon tropical pine forests	303	Indomalayan	Tropical & Subtropical Coniferous Forests	Tropical & Subtropical Grasslands, Savannas & Shrublands
Narmada Valley dry deciduous forests	296	Indomalayan	Tropical & Subtropical Dry Broadleaf Forests	Tropical & Subtropical Grasslands, Savannas & Shrublands
North Deccan dry deciduous forests	297	Indomalayan	Tropical & Subtropical Dry Broadleaf Forests	Tropical & Subtropical Grasslands, Savannas & Shrublands
South Deccan Plateau dry deciduous forests	298	Indomalayan	Tropical & Subtropical Dry Broadleaf Forests	Tropical & Subtropical Grasslands, Savannas & Shrublands
Southeast Indochina dry evergreen forests	299	Indomalayan	Tropical & Subtropical Dry Broadleaf Forests	Tropical & Subtropical Grasslands, Savannas & Shrublands
Southern Vietnam lowland dry forests	300	Indomalayan	Tropical & Subtropical Dry Broadleaf Forests	Tropical & Subtropical Grasslands, Savannas & Shrublands
Timor and Wetar deciduous forests	166	Australasia	Tropical & Subtropical Dry Broadleaf Forests	Tropical & Subtropical Grasslands, Savannas & Shrublands
Angolan montane forest-grassland	77	Afrotropic	Montane Grasslands & Shrublands	Tropical & Subtropical Grasslands, Savannas & Shrublands
Deccan thorn scrub forests	315	Indomalayan	Deserts & Xeric Shrublands	Tropical & Subtropical Grasslands, Savannas & Shrublands
Fiji tropical dry forests	635	Oceania	Tropical & Subtropical Dry Broadleaf Forests	Tropical & Subtropical Grasslands, Savannas & Shrublands
Hawai'i tropical dry forests	636	Oceania	Tropical & Subtropical Dry Broadleaf Forests	Tropical & Subtropical Grasslands, Savannas & Shrublands
Sri Lanka dry-zone dry evergreen forests	301	Indomalayan	Tropical & Subtropical Dry Broadleaf Forests	Tropical & Subtropical Grasslands, Savannas & Shrublands
Sumba deciduous forests	165	Australasia	Tropical & Subtropical Dry Broadleaf Forests	Tropical & Subtropical Grasslands, Savannas & Shrublands

Zambezian evergreen dry forests	33	Afrotropic	Tropical & Subtropical Dry Broadleaf Forests	Tropical & Subtropical Grasslands, Savannas & Shrublands
Godavari-Krishna mangroves	316	Indomalayan	Deserts & Xeric Shrublands	Mangroves

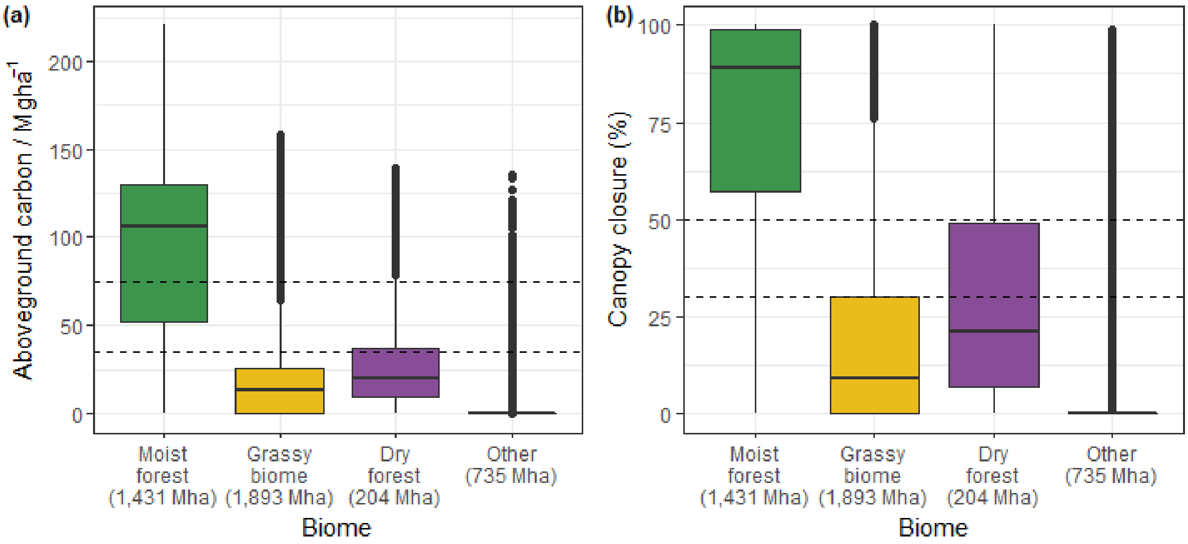


Figure S2.8. Boxplots of aboveground carbon stock and canopy closure for all natural habitat in the tropics (including primary vegetation, secondary vegetation and pasture, and excluding cropland, urban areas and tree plantations) for each biome. Central bars show the median, lower and upper hinges show the first and third quartiles respectively, whiskers extend to the maximum and minimum values within 1.5*inter-quartile range, and outliers are plotted individually. Total areas of natural habitat of each biome (across the tropics) are labelled on the x axis. Dashed lines represent the two sets of protection thresholds for zero-deforestation under the High Carbon Stock Approach (see main text Methods).

Supplementary Information 2.3: sensitivity analyses of suitability for rainfed oil palm cultivation

We found that our model estimates of total suitable area for oil palm cultivation, and hence total suitable area potentially available for expansion under zero-deforestation commitments, are highly sensitive to the model threshold (MPA_{95}, MPA_{99}, MPA_{100}) for determining suitability (table S2.4; fig. S2.9; fig. S2.10). For each thresholded model, we also found that applying the threshold for compulsory habitat protection under zero-deforestation (following the High Carbon Stock Approach, where all natural habitat of ≥75 Mg ha^{-1} and ≥50% canopy closure is protected) increases our estimates of total suitable area for oil palm potentially available for expansion under zero-deforestation commitments, in comparison to applying the threshold for potential protection (where all natural habitat of of ≥35 Mg ha^{-1} and ≥30% canopy closure is protected, as presented in the main article) (table S2.4). Nevertheless, the relative area of habitat potentially suitable for zero-deforestation oil palm expansion remains similar between biomes and biogeographic realms under the different thresholds of suitability for oil palm and habitat protection (fig. S2.9; fig. S2.10). The majority of the variation in total suitable area is within areas of low expected productivity, which comprise 87.4% - 97.4% of the total suitable area (natural habitat outside existing protected areas) in all models (fig. S2.11).

We found that the absolute difference in the area of moist forest potentially suitable for zero-deforestation oil palm expansion (i.e. not protected by zero-deforestation commitments) between habitat protection thresholds (potential and compulsory protection) is greater than that for other biomes, when comparing protection thresholds within a given threshold of model suitability (fig. S2.9; fig. S2.10; fig. S2.11). Thus, the area of degraded tropical moist forest available for zero-deforestation oil palm expansion appears highly sensitive to the choice of threshold for protection under zero-deforestation, which in turn depends on local identification of additional conservation values (as areas designated for potential protection under the High Carbon Stock Approach are protected depending on identification of additional conservation values).

Table S2.4. Estimates of total climatically suitable area for rainfed oil palm cultivation, across the three thresholds for suitability (see above). Results for MPA$_{99}$ are presented in the main text. Natural habitat includes primary vegetation, secondary vegetation and pasture, and excludes cropland, urban areas and tree plantations. Protected areas refer to IUCN class I and II protected areas. We estimated protection under zero-deforestation following HCSA (High Carbon Stocks Approach) thresholds: for compulsory protection, locations with aboveground carbon stocks of ≥75 Mg ha^{-1} and ≥50% canopy closure, and/or peat soil are protected; for potential protection (where in practice, protection of low-carbon areas can depend on additional conservation values), locations with aboveground carbon stocks of ≥35 Mg ha^{-1} and ≥30% canopy closure, and/or peat soil are protected.

Threshold for suitability	**Areal estimate (Mha)**				
	Total suitable area	**Total suitable natural habitat**	**Total suitable natural habitat outside protected areas**	**Total suitable natural habitat not protected by zero-deforestation (compulsory protection)**	**Total suitable natural habitat not protected by zero-deforestation (potential protection)**
MPA$_{95}$	960	889	840	169	69.8
MPA$_{99}$	1,368	1,264	1,198	358	167
MPA$_{100}$	1,860	1,674	1,594	694	375

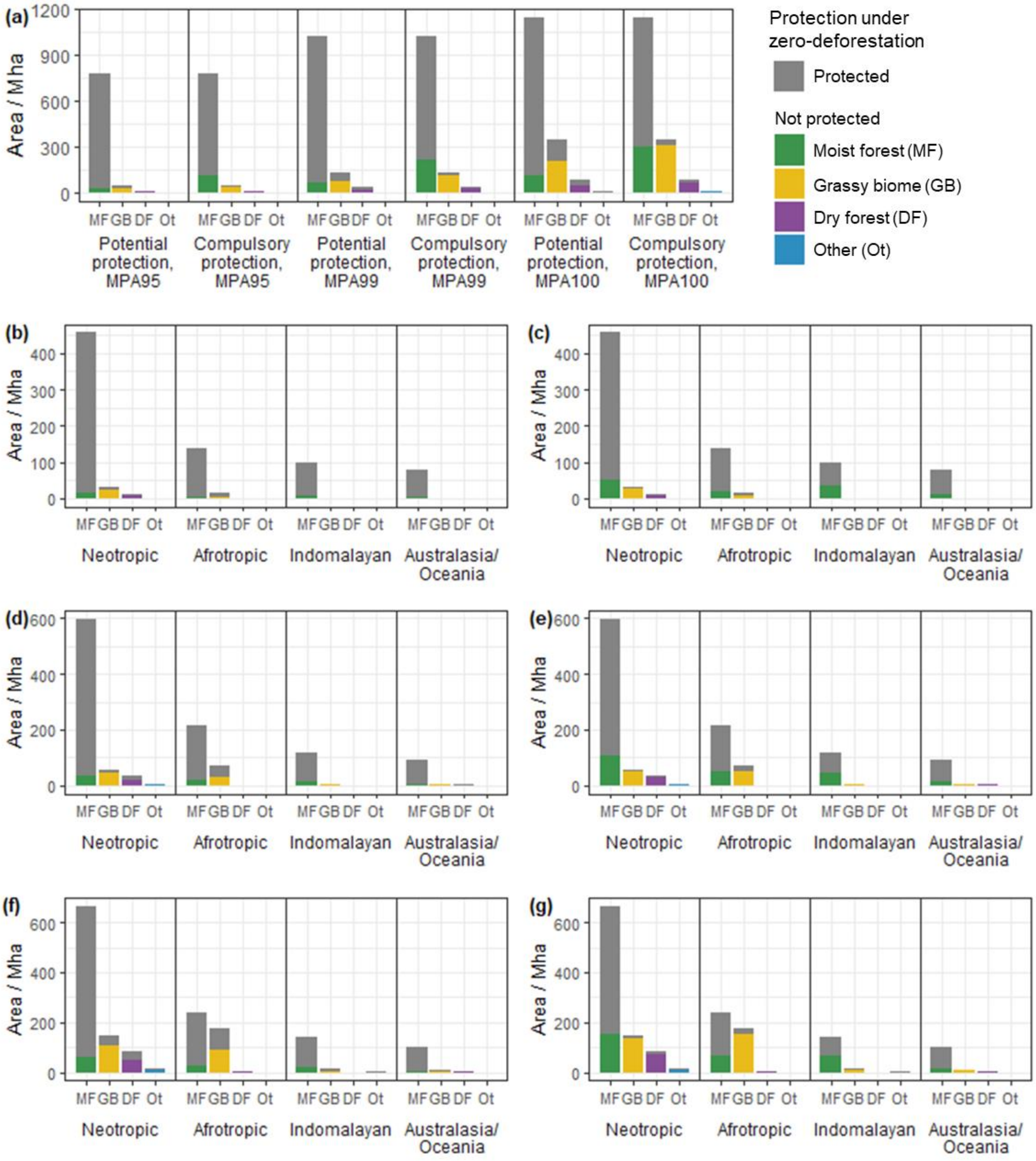


Figure S2.9. Area of natural habitat climatically-suitable for rainfed oil palm cultivation, compared between thresholds for oil palm suitability and thresholds of habitat protection under zero-deforestation commitments. (a) Globally, compared between thresholds of habitat protection under zero-deforestation commitments (potential, compulsory), and between model thresholds for suitability (MPA95, MPA99, MPA100; see table S2.2). (b-g) By biogeographic realm, for potential protection under zero-deforestation commitments (b,d,f), and for compulsory protection under zero-deforestation commitments (c,e,g); for suitability threshold MPA95 (b,c), MPA99 (d,e) and MPA100 (f,g). For compulsory protection, locations with aboveground carbon stocks of ≥75 Mg ha^{-1} and ≥50% canopy closure, and/or peat soil are protected; for potential protection (where in practice, protection of low-carbon areas can depend on additional conservation values), locations with aboveground carbon stocks of ≥35 Mg ha^{-1} and ≥30% canopy closure, and/or peat soil are protected. Locations of cropland, urban areas and tree plantations are excluded; as are all IUCN class I/II protected areas. Note that results for MPA99 under potential protection are presented in the main article.

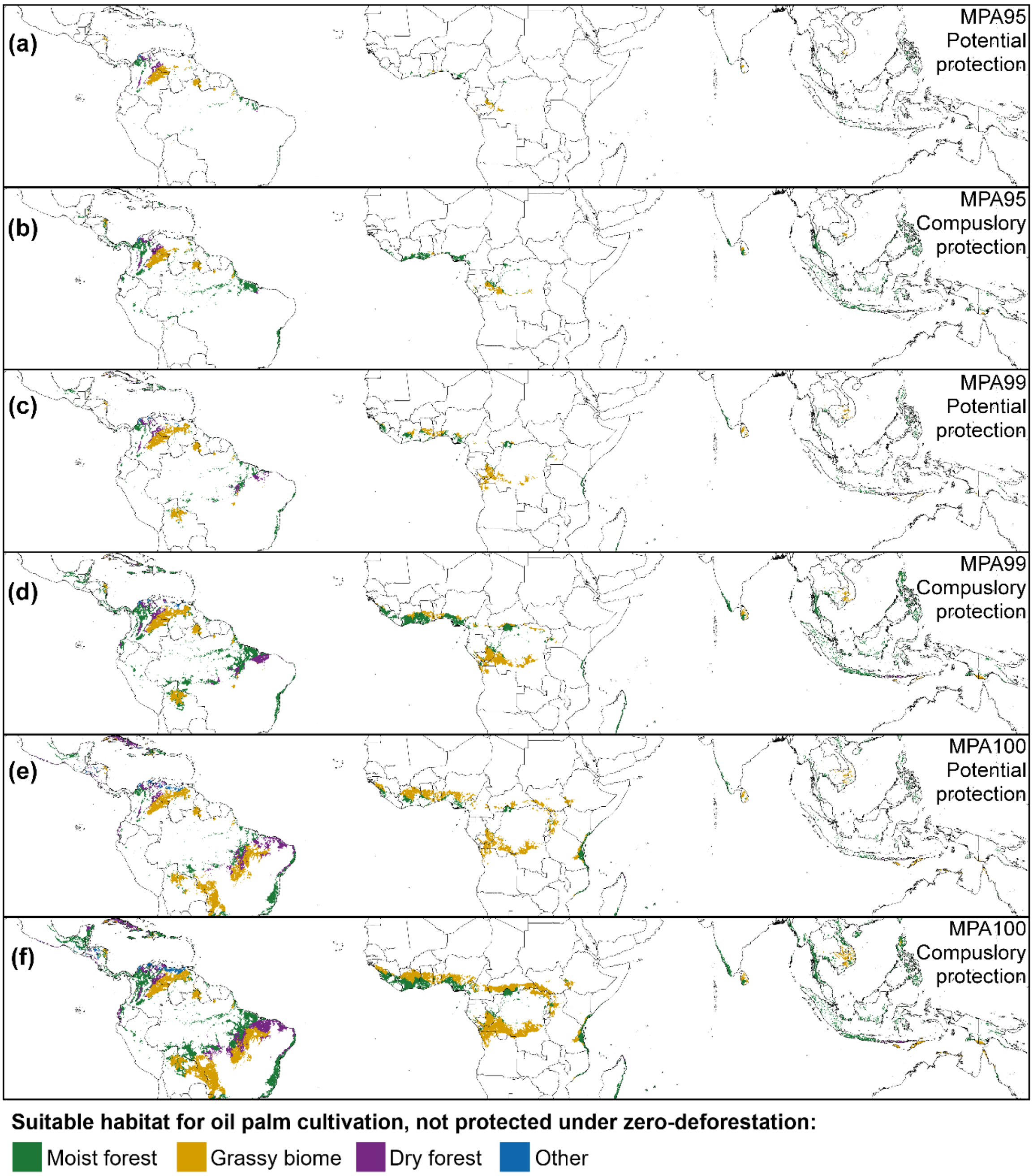


Figure S2.10. Maps of natural habitat climatically-suitable for rainfed oil palm cultivation under zero-deforestation commitments, compared between thresholds for oil palm suitability (MPA95, MPA99, MPA100; see table S2.2) and thresholds of habitat protection under zero-deforestation commitments (compulsory, potential). These maps correspond to coloured areas in fig. S2.9. For compulsory protection, locations with aboveground carbon stocks of ≥75 Mg ha^{-1} and ≥50% canopy closure, and/or peat soil are protected; for potential protection (where in practice, protection of low-carbon areas can depend on additional conservation values), locations with aboveground carbon stocks of ≥35 Mg ha^{-1} and ≥30% canopy closure, and/or peat soil are protected. Locations of cropland, urban areas and tree plantations are excluded; as are all IUCN class I/II protected areas. Note that results for MPA99 under potential protection are presented in the main article.

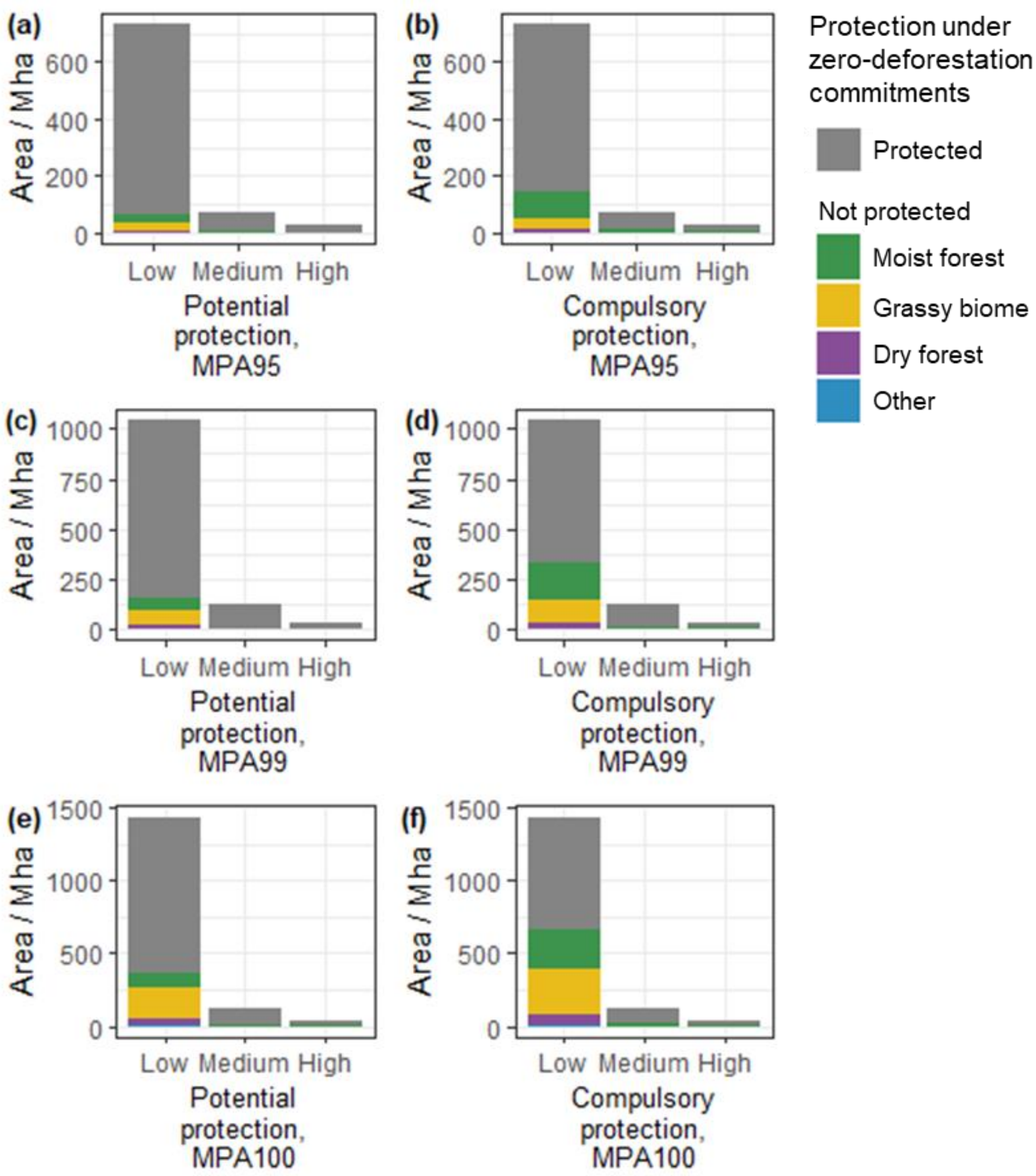


Figure S2.11. Area of natural habitat climatically-suitable for rainfed oil palm cultivation, for each of the three classes of suitability classes, compared between model thresholds for suitability (MPA95, MPA99, MPA100; see table S2.2) and thresholds of habitat protection under zero-deforestation commitments (potential, compulsory). For compulsory protection, locations with aboveground carbon stocks of ≥75 Mg ha^{-1} and ≥50% canopy closure, and/or peat soil are protected; for potential protection (where in practice, protection of low-carbon areas can depend on additional conservation values), locations with aboveground carbon stocks of ≥35 Mg ha^{-1} and ≥30% canopy closure, and/or peat soil are protected. Locations of cropland, urban areas and tree plantations are excluded; as are all IUCN class I/II protected areas. Values in (c) under potential protection correspond to those presented in main article figure 3.3.

Supplementary Information 2.4: sensitivity analyses of suitability for irrigated oil palm cultivation

Excluding locations suitable for rainfed oil palm cultivation, we estimate that irrigation could allow an additional 63-138 Mha of land to be climatically suitable for cultivation (table S2.5). We found that these estimates of total additional suitable area (i.e. area requiring irrigation) are sensitive to water availability, as using up to 100% of surplus available water consistently renders a greater area suitable than using only 50% surplus available water (table S2.5, fig. S2.12). These total areal estimates are somewhat sensitive to thresholds of model suitability threshold (MPA_{95}, MPA_{99}, MPA_{100}) and habitat protection under zero-deforestation commitments (compulsory potential), but less so than the sensitivity of areas suitable for rainfed cultivation overall (table S2.5, fig. S2.12; see table S2.4 for estimates of rainfed suitability). Because we excluded locations suitable for rainfed cultivation from our estimates of locations suitable for irrigation-only, we found that the locations predicted as suitable alter with model suitability threshold, although the areal estimates are broadly similar (table S2.5, fig. S2.13, fig. S2.14). Moreover, the majority of locations suitable for irrigated-only cultivation are not in areas which fall under protection by zero-deforestation commitments (fig. S2.12; fig. S2.16). Thus, as for rainfed cultivation, the distribution of areas suitable for oil palm under irrigation-only remains similar between biomes for different model permutations (fig. S2.12). As for rainfed suitability, the majority of the variation in suitable areas requiring irrigation is within areas of low expected productivity, which comprises 91.8% - 98.3% of the total suitable natural habitat requiring irrigation for all model permutations (fig. S2.15; fig. S2.16).

Table S2.5. Estimates of total climatically-suitable area for irrigated-only oil palm cultivation, across the three thresholds for suitability, and two levels of water use for irrigation. We have excluded locations suitable for rainfed oil palm cultivation for each model, so that some models with greater total rainfed extent (e.g. MPA$_{100}$) have smaller additional suitable areas under irrigation than other models (see table S2.4 for rainfed areas). Results for MPA$_{99}$ are presented in the main text. We simulated irrigation for in locations where annual cumulative water deficit > 100mm, by using either 50% or 100% of surplus available water to supplement rainfall. As above (see table S2.4 for results for rainfed cultivation only), natural habitat includes primary vegetation, secondary vegetation and pasture, and excludes cropland, urban areas and tree plantations. Protected areas refer to IUCN class I and II protected areas. We estimated protection under zero-deforestation commitments following HCSA (High Carbon Stocks Approach) thresholds: for compulsory protection, locations with aboveground carbon stocks of ≥75 Mg ha^{-1} and ≥50% canopy closure, and/or peat soil are protected; for potential protection (where in practice, protection of low-carbon areas depends on additional conservation values), locations with aboveground carbon stocks of ≥35 Mg ha^{-1} and ≥30% canopy closure, and/or peat soil are protected.

Surplus available water used for irrigation	**Threshold for suitability**	**Areal estimate (Mha)**				
		Total suitable area	**Total suitable natural habitat**	**Total suitable natural habitat outside protected areas**	**Total suitable natural habitat not protected by zero-deforestation (compulsory protection)**	**Total suitable natural habitat not protected by zero-deforestation (potential protection)**
50%	**MPA$_{95}$**	147	128	125	90.7	63.0
	MPA$_{99}$	123	84.4	83.0	80.0	64.4
	MPA$_{100}$	110	66.4	65.3	64.8	57.6
100%	**MPA$_{95}$**	228	197	193	137	92.5
	MPA$_{99}$	206	148	145	138	108
	MPA$_{100}$	179	114	112	111	95.7

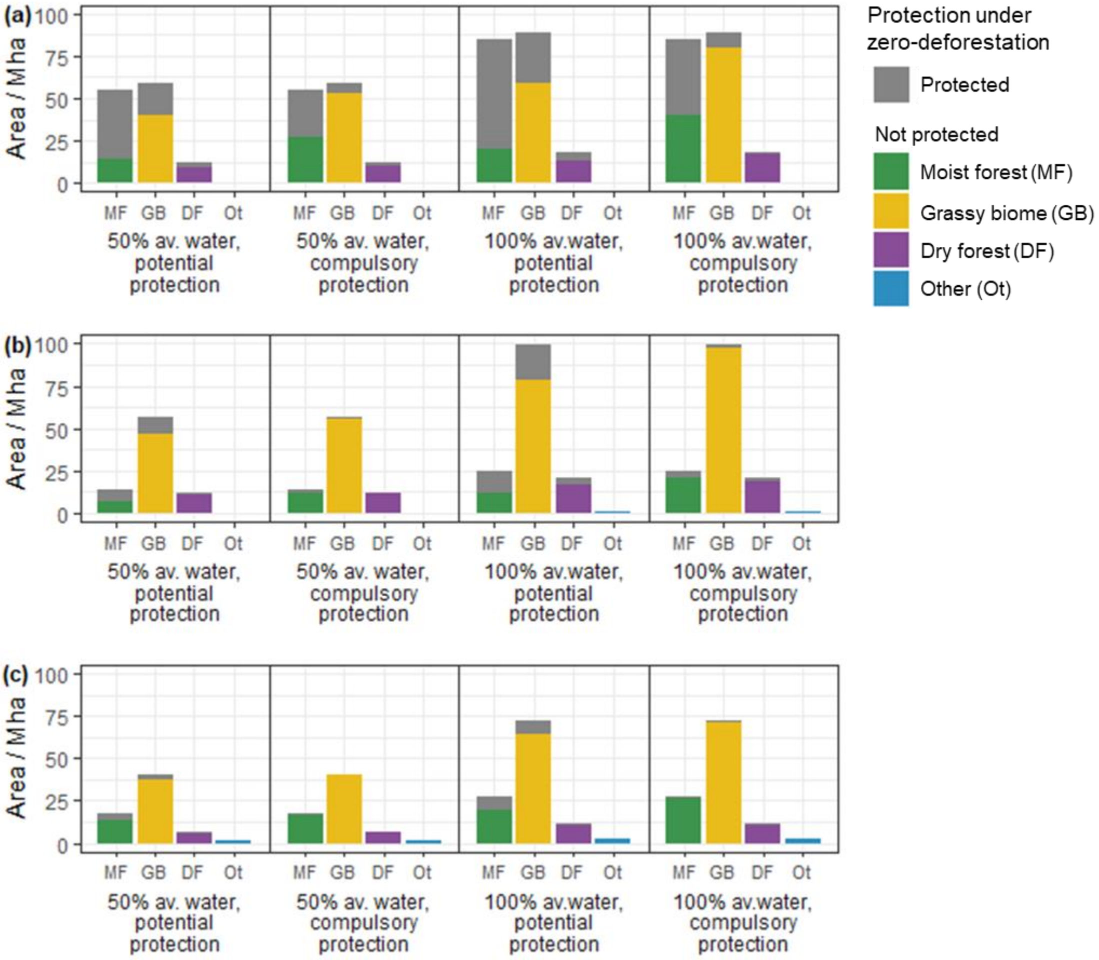


Figure S2.12. Area of natural habitat climatically-suitable for irrigated-only oil palm cultivation, compared between the two levels of water use for irrigation (50% and 100% of surplus available water), the two thresholds for protection under zero-deforestation (potential, compulsory), and the three thresholds of suitability: (a) MPA95 threshold for suitability; (b) MPA99 threshold for suitability; (c) MPA100 threshold for suitability. We simulated irrigation for in locations where annual cumulative water deficit >100mm, by using either 50% or 100% of surplus available water ('av. water') to supplement rainfall. For compulsory protection, locations with aboveground carbon stocks of ≥75 Mg ha^{-1} and ≥50% canopy closure, and/or peat soil are protected; for potential protection (where in practice, protection of low-carbon areas can depend on additional conservation values), locations with aboveground carbon stocks of ≥35 Mg ha^{-1} and ≥30% canopy closure, and/or peat soil are protected. Locations of cropland, urban areas and tree plantations are excluded; as are all IUCN class I/II protected areas. We have excluded locations suitable for rainfed oil palm cultivation for each model, so that some models with greater total rainfed extent (e.g. MPA_{100}) have smaller additional suitable areas under irrigation than other models. Results for MPA99 under potential protection and using 100% of surplus available water are presented in the main article.

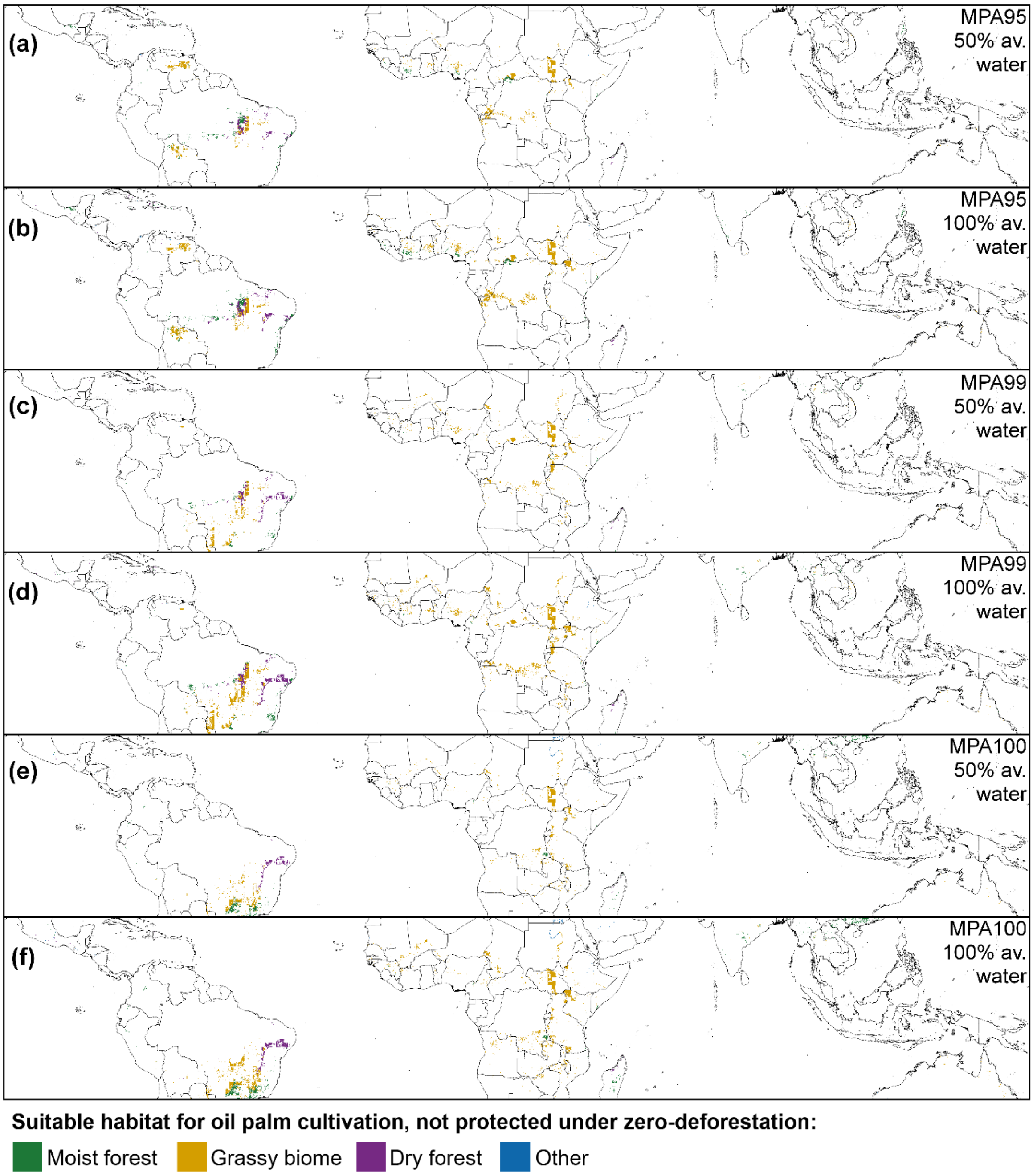


Figure S2.13. Maps of climatically-suitable habitat for irrigated-only oil palm cultivation, assuming all locations potentially protected under zero-deforestation commitments are unavailable. Maps are compared between model thresholds for suitability (MPA95, MPA99, MPA100; see table S2.2) and percentage of surplus available water ('av. water') applied as irrigation (in locations where annual cumulative water deficit > 100mm; up to either 50% or 100% surplus available water used for irrigation). For potential protection under zero-deforestation commitments, locations with aboveground carbon stocks of ≥35 Mg ha^{-1} and ≥30% canopy closure, and/or peat soil are protected from expansion. Locations of cropland, urban areas and tree plantations are excluded; as are all IUCN class I/II protected areas. Locations suitable for rainfed cultivation are not shown (see fig. S2.10); note that some locations estimated as suitable under irrigation in models with low suitability thresholds are estimated as suitable if rainfed in models with higher suitability thresholds. Areas of (c,d) are presented in the main article fig. 3.

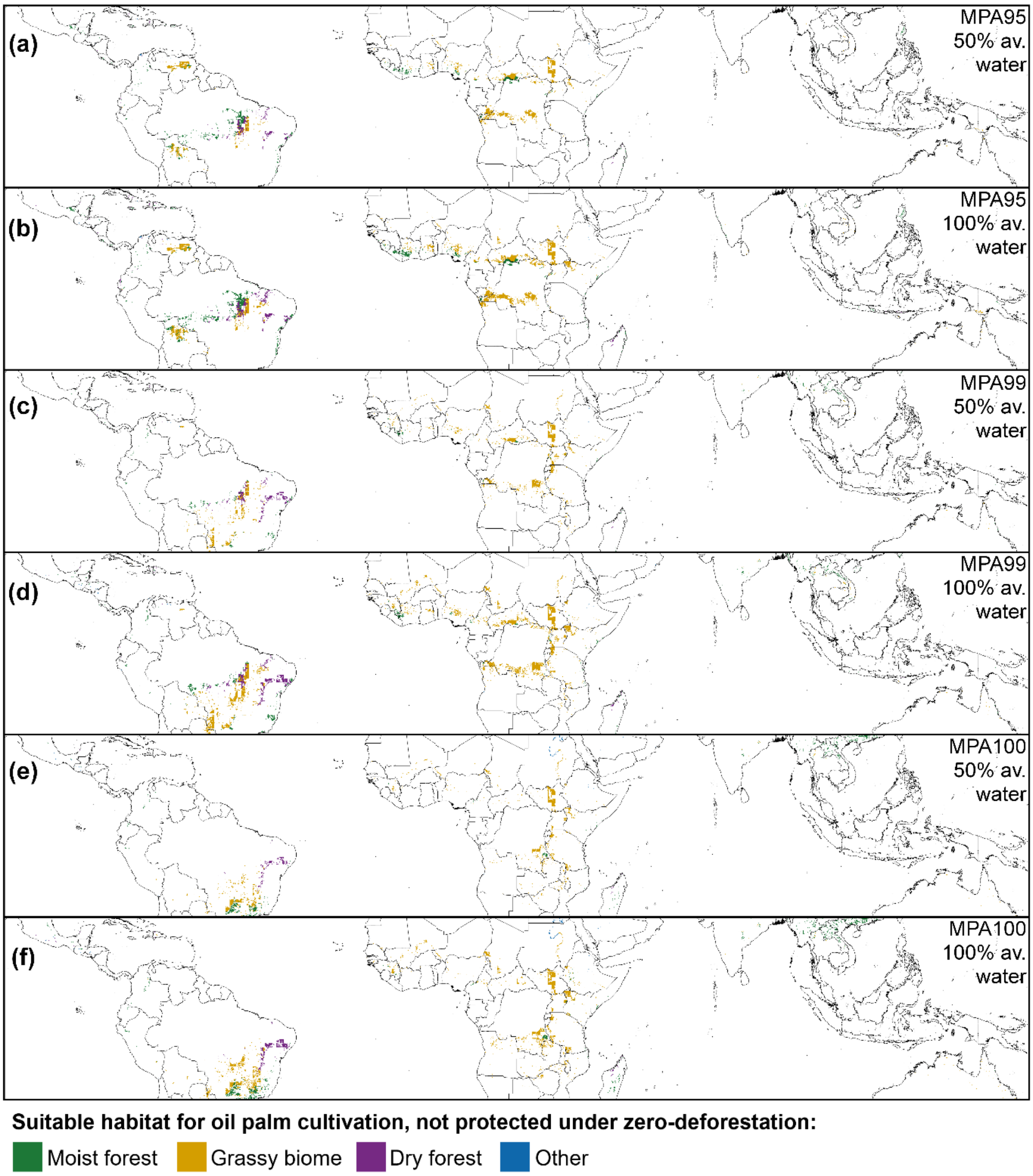


Figure S2.14. Maps of climatically-suitable habitat for irrigated-only oil palm cultivation, assuming all locations under 'compulsory' protection from zero-deforestation commitments are unavailable. Maps are compared between model thresholds for suitability (MPA95, MPA99, MPA100; see table S2.2) and percentage of surplus available water ('av. water') applied as irrigation (in locations where annual cumulative water deficit > 100mm; up to either 50% or 100% surplus available water used for irrigation). For compulsory protection under zero-deforestation commitments, locations with aboveground carbon stocks of ≥75 Mg ha^{-1} and ≥50% canopy closure, and/or peat soil are protected**.** Locations of cropland, urban areas and tree plantations are excluded; as are all IUCN class I/II protected areas.

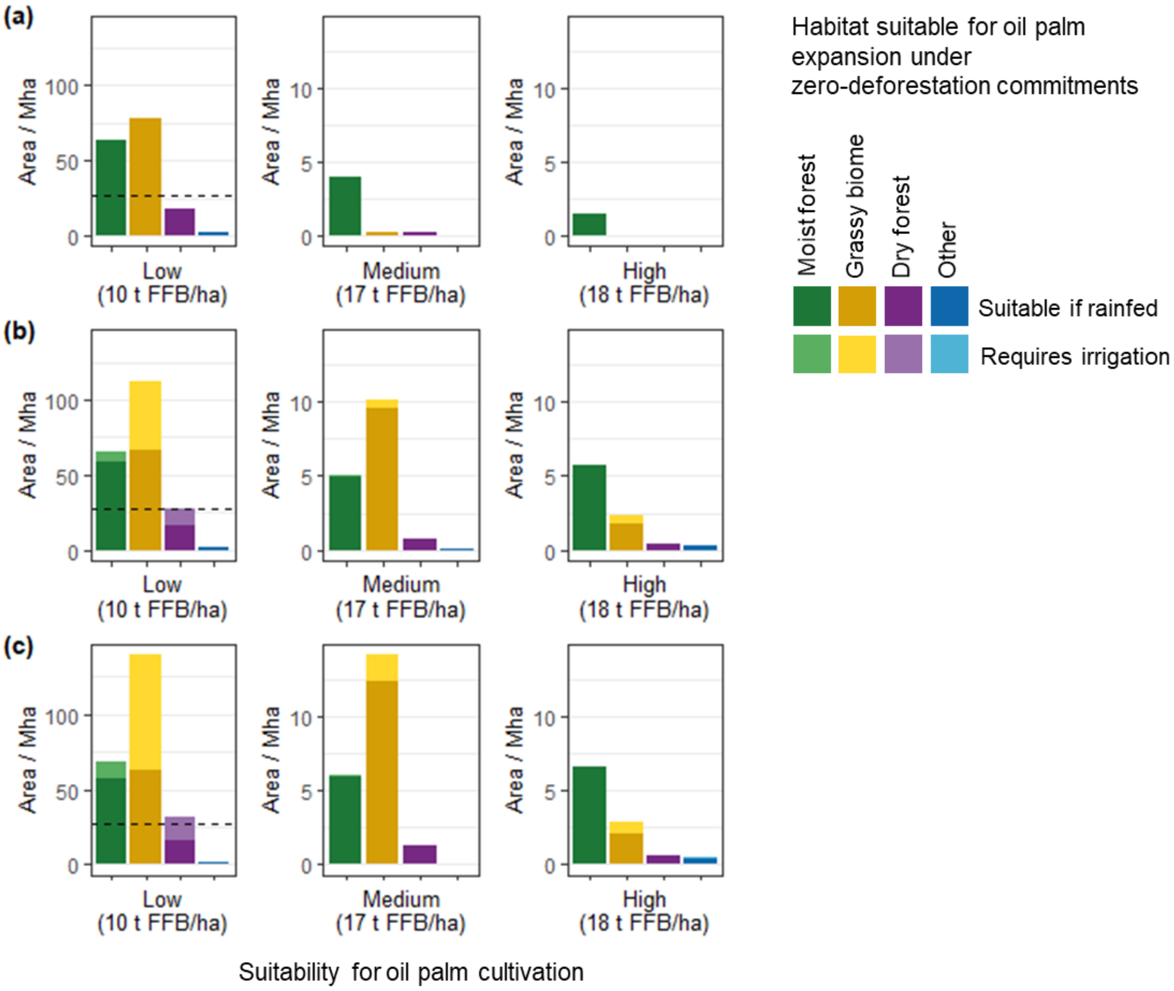


Figure S2.15. Total areas of non-cultivated land climatically-suitable for oil palm expansion under zero-deforestation commitments, classified according to suitability (and expected yield), by biome. (a) Under rainfed cultivation, (b) under irrigation, using 50% available water, (c) under irrigation, using 100% available water. The suitability and classes are for MPA99 (see table S2.2): this is a replicate of fig. 3 (main article) but also includes irrigation estimated using 50% water availability (only (a) and (c) are shown in main article). The dashed line in 'Low Yield' panels shows the current area of oil palm plantations globally, which is outside the axis range of the other yield classes. Note differences in y axes. For the (b) and (c), dark colours represent the expected yield of locations which are also suitable if rainfed (i.e. those shown in (a)), but under irrigation; and pale colours represent locations only suitable under irrigation.

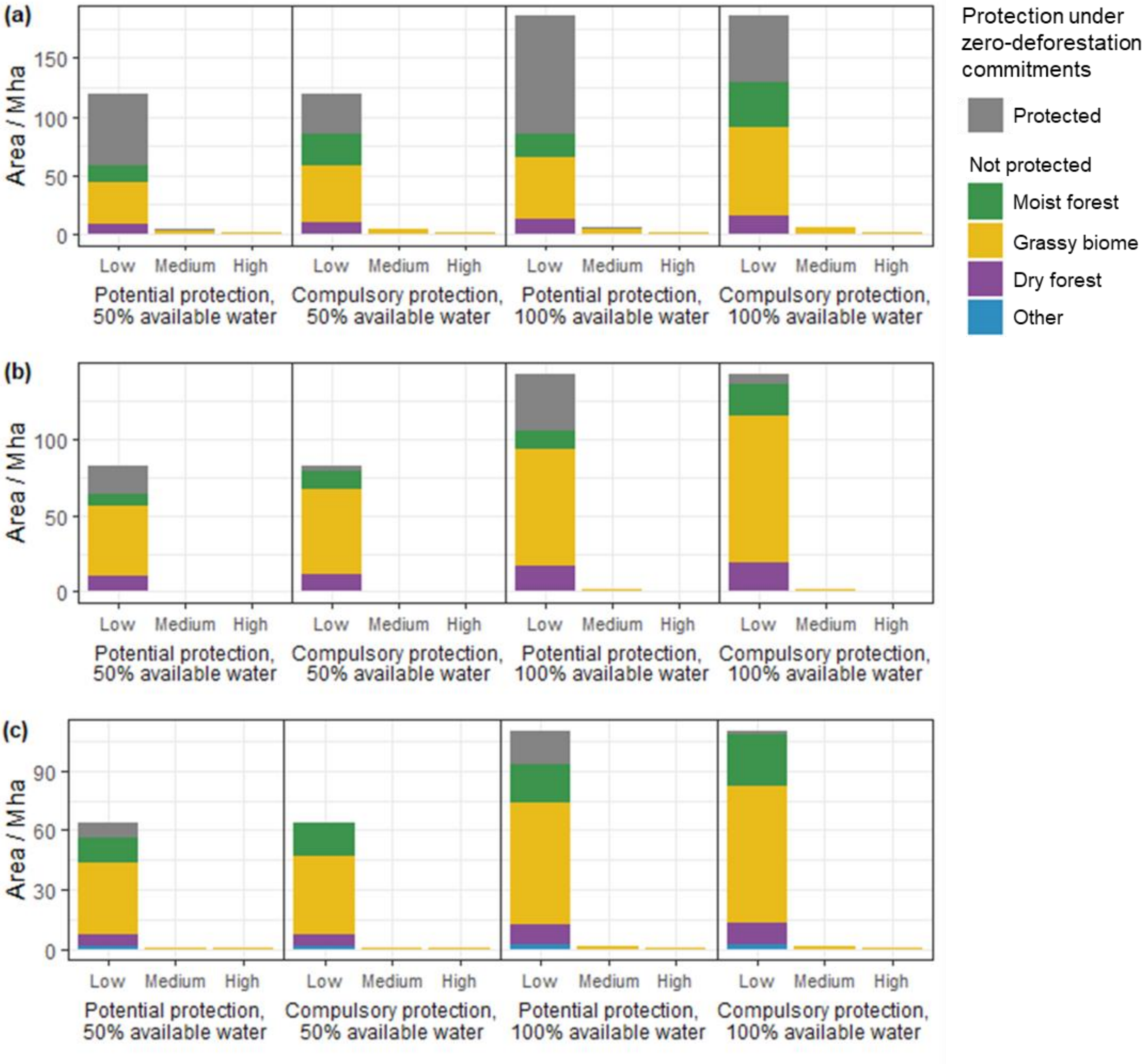


Figure S2.16. Area of non-cultivated land climatically-suitable for rainfed oil palm cultivation, for each of the three classes of suitability classes, compared between three model thresholds for suitability (a) MPA95, (b) MPA99, (c) MPA100 (see table S2.2); two thresholds of habitat protection under zero-deforestation commitments (potential, compulsory); and two thresholds percentage of surplus available water applied as irrigation (in locations where annual cumulative water deficit > 100mm; up to either 50% or 100% surplus available water used for irrigation). We have excluded locations suitable for rainfed oil palm cultivation for each model, so that some models with greater total rainfed extent (e.g. MPA_{100}) have smaller additional suitable areas under irrigation than other models. For compulsory protection, locations with aboveground carbon stocks of ≥75 Mg ha^{-1} and ≥50% canopy closure, and/or peat soil are protected; for potential protection (where in practice, protection of low-carbon areas can depend on additional conservation values), locations with aboveground carbon stocks of ≥35 Mg ha^{-1} and ≥30% canopy closure, and/or peat soil are protected. Locations of cropland, urban areas and tree plantations are excluded; as are all IUCN class I/II protected areas. Note differences in y axes. Values in (c) under potential protection and up to 100% available water use correspond to those presented in main article figure 3.3.

Supplementary Information 2.5: potential impacts of oil palm expansion on vertebrate diversity, including under irrigation

We refined range maps of terrestrial vertebrates according to non-cultivated and transformed habitat types in which each species could persist (see main article Methods) according to the matching in table S2.6, and estimated potential vertebrate species richness loss from conversion of non-cultivated habitat to oil palm plantation (fig. S2.17). Our results that zero-deforestation commitments could exacerbate richness loss from oil palm expansion in grassy and dry forest biomes, by prioritising locations of greater potential richness loss for conversion, held true across all model permutations that we tested (including locations suitable for both irrigated and rainfed expansion, compared to rainfed alone; and classifying protection under zero-deforestation commitments according to potential or compulsory thresholds; fig. S2.18). We found that the number of threatened vertebrate species that could undergo range loss from zero-deforestation oil palm expansion was considerably greater for compulsory protection under zero-deforestation commitments (protection of locations with aboveground carbon stocks of ≥75 Mg ha-1 and ≥50% canopy closure; 1273 threatened species could undergo range loss in total) than for potential protection (protection of locations with aboveground carbon stocks of ≥35 Mg ha-1 and ≥30% canopy closure; 879 threatened species could undergo range loss in total) (fig. S2.19). Including locations suitable for irrigated oil palm expansion increased the number of threatened vertebrates that could undergo range loss (1071 species) compared to rainfed expansion alone (879 species), although the impact of this was less than that of the thresholds for habitat protection under zero-deforestation commitments (fig. S2.19). Compulsory protection under zero-deforestation commitments allowed considerably greater range loss for these species than potential protection, although this largely impacted the tropical moist forest biome; whereas including irrigated oil palm expansion had little impact on the percentage of range that could be lost (fig. S2.19). Of moist forest, grassy biome and dry forest, the percentage of remaining non-cultivated habitat of individual ecoregions suitable for zero-deforestation oil palm expansion is highest for dry forest in all permutations (compulsory vs potential habitat protection under zero-deforestation commitments, and rainfed-only expansion or also including locations requiring irrigation) (fig. S2.20). Reducing protection under zero-deforestation commitments from potential to compulsory (i.e. less area protected) increases the percentage of tropical moist and dry forest ecoregions suitable for oil palm expansion more than for the other biomes, highlighting the sensitivity of potential biodiversity impacts of expansion in these biomes to the precise habitat protection applied in the field (fig. S2.20).

Table S2.6. Matching IUCN Red List habitat classifications (BirdLife International and Handbook of the Birds of the World, 2016; IUCN, 2018) with habitat classes of Terrestrial Ecoregions of the World (Dinerstein *et al.*, 2017) **and global spatial data on locations of cropland, urban areas** (Buchhorn *et al.*, 2019; Copernicus *et al.*, 2019) **and tree plantations** (Harris, Goldman and Gibbes, 2019). We considered a species as present in a given grid-cell (5 arc-minute resolution) if its range contained the grid cell centre, and if the habitat type (habitat according to Terrestrial Ecoregions of the World, masked by cropland, urban areas and tree plantations) was listed as a suitable habitat, according to this matching table.

IUCN	**Terrestrial ecoregions 2017**
Boreal forest	Boreal forests/taiga
Subarctic forest; Subantarctic forest	Boreal forests/taiga; Tundra
Temperate forest	Temperate broadleaf and mixed forests; temperate conifer forests
Subtropical/tropical dry forest	Tropical and subtropical dry broadleaf forests; tropical and subtropical coniferous forests
Subtropical/tropical moist lowland forest; subtropical/tropical swamp forest; subtropical/tropical moist montane forest	Tropical and subtropical moist broadleaf forests; tropical and subtropical coniferous forests
Subtropical/tropical mangrove forest vegetation	Mangroves
Dry savanna	Tropical and subtropical grasslands, savannas and shrublands; temperate grasslands, savannas and shrublands; montane grasslands and shrublands
Moist savanna	Tropical and subtropical grasslands, savannas and shrublands; temperate grasslands, savannas and shrublands; flooded grasslands and shrublands; montane grasslands and shrublands
Subarctic shrubland; subantarctic shrubland; boreal shrubland; tundra; subarctic grassland; subantarctic grassland	Tundra
Temperate shrubland; temperate grassland	Temperate grasslands, savannas and shrublands; montane grasslands and shrublands
Subtropical/tropical dry shrubland; subtropical/tropical moist shrubland	Tropical and subtropical grasslands, savannas and shrublands; montane grasslands and shrublands; flooded grasslands and savannas
Subtropical/tropical high altitude shrubland	Montane grasslands and shrublands
Mediterranean-type shrubby vegetation	Mediterranean forests, woodland and scrub
Subtropical/tropical dry lowland grassland	Tropical and subtropical grasslands, savannas and shrublands
Subtropical/tropical wet/flooded lowland grassland	Tropical and subtropical grasslands, savannas and shrublands; flooded grasslands and savannas
Subtropical/tropical high altitude grassland	Tropical and subtropical grasslands, savannas and shrublands; Montane grasslands and shrublands
Wetlands (inland)	Flooded grasslands and savannas

Inland rocky areas	
Caves & subterranean habitats	
Desert (hot desert, temperate desert, cold desert)	Deserts and xeric shrublands; tundra
	Copernicus landcover map
Arable land	Cropland
Urban areas	Urban
	Spatial Database of Planted Trees
Plantations	Tree plantations (including oil palm)

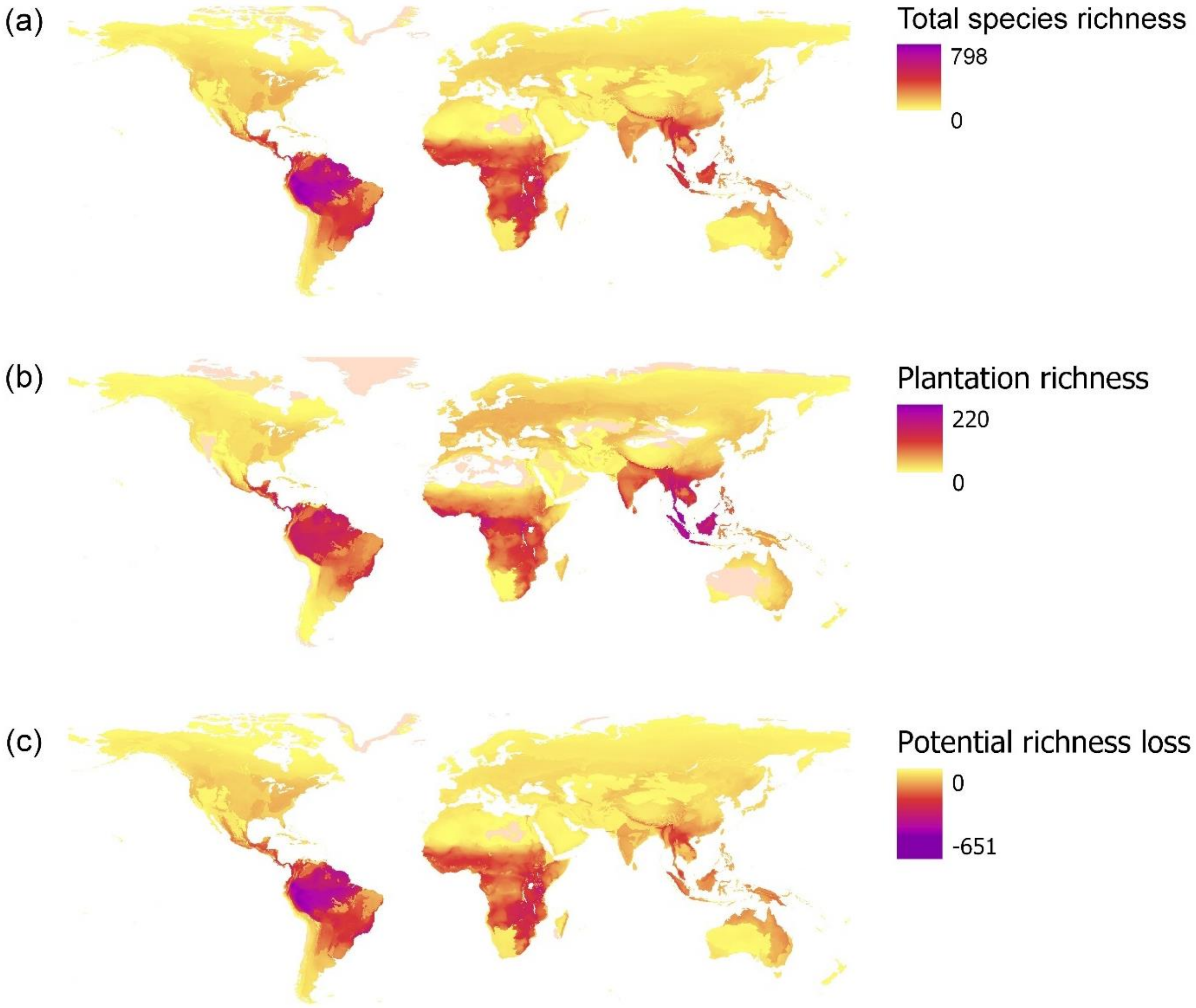


Figure S2.17. Global maps of estimated vertebrate species richness, from refined range maps. (a) Total richness in current landcover (assuming land outside cropland, urban areas and tree plantations is non-cultivated land); (b) potential richness of tree plantations (including oil palm plantations); (c) potential richness loss from conversion of non-cultivated land to oil palm plantation (i.e. the difference between (b) and (a)).

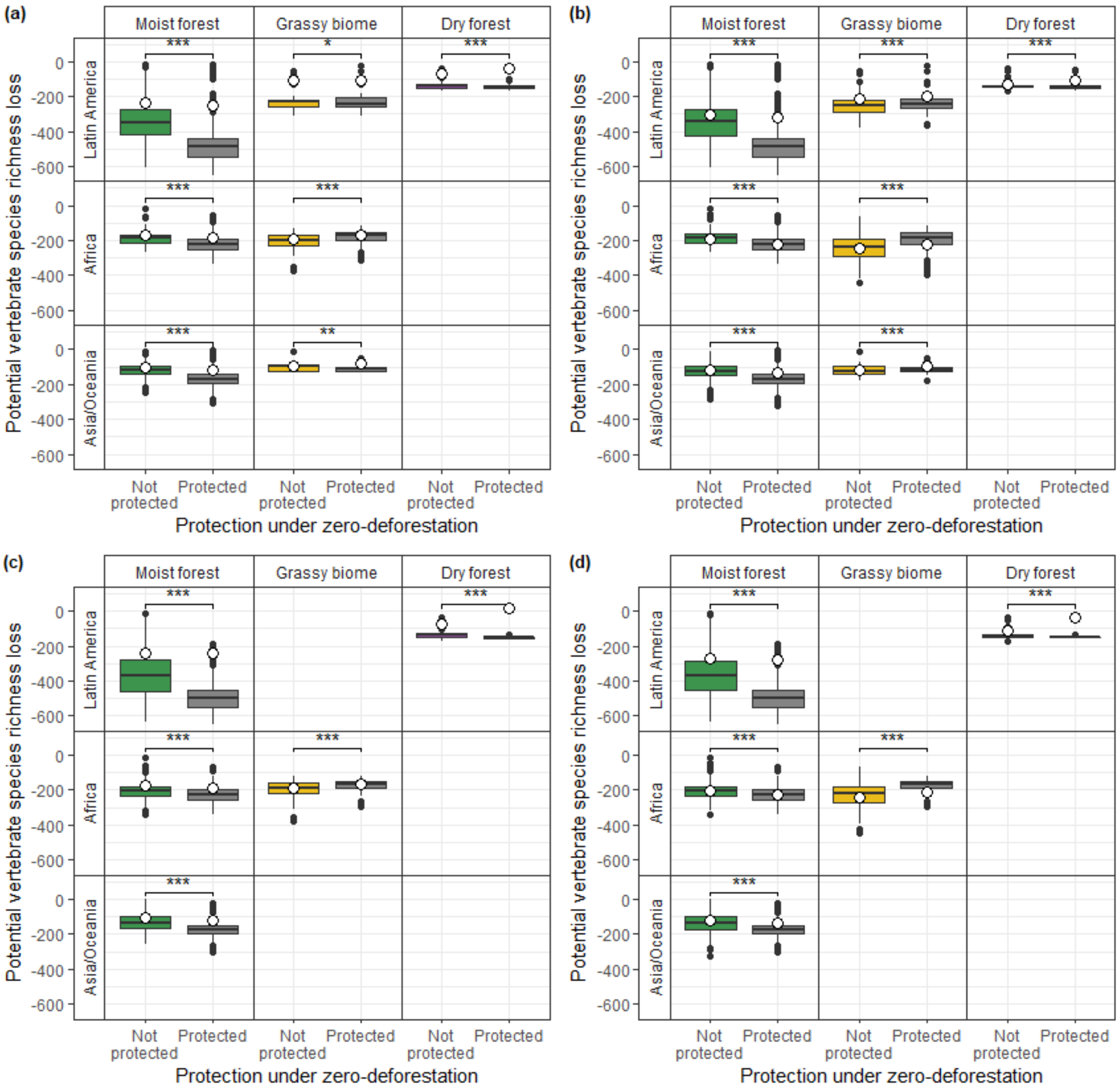


Figure S2.18. Potential impacts of zero-deforestation oil palm expansion on vertebrate richness, compared for rainfed and both rainfed and irrigated expansion, and for different habitat protection thresholds under zero-deforestation commitments (compulsory, potential). (a) Rainfed oil palm expansion, potential protection; (b) both rainfed and irrigated oil palm expansion, potential protection; (c) rainfed oil palm expansion, compulsory protection only; (d) both rainfed and irrigated oil palm expansion, compulsory protection only. For compulsory protection, locations with aboveground carbon stocks of ≥75 Mg ha^{-1} and ≥50% canopy closure, and/or peat soil are protected; for potential protection (where in practice, protection of low-carbon areas can depend on additional conservation values), locations with aboveground carbon stocks of ≥35 Mg ha^{-1} and ≥30% canopy closure, and/or peat soil are protected. Locations of cropland, urban areas and tree plantations are excluded; as are all IUCN class I/II protected areas. All estimates of irrigated expansion assume up to 100% of surplus available water could be applied for irrigation. Boxplots show potential richness loss for all grid-cells; white circles show the expected richness loss after accounting for spatial autocorrelation (non-spatial parameters of simultaneous autoregressive error models), and brackets denote significant differences (*p* <0.05) between these (* *p* <0.05, ** *p* <0.01, *** *p* <0.001). We conducted simultaneous autoregressive models on a systematic subset of all 5 arc-minute grid cells of non-cultivated land potentially suitable for oil palm expansion (every

16th grid-cell is included in the models). We excluded groups with insufficient sample size (*n* <30) from the models, so some locations in dry forest, grassy biome, and all 'other' biomes are not displayed.

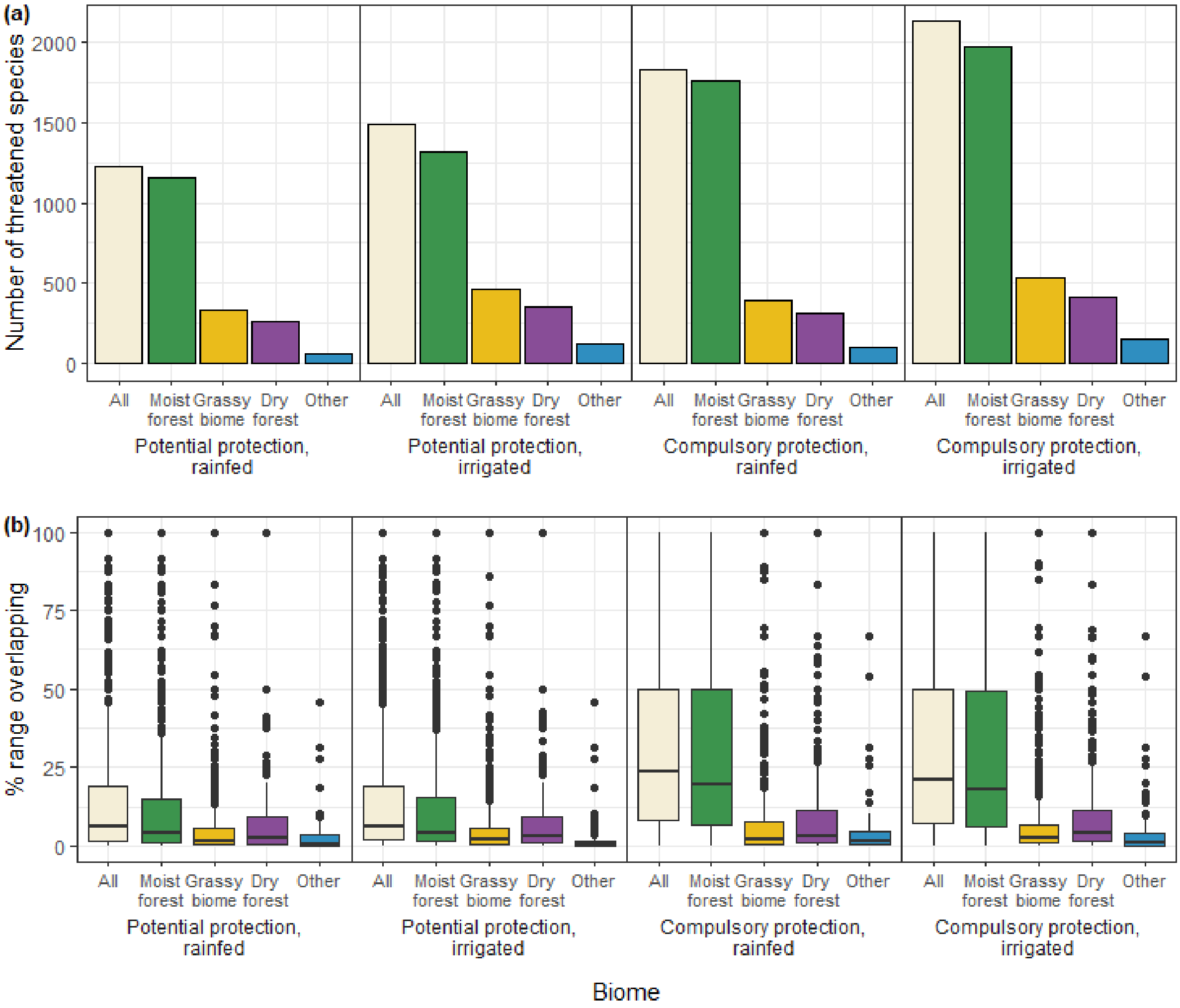


Figure S2.19. Comparison of potential impacts of zero-deforestation oil palm expansion on threatened vertebrates for rainfed and irrigated expansion, and for different habitat protection thresholds. (a) Number of threatened vertebrate species (of a global total of N = 4,895, excluding marine mammals) with overlapping ranges with locations climatically-suitable for zero-deforestation oil palm expansion. (b) Percentage of threatened species' ranges which overlap with locations climatically-suitable for zero-deforestation oil palm expansion. (b) excludes zero values (i.e. where a species does not occur in climatically-suitable, unprotected locations in a given biome). For compulsory protection, locations with aboveground carbon stocks of ≥75 Mg ha^{-1} and ≥50% canopy closure, and/or peat soil are protected; for potential protection (where in practice, protection of low-carbon areas can depend on additional conservation values), locations with aboveground carbon stocks of ≥35 Mg ha^{-1} and ≥30% canopy closure, and/or peat soil are protected. Locations of cropland, urban areas and tree plantations are excluded; as are all IUCN class I/II protected areas. Results for rainfed cultivation and potential habitat protection under zero-deforestation commitments are shown in figure 3.4 of the main article. Here we assume that up to 100% of surplus available water is used for irrigation; panels for 'irrigation' also include suitability for rainfed oil palm.

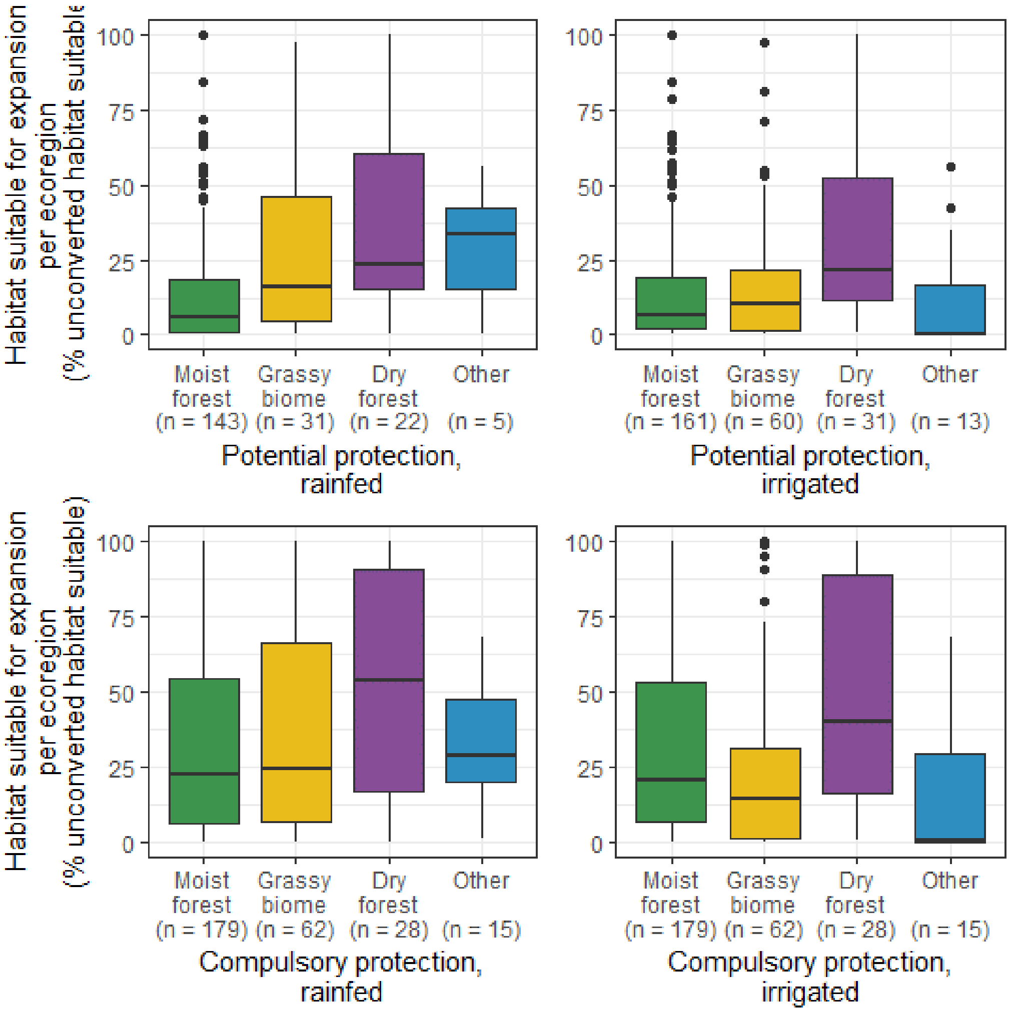


Figure S2.20 Percentages of remaining non-cultivated land per-ecoregion, suitable for oil palm expansion under zero-deforestation commitments, by biome, compared for rainfed and irrigated expansion, and for different thresholds of protection under zero-deforestation commitments (compulsory, potential)**.** For compulsory protection, locations with aboveground carbon stocks of ≥75 Mg ha^{-1} and ≥50% canopy closure, and/or peat soil are protected; for potential protection (where in practice, protection of low-carbon areas can depend on additional conservation values), locations with aboveground carbon stocks of ≥35 Mg ha^{-1} and ≥30% canopy closure, and/or peat soil are protected. Locations of cropland, urban areas and tree plantations are excluded; as are all IUCN class I/II protected areas. Results for rainfed cultivation and potential habitat protection under zero-deforestation commitments are shown in figure 3.4 of the main article. Here we assume that up to 100% of surplus available water is used for irrigation; panels for ‘irrigation’ also include suitability for rainfed oil palm.

Table S2.7. Results of spatial Simultaneous Autoregressive (SAR) error models, examining the potential species richness loss from oil palm expansion, for rainfed expansion and potential protection under zero-deforestation commitments (as presented in the main article). We conducted a separate model for each continental region (Latin America, Africa, Asia/Oceania), for a systematic subset of all 5 arc-minute grid cells of non-cultivated land potentially suitable for oil palm expansion (every 16th grid-cell is included in the models). We obtained estimates of parameter significance (likelihood ratio and *p*-value) by comparing models without the given parameter to the full model, so significant parameters have a higher AIC value than the full model. All full models were fitted with biome, protection under zero-deforestation commitments (ZDC-protection) and the interaction between these. We excluded groups with insufficient sample size (*n* <30) from the models, so some combinations of biome and continent are not displayed (including all 'other' biome; see fig. S2.18).

Latin America full model

Full (final) model: Nagelkerke pseudo-R^2 = 0.957

Spatial error term: lambda = 0.984, likelihood ratio = 11637, *p*-value <0.001

Effect removed	**AIC**	**Log likelihood**	**Likelihood ratio**	**Degrees of freedom**	***p*-value**
None (full model)	48239	-24111		8	
Biome * ZDC-protection interaction	48468	-24228	233.7	6	<0.001
Biome	53720	-26856	5489.3	4	<0.001
ZDC-protection	48467	-24229	234.4	5	<0.001
ZDC-protection (moist forest)	48309	-24148	72.4	7	<0.001
ZDC-protection (grassy biome)	48241	-24113	4.00	7	0.045
ZDC-protection (dry forest)	48378	-24182	141.3	7	<0.001

Africa full model

Full (final) model: Nagelkerke pseudo-R^2 = 0.828

Spatial error term: lambda = 0.924, likelihood ratio = 3316, *p*-value <0.001

Effect removed	**AIC**	**Log likelihood**	**Likelihood ratio**	**Degrees of freedom**	***p*-value**
None (full model)	18356	-9172		6	
Biome * ZDC-protection interaction	18608	-9299	253.5	5	<0.001
Biome	18619	-9306	266.7	4	<0.001
ZDC-protection	18608	-9300	255.2	4	<0.001
ZDC-protection (moist forest)	18453	-9222	98.7	5	<0.001
ZDC-protection (grassy biome)	18483	-9236	128	5	<0.001

Asia/Australasia full model

Full (final) model: Nagelkerke pseudo-R^2 = 0.726

Spatial error term: lambda = 0.876, likelihood ratio = 1914, *p*-value <0.001

Effect removed	**AIC**	**Log likelihood**	**Likelihood ratio**	**Degrees of freedom**	***p*-value**
None (full model)	15308	-7648		6	
Biome * ZDC-protection interaction	15328	-7659	22.2	5	<0.001
Biome	15353	-7673	49.3	4	<0.001
ZDC-protection	15350	-7671	45.7	4	<0.001
ZDC-protection (moist forest)	15345	-7668	39.1	5	<0.001
ZDC-protection (grassy biome)	15313	-7651	6.8	5	0.009

Table S2.8 Results of spatial Simultaneous Autoregressive (SAR) error models, examining the potential species richness loss from oil palm expansion, for rainfed expansion and compulsory-only protection under zero-deforestation commitments. See table S2.7 legend for details.

Latin America full model

Full (final) model: Nagelkerke pseudo-R^2 = 0.955

Spatial error term: lambda = 0.985, likelihood ratio = 10677, *p*-value <0.001

Effect removed	**AIC**	**Log likelihood**	**Likelihood ratio**	**Degrees of freedom**	***p*-value**
None (full model)	43786	-21887		6	
Biome * ZDC-protection interaction	44295	-22142	511	5	<0.001
Biome	48510	-24251	4728	4	<0.001
ZDC-protection	44302	-22147	520	4	<0.001
ZDC-protection (moist forest)	43822	-21906	34.9	5	<0.001
ZDC-protection (dry forest)	44223	-22107	439	5	<0.001

Africa full model

Full (final) model: Nagelkerke pseudo-R^2 = 0.830

Spatial error term: lambda = 0.924, likelihood ratio = 3364, *p*-value <0.001

Effect removed	**AIC**	**Log likelihood**	**Likelihood ratio**	**Degrees of freedom**	***p*-value**
None (full model)	18324	-9156		6	

Biome * ZDC-protection interaction	18609	-9300	287.1	5	<0.001
Biome	18620	-9306	266.7	4	<0.001
ZDC-protection	18608	-9300	287.5	4	<0.001
ZDC-protection (moist forest)	18430	-9210	107.9	5	<0.001
ZDC-protection (grassy biome)	18467	-9229	145	5	<0.001

Asia/Australasia full model

Full (final) model: Nagelkerke pseudo-R^2 = 0.725

Spatial error term: lambda = 0.879, likelihood ratio = 1792, *p*-value <0.001

Effect removed	**AIC**	**Log likelihood**	**Likelihood ratio**	**Degrees of freedom**	***p*-value**
None (full model)	14539	-7266		4	
ZDC-protection (moist forest only)	14593	-7294	56.1	3	<0.001

Table S2.9. Results of spatial Simultaneous Autoregressive (SAR) error models, examining the potential species richness loss from oil palm expansion, for both rainfed and irrigated expansion and potential protection under zero-deforestation commitments. See table S2.7 legend for details.

Latin America full model

Full (final) model: Nagelkerke pseudo-R^2 = 0.951

Spatial error term: lambda = 0.968, likelihood ratio = 11177, *p*-value <0.001

Effect removed	**AIC**	**Log likelihood**	**Likelihood ratio**	**Degrees of freedom**	***p*-value**
None (full model)	54163	-27074		8	
Biome * ZDC-protection interaction	54339	-27164	180	6	<0.001
Biome	59216	-29604	5061.1	4	<0.001
ZDC-protection	54338	-27164	180.6	5	<0.001
ZDC-protection (moist forest)	54238	-27112	77.0	7	<0.001
ZDC-protection (grassy biome)	54183	-27085	22.1	7	0.045
ZDC-protection (dry forest)	54232	-27109	70.6	7	<0.001

Africa full model

Full (final) model: Nagelkerke pseudo-R^2 = 0.741

Spatial error term: lambda = 0.860, likelihood ratio = 3198, *p*-value <0.001

Effect removed	**AIC**	**Log likelihood**	**Likelihood ratio**	**Degrees of freedom**	***p*-value**
None (full model)	24631	-12309		6	
Biome * ZDC-protection interaction	24851	-12421	223	5	<0.001
Biome	24924	-12458	297.4	4	<0.001
ZDC-protection	24851	-12421	223.9	4	<0.001
ZDC-protection (moist forest)	24747	-12368	118.3	5	<0.001
ZDC-protection (grassy biome)	24717	-12354	88.7	5	<0.001

Asia/Australasia full model

Full (final) model: Nagelkerke pseudo-R^2 = 0.660

Spatial error term: lambda = 0.823, likelihood ratio = 1646, *p*-value <0.001

Effect removed	**AIC**	**Log likelihood**	**Likelihood ratio**	**Degrees of freedom**	***p*-value**
None (full model)	16269	-8129		6	
Biome * ZDC-protection interaction	16300	-8145	32.3	5	<0.001
Biome	16320	-8156	54.9	4	<0.001
ZDC-protection	16308	-8150	42.4	4	<0.001
ZDC-protection (moist forest)	16294	-8142	27.1	5	<0.001
ZDC-protection (grassy biome)	16283	-8136	15.6	5	0.009

Table S2.10 Results of spatial Simultaneous Autoregressive (SAR) error models, examining the potential species richness loss from oil palm expansion, for both rainfed and irrigated expansion and compulsory-only protection under zero-deforestation commitments. See table S2.7 legend for details.

Latin America full model

Full (final) model: Nagelkerke pseudo-R^2 = 0.956

Spatial error term: lambda = 0.979, likelihood ratio = 10497, *p*-value <0.001

Effect removed	**AIC**	**Log likelihood**	**Likelihood ratio**	**Degrees of freedom**	***p*-value**
None (full model)	46559	-23273		6	
Biome * ZDC-protection interaction	46977	-23484	421	5	<0.001
Biome	51300	-25646	4745	4	<0.001
ZDC-protection	46983	-23488	429	4	<0.001

ZDC-protection (moist forest)	46594	-23292	37.4	5	<0.001
ZDC-protection (dry forest)	46911	-23451	354.4	5	<0.001

Africa full model

Full (final) model: Nagelkerke pseudo-R^2 = 0.865

Spatial error term: lambda = 0.865, likelihood ratio = 3362, *p*-value <0.001

Effect removed	**AIC**	**Log likelihood**	**Likelihood ratio**	**Degrees of freedom**	***p*-value**
None (full model)	24549	-12269		6	
Biome * ZDC-protection interaction	24853	-12421	305	5	<0.001
Biome	24928	-12460	382	4	<0.001
ZDC-protection	24851	-12421	305	4	<0.001
ZDC-protection (moist forest)	24667	-12328	119.3	5	<0.001
ZDC-protection (grassy biome)	24699	-12345	152	5	<0.001

Asia/Australasia full model

Full (final) model: Nagelkerke pseudo-R^2 = 0.653

Spatial error term: lambda = 0.827, likelihood ratio = 1521, *p*-value <0.001

Effect removed	**AIC**	**Log likelihood**	**Likelihood ratio**	**Degrees of freedom**	***p*-value**
None (full model)	15322	-7657		4	
ZDC-protection (moist forest only)	15350	-7672	30.8	3	<0.001

Appendix 3

Climate has limited but varied impacts on oil palm yield in industrial plantations: Supplementary information

Supplementary Information 3.1. Calculating anomalies of yield and climate variables

To improve the sensitivity of our analyses to relationships of yield with temperature and rainfall, and to assess the reliability of the relationships we detected for the raw variables, we calculated standardised monthly anomalies for each of the variables (yield, rainfall, Tmax and Tmin) in our analyses. Our analyses of the relationships between raw climate and yield variables incorporated substantial seasonal fluctuations in the climatic predictors of yield (main article fig. 4.2, fig. S3.2), and could therefore result in spurious correlations between the yield and climate variables, which both have regular seasonal cycles (Tinker and Corley, 2015). Additionally, the high autocorrelation among timelags of the raw climatic predictors (fig. S3.3) means that potentially important effects at different timelags could have been masked by the effect at the strongest lag; and we could not include multiple lags of temperature in the same model because of their autocorrelation. We therefore removed regular seasonal patterns from each variable by computing anomalies, enabling us to analyse relationships between 'unexpected' variation in climate and yield for a given month of the year at each oil palm field (see fig. S3.4 for example timeseries of raw and anomalised oil palm yield).

We computed anomalies for each variable (yield, rainfall, Tmax and Tmin) as the difference between each value and the mean of all values for that month for each oil palm field, scaled by the standard deviation of all values for each month and field (i.e. anomalised per time series of oil palm yield data) (equation S3.1).

$$anom_{i,j,k} = \frac{x_{i,j,k} - \bar{x}_{i,j}}{\sigma_{i,j}}$$

Equation S3.1. Calculation of anomalies for month *i* in field *j* and year *k*.

The computed anomaly timeseries were therefore centred at zero and did not incorporate differences in yield mean or variation between spatial locations (oil palm fields or plantations) (see fig. S3.4, S3.9). To ensure that the anomalies were comparable, we only used time series (i.e. data per oil palm field) of a length of one decade, from July 2007 to June 2017, in this analysis, therefore using data from a total of 56 oil palm fields across 12 plantations, and excluding any months for which we had data outside this range.

Supplementary Information 3.2. Determining timelags of climatic predictors of oil palm yield for inclusion in models

For the raw climatic predictors, we found that the strongest absolute correlations of raw yield with Tmax and rainfall occurred at a lag of 14 months (Spearman's Rho of 0.30 with Tmax, and -0.15 with rainfall), and the strongest absolute correlation with Tmin occurred at a lag of 28 months (Spearman's Rho of 0.247) (main text fig. 4.3). Because Tmax and Tmin had high autocorrelation through time (fig. S3.3), and were strongly intercorrelated with each other (table S3.1), including between Tmax at a 14 month lag and Tmin at a 28 month lag (fig. S3.5), we selected the single lag period with the highest absolute correlation with yield from both of these variables: Tmax at a 14 month lag. Our choice of Tmax over Tmin as a predictor of yield was supported by the consistently higher correlation coefficients of Tmax with yield than those for Tmin (main text fig. 3). In addition, we found that yield had the strongest positive correlation with rainfall at a lag of 10 months (Spearman's Rho of 0.082), which appears to be unrelated to the negative correlation at a lag of 14 months because the autocorrelation of rainfall between time periods 4 months apart is very low (Spearman's Rho of 0.025; figs. S3.3, S3.5). We therefore included Tmax and rainfall at a 14 month lag, corresponding to inflorescence development and determination of the number of spikelets per infloresence, and rainfall at a 10 month lag, corresponding to the inflorescence abortion period, as candidate predictors of raw oil palm yield (main text table 4.1, fig. 4.3).

For the anomalised climatic predictors, we found that the correlation coefficients for the climatic predictors of raw yield (climatic variables at specific timelags) were in the same direction as for the raw variables, but considerably weaker (Spearman's Rho of 0.037, -0.075 and 0.062 for Tmax at a 14 month lag, rainfall at a 14 month lag and rainfall at a 10 month lag respectively; main text fig. 4.3). We therefore included the anomalised versions of all three climatic predictors of raw yield as candidate predictors of anomalised yield (Tmax at a 14 month lag, rainfall at a 14 month lag, and rainfall at a 10 month lag), in order to test the robustness of the relationships we derived for raw climate and yield when regular seasonal cycles were removed from the variables. In addition, we found relatively high correlation coefficients of climatic variables at other timelags important for fruit development, suggesting potential additional relationships between climate and yield which we were unable to detect in the analysis of raw climate and yield: Tmax at the month of harvest (Spearman's Rho -0.138), suggesting potential impacts of climate on the harvest itself; Tmin at a 6 month lag (-0.117), corresponding to fruit ripening and pollination, and both Tmin and rainfall at a 29 month lag (0.121 and 0.080 respectively), corresponding to sex determination (main text table 4.1, fig. 4.2). However, Tmin at a 6 month lag was positively correlated with both Tmax at the month of harvest and Tmax at a 14 month lag (Spearman's Rho = 0.327 and 0.304), which could have been driven by high autocorrelation between Tmin lags of up to ~10 months apart, and high correlation between Tmin and Tmax in the same month (figs. S3.3, S3.6, table S3.1). Therefore, we did not include Tmin at a 6 month lag in the models, but included the other six candidate anomalised predictors (Tmax at month of harvest, rainfall at a 10 month lag, Tmax and rainfall at a 14 month lag, and Tmin and rainfall at a 29 month lag).

Supplementary Information 3.3. Specification and selection of optimal model for raw climatic variables and yield

We fitted the initial 'full model' of raw oil palm yield with the following terms: random intercept for plantation; linear and quadratic effects for the three climatic predictors (Tmax at a 14 month lag, rainfall at a 14 month lag, and rainfall at a 10 month lag), and an interaction between Tmax and rainfall at a 14 month lag; a thin plate regression spline for oil palm age (Wood, 2003), to control for the expected non-linear relationship between age and yield (Woittiez *et al.*, 2017); cyclic cubic regression splines for months of the year in each plantation, to account for regular seasonal fluctuations in oil palm yield, with differences in seasonality between plantations. We restricted the basis dimension of each cyclic seasonality spline to a value of 5 (representing wiggliness, corresponding to a maximum of two peaks or troughs per year) to allow for the potential influence of two monsoon seasons (i.e. two peaks within a year) but avoid overfitting (Tang, 2019).

We followed the model selection approach of (i) finding an initial 'full' model which met statistical assumptions and contained all plausible fixed effects, followed by (ii) selection of the optimal error structure (random and autocorrelation terms) fitted with Restricted Maximum Likelihood (REML), and finally (iii) the selection of the optimal fixed effect structure (climatic predictors and smoothers fitted to month and oil palm age) fitted with Maximum Likelihood (ML) (Zuur, Ieno and Smith, 2007). We describe our decisions during model fitting and selection following this approach.

To obtain an initial model with Gaussian, homoscedastic residuals, we found that yield required a square-root transformation (fig. S3.8). During initial model fitting, we identified two outliers of zero-values for yield (interspersed among otherwise positive values), which we removed from subsequent analyses, leaving a dataset of N = 9,731 data points. We proceeded to fit the GAMMs of square-root yield with a Gaussian error function and identity link.

To find the optimal error structure accounting for temporal autocorrelation within the time-series of yield per oil palm field, we compared the AIC values of models fitted with an autocorrelation-moving average structure, for varying orders of autoregressive parameters p and moving average parameters q (i.e. varying in the number of adjacent months that each process operates over). We fitted 49 models with all combinations of p and q of orders 0-6, and found that the model with the lowest AIC had p of order 4 and q of order 4 (table S3.2). We proceeded to optimize the error structure of the model with $p = 4$, $q = 4$, by testing for the optimal random intercept term to account for spatial clustering of the study sites. We found that including a random intercept for plantation (AIC = -4701, fitted with REML) gave a substantially better model fit than with no random intercept term (AIC = -4634), but that including a random intercept for oil palm field within plantation (AIC = -4695) did not improve the model fit compared to plantation alone, so we proceeded with a random intercept of plantation only.

To find the optimal climatic predictor terms, we compared the AIC of models fitted with all combinations of the climatic predictors, on the conditions that (i) we only included quadratic terms when the first-order term was also included and (ii) we fitted interactions for all orders of the interacting terms, and did not separate them to allow interactions for some orders of a term only. Including a model with no climatic predictors, we therefore ran a total of 39 models to find the optimal climatic predictors. All models also included smoothers for seasonality per plantation, and oil palm age, a random intercept for plantation, and an autocorrelation-moving average structure of order $p = 4$, $q = 4$. Because the approximated p-values of the oil palm age smoother and the majority (9 of 12) of seasonality smoothers were very low ($p < 0.001$), and these terms were controlling for sources of variation which were likely to be highly important for oil palm yield, we did not test the importance of these smoother terms by dropping them from the model in combination with the climatic predictors; instead, we verified their importance after finding the optimal set of climatic predictors. We found that the optimal climatic predictor terms were a linear term for rainfall with a 14 month lag, a quadratic term for Tmax at a 14 month lag, and a quadratic term for rainfall at a 10 month lag, with an interaction term between rainfall and Tmax at 14 month lag periods (table S3.3). With these climatic predictors, the smoothers for seasonality per plantation and oil palm age were still highly significant ($p < 0.001$ for oil palm age and 9 of 12 seasonality smoothers); and model fit was considerably better when including these smoothers, and fitting the seasonality smoothers per plantation rather than using a single universal smoother (table S3.4). We therefore proceeded with the final model of square-root oil palm yield predicted by rainfall with a 14 month lag, Tmax at a 14 month lag, rainfall at a 10 month lag, smoothers for seasonality per plantation and oil palm age, a random intercept for plantation and an autocorrelation-moving average error structure of order $p = 4$, $q = 4$ (table S3.5).

Supplementary Information 3.4. Selection of optimal model for climate and yield anomalies

We fitted the initial ‘full model’ of oil palm yield anomalies with the following terms: linear and effects for the six climatic anomaly predictors (Tmax and rainfall at a 14 month lag, rainfall at a 10 month lag, Tmax at a 0 month lag, and Tmin and rainfall at a 29 month lag), and interaction terms between the two pairs of temperature and rainfall variables at the same timelag (Tmax and rainfall at a 14 month lag, and Tmin and rainfall at a 29 month lag); and a thin plate regression spline for oil palm age (Wood, 2003), to control for the expected non-linear relationship between age and yield (Woittiez *et al.*, 2017). We did not include quadratic terms for the climatic anomaly predictors because each anomaly value could correspond to a range of actual climatic values (fig. S3.9), so the optimal value (i.e. expected peak of a quadratic curve) for each predictor would have different anomaly values depending on the oil palm field and month. As for the model of raw climate and yield, we fitted an autoregression-moving average error structure to account for temporal autocorrelation between data points from the same yield time series (i.e. in the same oil palm field). We proceeded with selection of the optimal error structure and fixed effects for GAMs of anomalised yield using a Gaussian error function and identity link, which met model assumptions (fig. S3.10), following the procedure outlined for the models of raw yield (i.e. finding optimal error structure, then finding optimal fixed effects structure; see Supplementary Information 3.3).

To find the optimal error structure accounting for temporal autocorrelation within the time-series of anomalised yield per oil palm field, we compared AIC values of 49 models with all combinations of p and q (autoregressive and moving-average parameters respectively) of orders 0-6, as for the models of raw oil palm yield (see above). We found that the model with the lowest AIC had p of order 6 and q of order 3 (table S3.6).

As for the models of raw oil palm yield, we selected the optimal climatic predictor terms by comparing the AIC of models with different predictor combinations, on the condition that interaction terms were only included when the main effects of the component predictors were also present. We found that the optimal climatic predictor terms were Tmax at a 0 month lag (month of harvest), rainfall at a 10 month lag, Tmax and rainfall at a 14 month lag, and Tmin and rainfall at a 29 month lag; including an interaction term for rainfall and Tmax at a 14 month lag (but not for Tmin and rainfall at a 29 month lag; table S3.7). As during selection of climatic predictors of raw oil palm yield, we maintained the smoother for oil palm age as a fixed effect throughout anomalised climatic predictor selection, as its approximated p-value was very low in the model with full climatic predictor terms ($p < 0.001$). For the optimal climatic predictor terms, we then tested the impact of dropping the smoother for age, and found that model fit was substantially better when the age term was included (AIC = 16936 without age, and AIC = 16779 with age), so we retained it in the model. We therefore proceeded with the final model of anomalised oil palm yield predicted by anomalised Tmax at a 0 month lag, rainfall at a 10 month lag, rainfall at a 14 month lag, Tmax at a 14 month lag, rainfall at a 29 month lag and Tmin at a 29 month lag, with a smoother for oil palm age, and an autocorrelation-moving average error structure of order $p = 6$, $q = 3$ (table S3.8).

Supplementary Information 3.5. Supplementary figures and tables

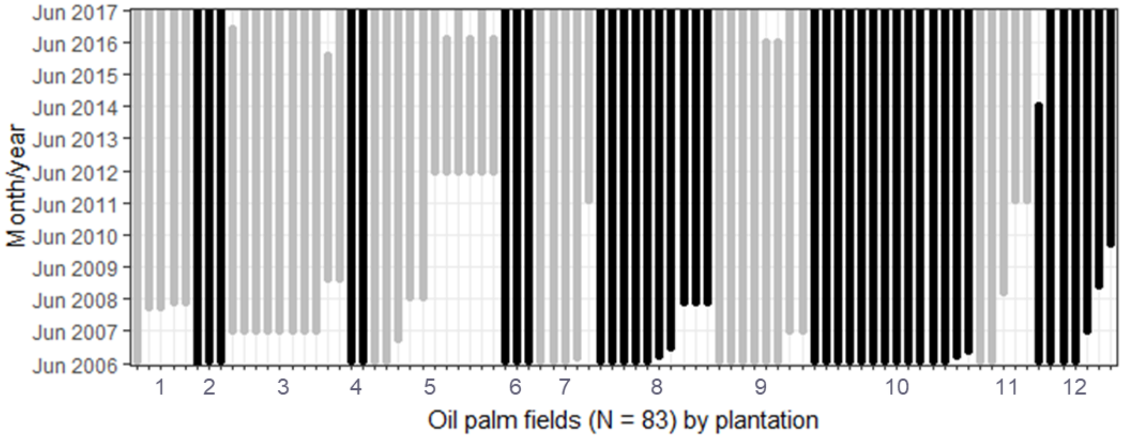


Figure S3.1. Availability of yield data through time for each of the 83 oil palm fields across the 12 plantations. x axis labels refer to the plantation codes (see main article table 4.2) and colours for each plantation alternate between grey and black. The analysis of yield anomalies included data for July 2007 to June 2017 only, so we excluded oil palm fields which did not span this range, giving N = 56.

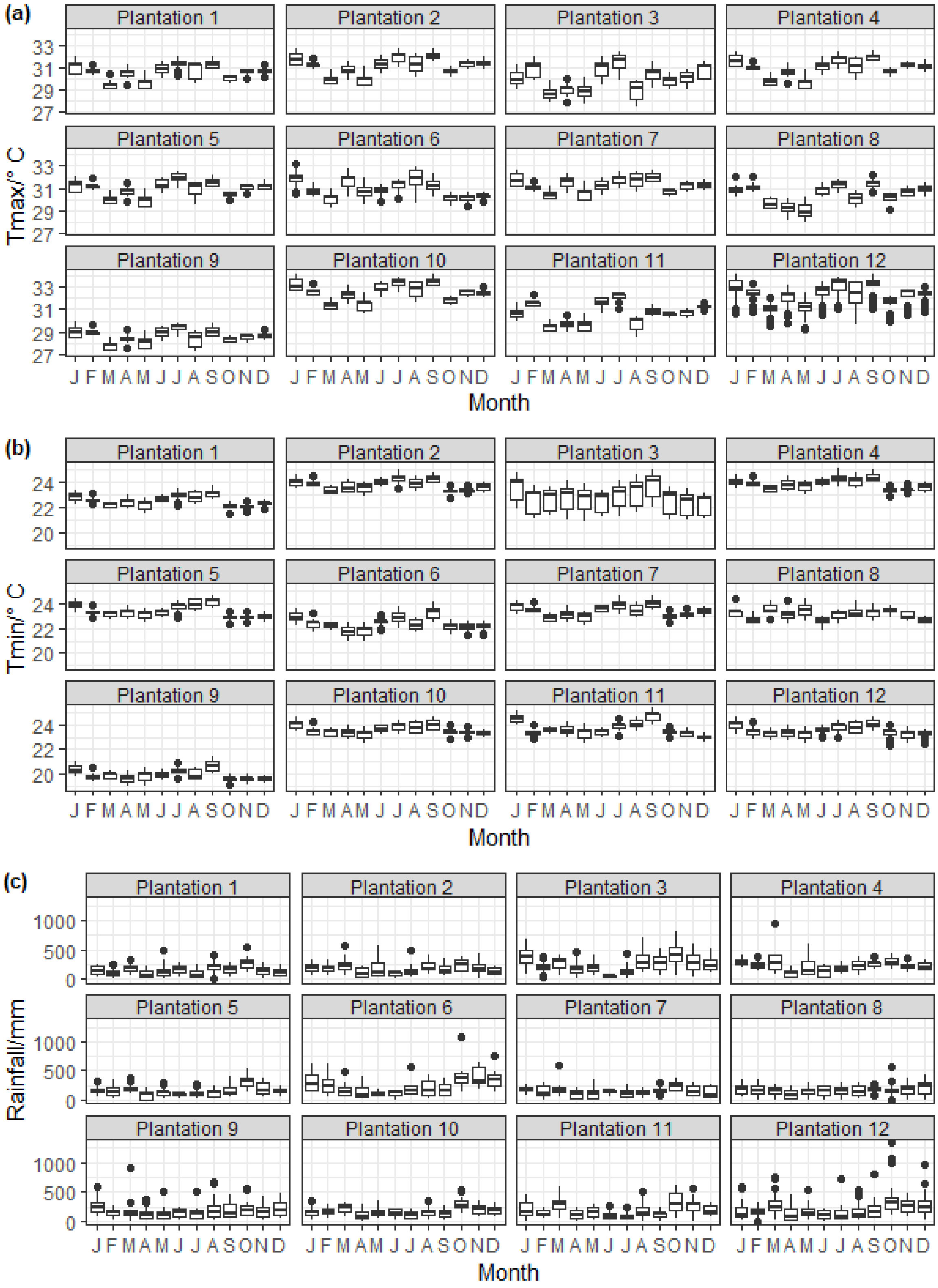


Figure S3.2. Boxplots of monthly values climatic predictors, for the 12 oil palm plantations by month: (a) Tmax; (b) Tmin; (c) rainfall. The plantations are ranked by mean annual yield; note that Plantation 8 is in Sabah whereas the others are all in Peninsular Malaysia (see main article table 4.2).

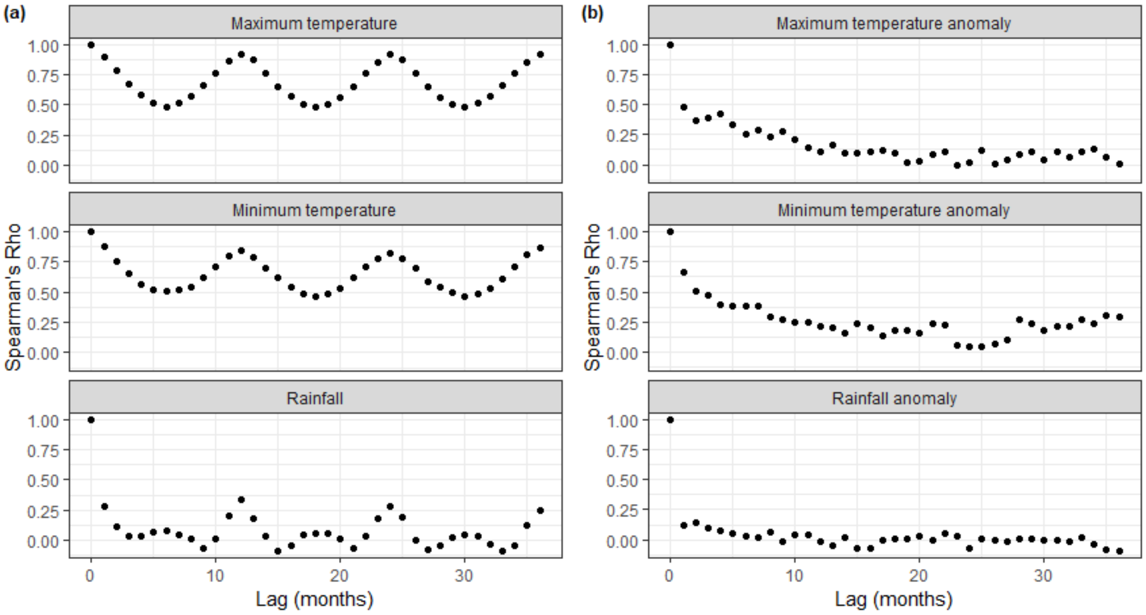


Figure S3.3. Spearman's Rho of autocorrelation of each climatic variable, between the climatic variable and a lagged version of itself, for lags of 0-36 months prior to harvest. (a) raw climatic variables; (b) anomalised climatic variables.

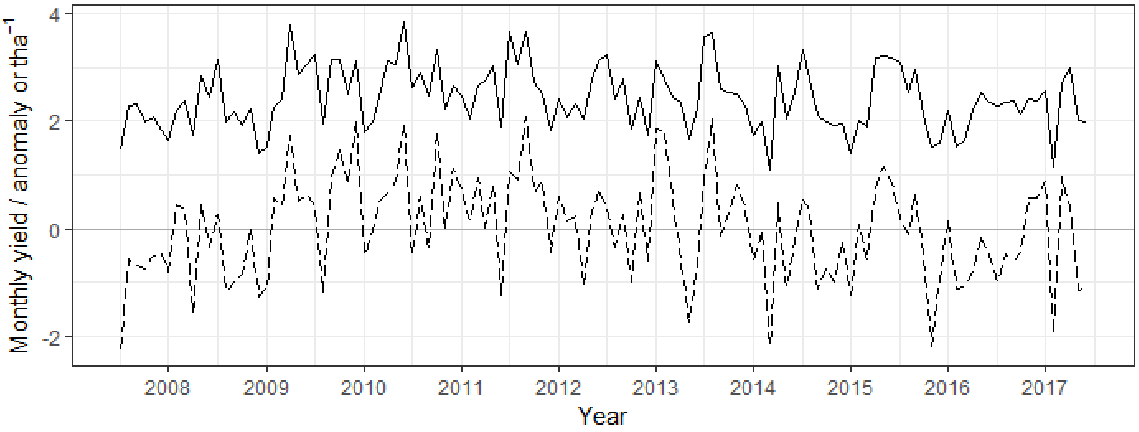


Figure S3.4. Example timeseries of monthly oil palm yield data for a single oil palm field, July 2007 to June 2017. Solid line: raw oil palm yield; dashed line: anomalised oil palm yield.

Table S3.1. Spearman's Rho values for intercorrelation of climatic predictors (without timelags) of oil palm yield. Correlations given in the upper right of the table in normal font are for raw climate variables; correlations given in the lower left of the table in *italic* font are for anomalised climatic variables. Highly intercorrelated predictors (Spearman's Rho >|0.6|) are given in bold text. Rainfall data were obtained from the oil palm company alongside yield data; Tmax and Tmin were obtained from CRU TS v. 4.04 (Harris *et al.*, 2020).

	Rainfall	**Tmax**	**Tmin**
Rainfall	-	-0.138	-0.050
Tmax	*-0.133*	-	**0.618**
Tmin	*-0.0212*	***0.680***	-

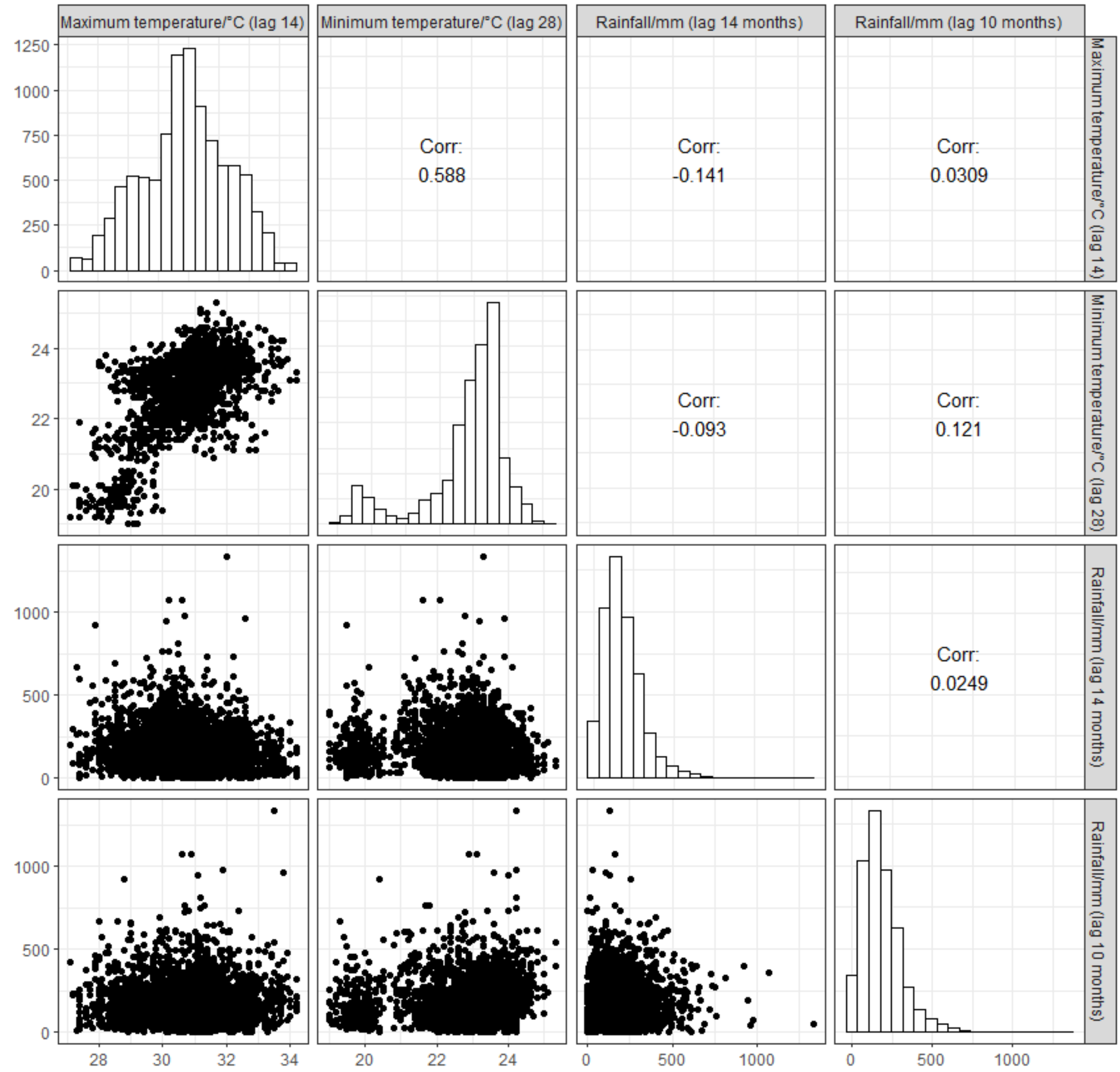


Figure S3.5. Pairwise plot of the four climatic predictors of raw oil palm yield with high correlations with yield (maximum temperature with a lag of 14 months, minimum temperature with a lag of 28 months, rainfall with a lag of 14 months, and rainfall with a lag of 10 months), showing (i) Spearman's Rho correlation coefficients for each pair of predictors; (ii) histograms of each predictor; and (iii) scatterplots of each pair of predictors. We did not include minimum temperature with a lag of 28 months in the GAMM of raw oil palm yield because of its high correlation with maximum temperature at a lag of 14 months.

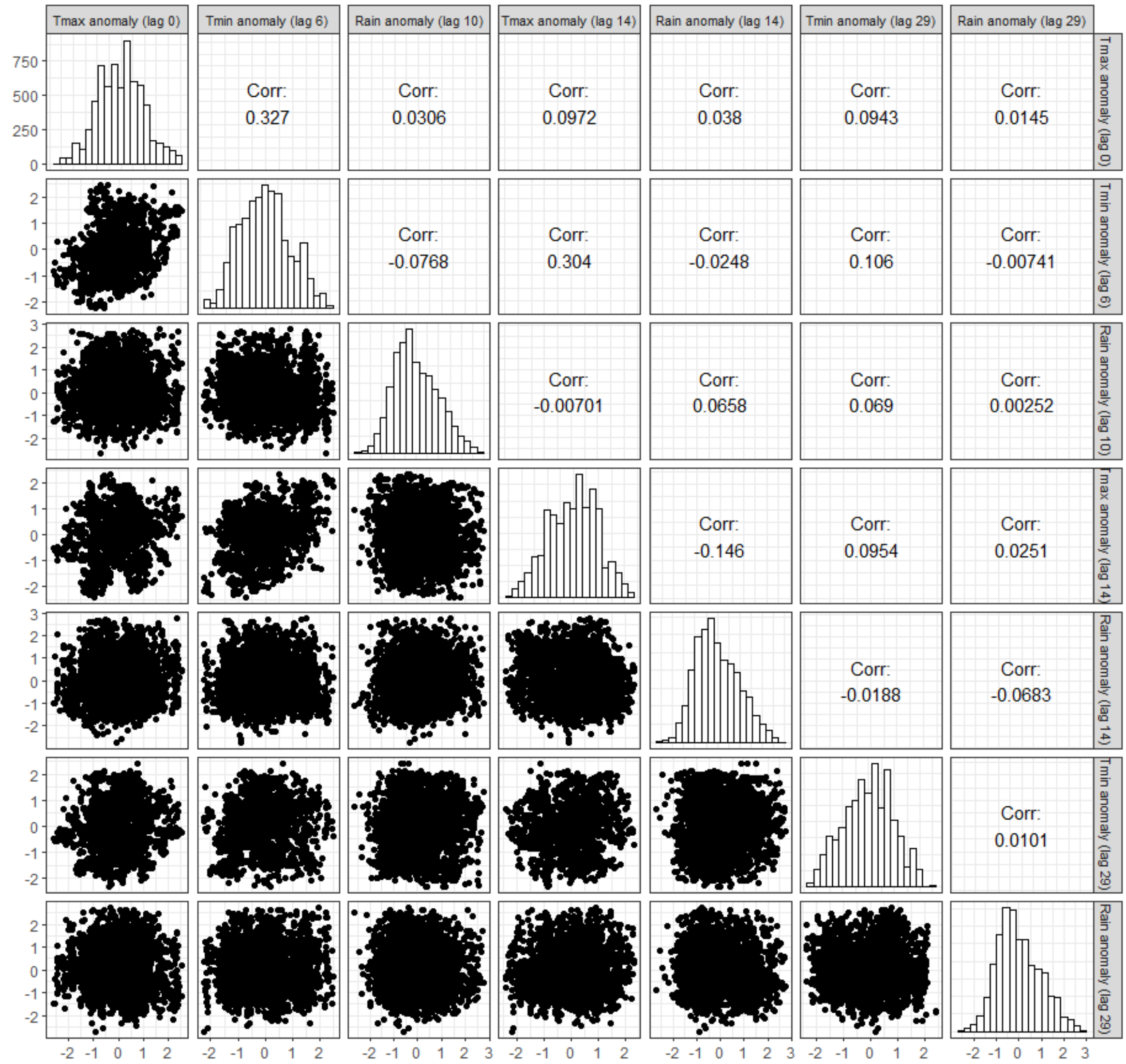


Figure S3.6. Pairwise plot of the seven candidate climatic anomaly predictors of oil palm yield anomalies (maximum temperature with a lag of 0 months, minimum temperature with a lag of 6 months, rainfall with a lag of 10 months, maximum temperature with a lag of 14 months, rainfall with a lag of 14 months, minimum temperature with a lag of 2 months, and rainfall with a lag of 29 months), showing (i) Spearman's Rho correlation coefficients for each pair of predictors; (ii) histograms of each predictor; and (iii) scatterplots of each pair of predictors. We did not include minimum temperature with a lag of 6 months in the GAM of anomalised oil palm yield because of its correlations with maximum temperature at lags of 0 and 14 months, which correspond to the autocorrelation between timesteps of the temperature variables ~6-8 months apart (fig. S3.3).

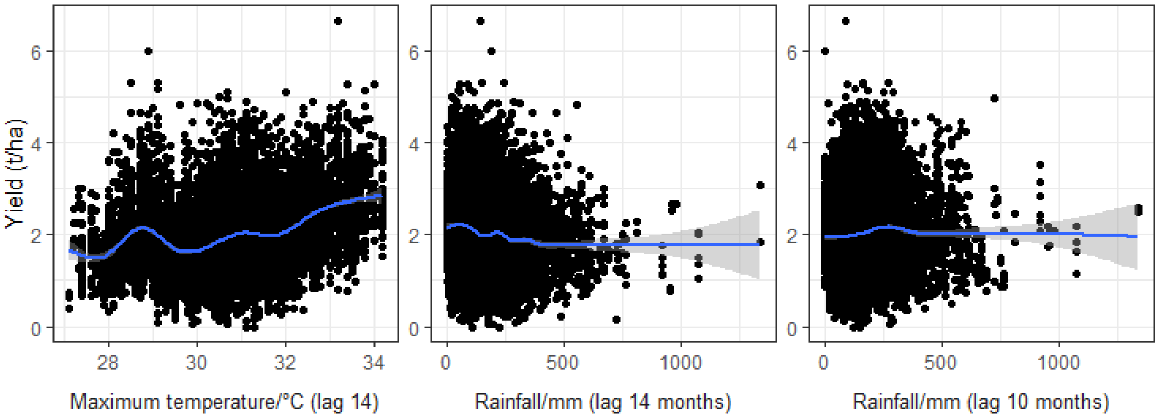


Figure S3.7. Scatterplots of raw oil palm yield and each of its candidate climatic predictors, with smoothing splines (blue lines, cubic spline with shrinkage) and 95% confidence intervals (shading) to indicate the potential shapes of relationships between these.

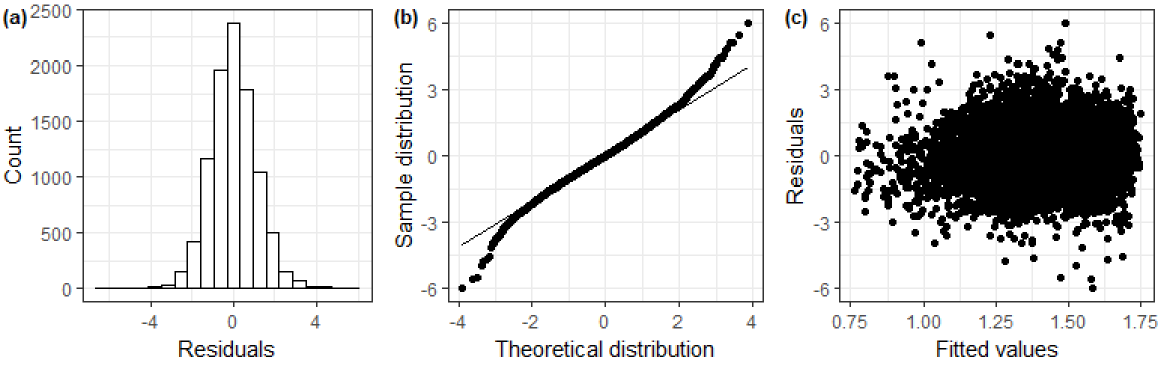


Figure S3.8. Diagnostic plots for checking that error distribution meets model assumptions (of homogeneity of variance, and approximate Normality), for model of raw climate and square-root yield. (a) Histogram of final model residuals (Normalized to account for the fitted error structure); (b) scatterplot of quantiles of the Normalized residuals compared to a theoretical Normal distribution; (c) scatterplot of final model residuals (also Normalized) and fitted values.

Table S3.2. AIC values of full models of raw oil palm yield, fitted with autoregressive-moving average correlation structures of varying orders, using REML. *p* represents the order of autoregressive parameters and *q* represents the order of moving average parameters. NC: No Convergence following 600 iterations of the mixed-effects model optimization algorithm. The best-fitting error structure (i.e. with the lowest AIC) has orders *p* = 4, *q* = 4 and is given in bold. All models included full candidate climatic predictors, smoothing splines for oil palm age and seasonality, and a random intercept for plantation.

		q						
		0	**1**	**2**	**3**	**4**	**5**	**6**
p	**0**	-1461	-2784	-3654	-4044	-4199	-4268	-4303
	1	-3603	-4142	-4279	-4265	-4249	NC	NC
	2	-4241	-4250	-4317	-4286	NC	NC	NC
	3	-4254	-4260	-4318	-4314	NC	-4316	-4305
	4	-4271	-4282	-4425	-4699	**-4701**	NC	NC
	5	-4286	-4287	-4503	NC	-4696	NC	NC
	6	-4292	-4290	-4657	-4500	-4438	NC	NC

Table S3.3. Comparison of model AIC for all combinations of candidate climatic predictors, for the model of raw oil palm yield, by ascending AIC score fitted by ML. We fitted models with an autoregressive-moving average correlation structure of $p = 4$, q = 4, plantation as a random intercept, and smoothing terms for oil palm age and for seasonality per plantation. Rain$_{14}$: rainfall with 14 month timelag; Tmax$_{14}$: Tmax with 14 month timelag; Rain$_{10}$: rainfall with a 10 month timelag. * represents an interaction and + is additive effects. Of the 39 different combinations of climatic predictors, five models did not converge following 1500 iterations of the mixed-effects model optimization algorithm, these are listed at the end ('NC' no convergence). The best model (first row) and all models nested within this are given in **bold** text.

Climatic predictors	**Degrees of freedom**	**AIC**
Rain$_{14}$ * (Tmax$_{14}$ + Tmax$_{14}^2$) + (Rain$_{10}$ + Rain$_{10}^2$)	**32**	**-4679.5**
(Rain$_{14}$ + Rain$_{14}^2$) * Tmax$_{14}$ + (Rain$_{10}$ + Rain$_{10}^2$)	32	-4670.9
(Rain$_{14}$ + Rain$_{14}^2$) + Tmax$_{14}$ + Rain$_{10}$	29	-4670.9
(Rain$_{14}$ + Rain$_{14}^2$) * (Tmax$_{14}$ + Tmax$_{14}^2$) + Rain$_{10}$	34	-4669.4
Rain$_{14}$ * (Tmax$_{14}$ + Tmax$_{14}^2$)	**30**	**-4666.9**
(Rain$_{14}$ + Rain$_{14}^2$) * Tmax$_{14}$	30	-4666.4
(Rain$_{14}$ + Rain$_{14}^2$) + (Tmax$_{14}$ + Tmax$_{14}^2$) + Rain$_{10}$	30	-4666.1
(Rain$_{14}$ + Rain$_{14}^2$) + (Tmax$_{14}$ + Tmax$_{14}^2$)	29	-4666.1
Rain$_{14}$ * Tmax$_{14}$ + Rain$_{10}$	**29**	**-4663.2**
(Rain$_{14}$ + Rain$_{14}^2$) + Tmax$_{14}$	28	-4656.3
Rain$_{14}$ + Tmax$_{14}$	**27**	**-4654.5**
Tmax$_{14}$ + (Rain$_{10}$ + Rain$_{10}^2$)	**28**	**-4642.0**
(Tmax$_{14}$ + Tmax$_{14}^2$) + Rain$_{10}$	**28**	**-4638.8**
(Tmax$_{14}$ + Tmax$_{14}^2$)	**27**	**-4636.6**
Tmax$_{14}$	**26**	**-4636.5**
(Rain$_{14}$ + Rain$_{14}^2$)	27	-4592.6
(Rain$_{14}$ + Rain$_{14}^2$) + Rain$_{10}$	28	-4587.0
Rain$_{14}$	**26**	**-4578.1**
Rain$_{14}$ + (Rain$_{10}$ + Rain$_{10}^2$)	**28**	**-4575.9**
Rain$_{10}$	**26**	**-4544.0**
(Rain$_{10}$ + Rain$_{10}^2$)	**27**	**-4530.4**
(Rain$_{14}$ + Rain$_{14}^2$) * (Tmax$_{14}$ + Tmax$_{14}^2$) + (Rain$_{10}$ + Rain$_{10}^2$)	35	-4436.5
(Rain$_{14}$ + Rain$_{14}^2$) + (Tmax$_{14}$ + Tmax$_{14}^2$) + (Rain$_{10}$ + Rain$_{10}^2$)	31	-4434.4
(Rain$_{14}$ + Rain$_{14}^2$) * Tmax$_{14}$ + Rain$_{10}$	31	-4427.7
Rain$_{14}$ * (Tmax$_{14}$ + Tmax$_{14}^2$) + Rain$_{10}$	**31**	**-4426.1**
Rain$_{14}$ + (Tmax$_{14}$ + Tmax$_{14}^2$) + (Rain$_{10}$ + Rain$_{10}^2$)	**30**	**-4423.2**
Rain$_{14}$ + (Tmax$_{14}$ + Tmax$_{14}^2$) + Rain$_{10}$	**29**	**-4419.0**
(Tmax$_{14}$ + Tmax$_{14}^2$) + (Rain$_{10}$ + Rain$_{10}^2$)	**29**	**-4404.7**
Tmax$_{14}$ + Rain$_{10}$	**27**	**-4400.5**
(Rain$_{14}$ + Rain$_{14}^2$) + (Rain$_{10}$ + Rain$_{10}^2$)	29	-4384.8
Rain$_{14}$ + Rain$_{10}$	**27**	**-4367.3**
Rain$_{14}$ + Tmax$_{14}$ + (Rain$_{10}$ + Rain$_{10}^2$)	**28**	**-4283.7**
Rain$_{14}$ + Tmax$_{14}$ + Rain$_{10}$	**28**	**-4272.3**
-	**25**	**-4169.5**
Rain$_{14}$ * Tmax$_{14}$ + (Rain$_{10}$ + Rain$_{10}^2$)	**NC**	**NC**

(Rain$_{14}$ + Rain$_{14}^2$) * (Tmax$_{14}$ + Tmax$_{14}^2$)	NC	NC
Rain$_{14}$ + (Tmax$_{14}$ + Tmax$_{14}^2$)	**NC**	**NC**
(Rain$_{14}$ + Rain$_{14}^2$) + Tmax$_{14}$ + (Rain$_{10}$ + Rain$_{10}^2$)	NC	NC
Rain$_{14}$ * Tmax$_{14}$	**NC**	**NC**

Table S3.4. Comparison of model AIC for models excluding smoothing terms, for the model of raw oil palm yield, by ascending AIC score fitted by ML. The age smoother was a thin plate regression spline; and the seasonality smoother was a cyclic cubic regression spline fitted over months, with basis dimension restricted to a value of 5, fitted either per plantation (12 separate smoothers) or with a single universal smoother. We fitted models with the best climatic predictor terms (table S3.3, and first model in this table), with an autoregressive-moving average correlation structure of p = 4, q = 4, and plantation as a random intercept. NC: models did not converge following 1500 iterations of the mixed-effects model optimization algorithm.

Smoothed predictors	**Degrees of freedom**	**AIC**
Age + seasonality (per plantation)	32	-4679.5
Age + seasonality (universal)	21	-4565.6
Seasonality (per plantation)	30	-4504.3
Age	20	-4473.8
Seasonality (universal)	NC	NC
-	NC	NC

Table S3.5. Fitted effects for final GAMM explaining raw oil palm yield (fitted with square-root yield as the response). We do not provide *p*-values for the effects as accurate *p*-values are not currently available for GAMMs. Quadratic terms were fitted using orthogonal polynomials. Rain$_{14}$: rainfall with 14 month timelag; Tmax$_{14}$: Tmax with 14 month timelag; Rain$_{10}$: rainfall with a 10 month timelag; ϕ_i: autoregressive term of order *i*; θ_i: moving-average term of order *i*. The interaction between two terms is represented by a colon (:).

Parametric fixed effects		
Term	**Estimated effect value**	**Standard error**
Intercept	1.37	0.038
Rain$_{14}$	-0.01	0.002
Tmax$_{14}$	5.32	0.56
Tmax$_{14}^2$	-0.96	0.36
Rain$_{10}$	0.64	0.20
Rain$_{10}^2$	-0.49	0.18
Rain$_{14}$: Tmax$_{14}$	-0.65	0.22
Rain$_{14}$: Tmax$_{14}^2$	0.33	0.19
Smooth terms		
Term	**Estimated degrees of freedom**	
Age	7.62	
Seasonality (Plantation 1)	2.90	
Seasonality (Plantation 2)	2.75	
Seasonality (Plantation 3)	0.00	
Seasonality (Plantation 4)	2.83	
Seasonality (Plantation 5)	2.01	
Seasonality (Plantation 6)	2.85	
Seasonality (Plantation 7)	2.87	
Seasonality (Plantation 8)	2.75	
Seasonality (Plantation 9)	2.90	
Seasonality (Plantation 10)	1.95	
Seasonality (Plantation 11)	2.73	
Seasonality (Plantation 12)	2.03	

Random intercept (plantation)	
Fitted intercepts	**Standard deviation**
See table S3.1	0.375
Autoregression-moving average error structure	
Term	**Fitted parameter estimate**
ϕ_1	2.14
ϕ_2	-1.22
ϕ_3	-0.32
ϕ_4	0.40
θ_1	-1.85
θ_2	0.93
θ_3	0.22
θ_4	-0.26

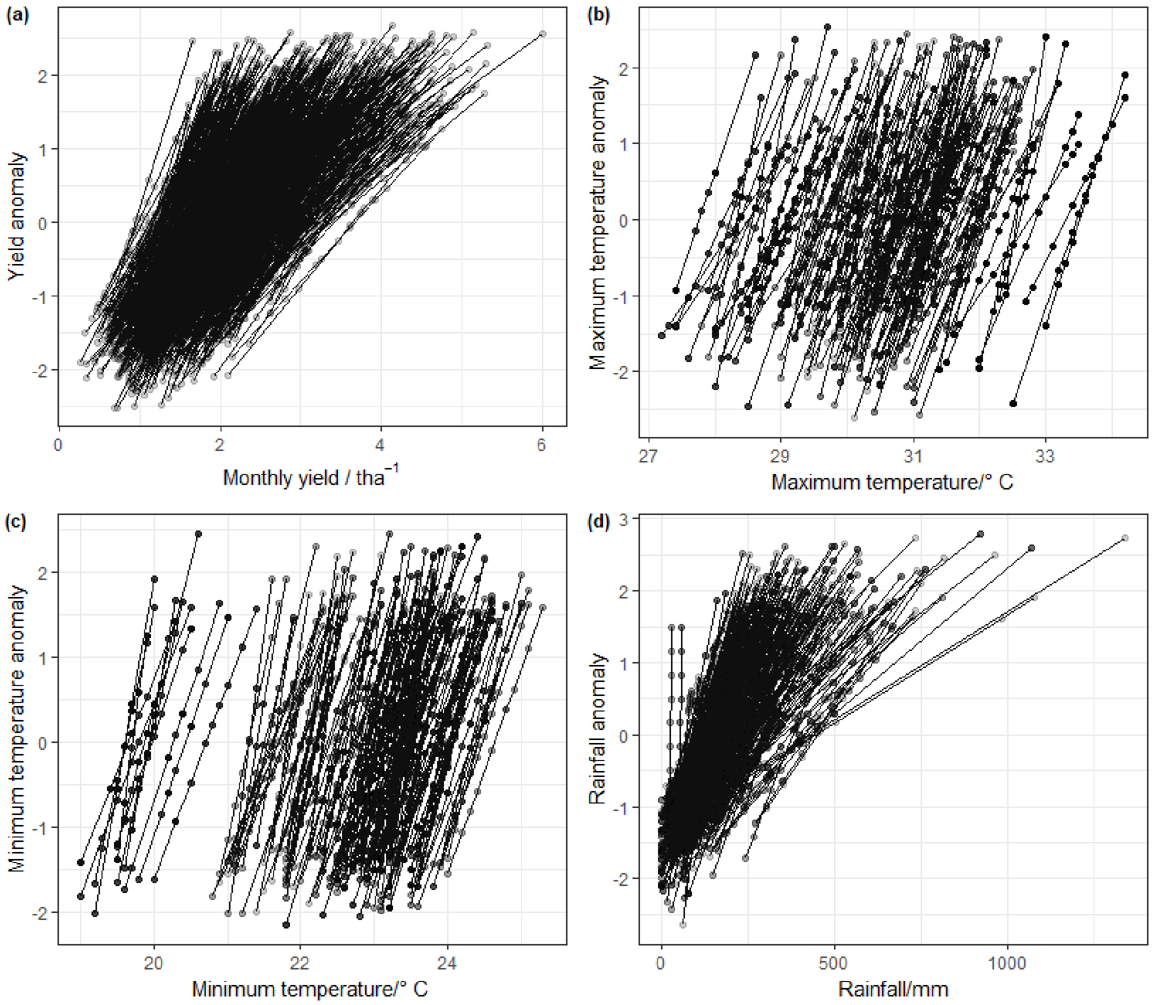


Figure S3.9. Comparison of raw and anomalised values of yield and the three climatic variables. Lines connect points within the same month and same oil palm field (the resolution of anomaly calculations). Points are translucent and therefore darker where data overlap. There are fewer lines for temperature than yield and rainfall because temperature data was at a lower spatial resolution and therefore repeated between some oil palm fields (see main text Methods and fig. 4.1).

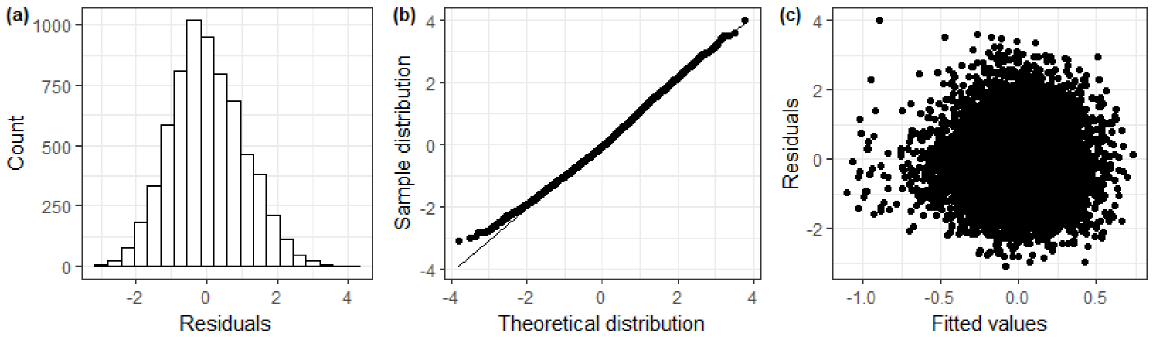


Figure S3.10. Diagnostic plots for checking that error distribution meets model assumptions (of homogeneity of variance, and approximate Normality), for model of anomalised climate and yield. (a) Histogram of final model residuals (Normalized to account for the fitted error structure); (b) scatterplot of quantiles of the Normalized residuals compared to a theoretical Normal distribution; (c) scatterplot of final model residuals (also Normalized) and fitted values.

Table S3.6. AIC values of full models of anomalised oil palm yield, fitted with autoregressive-moving average correlation structures of varying orders, using REML. *p* represents the order of autoregressive parameters and *q* represents the order of moving average parameters. NC: No Convergence following 600 iterations of the mixed-effects model optimization algorithm. The best-fitting error structure (i.e. with the lowest AIC) has orders *p* = 6, *q* = 3 and is given in bold. All models included full candidate climatic predictors, smoothing splines for oil palm age and seasonality, and a random intercept for plantation.

		q						
		0	**1**	**2**	**3**	**4**	**5**	**6**
p	**0**	17840	17543	17197	17047	17022	17021	17023
	1	17401	17163	17056	17033	NC	17023	17025
	2	17073	17066	17015	17025	17025	17027	NC
	3	17060	17055	17002	17003	NC	17011	NC
	4	17039	17015	17002	16930	16909	NC	17002
	5	17014	17009	16909	16925	16901	16914	NC
	6	17009	17010	16907	**16842**	NC	16903	NC

Table S3.7. Comparison of model AIC for all combinations of predictors, for the model of oil palm yield anomalies, by ascending AIC score fitted by ML. We fitted models with an autoregressive-moving average correlation structure of *p* = 6, q = 3; and varied the combinations of the predictors of anomalised climatic variables at specified lags, and a smoother for oil palm age. Tmax$_0$: Tmax with 0 month timelag (at month of harvest); Rain$_{10}$: rainfall with a 10 month timelag; Rain$_{14}$: rainfall with 14 month timelag; Tmax$_{14}$: Tmax with 14 month timelag; Tmin$_{29}$: Tmin with 29 month timelag; Rain$_{29}$: rainfall with 29 month timelag; * represents an interaction and + is additive effects. Of the 200 possible combinations of climatic predictors, only 48 models converged following 1500 iterations of the mixed-effects model optimization algorithm, and only these are included in the table. The best model (first row) and all models nested within this are given in **bold** text.

Climatic predictors	Degrees of freedom	AIC
Tmax$_0$ + Rain$_{10}$ + Rain$_{14}$ * Tmax$_{14}$ + Rain$_{29}$ * Tmin$_{29}$	21	16779.0
Tmax$_0$ + Rain$_{10}$ + Rain$_{14}$ * Tmax$_{14}$ + Rain$_{29}$ + Tmin$_{29}$	**20**	**16780.7**
Tmax$_0$ + Rain$_{10}$ + Tmax$_{14}$ + Rain$_{29}$ * Tmin$_{29}$	19	16786.7
Tmax$_0$ + Rain$_{10}$ + Rain$_{14}$ + Rain$_{29}$ * Tmin$_{29}$	19	16791.7
Tmax$_0$ + Rain$_{10}$ + Rain$_{14}$ + Rain$_{29}$ + Tmin$_{29}$	**18**	**16794.3**
Tmax$_0$ + Rain$_{14}$ * Tmax$_{14}$ + Rain$_{29}$ + Tmin$_{29}$	**19**	**16798.9**
Tmax$_0$ + Rain$_{10}$ + Rain$_{29}$ * Tmin$_{29}$	18	16804.0
Tmax$_0$ + Tmax$_{14}$ + Rain$_{29}$ + Tmin$_{29}$	**17**	**16805.0**
Tmax$_0$ + Rain$_{10}$ + Rain$_{14}$ + Tmax$_{14}$ + Tmin$_{29}$	**18**	**16808.6**
Tmax$_0$ + Rain$_{14}$ + Rain$_{29}$ * Tmin$_{29}$	18	16810.4
Tmax$_0$ + Rain$_{14}$ + Rain$_{29}$ + Tmin$_{29}$	**17**	**16812.1**
Tmax$_0$ + Rain$_{14}$ + Tmin$_{29}$	**16**	**16837.5**
Rain$_{10}$ + Rain$_{14}$ * Tmax$_{14}$ + Rain$_{29}$ * Tmin$_{29}$	20	16845.7
Rain$_{10}$ + Tmax$_{14}$ + Rain$_{29}$ * Tmin$_{29}$	18	16852.7
Rain$_{10}$ + Rain$_{14}$ + Rain$_{29}$ * Tmin$_{29}$	18	16863.2
Tmax$_{14}$ + Rain$_{29}$ + Tmin$_{29}$	**16**	**16866.2**
Rain$_{10}$ + Rain$_{14}$ + Tmax$_{14}$ + Tmin$_{29}$	**17**	**16874.8**
Rain$_{10}$ + Rain$_{14}$ * Tmax$_{14}$ + Tmin$_{29}$	**18**	**16875.5**
Rain$_{14}$ + Rain$_{29}$ * Tmin$_{29}$	17	16876.9
Rain$_{10}$ + Tmax$_{14}$ + Tmin$_{29}$	**16**	**16885.8**
Rain$_{14}$ * Tmax$_{14}$ + Tmin$_{29}$	**17**	**16888.0**
Rain$_{29}$ + Tmin$_{29}$	**15**	**16889.2**
Tmax$_0$ + Rain$_{10}$ + Rain$_{14}$ + Tmax$_{14}$ + Rain$_{29}$	**18**	**16910.6**
Tmax$_0$ + Rain$_{10}$ + Rain$_{14}$ * Tmax$_{14}$ + Rain$_{29}$	**19**	**16912.3**
Tmax$_0$ + Rain$_{10}$ + Rain$_{14}$ + Tmax$_{14}$	**17**	**16932.1**
Tmax$_0$ + Rain$_{14}$ * Tmax$_{14}$ + Rain$_{29}$	**18**	**16933.5**
Tmax$_0$ + Rain$_{10}$ + Rain$_{14}$ * Tmax$_{14}$	**18**	**16933.9**
Tmax$_0$ + Rain$_{14}$ + Rain$_{29}$	**16**	**16937.6**
Tmax$_0$ + Rain$_{10}$ + Rain$_{14}$	**16**	**16937.6**
Tmax$_0$ + Rain$_{10}$	**15**	**16952.4**
Tmax$_0$ + Rain$_{14}$ + Tmax$_{14}$	**16**	**16952.6**
Rain$_{10}$ + Rain$_{14}$ + Tmax$_{14}$ + Rain$_{29}$	**17**	**16987.1**
Tmax$_0$ + Rain$_{10}$ + Tmax$_{14}$ + Rain$_{29}$	**17**	**16989.2**
Rain$_{10}$ + Tmax$_{14}$ + Rain$_{29}$	**16**	**16995.1**

$\text{Rain}_{10} + \text{Rain}_{14} + \text{Rain}_{29}$	**16**	**16996.1**
$\text{Rain}_{14} * \text{Tmax}_{14} + \text{Rain}_{29}$	**17**	**17005.1**
$\text{Tmax}_{0} + \text{Rain}_{10} + \text{Tmax}_{14}$	**16**	**17007.7**
$\text{Tmax}_{0} + \text{Rain}_{14} + \text{Tmax}_{14} + \text{Rain}_{29}$	**17**	**17007.9**
$\text{Rain}_{10} + \text{Rain}_{14} + \text{Tmax}_{14}$	**16**	**17008.9**
$\text{Tmax}_{14} + \text{Rain}_{29}$	**15**	**17009.6**
$\text{Tmax}_{0} + \text{Tmax}_{14} + \text{Rain}_{29}$	**16**	**17010.0**
$\text{Rain}_{10} + \text{Rain}_{14} * \text{Tmax}_{14}$	**17**	**17010.9**
$\text{Rain}_{14} + \text{Rain}_{29}$	**15**	**17011.5**
$\text{Rain}_{10} + \text{Rain}_{14}$	**15**	**17017.0**
Rain_{29}	**14**	**17021.6**
$\text{Rain}_{14} + \text{Tmax}_{14}$	**15**	**17024.2**
$\text{Tmax}_{0} + \text{Rain}_{29}$	**15**	**17024.8**
$\text{Rain}_{14} * \text{Tmax}_{14}$	**16**	**17026.1**
Rain_{10}	**14**	**17032.3**
Tmax_{14}	**14**	**17033.3**
Tmax_{0}	**14**	**17041.7**

Table S3.8. Fitted effects for final GAM explaining oil palm yield anomalies. We do not provide *p*-values for the effects as accurate *p*-values are not currently available for models fitted with this R function (see main text Methods). All climatic variables are anomalised. Tmax_0: Tmax with 0 month timelag (at month of harvest); Rain_{10}: rainfall with a 10 month timelag; Rain_{14}: rainfall with 14 month timelag; Tmax_{14}: Tmax with 14 month timelag; Tmin_{29}: Tmin with 29 month timelag; Rain_{29}: rainfall with 29 month timelag; ϕ_i: autoregressive term of order *i*; θ_i: moving-average term of order *i*. The interaction between two terms is represented by a colon (:).

Parametric fixed effects		
Term	**Estimated effect value**	**Standard error**
Intercept	-0.00548	0.0201
Tmax_0	-0.105	0.0126
Rain_{10}	0.0487	0.0108
Rain_{14}	-0.0343	0.0110
Tmax_{14}	0.0492	0.0125
Rain_{29}	0.0601	0.0109
Tmin_{29}	0.152	0.0126
$\mathrm{Rain}_{14} : \mathrm{Tmax}_{14}$	0.0153	0.0104
Smooth terms		
Term	**Estimated degrees of freedom**	
Age	7.47	
Autoregression-moving average error structure		
Term	**Fitted parameter estimate**	
ϕ_1	1.009	
ϕ_2	0.974	
ϕ_3	-1.13	
ϕ_4	-0.185	
ϕ_5	0.158	
ϕ_6	0.107	
θ_1	-0.815	
θ_2	-0.937	
θ_3	0.878	

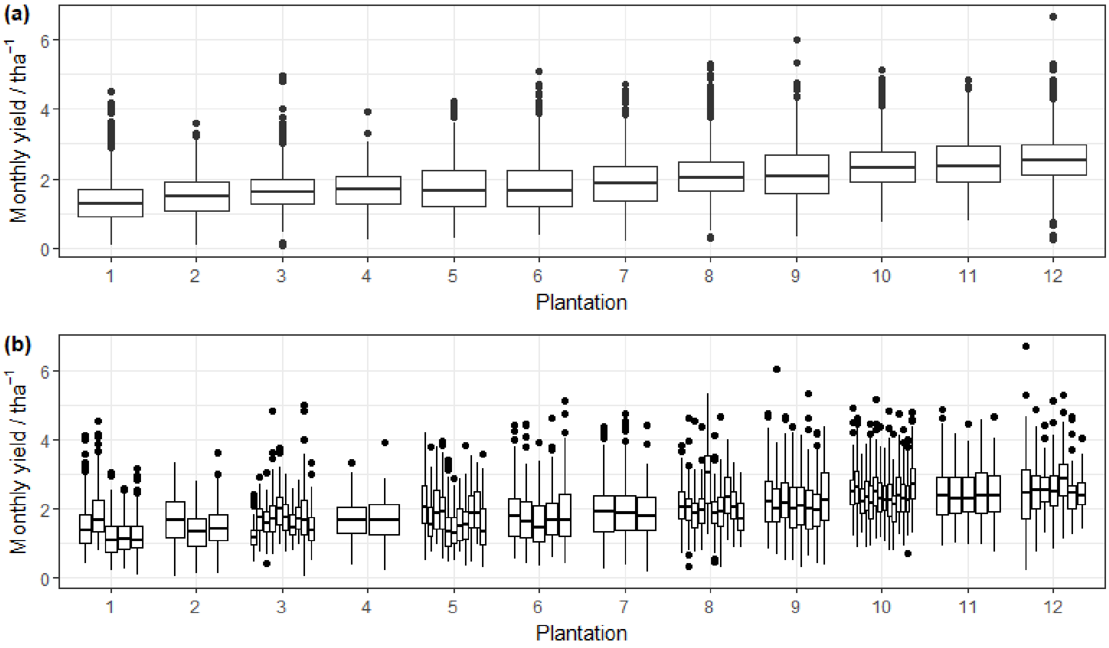


Figure S3.11. Boxplots of monthly yield values for the 12 oil palm plantations, ranked by mean annual yield (see main text table 4.2). (a) All monthly yield values for a plantation; (b) Monthly yield values are shown by oil palm field (smallest level of management, at which we have one oil palm yield value per month) within each plantation.

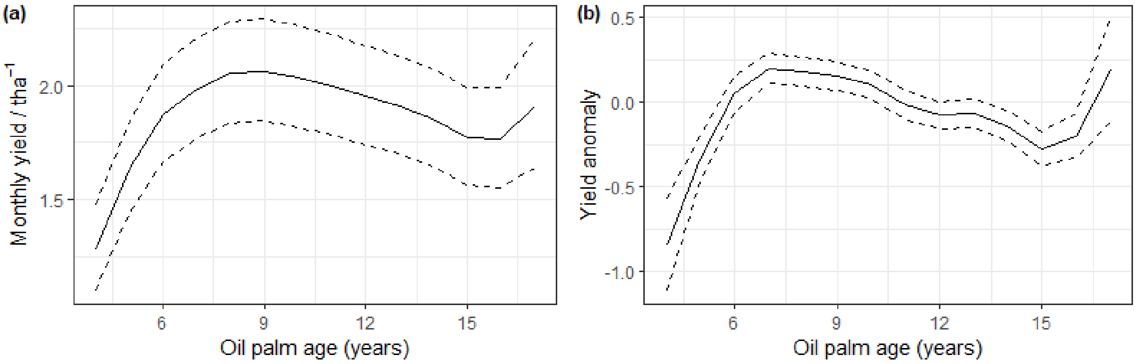


Figure S3.12. Relationship of oil palm age with yield (expected values and 95% confidence intervals). (a) Predicted raw yield values for oil palm age from the final GAMM of raw climatic variables and raw yield, with all other numeric predictors held at median value. (b) Predicted yield anomaly values for oil palm age from the final GAM of yield and climate anomalies, with all anomalised climate predictors held at 0. In both models, oil palm age was fitted by a thin plate regression spline smoother.

Table S3.9. Approximate R^2 values (proportion of variation explained) of the final models of climate and yield, and the change in R^2 when predictors are dropped from the model (ΔR^2), for (a) raw yield and climate variables, and (b) yield and climate anomalies. Negative ΔR^2 values of high magnitude indicate that predictors explain a substantial proportion of the total variation explained. We calculated R^2 as the squared correlation between the response variable and the predicted values (including the effect of the random intercept in predictions when stated), so it is therefore an approximation of the proportion of variance explained by the model, and does not incorporate the multiple levels of variance structure in the models (fixed effects, random intercept and autoregressive-moving average error structure). Whilst some very small, positive ΔR^2 values suggest that certain predictors do not improve model fit to the data, all predictors improved model AIC and we therefore retained them in the model for improved predictive accuracy (Supplementary Information 3.3, 3.4). RI(Plantation): random intercept term for plantation; s(Month): cyclic smoother for months of the year, representing regular seasonal fluctuations in yield; s(Age): smoother for oil palm age. NC: model convergence not achieved.

(a) Model of raw climatic variables and raw oil palm yield			
Predictor removed	**Predictors in model**	**R^2 (approx.)**	**ΔR^2**
None (full model)	$Rain_{14}$ * ($Tmax_{14}$ + $Tmax_{14}^2$) + ($Rain_{10}$ + $Rain_{10}^2$) + s(Month) * Plantation + s(Age) + RI(Plantation)	0.384	
All climatic variables	s(Month) * Plantation + s(Age) + RI(Plantation)	0.383	-0.001
$Tmax_{14}$	$Rain_{14}$ + ($Rain_{10}$ + $Rain_{10}^2$) + s(Month) * Plantation + s(Age) + RI(Plantation)	0.370	-0.014
$Rain_{14}$	($Tmax_{14}$ + $Tmax_{14}^2$) + ($Rain_{10}$ + $Rain_{10}^2$) + s(Month) * Plantation + s(Age) + RI(Plantation)	0.389	0.005
$Rain_{10}$	$Rain_{14}$ * ($Tmax_{14}$ + $Tmax_{14}^2$) + s(Month) * Plantation + s(Age) + RI(Plantation)	0.383	-0.001
$Rain_{14}$ * $Tmax_{14}$ interaction	$Rain_{14}$ + ($Tmax_{14}$ + $Tmax_{14}^2$) + ($Rain_{10}$ + $Rain_{10}^2$) + s(Month) * Plantation + s(Age) + RI(Plantation)	0.391	0.007
Plantation (all terms)	$Rain_{14}$ * ($Tmax_{14}$ + $Tmax_{14}^2$) + ($Rain_{10}$ + $Rain_{10}^2$) + s(Month) + s(Age)	0.177	-0.207
Plantation (interaction with Month only)	$Rain_{14}$ * ($Tmax_{14}$ + $Tmax_{14}^2$) + ($Rain_{10}$ + $Rain_{10}^2$) + s(Month) + s(Age) + RI(Plantation)	0.343	-0.041

Plantation (random intercept only)	Rain$_{14}$ * (Tmax$_{14}$ + Tmax$_{14}^{2}$) + (Rain$_{10}$ + Rain$_{10}^{2}$) + s(Month) * Plantation + s(Age)	0.213	-0.171
Age	Rain$_{14}$ * (Tmax$_{14}$ + Tmax$_{14}^{2}$) + (Rain$_{10}$ + Rain$_{10}^{2}$) + s(Month) * Plantation + RI(Plantation)	0.325	-0.059
Month	Rain$_{14}$ * (Tmax$_{14}$ + Tmax$_{14}^{2}$) + (Rain$_{10}$ + Rain$_{10}^{2}$) + s(Age) + RI(Plantation)	0.308	-0.076
(b) Model of climatic anomalies and oil palm yield anomalies			
Predictor removed	**Predictors in model**	***R*^{2}**	**Δ*R*^{2}**
None (full model)	Tmax$_{0}$ + Rain$_{10}$ + Rain$_{14}$ * Tmax$_{14}$ + Rain$_{29}$ + Tmin$_{29}$ + s(Age)	0.090	
All climatic variables	s(Age)	NC	NC
Tmax$_{0}$	Rain$_{10}$ + Rain$_{14}$ * Tmax$_{14}$ + Rain$_{29}$ + Tmin$_{29}$ + s(Age)	NC	NC
Rain$_{10}$	Tmax$_{0}$ + Rain$_{14}$ * Tmax$_{14}$ + Rain$_{29}$ + Tmin$_{29}$ + s(Age)	0.087	-0.003
Tmax$_{14}$	Tmax$_{0}$ + Rain$_{10}$ + Rain$_{14}$ + Rain$_{29}$ + Tmin$_{29}$ + s(Age)	0.084	-0.006
Rain$_{14}$	Tmax$_{0}$ + Rain$_{10}$ + Tmax$_{14}$ + Rain$_{29}$ + Tmin$_{29}$ + s(Age)	NC	NC
Rain$_{14}$ * Tmax$_{14}$ interaction	Tmax$_{0}$ + Rain$_{10}$ + Rain$_{14}$ + Tmax$_{14}$ + Rain$_{29}$ + Tmin$_{29}$ + s(Age)	NC	NC
Tmin$_{29}$	Tmax$_{0}$ + Rain$_{10}$ + Rain$_{14}$ * Tmax$_{14}$ + Rain$_{29}$ + s(Age)	0.062	-0.028
Rain$_{29}$	Tmax$_{0}$ + Rain$_{10}$ + Rain$_{14}$ * Tmax$_{14}$ + Rain$_{29}$ + Tmin$_{29}$ + s(Age)	NC	NC
Age	Tmax$_{0}$ + Rain$_{10}$ + Rain$_{14}$ * Tmax$_{14}$ + Rain$_{29}$ + Tmin$_{29}$	0.053	-0.037

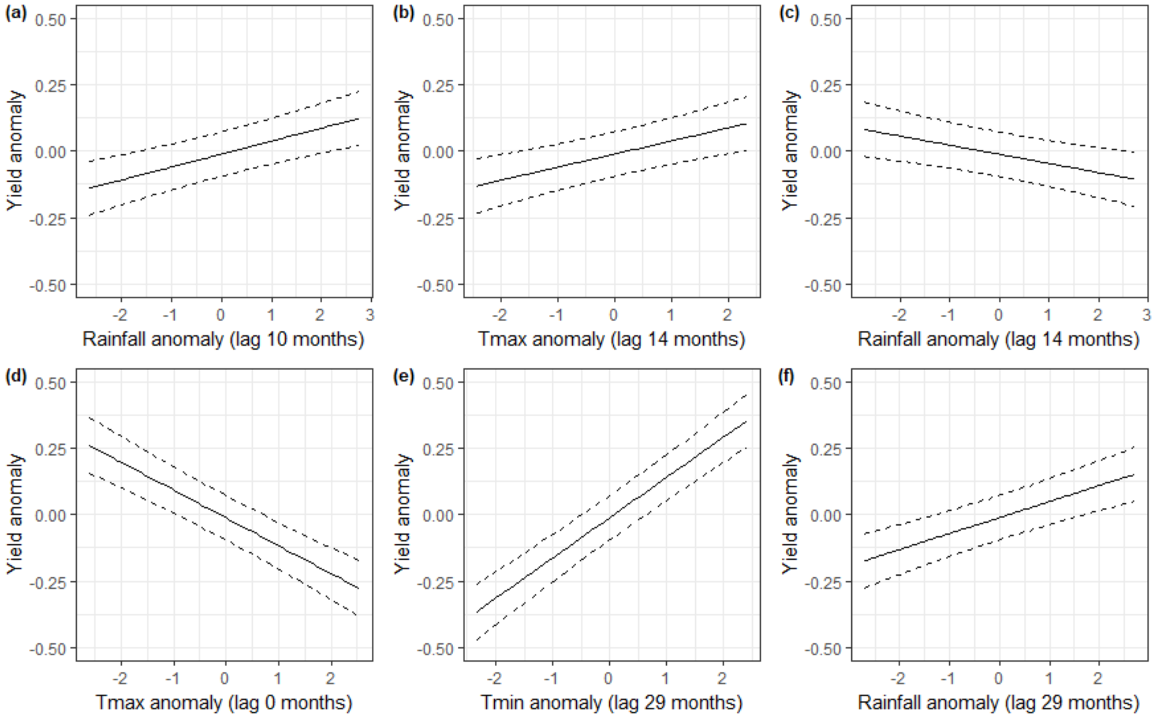


Figure S3.13. Expected yield anomaly values and 95% confidence intervals for the main effects of the six climatic anomaly predictors in the final GAM modelling yield anomalies: (a, b, c) predictors which were also included in the final GAMM modelling raw oil palm yield, as raw climatic variables; (d, e, f) predictors which were only included in the anomaly analyses. The yield anomaly values in these plots were predicted with all other climate anomaly predictors held at zero, and oil palm age held at the median value in the dataset. See table S3.8 for final model coefficients; and see fig. S3.12 for the fitted smoother of oil palm age and yield anomalies.

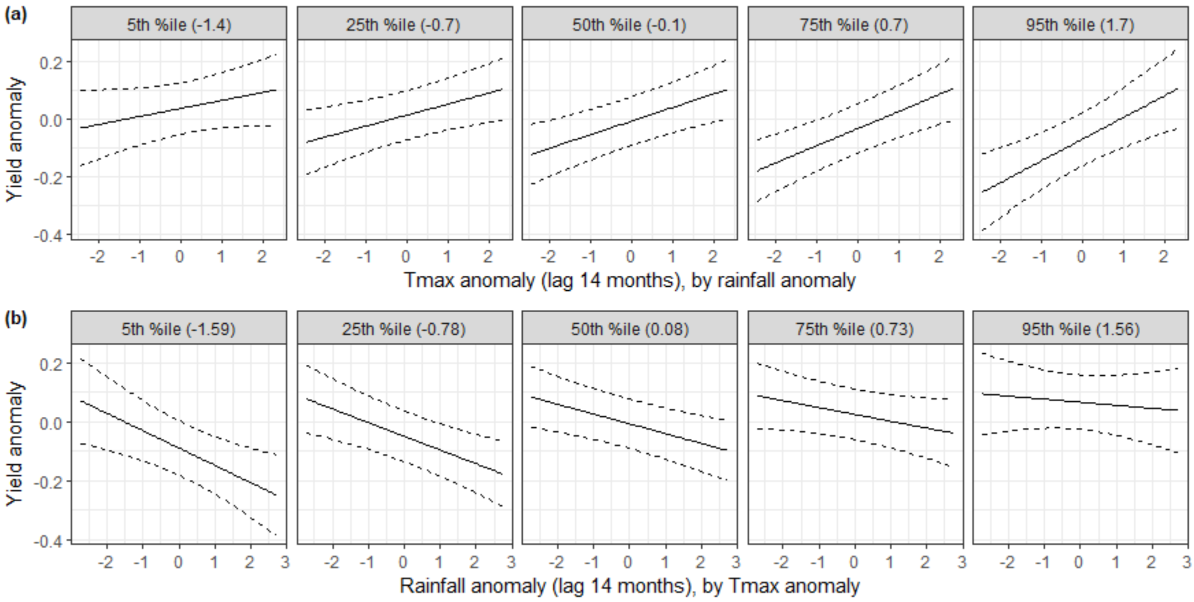


Figure S3.14. Expected yield anomaly values and 95% confidence intervals for the interaction of Tmax and rainfall at 14-month timelags prior to harvest, in the final GAM modelling yield anomalies. (a) Relationship of Tmax and yield anomalies for different values of rainfall anomaly (increasingly wet from left to right); (b) Relationship of rainfall and yield anomalies for different values of Tmax anomaly (increasingly hot from left to right. The yield anomaly values in these plots were predicted with all other climate anomaly predictors held at zero, and oil palm age held at the median value in the dataset. See table S3.8 for final model coefficients; and see fig. S3.12 for the fitted smoother of oil palm age and yield anomalies.

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