Edge effects on rainforest trees and carbon stocks

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Abstract

Agricultural expansion has driven widespread fragmentation of tropical rainforests, and many forest areas are now close to edges. Edges can have deleterious impacts on forest trees and aboveground carbon (AGC) stocks, but these edge effects are variable in strength. Focusing on Sabah, Malaysian Borneo, I studied edge effects in landscapes dominated by oil palm plantations, to better understand the environmental impacts of oil palm agriculture and to inform management strategies to ameliorate detrimental edge impacts on remaining forest areas. I collected field data to quantify edge effects on tree communities and AGC in forests bordered by oil palm plantations. The largest trees were up to 21% smaller near edges, causing reductions in local plot-level carbon of up to 30% (30% reduction at 50m from edge), with the strongest effects within 300m of edges. However, these edge effects were weak relative to existing variation in forest structure and carbon, and there were no observable edge effects on tree community composition or diversity. I used remotely-sensed data to examine whether AGC losses were stronger in areas close to multiple edges, and found that forest carbon stocks were 23% lower close to multiple edges than adjacent to a single edge. I also explored the role of the non-forest matrix and examined forest AGC losses at edges adjacent to high-contrast matrices (e.g. pasture) compared with low-contrast matrices (e.g. mature palms and trees). High-contrast edges lost twice as much carbon as low-contrast edges (21% loss vs 10% loss). Taken together, my results show that forest edge AGC is highly variable and that edge effects are relatively weak, but are nevertheless worse in proximity to multiple edges and when adjacent to high-contrast matrices. Management strategies to buffer edge contrast and minimize edge:area ratios of fragments may help maintain forest carbon stocks in fragmented landscapes.

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Author's declaration

I declare that this thesis is a presentation of original work and I (**JAA**) am the sole author. This work has not previously been presented for a degree or other qualification 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. Please note that thesis figure 2.1 was originally published in the supplementary materials as figure S1, but was moved to the main text to improve the flow of the thesis. Please also note that supplementary materials will be produced for chapter 4 before submitting for publication, however these will primarily comprise methodological details already discussed in depth in chapter 3. Thus, an appendix for chapter 4 has not been included in this thesis, to avoid repetition of information.

Chapter 1 - **General Introduction**

Emergent *Koompassia excelsa* in a forest edge adjacent to oil palm

1.1 Abstract

In recent decades, global population growth and increasing consumption have driven a rapid expansion of tropical agriculture. This has primarily occurred at the expense of tropical rainforests, globally important ecosystems which harbour more than half of all terrestrial species and store the majority of global forest carbon. Agricultural expansion in the tropics has therefore driven substantial reductions in biodiversity and is a significant source of greenhouse gas emissions. However, the negative effects of tropical land-use change are not limited to those arising directly from forest loss; degradation of remaining forest areas is also a contributing factor. Forest fragmentation is one of the primary drivers of degradation, resulting in the creation of forest edges which have a range of persistent and deleterious impacts. However, edge effects are highly variable in strength and are poorly studied in many landscapes, such as those dominated by oil palm plantations. Such landscapes are common throughout Southeast Asia, yet the influence of edges on trees and carbon stocks in forests adjacent to oil palm plantations remains poorly understood. Furthermore, the structure of the adjacent non-forest habitat and the combined effects of multiple edges are both thought to mediate edge effects on forest trees and carbon stocks, but have received relatively little research attention. In this introductory chapter I provide an overview of tropical land-use change and its direct and indirect consequences for tropical forests, and then summarise the extent and impacts of tropical forest fragmentation and edge effects. I discuss factors which may mediate the strength of edge effects, and introduce Southeast Asia as a study system in which to examine these concepts further. These topics contextualise the main objective of my thesis: to examine the impacts of edge creation on forest trees and carbon stocks in oil palm landscapes. I aim to better understand the environmental impacts of oil palm agriculture and to inform management strategies to ameliorate detrimental edge impacts.

1.2 Tropical land-use change

Today, the global human population stands at around 8 billion, over three times larger than it was seventy years ago (United Nations, 2022). By the year 2050, it is projected to reach almost 10 billion (United Nations, 2022). As the population has increased, so too have levels of individual consumption, which are now at the highest level in human history (Millward-Hopkins et al., 2020). This combination of population growth and increasing consumption has resulted in the increased conversion of natural landscapes to anthropogenic land uses, such as urban centres and agricultural land to produce food, animal feed and biofuels (Foley et al., 2005; Defries et al., 2010). Most of the global land area is, or has been, subject to land management (Luyssaert et al., 2014; Ellis et al., 2021), and almost a third has been subject to land-use change within the last six decades (Winkler et al., 2021). The majority of these land conversions have typically resulted in the same outcome: the degradation of natural ecosystems and environmental conditions, in order to acquire resources to meet immediate human needs (Foley et al., 2005). However, whilst the majority of these resources are used by the Global North (Oswald et al., 2020), increasing globalisation has facilitated the displacement of land conversions, and patterns of change are therefore divergent across the globe (Lambin and Meyfroidt, 2011; Meyfroidt et al., 2013; Yu et al., 2013). The recent expansion of agriculture has primarily occurred in the tropics (Winkler et al., 2021), where productivity is high and land and labour are relatively cheap (Akram-Lodhi, 2012; Laurance et al., 2014; Kastner et al., 2014; Mechiche-Alami et al., 2019). Agricultural land (i.e. cropland and pasture) made up at least a fifth of the tropical land area in 2005 (Malhi, 2010), and industries such as beef (Macedo et al., 2012), sugar cane (Picoli and Machado, 2021), soybean (Barona et al., 2010), oil palm (Gaveau et al., 2016), and cocoa (Ordway et al., 2017) have continued expanding throughout tropical regions. This agricultural expansion has largely occurred at the expense of tropical forests (Henders et al., 2015; Curtis et al., 2018). Between 1980 and 2000, over 80% of new agricultural land across the tropics was converted from forests, with intact (i.e. undisturbed) tropical forests being particularly vulnerable to conversion (Gibbs et al., 2010). This trend has continued into the 21st Century, with over 90% of tropical deforestation between 2011 and 2015 linked with agriculture (Pendrill et al., 2022), and is expected to continue as the human population continues to grow (Laurance et al., 2014; Lewis et al., 2015).

Agricultural expansion and associated forest loss primarily occurs in the tropics, but the environmental impacts are significant at both local and global scales. Humid tropical forests contain disproportionately high levels of biodiversity (e.g. Figure 1.1), and are home to over half of all terrestrial species (Myers et al., 2000; Scheffers et al., 2012; Barlow et al., 2018), despite covering less than 10% of the land surface (Eiserhardt et al., 2017). Deforestation is therefore driving substantial reductions in biodiversity (Pimm et al., 2014; Newbold et al., 2015; Nunes et al., 2022; Oakley and Bicknell, 2022). Deforestation is also reducing the capacity of tropical forests to provide ecosystem services (Laurance et al., 2014; Watson et al., 2018; Brouwer et al., 2022), due to both the loss of forests and the long-term impacts that this loss has on soils (Don et al., 2011; Veldkamp et al., 2020), which is concerning given that over 1 billion people directly rely on these services (Vira et al., 2015). Tropical deforestation also influences the global carbon cycle. Intact tropical forests have exceptionally high levels of carbon storage; they contain approximately 55% of all global forest carbon (Pan et al., 2011), which is roughly a third as much as is held in the atmosphere (Le Quéré et al., 2016), and they sequester about 437 TgC each year

(Baccini et al., 2017). Tropical forests therefore play a key role in global climate regulation, and are essential for mitigating anthropogenic climate warming (Mitchard, 2018). However, their capacity to act as carbon sinks is compromised by agricultural expansion (Harris et al., 2021; Li et al., 2022). Forest clearance, alongside factors which degrade remaining forest areas (see below), may be causing tropical forests to shift to net carbon sources of around 425 Tg C year^{-1} (Baccini et al., 2017). Some evidence indicates that tropical forests have a neutral contribution to the global carbon cycle, but continued anthropogenic pressures and rising global temperatures are likely to result in them becoming a carbon source in the future (Qie et al., 2017; Mitchard, 2018).

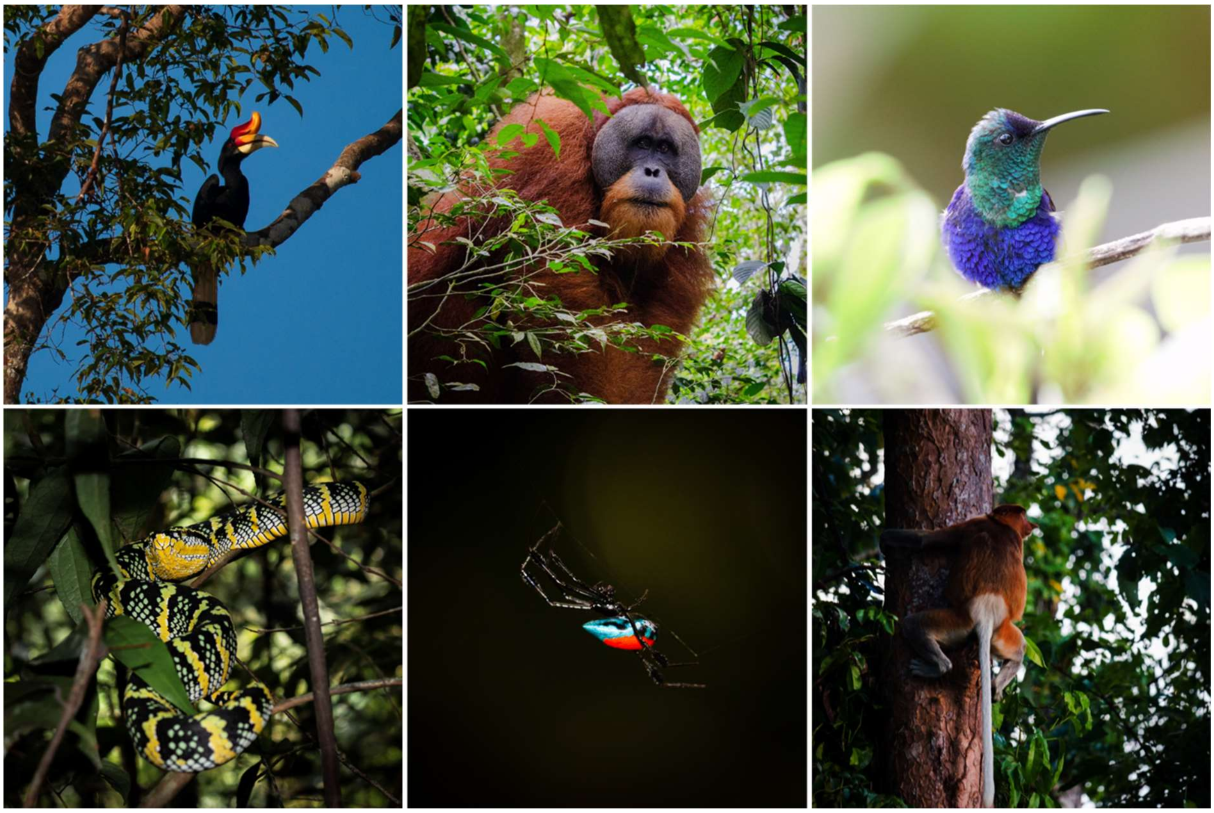


Figure 1.1. Tropical rainforests are home to a huge diversity of species. Clockwise from top left: Rhinoceros hornbill *Buceros rhinoceros* (Sabah, Malaysia), Sumatran orangutan *Pongo abelii* (Sumatra, Indonesia), crowned woodnymph *Thalurania colombica* (Sierra Nevada de Santa Marta, Colombia), proboscis monkey *Nasalis larvatus* (Sabah, Malaysia), long-jawed orb weaver *Opadometa sarawakensis* (Sabah, Malaysia), Wagler's pit viper *Tropidolaemus wagleri* (Sumatra, Indonesia). Photos by J Anderson.

Forest degradation

The environmental impacts of tropical land-use change are not limited to the direct effects of forest loss. Substantial impacts also arise from the degradation of remaining forest areas; that is, temporary or long-term deleterious changes in forest condition (functions, properties and services; Lapola et al., 2023). Degraded forests account for around 25% of tropical moist forests (Zhu et al., 2023), and in some regions the area affected by degradation now surpasses the extent of deforestation (Matricardi et al., 2020). Forest degradation typically occurs alongside land-use change, resulting in cascading and indirect effects (Malhi et al., 2014). Degradation is driven by a variety of factors such as invasive species, disease outbreaks, wildfires, pollution, climate change, unsustainable extraction of forest resources, and forest fragmentation (Laurance et al., 2014; Lewis et al., 2015; Barlow et al., 2018). Land-use change facilitates the invasion of non-native species into remnant forests (Waddell et al., 2020; Franklin et al., 2020) and the increased occurrence of diseases (Castro et al., 2019), with detrimental consequences for ecosystem function, local wildlife populations, and people’s health and livelihoods (Lewis et al., 2015; Corlett, 2019). Landscapes subject to deforestation for agriculture often experience forest fires, due to ‘slash and burn’ practices used to clear and manage land, and the increased susceptibility of remnant forests to drought from climate change (Cochrane, 2003; Qie et al., 2017), resulting in significant carbon emissions (Van Der Werf et al., 2010). These fires are not only limited to remnant forest areas; underground fires in tropical peatlands that have been drained are also a significant source of carbon emissions, and are detrimental to wildlife and people’s health (Harrison et al., 2009; Hoyt et al., 2020). In Indonesia, for example, deforestation and soil drainage for agricultural development has made peatlands highly susceptible to burning (Turetsky et al., 2014), resulting in widespread fires such as those observed in 2015. These fires pushed Indonesia into the top five carbon emitting countries, cost the Indonesian government over USD 16 billion, and had significant long-term health impacts on people throughout Southeast Asia (Atwood et al., 2016; Uda et al., 2019). Deforestation also increases the accessibility of remnant forests, increasing the extraction of timber and non-timber forest products, as well as substantial defaunation via hunting and poaching (Asner et al., 2009; Lewis et al., 2015; Harrison et al., 2016). Collectively, the drivers of forest degradation result in loss of biodiversity across multiple taxonomic groups (Gibson et al., 2011; Laurance et al., 2012; Nunes et al., 2022). It has been estimated that degradation can double biodiversity losses caused by deforestation alone (Barlow et al., 2016), and can triple the carbon emissions arising from tropical land-use change (Maxwell et al., 2019).

Forest fragmentation, the division of forests into smaller and more isolated patches, is one of the most significant drivers of forest degradation, with deleterious consequences (Lindenmayer and Fischer, 2006; Haddad et al., 2015). These consequences include the impacts of fragment size and isolation, matrix effects (the impacts of the surrounding land use), and edge effects (the impacts of forest edge creation and maintenance). These fragmentation effects are reviewed in the following sections, with a particular focus on edge effects, which are the central topic of my thesis. Edge effects are one of the primary drivers of degradation and ecological change in human-modified tropical landscapes (Laurance et al., 2011; Berenguer et al., 2014; Chaplin-Kramer, Ramler, et al., 2015; Pfeifer et al., 2017), and have the largest global footprint of all the drivers of tropical forest degradation (Zhu et al., 2023). However, edge effects are highly variable across study systems and are commonly perceived as being idiosyncratic (Ries et al., 2017). Thus, in order to quantify the impacts of tropical land-use change, and devise management strategies to mitigate these impacts, there is a clear need for system-specific research on edge effects and an improved understanding of the factors which drive their variability (Chaplin-Kramer, Sharp, et al., 2015; Chaplin-Kramer, Ramler, et al., 2015). My thesis examines the impacts of edge effects on tree communities and aboveground carbon stocks in oil palm landscapes, which are common throughout tropical Southeast Asia but are understudied in this context, and also examines factors which may mediate their detrimental effects.

1.3 Forest fragmentation

Conversion of forest to agriculture and other land-uses results in the fragmentation of remaining forest areas (Figure 1.2), and fragments are often small, isolated amidst a matrix of non-forest habitat, and exposed to further disturbances and variable levels of protection (Curran et al., 2004; Broadbent et al., 2008; Taubert et al., 2018). Throughout the tropics, agricultural expansion has caused widespread fragmentation of tropical forests (Lewis et al., 2015). Analyses of high-resolution forest cover maps (30m resolution) show that between 2000 and 2010 the number of tropical forest fragments (identified based on forest pixel connectivity, 0.09 ha minimum fragment size threshold) increased by approximately 20 million, a 16% increase (Fischer et al., 2021), and fragments are also getting smaller (Hansen et al., 2020), with large tracts of continuous forest becoming increasingly rare. On average, around 10% of tropical forests are now comprised of fragments smaller than 10,000 ha, and the average size of fragments is only about 17 ha (Taubert et al., 2018). Over the next 50 years, the number of tropical forest fragments is predicted to increase by a factor of 33, with a concurrent decrease in mean fragment size to 0.25 ha (Taubert et al., 2018). Understanding the impacts of forest fragmentation is therefore critical for landscape management and biodiversity conservation.

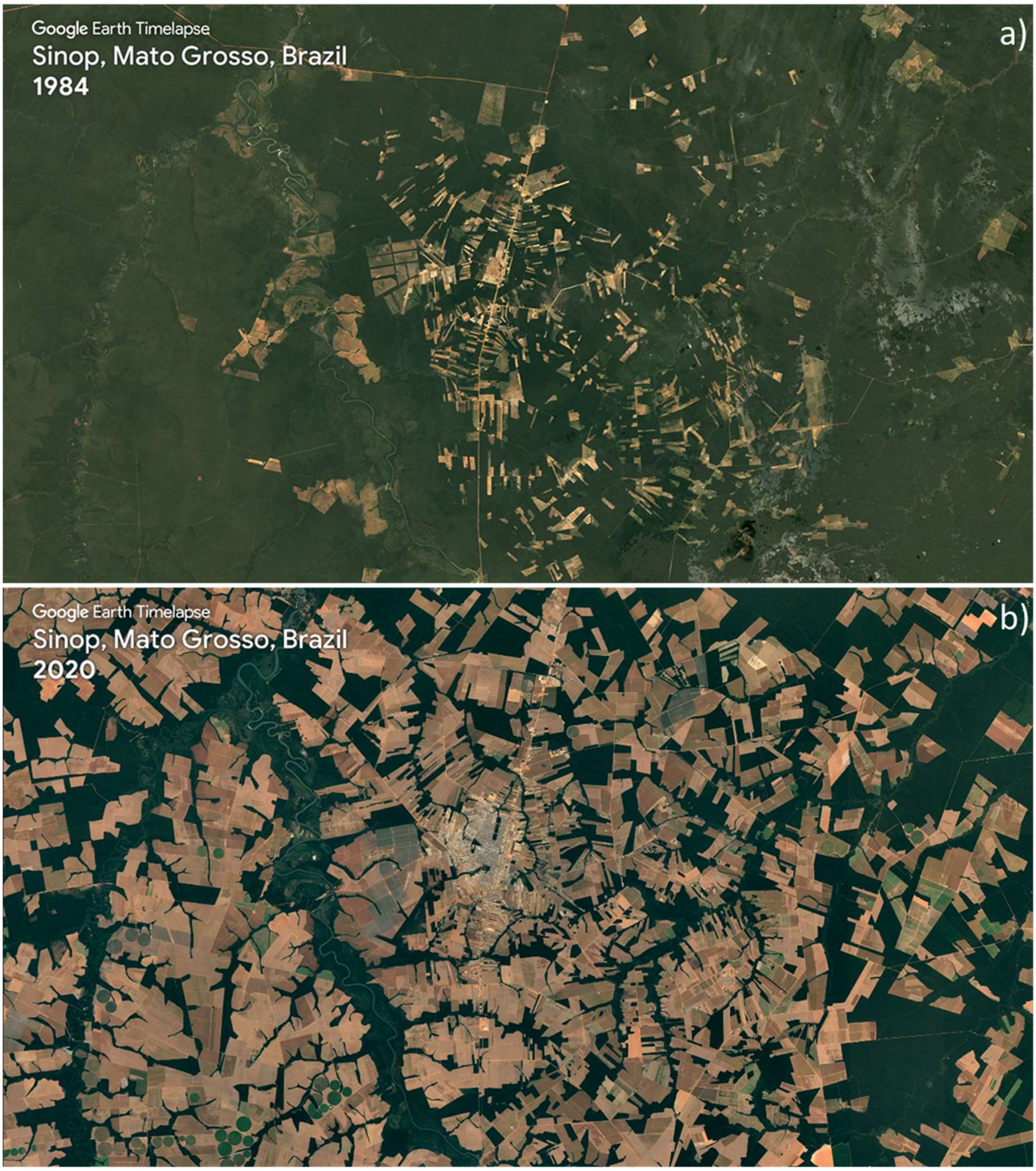


Figure 1.2 - Deforestation and tropical forest fragmentation in Mato Grosso, Brazil, from **a)** 1984 to **b)** 2020, due to expansion of soybean agriculture. Area shown is approx. 60km x 110km. Taken from Google Earth Timelapse (Google, Landsat, Copernicus) video, available under a Creative Commons Attribution 4.0 International License, from https://developers.google.com/earth-engine/timelapse/videos.

Although they are distinct processes (Fahrig, 2003), habitat loss and fragmentation tend to occur simultaneously (e.g. Figure 1.2), which can make it difficult to disentangle their relative effects (Didham et al., 2012). Nonetheless, there is clear evidence that fragmentation has its own set of impacts separate from those caused directly by habitat loss, and that these are widespread, pervasive and long-lasting (Ibáñez et al., 2014; Haddad et al., 2015; Fletcher et al., 2018; Püttker et al., 2020). These fragmentation effects are driven by a variety of processes, and are underpinned by fundamental ecological theories such as the Theory of Island Biogeography (MacArthur and Wilson, 1967), Species-Area Relationships (Preston, 1962), and metapopulation theory (Hanski, 1998). Smaller forest fragments tend to support fewer species ('area effects'), and this has been observed in a variety of taxa including birds, mammals, plants and invertebrates (Struebig et al., 2008; Hill et al., 2011; Lucey et al., 2014; Haddad et al., 2015; Laurance et al., 2018; Stride et al., 2018). There are fewer species in smaller fragments because they are less capable of supporting viable population sizes, and also because of 'sample' effects in habitats with high levels of species rarity, such as tropical forests, whereby smaller fragments are unlikely to contain all species present in the original forest community (Laurance et al., 2018). Smaller fragments also lose species more quickly than large fragments, which often experience extinction debts (time delays in species loss following disturbance) (Ferraz et al., 2003; Stouffer et al., 2009). Fragment isolation also contributes to biodiversity loss, because landscapes with more isolated fragments have reduced patch connectivity. This compromises the persistence of plant and animal populations by limiting dispersal and by reducing re-colonisation of habitat patches following local extinctions ('isolation effects'; Haddad et al., 2015; Hanski, 2015). Compared to larger fragments, smaller and more isolated fragments are also more likely to disappear over time (Gascon et al., 2000; Hansen et al., 2020). Thus, fragment area and isolation effects cause biodiversity declines across multiple taxa. These effects generally worsen over time, because populations which are no longer viable within fragments become functionally extinct and eventually disappear ('extinction debts'; Haddad et al., 2015). In taxa with very long generation times, such as trees, these extinction debts can last for several centuries (Vellend et al., 2006; Stride et al., 2018).

Edge effects

Forest edges, the human-made boundaries between forest and non-forest habitats (Figure 1.3a), are often dominating drivers of ecological change in fragmented tropical forests, via 'edge effects' (Laurance et al., 2011; Berenguer et al., 2014; Benchimol and Peres, 2015; Püttker et al., 2020). Edge effects are the biotic and abiotic changes which occur near the forest edge as a result of edge creation and maintenance, and therefore arise from forest fragmentation (Murcia, 1995).

Edge effects occur on both sides of the edge (i.e. in both the forest and adjacent matrix), but I focus on forest edge effects in this thesis. A wide variety of edge effects have been documented in fragmented tropical forests, and although the most severe effects tend to occur within 100m – 300m of the edge (Laurance et al., 2002; Broadbent et al., 2008), some have been observed at much greater distances of over 1.5km (Cochrane and Laurance, 2002; Briant et al., 2010; Chaplin-Kramer, Ramler, et al., 2015; Luskin et al., 2017). Anthropogenically-created edges have increased light penetration, decreased humidity, increased temperatures and increased wind turbulence and windthrow (Figure 1.3b; Kapos, 1989; Laurance and Curran, 2008; Ewers and Banks-Leite, 2013; Magnago et al., 2015; Magnago et al., 2017; Zhu et al., 2023). Fires also increase in frequency and intensity near edges (Cochrane, 2001; Cochrane and Laurance, 2002; Benchimol and Peres, 2015; Brando et al., 2019), due to human activities in adjacent land-uses and increased desiccation of the forest (Zhao et al., 2021).

Altered abiotic conditions influence species abundances and the structure and diversity of animal and plant communities near edges (Didham et al., 1996; Laurance et al., 2011; Ibáñez et al., 2014; Pfeifer et al., 2017; Willmer et al., 2022). For example, a global analysis revealed that 85% of 1,673 studied vertebrate species were affected by edges, with either an increase or decrease in their abundance, and species classified as threatened by the IUCN were less likely to be present at edges (Pfeifer et al., 2017). Species responses to edges reflect material and energy flows across the edge boundary and altered resource availability, as well as biotic interactions (Ries et al., 2004; Ewers and Didham, 2006; Ries et al., 2017), and species life-history strategies and traits determine their ability to persist at edges (Pfeifer et al., 2017). Relatively low historical disturbance levels (e.g. from fires, glaciation, hurricanes, and deforestation) may mean that the tropics contain more species that are vulnerable to edge effects than in higher-latitudinal regions (Betts et al., 2019), thus species richness tends to decline at tropical forest edges (Willmer et al., 2022). Over 30% of remaining tropical forest is estimated to be within 100m of an edge, and this is anticipated to rise to 50% by 2100 (Fischer et al., 2021); edges are therefore increasingly important ecological features within human-dominated tropical landscapes. Understanding the impacts of edge effects on forest trees is of critical importance, because trees are key structural elements in forests and play critical functional roles in primary production, carbon storage and resource provision for fauna.

1.4 Edge effects on tropical forest trees and carbon stocks

Altered abiotic conditions drive substantial changes in plant community structure and processes near edges (Harper et al., 2005; Figure 1.3c), with rapid species turnover of forest tree communities (Laurance et al., 1998 a; Laurance et al. 2006 a; Qie et al., 2017). Disturbance-adapted species with lower wood densities tend to proliferate at edges, whilst shade-tolerant, forest-interior species with higher wood densities decline (Laurance et al. 1998 b; Oliveira et al., 2004; Laurance et al. 2006 b; Michalski et al., 2007; de Paula et al., 2011). Large trees, which are key structural and ecological components of forests (Slik et al., 2013; Pinho et al., 2020), are disproportionately affected (Oliveira et al., 2008; de Paula et al., 2011), with mortality rates increasing by almost 300% within 300m of an edge (Laurance et al., 2000). Large tree mortality is due to microclimatic stress, lianas (which increase in abundance at edges, and can reduce tree survival), fire and increased wind turbulence (D'Angelo et al., 2004; Magnago et al., 2015; Campbell et al., 2018; Gora and Esquivel-Muelbert, 2021; Zhao et al., 2021). Canopy and emergent trees are prone to canopy desiccation caused by local phenomena such as the 'vegetation breeze', whereby local evaporation and convection dynamics are altered by the proximity of cleared land (Briant et al., 2010; Laurance et al., 2018), which can be exacerbated by regional droughts (Qie et al., 2017; Nunes et al., 2021). In combination, these compositional changes can culminate in phylogenetic impoverishment (Santos et al., 2010; Razafindratsima et al., 2018), biotic homogenisation (Oliveira et al., 2004) and a 'retrogressive succession' of tree communities near edges (Figure 1.3d; Michalski et al., 2007; Santos et al., 2008; Tabarelli et al., 2008; Tabarelli et al., 2012; Benchimol and Peres, 2015), which may persist for centuries (Pütz et al., 2011). There are associated changes in forest structure near edges (Figure 1.3d), with reductions in forest height (Almeida et al., 2019; Ordway and Asner, 2020), canopy density (Scriven et al., 2018), and emergent tree abundance (de Paula et al., 2011), whilst understorey stem and foliage density can increase due to recruitment of disturbance-adapted species (Broadbent et al., 2008). These structural changes further contribute to altered abiotic conditions. Tree communities near edges can suffer from reductions in species richness (Oliveira et al., 2004; Krishnadas et al., 2019; Krishnadas and Stump, 2021; Willmer et al., 2022), though not always (Ibáñez et al., 2014), and non-native trees are also more common (Franklin et al., 2020). In summary, increased levels of abiotic disturbance at tropical forest edges cause substantial changes in the structure, composition and diversity of tree communities within the forest (Figure 1.3).

Abiotic effects on trees are further compounded by changes in species interactions near edges, such as altered animal behaviour and resource use. For example, increased abundance of wild pigs in agricultural plantations can reduce tree sapling density by almost 80% in adjacent forests (Luskin et al., 2017) and facilitate the invasion of non-native shrubs (Peters, 2001), whilst increased vertebrate seed predation can hinder tree recruitment (Curran et al., 1999). Changes in the abundance, composition and behaviour of seed-dispersing birds and mammals, as well as pollinating insects, can also reduce tree recruitment (de Melo et al., 2006; Cramer et al., 2007; Brosi et al., 2008; Melo et al., 2010), particularly in regions with many animal-dispersed trees (Osuri et al., 2016). The regulation of seedling recruitment by fungal pathogens and insect herbivores can also be compromised by edge proximity, thus reducing tree diversity near edges (Krishnadas et al., 2018). Increased felling and hunting near edges (Peres, 2001; Lewis et al., 2015) also contributes to the loss of large, late-successional tree species with high wood densities, because these are typically the main targets for timber extraction (Lindenmayer et al., 2012) and are often animal-dispersed (Harrison et al., 2013; Bello et al., 2015). Edges can therefore have many deleterious impacts on forest tree communities, which have consequences for ecological processes and ecosystem functions, such as carbon storage.

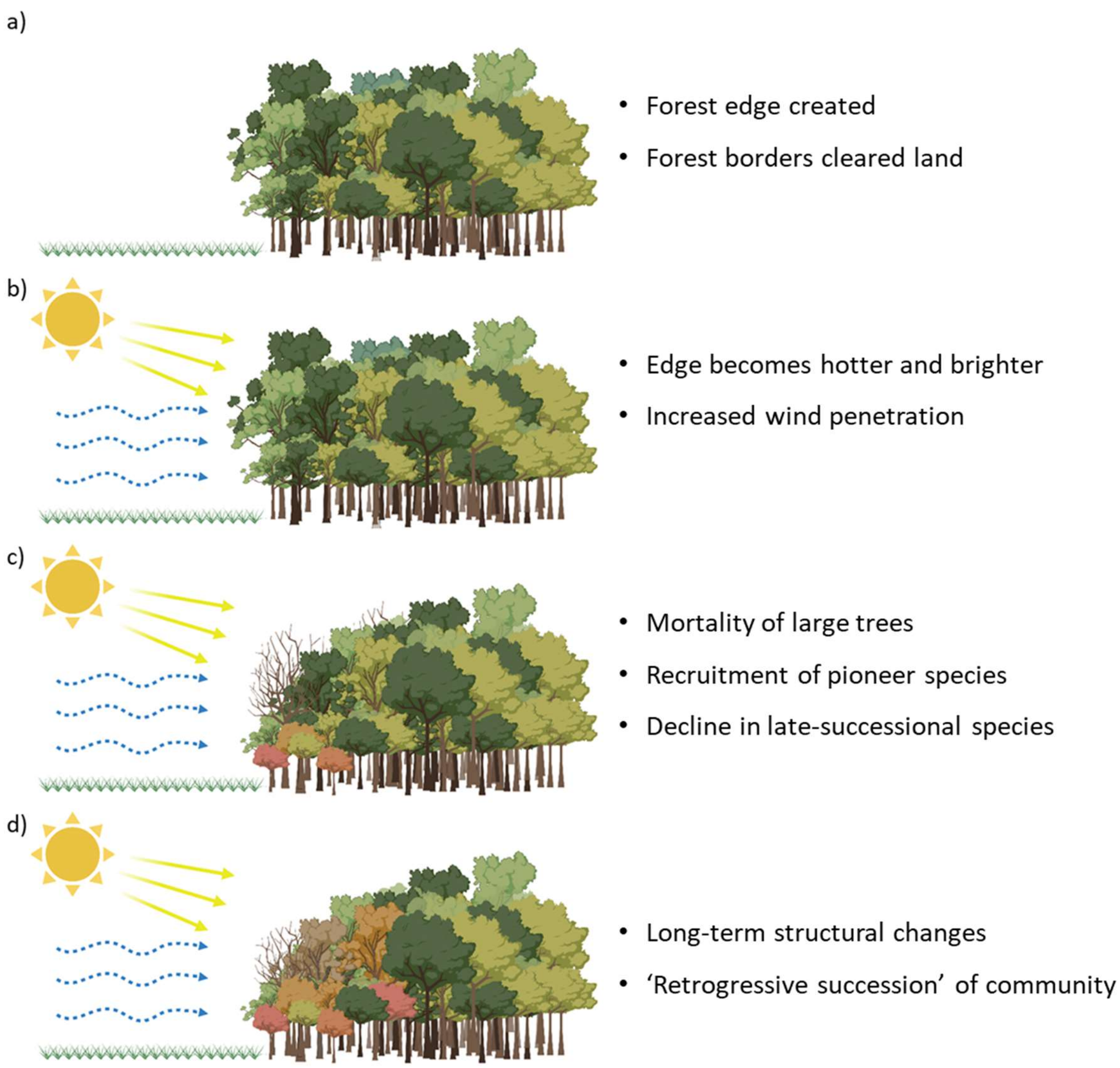


Figure 1.3 – Conceptualized diagram of abiotic edge effects on tropical forest trees, showing: **a)** a recently created edge, **b)** abiotic gradients (wind, sunlight) penetrating laterally from the adjacent non-forest into the forest, **c)** increased mortality of large trees and increased recruitment of disturbance-adapted species (pink and orange trees), and **d)** significant long-term alterations in tree community structure and composition. Figure produced with BioRender premium plan.

Edge effects on forest carbon

Tropical trees store around a third as much carbon as is held in the atmosphere (Mitchard, 2018), and the majority of this carbon is stored as aboveground biomass (AGB) (Pan et al., 2011). Changes in the structure and composition of forest tree communities therefore have profound implications for forest carbon stocks, and any reduction in AGB also reduces the amount of aboveground carbon (AGC) stored in the forest. Following edge creation there is typically a pulse in tree mortality near the edge, due to the harsh abiotic conditions (e.g. wind turbulence, canopy desiccation) which the tree community is not adapted to (D’Angelo et al., 2004). This can cause an immediate reduction in AGB, typically within 100-300m of forest edges (Laurance et al., 1997; Dantas de Paula et al., 2015; Ordway and Asner, 2020; Silva Junior et al., 2020). The loss of large trees in particular is responsible for much of this biomass loss (Laurance et al., 2000; de Paula et al., 2011), because the density of large trees (over 70cm diameter) drives around 70% of the variation in AGB in tropical forests (Slik et al., 2013). Subsequent changes in tree community composition can contribute to long-term declines in AGB, because the early-successional, fast-growing trees which tend to dominate near edges typically have lower wood densities and grow to smaller sizes than the late-successional species that they replace (Qie et al., 2017). Thus, increased recruitment of these pioneer species does not offset the loss of AGB from the mortality of large and late-successional trees (Laurance et al., 1997; Nascimento and Laurance, 2004; de Paula et al., 2011). Whilst regrowth of forest vegetation at the edge can buffer abiotic gradients over time (Didham and Lawton, 1999), wind disturbance and fire frequency remain elevated and can increase, therefore mortality and biomass loss can increase as the edge ages (Laurance and Curran, 2008; Zhao et al., 2021). Furthermore, human activities near edges (see above) are likely to remain persistent drivers of biomass loss.

Abiotic and biotic edge effects on tropical forest trees can therefore drive a substantial reduction in AGB and AGC near edges (Smith et al., 2018), and this depletion in carbon stocks can persist indefinitely and worsen over time (Pütz et al., 2014; Ordway and Asner, 2020; Silva Junior et al., 2020). However, despite the general recognition of this trend, a recent systematic review concluded that overall there is insufficient quantification of AGB declines at tropical forest edges, and the studies which have examined this relationship have observed that declines are variable (Melito et al., 2018). For example, Laurance et al. (1997) observed biomass declines of up to 36% in Amazonian forest edges, whereas in Atlantic forest edges de Paula et al. (2011) and Magnago et al. (2017) found AGC declines of 50% and 70% respectively. By contrast, Ordway and Asner (2020) recorded average AGC declines of only 22% in Southeast Asian forest edges. The depth of edge effects on AGB and AGC is also variable, with estimates ranging from 100 m (Laurance et al., 1997; Ordway and Asner, 2020; Zhao et al., 2021) to 500 m (Chaplin-Kramer, Ramler, et al., 2015; Qie et al., 2017), or even up to several kilometres in some edges (Chaplin-Kramer, Ramler, et al., 2015). Furthermore, whilst some study systems find that edge effects are a major driver of AGC (e.g. Berenguer et al., 2014), others report little to no change near edges (Phillips et al., 2006; Schedlbauer et al., 2007; Numata et al., 2017), and there is evidence that depleted forest edge carbon stocks can sometimes recover within a few decades (Almeida et al., 2019). Moreover, most studies are from only a few Neotropical regions, and there is a paucity of research in many tropical landscapes and study systems (Melito et al., 2018).

Given the expected increase in tropical forest fragmentation over the coming decades (Taubert et al., 2018), it is important to quantify the impact of edges on AGC and to understand drivers of variation. Edge effects are key drivers of tropical forest degradation (Zhu et al., 2023), therefore properly accounting for the impacts of edge-related degradation will improve carbon stock assessments, which typically do not consider edge effects (Chaplin-Kramer, Ramler, et al., 2015; Pearson et al., 2017). This information is crucial for monitoring and reporting carbon emissions, such as REDD+, to avoid inaccurate emissions estimates (Gibbs et al., 2007; Goetz et al., 2015; Silva Junior et al., 2021), and will improve the robustness of climate change models (Melito et al., 2018). For example, accounting for edge effects increases estimates of deforestation-linked carbon emissions by around 40% in Amazonia (Silva Junior et al., 2020), and by 30% across the entire tropics (Fischer et al., 2021). The tropical forest component of the global carbon budget is the least certain (Le Quéré et al., 2017), due to uncertainties in the impacts of forest degradation (Mitchard, 2018). Improved estimation of carbon losses from edge effects will also improve ecosystem service assessments (Chaplin-Kramer, Sharp, et al., 2015; Metzger et al., 2021), footprinting studies of tropical agricultural products (Chaplin-Kramer et al., 2017; Lam et al., 2019), and landscape planning decisions to protect carbon stocks (Laurance, 1991; Gascon et al., 2000). Thus, it is important to identify the factors which drive variability in edge effects on forest trees and AGC. This thesis therefore focuses on quantifying edge effects on forest trees and AGC in an understudied tropical system in Southeast Asia (Chapter 2), and examines drivers of variation in edge effect strength (Chapters 3 & 4). In the next section, I review current knowledge about the factors which drive variability in edge effects and discuss the underlying ecological mechanisms.

1.5 Edge effect variability

Edge effects are highly variable in strength and penetration (Ries et al., 2004; Laurance et al., 2007; Ries et al., 2017). This variation is due to a range of factors including landscape configuration (Laurance et al., 2007), edge orientation (Ries et al., 2004), edge age (Ordway and Asner, 2020; Silva Junior et al., 2020), soil type (Ordway and Asner, 2020), neighbouring land-use matrix (Mesquita et al., 1999), interacting effects between nearby edges (Porensky and Young, 2013), and forest type (Chaplin-Kramer, Ramler, et al., 2015; Zhao et al., 2021). In short, edge effects are context-specific. However, many of these factors have been poorly studied, and the influence of multiple edges and neighbouring matrix have received relatively little research attention, limiting our capacity to make large-scale predictions about edge impacts (Ries et al., 2017).

Multiple edge effects

Many human-dominated tropical landscapes have complex patterns of fragmentation, with forest fragments in a variety of shapes and sizes (e.g. Figure 1.2). In small fragments and in forest areas with complex geometries (i.e. corners and corridors), it is therefore common for multiple edges to be near to one another (Malcolm, 1994; Fernández et al., 2002). However, the majority of edge effect studies examine the influence of the nearest edge only, under the assumption that the nearest edge is the key driver of ecological change. Yet there is evidence that the presence of multiple nearby edges may increase the overall edge effect (Porensky and Young, 2013; Laurance et al., 2018), a concept termed 'edge additivity' (Malcolm, 1994). There is evidence for these stronger edge effects on the abundance and diversity of birds (Lack, 1988; Fletcher, 2005; Lindenmayer et al., 2007), plants (Harper et al., 2007; Porensky, 2011; Malcolm et al., 2017; Laurance et al., 2018), herbivores (Porensky, 2011) and invertebrates (Porensky, 2011; Malcolm et al., 2017; van Schalkwyk et al., 2020). Whilst there has been some research on this topic, it is largely neglected in the literature, and we lack a comprehensive understanding of how multiple edges interact (Ries et al., 2017).

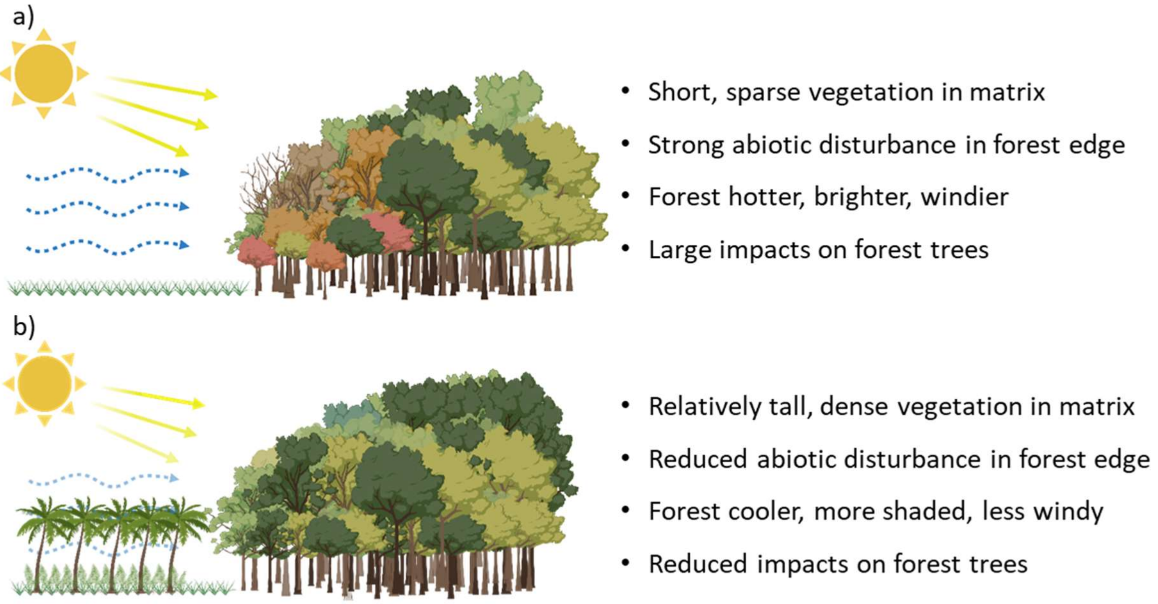
Edge effects on forest trees and AGC may be stronger in the presence of multiple edges, because these forest areas are likely to experience greater abiotic disturbances. For example, wind disturbance is typically greater in smaller, 'edgier' fragments (Laurance and Curran, 2008; Schwartz et al., 2017), and forest temperature is likely to be hotter in these areas (Malcolm, 1998). Furthermore, modelling studies have shown that multiple edges can facilitate more severe fires in fragmented forests (LaCroix et al., 2008). Thus, in tropical forest areas close to multiple edges, there is evidence of stronger edge effects on vegetation thickness (Malcolm, 1994), tree species richness and community composition (Benitez-Malvido and Martinez-Ramos, 2003; Laurance et al. 2006 a), biotic damage from leaf-fungi (Benítez-Malvido et al., 2018) and tree mortality and density (Laurance et al. 2006 a; Malcolm et al., 2017), but effects on AGC remain unquantified. As tropical forest fragmentation continues and fragments become smaller (Taubert et al., 2018), remnant forest areas will increasingly be subject to influence from multiple edges. If AGC declines further in the presence of multiple edges, then studies which estimate carbon emissions based on assumptions of single-edge effects (e.g. Brinck et al., 2017; Fischer et al., 2021) may underestimate emissions from tropical land-use change. A metric which accounts for proximity to multiple edges may explain more variation in edge-affected features such as AGC, thereby offering an improvement over a simple metric of ‘distance to nearest edge’. In Chapter 3, I therefore adapt a metric of ‘edginess’ which accounts for the proximity of multiple edges, in order to test whether forest AGC is lower in ‘edgier’ forest areas, and to determine whether an edginess metric explains more variation in AGC than a ‘nearest edge’ metric.

Matrix impacts

Traditionally, ecological theories of forest fragmentation impacts (e.g. Island Biogeography) have viewed forest fragments as habitat islands surrounded by an uninhabitable non-forest matrix. However, this viewpoint does not consider the ecological role of the matrix itself, which may act as habitat for some forest species and mediate the ecological impacts of fragmentation (Jules and Shahani, 2003; Ewers and Didham, 2006; Kupfer et al., 2006; Prugh et al., 2008; Arroyo-Rodríguez, Melo, et al., 2017). The relative ‘quality’ of the matrix determines the capacity of forest species to use, and move through, the matrix (Driscoll et al., 2013). The matrix can therefore influence metapopulation dynamics within patch networks, and facilitate the colonisation of species at forest edges (Laurance et al., 2011). For example, tree community composition in fragment edges in the Brazilian Amazon is strongly related to composition in the adjacent matrix (Laurance et al. 2006 a; Nascimento et al., 2006; Ewers et al., 2017), and similar ‘spillover’ effects have been observed in a variety of taxa across different study systems (Sisk et al., 1997; Rand et al., 2006; Kennedy et al., 2010; Luskin et al., 2017). Variation in human activities and management regimes within the adjacent matrix can also determine the level of disturbance experienced by edge forest (Maeda et al., 2023). For example, fire frequency in fragmented forests is related to the surrounding land-use (Cochrane et al., 1999), livestock browsing intensity can modify vegetation in adjacent edges (Benítez-Malvido et al., 2014), and human activities such as timber extraction and hunting are likely to be higher in forest fragments closer to human settlements (Chaplin-Kramer, Ramler, et al., 2015).

The physical structure of the matrix can also mediate edge effect strength (Harper et al., 2005; Ries et al., 2017; Melito et al., 2018; Willmer et al., 2022). Structural contrast between the forest and adjacent non-forest habitat mediates abiotic gradients, such as wind, temperature and light penetration (Harper et al., 2005). This is because matrices which are more similar in structure to natural forests (i.e. tall, dense vegetation with greater structural complexity) have abiotic conditions more similar to those within the forest (Hardwick et al., 2015; Jucker et al., 2018), and will therefore buffer edges against the very different abiotic conditions in high-contrast matrices (Figure 1.4). Thus, forests bordering high-contrast matrices experience more severe abiotic disturbances at the edge (Camargo and Kapos, 1995; Laurance and Curran, 2008; Arroyo-

Rodríguez, Saldaña-Vázquez, et al., 2017; Permana et al., 2022), with deleterious consequences for a variety of taxa including birds, amphibians, invertebrates and plants (Mesquita et al., 1999; Santos-Barrera and Urbina-Cardona, 2011; Campbell et al., 2011; Hatfield et al., 2020). Some high-contrast forest edges may support a greater diversity of species if there is resource complementarity with the adjacent habitats (Willmer et al., 2022), although this is unlikely in intensive agricultural systems. The majority of studies examining edge effects on tropical forests have been in edges bordering pastures, with relatively little research on edges bordering other land-use types (Franklin et al., 2020). Furthermore, the effects of matrix contrast may be mediated by variation in local 'core' forest structure and carbon, because high-carbon forests may be more resilient to fragmentation effects (Melito et al., 2018), but these effects remain unquantified. Thus, in Chapter 4 I examine the influence of matrix structure on forest edge AGC in a region with a wide variety of matrix types and edge contrast, and also examine whether high-carbon forests are more resilient to edge and matrix effects.



a)

- Short, sparse vegetation in matrix
- Strong abiotic disturbance in forest edge
- Forest hotter, brighter, windier
- Large impacts on forest trees

b)

- Relatively tall, dense vegetation in matrix
- Reduced abiotic disturbance in forest edge
- Forest cooler, more shaded, less windy
- Reduced impacts on forest trees

Figure 1.4 – Conceptualized diagram of the abiotic buffering capacity provided by different matrices. Abiotic gradients such as wind and light are typically stronger in edges bordering **a)** high-contrast matrices (e.g. pasture) than in those bordering **b)** low-contrast matrices (e.g. mature palm plantation), because matrix structure mediates these effects. This may reduce edge influence on tree communities within forest. Figure produced with BioRender premium plan.

1.6 Southeast Asia as a study region

Edge effects can vary considerably between regions, due to differences in factors such as forest type and climate (Harper et al., 2005). Whilst there has been a recent increase in edge effect studies in Southeast Asia (Franklin et al., 2020), there is still a paucity of research in the region, with most tropical edge effect studies taking place in the Neotropics (Ries et al., 2017). Such studies are important because Southeast Asia differs from the Neotropics in its biota, forest types and climate (Corlett, 2019), therefore edge effects are likely to differ. The region supports exceptionally high levels of biodiversity, and contains four of the world's biodiversity hotspots (Myers et al., 2000; Figure 1.5). The biodiversity hotspot of Sundaland, which is spread across Malaysia, Indonesia, Singapore and Brunei, is particularly rich in flora and fauna. It contains more than 15,000 endemic plant species and over 700 endemic vertebrate species, despite retaining less than 8% of its primary vegetation (Myers et al., 2000; Brooks et al., 2002). There is a variety of forest types throughout this region, however the majority of terrestrial diversity is contained within lowland tropical rainforests, which have the greatest height, biomass and plant diversity of any vegetation type in Southeast Asia (Corlett, 2019). However, Southeast Asia has experienced very high rates of forest clearance and degradation (Miettinen et al., 2011; Hansen et al., 2013; Zhu et al., 2023) and its biota is highly sensitive to land-use change and forest degradation impacts (Gibson et al., 2011), with its natural forests shifting from carbon sinks to sources (Harris et al., 2021). Much of Southeast Asia's lowland forest area occurs on the island of Borneo, the world's second largest tropical island.

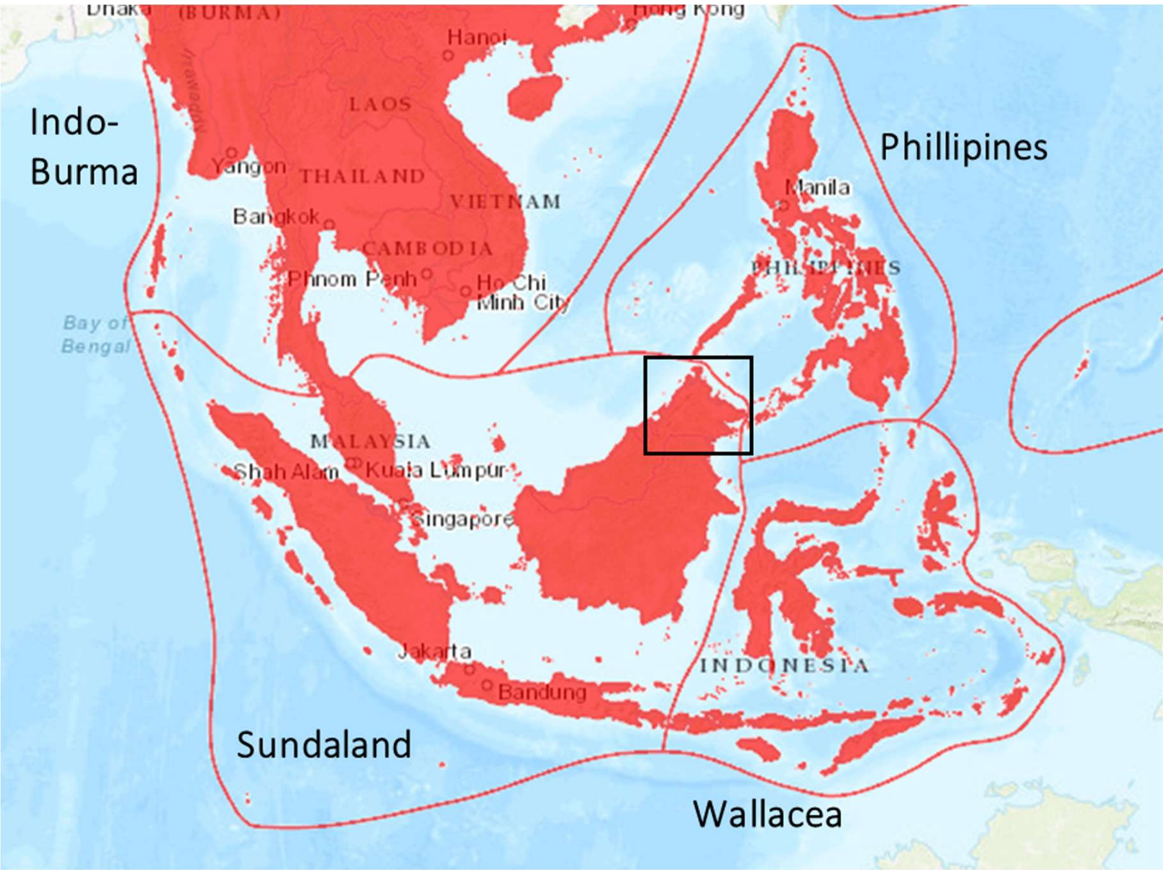


Figure 1.5 – Map of Southeast Asian biodiversity hotspots (delineated by red lines). Black box shows Sabah, Malaysian Borneo, which is the study area of my thesis. Map produced using Data Basin (owned by the Conservation Biology Institute), with layer 'Biodiversity Hotspots 2016' (available under a CC BY 3.0 license - https://creativecommons.org/licenses/by/3.0/legalcode) and addition of hotspot names and black box. Data downloadable from https://databasin.org/.

Bornean rainforests

The lowland rainforests of Borneo primarily comprise mixed dipterocarp forests (Whitmore, 1984; e.g. Figure 1.6), and are home to the majority of the island's biodiversity (MacKinnon et al., 1997; Curran et al., 2004; Ashton, 2010). These forests contain a greater diversity of vascular plants than any other ecoregion on earth, with over 10,000 known plant species including 3000 tree species (MacKinnon et al., 1997; Kier et al., 2005). Trees in the family *Dipterocarpaceae* are the dominant component of lowland rainforests in Borneo, particularly amongst the canopy and emergent layers (Slik et al., 2003). Lowland dipterocarp forests are characterised by their unique structure, with a relatively open upper canopy and greater height and density of tall emergent trees (Paoli et al., 2008; Figure 1.6). Canopy height is generally 30-40m, with a scattered emergent layer over 50m tall (Corlett, 2019), however some dipterocarp species reach heights of almost 100m, making them the tallest tropical trees in the world (Shenkin et al., 2019). These forests experience supraannual mast-fruiting events of dipterocarp trees every 2-10 years (Appanah, 1993) which are triggered by El Niño-Southern Oscillation (ENSO) events (Curran et al., 1999). Dipterocarps are primarily wind-dispersed, with tall, straight boles to facilitate this fruiting strategy (Slik et al., 2010). The dominance of large emergent dipterocarp trees means that Bornean forests harbour exceptionally high levels of AGB and AGC (Asner et al., 2018), with average AGB in Borneo around 60% higher than in Amazonian forests (Slik et al., 2010). However, the height and hardwood qualities of dipterocarps also make them important timber species and the focus of commercial logging activities (Meijaard et al., 2006; Edwards et al., 2011).

Figure 1.6 – Lowland mixed dipterocarp forest in Danum Valley Conservation Area. Sabah, Malaysian Borneo. Photo by J Anderson.

Since the 1950s, the majority of Southeast Asia's lowland forests have been subject to commercial selective logging (Sodhi et al., 2004; Edwards et al., 2011). Historically, timber exports from Borneo exceed the timber exports from all of Latin America and tropical Africa combined (Curran et al., 2004), and around half of the remaining forest on Borneo has been logged at least once (Gaveau et al., 2014). The majority of remaining forest areas in the Malaysian state of Sabah, in the north of Borneo (Figure 1.5), have been selectively logged (Reynolds et al., 2011; Bryan et al., 2013; Gaveau et al., 2014), reducing forest carbon stocks by around 50% (Asner et al., 2018). Timber production peaked in Sabah in the 1970s and 1980s, but was generally not carried out sustainably, and so the primary threat to lowland rainforests has been the expansion of agricultural croplands to replace heavily-degraded natural forest with low timber revenues (Reynolds et al., 2011). From 1973 to 2010, Sabah lost around 1.9 M ha of forest, equivalent to 40% of its forest cover (Gaveau et al., 2014). Approximately 1.2 M ha of forest, both selectively logged and primary, were converted to oil palm (*Elaeis guineensis*), as well as pulpwood (*Acacia spp* and *Eucalyptus spp*) and rubber (*Hevea brasiliensis*). Oil palm plantations and smallholdings now dominate much of Sabah's land area, with over 1.5 M ha (i.e. 20% of the total land area) dedicated to plantations, most of which are monocultures (MPOB, 2022; Figure 1.7). Sabah's remaining forest areas, which cover around 3.7 M ha (50% of the total land area), include forest reserves, parks and wildlife sanctuaries, with variable management and protection classifications (Reynolds et al., 2011; Asner et al., 2018). This agricultural expansion and previous selective logging means that most remaining areas of lowland forest, except for some primary forest reserves, are heavily degraded and fragmented in landscapes dominated by oil palm plantations.

Figure 1.7 – Commercial oil palm monoculture in Sabah, Malaysian Borneo. Photo by J Anderson.

Oil palm

Oil palm originates from equatorial Africa and is the most productive and widely-used vegetable oil crop in the world (Meijaard et al., 2020). Its products have a variety of uses, including food products, biofuels, and personal care products and cosmetics (Corley and Tinker, 2015). Oil palm cultivation has grown substantially in recent decades, particularly in Southeast Asia, where >90% of global palm oil is produced in Indonesia and Malaysia (Descals et al., 2021). This expansion has had significant environmental impacts associated with forest clearance, habitat fragmentation, pollution, and greenhouse gas emissions (Fitzherbert et al., 2008; Wilcove and Koh, 2010; Sodhi et al., 2010; Pendrill et al., 2019; Meijaard et al., 2020). Many studies of the environmental impacts of palm oil have focused on forest loss and peatland drainage (e.g. Carlson et al., 2012; Senior et al., 2013; Savilaakso et al., 2014; Meijaard et al., 2020), but fragmentation effects are also important, affecting biodiversity patterns in multiple taxa in oil palm-dominated landscapes (Benedick et al., 2006; Edwards et al., 2010; Stride et al., 2018). Oil palm can act as a barrier to the dispersal of forest species (Scriven et al., 2017), but may buffer adjacent forest stands (e.g. Figure 1.8) and so lessen the intensity of edge effects (Fitzherbert et al., 2008), therefore more studies are needed to quantify these impacts.

Studies of edge effects in oil palm landscapes have revealed contrasting effects, with declines in forest amphibian richness near oil palm plantations (Scriven et al., 2018) but variable or no change in insect or mammal diversity (Maeto et al., 1999; Lucey and Hill, 2012; Yue et al., 2015; Chapman et al., 2019; Williamson et al., 2021). Analyses of remotely-sensed data reveal AGC losses averaging 22% within 114 m of edges (Ordway and Asner, 2020), but considerable variation, from 16-30% losses between 35m – 300m in edges in the same landscape (Ordway and Asner, 2020). Remotely-sensed studies have also documented reductions in canopy growth within 300m of plantations (Nunes et al., 2021), and an overall decrease in canopy height near edges (Nguyen et al., 2023). However, with the exception of Permana et al. (2022), who recently documented compositional shifts of forest seedling communities towards early-successional assemblages, and Luskin et al. (2017), who found reduced sapling densities due to spillover of wild boar from plantations, there is a paucity of field research examining edge effects on forest tree communities adjacent to oil palm. Global demand for vegetable oil is projected to double by 2050, with palm oil expected to fulfil much of this demand (Corley, 2009). Tropical landscapes dominated by oil palm plantations will therefore become more common throughout the tropics, and without quantifying the indirect impacts of deforestation for oil palm via edge effects, we may be underestimating the environmental impacts of this expansion. Given the highly fragmented nature of Sabah’s forests and the dominance of oil palm plantations, it is an ideal study landscape in which to examine edge effects. Furthermore, the availability of high-resolution data on forest AGC (Asner et al., 2018) provides an opportunity to study the drivers of AGC at forest edges across large regions.

Figure 1.8 – Forest edge bordering oil palm monoculture in Sabah, Malaysian Borneo, as seen from satellite imagery (sourced from Google Earth Pro) and on the ground (photo by J Anderson). Oil palm is on the left in both panels, with forest on the right.

1.7 Thesis aims and rationale

In this thesis, I examine the impacts of edges on the composition, diversity and aboveground carbon stocks of forest remnants in oil palm landscapes. I provide new information to improve our understanding of the drivers of edge effect variability, and to help inform management strategies aimed at preserving forest diversity and carbon stocks. In chapter 2, I collect field data to quantify the effects of edge proximity on the composition, diversity, microclimate, structure and AGC stocks of tree communities in forest remnants bordering oil palm plantations in Sabah, Malaysian Borneo. In chapter 3, I use remotely-sensed data for Sabah to examine the influence of multiple edges on forest AGC, to determine how AGC is affected by proximity to additional edges. In chapter 4, I extend the analysis of these remotely-sensed data to examine the influence of adjacent matrix structure on AGC in forest edges, to determine whether edge effects are mediated by the matrix. In the General Discussion in chapter 5, I synthesise my findings, draw conclusions about the drivers of edge effect variability and relative importance of edge effects in Sabah’s fragmented forests, and suggest management recommendations to help preserve the integrity of forest remnants. The main objectives of these chapters are described below.

Chapter 2: Weak edge effects on trees in Bornean rainforest remnants bordering oil palm

In this chapter, I carry out field work to examine edge effects on forest structure, AGC stocks, microclimate and tree community composition and richness, in protected lowland forest remnants bordering mature oil palm plantations. I analyse data from field sites in Sabah, Malaysian Borneo to test the following hypotheses:

(1) Edge plots contain fewer and smaller stems, and lower AGC stocks, than forest interior plots

(2) Edge plots have reduced canopy cover, higher temperatures, and higher light levels than forest interior plots

(3) Tree community composition near edges is distinct from forest interior plots, with taxonomic and functional shifts toward low wood density pioneer trees, the loss of some taxa, and lower tree genus richness

Chapter 3: Proximity to multiple edges reduces carbon stocks in fragmented tropical rainforests

In this chapter, I use published remotely-sensed data and a heat-diffusion modelling approach to develop a state-wide map of forest ‘edginess’ for Sabah. My edginess metric accounts for the number and proximity of nearby edges in oil palm-dominated landscapes. I combine this information with data on forest AGC stocks (Asner et al., 2018) to test whether:

(1) AGC is reduced in forest areas that are influenced by multiple nearby edges
(2) My metric of edginess explains more variation in AGC than the commonly-used measure of ‘distance to nearest edge’

Chapter 4: Carbon stocks at rainforest edges are mediated by adjacent habitat structure

In this chapter, I use remotely-sensed data on AGC stocks (Asner et al., 2018) to examine how structural characteristics of the adjacent land-use matrix influence AGC at forest edge sites throughout Sabah. My analysis spans a range of matrix types, including oil palm, timber plantations, annual crops and pasture. I also examine whether edge age (time since edge creation) and local interior forest AGC mediate the effects of the neighbouring matrix structure. I test the following hypotheses:

(1) Forest AGC is higher in edges adjacent to low-contrast land-uses (i.e. land-uses with tall, dense vegetation such as mature oil palm) compared with edges adjacent to high-contrast land-uses (i.e. land-uses with short, sparse vegetation such as cattle pasture)
(2) AGC at edges declines over time
(3) Forest sites with high AGC in their interior are more resilient to edge effects and the effects of the matrix

1.8 References

Akram-Lodhi, A.H. 2012. Contextualising land grabbing: contemporary land deals, the global subsistence crisis and the world food system. *Canadian Journal of Development Studies*. **33**(2), pp.119–142.

Almeida, D.R.A., Stark, Scott C, Schietti, Juliana, Camargo, Jose L C, Amazonas, Nino T, Gorgens, Eric B, … Silva, C A 2019. Persistent effects of fragmentation on tropical rainforest canopy structure after 20 yr of isolation. *Ecological Applications*. **29**(6), p.e01952.

Appanah, S. 1993. Mass flowering of dipterocarp forests in the aseasonal tropics. *J. Biosci*. **18**(4), pp.457–474.

Arroyo-Rodríguez, V., Melo, F.P.L., Martínez-Ramos, M., Bongers, F., Chazdon, R.L., Meave, J.A., … Tabarelli, M. 2017. Multiple successional pathways in human-modified tropical landscapes: new insights from forest succession, forest fragmentation and landscape ecology research. *Biological Reviews*. **92**(1), pp.326–340.

Arroyo-Rodríguez, V., Saldaña-Vázquez, R.A., Fahrig, L., & Santos, B.A. 2017. Does forest fragmentation cause an increase in forest temperature? *Ecological Research*. **32**(1), pp.81–88.

Ashton, P.S. 2010. Conservation of Borneo biodiversity: Do small lowland parks have a role, or are big inland sanctuaries sufficient? Brunei as an example. *Biodiversity and Conservation*. **19**(2), pp.343–356.

Asner, G.P., Brodrick, P.G., Philipson, C., Vaughn, N.R., Martin, R.E., Knapp, D.E., … Coomes, D.A. 2018. Mapped aboveground carbon stocks to advance forest conservation and recovery in Malaysian Borneo. *Biological Conservation*. **217**, pp.289–310.

Asner, G.P., Rudel, T.K., Aide, T.M., Defries, R., & Emerson, R. 2009. A Contemporary Assessment of Change in Humid Tropical Forests. *Conservation Biology*. **23**(6), pp.1386–1395.

Atwood, E.C., Englhart, S., Lorenz, E., Halle, W., Wiedemann, W., & Siegert, F. 2016. Detection and Characterization of Low Temperature Peat Fires during the 2015 Fire Catastrophe in Indonesia Using a New High-Sensitivity Fire Monitoring Satellite Sensor (FireBird). *PLOS ONE*. **11**(8), p.e0159410.

Baccini, A., Walker, W., Carvalho, L., Farina, M., Sulla-Menashe, D., & Houghton, R.A. 2017. Tropical forests are a net carbon source based on aboveground measurements of gain and loss. *Science*. **358**(6360), pp.230–234.

Barlow, J., França, F., Gardner, T.A., Hicks, C.C., Lennox, G.D., Berenguer, E., … Graham, N.A.J. 2018. The future of hyperdiverse tropical ecosystems. *Nature 2018 559:7715*. **559**(7715), pp.517–526.

Barlow, J., Lennox, G.D., Ferreira, J., Berenguer, E., Lees, A.C., Nally, R. Mac, … Gardner, T.A. 2016. Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. *Nature*. **535**(7610), pp.144–147.

Barona, E., Ramankutty, N., Hyman, G., & Coomes, O.T. 2010. The role of pasture and soybean in deforestation of the Brazilian Amazon. *Environ. Res. Lett*. **5**, pp.24002–24011.

Bello, C., Galetti, M., Pizo, M.A., Magnago, L.F.S., Rocha, M.F., Lima, R.A.F., … Jordano, P. 2015. Defaunation affects carbon storage in tropical forests. *Science Advances*. **1**(11).

Benchimol, M., & Peres, C.A. 2015. Edge-mediated compositional and functional decay of tree assemblages in Amazonian forest islands after 26 years of isolation. *Journal of Ecology*. **103**(2), pp.408–420.

Benedick, S., Hill, J.K., Mustaffa, N., Chey, V.K., Maryati, M., Searle, J.B., … Hamer, K.C. 2006. Impacts of rain forest fragmentation on butterflies in northern Borneo: species richness, turnover and the value of small fragments. *Journal of Applied Ecology*. **43**(5), pp.967–977.

Benítez-Malvido, J., Gallardo-Vásquez, J.C., Alvarez-Añorve, M.Y., & Avila-Cabadilla, L.D. 2014. Influence of matrix type on tree community assemblages along tropical dry forest edges. *American Journal of Botany*. **101**(5), pp.820–829.

Benítez-Malvido, J., Lázaro, A., & Ferraz, I.D.K. 2018. Effect of distance to edge and edge interaction on seedling regeneration and biotic damage in tropical rainforest fragments: A long-term experiment. *Journal of Ecology*. **106**(6), pp.2204–2217.

Benitez-Malvido, J., & Martinez-Ramos, M. 2003. Influence of Edge Exposure on Tree Seedling Species Recruitment in Tropical Rain Forest Fragments1. *Biotropica*. **35**(4), pp.530–541.

Berenguer, E., Ferreira, J., Gardner, T.A., Aragão, L.E.O.C., De Camargo, P.B., Cerri, C.E., … Barlow, J. 2014. A large-scale field assessment of carbon stocks in human-modified tropical forests. *Global Change Biology*. **20**(12), pp.3713–3726.

Betts, M.G., Wolf, C., Pfeifer, M., Banks-Leite, C., Arroyo-Rodríguez, V., Ribeiro, D.B., … Ewers, R.M. 2019. Extinction filters mediate the global effects of habitat fragmentation on animals. *Science*. **366**(6470), pp.1236–1239.

Brando, P.M., Silvério, D., Maracahipes-Santos, L., Oliveira-Santos, C., Levick, S.R., Coe, M.T., … Trumbore, S. 2019. Prolonged tropical forest degradation due to compounding disturbances: Implications for CO2 and H2O fluxes. *Global Change Biology*. **25**(9), pp.2855–2868.

Briant, G., Gond, V., & Laurance, S.G.W. 2010. Habitat fragmentation and the desiccation of forest canopies: A case study from eastern Amazonia. *Biological Conservation*. **143**(11), pp.2763–2769.

Brinck, K., Fischer, R., Groeneveld, J., Lehmann, S., Dantas De Paula, M., Pütz, S., … Huth, A. 2017. High resolution analysis of tropical forest fragmentation and its impact on the global carbon cycle. *Nature Communications*. **8**(Article no:14855).

Broadbent, E.N., Asner, G.P., Keller, Michael, Knapp, David E, Oliveira, Paulo J C, Silva, Jose N, … Silva, J N 2008. Forest fragmentation and edge effects from deforestation and selective logging in the Brazilian Amazon.

Brooks, T.M., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Rylands, A.B., Konstant, W.R., … Hilton-Taylor, C. 2002. Habitat Loss and Extinction in the Hotspots of Biodiversity. *Conservation Biology*. **16**(4), pp.909–923.

Brosi, B.J., Daily, G.C., Shih, T.M., Oviedo, F., & Durán, G. 2008. The effects of forest fragmentation on bee communities in tropical countryside. *Journal of Applied Ecology*. **45**(3), pp.773–783.

Brouwer, R., Pinto, R., Dugstad, A., & Navrud, S. 2022. The economic value of the Brazilian Amazon rainforest ecosystem services: A meta-analysis of the Brazilian literature. *PLOS ONE*. **17**(5), p.e0268425.

Bryan, J.E., Shearman, P.L., Asner, G.P., Knapp, D.E., Aoro, G., & Lokes, B. 2013. Extreme Differences in Forest Degradation in Borneo: Comparing Practices in Sarawak, Sabah, and Brunei. *PLOS ONE*. **8**(7), p.e69679.

Camargo, J.L., & Kapos, V. 1995. Complex edge effects on soil moisture and microclimate in central Amazonian forest. *Journal of Tropical Ecology*. **11**(2), pp.205–221.

Campbell, M.J., Edwards, W., Magrach, A., Alamgir, M., Porolak, G., Mohandass, D., & Laurance, W.F. 2018. Edge disturbance drives liana abundance increase and alteration of liana–host tree interactions in tropical forest fragments. *Ecology and Evolution*. **8**(8), pp.4237–4251.

Campbell, R.E., Harding, J.S., Ewers, R.M., Thorpe, S., & Didham, R.K. 2011. Production land use alters edge response functions in remnant forest invertebrate communities. *Ecological Applications*. **21**(8), pp.3147–3161.

Carlson, K.M., Curran, L.M., Ratnasari, D., Pittman, A.M., Soares-Filho, B.S., Asner, G.P., … Rodrigues, H.O. 2012. Committed carbon emissions, deforestation, and community land conversion from oil palm plantation expansion in West Kalimantan, Indonesia. *Proceedings of the National Academy of Sciences of the United States of America*. **109**(19), pp.7559–7564.

Castro, M.C., Baeza, A., Codeço, C.T., Cucunubá, Z.M., Dal'Asta, A.P., De Leo, G.A., … Santos-Vega, M. 2019. Development, environmental degradation, and disease spread in the Brazilian Amazon. *PLOS Biology*. **17**(11), p.e3000526.

Chaplin-Kramer, R., Ramler, I., Sharp, R., Haddad, N.M., Gerber, J.S., West, P.C., … King, H. 2015. Degradation in carbon stocks near tropical forest edges. *Nature Communications*. **6**(Article no: 10158).

Chaplin-Kramer, R., Sharp, R., Mandle, L., Sim, S., Johnson, J., Butnar, I., … Kareiva, P.M. 2015. Spatial patterns of agricultural expansion determine impacts on biodiversity and carbon storage. *Proceedings of the National Academy of Sciences of the United States of America*. **112**(24), pp.7402–7407.

Chaplin-Kramer, R., Sim, S., Hamel, P., Bryant, B., Noe, R., Mueller, C., … Daily, G. 2017. Life cycle assessment needs predictive spatial modelling for biodiversity and ecosystem services. *Nature Communications*. **8**, p.15065.

Chapman, P.M., Loveridge, R., Rowcliffe, J.M., Carbone, C., Bernard, H., Davison, C.W., & Ewers, R.M. 2019. Minimal Spillover of Native Small Mammals From Bornean Tropical Forests Into Adjacent Oil Palm Plantations. *Frontiers in Forests and Global Change*. **2**, p.2.

Cochrane, M.A. 2003. Fire science for rainforests. *Nature 2003 421:6926*. **421**(6926), pp.913–919.

Cochrane, M.A. 2001. Synergistic Interactions between Habitat Fragmentation and Fire in Evergreen Tropical Forests. *Conservation Biology*. **15**(6), pp.1515–1521.

Cochrane, M.A., Alencar, A., Schulze, M.D., Souza, C.M., Nepstad, D.C., Lefebvre, P., & Davidson, E.A. 1999. Positive feedbacks in the fire dynamic of closed canopy tropical forests. *Science*. **284**(5421), pp.1832–1835.

Cochrane, M.A., & Laurance, W.F. 2002. Fire as a large-scale edge effect in Amazonian forests. *Journal of Tropical Ecology*. **18**(3), pp.311–325.

Corlett, R.T. 2019. *The Ecology of Tropical East Asia* Third Edit. Oxford, UK: Oxford University Press.

Corley, R.H.V. 2009. How much palm oil do we need? *Environmental Science & Policy*. **12**(2), pp.134–139.

Corley, R.H.V., & Tinker, P.B. 2015. *The Oil Palm* [Online] Fifth Edition. John Wiley & Sons. [Accessed 26 March 2023]. Available from: https://onlinelibrary.wiley.com/doi/book/10.1002/9781118953297.

Cramer, J.M., Mesquita, R.C.G., & Bruce Williamson, G. 2007. Forest fragmentation differentially affects seed dispersal of large and small-seeded tropical trees. *Biological Conservation*. **137**(3), pp.415–423.

Curran, L.M., Caniago, I., Paoli, G.D., Astianti, D., Kusneti, M., Leighton, M., … Haeruman, H. 1999. Impact of El Nino and logging on canopy tree recruitment in Borneo. *Science*. **286**(5447), pp.2184–2188.

Curran, L.M., Trigg, S.N., McDonald, A.K., Astiani, D., Hardiono, Y.M., Siregar, P., … Kasischke, E. 2004. Lowland Forest Loss in Protected Areas of Indonesian Borneo. *Science*. **303**(5660), pp.1000–1003.

Curtis, P.G., Slay, C.M., Harris, N.L., Tyukavina, A., & Hansen, M.C. 2018. Classifying drivers of global forest loss. *Science*. **361**(6407), pp.1108–1111.

D’Angelo, S.A., Andrade, A.C.S., Laurance, S.G., Laurance, W.F., & Mesquita, R.C.G. 2004. Inferred causes of tree mortality in fragmented and intact Amazonian forests. *Journal of Tropical Ecology*. **20**, pp.243–246.

Dantas de Paula, M., Groeneveld, J., & Huth, A. 2015. Tropical forest degradation and recovery in fragmented landscapes — Simulating changes in tree community, forest hydrology and carbon balance. *Global Ecology and Conservation*. **3**, pp.664–677.

Defries, R.S., Rudel, T., Uriarte, M., & Hansen, M. 2010. Deforestation driven by urban population growth and agricultural trade in the twenty-first century. *Nature Geoscience 2010 3:3*. **3**(3), pp.178–181.

Descals, A., Wich, S., Meijaard, E., Gaveau, D.L.A., Peedell, S., & Szantoi, Z. 2021. High-resolution global map of smallholder and industrial closed-canopy oil palm plantations. *Earth System Science Data*. **13**(3), pp.1211–1231.

Didham, R.K., Ghazoul, J., Stork, N.E., & Davis, A.J. 1996. Insects in fragmented forests: a functional approach. *Trends in Ecology & Evolution*. **11**(6), pp.255–260.

Didham, R.K., Kapos, V., & Ewers, R.M. 2012. Rethinking the conceptual foundations of habitat fragmentation research. *Oikos*. **121**(2), pp.161–170.

Didham, R.K., & Lawton, J.H. 1999. Edge structure determines the magnitude of changes in microclimate and vegetation structure in tropical forest fragments. *Biotropica*. **31**, pp.17–30.

Don, A., Schumacher, J., & Freibauer, A. 2011. Impact of tropical land-use change on soil organic carbon stocks – a meta-analysis. *Global Change Biology*. **17**(4), pp.1658–1670.

Driscoll, D.A., Banks, S.C., Barton, P.S., Lindenmayer, D.B., & Smith, A.L. 2013. Conceptual domain of the matrix in fragmented landscapes. *Trends in Ecology and Evolution*. **28**(10), pp.605–613.

Edwards, D.P., Hodgson, J.A., Hamer, K.C., Mitchell, S.L., Ahmad, A.H., Cornell, S.J., & Wilcove, D.S. 2010. Wildlife-friendly oil palm plantations fail to protect biodiversity effectively. *Conservation Letters*. **3**(4), pp.236–242.

Edwards, D.P., Larsen, T.H., Docherty, T.D.S., Ansell, F.A., Hsu, W.W., Derhé, M.A., … Wilcove, D.S. 2011. Degraded lands worth protecting: the biological importance of Southeast Asia's repeatedly logged forests. *Proceedings of the Royal Society B: Biological Sciences*. **278**(1702), pp.82–90.

Eiserhardt, W.L., Couvreur, T.L.P., & Baker, W.J. 2017. Plant phylogeny as a window on the evolution of hyperdiversity in the tropical rainforest biome. *New Phytologist*. **214**(4), pp.1408–1422.

Ellis, E.C., Gauthier, N., Goldewijk, K.K., Bird, R.B., Boivin, N., Díaz, S., … Watson, J.E.M. 2021. People have shaped most of terrestrial nature for at least 12,000 years. *Proceedings of the National Academy of Sciences of the United States of America*. **118**(17), p.e2023483118.

Ewers, R.M., Andrade, A., Laurance, S.G., Camargo, J.L., Lovejoy, T.E., & Laurance, W.F. 2017. Predicted trajectories of tree community change in Amazonian rainforest fragments. *Ecography*. **40**(1), pp.26–35.

Ewers, R.M., & Banks-Leite, C. 2013. Fragmentation Impairs the Microclimate Buffering Effect of Tropical Forests G. Bohrer, ed. *PLoS ONE*. **8**(3), p.e58093.

Ewers, R.M., & Didham, R.K. 2006. Confounding factors in the detection of species responses to habitat fragmentation. *Biological Reviews*.

Fahrig, L. 2003. Effects of Habitat Fragmentation on Biodiversity. *Annual Review of Ecology,* *Evolution, and Systematics*. **34**, pp.487–515.

Fernández, C., Acosta, F.J., Abellá, G., López, F., & Díaz, M. 2002. Complex edge effect fields as additive processes in patches of ecological systems. *Ecological Modelling*. **149**(3), pp.273–283.

Ferraz, G., Russell, G.J., Stouffer, P.C., Bierregaard, R.O., Pimm, S.L., & Lovejoy, T.E. 2003. Rates of species loss from Amazonian forest fragments. *Proceedings of the National Academy of Sciences of the United States of America*. **100**(SUPPL. 2), pp.14069–14073.

Fischer, R., Taubert, F., Müller, M.S., Groeneveld, J., Lehmann, S., Wiegand, T., & Huth, A. 2021. Accelerated forest fragmentation leads to critical increase in tropical forest edge area. *Science Advances*. **7**(37).

Fitzherbert, E.B., Struebig, M.J., Morel, A., Danielsen, F., Brühl, C.A., Donald, P.F., & Phalan, B. 2008. How will oil palm expansion affect biodiversity? *Trends in Ecology and Evolution*. **23**(10), pp.538–545.

Fletcher, R.J. 2005. Multiple edge effects and their implications in fragmented landscapes. *Journal of Animal Ecology*. **74**(2), pp.342–352.

Fletcher, R.J., Didham, R.K., Banks-Leite, C., Barlow, J., Ewers, R.M., Rosindell, J., … Haddad, N.M. 2018. Is habitat fragmentation good for biodiversity? *Biological Conservation*. **226**, pp.9–15.

Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., … Snyder, P.K. 2005. Global consequences of land use. *Science*. **309**(5734), pp.570–574.

Franklin, C.M.A., Harper, K.A., & Clarke, M.J. 2020. Trends in studies of edge influence on vegetation at human-created and natural forest edges across time and space. *Canadian Journal of Forest Research*., pp.1–9.

Gascon, C., Williamson, G.B., & Da Fonseca, G.A.B. 2000. Receding forest edges and vanishing reserves. *Science*. **288**(5470), pp.1356–1358.

Gaveau, D.L.A., Sheil, D., Husnayaen, Salim, M.A., Arjasakusuma, S., Ancrenaz, M., … Meijaard, E. 2016. Rapid conversions and avoided deforestation: examining four decades of industrial plantation expansion in Borneo. *Scientific Reports*. **6**(Article no: 32017).

Gaveau, D.L.A., Sloan, S., Molidena, E., Yaen, H., Sheil, D., Abram, N.K., … Meijaard, E. 2014. Four Decades of Forest Persistence, Clearance and Logging on Borneo. *PLoS One*. **9**(7), p.e101654.

Gibbs, H.K., Brown, S., Niles, J.O., & Foley, J.A. 2007. Monitoring and estimating tropical forest carbon stocks: making REDD a reality. *Environ. Res. Lett*. **2**, p.13.

Gibbs, H.K., Ruesch, A.S., Achard, F., Clayton, M.K., Holmgren, P., Ramankutty, N., & Foley, J.A. 2010. Tropical forests were the primary sources of new agricultural land in the 1980s and 1990s. *Proceedings of the National Academy of Sciences of the United States of America*. **107**(38), pp.16732–7.

Gibson, L., Lee, T.M., Koh, L.P., Brook, B.W., Gardner, T.A., Barlow, J., … Sodhi, N.S. 2011. Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature*. **478**(7369), pp.378–381.

Goetz, S.J., Hansen, M., Houghton, R.A., Walker, W., Laporte, N., & Busch, J. 2015. Measurement and monitoring needs, capabilities and potential for addressing reduced emissions from deforestation and forest degradation under REDD+. *Environmental Research Letters*. **10**(12), p.123001.

Gora, E.M., & Esquivel-Muelbert, A. 2021. Implications of size-dependent tree mortality for tropical forest carbon dynamics. *Nature Plants*., pp.384–391.

Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., … Townshend, J.R. 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances*. **1**(2).

Hansen, M.C., Potapov, P. V, Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., … Townshend, J.R.G. 2013. High-resolution global maps of 21st-century forest cover change. *Science (New York, N.Y.)*. **342**(6160), pp.850–3.

Hansen, M.C., Wang, L., Song, X.P., Tyukavina, A., Turubanova, S., Potapov, P. V., & Stehman, S. V. 2020. The fate of tropical forest fragments. *Science Advances*. **6**(11), pp.8574–8585.

Hanski, I. 2015. Habitat fragmentation and species richness. *Journal of Biogeography*. **42**(5), pp.989–993.

Hanski, I. 1998. Metapopulation dynamics. *Nature*. **396**(6706), pp.41–49.

Hardwick, S.R., Toumi, R., Pfeifer, M., Turner, E.C., Nilus, R., & Ewers, R.M. 2015. The relationship between leaf area index and microclimate in tropical forest and oil palm plantation: Forest disturbance drives changes in microclimate. *Agricultural and Forest Meteorology*. **201**, pp.187–195.

Harper, K.A., Macdonald, S.E., Burton, P.J., Chen, J., Brosofske, K.D., Saunders, S.C., … Esseen, P.A. 2005. Edge Influence on Forest Structure and Composition in Fragmented Landscapes.

Conservation Biology. **19**(3), pp.768–782.

Harper, K.A., Mascarúa-López, L., Macdonald, S.E., & Drapeau, P. 2007. Interaction of edge influence from multiple edges: Examples from narrow corridors. *Plant Ecology*. **192**(1), pp.71–84.

Harris, N.L., Gibbs, D.A., Baccini, A., Birdsey, R.A., de Bruin, S., Farina, M., … Tyukavina, A. 2021. Global maps of twenty-first century forest carbon fluxes. *Nature Climate Change 2021 11:3*. **11**(3), pp.234–240.

Harrison, M., Page, S., & Limin, S. 2009. The global impact of Indonesian forest fires. *Biologist*. **56**, pp.156–163.

Harrison, R.D., Sreekar, R., Brodie, J.F., Brook, S., Luskin, M., O'Kelly, H., … Velho, N. 2016. Impacts of hunting on tropical forests in Southeast Asia. *Conservation Biology*. **30**(5), pp.972–981.

Harrison, R.D., Tan, S., Plotkin, J.B., Slik, F., Detto, M., Brenes, T., … Davies, S.J. 2013. Consequences of defaunation for a tropical tree community. *Ecology Letters*. **16**(5), pp.687–694.

Hatfield, J.H., Barlow, J., Joly, C.A., Lees, A.C., Parruco, C.H. de F., Tobias, J.A., … Banks-Leite, C. 2020. Mediation of area and edge effects in forest fragments by adjacent land use. *Conservation Biology*. **34**(2), pp.395–404.

Henders, S., Persson, U.M., & Kastner, T. 2015. Trading forests: land-use change and carbon emissions embodied in production and exports of forest-risk commodities. *Environmental Research Letters*. **10**(12), p.125012.

Hill, J.K., Gray, M.A., Khen, C.V., Benedick, S., Tawatao, N., & Hamer, K.C. 2011. Ecological impacts of tropical forest fragmentation: how consistent are patterns in species richness and nestedness? *Philosophical Transactions of the Royal Society B: Biological Sciences*. **366**(1582), pp.3265–3276.

Hoyt, A.M., Chaussard, E., Seppalainen, S.S., & Harvey, C.F. 2020. Widespread subsidence and carbon emissions across Southeast Asian peatlands. *Nature Geoscience 2020 13:6*. **13**(6), pp.435–440.

Ibáñez, I., Katz, D.S.W., Peltier, D., Wolf, S.M., & Connor Barrie, B.T. 2014. Assessing the integrated effects of landscape fragmentation on plants and plant communities: the challenge of multiprocess-multiresponse dynamics. *Journal of Ecology*. **102**(4), pp.882–895.

Jucker, T., Hardwick, S.R., Both, S., Elias, D.M.O., Ewers, R.M., Milodowski, D.T., … Coomes, D.A. 2018. Canopy structure and topography jointly constrain the microclimate of human-modified tropical landscapes. *Global Change Biology*. **24**(11), pp.5243–5258.

Jules, E.S., & Shahani, P. 2003. A broader ecological context to habitat fragmentation: Why matrix habitat is more important than we thought. *Journal of Vegetation Science*. **14**(3), pp.459–464.

Kapos, V. 1989. Effects of isolation on the water status of forest patches in the Brazilian Amazon. *Journal of Tropical Ecology*. **5**(2), pp.173–185.

Kastner, T., Erb, K.H., & Haberl, H. 2014. Rapid growth in agricultural trade: effects on global area efficiency and the role of management. *Environmental Research Letters*. **9**(3), p.034015.

Kennedy, C.M., Marra, P.P., Fagan, W.F., & Neel, M.C. 2010. Landscape matrix and species traits mediate responses of Neotropical resident birds to forest fragmentation in Jamaica. *Ecological Monographs*. **80**(4), pp.651–669.

Kier, G., Mutke, J., Dinerstein, E., Ricketts, T.H., Küper, W., Kreft, H., & Barthlott, W. 2005. Global patterns of plant diversity and floristic knowledge. *Journal of Biogeography*. **32**(7), pp.1107–1116.

Krishnadas, M., Bagchi, R., Sridhara, S., & Comita, L.S. 2018. Weaker plant-enemy interactions decrease tree seedling diversity with edge-effects in a fragmented tropical forest. *Nature Communications*. **9**(1), pp.1–7.

Krishnadas, M., Kumar, A.N., & Comita, L.S. 2019. Edge effects reduce α-diversity but not β-diversity during community assembly in a human-modified tropical forest. *Ecological Applications*. **29**(8), p.e01996.

Krishnadas, M., & Stump, S.M. 2021. Dispersal limitation and weaker stabilizing mechanisms mediate loss of diversity with edge effects in forest fragments. *Journal of Ecology*. **109**(5), pp.2137–2151.

Kupfer, J.A., Malanson, G.P., & Franklin, S.B. 2006. Not seeing the ocean for the islands: the mediating influence of matrix-based processes on forest fragmentation effects. *Global Ecology and Biogeography*. **15**(1), pp.8–20.

Lack, P.C. 1988. Hedge intersections and breeding bird distribution in farmland. *Bird Study*. **35**(2), pp.133–136.

LaCroix, J.J., Li, Q., Chen, J., Henderson, R., & John, R. 2008. Edge effects on fire spread in a disturbed Northern Wisconsin landscape. *Landscape Ecology*. **23**(9), pp.1081–1092.

Lam, W.Y., Kulak, M., Sim, S., King, H., Huijbregts, M.A.J., & Chaplin-Kramer, R. 2019. Greenhouse gas footprints of palm oil production in Indonesia over space and time. *Science of the Total Environment*. **688**, pp.827–837.

Lambin, E.F., & Meyfroidt, P. 2011. Global land use change, economic globalization, and the looming land scarcity. *Proceedings of the National Academy of Sciences of the United States of America*. **108**(9), pp.3465–3472.

Lapola, D.M., Pinho, P., Barlow, J., Aragão, L.E.O.C., Berenguer, E., Carmenta, R., … Walker, W.S. 2023. The drivers and impacts of Amazon forest degradation. *Science*. **379**(6630).

Laurance, Ferreira, L. V., Rankin-De Merona, J.M., & Laurance, S.G. 1998. Rain forest fragmentation and the dynamics of Amazonian tree communities. *Ecology*. **79**(6), pp.2032–2040.

Laurance, Nascimento, H, Laurance, S., Andrade, A.C., Fearnside, P.M., Ribeiro, J.E.L., & Capretz, R.L. 2006. Rain forest fragmentation and the proliferation of successional trees. *Wiley Online Library*. **87**(2), pp.469–482.

Laurance, Nascimento, Henrique E M, Laurance, S.G., Andrade, A., Ribeiro, J.E.L.S., Giraldo, J.P., … D'Angelo, S. 2006. Rapid decay of tree-community composition in Amazonian forest fragments. *Proceedings of the National Academy of Sciences of the United States of America*. **103**(50), pp.19010–19014.

Laurance, Nascimento, Henrique E. M., Laurance, S.G., Andrade, A.C., Fearnside, P.M., Ribeiro, J.E.L., & Capretz, R.L. 2006. RAIN FOREST FRAGMENTATION AND THE PROLIFERATION OF SUCCESSIONAL TREES. *Ecology*. **87**(2), pp.469–482.

Laurance, W., Ferreira, L. V., Merona, J.M.R.-D., Laurance, S.G., Hutchings, R.W., & Lovejoy, T.E. 1998. Effects of Forest Fragmentation on Recruitment Patterns in Amazonian Tree Communities. *Conservation Biology*. **12**(2), pp.460–464.

Laurance, W.F. 1991. Edge effects in tropical forest fragments: Application of a model for the design of nature reserves. *Biological Conservation*. **57**(2), pp.205–219.

Laurance, W.F., Camargo, J.L.C., Fearnside, P.M., Lovejoy, T.E., Williamson, G.B., Mesquita, R.C.G., … Laurance, S.G.W. 2018. An Amazonian rainforest and its fragments as a laboratory of global change. *Biological Reviews*. **93**(1), pp.223–247.

Laurance, W.F., Camargo, J.L.C., Luizão, R.C.C., Laurance, S.G., Pimm, S.L., Bruna, E.M., … Lovejoy, T.E. 2011. The fate of Amazonian forest fragments: A 32-year investigation. *Biological Conservation*. **144**(1), pp.56–67.

Laurance, W.F., Carolina Useche, D., Rendeiro, J., Kalka, M., Bradshaw, C.J.A., Sloan, S.P., … Zamzani, F. 2012. Averting biodiversity collapse in tropical forest protected areas. *Nature 2012 489:7415*. **489**(7415), pp.290–294.

Laurance, W.F., & Curran, T.J. 2008. Impacts of wind disturbance on fragmented tropical forests: A review and synthesis. *Austral Ecology*. **33**(4), pp.399–408.

Laurance, W.F., Delamônica, P., Laurance, S.G., Vasconcelos, H.L., & Lovejoy, T.E. 2000. Rainforest fragmentation kills big trees. *Nature*. **404**, p.836.

Laurance, W.F., Laurance, S.G., Ferreira, L. V., Rankin-de Merona, J.M., Gascon, C., & Lovejoy, T.E. 1997. Biomass collapse in Amazonian forest fragments. *Science*. **278**(5340), pp.1117–1118.

Laurance, W.F., Lovejoy, T.E., Vasconcelos, H.L., Bruna, E.M., Didham, R.K., Stouffer, P.C., … Sampaio, E. 2002. Ecosystem decay of Amazonian forest fragments: a 22-year investigation. *Conservation Biology*. **16**(3), pp.605–618.

Laurance, W.F., Nascimento, H.E.M., Laurance, S.G., Andrade, A., Ewers, R.M., Harms, K.E., … Ribeiro, J.E. 2007. Habitat fragmentation, variable edge effects, and the landscape-divergence hypothesis. *PLoS ONE*. **2**(10), p.e1017.

Laurance, W.F., Sayer, J., & Cassman, K.G. 2014. Agricultural expansion and its impacts on tropical nature. *Trends in Ecology & Evolution*. **29**(2), pp.107–116.

Lewis, S.L., Edwards, D.P., & Galbraith, D. 2015. Increasing human dominance of tropical forests. *Science*. **349**(6250), pp.827–32.

Li, Y., Brando, P.M., Morton, D.C., Lawrence, D.M., Yang, H., & Randerson, J.T. 2022. Deforestation-induced climate change reduces carbon storage in remaining tropical forests. *Nature Communications 2022 13:1*. **13**(1), pp.1–13.

Lindenmayer, D., & Fischer, J. 2006. *Habitat fragmentation and landscape change : an ecological and conservation synthesis*. Washington: Island Press.

Lindenmayer, D.B., Cunningham, R., Crane, M., Michael, D., & Montague-Drake, R. 2007. Farmland bird responses to intersecting replanted areas. *Landscape Ecology*. **22**(10), pp.1555–1562.

Lindenmayer, D.B., Laurance, W.F., & Franklin, J.F. 2012. Global decline in large old trees. *Science*. **338**(6112), pp.1305–1306.

Lucey, J.M., & Hill, J.K. 2012. Spillover of Insects from Rain Forest into Adjacent Oil Palm Plantations. *Biotropica*. **44**(3), pp.368–377.

Lucey, J.M., Tawatao, N., Senior, M.J.M., Chey, V.K., Benedick, S., Hamer, K.C., … Hill, J.K. 2014. Tropical forest fragments contribute to species richness in adjacent oil palm plantations. *Biological Conservation*. **169**, pp.268–276.

Luskin, M.S., Brashares, J.S., Ickes, K., Sun, I.F., Fletcher, C., Wright, S.J., & Potts, M.D. 2017. Cross-boundary subsidy cascades from oil palm degrade distant tropical forests. *Nature Communications*. **8**(Article no: 2231).

Luyssaert, S., Jammet, M., Stoy, P.C., Estel, S., Pongratz, J., Ceschia, E., … Dolman, A.J. 2014. Land management and land-cover change have impacts of similar magnitude on surface temperature. *Nature Climate Change 2014 4:5*. **4**(5), pp.389–393.

MacArthur, R., & Wilson, E. 1967. *The theory of island biogeography*. The University of Chicago Press Princeton.

Macedo, M.N., DeFries, R.S., Morton, D.C., Stickler, C.M., Galford, G.L., & Shimabukuro, Y.E. 2012. Decoupling of deforestation and soy production in the southern Amazon during the late 2000s. *Proceedings of the National Academy of Sciences of the United States of America*. **109**(4), pp.1341–1346.

MacKinnon, K., Hatta, G., Halim, H., & Mangalik, A. 1997. The ecology of Kalimantan. *Oxford University Press*., p.880.

Maeda, E.E., Aragão, L.E.O.C., Baker, J.C.A., Balbino, L.C., de Moura, Y.M., Nobre, A.D., … dos Reis, J.C. 2023. Land use still matters after deforestation. *Communications Earth & Environment 2023 4:1*. **4**(1), pp.1–4.

Maeto, K., Fukuyama, K., & Kirton, L. 1999. Edge effects on ambrosia beetle assemblages in a lowland rain forest, bordering oil palm plantations, in peninsular Malaysia. *Journal of Tropical Forest Science*. **11**(3), pp.537–547.

Magnago, L.F.S., Magrach, A., Barlow, J., Schaefer, C.E.G.R., Laurance, W.F., Martins, S.V., & Edwards, D.P. 2017. Do fragment size and edge effects predict carbon stocks in trees and lianas in tropical forests? *Functional Ecology*. **31**, pp.542–552.

Magnago, L.F.S., Rocha, M.F., Meyer, L., Martins, S.V., & Meira-Neto, J.A.A. 2015. Microclimatic conditions at forest edges have significant impacts on vegetation structure in large Atlantic forest fragments. *Biodiversity and Conservation*. **24**(9), pp.2305–2318.

Malcolm, J.R. 1998. A model of conductive heat flow in forest edges and fragmented landscapes. *Climatic Change*. **39**(2–3), pp.487–502.

Malcolm, J.R. 1994. Edge Effects in Central Amazonian Forest Fragments. *Ecology*. **75**(8), pp.2438–2445.

Malcolm, J.R., Valenta, K., & Lehman, S.M. 2017. Edge effects in tropical dry forests of Madagascar: additivity or synergy? *Landscape Ecology*. **32**(2), pp.327–341.

Malhi, Y. 2010. The carbon balance of tropical forest regions, 1990–2005. *Current Opinion in Environmental Sustainability*. **2**(4), pp.237–244.

Malhi, Y., Gardner, T.A., Goldsmith, G.R., Silman, M.R., & Zelazowski, P. 2014. Tropical forests in the anthropocene. *Annual Review of Environment and Resources*. **39**, pp.125–159.

Matricardi, E.A.T., Skole, D.L., Costa, O.B., Pedlowski, M.A., Samek, J.H., & Miguel, E.P. 2020. Long-term forest degradation surpasses deforestation in the Brazilian Amazon. *Science*. **369**(6509), pp.1378–1382.

Maxwell, S.L., Evans, T., Watson, J.E.M., Morel, A., Grantham, H., Duncan, A., … Malhi, Y. 2019. Degradation and forgone removals increase the carbon impact of intact forest loss by 626%. *Science Advances*. **5**(10).

Mechiche-Alami, A., Piccardi, C., Nicholas, K.A., & Seaquist, J.W. 2019. Transnational land acquisitions beyond the food and financial crises. *Environmental Research Letters*. **14**(8), p.084021.

Meijaard, E., Brooks, T.M., Carlson, K.M., Slade, E.M., Garcia-Ulloa, J., Gaveau, D.L.A., … Sheil, D. 2020. The environmental impacts of palm oil in context. *Nature Plants*. **6**, pp.1418–1426.

Meijaard, E., Sheil, D., Nasi, R., & Stanley, S.A. 2006. Wildlife Conservation in Bornean Timber Concessions. . **11**(1).

Melito, M., Metzger, J.P., & de Oliveira, A.A. 2018. Landscape-level effects on aboveground biomass of tropical forests: A conceptual framework. *Global Change Biology*. **24**(2), pp.597–607.

de Melo, F.P.L., Dirzo, R., & Tabarelli, M. 2006. Biased seed rain in forest edges: Evidence from the

Brazilian Atlantic forest. *Biological Conservation*. **132**(1), pp.50–60.

Melo, F.P.L., Martnez-Salas, E., Bentez-Malvido, J., & Ceballos, G. 2010. Forest fragmentation reduces recruitment of large-seeded tree species in a semi-deciduous tropical forest of southern Mexico. *Journal of Tropical Ecology*. **26**(1), pp.35–43.

Mesquita, R.C.G., Delamônica, P., & Laurance, W.F. 1999. Effect of surrounding vegetation on edge-related tree mortality in Amazonian forest fragments. *Biological Conservation*. **91**(2–3), pp.129–134.

Metzger, J.P., Villarreal-Rosas, J., Suárez-Castro, A.F., López-Cubillos, S., González-Chaves, A., Runting, R.K., … Rhodes, J.R. 2021. Considering landscape-level processes in ecosystem service assessments. *Science of The Total Environment*. **796**, p.149028.

Meyfroidt, P., Lambin, E.F., Erb, K.H., & Hertel, T.W. 2013. Globalization of land use: distant drivers of land change and geographic displacement of land use. *Current Opinion in Environmental Sustainability*. **5**(5), pp.438–444.

Michalski, F., Nishi, I., & Peres, C.A. 2007. Disturbance-mediated drift in tree functional groups in Amazonian forest fragments. *Biotropica*. **39**(6), pp.691–701.

Miettinen, J., Shi, C., & Liew, S.C. 2011. Deforestation rates in insular Southeast Asia between 2000 and 2010. *Global Change Biology*. **17**(7), pp.2261–2270.

Millward-Hopkins, J., Steinberger, J.K., Rao, N.D., & Oswald, Y. 2020. Providing decent living with minimum energy: A global scenario. *Global Environmental Change*. **65**, p.102168.

Mitchard, E.T.A. 2018. The tropical forest carbon cycle and climate change. *Nature*. **559**(7715), pp.527–534.

MPOB 2022. Oil Palm Planted Area 2022.

Murcia, C. 1995. Edge effects in fragmented forests: implications for conservation. *Trends in Ecology & Evolution*. **10**(2), pp.58–62.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., & Kent, J. 2000. Biodiversity hotspots for conservation priorities. *Nature*. **403**, pp.853–858.

Nascimento, H.E.M., Andrade, A.C.S., Camargo, J.L.C., Laurance, W.F., Laurance, S.G., & Ribeiro, J.E.L. 2006. Effects of the surrounding matrix on tree recruitment in Amazonian forest fragments. *Conservation Biology*. **20**(3), pp.853–860.

Nascimento, H.E.M., & Laurance, W.F. 2004. Biomass dynamics in amazonian forest fragments. *Ecological Applications*. **14**(4 SUPPL.).

Newbold, T., Hudson, L.N., Hill, S.L.L., Contu, S., Lysenko, I., Senior, R.A., … Purvis, A. 2015. Global effects of land use on local terrestrial biodiversity. *Nature*. **520**(7545), pp.45–50.

Nguyen, T.A., Ehbrecht, M., & Camarretta, N. 2023. Application of point cloud data to assess edge effects on rainforest structural characteristics in tropical Sumatra, Indonesia. *Landscape Ecology*. **3**, pp.1–18.

Numata, I., Silva, S.S., Cochrane, M.A., & d'Oliveira, M. V. 2017. Fire and edge effects in a fragmented tropical forest landscape in the southwestern Amazon. *Forest Ecology and Management*. **401**, pp.135–146.

Nunes, C.A., Berenguer, E., França, F., Ferreira, J., Lees, A.C., Louzada, J., … Barlow, J. 2022. Linking land-use and land-cover transitions to their ecological impact in the Amazon. *Proceedings of the National Academy of Sciences of the United States of America*. **119**(27), p.e2202310119.

Nunes, M.H., Jucker, T., Riutta, T., Svátek, M., Kvasnica, J., Rejžek, M., … Coomes, D.A. 2021. Recovery of logged forest fragments in a human-modified tropical landscape during the 2015-16 El Niño. *Nature Communications*. **12**(Article no: 1526).

Oakley, J.L., & Bicknell, J.E. 2022. The impacts of tropical agriculture on biodiversity: A meta-analysis. *Journal of Applied Ecology*. **59**(12), pp.3072–3082.

Oliveira, M.A., Grillo, A.S., & Tabarelli, M. 2004. Forest edge in the Brazilian Atlantic forest: Drastic changes in tree species assemblages. *Oryx*. **38**(4), pp.389–394.

Oliveira, M.A., Santos, A.M.M., & Tabarelli, M. 2008. Profound impoverishment of the large-tree stand in a hyper-fragmented landscape of the Atlantic forest. *Forest Ecology and Management*. **256**(11), pp.1910–1917.

Ordway, E.M., & Asner, G.P. 2020. Carbon declines along tropical forest edges correspond to heterogeneous effects on canopy structure and function. *Proceedings of the National Academy of Sciences of the United States of America*. **117**(14), pp.7863–7870.

Ordway, E.M., Asner, G.P., & Lambin, E.F. 2017. Deforestation risk due to commodity crop expansion in sub-Saharan Africa. *Environmental Research Letters*. **12**(4), p.044015.

Osuri, A.M., Ratnam, J., Varma, V., Alvarez-Loayza, P., Hurtado Astaiza, J., Bradford, M., … Sankaran, M. 2016. Contrasting effects of defaunation on aboveground carbon storage across the global tropics. *Nature Communications*. **7**(1), p.11351.

Oswald, Y., Owen, A., & Steinberger, J.K. 2020. Large inequality in international and intranational energy footprints between income groups and across consumption categories. *Nature Energy 2020 5:3*. **5**(3), pp.231–239.

Pan, Y., Birdsey, R.A., Fang, J., Houghton, R., Kauppi, P.E., Kurz, W.A., … Hayes, D. 2011. A large and persistent carbon sink in the world's forests. *Science (New York, N.Y.)*. **333**(6045), pp.988–93.

Paoli, G.D., Curran, L.M., & Slik, J.W.F. 2008. Soil nutrients affect spatial patterns of aboveground biomass and emergent tree density in southwestern Borneo. *Oecologia*. **155**(2), pp.287–299.

de Paula, M.D., Costa, C.P.A., & Tabarelli, M. 2011. Carbon storage in a fragmented landscape of Atlantic forest: the role played by edge-affected habitats and emergent trees. *Tropical Conservation Science*. **4**(3), pp.349–358.

Pearson, T.R.H., Brown, S., Murray, L., & Sidman, G. 2017. Greenhouse gas emissions from tropical forest degradation: An underestimated source. *Carbon Balance and Management*. **12**(1), pp.1–11.

Pendrill, F., Gardner, T.A., Meyfroidt, P., Persson, U.M., Adams, J., Azevedo, T., … West, C. 2022. Disentangling the numbers behind agriculture-driven tropical deforestation. *Science*. **377**(6611).

Pendrill, F., Persson, U.M., Godar, J., Kastner, T., Moran, D., Schmidt, S., & Wood, R. 2019. Agricultural and forestry trade drives large share of tropical deforestation emissions. *Global Environmental Change*. **56**, pp.1–10.

Peres, C.A. 2001. Synergistic Effects of Subsistence Hunting and Habitat Fragmentation on Amazonian Forest Vertebrates. *Conservation Biology*. **15**(6), pp.1490–1505.

Permana, G., Marliana, S.N., Susandarini, R., & Addaha, H. 2022. Sustaining rainforest remnants in plantation landscapes: degree of oil palm stand-induced edge effects on forest microclimate and regeneration. *CERNE*. **28**(1).

Peters, H.A. 2001. Clidemia hirta Invasion at the Pasoh Forest Reserve: An Unexpected Plant Invasion in an Undisturbed Tropical Forest1. *Biotropica*. **33**(1), pp.60–68.

Pfeifer, M., Lefebvre, V., Peres, C.A., Banks-Leite, C., Wearn, O.R., Marsh, C.J., … Ewers, R.M. 2017. Creation of forest edges has a global impact on forest vertebrates. *Nature*. **551**, pp.187–191.

Phillips, O.L., Rose, S., Mendoza, A.M., & Vargas, P.N. 2006. Resilience of southwestern Amazon forests to anthropogenic edge effects. *Conservation Biology*. **20**(6), pp.1698–1710.

Picoli, M.C.A., & Machado, P.G. 2021. Land use change: the barrier for sugarcane sustainability. *Biofuels, Bioproducts and Biorefining*. **15**(6), pp.1591–1603.

Pimm, S.L., Jenkins, C.N., Abell, R., Brooks, T.M., Gittleman, J.L., Joppa, L.N., … Sexton, J.O. 2014. The biodiversity of species and their rates of extinction, distribution, and protection. *Science*. **344**(6187).

Pinho, B.X., Peres, C.A., Leal, I.R., & Tabarelli, M. 2020. Critical role and collapse of tropical mega-trees: A key global resource. *Advances in Ecological Research*. **62**, pp.253–294.

Porensky, L.M. 2011. When edges meet: interacting edge effects in an African savanna. *Journal of Ecology*. **99**(4), pp.923–934.

Porensky, L.M., & Young, T.P. 2013. Edge-Effect Interactions in Fragmented and Patchy Landscapes. *Conservation Biology*. **27**(3), pp.509–519.

Preston, F.W. 1962. The Canonical Distribution of Commonness and Rarity: Part I. *Ecology*. **43**(2), p.185.

Prugh, L.R., Hodges, K.E., Sinclair, A.R.E., & Brashares, J.S. 2008. Effect of habitat area and isolation on fragmented animal populations. *Proceedings of the National Academy of Sciences of the United States of America*. **105**(52), pp.20770–20775.

Püttker, T., Crouzeilles, R., Almeida-Gomes, M., Schmoeller, M., Maurenza, D., Alves-Pinto, H., … Prevedello, J.A. 2020. Indirect effects of habitat loss via habitat fragmentation: A cross-taxa analysis of forest-dependent species. *Biological Conservation*. **241**, p.108368.

Pütz, S., Groeneveld, J., Alves, L.F., Metzger, J.P., & Huth, A. 2011. Fragmentation drives tropical forest fragments to early successional states: A modelling study for Brazilian Atlantic forests. *Ecological Modelling*. **222**(12), pp.1986–1997.

Pütz, S., Groeneveld, J., Henle, K., Knogge, C., Martensen, A.C., Metz, M., … Huth, A. 2014. Long-term carbon loss in fragmented Neotropical forests. *Nature Communications*. **5**(1), p.5037.

Qie, L., Lewis, S.L., Sullivan, M.J.P., Lopez-Gonzalez, G., Pickavance, G.C., Sunderland, T., … Phillips, O.L. 2017. Long-term carbon sink in Borneo's forests halted by drought and vulnerable to edge effects. *Nature Communications*. **8**(Article no: 1966).

Le Quéré, C., Andrew, R.M., Canadell, J.G., Sitch, S., Korsbakken, J.I., Peters, G.P., … Zaehle, S.

2016. Global Carbon Budget 2016. *Earth System Science Data*. **8**(2), pp.605–649.

Le Quéré, C., Andrew, R.M., Friedlingstein, P., Sitch, S., Pongratz, J., Manning, A.C., … Zhu, D. 2017. Global Carbon Budget 2017. *Earth System Science Data Discussions*., pp.1–79.

Rand, T.A., Tylianakis, J.M., & Tscharntke, T. 2006. Spillover edge effects: the dispersal of agriculturally subsidized insect natural enemies into adjacent natural habitats. *Ecology Letters*. **9**(5), pp.603–614.

Razafindratsima, O.H., Brown, K.A., Carvalho, F., Steig, |, Johnson, E., Wright, P.C., … Razafindratsima, H. 2018. Edge effects on components of diversity and above-ground biomass in a tropical rainforest. *J Appl Ecol*., p.55.

Reynolds, G., Payne, J., Sinun, W., Mosigil, G., & Walsh, R.P.D. 2011. Changes in forest land use and management in Sabah, Malaysian Borneo, 1990-2010, with a focus on the Danum Valley region. *Philosophical Transactions of the Royal Society B: Biological Sciences*. **366**(1582), pp.3168–3176.

Ries, L., Fletcher, R.J., Battin, J., & Sisk, T.D. 2004. Ecological responses to habitat edges: mechanisms, models, and variability explained. *Annual Review of Ecology, Evolution, and Systematics*. **35**, pp.491–522.

Ries, L., Murphy, S.M., Wimp, G.M., & Fletcher, R.J. 2017. Closing persistent gaps in knowledge about edge ecology. *Current Landscape Ecology Reports*. **2**, pp.30–41.

Santos-Barrera, G., & Urbina-Cardona, J.N. 2011. The role of the matrix-edge dynamics of amphibian conservation in tropical montane fragmented landscapes. *Revista mexicana de biodiversidad*. **82**(2), pp.679–687.

Santos, B.A., Arroyo-Rodríguez, V., Moreno, C.E., & Tabarelli, M. 2010. Edge-Related Loss of Tree Phylogenetic Diversity in the Severely Fragmented Brazilian Atlantic Forest J. Chave, ed. *PLoS ONE*. **5**(9), p.e12625.

Santos, B.A., Peres, C.A., Oliveira, M.A., Grillo, A., Alves-Costa, C.P., & Tabarelli, M. 2008. Drastic erosion in functional attributes of tree assemblages in Atlantic forest fragments of northeastern Brazil. *Biological Conservation*. **141**(1), pp.249–260.

Savilaakso, S., Garcia, C., Garcia-Ulloa, J., Ghazoul, J., Groom, M., Guariguata, M.R., … Zrust, M. 2014. Systematic review of effects on biodiversity from oil palm production. *Environmental Evidence*. **3**(1), pp.1–21.

van Schalkwyk, J., Pryke, J.S., Samways, M.J., & Gaigher, R. 2020. Corridor width determines strength of edge influence on arthropods in conservation corridors. *Landscape Ecology*. **35**(5), pp.1175–1185.

Schedlbauer, J.L., Finegan, B., & Kavanagh, K.L. 2007. Rain Forest Structure at Forest-Pasture Edges in Northeastern Costa Rica. *Biotropica*. **39**(5), pp.578–584.

Scheffers, B.R., Joppa, L.N., Pimm, S.L., & Laurance, W.F. 2012. What we know and don't know about Earth's missing biodiversity. *Trends in Ecology & Evolution*. **27**(9), pp.501–510.

Schwartz, N.B., Uriarte, M., Defries, R., Bedka, K.M., Fernandes, K., Gutiérrez-Vélez, V., & Pinedo-Vasquez, M.A. 2017. Fragmentation increases wind disturbance impacts on forest structure and carbon stocks in a western Amazonian landscape. *Ecological Applications*. **27**(6), pp.1901–1915.

Scriven, S.A., Beale, C.M., Benedick, S., & Hill, J.K. 2017. Barriers to dispersal of rain forest butterflies in tropical agricultural landscapes. *Biotropica*. **49**(2), pp.206–216.

Scriven, S.A., Gillespie, G.R., Laimun, S., & Goossens, B. 2018. Edge effects of oil palm plantations on tropical anuran communities in Borneo. *Biological Conservation*. **220**, pp.37–49.

Senior, M.J.M., Hamer, K.C., Bottrell, S., Edwards, D.P., Fayle, T.M., Lucey, J.M., … Hill, J.K. 2013. Trait-dependent declines of species following conversion of rain forest to oil palm plantations. *Biodiversity and Conservation*. **22**(1), pp.253–268.

Shenkin, A., Chandler, C.J., Boyd, D.S., Jackson, T., Disney, M., Majalap, N., … Malhi, Y. 2019. The World's Tallest Tropical Tree in Three Dimensions. *Frontiers in Forests and Global Change*. **2**, p.32.

Silva Junior, C.H.L., Aragão, L.E.O.C., Anderson, L.O., Fonseca, M.G., Shimabukuro, Y.E., Vancutsem, C., … Saatchi, S.S. 2020. Persistent collapse of biomass in Amazonian forest edges following deforestation leads to unaccounted carbon losses. *Science Advances*. **6**(40), p.eaaz8360.

Silva Junior, C.H.L., Carvalho, N.S., Pessôa, A.C.M., Reis, J.B.C., Pontes-Lopes, A., Doblas, J., … Aragão, L.E.O.C. 2021. Amazonian forest degradation must be incorporated into the COP26 agenda. *Nature Geoscience 2021 14:9*. **14**(9), pp.634–635.

Sisk, T.D., Haddad, N.M., & Ehrlich, P.R. 1997. Bird Assemblages in Patchy Woodlands: Modeling the Effects of Edge and Matrix Habitats. *Ecological Applications*. **7**(4), pp.1170–1180.

Slik, J.W.F., Aiba, S.I., Brearley, F.Q., Cannon, C.H., Forshed, O., Kitayama, K., … van Valkenburg, J.L.C.H. 2010. Environmental correlates of tree biomass, basal area, wood specific gravity and stem density gradients in Borneo’s tropical forests. *Global Ecology and Biogeography*. **19**(1), pp.50–60.

Slik, J.W.F., Paoli, G., Mcguire, K., Amaral, I., Barroso, J., Bastian, M., … Zweifel, N. 2013. Large trees drive forest aboveground biomass variation in moist lowland forests across the tropics. *Global Ecology and Biogeography*. **22**(12), pp.1261–1271.

Slik, J.W.F., Poulsen, A.D., Ashton, P.S., Cannon, C.H., Eichhorn, K.A.O., Kartawinata, K., … Wilkie, P. 2003. A floristic analysis of the lowland dipterocarp forests of Borneo. *Journal of Biogeography*. **30**(10), pp.1517–1531.

Smith, I.A., Hutyra, L.R., Reinmann, A.B., Marrs, J.K., & Thompson, J.R. 2018. Piecing together the fragments: elucidating edge effects on forest carbon dynamics. *Frontiers in Ecology and the Environment*. **16**(4), pp.213–221.

Sodhi, N.S., Koh, L.P., Brook, B.W., & Ng, P.K.L. 2004. Southeast Asian biodiversity: An impending disaster. *Trends in Ecology and Evolution*. **19**(12), pp.654–660.

Sodhi, N.S., Koh, L.P., Clements, R., Wanger, T.C., Hill, J.K., Hamer, K.C., … Lee, T.M. 2010. Conserving Southeast Asian forest biodiversity in human-modified landscapes. *Biological Conservation*. **143**(10), pp.2375–2384.

Stouffer, P.C., Strong, C., & Naka, L.N. 2009. Twenty years of understorey bird extinctions from Amazonian rain forest fragments: consistent trends and landscape-mediated dynamics. *Diversity and Distributions*. **15**(1), pp.88–97.

Stride, G., Thomas, C.D., Benedick, S., Hodgson, J.A., Jelling, A., Senior, M.J.M., & Hill, J.K. 2018. Contrasting patterns of local richness of seedlings, saplings, and trees may have implications for regeneration in rainforest remnants. *Biotropica*. **50**(6), pp.889–897.

Struebig, M.J., Kingston, T., Zubaid, A., Mohd-Adnan, A., & Rossiter, S.J. 2008. Conservation value of forest fragments to Palaeotropical bats. *Biological Conservation*. **141**(8), pp.2112–2126.

Tabarelli, M., Lopes, A. V., & Peres, C.A. 2008. Edge-effects Drive Tropical Forest Fragments Towards an Early-Successional System. *Biotropica*. **40**(6), pp.657–661.

Tabarelli, M., Peres, C.A., & Melo, F.P.L. 2012. The ‘few winners and many losers’ paradigm revisited: Emerging prospects for tropical forest biodiversity. *Biological Conservation*. **155**, pp.136–140.

Taubert, F., Fischer, R., Groeneveld, J., Lehmann, S., Müller, M.S., Rödig, E., … Huth, A. 2018. Global patterns of tropical forest fragmentation. *Nature*. **554**, pp.519–522.

Turetsky, M.R., Benscoter, B., Page, S., Rein, G., Van Der Werf, G.R., & Watts, A. 2014. Global vulnerability of peatlands to fire and carbon loss. *Nature Geoscience 2015 8:1*. **8**(1), pp.11–14.

Uda, S.K., Hein, L., & Atmoko, D. 2019. Assessing the health impacts of peatland fires: a case study for Central Kalimantan, Indonesia. *Environmental Science and Pollution Research*. **26**(30), pp.31315–31327.

United Nations 2022. *World Population Prospects 2022: Summary of Results* [Online]. [Accessed 26 March 2023]. Available from: http://www.unpopulation.org/.

Veldkamp, E., Schmidt, M., Powers, J.S., & Corre, M.D. 2020. Deforestation and reforestation impacts on soils in the tropics. *Nature Reviews Earth & Environment 2020 1:11*. **1**(11), pp.590–605.

Vellend, M., Verheyen, K., Jacquemyn, H., Kolb, A., Van Calster, H., Peterken, G., & Hermy, M. 2006. Extinction debt of forest plants persists for more than a century following habitat fragmentation. *Ecology*. **87**(3), pp.542–548.

Vira, B., Wildburger, C., & Mansourian, S. 2015. *Forests, Trees and Landscapes for Food Security and Nutrition. A Global Assessment Report* [Online]. Vienna. [Accessed 25 March 2023]. Available from: www.iufro.org.

Waddell, E.H., Banin, L.F., Fleiss, S., Hill, J.K., Hughes, M., Jelling, A., … Chapman, D.S. 2020. Land-use change and propagule pressure promote plant invasions in tropical rainforest remnants. *Landscape Ecology*. **35**, pp.1891–1906.

Watson, J.E.M., Evans, T., Venter, O., Williams, B., Tulloch, A., Stewart, C., … Lindenmayer, D. 2018. The exceptional value of intact forest ecosystems. *Nature Ecology & Evolution 2018 2:4*. **2**(4), pp.599–610.

Van Der Werf, G.R., Randerson, J.T., Giglio, L., Collatz, G.J., Mu, M., Kasibhatla, P.S., … Van Leeuwen, T.T. 2010. Global fire emissions and the contribution of deforestation, savanna, forest, agricultural, and peat fires (1997-2009). *Atmospheric Chemistry and Physics*. **10**(23), pp.11707–11735.

Whitmore, T.. 1984. *Tropical rain forests of the Far East* 2nd editio. Oxford, UK: Clarendon Press.

Wilcove, D.S., & Koh, L.P. 2010. Addressing the threats to biodiversity from oil-palm agriculture. *Biodiversity and Conservation*. **19**(4), pp.999–1007.

Williamson, J., Slade, E.M., Luke, S.H., Swinfield, T., Chung, A.Y.C., Coomes, D.A., … Struebig, M.J. 2021. Riparian buffers act as microclimatic refugia in oil palm landscapes. *Journal of Applied Ecology*. **58**(2), pp.431–442.

Willmer, J.N.G., Püttker, T., & Prevedello, J.A. 2022. Global impacts of edge effects on species richness. *Biological Conservation*. **272**, p.109654.

Winkler, K., Fuchs, R., Rounsevell, M., & Herold, M. 2021. Global land use changes are four times greater than previously estimated. *Nature Communications 2021 12:1*. **12**(1), pp.1–10.

Yu, Y., Feng, K., & Hubacek, K. 2013. Tele-connecting local consumption to global land use. *Global Environmental Change*. **23**(5), pp.1178–1186.

Yue, S., Brodie, J.F., Zipkin, E.F., & Bernard, H. 2015. Oil palm plantations fail to support mammal diversity. *Ecological Applications*. **25**(8), pp.2285–2292.

Zhao, Z., Li, W., Ciais, P., Santoro, M., Cartus, O., Peng, S., … Wang, J. 2021. Fire enhances forest degradation within forest edge zones in Africa. *Nature Geoscience 2021 14:7*. **14**(7), pp.479–483.

Zhu, L., Li, W., Ciais, P., He, J., Cescatti, A., Santoro, M., … Wang, J. 2023. Comparable biophysical and biogeochemical feedbacks on warming from tropical moist forest degradation. *Nature Geoscience 2023 16:3*. **16**(3), pp.244–249.

Chapter 2 - **Weak edge effects on trees in Bornean rainforest remnants bordering oil palm**

Conducting carbon stock assessments in a lowland rainforest remnant

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2.1 Abstract

Many tropical forests are dominated by edge habitat, with consequences for forest structure, carbon stocks and biodiversity. However, edge effects are highly variable and context-dependent, and are poorly quantified in oil palm landscapes. We studied edge effects in 10 lowland rainforest remnants bordering mature oil palm plantations on Borneo, by surveying 0.2 ha plots along transects running perpendicular to the forest edge (ten 1.6 km transects, 5-6 plots per transect; 57 plots in total). We examined how edge proximity affected plot-level forest structure (canopy cover, number and size of stems ⩾10 cm diameter), aboveground carbon stocks, microclimate (air temperature and light intensity), and tree community composition and richness. The largest trees were significantly smaller (up to 21% reduced diameter) in plots near edges, and plot-level carbon was up to 30% lower (model-fitted average = 64.7 Mg ha^{-1} at 50m from the edge, versus 92.3 Mg ha^{-1} at 1600 m), with the strongest effects within 300m of edges. However, these significant effects of edge proximity were relatively small in the context of existing variation, with distance-from-edge explaining <13% of the total variability in maximum tree size or carbon. Additionally, there were generally no effects of edge proximity on any other component of forest structure, composition or diversity, and only a weak effect on microclimate. We conclude that limited edge effects in this system may reflect low structural contrast between forest and mature oil palm, and limited invasion of pioneer trees from plantations, which diminished edge influence in highly heterogeneous forest remnants.

Keywords

Agricultural expansion, biodiversity, carbon storage, forest fragmentation, forest structure, microclimate, tropical trees

Data availability - The data that support the findings of this study are openly available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.gqnk98sqj (Anderson et al., 2022).

2.2 Introduction

Agricultural expansion has caused widespread loss of tropical rainforests, which support an outstanding diversity of species and provide valuable ecosystem services (Lewis et al., 2015). This expansion is predicted to continue in the coming decades to provide food and resources for a growing human population (Laurance et al., 2014). Deforestation for agriculture causes a reduction in forest area and increased fragmentation of remaining forest, with consequences for biodiversity and key ecosystem functions such as carbon storage (Haddad et al., 2015). Forest fragmentation creates edges, where abiotic and biotic changes (‘edge effects’) can drive significant ecological changes within remnants (Laurance et al., 2002; Pfeifer et al., 2017). Approximately 20% of remaining tropical forest is within 100m of an edge (Brinck et al., 2017); it is therefore critical that we understand the impacts that edges have on rainforest tree communities, both to quantify the environmental impacts of agricultural expansion and to devise management strategies to limit detrimental effects.

Forest edges are typically hotter, drier, brighter and windier than interior forest, with increased vulnerability to desiccation and fire (Laurance et al., 2002). Abiotic changes lead to biotic edge effects, such as elevated tree recruitment and mortality, causing rapid community turnover (Laurance et al., 2006). This typically manifests in declines of slow-growing, late successional species with higher wood densities, whilst fast-growing pioneers with lower wood densities, better suited to the disturbed conditions at edges, become more dominant (Tabarelli et al., 2012). Thus, long-term compositional shifts can occur, resulting in taxonomically and functionally distinct tree communities at forest edges (Santos et al., 2008), changes to stand-level structure (e.g. stem number, stem size, canopy density) (Broadbent et al., 2008) and reduced species richness (Oliveira et al., 2004), but not always (Ibáñez et al., 2014). Increased mortality of large and high wood density trees can cause declines in aboveground biomass and carbon (de Paula et al., 2011), but edge effect magnitude is highly variable, and can be mediated by structural contrast with the adjacent matrix (i.e. land cover) type (Melito et al., 2018).

Not only do edge effects vary in magnitude, but it is often unclear how far they permeate into the forest. Many studies report penetration distances of less than 500m, albeit with considerable variation in exact distances (Broadbent et al., 2008). Estimates from remotely-sensed data, however, indicate that biomass losses of >10% can penetrate at least 1.5km into the forest, but this is highly variable among regions (Chaplin-Kramer et al., 2015). Hence, variable edge effects are commonly reported (Ries et al., 2004); this may in part be due to variable study designs, but is also due to the context-dependent nature of edge effects (Ries et al., 2017). Landscape composition and configuration exert a strong influence on edge effect magnitude and penetration depth, and also define the ecological context within which to assess their significance (Harper et al., 2005). Given that forest fragmentation is becoming increasingly common (Fischer et al., 2021), and that remaining forest patches are important refuges for wildlife and contribute to carbon stocks in agricultural landscapes (Fleiss et al., 2020), it is important to examine edge effects across a range of human-modified landscapes.

To date, there has been relatively little research on rainforest edges that border oil palm (*Elaeis guineensis*) plantations. This is surprising given that palm oil is the world's most consumed vegetable oil (Meijaard et al., 2020), with plantations estimated to cover over 20 M ha globally (Descals et al., 2021) and with around half of all new plantations occupying land converted from forest (Meijaard et al., 2018). Oil palm is a perennial crop that can reach over 13m in height in industrial plantations, forming a closed canopy with a stable understory microclimate (Luskin & Potts, 2011). It may therefore buffer the severity of edge effects in neighbouring forest (Fitzherbert et al., 2008), explaining the lack of edge effects found by Fleiss et al. (2020) in forest remnants within plantations. However, remotely-sensed data from Borneo suggest that edge effects may have large impacts on aboveground carbon (AGC) in forest remnants, resulting in average declines of 22.5% up to 114 metres from oil palm plantations (Ordway & Asner, 2020). Similarly, Nunes et al. (2021) found that forest within 300 metres of oil palm plantations had reduced canopy growth during the 2015-16 El Niño event. Additionally, there is evidence of increased stem turnover and reduced biomass accumulation up to 448 metres from edges in oil palm landscapes (Qie et al., 2017), suggesting that biomass loss may be due to compositional shifts towards low wood density taxa. However, Qie et al. (2017) also included edges bordering other matrix types in their study, such as inhabited areas, clear cut logging, regenerating forest and logging roads. Thus, it is unclear if there are changes in plant community composition or diversity in edges bordering oil palm, and there is also a lack of consensus on the magnitude and scale over which edge effects may operate.

The growth of the palm oil industry is expected to continue (Meijaard et al., 2020), and it is important to consider edge effects when quantifying the environmental impacts of oil palm expansion. Edge effects can account for 19% of palm oil production greenhouse gas (GHG) emissions, but are typically not included in GHG footprint studies (Lam et al., 2019); these will benefit from robust estimates of AGC loss at edges. Additionally, the Roundtable on Sustainable Palm Oil (RSPO) has Zero-Deforestation Commitments and requires patches of forest with 'High Conservation Values' (e.g. high biodiversity) and 'High Carbon Stocks' to be conserved (Rosoman et al., 2017; RSPO, 2018). Estimates of carbon stocks and biodiversity levels could be significantly enhanced with better understanding of edge effects within oil palm landscapes, potentially enabling better conservation and management practices and outcomes.

In this study, we conducted field surveys to quantify edge effects on rainforest tree communities in forest remnants bordering mature oil palm plantations in Sabah, Malaysian Borneo. Forests in this region contain some of the highest levels of AGC of any tropical forests (Asner et al., 2018) and are important biodiversity hotspots (Myers et al., 2000). However, Sabah has lost approximately 40% of its forest cover since 1973 (Gaveau et al., 2014) and the remaining forest is highly fragmented within oil palm plantation landscapes, with plantations now accounting for >20% of Sabah's land cover (MPOB, 2019). We quantify changes in plot-level forest structure, AGC and microclimate at increasing distances into forest remnants from edges bordering plantations, and examine how the composition and diversity of tree communities change, up to 1.6 km from edges. We studied effects over these distances because edge influence can persist up to 1.5 km from edges (Chaplin-Kramer et al., 2015). We test the hypotheses that edge plots contain fewer and smaller stems and have lower AGC stocks than interior plots, and also have reduced canopy cover, higher temperatures and higher light levels. We also test the hypothesis that tree community composition near edges is distinct from forest interior plots, with taxonomic and functional shifts towards low wood density pioneer trees, the loss of some taxa, and lower tree richness.

2.3 Methods

2.3.1 Study region and field sites

We studied 10 lowland (<500 m a.s.l.) mixed dipterocarp rainforest remnants in the State of Sabah, Malaysian Borneo (Figure 2.1; Table S1), between June and October 2019. All sites were forest reserves protected from disturbance (i.e. timber logging, hunting), containing interior forest areas at least 1.6 km from any edges, except Site 6 which only had interior forest 1 km from edges. Whilst detailed management histories of sites are not available, most have likely been selectively logged at variable intensities in the past (Gaveau et al., 2014). However, there has been no commercial logging in any site since at least 1984, when they were formally declared as protected areas, although many may have experienced low levels of encroachment (e.g. felling and hunting) (Stride et al., 2018). Edges were 19-49 years old (mean = 36 years), and bordered by large expanses of mature oil palm plantations. Neighbouring palms were on average 12.6m tall (SD = 3.75m) and 7.5m apart, with varied understory vegetation typical of mature plantations (Luke et al., 2019).

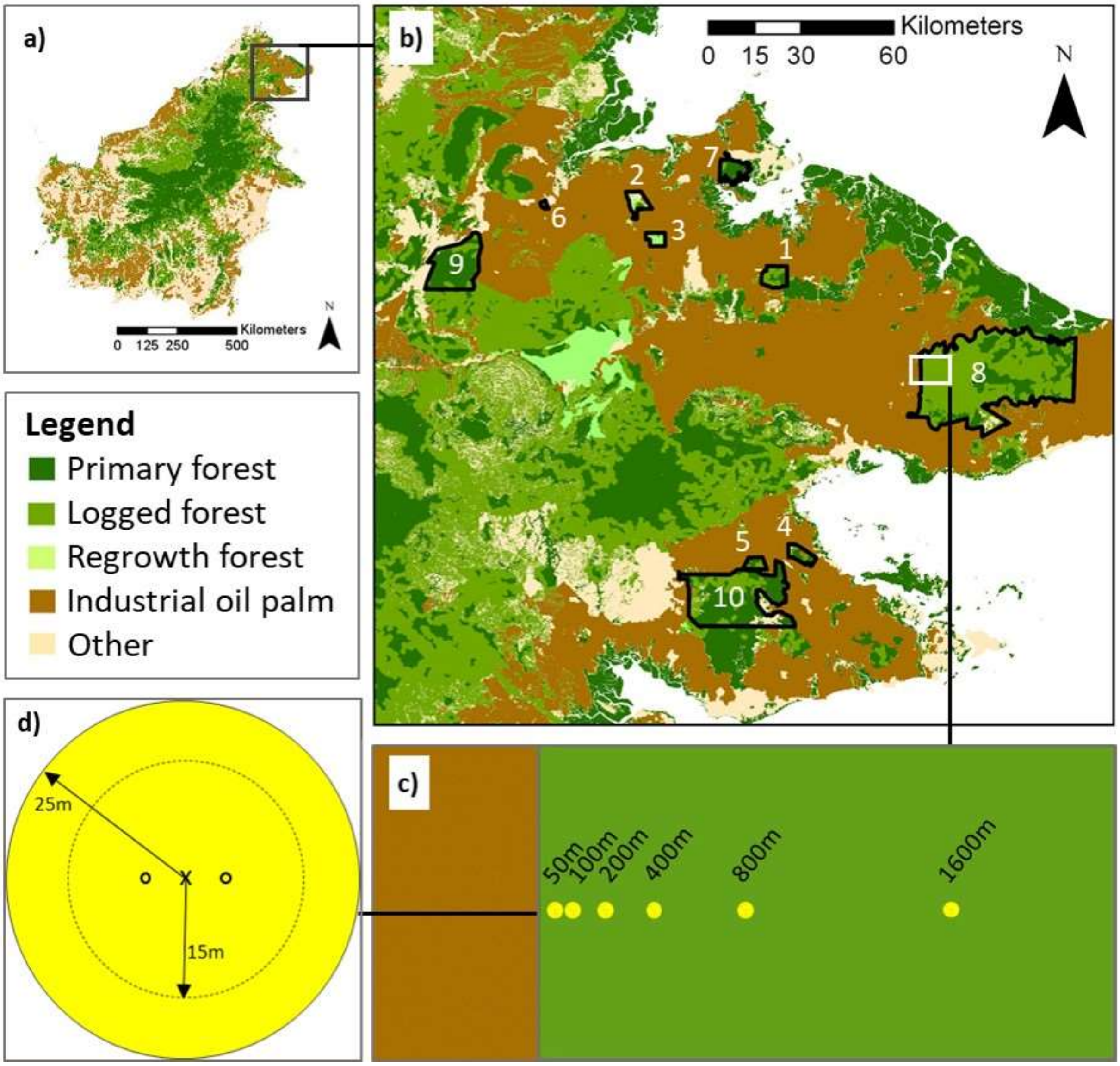


Figure 2.1. Clockwise from left: (**a**) Location of study area in Sabah, Malaysian Borneo and (**b**) location of the 10 forest remnant sites (see Table S1 for information on each). Maps of forest cover and oil palm plantations were obtained from CIFOR (Gaveau et al., 2014; Gaveau et al., 2016), reserve outlines were downloaded from the World Database of Protected Areas (WDPA; http://www.protectedplanet.net). (**c**) Transects ran perpendicular from the edge and contained five or six 0.2 ha circular plots, with plot centres at 50 m, 100 m, 200 m, 400 m, 800 m and (in seven sites) 1600 m from the edge. (**d**) Nested sampling plot design. We inventoried live stems ≥25 cm dbh in the main plot of 25 m radius (0.2 ha), and live stems ≥10 cm and <25 cm dbh in the subplot of 15 m radius (0.07 ha). Canopy density was measured in 4 compass directions from the plot centre, and microclimate data loggers were placed 5 m to the East and West of the plot centre (hollow circles), 1.8 m from the ground.

2.3.2 Vegetation surveys

We placed a single transect in each site, running perpendicular from the edge to the interior and >800 m from any other edges, to avoid influence from multiple edges (Porensky & Young, 2013). Transects were >4 km apart to avoid spatial autocorrelation. Forest edge was defined as the point where natural vegetation became taller than 5 m in height (UN FAO, 2012), however edges were usually characterised by a hard boundary between natural forest and oil palm at our sites, sometimes separated by minor plantation tracks. Transects comprised six circular plots (25 m radius, 0.2 ha) spaced to concentrate sampling effort close to the edge (Figure 2.1c), where the greatest effect of edge proximity was expected. Transects at three sites contained only five plots, either due to small remnant size or because natural features made the final plot inaccessible. In total we sampled 57 plots (total area of 11.2 ha).

Within each plot we used a nested survey design to maximise sampling efficiency (Figure 2.1d) and followed standard protocols (Marthews et al., 2014; Phillips et al., 2016) to inventory live trees (including palms) above 10 cm diameter at breast height (dbh). Trees were identified to genus level, or to species when known (23.1% of stems), either in the field or in consultation with botanists at Danum Valley Field Centre herbarium. Tree height was estimated by eye, always by the same person (AJ). AJ's estimates have been validated against the 'tangent method', which is commonly used to estimate tree height (Larjavaara & Muller-Landau, 2013), and were closely correlated (Fleiss et al., 2020), giving us confidence in our estimates.

2.3.3 Forest structure and microclimate measures and AGC estimation

For each plot we calculated the total number of individual stems sampled, and the mean and maximum dbh (cm) and height (m), to characterise plot-level forest structure. We also measured canopy density using a spherical crown densiometer, taking four readings (N, E, S & W) from the plot centre then converting these to a single plot-level measure (proportion cover from 0-1). We measured mean daily air temperature (°C) and mean daytime light intensity (lum/ft^2) within each plot, using Hobo® loggers (see Supplementary Information for details).

We assigned wood density (g/cm^3) values to each stem at the finest taxonomic level available, using the Global Wood Density Database (Chave et al., 2009; Zanne et al., 2009), then used published allometric equations (Chave et al., 2014; Goodman et al., 2013) to produce plot-level AGC (Mg C ha^{-1}) estimates (see Supplementary Information for details).

2.3.4 Tree diversity and community composition measures

As a measure of functional composition we calculated plot-level community-weighted mean (CWM) wood density (g/cm^3), using mixed-resolution wood density values (12.9% of stems at species level, 82.4% at genus level, 4.6% at family level) and plot-level abundance weightings. Wood density is a functional trait linked to growth strategy, with lower-wood density trees typically having faster growth rates, increased light preference and earlier successional status (Slik, 2005). We used genus-level data for analyses of taxonomic composition, and calculated plot-level genus richness (number of genera) as our measure of tree diversity. We worked at genus level because there are challenges with reliably identifying trees to species in Borneo, and analysing genus-level data can give more reliable results than species-level identifications (Slik et al., 2003), whilst also increasing sampling efficiency to give greater sample sizes (Imai et al., 2014). Genus-level data are also commonly used in studies of disturbance-driven floristic changes (e.g. Laurance et al., 2006; Michalski et al., 2007; Slik et al., 2008). Furthermore, patterns of floristic richness and composition are highly correlated between taxonomic levels in Borneo forests, making fragmentation and disturbance effects detectable at multiple taxonomic resolutions (Ganivet et al., 2020; Imai et al., 2014; Stride et al., 2018), and wood density is a highly taxonomically-conserved trait, with 72.5% of species-level variation explained at the genus-level (Slik, 2006). Our analyses of taxonomic and functional composition and diversity are therefore robust to genus-level information.

2.3.5 Data analysis of forest structure, AGC and microclimate

We conducted all analyses in R version 4.0.2 (R Core Team, 2020), using generalised mixed-effects models to test for edge effects on: number of trees (stems per plot), mean and maximum tree dbh (cm), mean and maximum tree height (m), canopy density (proportion cover from 0-1), AGC (Mg ha^{-1}), mean daily temperature (°C), and mean daytime light intensity (lum/ft^2) (nine models in total; Table 2.1). Data were analysed at plot level, using the glmer function in the lme4 package (Bates et al., 2015). Maximum dbh and mean daytime light intensity were both ln-(natural log) transformed to improve model fits, based on diagnostic plots. For all models, we used ln-transformed distance of plots from the forest edge as our fixed effect in order to linearize predicted edge-response curves, following Ibanez et al. (2017), which is appropriate given our concentrated sampling effort closer to the edge, and we assessed statistical significance using a threshold of $p < 0.05$ for the fixed effect term. We fitted models with appropriate error distribution families and link functions (Table 2.1) to ensure model assumptions were met, and model fits were assessed using residual plots. We included ‘site’ as a random intercept in all models to account for site-level variation in response variables.

2.3.6 Community composition and diversity analyses

We used the same modelling procedure to test for edge effects on plot-level CWM wood density and genus richness (two models; Table 2.1). To evaluate taxonomic similarity between plots in relation to edge proximity, we computed a Bray-Curtis dissimilarity matrix of all plots (Magurran, 2004), based on relative abundances of genera. We then performed an ordination using non-metric multidimensional scaling (NMDS) with 1000 iterations, using the metaMDS function in the R vegan package (Oksanen et al., 2020). We used the adonis2 function in vegan to perform a permutational multivariate analysis of variance (PERMANOVA), to assess differences in plot-level community composition between the six distance classes (treated categorically for this analysis), with 999 permutations to calculate significance.

To determine whether some taxa may be lost from edges even in the absence of detectable edge effects on plot-level richness or community composition, we pooled data from the 10 sites into 3 distance classes: ‘edge’ (50m + 100m plots), ‘intermediate’ (200m + 400m plots) and ‘core’ (800m + 1600m plots). We used a randomisation approach to generate a random (abundance-based) distribution of genera amongst categories (Supplementary Information), then used a chi-square goodness-of-fit test (chisq.test function; R Core Team, 2020) to determine if the actual distribution of genera differed from what we would expect by chance (i.e. our randomisation approach). If compositional shifts are resulting in the loss or gain of genera at edges (as distinct communities form), we would expect to see more genera unique to each individual distance class, and fewer genera found in all three classes, than predicted by chance alone. To confirm that our results are robust to the taxonomic resolution of our data, we also repeated all diversity and composition analyses on higher-resolution subsets of our data as a sensitivity analysis (Supplementary Information).

2.4 Results

In total we surveyed 2,403 individual stems from 57 plots at 10 sites, representing 138 genera (Table S3) and 54 families. We found high levels of heterogeneity among plots. For example, AGC varied from 11.3 to 255.9 Mg ha^{-1} (mean = 81.9 Mg ha^{-1} ± 44.4 SD), and genus richness varied from 8 to 31 genera per plot (mean = 20 genera ± 4.8 SD). There was also high floristic dissimilarity between plots according to Bray-Curtis index scores (mean = 0.8 ± 0.11 SD, on a 0-1 scale).

Table 2.1. Summary of mixed-effects models used to analyse the effect of ln-(natural log) transformed distance-from-edge on plot-level variables, with site included as a random intercept in all models. Models with a significant effect of distance ($p < 0.05$) are denoted in **bold**. Marginal (R^2_M) and conditional (R^2_C) R^2 values are given for these models, representing the proportion of variance explained by the fixed effect (ln-distance), and the entire model, respectively.

Response variable	**Error family (link function)**	**β (± SE)**	***p***	**R^2_M**	**R^2_C**
Stem number	Negative binomial (log link)	0.01	0.74		
Mean dbh (cm)	Gamma (log link)	0.001	0.94		
ln(Max dbh (cm))	Gaussian (identity link)	**0.07 (± 0.02)**	**0.004**	**0.13**	**0.20**
Mean height (m)	Gamma (log link)	0.02	0.23		
Max height (m)	Gaussian (identity link)	**3.4 (+/- 1)**	**0.002**	**0.10**	**0.50**
Canopy density (proportional)	Binomial (identity link)	-0.0002	0.96		
Aboveground carbon (Mg ha^{-1})	Gamma (log link)	**0.103 (± 0.05)**	**0.027**	**0.05**	**0.27**
Mean daily temperature (°C)	Gaussian (identity link)	**-0.05 (± 0.02)**	**0.02**	**0.005**	**0.95**
ln(Mean daylight intensity (lum/ft^2))	Gamma (log link)	-0.01	0.20		
CWM wood density (g/cm^3)	Gamma (identity link)	0.005	0.12		
Genus richness	Poisson (log link)	-0.007	0.79		

2.4.1 Variation in forest structure, AGC and microclimate with distance from edge

We found a significant effect of distance-from-edge on some components of forest structure, with maximum tree height, maximum dbh and AGC declining closer to edges (Table 2.1). Model-predicted values showed a 26.2% decrease in maximum height in plots at 50 m (mean = 32.9 m) versus 1600 m (mean = 44.6 m; Figure 2.2a; $p < 0.01$), and a similar decrease (21.3%) in maximum dbh (65.9 cm compared with 83.7 cm; Figure 2.2b; $p < 0.01$). The loss of very large trees in plots near edges resulted in a 29.9% decline in plot-level AGC (from 92.3 to 64.7 Mg ha^{-1} in plots at 1600 m versus 50 m; Figure 2.2c; $p < 0.05$). Edge effects on these three variables weakened with distance, with more than half of the change occurring within approximately 300 m of the edge. Edge proximity explained only 13% of the total variance in maximum dbh, 10% of total variance in maximum height, and 5% of total variance in AGC (Table 2.1 R^2_M). Hence, whilst significant, distance-from-edge explained only a small proportion of the total variation in these three variables. There was no effect of edge proximity on any other structural variable we measured (mean height, mean dbh, number of stems, canopy density; Table 2.1; Figure S2).

Edge plots were marginally hotter, but there was no significant effect of edge proximity on mean daytime light intensity (Table 2.1; Figure S2f). Model-predicted values showed a significant but small temperature increase from 25.54°C at 1600 m to 25.71°C at 50 m ($p < 0.05$; Figure 2.2d), and edge proximity explained only 0.5% of the total variance. There was a large effect of site in the model ($R^2_C = 0.95$), likely because sites were sampled on different days.

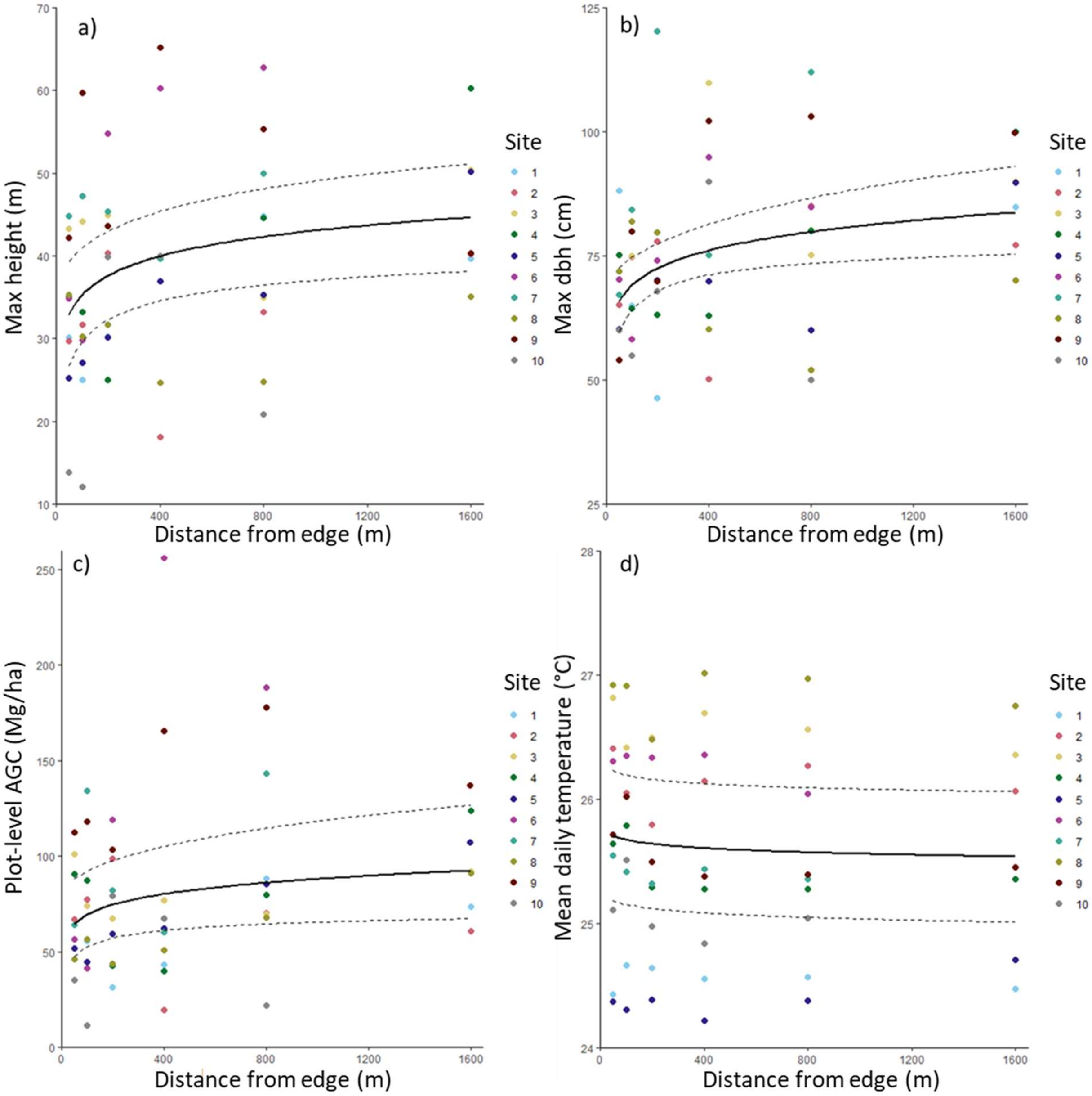


Figure 2.2. Significant effect of edge proximity (ln-transformed) on (**a**) maximum height (m), (**b**) maximum dbh (cm), (**c**) AGC (Mg ha^{-1}) and (**d**) mean daily temperature (°C), with 95% confidence intervals. Relationships are plotted against untransformed distance in order to visualise the non-linear edge effect. All models include 'site' as a random intercept but only a single trend line is presented here for each model, using predicted values for the entire sample, to aid visualisation of the effect (see Figure S3 for individual trend lines for each site). Maximum dbh was ln-transformed prior to analysis, therefore the exponents of predicted values were taken to make results more interpretable. Minor jitter applied to all figures to aid visualisation of overlapping data points. See Table 2.1 for model structures, coefficients and significance values.

2.4.2 Community composition and diversity

There was no significant effect of distance-from-edge on plot-level genus richness (Table 2.1; Figure 2.3b). There was also no evidence of plots clustering by distance in the NMDS ordination (Figure 2.3a), and results of the PERMANOVA supported this conclusion ($R^2 = 0.07$, $p = 0.98$), indicating that edge communities were not taxonomically distinct from forest interior communities. There was no significant effect of distance-from-edge on CWM wood density (Table 2.1; Figure S2e), indicating that there was also no edge effect on tree functional composition. This lack of edge effects on tree richness or composition was supported by analyses on data pooled into three distance classes (edge, intermediate and core); there was no significant difference between the observed distribution of genera among distance classes and their expected random abundance-based distribution ($\chi^2(6) = 7.47$, $p = 0.3$). Sensitivity analyses generally showed no qualitative change in results, and whilst a minority did give significant results indicative of possible edge effects, these were biologically weak and were driven entirely by outlier plots or rare (<1 individual/ha) species (Supplementary Information). Thus, our findings are robust to the taxonomic resolution of our data, and we conclude that distance-from-edge generally had no effect on tree diversity or community composition.

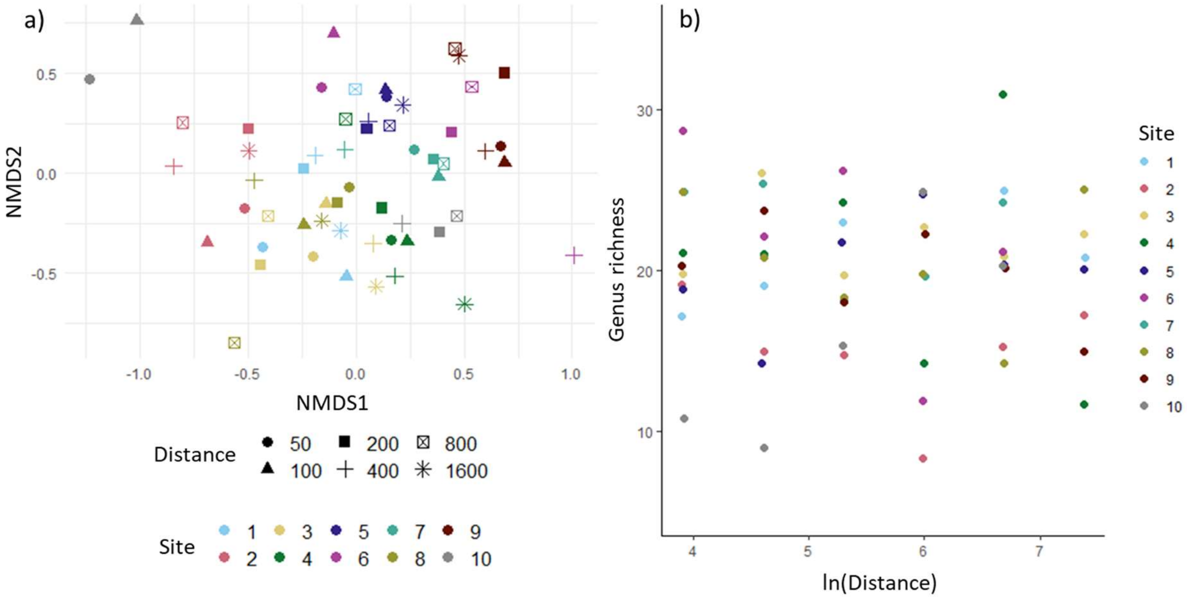


Figure 2.3 (**a**) Non-metric multidimensional scaling (NMDS) of plot genus composition, using Bray–Curtis index scores based on relative abundances (stress = 0.25), (**b**) No effect of edge proximity (ln-transformed) on plot-level genus richness, with minor jitter applied to aid visualisation of overlapping data points (see Table 2.1 for model structure, coefficients and significance value).

2.5 Discussion

2.5.1 Edge effects on the largest trees and AGC

We found reduced AGC in forest edges bordering oil palm plantations, with a 30% reduction in predicted plot-level AGC from 1600 m to 50 m (Figure 2.2c). This is similar to estimates from remotely-sensed data, with Ordway and Asner (2020) reporting AGC declines of up to 30% in some edges. Given the absence of edge effects on stand-level structure and composition, but declines in maximum tree dbh and height, we conclude that AGC loss is driven primarily by edge effects on large trees (i.e. those over 70cm dbh; Slik et al., 2013; Figure 2.2b). Thus, declines in biomass and AGC occurred independent of any compositional shifts, as observed elsewhere (Silva et al., 2021), probably because large trees make up a small proportion of stems but make a disproportionately large contribution to biomass (Slik et al., 2013).

Large trees (e.g. Figure S5) are commonly among the worst affected by edge effects (Laurance et al., 2000). They are highly susceptible to wind damage and canopy desiccation (Gora & Esquivel-Muelbert, 2021), which tend to be higher near edges and can cause increased mortality (Magnago et al., 2015). Indeed, the largest trees on Borneo are sensitive to drought-induced mortality (Phillips et al., 2010) and are typically found in sheltered areas where wind speeds are low (Jackson et al., 2021). Thus, abiotic changes at edges can reduce forest biomass (Qie et al., 2017). Many edges in our study were created after commercial logging had ceased, but subsequent encroachment and felling of large trees could also have contributed to the observed patterns, if removal rates have been higher near edges, where trees are more accessible. Nonetheless, even if logging has contributed to tree mortality at edges, we argue that this is still an edge-related effect, given that it results from edge creation and maintenance (Ries et al., 2017). Our finding that the largest trees are smaller at edges (21% reduced dbh, 26% reduced height) may therefore indicate increased mortality (via abiotic effects or edge-facilitated felling), and/or inhibited growth (Nunes et al., 2021), of the largest trees near plantations.

Over half of the observed reduction in AGC and maximum tree size occurred within approximately 300m from the edge (Figure 2.2), supporting studies that found edge effects within 300 - 500 m of edges (e.g. Nunes et al., 2021; Ordway & Asner, 2020; Qie et al., 2017). Small forest remnants will increasingly dominate many fragmented tropical landscapes (Taubert et al., 2018), and remnants without interior forest areas further than 300m from edges may therefore experience severe degradation of the large tree stand and associated carbon stocks. Effects on the largest trees could also have wider consequences, given their importance for numerous ecosystem processes and the many species they support (Pinho et al., 2020), and their loss may also have contributed to the small increase in understory temperature we observed near edges.

2.5.2 Weak edge influence - the importance of local context

Contextualising the influence of edge effects against existing variability within a system is essential to evaluate their relative importance (Harper et al., 2005). Whilst distance-from-edge caused a significant and meaningful decline in both AGC and maximum tree size ($p < 0.05$, 0.01 and 0.01 respectively; Table 2.1), these effects were relatively small in the context of the high baseline heterogeneity within the forest. Distance-from-edge explained only 13%, 10% and 5% of the total variation in maximum dbh, maximum height and AGC, whilst including site as a random effect in the models accounted for an additional 7%, 40% and 22% of variation respectively (Table 2.1 R^2 values). Thus, the ecological importance of edge influence in our study system is low compared to other drivers of variation, such as inter-site differences in factors like disturbance (e.g. from selective logging) or topography, which can outweigh fragmentation effects (Fleiss et al., 2020; Liu & Slik, 2014). Additionally, contrary to our hypotheses, many effects found in other systems were absent. We generally found no effect of edge proximity on community composition or tree diversity, no effect on most forest structural variables (e.g. stem number, canopy density), and only a weak effect on microclimate (< 0.2°C increase in temperature). Thus, overall edge effects do not appear to be as dominant here as in other systems (e.g. Laurance et al., 2018). We think this finding is unlikely to be due to the taxonomic resolution of our data, because analyses on a sub-set of stems identified to species-level support our conclusions (Supplementary Information). Other studies have shown that the adjacent matrix is a key determinant of ecological change within forest fragments, and has a mediating influence on fragmentation effects (Driscoll et al., 2013; Hatfield et al., 2020; Kupfer et al., 2006), and so the nature of the oil palm matrix (i.e. its structure, composition and extent) is likely to be an important factor in explaining the limited influence of edges in our study.

The average height of palms bordering our sites was 12.6m; at this height, plantations have typically developed closed canopies and some level of understory complexity (Luskin & Potts, 2011). Thus, compared with forest bordering open habitats like pastureland (Laurance et al., 2002) or annual crops such as sugarcane (Santos et al., 2008), structural contrast is maintained at relatively low levels at these plantation-forest edges. Structural contrast directly mediates the strength of abiotic gradients at edges, which control the magnitude and distance of effects on tree communities (Arroyo-Rodríguez et al., 2017; Mesquita et al., 1999), thus palm maturation may have provided a buffer against edge influence. For example, plantations are typically only around 2.8°C hotter than forest once mature (Luskin & Potts, 2011), hence the very small increase in temperature we observed near edges, which may also have been buffered by vegetation regrowth ‘sealing’ the forest edge (Didham & Lawton, 1999) and may only occur over very short distances (Ewers & Banks-Leite, 2013). Oil palm plantations may also act as a barrier to the dispersal of disturbance-adapted trees into forest edges, thus minimising compositional shifts. Study systems in which tree communities experience strong edge effects often contain many small, degraded forest remnants in close proximity to one another (e.g. Benchimol & Peres, 2015; Laurance et al., 2002; Magnago et al., 2017; Santos et al., 2008), which can act as a source of seed rain and facilitate the spread of pioneer trees into edges (Jesus et al., 2012), and trees within the matrix can also act as a source of propagule pressure (Nascimento et al., 2006). However, management practices that prevent the establishment of mature trees within monoculture oil palm plantations, and the isolation of forest remnants within the plantation landscape (Figure 2.1; Scriven et al., 2015), will probably limit pioneer tree seed rain into edges, given that the maximum dispersal distance of most trees in the region is 100-1000m (Corlett, 2009). Hence, the composition and configuration of forest remnants and the plantation landscape have likely mediated the ecological influence of edges in this study system. This suggests that mature tree communities in remnants within these oil palm landscapes may have some resilience to fragmentation effects, although it is important to note that edge effects can vary considerably even within the same study system, for example due to variation in local topography, soil type, climate or patch geometry (Laurance et al., 2007; Ordway & Asner, 2020), and it is therefore possible that effects may be more severe in other edges bordered by oil palm.

2.5.3 Potential time lags in edge effects

The average age of edge formation in our study was around 36 years, and so we conclude that there are long-term consequences of edge creation for the largest rainforest trees and AGC. However, it is unclear if these edge effects are ongoing or if they are residual effects following high mortality shortly after edge creation. There is little variation in edge age amongst our sites, which are biased towards older edges created 46-49 years ago (Table S1), therefore any conclusions about the temporal dynamics of effects are limited. However, there is evidence that AGC loss increases with edge age (Ordway & Asner, 2020), suggesting that edge effects may continue to impact the largest trees in our study, particularly in the younger edges established 19 years ago. Mortality at edges could also increase if management practices within plantations (e.g. periodic replanting) increase structural contrast at edges, or if edge effects are worsened by droughts, which are becoming more frequent and severe due to climate change (Cai et al., 2018;

Nunes et al., 2021). Thus, edge effects on large trees may worsen, and forest remnants within oil palm landscapes could experience long-term decays of carbon stocks.

Although we found no edge effects on the composition or diversity of trees in our plots, edge effects may be present in younger cohorts smaller than our 10 cm dbh stem threshold. Edge effects on seedlings and saplings can occur independently of effects on adult trees, for example due to their establishment post-edge creation or due to altered biotic interactions during early life stages (Krishnadas et al., 2019; Luskin et al., 2017; Slik et al., 2011). Stride et al. (2018) found that forest area and isolation effects reduced richness of tree seedlings but not adult trees in Bornean forest remnants, signalling a potential extinction debt. It is therefore possible that compositional shifts, loss of diversity and greater reductions of carbon could occur in these edges in the future. Further research on younger tree cohorts is needed to determine whether there are potential time lags, which may pose a threat to the long-term integrity of small remnants. Studies should also seek to determine the temporal dynamics of edge effects on mature trees and any potential impacts of plantation management, such as palm replanting.

2.5.4 Conclusions and implications for sustainable oil palm landscapes

Whilst edge proximity explained relatively little of the total plot-level variation within this system, it nevertheless caused a significant decline in maximum tree size and AGC, therefore edge effects do have implications for the future of sustainable oil palm landscapes. Adoption of sustainability criteria, such as the retention of forest patches that support ‘High Conservation Values’ or ‘High Carbon Stocks’ within plantations (Rosoman et al., 2017; RSPO, 2018), can boost local carbon stocks by 20% (Fleiss et al., 2020). However, their long-term persistence and integrity must be considered; for this reason, there are recommendations to prioritise the conservation of forest remnants with ‘core’ areas >200 ha (Lucey et al., 2017; recognising the detrimental effects of edges). Most remnants within plantations fall well short of this target (Scriven et al. unpublished data), and an edge penetration distance of around 300m, as indicated by this study, would compromise the ability of small or irregularly-shaped forest remnants to maintain carbon stocks, and the associated biodiversity that high-carbon forests support (Fleiss et al., 2020). Thus, if oil palm agriculture is to become sustainable as the industry continues to grow, it is important that these effects are taken into account when developing sustainability criteria, to ensure the long-term integrity of forest remnants.

Overall however, our results, like those of Fleiss et al. (2020) and Stride et al. (2018), suggest that fragmentation effects on mature tree communities in oil palm landscapes may be weak relative to existing levels of variation within forest remnants. Thus, tree communities in these landscapes may be less vulnerable to fragmentation effects than those in other agricultural landscapes, with remnants possibly maintaining their integrity in the longer term. We suspect that this is probably because of the current configuration and composition of the oil palm matrix (extensive and mature) and the forest remnants themselves (isolated and heterogeneous). However, given that edge effects can vary even within the same study system (Ordway & Asner, 2020), it is possible that effects may be more severe in other edges bordered by oil palm, such as those bordered by young palms or in close proximity to additional edges, and effects may also become more severe if there are time lags. Thus, whilst we conclude that strong edge effects are not ubiquitous, and are absent from some edges bordering oil palm, future research should seek to understand the patterns and drivers of spatial and temporal variability in these effects at a landscape scale, in order to inform the management of sustainable oil palm landscapes into the future.

2.6 References

Anderson, J. A., McClean, C. J., Sim, S., Pettorelli, N., Jelling, A., Tangah, J., Hill, J. K. (2022). Data from: Weak edge effects on trees in Bornean rainforest remnants bordering oil palm. Dryad Digital Repository. https://doi.org/10.5061/dryad.gqnk98sqj

Arroyo-Rodríguez, V., Saldaña-Vázquez, R. A., Fahrig, L., & Santos, B. A. (2017). Does forest fragmentation cause an increase in forest temperature? *Ecological Research*, *32*(1), 81–88. https://doi.org/10.1007/s11284-016-1411-6

Asner, G. P., Brodrick, P. G., Philipson, C., Vaughn, N. R., Martin, R. E., Knapp, D. E., Heckler, J., Evans, L. J., Jucker, T., Goossens, B., Stark, D. J., Reynolds, G., Ong, R., Renneboog, N., Kugan, F., & Coomes, D. A. (2018). Mapped aboveground carbon stocks to advance forest conservation and recovery in Malaysian Borneo. *Biological Conservation*, *217*, 289–310. https://doi.org/10.1016/J.BIOCON.2017.10.020

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Benchimol, M., & Peres, C. A. (2015). Edge-mediated compositional and functional decay of tree assemblages in Amazonian forest islands after 26 years of isolation. *Journal of Ecology*, *103*(2), 408–420. https://doi.org/10.1111/1365-2745.12371

Brinck, K., Fischer, R., Groeneveld, J., Lehmann, S., Dantas De Paula, M., Pütz, S., Sexton, J. O., Song, D., & Huth, A. (2017). High resolution analysis of tropical forest fragmentation and its impact on the global carbon cycle. *Nature Communications*, *8*, 14855. https://doi.org/10.1038/ncomms14855

Broadbent, E. N., Asner, G. P., Keller, M., Knapp, D. E., Oliveira, P. J. C., & Silva, J. N. (2008). Forest fragmentation and edge effects from deforestation and selective logging in the Brazilian Amazon. *Biological Conservation*, *141*(7), 1745–1757. https://doi.org/10.1016/J.BIOCON.2008.04.024

Cai, W., Wang, G., Dewitte, B., Wu, L., Santoso, A., Takahashi, K., Yang, Y., Carréric, A., & McPhaden, M. J. (2018). Increased variability of eastern Pacific El Niño under greenhouse warming. *Nature*, *564*, 201–206. https://doi.org/10.1038/s41586-018-0776-9

Chaplin-Kramer, R., Ramler, I., Sharp, R., Haddad, N. M., Gerber, J. S., West, P. C., Mandle, L., Engstrom, P., Baccini, A., Sim, S., Mueller, C., & King, H. (2015). Degradation in carbon stocks near tropical forest edges. *Nature Communications*, *6*. https://doi.org/10.1038/ncomms10158

Chave, J., Coomes, D., Jansen, S., Lewis, S. L., Swenson, N. G., & Zanne, A. E. (2009). Towards a worldwide wood economics spectrum. *Ecology Letters*, *12*(4), 351–366. https://doi.org/10.1111/j.1461-0248.2009.01285.x

Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M. S., Delitti, W. B. C., Duque, A., Eid, T., Fearnside, P. M., Goodman, R. C., Henry, M., Martínez-Yrízar, A., Mugasha, W. A., Muller-Landau, H. C., Mencuccini, M., Nelson, B. W., Ngomanda, A., Nogueira, E. M., Ortiz-Malavassi, E., … Vieilledent, G. (2014). Improved allometric models to estimate the aboveground biomass of tropical trees. *Global Change Biology*, *20*(10), 3177–3190. https://doi.org/10.1111/gcb.12629

Corlett, R. T. (2009). Seed dispersal distances and plant migration potential in tropical East Asia. *Biotropica*, *41*(5), 592–598. https://doi.org/10.1111/j.1744-7429.2009.00503.x

de Paula, M. D., Costa, C. P. A., & Tabarelli, M. (2011). Carbon storage in a fragmented landscape of Atlantic forest: the role played by edge-affected habitats and emergent trees. *Tropical Conservation Science*, *4*(3), 349–358. https://doi.org/10.1177/194008291100400310

Descals, A., Wich, S., Meijaard, E., Gaveau, D. L. A., Peedell, S., & Szantoi, Z. (2021). High-resolution global map of smallholder and industrial closed-canopy oil palm plantations. *Earth System Science Data*, *13*(3), 1211–1231. https://doi.org/10.5194/essd-13-1211-2021

Didham, R. K., & Lawton, J. H. (1999). Edge structure determines the magnitude of changes in microclimate and vegetation structure in tropical forest fragments. *Biotropica*, *31*, 17–30. https://doi.org/10.1111/j.1744-7429.1999.tb00113.x

Driscoll, D. A., Banks, S. C., Barton, P. S., Lindenmayer, D. B., & Smith, A. L. (2013). Conceptual domain of the matrix in fragmented landscapes. *Trends in Ecology and Evolution*, *28*(10), 605–613. https://doi.org/10.1016/j.tree.2013.06.010

Ewers, R. M., & Banks-Leite, C. (2013). Fragmentation Impairs the Microclimate Buffering Effect of Tropical Forests. *PLoS ONE*, *8*(3), e58093. https://doi.org/10.1371/journal.pone.0058093

Fischer, R., Taubert, F., Müller, M. S., Groeneveld, J., Lehmann, S., Wiegand, T., & Huth, A. (2021). Accelerated forest fragmentation leads to critical increase in tropical forest edge area. *Science Advances*, *7*(37). https://doi.org/10.1126/SCIADV.ABG7012

Fitzherbert, E. B., Struebig, M. J., Morel, A., Danielsen, F., Brühl, C. A., Donald, P. F., & Phalan, B. (2008). How will oil palm expansion affect biodiversity? *Trends in Ecology and Evolution*, *23*(10), 538–545. https://doi.org/10.1016/j.tree.2008.06.012

Fleiss, S., Waddell, E. H., Bala Ola, B., Banin, L. F., Benedick, S., Bin Sailim, A., Chapman, D. S., Jelling, A., King, H., McClean, C. J., Yeong, K. L., & Hill, J. K. (2020). Conservation set-asides improve carbon storage and support associated plant diversity in certified sustainable oil palm plantations. *Biological Conservation*, *248*, 108631. https://doi.org/10.1016/j.biocon.2020.108631

Ganivet, E., Unggang, J., Bodos, V., Demies, M., Ling, C. Y., Sang, J., & Bloomberg, M. (2020). Assessing tree species diversity and structure of mixed dipterocarp forest remnants in a fragmented landscape of north-western Borneo, Sarawak, Malaysia. *Ecological Indicators*, *112*, 106117. https://doi.org/10.1016/j.ecolind.2020.106117

Gaveau, D. L. A., Sloan, S., Molidena, E., Yaen, H., Sheil, D., Abram, N. K., Ancrenaz, M., Nasi, R., Quinones, M., Wielaard, N., & Meijaard, E. (2014). Four Decades of Forest Persistence, Clearance and Logging on Borneo. *PLoS One*, *9*(7), e101654. https://doi.org/10.1371/journal.pone.0101654

Goodman, R. C., Phillips, O. L., Del Castillo Torres, D., Freitas, L., Cortese, S. T., Monteagudo, A., & Baker, T. R. (2013). Amazon palm biomass and allometry. *Forest Ecology and Management*, *310*, 994–1004. https://doi.org/10.1016/j.foreco.2013.09.045

Gora, E. M., & Esquivel-Muelbert, A. (2021). Implications of size-dependent tree mortality for tropical forest carbon dynamics. *Nature Plants*, *7*, 384–391. https://doi.org/10.1038/s41477-

021-00879-0

Haddad, N. M., Brudvig, L. A., Clobert, J., Davies, K. F., Gonzalez, A., Holt, R. D., Lovejoy, T. E., Sexton, J. O., Austin, M. P., Collins, C. D., Cook, W. M., Damschen, E. I., Ewers, R. M., Foster, B. L., Jenkins, C. N., King, A. J., Laurance, W. F., Levey, D. J., Margules, C. R., … Townshend, J. R. (2015). Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances*, *1*(2). https://doi.org/10.1126/sciadv.1500052

Harper, K. A., Macdonald, S. E., Burton, P. J., Chen, J., Brosofske, K. D., Saunders, S. C., Euskirchen, E. S., Roberts, D. A. R., Jaiteh, M. S., & Esseen, P. A. (2005). Edge Influence on Forest Structure and Composition in Fragmented Landscapes. *Conservation Biology*, *19*(3), 768–782. https://doi.org/10.1111/j.1523-1739.2005.00045.x

Hatfield, J. H., Barlow, J., Joly, C. A., Lees, A. C., Parruco, C. H. de F., Tobias, J. A., Orme, C. D. L., & Banks-Leite, C. (2020). Mediation of area and edge effects in forest fragments by adjacent land use. *Conservation Biology*, *34*(2), 395–404. https://doi.org/10.1111/cobi.13390

Ibáñez, I., Katz, D. S. W., Peltier, D., Wolf, S. M., & Connor Barrie, B. T. (2014). Assessing the integrated effects of landscape fragmentation on plants and plant communities: the challenge of multiprocess-multiresponse dynamics. *Journal of Ecology*, *102*(4), 882–895. https://doi.org/10.1111/1365-2745.12223

Ibanez, T., Hequet, V., Chambrey, C., Jaffré, T., & Birnbaum, P. (2017). How does forest fragmentation affect tree communities? A critical case study in the biodiversity hotspot of New Caledonia. *Landscape Ecology*, *32*(8), 1671–1687. https://doi.org/10.1007/s10980-017-0534-7

Imai, N., Tanaka, A., Samejima, H., Sugau, J. B., Pereira, J. T., Titin, J., Kurniawan, Y., & Kitayama, K. (2014). Tree community composition as an indicator in biodiversity monitoring of REDD+. *Forest Ecology and Management*, *313*, 169–179. https://doi.org/10.1016/J.FORECO.2013.10.041

Jackson, T. D., Shenkin, A. F., Majalap, N., Bin Jami, J., Bin Sailim, A., Reynolds, G., Coomes, D. A., Chandler, C. J., Boyd, D. S., Burt, A., Wilkes, P., Disney, M., & Malhi, Y. (2021). The mechanical stability of the world's tallest broadleaf trees. *Biotropica*, *53*(1), 110–120. https://doi.org/10.1111/btp.12850

Jesus, F. M., Pivello, V. R., Meirelles, S. T., Franco, G. A. D. C., & Metzger, J. P. (2012). The importance of landscape structure for seed dispersal in rain forest fragments. *Journal of*

Vegetation Science, *23*(6), 1126–1136. https://doi.org/10.1111/j.1654-1103.2012.01418.x

Krishnadas, M., Kumar, A. N., & Comita, L. S. (2019). Edge effects reduce α-diversity but not β-diversity during community assembly in a human-modified tropical forest. *Ecological Applications*, *29*(8), e01996. https://doi.org/10.1002/eap.1996

Kupfer, J. A., Malanson, G. P., & Franklin, S. B. (2006). Not seeing the ocean for the islands: the mediating influence of matrix-based processes on forest fragmentation effects. *Global Ecology and Biogeography*, *15*(1), 8–20. https://doi.org/10.1111/j.1466-822X.2006.00204.x

Lam, W. Y., Kulak, M., Sim, S., King, H., Huijbregts, M. A. J., & Chaplin-Kramer, R. (2019). Greenhouse gas footprints of palm oil production in Indonesia over space and time. *Science of the Total Environment*, *688*, 827–837. https://doi.org/10.1016/j.scitotenv.2019.06.377

Larjavaara, M., & Muller-Landau, H. C. (2013). Measuring tree height: a quantitative comparison of two common field methods in a moist tropical forest. *Methods in Ecology and Evolution*, *4*(9), 793–801. https://doi.org/10.1111/2041-210X.12071

Laurance, W. F., Camargo, J. L. C., Fearnside, P. M., Lovejoy, T. E., Williamson, G. B., Mesquita, R. C. G., Meyer, C. F. J., Bobrowiec, P. E. D., & Laurance, S. G. W. (2018). An Amazonian rainforest and its fragments as a laboratory of global change. *Biological Reviews*, *93*(1), 223–247. https://doi.org/10.1111/brv.12343

Laurance, W. F., Delamônica, P., Laurance, S. G., Vasconcelos, H. L., & Lovejoy, T. E. (2000). Rainforest fragmentation kills big trees. *Nature*, *404*, 836. https://doi.org/10.1038/35009032

Laurance, W. F., Lovejoy, T. E., Vasconcelos, H. L., Bruna, E. M., Didham, R. K., Stouffer, P. C., Gascon, C., Bierregaard, R. O., Laurance, S. G., & Sampaio, E. (2002). Ecosystem decay of Amazonian forest fragments: a 22-year investigation. *Conservation Biology*, *16*(3), 605–618. https://doi.org/10.1046/j.1523-1739.2002.01025.x

Laurance, W. F., Nascimento, H. E. M., Laurance, S. G., Andrade, A., Ewers, R. M., Harms, K. E., Luizão, R. C. C., & Ribeiro, J. E. (2007). Habitat fragmentation, variable edge effects, and the landscape-divergence hypothesis. *PLoS ONE*, *2*(10), e1017. https://doi.org/10.1371/journal.pone.0001017

Laurance, W. F., Nascimento, H. E. M., Laurance, S. G., Andrade, A., Ribeiro, J. E. L. S., Giraldo, J. P., Lovejoy, T. E., Condit, R., Chave, J., Harms, K. E., & D'Angelo, S. (2006). Rapid decay of tree-community composition in Amazonian forest fragments. *Proceedings of the National Academy of Sciences of the United States of America*, *103*(50), 19010–19014.

https://doi.org/10.1073/pnas.0609048103

Laurance, W. F., Sayer, J., & Cassman, K. G. (2014). Agricultural expansion and its impacts on tropical nature. *Trends in Ecology & Evolution*, *29*(2), 107–116. https://doi.org/10.1016/J.TREE.2013.12.001

Lewis, S. L., Edwards, D. P., & Galbraith, D. (2015). Increasing human dominance of tropical forests. *Science*, *349*(6250), 827–832. https://doi.org/10.1126/science.aaa9932

Liu, J. J., & Slik, J. W. F. (2014). Forest fragment spatial distribution matters for tropical tree conservation. *Biological Conservation*, *171*, 99–106. https://doi.org/10.1016/j.biocon.2014.01.004

Lucey, J. M., Palmer, G., Yeong, K. L., Edwards, D. P., Senior, M. J. M., Scriven, S. A., Reynolds, G., & Hill, J. K. (2017). Reframing the evidence base for policy-relevance to increase impact: a case study on forest fragmentation in the oil palm sector. *Journal of Applied Ecology*, *54*(3), 731–736. https://doi.org/10.1111/1365-2664.12845

Luke, S. H., Purnomo, D., Advento, A. D., Aryawan, A. A. K., Naim, M., Pikstein, R. N., Ps, S., Rambe, T. D. S., Soeprapto, Caliman, J.-P., Snaddon, J. L., Foster, W. A., & Turner, E. C. (2019). Effects of understory vegetation management on plant communities in oil palm plantations in Sumatra, Indonesia. *Frontiers in Forests and Global Change*, *2*. https://doi.org/10.3389/ffgc.2019.00033

Luskin, M. S., Brashares, J. S., Ickes, K., Sun, I. F., Fletcher, C., Wright, S. J., & Potts, M. D. (2017). Cross-boundary subsidy cascades from oil palm degrade distant tropical forests. *Nature Communications*, *8*, 2231. https://doi.org/10.1038/s41467-017-01920-7

Luskin, M. S., & Potts, M. D. (2011). Microclimate and habitat heterogeneity through the oil palm lifecycle. *Basic and Applied Ecology*, *12*(6), 540–551. https://doi.org/10.1016/j.baae.2011.06.004

Magnago, L. F. S., Magrach, A., Barlow, J., Schaefer, C. E. G. R., Laurance, W. F., Martins, S. V., & Edwards, D. P. (2017). Do fragment size and edge effects predict carbon stocks in trees and lianas in tropical forests? *Functional Ecology*, *31*, 542–552. https://doi.org/10.1111/1365-2435.12752

Magnago, L. F. S., Rocha, M. F., Meyer, L., Martins, S. V., & Meira-Neto, J. A. A. (2015). Microclimatic conditions at forest edges have significant impacts on vegetation structure in large Atlantic forest fragments. *Biodiversity and Conservation*, *24*(9), 2305–2318.

https://doi.org/10.1007/s10531-015-0961-1

Magurran, A. E. (2004). *Measuring biological diversity*. John Wiley & Sons.

Malaysian Palm Oil Board. (2019). Oil Palm Planted Area 2019. Retrieved May 25, 2020, from http://bepi.mpob.gov.my/index.php/en/area/area-2019/oil-palm-planted-area-as-at-dec-2019.html

Marthews, T., Riutta, T., Oliveras Menor, I., Urrutia, R., Moore, S., Metcalfe, D., Malhi, Y., Phillips, O. L., Huaraca Huasco, W., Ruiz Jaén, M., Girardin, C., Butt, N., Cain, R., & colleagues from the RAINFOR and GEM networks. (2014). Measuring Tropical Forest Carbon Allocation and Cycling: A RAINFOR-GEM Field Manual for Intensive Census Plots (v3.0). Retrieved from http://gem.tropicalforests.ox.ac.uk/

Meijaard, E., Brooks, T. M., Carlson, K. M., Slade, E. M., Garcia-Ulloa, J., Gaveau, D. L. A., Lee, J. S. H., Santika, T., Juffe-Bignoli, D., Struebig, M. J., Wich, S. A., Ancrenaz, M., Koh, L. P., Zamira, N., Abrams, J. F., Prins, H. H. T., Sendashonga, C. N., Murdiyarso, D., Furumo, P. R., … Sheil, D. (2020). The environmental impacts of palm oil in context. *Nature Plants*, *6*, 1418–1426. https://doi.org/10.1038/s41477-020-00813-w

Meijaard, E., Garcia-Ulloa, J., Sheil, D., Wich, S. A., Carlson, K. M., Juffe-Bignoli, D., & Brooks, T. M. (2018). *Oil palm and biodiversity: A situation analysis by the IUCN Oil Palm Task Force*. International Union for Conservation of Nature and Natural Resources (IUCN). https://doi.org/https://doi.org/10.2305/IUCN.CH.2018.11.en

Melito, M., Metzger, J. P., & de Oliveira, A. A. (2018). Landscape-level effects on aboveground biomass of tropical forests: A conceptual framework. *Global Change Biology*, *24*(2), 597–607. https://doi.org/10.1111/gcb.13970

Mesquita, R. C. G., Delamônica, P., & Laurance, W. F. (1999). Effect of surrounding vegetation on edge-related tree mortality in Amazonian forest fragments. *Biological Conservation*, *91*(2–3), 129–134. https://doi.org/10.1016/S0006-3207(99)00086-5

Michalski, F., Nishi, I., & Peres, C. A. (2007). Disturbance-mediated drift in tree functional groups in Amazonian forest fragments. *Biotropica*, *39*(6), 691–701. https://doi.org/10.1111/j.1744-7429.2007.00318.x

Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, *403*, 853–858. https://doi.org/10.1038/35002501

Nascimento, H. E. M., Andrade, A. C. S., Camargo, J. L. C., Laurance, W. F., Laurance, S. G., & Ribeiro, J. E. L. (2006). Effects of the surrounding matrix on tree recruitment in Amazonian forest fragments. *Conservation Biology*, *20*(3), 853–860. https://doi.org/10.1111/j.1523-1739.2006.00344.x

Nunes, M. H., Jucker, T., Riutta, T., Svátek, M., Kvasnica, J., Rejžek, M., Matula, R., Majalap, N., Ewers, R. M., Swinfield, T., Valbuena, R., Vaughn, N. R., Asner, G. P., & Coomes, D. A. (2021). Recovery of logged forest fragments in a human-modified tropical landscape during the 2015-16 El Niño. *Nature Communications*, *12*, 1526. https://doi.org/10.1038/s41467-020-20811-y

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., & Wagner, H. (2020). *vegan: Community Ecology Package*.

Oliveira, M. A., Grillo, A. S., & Tabarelli, M. (2004). Forest edge in the Brazilian Atlantic forest: Drastic changes in tree species assemblages. *Oryx*, *38*(4), 389–394. https://doi.org/10.1017/S0030605304000754

Ordway, E. M., & Asner, G. P. (2020). Carbon declines along tropical forest edges correspond to heterogeneous effects on canopy structure and function. *Proceedings of the National Academy of Sciences of the United States of America*, *117*(14), 7863–7870. https://doi.org/10.1073/pnas.1914420117

Pfeifer, M., Lefebvre, V., Peres, C. A., Banks-Leite, C., Wearn, O. R., Marsh, C. J., Butchart, S. H. M., Arroyo-Rodríguez, V., Barlow, J., Cerezo, A., Cisneros, L., D'Cruze, N., Faria, D., Hadley, A., Harris, S. M., Klingbeil, B. T., Kormann, U., Lens, L., Medina-Rangel, G. F., … Ewers, R. M. (2017). Creation of forest edges has a global impact on forest vertebrates. *Nature*, *551*, 187–191. https://doi.org/10.1038/nature24457

Phillips, O. L., Baker, T., Feldpausch, T., & Brienen, R. (2016). RAINFOR Field Manual for Plot Establishment and Remeasurement. Retrieved from http://www.forestplots.net/en/using-forestplots/in-the-field

Phillips, O. L., van der Heijden, G., Lewis, S. L., López-González, G., Aragão, L. E. O. C., Lloyd, J., Malhi, Y., Monteagudo, A., Almeida, S., Dávila, E. A., Amaral, I., Andelman, S., Andrade, A., Arroyo, L., Aymard, G., Baker, T. R., Blanc, L., Bonal, D., de Oliveira, A. C. A., … Vilanova, E. (2010). Drought-mortality relationships for tropical forests. *New Phytologist*, *187*(3), 631–646. https://doi.org/10.1111/j.1469-8137.2010.03359.x

Pinho, B. X., Peres, C. A., Leal, I. R., & Tabarelli, M. (2020). Critical role and collapse of tropical mega-trees: A key global resource. *Advances in Ecological Research*, *62*, 253–294. https://doi.org/10.1016/bs.aecr.2020.01.009

Porensky, L. M., & Young, T. P. (2013). Edge-Effect Interactions in Fragmented and Patchy Landscapes. *Conservation Biology*, *27*(3), 509–519. https://doi.org/10.1111/cobi.12042

Qie, L., Lewis, S. L., Sullivan, M. J. P., Lopez-Gonzalez, G., Pickavance, G. C., Sunderland, T., Ashton, P., Hubau, W., Abu Salim, K., Aiba, S.-I., Banin, L. F., Berry, N., Brearley, F. Q., Burslem, D. F. R. P., Dančák, M., Davies, S. J., Fredriksson, G., Hamer, K. C., Hédl, R., … Phillips, O. L. (2017). Long-term carbon sink in Borneo's forests halted by drought and vulnerable to edge effects. *Nature Communications*, *8*, 1966. https://doi.org/10.1038/s41467-017-01997-0

R Core Team. (2020). *R: A Language and Environment for Statistical Computing*. Vienna, Austria.

Ries, L., Fletcher, R. J., Battin, J., & Sisk, T. D. (2004). Ecological responses to habitat edges: mechanisms, models, and variability explained. *Annual Review of Ecology, Evolution, and Systematics*, *35*, 491–522. https://doi.org/10.1146/annurev.ecolsys.35.112202.130148

Ries, L., Murphy, S. M., Wimp, G. M., & Fletcher, R. J. (2017). Closing persistent gaps in knowledge about edge ecology. *Current Landscape Ecology Reports*, *2*, 30–41. https://doi.org/10.1007/s40823-017-0022-4

Rosoman, G., Sheun, S. S., Opal, C., Anderson, P., & Trapshah, R. (2017). The HCS Approach Toolkit. Retrieved from http://highcarbonstock.org/wp-content/uploads/2017/05/HCSA-Toolkit-v2.0-Module-1-Introduction-190917-web.pdf

RSPO. (2018). Roundtable on Sustainable Palm Oil Principles & Criteria for Sustainable Palm Oil. Retrieved from https://rspo.org/resources/certification/rspo-principles-criteria-certification

Santos, B. A., Peres, C. A., Oliveira, M. A., Grillo, A., Alves-Costa, C. P., & Tabarelli, M. (2008). Drastic erosion in functional attributes of tree assemblages in Atlantic forest fragments of northeastern Brazil. *Biological Conservation*, *141*(1), 249–260. https://doi.org/10.1016/j.biocon.2007.09.018

Scriven, S. A., Hodgson, J. A., McClean, C. J., & Hill, J. K. (2015). Protected areas in Borneo may fail to conserve tropical forest biodiversity under climate change. *Biological Conservation*, *184*, 414–423. https://doi.org/10.1016/j.biocon.2015.02.018

Silva, M. C., Melo, F. P. L., & Berg, E. (2021). Changes in tree size, not species diversity, underlie the low above-ground biomass in natural forest edges. *Journal of Vegetation Science*, *32*(2), e13003. https://doi.org/10.1111/jvs.13003

Slik, J. W. F. (2005). Assessing tropical lowland forest disturbance using plant morphological and ecological attributes. *Forest Ecology and Management*, *205*(1–3), 241–250. https://doi.org/10.1016/j.foreco.2004.10.011

Slik, J. W. F. (2006). Estimating species-specific wood density from the genus average in Indonesian trees. *Journal of Tropical Ecology*, *22*(4), 481–482. https://doi.org/10.1017/S0266467406003324

Slik, J. W. F., Bernard, C. S., Breman, F. C., Van Beek, M., Salim, A., & Sheil, D. (2008). Wood Density as a Conservation Tool: Quantification of Disturbance and Identification of Conservation-Priority Areas in Tropical Forests. *Conservation Biology*, *22*(5), 1299–1308. https://doi.org/10.1111/J.1523-1739.2008.00986.X

Slik, J. W. F., Paoli, G., Mcguire, K., Amaral, I., Barroso, J., Bastian, M., Blanc, L., Bongers, F., Boundja, P., Clark, C., Collins, M., Dauby, G., Ding, Y., Doucet, J. L., Eler, E., Ferreira, L., Forshed, O., Fredriksson, G., Gillet, J. F., … Zweifel, N. (2013). Large trees drive forest aboveground biomass variation in moist lowland forests across the tropics. *Global Ecology and Biogeography*, *22*(12), 1261–1271. https://doi.org/10.1111/geb.12092

Slik, J. W. F., Poulsen, A. D., Ashton, P. S., Cannon, C. H., Eichhorn, K. A. O., Kartawinata, K., Lanniari, I., Nagamasu, H., Nakagawa, M., Van Nieuwstadt, M. G. L., Payne, J., Saridan, A., Sidiyasa, K., Verburg, R. W., Webb, C. O., & Wilkie, P. (2003). A floristic analysis of the lowland dipterocarp forests of Borneo. *Journal of Biogeography*, *30*(10), 1517–1531. https://doi.org/10.1046/j.1365-2699.2003.00967.x

Slik, J. W. F., van Beek, M., Bernard, C., Bongers, F., Breman, F. C., Cannon, C. H., & Sidiyasa, K. (2011). Limited edge effects along a burned-unburned Bornean forest boundary seven years after disturbance. *Biotropica*, *43*(3), 288–298. https://doi.org/10.1111/j.1744-7429.2010.00706.x

Stride, G., Thomas, C. D., Benedick, S., Hodgson, J. A., Jelling, A., Senior, M. J. M., & Hill, J. K. (2018). Contrasting patterns of local richness of seedlings, saplings, and trees may have implications for regeneration in rainforest remnants. *Biotropica*, *50*(6), 889–897. https://doi.org/10.1111/btp.12605

Tabarelli, M., Peres, C. A., & Melo, F. P. L. (2012). The “few winners and many losers” paradigm revisited: Emerging prospects for tropical forest biodiversity. *Biological Conservation*, *155*, 136–140. https://doi.org/10.1016/j.biocon.2012.06.020

Taubert, F., Fischer, R., Groeneveld, J., Lehmann, S., Müller, M. S., Rödig, E., Wiegand, T., & Huth, A. (2018). Global patterns of tropical forest fragmentation. *Nature*, *554*, 519–522. https://doi.org/10.1038/nature25508

UN Food and Agriculture Organization. (2012). FRA 2015 Terms and Definitions. Retrieved from http://www.fao.org/publications/card/en/c/5d917495-a5de-5b0c-851a-c0010269d79d

Zanne, A. E., Lopez-Gonzalez, G., Coomes, D. A., Ilic, J., Jansen, S., Lewis, S. L., Miller, R. B., Swenson, N. G., Wiemann, M. C., & Chave, J. (2009). Global wood density database. Retrieved from https://doi.org/10.5061/dryad.234

Chapter 3 - **Proximity to multiple edges reduces carbon stocks in fragmented tropical rainforests**

Primary lowland dipterocarp forest at dawn

3.1 Abstract

Context

Tropical land-use change has resulted in highly fragmented landscapes, with remaining forest fragments being further degraded by edge effects. Edge effects reduce aboveground carbon (AGC), but it is unclear if these effects are magnified by proximity to multiple edges.

Objectives

We quantified the amount by which AGC is reduced in forest areas that are influenced by multiple nearby edges. We determined whether a metric of 'edginess' (a measure that accounts for the amount and proximity of nearby edges) explains more variation in AGC than the commonly used measure of 'distance to nearest edge'.

Methods

We used high-resolution (30m pixel) remotely-sensed datasets to study the influence of multiple edges on AGC in the forests of Sabah (Malaysian Borneo), a fragmented forest landscape dominated by oil palm plantations. We generated a state-wide map of forest edginess (index scaled from low = 0 to high = 1), and quantified the relationship between edginess and AGC for a stratified random sample of 600,000 forest pixels. We also quantified the relationship between 'Euclidean distance to nearest edge' and AGC for the same sample of pixels, and used a model comparison approach to determine which metric explained more variation in pixel-level AGC.

Results

AGC in forest directly adjacent to multiple edges (model-fitted AGC = 41.6 Mg C ha^{-1} at edginess = 1) was 23% lower than in forest directly adjacent to a single edge (model-fitted AGC = 53.9 Mg C ha^{-1} at edginess = 0.78), and less than half (38%) that of the forest core (model-fitted AGC = 108.84 Mg C ha^{-1} at edginess = 0). Proximity to multiple edges therefore caused a substantial reduction in AGC. A model of AGC using our edginess metric provided a better explanatory model than one using distance to nearest edge (ΔAIC = 21962 for edginess *vs* Euclidean distance model) and explained more variation in pixel-level AGC, particularly within 100m of edges, although neither model explained much of the total variation in AGC (R^2 for edginess model of 18.3% *vs* 15.3% for the Euclidean distance model). We estimate that almost half (41%) of the total forest area in Sabah is within 300m of an edge and that AGC in approximately a quarter (23%) of this edge-affected forest is impacted by multiple edges.

Conclusions

Our study reveals that proximity to multiple edges greatly reduces forest AGC, and that a metric which measures edginess explains more variation in AGC throughout a fragmented landscape than a more commonly used Euclidean distance metric. Proximity to multiple edges is likely to increase the impacts of detrimental abiotic factors on trees, leading to increased mortality at these sites. Our results emphasize the importance of forest reserve designs that minimize edge:area ratios, and that accounting for effects of multiple edges is important for understanding how edge effects impact AGC.

Keywords

Agricultural expansion, carbon storage, deforestation, forest fragmentation

3.2 Highlights

1. High-resolution remotely-sensed data were used to study the impact of multiple edges on aboveground forest carbon (AGC)
2. AGC is significantly lower when forest is close to multiple edges
3. A metric accounting for multiple edges ('edginess') explains more variation in AGC than a 'distance to nearest edge' metric, particularly in close proximity to edges
4. Failure to account for the influence of multiple edges may result in underestimation of edge effects
5. Forest reserves in fragmented tropical landscapes should be designed to minimize edge:area ratios, to preserve carbon stocks

3.3 Introduction

Tropical forests are essential components of the Earth system, supporting a considerable proportion of the global biodiversity and providing numerous ecosystem services (Barlow et al., 2007; Mitchard, 2018). However, land use change in the tropics has driven extensive deforestation and the fragmentation of remaining forest areas (Gibbs et al., 2010; Laurance et al., 2014; Brinck et al., 2017). Fragmentation results in the creation of forest edges, where remaining forest areas are in close proximity to new types of land use. Forest areas close to edges often experience significant ecological changes following edge creation, such as compositional shifts and biodiversity losses (Laurance et al., 2002; Oliveira et al., 2004). Recent estimates suggest over 30% of remaining tropical forest is within 100m of an edge, and this is predicted to increase to 50% by the year 2100 due to ongoing human activities (Fischer et al., 2021).

Of particular concern is the impact that edge creation has on aboveground carbon (AGC) stocks in fragmented tropical forests. Tropical trees store approximately one third as much carbon as is held in the Earth's atmosphere (Mitchard, 2018) and perform the majority of the terrestrial world’s photosynthesis (Beer et al., 2010), playing a key role in global climate regulation. However, there is evidence from multiple tropical systems that aboveground forest carbon stocks are degraded near edges (Laurance et al., 1997; de Paula et al., 2011; Anderson et al., 2022). These edge effects are primarily due to the abiotic disturbances that occur in edge-affected forest, driving an increase in the mortality of large trees and increased turnover of tree communities (Nascimento and Laurance, 2004; Magnago et al., 2015; Qie et al., 2017). Accounting for these edge effects is important for understanding the impacts of land-use change from agricultural expansion, such as oil palm cultivation (Lam et al., 2019), and for improving forest and climate policies (Gibbs et al., 2007; Chaplin-Kramer, Ramler, et al., 2015). However, there is a geographic bias in studies which have examined edge effects on forest carbon, with most studies occurring in the Neotropics, and there is considerable variability reported in the strength of these edge effects (Melito et al., 2018). Moreover, the impacts of edge effects are often determined from local studies, making it difficult to quantify impacts across regions and landscapes (Ries et al., 2017).

An additional complication is that studies typically only quantify the influence of the nearest forest edge, yet there is evidence that the presence of multiple edges worsens the overall edge effect on trees (Porensky and Young, 2013; Laurance et al., 2018). In forest areas that are close to multiple edges, such as in small or geometrically complex forest fragments, there is evidence of strengthened edge effects on vegetation thickness (Malcolm, 1994), tree species richness and community composition (Benitez-Malvido and Martinez-Ramos, 2003; Laurance et al., 2006) and tree mortality and density (Laurance et al., 2006). The influence of multiple edges on forest carbon, however, remains unquantified. Patch geometry in fragmented landscapes is often complex, and ongoing land-use change means that forest fragmentation continues to increase, with fragments becoming smaller and ‘edgier’ (Taubert et al., 2018; Hansen et al., 2020; Fischer et al., 2021). Thus, if forest carbon is reduced close to multiple edges, carbon declines may be greater than previously estimated (Pütz et al., 2014; Brinck et al., 2017; Fischer et al., 2021). Existing studies have also been limited by a previous lack of high-resolution datasets to study these patterns (Chaplin-Kramer, Ramler, et al., 2015).

In this study, we use high resolution (30m x 30m pixels) remotely-sensed data on forest cover and AGC in order to quantify the effect that proximity to multiple edges has on forest AGC in Sabah, Malaysian Borneo. These forests contain exceptionally high levels of biodiversity and AGC (Myers et al., 2000; Asner et al., 2018), but have experienced a large amount of deforestation and forest fragmentation in recent decades, primarily due to plantation industries such as oil palm (Gaveau et al., 2016; Gaveau et al., 2019). The remaining forest areas in this landscape are therefore highly fragmented. Field studies have revealed significant reductions in forest carbon (up to 30% loss) within 300m from edges bordering oil palm plantations (Anderson et al., 2022), as well as carbon reductions of over 50% in small fragments compared to continuous forest (Fleiss et al., 2020). There is also evidence of associated changes in canopy structure and foliar traits (Ordway and Asner, 2020), canopy growth dynamics (Nunes et al., 2021), stem turnover (Qie et al., 2017) and tree regeneration (Permana et al., 2022) near edges. Here we use remotely-sensed data to explore the impacts of close proximity to multiple edges on AGC, and test the utility of an edginess metric (i.e. proximity to multiple edges) compared to the commonly used measure of 'distance to nearest edge'. We test the hypotheses that AGC decreases with increasing forest edginess, and that a metric of edginess explains more variation in AGC than the 'Euclidean distance to nearest edge' metric, particularly in the most edge-affected forest.

3.4 Methods

Mapping and GIS analyses were performed in ArcGIS Pro version 2.3.3 and R version 4.1.1 (R Core Team, 2022), and all statistical analyses were performed in R version 4.1.1 (R Core Team, 2022).

3.4.1 Mapping forest cover in Sabah

We produced a natural forest cover map at 30m resolution for Sabah for 2016, using a combination of high-resolution tree cover and forest loss data (Hansen et al., 2013) overlaid with a map of industrial oil palm and timber plantations (Gaveau et al., 2014; Gaveau et al., 2016), to identify areas of natural forest, non-forest and forest edges (Figure 3.1). We focused on 2016 so that our forest cover data correspond with published data on AGC (Asner et al., 2018). To produce our forest cover map, we used the approach recommended by Carlson et al. (2018) as follows. We first downloaded a 30m resolution map of tree canopy cover (%), defined as canopy closure for all vegetation taller than 5m in height, for the year 2000 (Figure 3.1a; https://storage.googleapis.com/earthenginepartners-hansen/GFC-2020-v1.8/download.html; see Hansen et al. (2013) for details). Next, we produced a binary forest/non-forest map for the year 2000, using a minimum 30% tree cover threshold to define forested pixels. This tree cover threshold allows for the inclusion of degraded forest typically found in fragmented regions, and is therefore recommended for studies of forest fragmentation (Haddad et al., 2015; Brinck et al., 2017; Taubert et al., 2018; Hansen et al., 2020; Fischer et al., 2021). We then used data on tree cover loss between the years 2000-2016 (https://storage.googleapis.com/earthenginepartners-hansen/GFC-2020-v1.8/download.html; see Hansen et al. (2013) for details) to identify forest pixels that had changed to non-forest, and re-classified them as non-forest pixels (Figure 3.1b; approx. 17.5 million pixels or 1.6 M ha). The tree cover data we used do not distinguish between natural forest and tree crops such as oil palm plantations (Tropek et al., 2014), and so we used a manually digitised layer of industrial oil palm and timber plantations for 2016, produced by a team of local experts (https://www.cifor.org/knowledge/dataset/0049; see Gaveau et al. (2014) and Gaveau et al. (2016) for details), to reclassify forest pixels which were actually tree plantation pixels (approx. 8 million pixels or 0.7 M ha) as non-forest. Finally, we applied a 1ha minimum mapping unit (MMU) filter to reduce the influence of speckle and within-forest canopy gaps, re-coding any contiguous (Queen's case contiguity, i.e. pixels sharing a common edge or vertex) group of pixels (forest or non-forest) with a combined area of less than 1ha to the value of the surrounding pixels, following Haddad et al. (2015), giving a binary (forest, non-forest) land cover map for 2016 (Figure 3.1c). Our full binary land cover map for Sabah can be found in the Supplementary Materials (SI Figure 1).

3.4.2 Mapping forest edginess from proximity to multiple edges

To determine the influence of multiple edges on AGC, we generated a map of 'edginess' (i.e. a measure of edge influence that takes into account both the number and proximity of nearby edges) for 30m x 30m forest pixels throughout Sabah, by adapting the heat-conduction model created by Malcolm (1998) and refined by Malcolm et al. (2017). This model is an additive diffusion-based model of edge effects, which has proven effective at explaining fragmentation effects on tree community structure in fragmented tropical forests and invertebrate species richness in fragmented temperate forests (Malcolm et al., 2017). It simulates edge effects as the diffusion of 'heat' through neighbouring pixels in a binary land cover raster (forest vs non-forest), with heat diffusing from the non-forest matrix ('hot' pixels) into forest ('cold' pixels). The diffusion proceeds iteratively, with heat permeating inwards from non-forest into adjacent forest in a stepwise manner, therefore the number of iterations determines the depth of edge influence (DEI) parameterised. The model is additive, therefore modelled forest temperatures represent the summed influence of all nearby edges that are within the parameterised DEI. The end result of the diffusion is a 'heat map' representative of edge influence on forest pixels, with a negative exponential function within forest with increasing distance from combined edges. These 'heat' values serve purely as a proxy for edge influence, representing processes which are known to cause AGC declines in edge-affected tropical forest (e.g. wind disturbance and canopy desiccation (Laurance and Curran, 2008; Briant et al., 2010)), rather than actual forest temperatures. We used our binary forest cover map, and parameterised the edginess metric assuming effects penetrate forest to a depth of 300m in this landscape (Ordway and Asner, 2020; Nunes et al., 2021; Anderson et al., 2022). After running the diffusion model we scaled the resulting ‘heat’ values of forest pixels based on the minimum and maximum values present in forest (min-max scaling), to improve metric interpretability, thereby producing our final edginess metric which ranged from 0 - 1. A value of 0 indicates that a forest pixel is subject to zero edge influence (i.e. far from any edges), whilst a value of 1 indicates that a forest pixel is in close proximity to multiple edges (Figures 3.1e & 3.1f). Edginess is influenced by the geometry of forest patches, with higher edginess scores found in forest ‘peninsulas’ (Figure 3.1f; black circle) than in forest areas sheltered by patch geometry, e.g. when edges occur at a reflex angle (Figure 3.1f; blue circle). The map of edginess scores across Sabah is provided in the Supplementary Materials (SI Figure 2), along with full details of our parameterisation approach.

In order to compare the performance of our edginess metric with a ‘distance to nearest edge’ metric, we also calculated the Euclidean distance of each forest pixel to its nearest ‘edge’ pixel. We defined edge pixels in our landscape as forest pixels bordering a non-forest pixel (Queen’s case contiguity; Figure 3.1d). We did not distinguish between naturally-occurring and anthropogenic (i.e. human-made) edges because of the difficulties in doing so reliably (Fischer et al., 2021); however the majority of edges in this region are likely to be anthropogenic (Gaveau et al., 2016; Brinck et al., 2017).

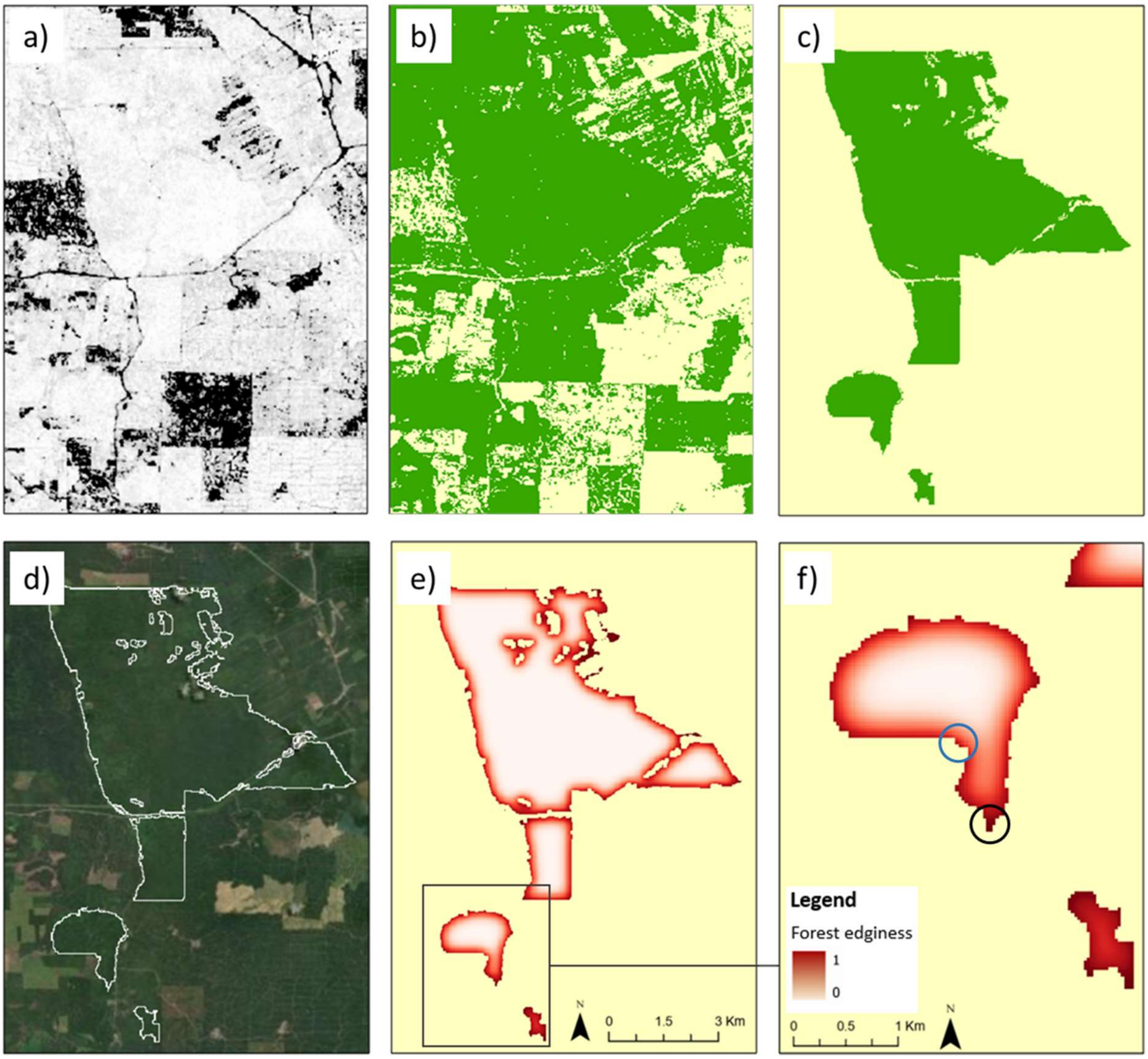


Figure 3.1 - Steps involved in creating a 30m-resolution binary land cover map (forest, non-forest) and map of forest edginess for Sabah, 2016, shown for a 14,000 ha sub-region - **a)** % tree cover map for the year 2000, **b)** 30% tree cover threshold applied, forest pixels (green) that experienced forest loss between 2000-2016 converted to non-forest pixels (cream), **c)** 2016 mask of industrial plantations applied to convert plantation pixels to non-forest, and 1ha MMU filter applied, to give final binary land cover map **d)** satellite imagery for comparison (arcgis.com) with edge pixels shown in white, **e)** heat diffusion model applied to produce edginess scores (0-1) for forest pixels, **f)** close-up view of small fragments in 1,750 ha sub-region. Blue circle exemplifies forest sheltered by patch geometry, e.g. when edges occur at a reflex angle, whilst black circle exemplifies forest exposed by patch geometry, e.g. when edges form a forest 'peninsula'.

3.4.3 Data sampling

Before conducting analyses we excluded forest pixels within 1.5km of a NoData pixel in our land cover map, or within 1.5km of the Sabah state boundary, to eliminate the potential for unaccounted edge influence (Chaplin-Kramer, Ramler, et al., 2015). We also excluded forest pixels bordering non-forest pixels (Figure 3.1d; see Methods 3.4.2) because these are likely to contain a mixture of forest and non-forest, reducing their AGC and inflating any edginess impacts we observe. We limited our study to pixels within 1km of an edge (i.e. Euclidean distance to nearest edge ≤1km), to focus on forest areas that encompass the majority of any edge effects in this landscape (Ordway and Asner, 2020; Nunes et al., 2021; Anderson et al., 2022), whilst still sampling the full gradient of edge-affected and 'core' forest (i.e. forest unaffected by edge effects) without over-sampling core forest. We analysed a stratified random sample of pixels from six equal-width distance bins, with 100,000 pixels (equivalent to 9000 ha) randomly sampled from each bin. Bins were assigned based on $\log_{10}$ transformed Euclidean distance to nearest edge, and so represent the following distance ranges: 30 m - 53.8 m, 53.8 m - 96.5 m, 96.5 m - 173.1 m, 173.1 m - 310.5 m, 310.5 m - 557 m, and 557m - 1000 m. This sampling approach (similar to the one used by Anderson et al. (2022)) prioritises representation of pixels close to edges (approximately 2/3rd of our sampled pixels are within 300m of an edge), and ensures that pixels with a lower edginess score, which are more common, are not over-represented in our analyses. It also limits the spatial proximity of sampled pixels, thus reducing the likelihood of pseudo-replication in our sampling.

We extracted the following data for each forest pixel in our final sample (n = 600,000 pixels; total of 54,000 ha): measure of edginess (metric from 0-1), Euclidean distance to nearest edge (m), and aboveground carbon density (hereafter AGC; Mg C ha^{-1}; from Asner et al. (2018)). These carbon data, produced using a combination of airborne Light Detection And Ranging (LiDAR), satellite imaging and geospatial data collected in 2016, have relatively high levels of uncertainty in some areas (>40% in some areas of low carbon storage, as is typical of these kinds of large-scale carbon maps (Asner et al., 2014)), however these errors are unbiased, meaning that AGC is not consistently over- or under-estimated in low-carbon areas (Asner et al., 2018). Thus, we are confident that the trends reported in our results are not sensitive to this uncertainty, and it is therefore not problematic for our overall conclusions. Furthermore, these data represent the best-available dataset of AGC for Sabah and offer significant advantages over alternative datasets produced at global or pantropical scales. Such large-scale datasets are typically validated using field plots from a limited subset of regions and so provide erroneous AGC estimates in unsampled regions (Ploton et al., 2020), unlike the data produced by Asner et al. (2018) which were validated with local field plots in our study region.

3.4.4 Data analyses

We modelled the effect of edginess on pixel-level AGC using a linear regression (lm function; R Core Team, 2022). We modelled a linear relationship because the non-linear effect of edge proximity is already accounted for by the heat-diffusion approach used to generate the metric (Malcolm et al., 2017), thus the resulting relationship between edginess and AGC is expected to be linear. We also used a linear regression (lm function; R Core Team, 2022) to model the effect of Euclidean distance on AGC, with Euclidean distance $\log_{10}$ transformed to linearize the relationship between the two variables (as in Anderson et al. (2022)). There was evidence of non-normality in the residuals of both models when raw AGC values were used, thus we used sqrt-transformed AGC (sqrt(AGC+1)) as our dependent variable for both models, to ensure model assumptions were met. To test whether edginess explains more AGC variation than Euclidean distance we used an Akaike Information Criterion (AIC) model comparison approach (AIC function; R Core Team, 2022) to determine the best-fitting model (Wagenmakers and Farrell, 2004). Finally, we also repeated these analyses using only sampled pixels within 100m of an edge (Euclidean distance < 100m; n = 200,000), where edge effects are typically strongest (Broadbent et al., 2008; Ordway and Asner, 2020; Anderson et al., 2022), to determine whether the benefits of an edginess metric are more pronounced in these areas.

3.5 Results

Our map of forest cover (SI Figure 1) includes a total forested area of approximately 4.16 M ha for Sabah in 2016 (excluding ‘edge’ pixels), of which 3 M ha are within 1km of an edge (72% of the total forest area), and 1.7 M ha within 300m of an edge (41% of the total forest area). Of the 3 M ha of forest within 1km of an edge, approximately 45% was designated a low edginess score of <0.1 (i.e. ‘core’ forest), with the remaining 55% of pixels approximately evenly distributed along the range of 0.1-1 edginess. The distribution of edginess values in our sampled pixels (SI Figure 3) therefore approximated the distribution of edginess scores throughout the entire Sabah landscape. For our study pixels, there was a non-linear relationship between edginess and nearest-edge distance, although the two metrics were generally poorly correlated, with variance in edginess scores decreasing at greater distances (Figure 3.2). Forest carbon varied considerably (Figures 3 & 4), with an overall mean pixel-level AGC of 91.6 Mg C ha^{-1} (+/- SD 58.3 Mg C ha^{-1}) in our sample.

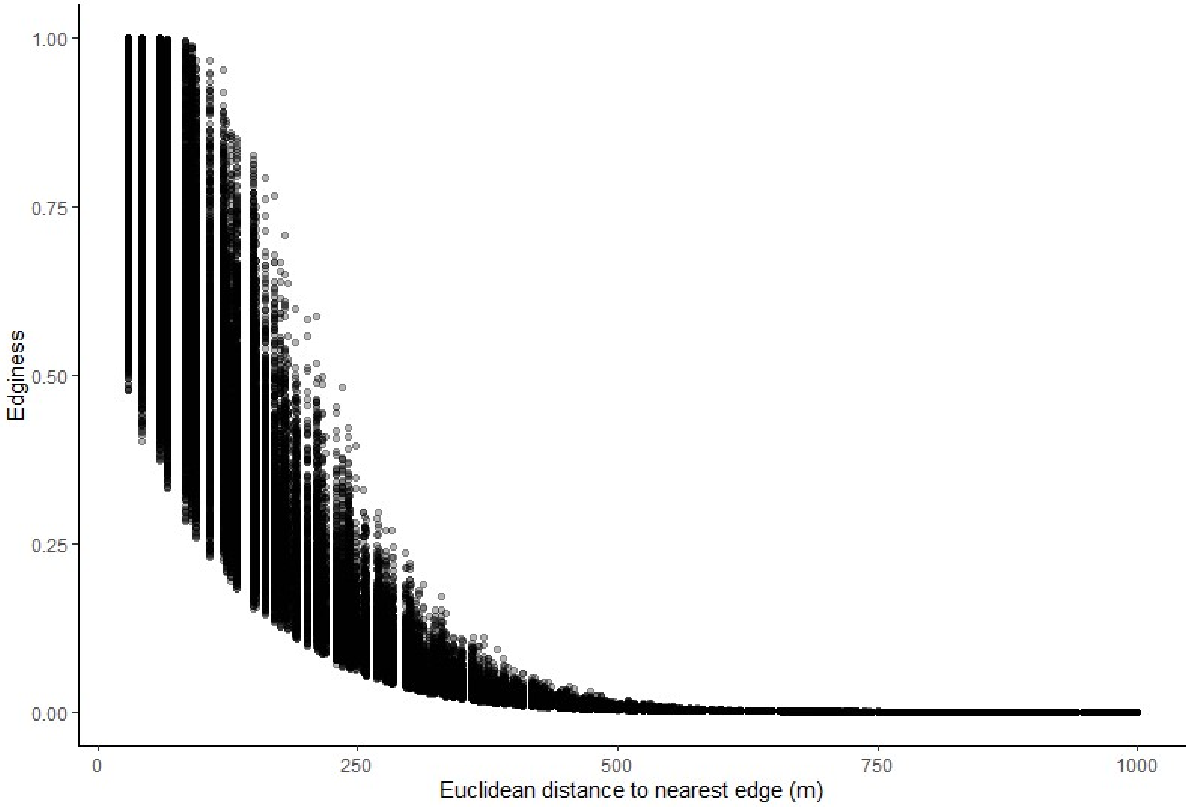


Figure 3.2 – Relationship between edginess and Euclidean distance to nearest edge (m), plotted for a subsample of 60,000 data points to aid visualisation.

3.5.1 Carbon declines with increasing edginess

We found a significant negative effect of edginess on forest carbon (linear regression of edginess on sqrt-transformed AGC; $\beta = -3.95$, $p < 0.0001$; Figure 3.3), with less than half (62% decline in model-fitted carbon) AGC in the most edgy pixels (41.6 Mg C ha^{-1} at edginess = 1) compared with the least edgy pixels (108.84 Mg C ha^{-1} at edginess = 0, i.e. forest 'core' pixels). In edge-adjacent forest pixels (those that are 30m from their nearest edge), model-fitted AGC declined from 73.8 Mg C ha^{-1} in pixels which are sheltered by patch geometry (at edginess = 0.463, e.g. when edges occur at a reflex angle; Figure 3.1f), to 53.9 Mg C ha^{-1} in pixels close to a single straight edge (at edginess = 0.78), to 41.6 Mg C ha^{-1} in pixels which are close to multiple edges (at edginess = 1, e.g. in small or geometrically complex fragments; Figure 3.1f). Thus, AGC in forest adjacent to multiple edges was reduced by almost a quarter (23%) relative to forest adjacent to only a single straight edge, confirming that the presence of multiple edges can substantially reduce AGC even when forest is in very close proximity to the nearest edge. We therefore conclude that forest carbon is impacted by multiple edges. 1.7 M ha of forest in Sabah is within 300m of an edge, and 0.39 M ha has a high edginess value > 0.78. This implies that AGC in about a quarter (23%) of edge-affected forest (i.e., forest within 300m of an edge) is further reduced by the impacts of multiple edges across this landscape.

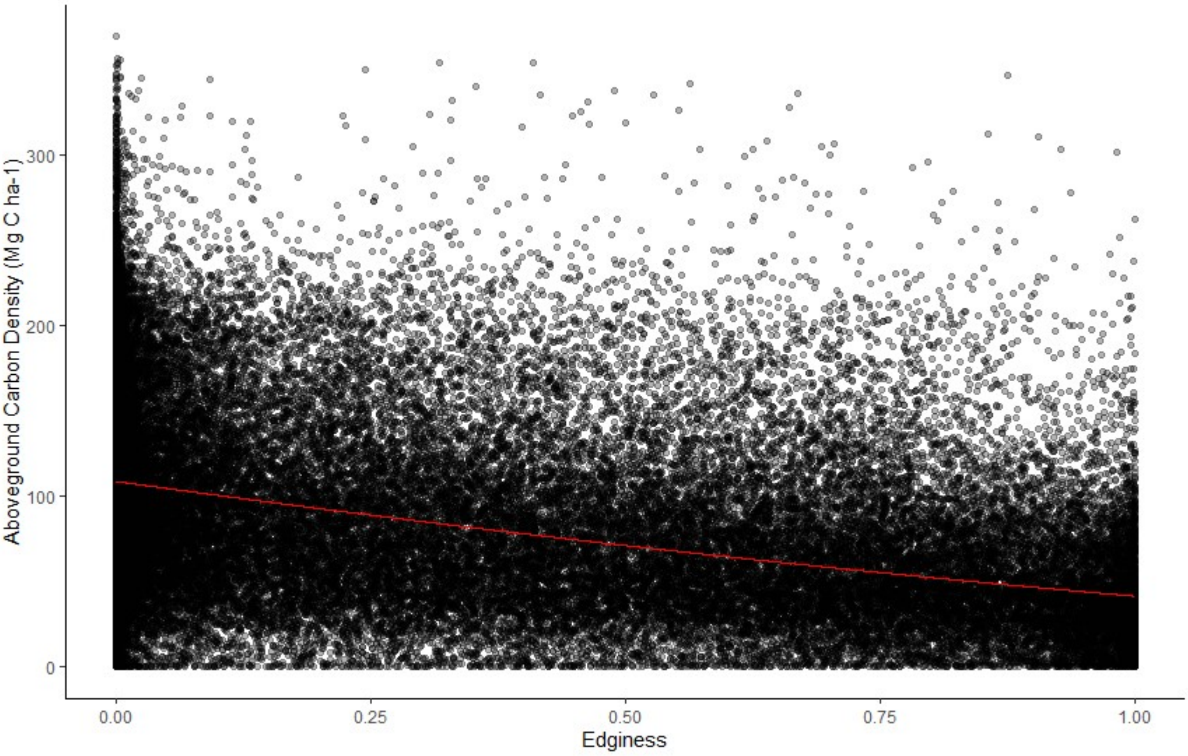


Figure 3.3 – Significant negative effect of edginess on AGC (Mg C ha^{-1}). Red line shows the fitted values of a linear regression of edginess against sqrt-transformed AGC for our sample of 600,000 data points, with model-fitted values back-transformed to give actual AGC values. A subsample of 60,000 data points are plotted to aid visualisation.

3.5.2 Edginess metric explains more AGC variation than Euclidean distance metric

Comparison of AIC scores shows that the edginess model was a better fit to forest AGC than the Euclidean distance model (ΔAIC = 21962). Neither explained a large amount of variation in pixel-level AGC across Sabah, but the edginess model did offer a slight improvement over Euclidean distance, explaining 18% of the variation in AGC (R^2 = 0.183; Figure 3.3; β = -3.95, $p < 0.0001$), compared to the 15% of variation explained by the Euclidean distance model (R^2 = 0.153; Figure 3.4; $\log_{10}$ transformed Euclidean distance against sqrt-AGC; β = 2.64, $p < 0.0001$). There was evidence of spatial autocorrelation in residuals of both models, but sensitivity analyses showed that our results are robust to this autocorrelation and it does not affect our conclusions (Supplementary Information). When analysing just 200,000 pixels within 100m of an edge, we found that edginess, whilst still only explaining a small amount of overall variation in pixel-level AGC, considerably outperformed Euclidean distance, explaining approximately 11% of AGC variation in these pixels, compared to the 1.5% explained by Euclidean distance ($R^2 = 0.108$ *vs* $R^2 = 0.015$).

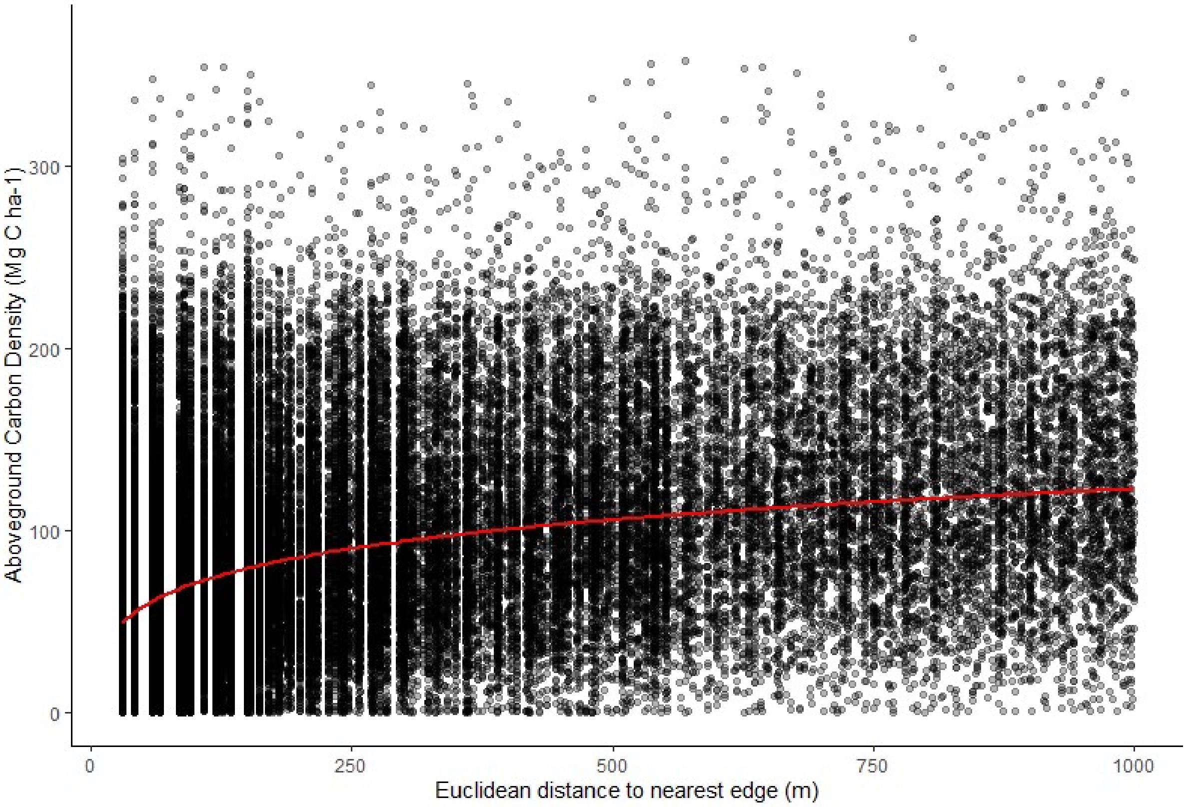


Figure 3.4 - Significant effect of $\log_{10}$(Euclidean distance (m)) on AGC (Mg C ha^{-1}). Red line shows the fitted values of a linear regression of $\log_{10}$(Euclidean distance) against sqrt-transformed AGC for our sample of 600,000 data points, with model-fitted values back-transformed to give actual AGC values. The relationship is plotted against untransformed distance in order to visualise the non-linear edge effect. A subsample of 60,000 data points are plotted to aid visualisation.

3.6 Discussion

3.6.1 Proximity to multiple edges reduces AGC in fragmented forests

We found evidence for a considerable (>60%) reduction in AGC in the most edge-affected forest areas relative to forest core, due to the impacts of multiple edges. Previous studies in this landscape have demonstrated AGC reductions of up to 30% in forest edges (Ordway and Asner, 2020; Anderson et al., 2022), however these focused on the effects of single edges, and here we demonstrate that AGC is further reduced by the proximity of additional edges. AGC levels were up to 23% lower in close proximity to multiple edges than in forest adjacent to a single straight edge, and were up to 44% lower than in edge-adjacent forest sheltered by forest patch geometry, for example where edges occur at a reflex angle (e.g. Figure 3.1f; blue circle). Thus, the influence of edge effects on AGC is strongly dependent upon the spatial configuration and number of nearby edges. Previous studies of multiple edges are limited and, unlike our study, do not find evidence for interacting edge effects on AGC (d'Albertas et al., 2018), though this may relate to the practical limitations of field studies (i.e. small sample sizes, placement of field plots). In our study, the use of high-resolution remotely-sensed data ensured a large sample size, and ability to sample across the full gradient of edginess in the studied landscape.

Edge-related losses of AGC in this landscape are primarily driven by the increased mortality of large trees (Anderson et al., 2022), which contribute disproportionately to forest biomass (Slik et al., 2013). These trees are disproportionally affected by edge proximity (Laurance et al., 2000) as they are susceptible to wind damage and canopy desiccation, which are higher near edges and result in increased mortality (D'Angelo et al., 2004; Magnago et al., 2015; Gora and Esquivel-Muelbert, 2021). Mortality may therefore be higher when forest is in proximity to multiple edges, where the underlying abiotic disturbances are also greater (Laurance and Curran, 2008; Schwartz et al., 2017). These disturbances can also cause compositional shifts near multiple edges (Laurance et al., 2006). Compositional shifts near edges can further contribute to biomass declines (Qie et al., 2017), but not always (Anderson et al., 2022). Thus, our results are probably due to increased levels of abiotic disturbance (e.g. wind turbulence, canopy desiccation) in the edgiest forest areas, resulting in greater mortality of large trees and possible compositional shifts in tree communities, which underlie the observed reductions in AGC near multiple edges. It is also possible that the observed patterns could be linked to area effects or variation in regional forest cover, which are likely correlated with edginess and could reduce carbon stocks by limiting tree regeneration and the ecological resilience of tree communities (Lucey et al., 2017; Melito et al., 2021; Arroyo-Rodríguez et al., 2023). Field studies should seek to provide an understanding of the mechanistic drivers of AGC loss we observed here, as well as measures of associated changes in tree community composition and diversity.

We estimate that around 1.7 M ha (41%) of Sabah's forest is edge-affected (i.e. within 300m of an edge), and that AGC is further reduced in approximately 23% of this edge-affected forest as a result of proximity to multiple edges. Our results therefore illustrate the substantial detrimental impact that patch size and geometry can have on edge-related AGC losses. Tropical forest fragmentation continues to increase with the ongoing expansion of agriculture, resulting in fragments becoming smaller and more geometrically complex (Taubert et al., 2018; Hansen et al., 2020; Fischer et al., 2021). It is therefore likely that edge-related carbon losses will become more severe, and forest areas with high edginess are also likely to experience associated changes in forest structure, community composition and diversity.

3.6.2 Accounting for multiple edges improves explanatory power

The vast majority of edge effect studies use ‘Euclidean distance to nearest edge’ as the explanatory variable by which to assess edge influence, under the assumption that proximity to the nearest edge drives ecological change. However, our results show that a metric which accounts for the proximity of multiple edges explains more variation in AGC than a metric which only considers the nearest edge. The proportion of variation explained by our edginess model (18.3%) is also larger than that observed in field studies in the same study landscape (Anderson et al., 2022), which found that distance from nearest edge explained only 5% of the variation in forest carbon. Whilst the improvement in explanatory power relative to the Euclidean distance model was fairly small (3%), and the proportion of AGC variance explained by our edginess model is similar to that found by Chaplin-Kramer et al. (2015) based on a model of Euclidean distance (20%), we observed a greater difference in metric performance when we repeated our analyses on pixels closer to edges. We find that the benefits of an edginess metric are most prominent close to edges (<100m), where there is the highest variation in edginess (Figure 3.2) and where a Euclidean distance model explains only 1.5% of the variation in AGC. This finding indicates that distance to the nearest edge becomes an increasingly poor predictor of variation in AGC across the most fragmented areas in our landscape, whilst an edginess metric still provides a reasonable level of explanatory power (R^2 = 11%).

Accounting for multiple edges through an edginess metric therefore provides improved ability to explain observed patterns in edge-affected features, particularly in highly fragmented landscapes where ‘core’ forest no longer exists. Whilst a Euclidean distance metric may suffice to generate overall estimates of edge influence across large regions (e.g. Chaplin-Kramer, Ramler, et al., 2015; Silva Junior et al., 2020), an edginess metric explains more variation in carbon stocks in very close proximity to edges. In these areas, there is very little variation in the ‘distance to nearest edge’ measure and so it becomes more categorical than continuous (Figure 3.4; vertical banding at left of plot), therefore this metric has too low a resolution to be useful in highly fragmented regions. Thus, an edginess metric is likely to be beneficial for spatially-explicit modelling of forest carbon stocks, and for more accurate estimates of carbon stock reduction in fragmented forests, making it useful for footprinting studies of tropical agricultural products (Chaplin-Kramer et al., 2017; Lam et al., 2019), ecosystem service assessments (Chaplin-Kramer, Sharp, et al., 2015; Metzger et al., 2021), and landscape management decisions (e.g. identifying priority areas for forest conservation and restoration (Lucey et al., 2017; Brancalion et al., 2019)). An edginess metric may also help resolve reported idiosyncrasies in edge effects (Laurance et al., 2007; Ries et al., 2017), and could help explain the apparent lack of edge effects on AGC in some studies (e.g. Fleiss et al., 2020), if they have not accounted for the influence of multiple edges. Further testing of the edginess metric at local spatial scales may help to bridge the gap between small-scale studies of edge influence and the extrapolation of results to regional scales (Ries et al., 2017).

3.6.3 Unexplained variation in forest carbon

Our edginess model explained more variation in AGC than the Euclidean distance model, but a substantial amount of unexplained variation in AGC remains. This is perhaps unsurprising given that forest carbon in this landscape is highly variable (Asner et al., 2018; Figures 3 & 4), driven by many factors in addition to fragmentation effects. Biomass levels in Borneo forests are driven by variables such as annual rainfall, soil fertility, soil drainage and historic disturbances (Slik et al., 2010; Asner et al., 2018), and local environmental variables can also modulate edge effects on AGC (Ordway and Asner, 2020). Furthermore, edge effects can be less important than the location of fragments in terms of driving patterns in tree diversity and composition (Liu and Slik, 2014). Thus, even in the most edge-affected areas (<100m), edge influence apparently only explains low levels of variation in AGC. Future studies could examine how edginess interacts with other environmental variables, as well as factors such as regional disturbance (Melito et al., 2018; Melito et al., 2021), in driving spatial patterns of AGC.

3.6.4 Wider implications for fragmented tropical landscapes

Our results improve understanding of the spatial distribution of AGC stocks in fragmented forests, and demonstrate that accounting for multiple edges is necessary in landscape management decisions aimed at long-term conservation of forest carbon. Whilst there is debate around the best configuration of forest reserves for the purpose of biodiversity conservation (Arroyo-Rodríguez et al., 2020; Banks-Leite et al., 2021), our results emphasize that, where possible, reserves should be large and circular (Laurance, 1991) for the purpose of maintaining carbon stocks, as this design minimizes their edge:area ratio. In our study landscape, where non-forest areas are dominated by oil palm plantations, these recommendations apply to the development of sustainable palm oil practices with respect to the size and shape of High Conservation Value (HCV) and High Carbon Stock (HCS) forest reserves within RSPO-certified plantations (Rosoman et al., 2017; RSPO, 2018), which are often small, with low AGC levels similar to those found in the edgiest forest pixels in our study (Fleiss et al., 2020).

Our finding that AGC is reduced when in proximity to multiple edges indicates that predictions of fragmentation-induced AGC declines may underestimate impacts in highly fragmented landscapes, if these are based on a ‘nearest edge’ understanding of edge influence. For example, studies which estimate edge-related carbon loss by combining core-area models with a simple carbon reduction factor (e.g. Brinck et al., 2017; Fischer et al., 2021) typically base their estimates on studies which only measure the influence of a single edge. Our results suggest that these estimates may be improved if they are parameterised for multiple edges. Accounting for multiple edges will be particularly important in highly fragmented landscapes with small and geometrically complex fragments, which are becoming increasingly common (Taubert et al., 2018), as these are the regions where interacting edge effects are likely to be most prevalent and cause the greatest reduction in forest carbon.

3.7 References

Anderson, J.A., McClean, C.J., Sim, S., Pettorelli, N., Jelling, A., Tangah, J., & Hill, J.K. 2022. Weak edge effects on trees in Bornean rainforest remnants bordering oil palm. *Biotropica*. **54**(4), pp.921–932.

Arroyo-Rodríguez, V., Fahrig, L., Tabarelli, M., Watling, J.I., Tischendorf, L., Benchimol, M., … Tscharntke, T. 2020. Designing optimal human-modified landscapes for forest biodiversity conservation. *Ecology Letters*. **23**(9), pp.1404–1420.

Arroyo-Rodríguez, V., Rito, K.F., Farfán, M., Navía, I.C., Mora, F., Arreola-Villa, F., … Martínez-Ramos, M. 2023. Landscape-scale forest cover drives the predictability of forest regeneration across the Neotropics. *Proceedings of the Royal Society B*. **290**(1990), pp.35–3069.

Asner, G.P., Brodrick, P.G., Philipson, C., Vaughn, N.R., Martin, R.E., Knapp, D.E., … Coomes, D.A. 2018. Mapped aboveground carbon stocks to advance forest conservation and recovery in Malaysian Borneo. *Biological Conservation*. **217**, pp.289–310.

Asner, G.P., Knapp, D.E., Martin, R.E., Tupayachi, R., Anderson, C.B., Mascaro, J., … Silman, M.R. 2014. Targeted carbon conservation at national scales with high-resolution monitoring. *Proceedings of the National Academy of Sciences of the United States of America*. **111**(47), pp.E5016–E5022.

Banks-Leite, C., Larrosa, C., Carrasco, L.R., Tambosi, L.R., & Milner-Gulland, E.J. 2021. The suggestion that landscapes should contain 40% of forest cover lacks evidence and is problematic. *Ecology Letters*. **24**(5), pp.1112–1113.

Barlow, J., Gardner, T.A., Araujo, I.S., Avila-Pires, T.C., Bonaldo, A.B., Costa, J.E., … Peres, C.A.

2007. Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. *Proceedings of the National Academy of Sciences*. **104**(47), pp.18555–18560.

Beer, C., Reichstein, M., Tomelleri, E., Ciais, P., Jung, M., Carvalhais, N., … Papale, D. 2010. Terrestrial gross carbon dioxide uptake: Global distribution and covariation with climate. *Science*. **329**(5993), pp.834–838.

Benitez-Malvido, J., & Martinez-Ramos, M. 2003. Influence of Edge Exposure on Tree Seedling Species Recruitment in Tropical Rain Forest Fragments. *Biotropica*. **35**(4), pp.530–541.

Brancalion, P.H.S., Niamir, A., Broadbent, E., Crouzeilles, R., Barros, F.S.M., Almeyda Zambrano, A.M., … Chazdon, R.L. 2019. Global restoration opportunities in tropical rainforest landscapes. *Science Advances*. **5**(7), pp.3223–3226.

Briant, G., Gond, V., & Laurance, S.G.W. 2010. Habitat fragmentation and the desiccation of forest canopies: A case study from eastern Amazonia. *Biological Conservation*. **143**(11), pp.2763–2769.

Brinck, K., Fischer, R., Groeneveld, J., Lehmann, S., Dantas De Paula, M., Pütz, S., … Huth, A. 2017. High resolution analysis of tropical forest fragmentation and its impact on the global carbon cycle. *Nature Communications*. **8**(Article no:14855).

Broadbent, E.N., Asner, G.P., Keller, M., Knapp, D.E., Oliveira, P.J.C., & Silva, J.N. 2008. Forest fragmentation and edge effects from deforestation and selective logging in the Brazilian Amazon. *Biological Conservation*. **141**(7), pp.1745–1757.

Carlson, K.M., Heilmayr, R., Gibbs, H.K., Noojipady, P., Burns, D.N., Morton, D.C., … Kremen, C. 2018. Effect of oil palm sustainability certification on deforestation and fire in Indonesia. *Proceedings of the National Academy of Sciences of the United States of America*. **115**(1), pp.121–126.

Chaplin-Kramer, R., Ramler, I., Sharp, R., Haddad, N.M., Gerber, J.S., West, P.C., … King, H. 2015. Degradation in carbon stocks near tropical forest edges. *Nature Communications*. **6**(Article no: 10158).

Chaplin-Kramer, R., Sharp, R., Mandle, L., Sim, S., Johnson, J., Butnar, I., … Kareiva, P.M. 2015. Spatial patterns of agricultural expansion determine impacts on biodiversity and carbon storage. *Proceedings of the National Academy of Sciences of the United States of America*. **112**(24), pp.7402–7407.

Chaplin-Kramer, R., Sim, S., Hamel, P., Bryant, B., Noe, R., Mueller, C., … Daily, G. 2017. Life cycle assessment needs predictive spatial modelling for biodiversity and ecosystem services. *Nature Communications*. **8**, p.15065.

d'Albertas, F., Costa, K., Romitelli, I., Barbosa, J.M., Vieira, S.A., & Metzger, J.P. 2018. Lack of evidence of edge age and additive edge effects on carbon stocks in a tropical forest. *Forest Ecology and Management*. **407**, pp.57–65.

D'Angelo, S.A., Andrade, A.C.S., Laurance, S.G., Laurance, W.F., & Mesquita, R.C.G. 2004. Inferred causes of tree mortality in fragmented and intact Amazonian forests. *Journal of Tropical Ecology*. **20**, pp.243–246.

Fischer, R., Taubert, F., Müller, M.S., Groeneveld, J., Lehmann, S., Wiegand, T., & Huth, A. 2021. Accelerated forest fragmentation leads to critical increase in tropical forest edge area. *Science Advances*. **7**(37).

Fleiss, S., Waddell, E.H., Bala Ola, B., Banin, L.F., Benedick, S., Bin Sailim, A., … Hill, J.K. 2020. Conservation set-asides improve carbon storage and support associated plant diversity in certified sustainable oil palm plantations. *Biological Conservation*. **248**(Article no: 108631).

Gaveau, D.L.A., Locatelli, B., Salim, M.A., Yaen, H., Pacheco, P., & Sheil, D. 2019. Rise and fall of forest loss and industrial plantations in Borneo (2000–2017). *Conservation Letters*. **12**(3), p.e12622.

Gaveau, D.L.A., Sheil, D., Husnayaen, Salim, M.A., Arjasakusuma, S., Ancrenaz, M., … Meijaard, E. 2016. Rapid conversions and avoided deforestation: examining four decades of industrial plantation expansion in Borneo. *Scientific Reports*. **6**(Article no: 32017).

Gaveau, D.L.A., Sloan, S., Molidena, E., Yaen, H., Sheil, D., Abram, N.K., … Meijaard, E. 2014. Four Decades of Forest Persistence, Clearance and Logging on Borneo. *PLoS One*. **9**(7), p.e101654.

Gibbs, H.K., Brown, S., Niles, J.O., & Foley, J.A. 2007. Monitoring and estimating tropical forest carbon stocks: making REDD a reality. *Environ. Res. Lett*. **2**, p.13.

Gibbs, H.K., Ruesch, A.S., Achard, F., Clayton, M.K., Holmgren, P., Ramankutty, N., & Foley, J.A. 2010. Tropical forests were the primary sources of new agricultural land in the 1980s and 1990s. *Proceedings of the National Academy of Sciences of the United States of America*. **107**(38), pp.16732–7.

Gora, E.M., & Esquivel-Muelbert, A. 2021. Implications of size-dependent tree mortality for tropical forest carbon dynamics. *Nature Plants*., pp.384–391.

Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., … Townshend, J.R. 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances*. **1**(2).

Hansen, M.C., Potapov, P. V, Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., … Townshend, J.R.G. 2013. High-resolution global maps of 21st-century forest cover change. *Science (New York, N.Y.)*. **342**(6160), pp.850–3.

Hansen, M.C., Wang, L., Song, X.P., Tyukavina, A., Turubanova, S., Potapov, P. V., & Stehman, S. V. 2020. The fate of tropical forest fragments. *Science Advances*. **6**(11), pp.8574–8585.

Lam, W.Y., Kulak, M., Sim, S., King, H., Huijbregts, M.A.J., & Chaplin-Kramer, R. 2019. Greenhouse gas footprints of palm oil production in Indonesia over space and time. *Science of the Total Environment*. **688**, pp.827–837.

Laurance, W.F. 1991. Edge effects in tropical forest fragments: Application of a model for the design of nature reserves. *Biological Conservation*. **57**(2), pp.205–219.

Laurance, W.F., Camargo, J.L.C., Fearnside, P.M., Lovejoy, T.E., Williamson, G.B., Mesquita, R.C.G., … Laurance, S.G.W. 2018. An Amazonian rainforest and its fragments as a laboratory of global change. *Biological Reviews*. **93**(1), pp.223–247.

Laurance, W.F., & Curran, T.J. 2008. Impacts of wind disturbance on fragmented tropical forests: A review and synthesis. *Austral Ecology*. **33**(4), pp.399–408.

Laurance, W.F., Delamônica, P., Laurance, S.G., Vasconcelos, H.L., & Lovejoy, T.E. 2000. Rainforest fragmentation kills big trees. *Nature*. **404**, p.836.

Laurance, W.F., Laurance, S.G., Ferreira, L. V., Rankin-de Merona, J.M., Gascon, C., & Lovejoy, T.E. 1997. Biomass collapse in Amazonian forest fragments. *Science*. **278**(5340), pp.1117–1118.

Laurance, W.F., Lovejoy, T.E., Vasconcelos, H.L., Bruna, E.M., Didham, R.K., Stouffer, P.C., … Sampaio, E. 2002. Ecosystem decay of Amazonian forest fragments: a 22-year investigation. *Conservation Biology*. **16**(3), pp.605–618.

Laurance, W.F., Nascimento, H.E.M., Laurance, S.G., Andrade, A., Ewers, R.M., Harms, K.E., … Ribeiro, J.E. 2007. Habitat fragmentation, variable edge effects, and the landscape-divergence hypothesis. *PLoS ONE*. **2**(10), p.e1017.

Laurance, W.F., Nascimento, H.E.M., Laurance, S.G., Andrade, A.C., Fearnside, P.M., Ribeiro, J.E.L., & Capretz, R.L. 2006. RAIN FOREST FRAGMENTATION AND THE PROLIFERATION OF

SUCCESSIONAL TREES. *Ecology*. **87**(2), pp.469–482.

Laurance, W.F., Sayer, J., & Cassman, K.G. 2014. Agricultural expansion and its impacts on tropical nature. *Trends in Ecology & Evolution*. **29**(2), pp.107–116.

Liu, J.J., & Slik, J.W.F. 2014. Forest fragment spatial distribution matters for tropical tree conservation. *Biological Conservation*. **171**, pp.99–106.

Lucey, J.M., Palmer, G., Yeong, K.L., Edwards, D.P., Senior, M.J.M., Scriven, S.A., … Hill, J.K. 2017. Reframing the evidence base for policy-relevance to increase impact: a case study on forest fragmentation in the oil palm sector. *Journal of Applied Ecology*. **54**(3), pp.731–736.

Magnago, L.F.S., Rocha, M.F., Meyer, L., Martins, S.V., & Meira-Neto, J.A.A. 2015. Microclimatic conditions at forest edges have significant impacts on vegetation structure in large Atlantic forest fragments. *Biodiversity and Conservation*. **24**(9), pp.2305–2318.

Malcolm, J.R. 1998. A model of conductive heat flow in forest edges and fragmented landscapes. *Climatic Change*. **39**(2–3), pp.487–502.

Malcolm, J.R. 1994. Edge Effects in Central Amazonian Forest Fragments. *Ecology*. **75**(8), pp.2438–2445.

Malcolm, J.R., Valenta, K., & Lehman, S.M. 2017. Edge effects in tropical dry forests of Madagascar: additivity or synergy? *Landscape Ecology*. **32**(2), pp.327–341.

Melito, M., Arroyo-Rodríguez, V., Metzger, J.P., Cazetta, E., Rocha-Santos, L., Melo, F.P.L., … Oliveira, A.A. 2021. Landscape forest loss decreases aboveground biomass of Neotropical forests patches in moderately disturbed regions. *Landscape Ecology*. **36**(2), pp.439–453.

Melito, M., Metzger, J.P., & de Oliveira, A.A. 2018. Landscape-level effects on aboveground biomass of tropical forests: A conceptual framework. *Global Change Biology*. **24**(2), pp.597–607.

Metzger, J.P., Villarreal-Rosas, J., Suárez-Castro, A.F., López-Cubillos, S., González-Chaves, A., Runting, R.K., … Rhodes, J.R. 2021. Considering landscape-level processes in ecosystem service assessments. *Science of The Total Environment*. **796**, p.149028.

Mitchard, E.T.A. 2018. The tropical forest carbon cycle and climate change. *Nature*. **559**(7715), pp.527–534.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., & Kent, J. 2000. Biodiversity hotspots for conservation priorities. *Nature*. **403**, pp.853–858.

Nascimento, H.E.M., & Laurance, W.F. 2004. Biomass dynamics in amazonian forest fragments. *Ecological Applications*. **14**(4 SUPPL.).

Nunes, M.H., Jucker, T., Riutta, T., Svátek, M., Kvasnica, J., Rejžek, M., … Coomes, D.A. 2021. Recovery of logged forest fragments in a human-modified tropical landscape during the 2015-16 El Niño. *Nature Communications*. **12**(Article no: 1526).

Oliveira, M.A., Grillo, A.S., & Tabarelli, M. 2004. Forest edge in the Brazilian Atlantic forest: Drastic changes in tree species assemblages. *Oryx*. **38**(4), pp.389–394.

Ordway, E.M., & Asner, G.P. 2020. Carbon declines along tropical forest edges correspond to heterogeneous effects on canopy structure and function. *Proceedings of the National Academy of Sciences of the United States of America*. **117**(14), pp.7863–7870.

de Paula, M.D., Costa, C.P.A., & Tabarelli, M. 2011. Carbon storage in a fragmented landscape of Atlantic forest: the role played by edge-affected habitats and emergent trees. *Tropical Conservation Science*. **4**(3), pp.349–358.

Permana, G., Marliana, S.N., Susandarini, R., & Addaha, H. 2022. Sustaining rainforest remnants in plantation landscapes: degree of oil palm stand-induced edge effects on forest microclimate and regeneration. *CERNE*. **28**(1).

Ploton, P., Mortier, F., Réjou-Méchain, M., Barbier, N., Picard, N., Rossi, V., … Pélissier, R. 2020. Spatial validation reveals poor predictive performance of large-scale ecological mapping models. *Nature Communications 2020 11:1*. **11**(1), pp.1–11.

Porensky, L.M., & Young, T.P. 2013. Edge-Effect Interactions in Fragmented and Patchy Landscapes. *Conservation Biology*. **27**(3), pp.509–519.

Pütz, S., Groeneveld, J., Henle, K., Knogge, C., Martensen, A.C., Metz, M., … Huth, A. 2014. Long-term carbon loss in fragmented Neotropical forests. *Nature Communications*. **5**(1), p.5037.

Qie, L., Lewis, S.L., Sullivan, M.J.P., Lopez-Gonzalez, G., Pickavance, G.C., Sunderland, T., … Phillips, O.L. 2017. Long-term carbon sink in Borneo's forests halted by drought and vulnerable to edge effects. *Nature Communications*. **8**(Article no: 1966).

R Core Team 2022. R: A language and environment for statistical computing.

Ries, L., Murphy, S.M., Wimp, G.M., & Fletcher, R.J. 2017. Closing persistent gaps in knowledge about edge ecology. *Current Landscape Ecology Reports*. **2**, pp.30–41.

Rosoman, G., Sheun, S.S., Opal, C., Anderson, P., & Trapshah (Eds.), R. 2017. The HCS Approach

Toolkit. Available from: http://highcarbonstock.org/wp-content/uploads/2017/05/HCSA-Toolkit-v2.0-Module-1-Introduction-190917-web.pdf.

RSPO 2018. Roundtable on Sustainable Palm Oil Principles & Criteria for Sustainable Palm Oil. Available from: https://rspo.org/resources/certification/rspo-principles-criteria-certification.

Schwartz, N.B., Uriarte, M., Defries, R., Bedka, K.M., Fernandes, K., Gutiérrez-Vélez, V., & Pinedo-Vasquez, M.A. 2017. Fragmentation increases wind disturbance impacts on forest structure and carbon stocks in a western Amazonian landscape. *Ecological Applications*. **27**(6), pp.1901–1915.

Silva Junior, C.H.L., Aragão, L.E.O.C., Anderson, L.O., Fonseca, M.G., Shimabukuro, Y.E., Vancutsem, C., … Saatchi, S.S. 2020. Persistent collapse of biomass in Amazonian forest edges following deforestation leads to unaccounted carbon losses. *Science Advances*. **6**(40), p.eaaz8360.

Slik, J.W.F., Aiba, S.I., Brearley, F.Q., Cannon, C.H., Forshed, O., Kitayama, K., … van Valkenburg, J.L.C.H. 2010. Environmental correlates of tree biomass, basal area, wood specific gravity and stem density gradients in Borneo’s tropical forests. *Global Ecology and Biogeography*. **19**(1), pp.50–60.

Slik, J.W.F., Paoli, G., Mcguire, K., Amaral, I., Barroso, J., Bastian, M., … Zweifel, N. 2013. Large trees drive forest aboveground biomass variation in moist lowland forests across the tropics. *Global Ecology and Biogeography*. **22**(12), pp.1261–1271.

Taubert, F., Fischer, R., Groeneveld, J., Lehmann, S., Müller, M.S., Rödig, E., … Huth, A. 2018. Global patterns of tropical forest fragmentation. *Nature*. **554**, pp.519–522.

Tropek, R., Sedláček, O., Beck, J., Keil, P., Musilová, Z., Šímová, I., & Storch, D. 2014. Comment on ‘High-resolution global maps of 21st-century forest cover change’. *Science*. **344**(6187).

Wagenmakers, E.J., & Farrell, S. 2004. AIC model selection using Akaike weights. *Psychonomic Bulletin and Review*. **11**(1), pp.192–196.

Chapter 4 - **Carbon stocks at rainforest edges are mediated by adjacent habitat structure**

Forest remnant surrounded by oil palm monoculture

4.1 Abstract

Tropical forests are becoming increasingly fragmented due to agricultural and forestry expansion, leading to a potential reduction in aboveground forest carbon near forest edges. However, forest edge effects are highly variable, and here we examine how the structural characteristics of the adjacent land use (‘matrix’) contribute to this variability.

We analysed high-resolution (30m pixels) remotely-sensed data on above-ground carbon (AGC), for 902 forest edge sites throughout Sabah, Malaysian Borneo. Sites bordered a range of matrix types, from high-contrast land-uses with very low AGC (e.g. pasture, bare earth), to low-contrast land-uses with more similar AGC to forest (e.g. tree plantations). Edge effects are expected to increase over time, and so we also examined the effect of edge age on AGC at edges.

Carbon stocks were lower in edges bordering high-contrast matrices than in those bordering low-contrast matrices ($\beta = 0.41$, $p < 0.001$). This equates to an average model-fitted loss of 21% AGC in edges bordering land-uses such as pasture, compared to an average loss of 10% AGC in edges bordering tree plantations. Older edges (8+ years) contained around 10% less AGC than younger edges (<8 years), however we found no interaction between edge age and matrix effects. Whilst adjacent matrix structure was an important determinant of edge carbon, the amount of carbon in the nearby forest ‘core’ had a greater impact ($\beta = 0.62$, $p < 0.001$), indicating that edge carbon stocks are lower in more degraded forests (i.e. sites with lower core forest AGC). Nonetheless, forest sites with high core forest AGC suffered the greatest reduction in carbon at edges (% loss), particularly when adjacent to high-contrast matrices.

Overall our results demonstrate that edge effects are weakest at sites adjacent to low-contrast matrices, such as tree plantations and oil palm, which may buffer forest edge exposure to microclimatic changes and windthrow. Carbon stocks at forest edges decline over time, although most losses occur within the first 8 years of edge formation. Management activities aimed at reducing edge contrast, such as the creation of matrix buffer habitats, may help to maintain carbon stocks in fragmented tropical landscapes.

Keywords

Agricultural expansion, carbon storage, deforestation, forest fragmentation, landscape management

4.2 Highlights

1. Aboveground carbon (AGC) losses at forest edges are mediated by adjacent land use
2. High-contrast edges have twice AGC loss of low-contrast edges (21% vs 10% loss)
3. Edge AGC declines over time but most AGC loss is within 8 years of edge creation
4. Edge AGC is more dependent on AGC in nearby ‘core’ forest than on edge contrast
5. Management strategies to buffer edge contrast may help maintain forest edge AGC

4.3 Introduction

The expansion of tropical agriculture and forestry has caused widespread fragmentation and loss of tropical forests, globally important ecosystems which play a key role in climate regulation (Malhi et al., 2014; Lewis et al., 2015; Mitchard, 2018; Curtis et al., 2018). The direct impacts of deforestation on tropical forests are substantial (Newbold et al., 2015; Tyukavina et al., 2015), however anthropogenic disturbances in remaining forest areas can also have large impacts (Barlow et al., 2016; Maxwell et al., 2019; Lapola et al., 2023), and are widespread (Matricardi et al., 2020; Zhu et al., 2023). Fragmented forests experience edge effects, the biotic and abiotic changes that occur within forest following edge creation. Edge effects are a leading driver of forest degradation in human-modified landscapes, and are responsible for significant changes in forest structure, composition, diversity and function (Laurance et al., 2011; Chaplin-Kramer et al., 2015; Pfeifer et al., 2017; Zhu et al., 2023). Around 30% of the remaining tropical forest area is within 100m of an edge, and this is expected to increase to 50% by the year 2100 (Fischer et al., 2021). However, edge effects are highly variable (Laurance et al., 2007; Ries et al., 2017), and so it is important to examine factors that modulate edge effects, and devise management strategies to limit their detrimental impacts.

Edges have a considerable impact on aboveground carbon (AGC) stocks in fragmented tropical forests. AGC declines with increasing proximity to edges (Chaplin-Kramer et al., 2015; Ordway and Asner, 2020; Anderson et al., 2022), and edge effects can cause a doubling of carbon emissions from deforestation in highly fragmented landscapes (Maxwell et al., 2019). These carbon losses are primarily driven by abiotic changes that occur near edges, such as increased wind speed, reduced humidity and increased temperature (Magnago et al., 2015), which can also increase fire occurrence (Cochrane, 2003). These factors contribute to increased mortality of large trees (Laurance et al., 2000; de Paula et al., 2011; Anderson et al., 2022), which store the majority of forest AGC (Slik et al., 2013). Edge effects can also cause compositional shifts in tree communities and increased stem turnover, which can further contribute to AGC losses (Nascimento and Laurance, 2004; Qie et al., 2017). However, edge effects on AGC are highly variable in strength (Melito et al., 2018), making it important to understand the drivers of this variability. The structure, composition and quality of the adjacent matrix habitat (i.e. non-forest land use) can play an important role in shaping the magnitude of edge effects (Harper et al., 2005; Laurance et al., 2011; Driscoll et al., 2013). The degree of structural contrast (i.e. difference in vegetation structure) between the forest and matrix determines the strength of abiotic gradients, in factors such as wind speed, temperature and humidity (Camargo and Kapos, 1995; Laurance and Curran, 2008; Arroyo-Rodríguez et al., 2017; Permana et al., 2022), with more severe abiotic gradients observed in high-contrast edges (e.g. forest adjacent to pasture) than low-contrast edges (e.g. forest adjacent to mature tree plantations). The structure of the matrix can therefore mediate biotic changes occurring at edges, and there is evidence of more severe edge effects on a variety of taxa including birds, amphibians and invertebrates (Santos-Barrera and Urbina-Cardona, 2011; Campbell et al., 2011; Hatfield et al., 2020), as well as increased tree mortality (Mesquita et al., 1999), at high-contrast edges. These findings suggest that matrix structure may also affect AGC in tropical forest edges (Melito et al., 2018), but this has not yet been quantified and is therefore the focus of our study.

Edge effects on AGC change over time, therefore consideration of edge age is also required when examining the impact of adjacent matrix structure on forest carbon. Edge-related tree mortality is typically greatest within the first few years after edge creation (Laurance et al., 2002), due to the severe microclimatic gradients adjacent to high-contrast felled areas, resulting in an initial pulse of tree death and a sharp decline in AGC (Silva Junior et al., 2020). Tree mortality declines as the edge ages (Laurance et al., 2018), but carbon stocks continue to deteriorate (Ordway and Asner, 2020). However, interactions between edge age and matrix contrast have so far not been considered in the literature. The influence of matrix contrast may be greatest in young edges, if forest regrowth has not yet ‘sealed’ the edge against subsequent abiotic disturbances (Camargo and Kapos, 1995).

Quantifying the influence of the adjacent matrix on edge AGC also requires consideration of local variation in core forest AGC, both to contextualise the local importance of edge effects and to determine whether the structure, and AGC, of the forest itself mediates the influence of matrix contrast (Harper et al., 2005). Whilst there is evidence that site-level variation in AGC can outweigh any local effects of fragmentation (Fleiss et al., 2020; Anderson et al., 2022), this is not always the case (Berenguer et al., 2014). These site-level differences in AGC are driven by variation in disturbance history, management regimes, topography, edaphic conditions and local environmental conditions (Slik et al., 2010; Asner et al., 2018), resulting in significant spatial heterogeneity in forest carbon stocks, even in ‘core’ forest not influenced by edge effects. This variation in core AGC could mediate the impacts of high-contrast edges. High-carbon forests may be more resilient to otherwise strong edge effects, due to increased seed flux from large tree species in the forest core (Melito et al., 2018), reduced synergisms between multiple disturbances (Berenguer et al., 2014; Silvério et al., 2019), and local climatic buffering provided by structurally complex forests with denser canopies (Mahmood et al., 2014; Chapman et al., 2020).

In this study, we use high resolution remotely-sensed data to study the impacts of matrix structure on carbon stocks in forest edges throughout Sabah, Malaysian Borneo. Sabah has experienced considerable forest loss and fragmentation due to commercial logging and the subsequent expansion of plantation industries such as timber and oil palm (Reynolds et al., 2011; Gaveau et al., 2014). Agriculture now comprises over 25% of the land area (Ministry of Agriculture and Fisheries (M.A.F), 2017). Non-forest areas in the region are dominated by oil palm plantations, but there is also a variety of other land-use types, such as clear-cut logging, timber and rubber plantations, livestock pastures, rice paddies, urban settlements and regenerating forests (M.A.F, 2017; Qie et al., 2017). Forest edges therefore border a wide variety of matrix types, providing a gradient from high-contrast edges (e.g. forest adjacent to pasture) to low-contrast edges (e.g. forest adjacent to mature palm and timber plantations). Prior to the expansion of plantation industries many forests in Sabah were selectively logged at variable intensities, and are still exposed to variable management regimes, leading to significant heterogeneity in tree biomass and AGC of forest remnants (McMorrow and Talip, 2001; Reynolds et al., 2011; Asner et al., 2018). The majority of deforestation occurred prior to 2010 (Gaveau et al., 2014), but agricultural expansion has continued (Gaveau et al., 2019) and around 20% of remaining forest in Sabah is within 100m of an edge (chapter 3). These edges vary considerably in the structure of the adjacent matrix, as well as their age and local core AGC, making it an ideal landscape for our study. We test the hypothesis that forest AGC is higher in edges adjacent to low-contrast land-uses (i.e. land-uses with tall, dense vegetation) compared with edges adjacent to high-contrast land-uses (i.e. land-uses with short, sparse vegetation), and we examine whether the effects of edge contrast are moderated by the effects of edge age and local forest AGC.

4.4 Methods

4.4.1 Selecting edge sites

Mapping and GIS analyses were performed in ArcGIS Pro version 2.3.3 and R version 4.1.1 (R Core Team, 2022). We selected edge sites using high-resolution (30m pixels) remotely-sensed data for Sabah in 2016, to generate a sample from the study landscape. We focused on 2016 so that our forest cover data correspond with published data on AGC (Asner et al., 2018). We used a binary land cover (forest vs non-forest) map for Sabah (Figure 4.1a), produced from a combination of tree-cover and forest-loss data (Hansen et al., 2013) and an industrial plantation map (Gaveau et al., 2014; Gaveau et al., 2016). This 2016 land cover map delineates forest cover (excluding mangroves) based on a minimum 30% tree cover threshold for pixels in the year 2000, the recommended threshold for studies of forest fragmentation (Haddad et al., 2015; Brinck et al., 2017; Taubert et al., 2018; Hansen et al., 2020; Fischer et al., 2021), but excludes forest pixels which experienced deforestation or conversion to plantations between 2000 and 2016 (see Chapter 3 for details). We used the land cover map to delineate forest edge boundaries (Figure 4.1a), defined as forest pixels adjacent to a non-forest pixel (Queen's case contiguity), in order to identify candidate locations for study sites. Edge effects on AGC vary depending on the number and proximity of nearby edges ('edginess'; Chapter 3), and we excluded sites affected by multiple edges to control for this. To do this, we filtered candidate sites based on a threshold of edginess applied to edge-adjacent forest pixels (30m from edge boundary), using the heat-diffusion approach developed by Malcolm et al. (2017; see Chapter 3 for details). Edginess values range from 0-1, with 0 representing 'core' forest beyond any edge influence, and 1 representing a forest pixel adjacent to multiple edges. We applied a threshold range of 0.65-0.8 to select potential edge-adjacent forest pixels for inclusion in the study, filtering out those pixels which were either close to multiple edges (edginess > 0.8) or were adjacent to only a small number of edge pixels (edginess < 0.65; e.g. when edges occur at a reflex angle or next to small clearings within forest). Thus, we included edge-adjacent forest pixels which bordered straight edges and were not influenced by additional edges. We selected pixels that formed 300m 'straight edge segments' (i.e. contiguous edge-adjacent forest pixels) and excluded any segments less than 300m (Figure 4.1b), to ensure a consistent sampling area across sites (see below), thus generating 4630 candidate edge study sites.

At each site we generated a transect (300m x 900m; 27ha) spanning the 300m straight edge segment, running perpendicular to the edge from 300m into the adjacent non-forest and 600m into the forest (Figure 4.1c). We included forest up to 600m from the edge to ensure sites contained core forest pixels, because edge effects typically occur within 100-500m of edges in this landscape (Qie et al., 2017; Ordway and Asner, 2020; Nunes et al., 2021; Anderson et al., 2022). We only included sites with at least 300m of non-forest adjacent to the edge, to exclude edges bordering narrow gaps such as rivers, roads and small forest clearings (Briant et al., 2010). Thus, edge sites (n = 4630) each comprised approximately 9 ha of non-forest and 18 ha of forest. We discarded sites with fewer than 2.7 ha of 'core forest' pixels (forest pixels 500-600m from the focal edge, with an edginess score of <0.05), as these were typically in very small forest fragments without a true forest 'core' (n = 3521 sites). We also excluded sites where the average AGC (Asner et al., 2018) of non-forest pixels was greater than that of core forest pixels (n = 63 sites), as these likely reflected incorrect land classifications. Finally, we imposed a minimum distance of 2km between sites to ensure spatial independence of sampling locations, leaving a final sample of 902 sites for analysis (Figure 4.1c). We categorized forest pixels within 120m of the edge as edge-influenced, because edge effects on AGC are typically strongest within around 100m (Ordway and Asner, 2020) and a 120m threshold is therefore recommended when using 30m-resolution data (Silva Junior et al., 2020). We did not include edge boundary pixels themselves (Figure 4.1; white shading) as these pixels likely contain a mixture of forest and non-forest.

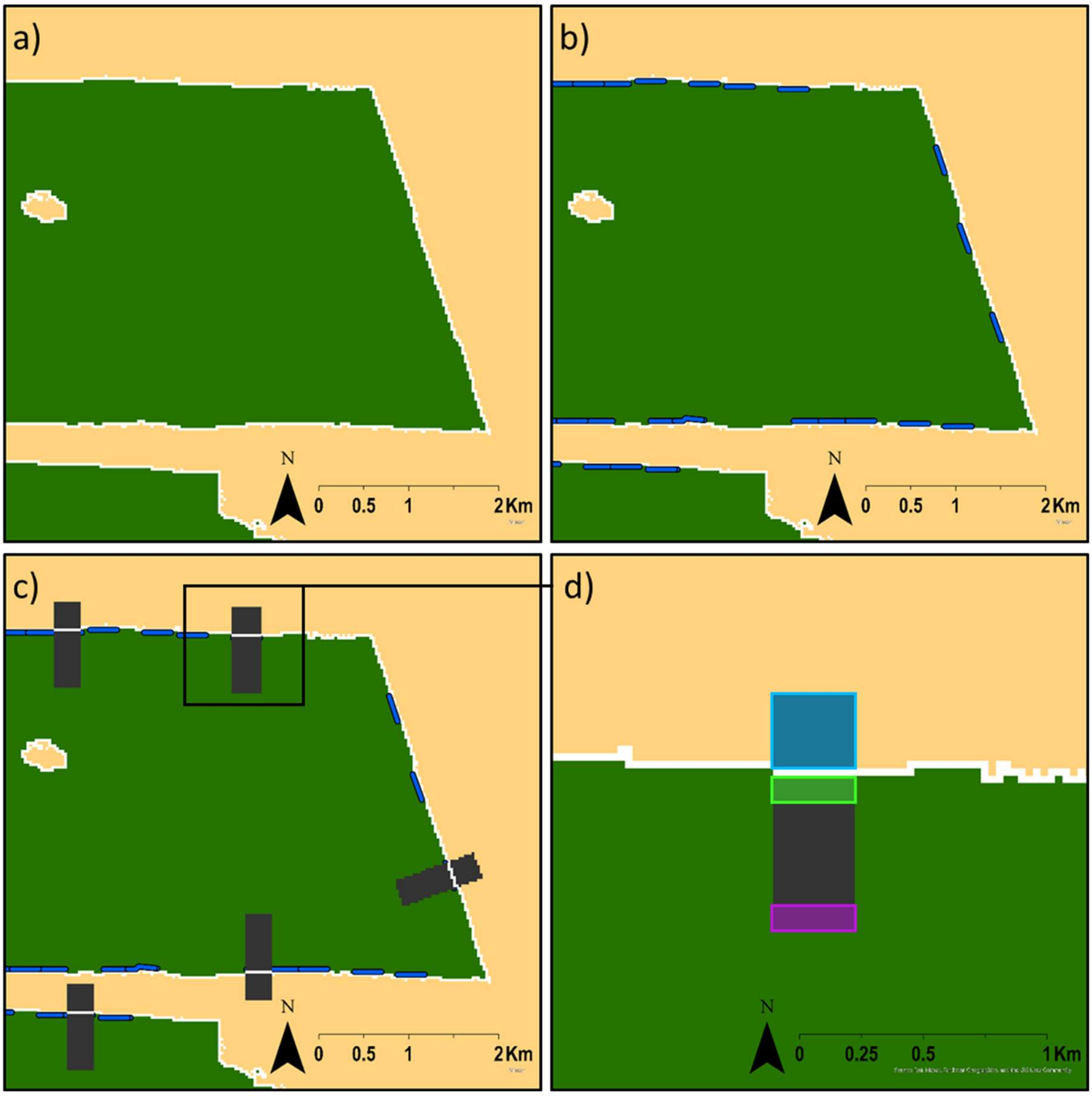


Figure 4.1 – Selection of edge study sites, shown for a 3,600 ha sub-region of Sabah: **a)** land-cover map for Sabah in 2016, showing forest (green), non-forest (cream) and edge boundary (white) pixels, **b)** 300m ‘straight-edge segments’ (blue), based on forest ‘edginess’ values to avoid sites in proximity to multiple edges, **c)** spatially-independent (>2km apart) edge sites (black rectangles) perpendicular to straight-edge segments, spanning 600m of forest and 300m of adjacent non-forest, **d)** close-up view of a single edge site, showing the non-forest zone (blue), edge-influenced forest zone (light green; ≤ 120m from edge) and core forest zone (pink; 500-600m from edge, edginess <0.05).

4.4.2 Sampling forest AGC, matrix structure and edge age

We computed four site-level metrics from our sample of 902 sites, to use in subsequent data analyses. We calculated the average aboveground carbon density (hereafter AGC; Mg C ha^{-1}) of forest pixels in the 'edge-influenced zone' (≤ 120m from edge; Figure 4.1d, light green zone), the average AGC of forest pixels in the local 'core forest zone' (500-600m from edge; Figure 4.1d, pink zone), and the average AGC of non-forest pixels (non-forest pixels within 300m adjacent to edge; Figure 4.1d, blue zone). These published AGC data from Asner et al. (2018) were produced using a combination of airborne Light Detection And Ranging (LiDAR), satellite imaging and geospatial data collected in 2016. They represent the best-available dataset of AGC for Sabah. We use mean AGC in the non-forest as our measure of matrix structure, given that AGC is primarily driven by aboveground biomass, a common measure of vegetation structure (Asner et al., 2018). Asner at al. calibrated the AGC data from forest plots but not from non-forest areas, and so AGC values of non-forest land classes may be less reliable than forest AGC values. However, they nevertheless provide a continuous measure of vegetation structure, which can distinguish between high-contrast and low-contrast land-uses. Thus, higher AGC in non-forest pixels is indicative of land-uses such as mature oil palm and tree plantations (taller, denser vegetation resulting in low-contrast edges; e.g. Figure 4.2a, mean non-forest AGC = 28 Mg C ha^{-1}), whereas low AGC represents land-uses such as pasture or bare earth (lower, sparser vegetation resulting in high-contrast edges; e.g. Figure 4.2b, mean non-forest AGC = 5 Mg C ha^{-1}).

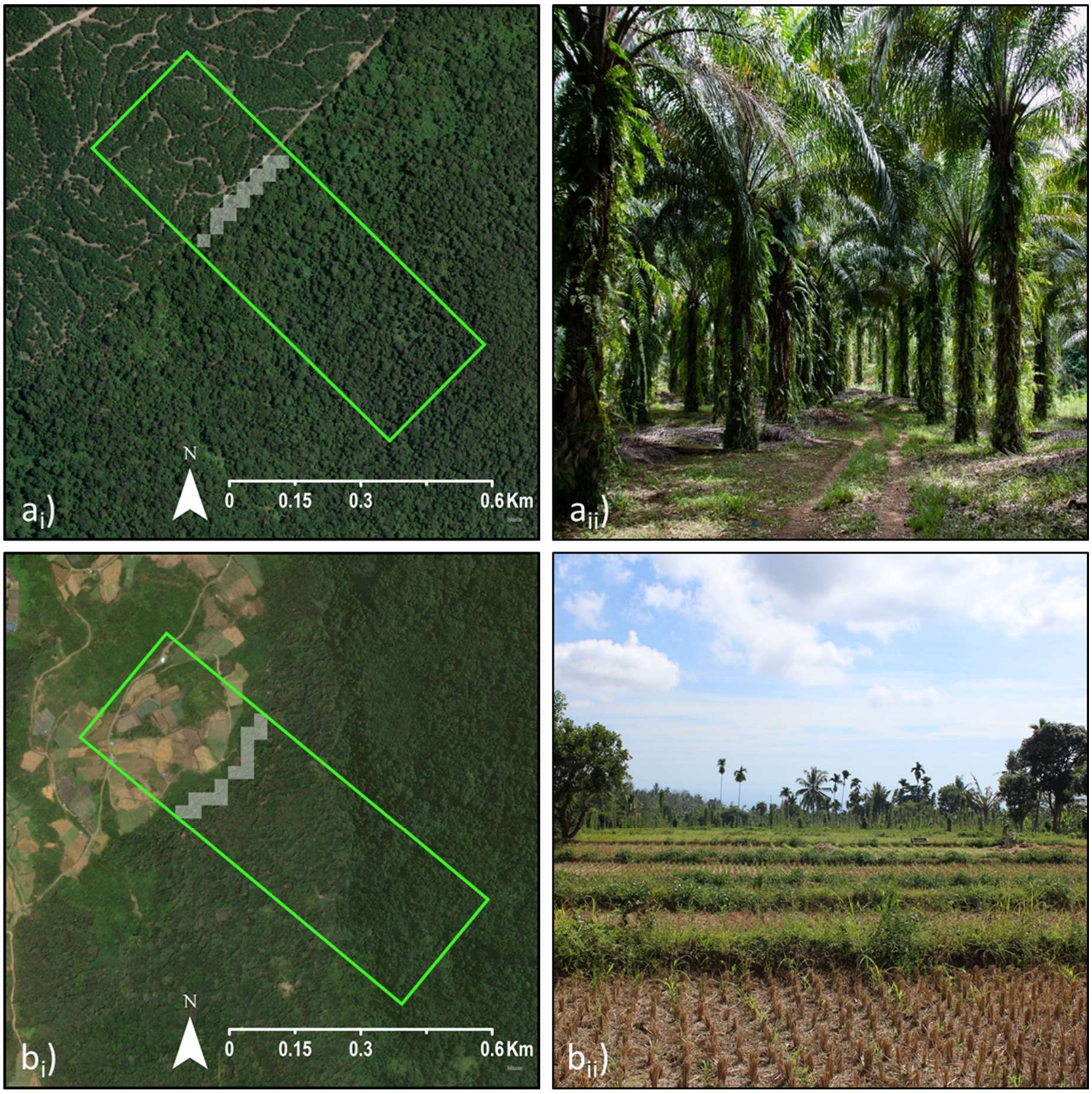


Figure 4.2 – Exemplar study sites with forest bordering **a)** a relatively low-contrast matrix (mature oil palm), with relatively high AGC non-forest pixels (mean AGC of non-forest pixels = 28 Mg C ha^{-1}), compared to sites bordering **b)** a relatively high-contrast matrix (pasture & annual crop mosaic) with relatively low AGC in the matrix (mean AGC of non-forest pixels = 5 Mg C ha^{-1}). Site boundaries are shown in light green and are represented by simplified polygons here, with edge boundary pixels shown in white (not included in analyses). On-ground photographs (J Anderson) are representative of respective land-uses in Sabah, but do not correspond to actual site locations. Satellite imagery sourced from arcgis.com.

We also computed edge age (time since edge creation; years before 2016) for each site. We used information on the year of forest loss for non-forest pixels, sourced from Gaveau et al. (2014; 2016) where available (where non-forest is industrial timber or oil palm plantations), and from Hansen et al. (2013) otherwise. Gaveau et al. provide forest-loss estimates dating back to 1973, although temporal resolution pre-2000 is generally patchy, whilst Hansen et al. provide yearly estimates dating back to the year 2000. Forest-loss estimates refer to initial deforestation events (when edges are created) rather than subsequent changes in the non-forest land cover (e.g. replanting events in oil palm and timber plantations). We calculated the mean age of all non-forest pixels in each site (i.e. time since deforested), then grouped sites into three age categories: young edges (mean age <8 years old, n = 332 sites), intermediate age edges (mean age 8-16 years old, n = 242 sites) and old edges (mean age 16+ years old, n = 328 sites). We used a categorical measure of edge age because exact dates of edge creation are unknown, particularly for edges created pre-2000. Previous research has shown that AGC losses tend to stabilise within 8 - 15 years following edge creation (Silva Junior et al., 2020), but AGC stocks can sometimes recover within 15-20 years (Almeida et al., 2019). Our three age categories should therefore allow us to identify key temporal trends in AGC loss, such as evidence of stabilisation or AGC recovery. These categories provide a reasonable level of resolution in edges <16 years old, and similar sample sizes in each category.

4.4.3 Data analysis

Statistical analyses were performed in R version 4.1.1 (R Core Team, 2022), on site-level metrics. We constructed a linear regression (lm function; R Core Team, 2022) to measure the influence of matrix structure (mean AGC in adjacent non-forest; Mg C ha^{-1}) on edge forest carbon (mean AGC in edge-influenced zone; Mg C ha^{-1}). We also included core forest carbon (mean AGC in core zone; Mg C ha^{-1}) and edge age (categorical) as independent variables. The inclusion of core forest AGC controls for local variation in forest AGC, and we also modelled an interaction term between edge age and matrix structure, to determine whether the influence of matrix structure on edge carbon differs depending upon the age of the edge. However, we found no significant interaction between edge age and matrix structure, therefore the interaction term was removed and hereafter we report results from the simplified model. Model residual plots were checked, and show that all necessary statistical assumptions of the linear regression were met (Thomas et al., 2017). Whilst there was a correlation between core forest carbon and matrix structure (r = 0.35; cor function; R Core Team, 2022), calculation of variance inflation factors (vif function; Fox and Weisberg, 2019) showed no evidence of concerning collinearity between variables (VIF < 3).

To aid interpretation of each of the main results, we calculated model-fitted edge AGC for various scenarios. We used the 'Predict' function (Fox and Weisberg, 2019) and model parameters (Table 4.1), holding the value of all independent variables constant other than the variable of interest, as specified below (see Table 4.2). Continuous variables were held constant at their mean value (98.3 Mg C ha^{-1} for core carbon, 24.9 Mg C ha^{-1} for matrix AGC) unless reported otherwise. Predictions were averaged across all age categories, except in section 4.5.3 (age effects on AGC). For comparisons of high and low contrast edges, we used a representative matrix AGC value of 3.2 Mg C ha^{-1} for high-contrast edges, as this is the mean AGC of pasture (Marín-Spiotta et al., 2007), and 30.3 Mg C ha^{-1} for low-contrast edges, as this is the mean AGC of oil palm (Fleiss et al., 2020).

4.5 Results

We sampled a range of edge contrast levels amongst our 902 sites, with considerable variation present in the structure of the adjacent matrix (Figure 4.3a). Around 11% of sites (*n* = 97) were at relatively high contrast edges (adjacent matrix AGC ≤ 5 Mg C ha^{-1}; e.g. Figure 4.2b), whilst 32% (*n* = 291) were at relatively low contrast edges (adjacent matrix AGC ≥ 28 Mg C ha^{-1}; e.g. Figure 4.2a). The average AGC in the adjacent matrix was 24.9 Mg C ha^{-1}, compared to the average AGC of 98.3 Mg C ha^{-1} in the forest core (though this also varied greatly; Figure 4.3c), demonstrating large differences in vegetation structure between forest and non-forest. We also observed substantial variation in edge forest carbon (Figure 4.3b), and our linear regression including matrix structure, core AGC and edge age explained 59% of this variation (adjusted R^2 = 0.59; Table 4.1).

Table 4.1 – Summary outputs of a linear regression used to analyse the influence of matrix structure (mean AGC in adjacent non-forest; Mg C ha^{-1}), core forest carbon (mean AGC in core zone; Mg C ha^{-1}) and edge age (categorical) on edge forest carbon (mean AGC in edge-influenced zone; Mg C ha^{-1}). Adjusted R^2 = 59%.

† Significance levels and intercept adjustments of edge age categories are relative to the y-intercept of young edges (<8 years).

Predictor variable	***β* (± SE)**	**Intercept adjustment (± SE)**	***p***
Matrix structure	0.41 (± 0.05)	-	<0.001
Core forest AGC	0.62 (± 0.02)	-	<0.001
Intermediate edges (8-16 years)	-	-8.4 (± 2.32) †	<0.001 †
Old edges (16+ years)	-	-7.2 (± 2.13) †	<0.001 †

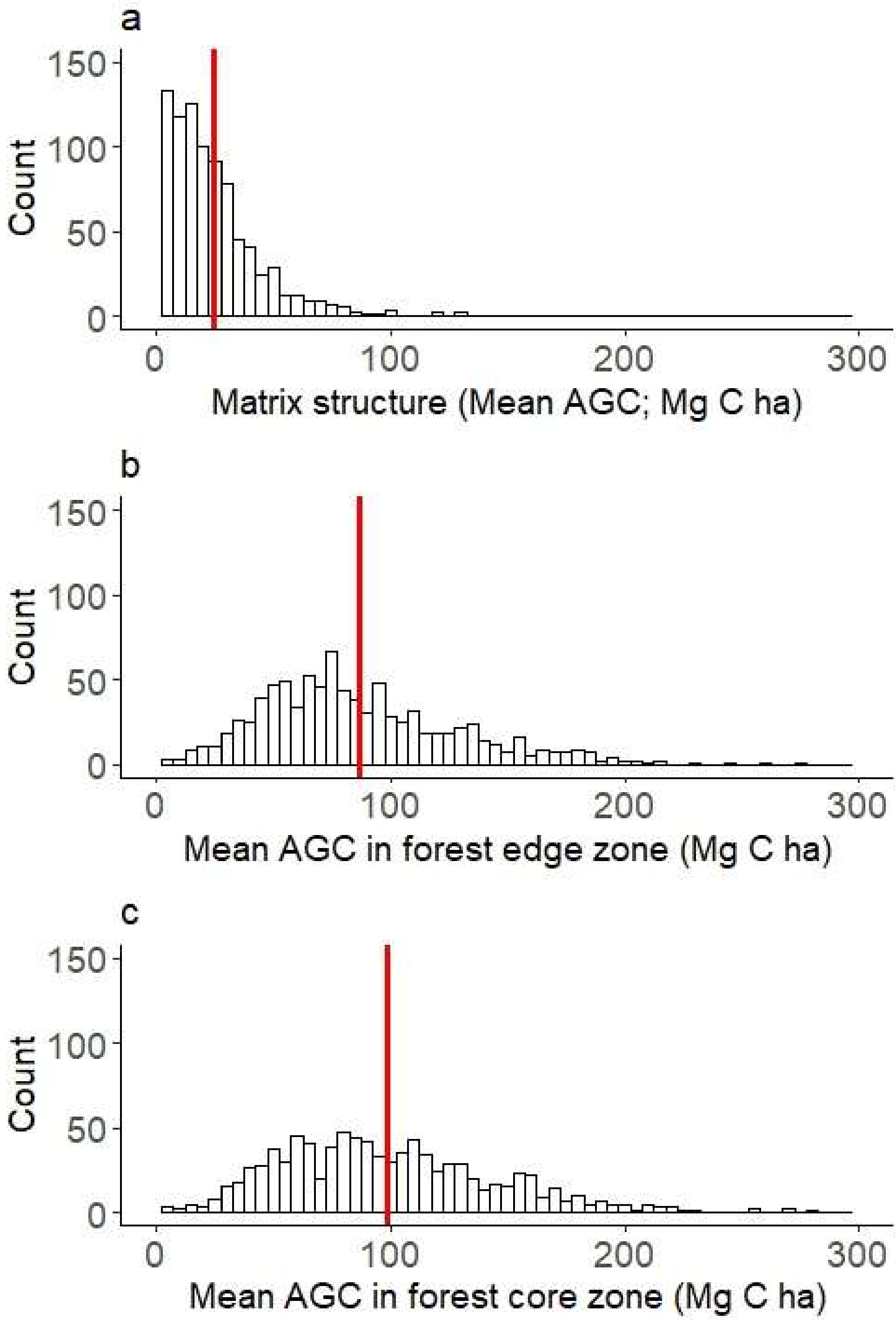


Figure 4.3 – Frequency histograms showing the considerable variation in AGC in 902 edge sites throughout Sabah, for **a)** the adjacent non-forest zone (non-forest ≤ 300m from edge), **b)** edge-influenced forest zone (forest ≤ 120m from edge) and **c)** core forest zone (forest 500-600m from edge). The mean AGC of each zone is shown in red.

4.5.1 Carbon stocks in high-contrast versus low-contrast edges

We found a significant positive effect of adjacent matrix structure on AGC at edges, with a fitted increase of 0.41 Mg C ha^{-1} edge forest carbon for every increase of 1 Mg C ha^{-1} AGC in the adjacent matrix (Figure 4.4; Table 4.1). Thus, carbon stocks were lower in edges that bordered high-contrast land-uses than in edges bordering low-contrast land-uses. At high-contrast edges (e.g. Figure 4.2b) average model-fitted AGC in edge forest was 77.43 Mg C ha^{-1} (averaged across all age categories, with core carbon held at mean value of 98.3 Mg C ha^{-1}; Table 4.2). This is approximately 13% lower than at low-contrast edges (e.g. Figure 4.2a), where average model-fitted edge carbon was 88.52 Mg C ha^{-1} (Table 4.2).

Relative to the mean core forest AGC value of 98.3 Mg C ha^{-1}, these edge values equate to an average predicted carbon loss of 21% in high-contrast edges (when matrix AGC = 3.2 Mg C ha^{-1}), compared to an average predicted loss of 10% in low-contrast edges (when matrix AGC = 30.3 Mg C ha^{-1}; Table 4.2). Whilst the relationship between matrix structure and edge forest carbon may appear to be driven by a few sites with high AGC in the matrix (Figure 4.4), model residual plots show no evidence of overly influential data points. Furthermore, restricting the analysis to only those sites with ≤ 50 Mg C ha^{-1} matrix AGC (n = 809) showed no qualitative change in results (effect of matrix structure on edge forest carbon when high matrix carbon sites are excluded: β = 0.5, $p < 0.001$), confirming that the observed relationship is not driven by these data points.

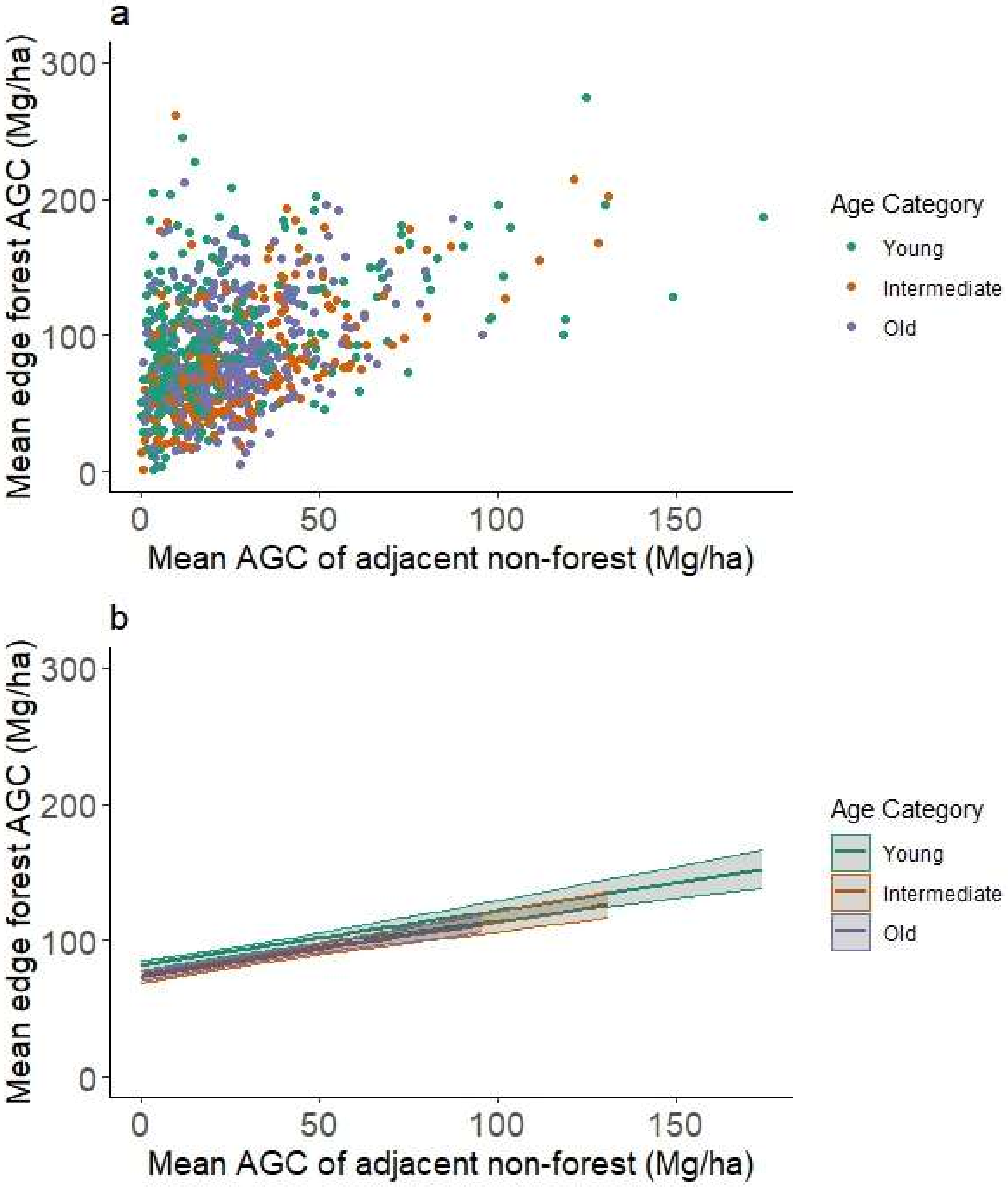


Figure 4.4– Significant effect of adjacent matrix AGC (mean AGC in adjacent non-forest; Mg C ha^{-1}) on forest edge AGC (mean AGC of forest ≤ 120m from edge; Mg C ha^{-1}), for 902 edge sites throughout Sabah, Malaysian Borneo. Raw data points (panel **a**) are coloured by the age category of edge sites, with young (< 8 years old) edges in green, intermediate (8-16 years old) edges in orange, and old (16+ years old) edges in purple. Model-fitted lines (panel **b**; also coloured by age category) show predicted values of edge forest AGC for different values of matrix AGC, as fitted by a linear regression, whilst holding core forest AGC constant at its mean value of 98.3 Mg C ha^{-1}. Shading shows 95% confidence intervals.

4.5.2 Local variation in forest AGC

We found a strong positive relationship between local forest AGC (mean core AGC) and edge forest carbon, with an increase of 0.6 Mg C ha^{-1} edge carbon for every increase of 1 Mg C ha^{-1} core carbon (Figure 4.5; Table 4.1). Furthermore, the inclusion of forest core AGC in the regression increased the explained variance in edge carbon by around 40% (adjusted R^2 = 0.59 with core AGC included *vs* 0.21 without). Thus, edge carbon was highly dependent upon core forest carbon, and the highest AGC stocks were found in sites where the core forest contains high levels of carbon. However, although carbon stocks were higher at these forest edges, the fitted relationship between edge forest carbon and core forest carbon indicates that these edges actually experience the greatest carbon losses relative to the core (Figure 4.5). Sites of an average quality (core AGC = 98.3 Mg C ha^{-1}) were predicted to experience around 12% AGC loss at the edge relative to the core (average model-fitted edge AGC = 86.6 Mg C ha^{-1}, when matrix AGC held at mean value of 24.9 Mg C ha^{-1}; Table 4.2), whereas sites with core carbon levels representative of protected forest reserves such as Danum Valley Conservation Area (207 Mg C ha^{-1} (Asner et al., 2018)), experience average predicted AGC losses of 26% at the edge (average model-fitted edge AGC = 153.4 Mg C ha^{-1}, when matrix AGC held at mean value of 24.9 Mg C ha^{-1}; Table 4.2). Edge impacts were even greater when sites bordered a high contrast matrix, with predicted edge AGC reductions of 21% in sites with average levels of core forest AGC, but 30% reductions in sites with high core AGC respectively (Table 4.2). Thus, the most severe AGC losses are predicted to occur at sites with high forest core AGC bordering high-contrast matrix habitats, such as pasture (Table 4.2).

Table 4.2 – Model-fitted edge AGC (Mg C ha^{-1}) and % loss (relative to core AGC) for various edge scenarios (determined by set values of core AGC and matrix AGC), averaged across all edge age categories. Values generated using the R Predict function (Fox and Weisberg, 2019) based on the parameters of a linear regression (Table 4.1).

Core AGC (Mg C ha^{-1})	**Matrix contrast (Mg C ha^{-1})**	**Model-fitted edge AGC (Mg C ha^{-1})**	**Model-fitted AGC loss at edge (%)**
Sample average (98.3)	High (matrix AGC = 3.2)	77.43	21
	Low (matrix AGC = 30.3)	88.52	10
	Sample average (matrix AGC = 24.9)	86.6	12
High (207)	Sample average (matrix AGC = 24.9)	153.4	26
	High (matrix AGC = 3.2)	144.6	30

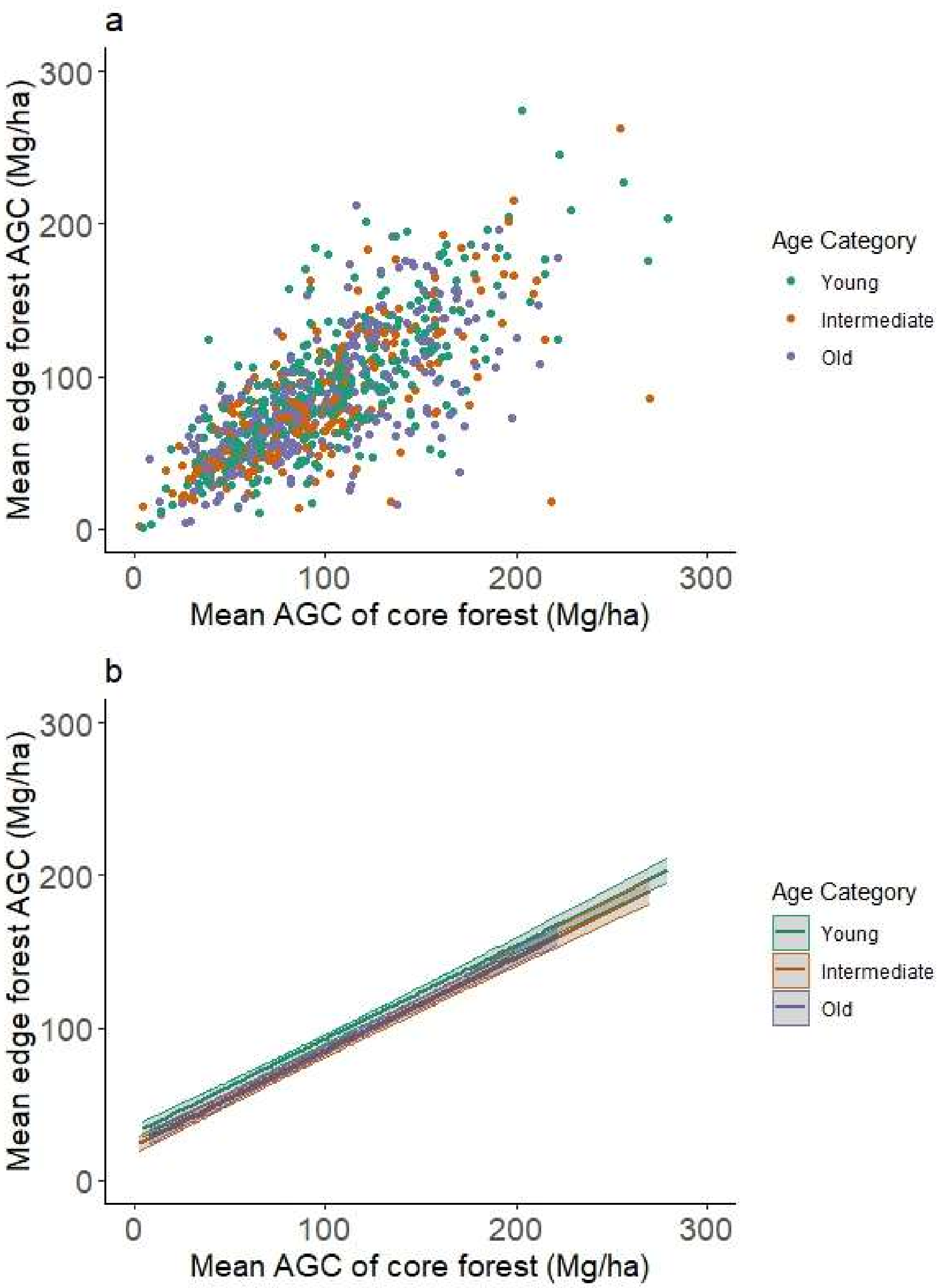


Figure 4.5 – Significant relationship between local forest core AGC (mean AGC in forest 500-600m from edge; Mg C ha^{-1}) and forest edge AGC (mean AGC of forest ≤ 120m from edge; Mg C ha^{-1}), for 902 edge sites throughout Sabah, Malaysian Borneo. Raw data points (panel **a**) are coloured by the age category of edge sites, with young (< 8 years old) edges in green, intermediate (8-16 years old) edges in orange, and old (16+ years old) edges in purple. Model-fitted lines (panel **b**; also coloured by age category) show the predicted values of edge forest AGC for different values of core forest AGC, as fitted by a linear regression, whilst holding adjacent matrix AGC constant at its mean value of 24.9 Mg C ha^{-1}. Shading shows 95% confidence intervals.

4.5.3 Effect of edge age on AGC

AGC stocks were significantly lower in intermediate (8-16 years) and old (16+ years) edges than in young (<8 years) edges, irrespective of matrix structure (Table 4.1; Figure 4.4). Post-hoc analysis confirmed that AGC was lower in both intermediate ($p < 0.001$) and old ($p < 0.01$) edges compared with young edges, but that there was no significant difference between intermediate and old edges (Tukey HSD test with Holm–Bonferroni correction for multiple comparisons; $p = 0.6$). On average, carbon stocks in edges over 8 years old were around 8 Mg C ha^{-1} lower than in edges under 8 years old. At high-contrast edges (adjacent matrix AGC = 3.2 Mg C ha^{-1}) over 8 years old, with average forest core AGC (core AGC = 98.3 Mg C ha^{-1}), this equates to a predicted 24% reduction in AGC at the edge relative to the forest core (average model-fitted edge AGC = 74.83 Mg C ha^{-1} when core AGC = 98.3 Mg C ha^{-1} and age >8). This is a considerably greater magnitude of edge effect than in edges under 8 years old, where model-fitted edge AGC is 16% lower than core AGC (fitted edge AGC = 82.63 Mg C ha^{-1} when core AGC = 98.3 Mg C ha^{-1} and age <8). Thus, we conclude that edge effects on AGC worsen over time, irrespective of matrix structure, and that most reductions in AGC occur within approximately 8 years following edge creation.

4.6 Discussion

Given the increasing fragmentation of tropical forests for agriculture, and the predicted increase in edge habitat throughout the tropics (Fischer et al., 2021), understanding the factors which affect carbon stocks in forest edges is increasingly important. Here, we found that the structure of the adjacent matrix habitat can have a large influence on AGC at forest edges, with the most severe AGC reductions found in edges bordering high-contrast matrices such as pasture. We also found that local variation in core forest AGC, probably driven by variation in disturbance history, mediates matrix impacts on AGC losses at edges, and that site-level differences in core AGC have a greater influence on edge forest AGC than matrix effects alone. Finally, we observed a negative effect of edge age on edge forest AGC, irrespective of adjacent matrix structure. The most severe AGC losses occurred within approximately eight years of edge creation, and there is evidence that AGC stocks in forest edges reach a post-disturbance equilibrium at lower levels than pre-fragmentation (no evidence of AGC recovery in edges over 16 years old; Table 4.1). These results improve our understanding of the drivers of edge effect variability, and have implications for the development of management strategies aimed at preserving carbon stocks in fragmented rainforests.

4.6.1 Matrix structure affects carbon at forest edges

We found that carbon stocks are highest in forest edges bordering low-contrast matrices. Carbon losses at the edge were estimated to be roughly doubled when forest bordered land-uses such as pasture, compared with land-uses characterized by taller, denser vegetation, such as mature palm trees or timber plantations, which provide a lower-contrast edge. Our results therefore provide the first empirical evidence that the structure of the adjacent matrix can mediate edge influence on forest carbon, as previous studies have suggested (Melito et al., 2018; Anderson et al., 2022). This aligns with studies showing more severe edge effects at high-contrast edges, with lower-contrast edges reportedly being more beneficial for bird and invertebrate communities in forest fragments (Campbell et al., 2011; Hatfield et al., 2020). Whilst this is the first study to directly quantify matrix impacts on forest AGC, a systematic review of edge effects on tropical forest biomass revealed that biomass loss is typically more severe at higher contrast edges (Melito et al., 2018), and Mesquita et al. (1999) showed that tree mortality is up to 110% greater in Amazonian forest edges bordering pasture compared to edges bordering regrowth forest. Thus, the mediating influence of matrix contrast on AGC loss at edges is likely to be present in other tropical study systems as well. This finding may help to explain some of the reported variability in edge influence (Laurance et al., 2007), and may help improve the general predictability of edge impacts across fragmented landscapes (Ries et al., 2017). Further studies should test for the generality of this relationship in other study systems.

Edge effects on forest carbon are primarily driven by abiotic gradients which increase the mortality of large trees (de Paula et al., 2011; Magnago et al., 2015; Anderson et al., 2022). Our finding that adjacent matrix structure affects forest edge AGC is therefore probably due to the increased buffering capacity of matrices with taller, denser vegetation, which likely limit wind speed and microclimatic changes at the forest edge (Harper et al., 2005). Increased vegetation height and density reduces air temperature and increases humidity in the matrix (Hardwick et al., 2015; Jucker, Hardwick, et al., 2018), whilst an increase in vegetation complexity diminishes wind speed adjacent to the forest (Davies-Colley et al., 2000). This is supported by the findings of Arroyo-Rodríguez et al. (2017), who report that edge effects only cause an increase in forest temperature when the adjacent matrix is high-contrast, and Permana et al. (2022), who found that increasing shade in the adjacent matrix (due to taller, denser vegetation) diminished edge influence on forest humidity, temperature and light intensity. Furthermore, increased canopy cover in a landscape can lessen the severity of drought-induced canopy desiccation, which is typically more severe at edges (Nunes et al., 2021), via its influence on local atmospheric circulation (Laurance et al., 2018). It is also possible that high-contrast edges facilitate increased access compared to low-contrast edges, which could contribute to the observed patterns (e.g. via increased selective logging or livestock browsing), though low-contrast land uses such as oil palm plantations typically contain high densities of workers, and encroachment is commonly observed in adjacent forest edges (Stride et al., 2018). We did not measure the influence of matrix structure on the penetration depth of edge effects, however it is possible that higher contrast edges may also suffer carbon losses over greater distances (Harper et al., 2005; Permana et al., 2022), and future studies could examine this relationship.

In this landscape, and throughout much of Southeast Asia, forest edges are typically bordered by low-contrast matrices such as oil palm and timber plantations. Whilst AGC loss is less severe in these sites, the modelled declines in AGC (average 10% reduction) are still considerable, particularly given that that a large proportion of the remaining forest area in this region is close to an edge (Zhu et al., 2023). Furthermore, carbon loss in low-contrast edges can be variable, with losses of up to 30% documented in some forest edges bordering mature oil palm plantations (Ordway and Asner, 2020; Anderson et al., 2022 (chapter 2)). This variability can be driven by a number of factors, such as local environmental conditions (Ordway and Asner, 2020), and our results suggest that local variation in ‘core’ forest AGC may also influence the magnitude, and relative importance, of these edge effects.

4.6.2 The importance of local core forest carbon

Whilst forest edge AGC is influenced by adjacent matrix structure, we found that edge AGC is more dependent on local core forest AGC. We observed a model-fitted increase of 0.6 Mg C ha^{-1} AGC at the edge for every increase of 1 Mg C ha^{-1} in the local forest core. Core forest AGC also explained most of the variation in edge carbon (adjusted R^2 = 59% with core AGC included *vs* 21% without). Thus, there is considerable local variation in forest carbon in this study landscape (Figure 4.3), and sites with higher AGC stocks in the forest core also tend to have higher AGC at the edge. This site-level variation in AGC may be related to variation in local climate, soil or tree community properties (Slik et al., 2010), however a large amount of the variation is likely driven by historic anthropogenic disturbance (Asner et al., 2018), and sites with lower AGC are therefore probably the most degraded, reflecting Sabah’s long history of commercial selective logging. Logged forests are a persistent carbon source (Mills et al., 2023) and typically contain at least 30-50% less AGC than intact forests, with these reductions persisting for decades (Berry et al., 2010; Asner et al., 2018; Nunes et al., 2022) due to the removal of large trees and associated degradation of topsoil, residual trees and recruitment (Pinard et al., 1996; Pillay et al., 2018; Riutta et al., 2021). The majority of remaining forest in Sabah is degraded due to commercial logging (Reynolds et al., 2011; Bryan et al., 2013; Gaveau et al., 2014). The high level of AGC heterogeneity we observed among sites is therefore probably linked to variability in historic exploitation, and these differences can be so large that they outweigh local fragmentation effects on trees (Stride et al., 2018; Fleiss et al., 2020; Anderson et al., 2022). Similar patterns have been observed in Atlantic forest remnants, where forest disturbance history plays a much greater role than fragmentation effects or environmental conditions in driving carbon stocks (Pyles et al., 2022).

Although high carbon sites (i.e. those with high levels of core AGC) had the highest AGC at edges, these edges also suffered the greatest carbon losses relative to the forest core, indicating that high carbon forests are the most vulnerable to edge effects. Furthermore, it appears that the effects of adjacent matrix structure and core forest AGC can act in tandem to mediate forest edge AGC. When adjacent to high-contrast matrix such as pasture, predicted carbon losses from edge effects were around 1.5 times greater in high-carbon sites than in those with average core AGC. This is probably because structural contrast at forest edges is dependent upon the structure of both the matrix and the forest itself (Harper et al., 2005), and forests with lower, sparser canopies (and thus, lower AGC (Chave et al., 2014; Jucker, Asner, et al., 2018)) tend to have microclimatic conditions more similar to non-forest areas (Hardwick et al., 2015; Jucker, Hardwick, et al., 2018), thereby reducing abiotic edge gradients (Harper et al., 2005). Other studies have reported similar results to those found here. Old-growth forests are more susceptible to biomass loss from wind disturbance than second-growth forests (Schwartz et al., 2017), and edge effects on canopy height growth are more pronounced in mature forests than in logged forests (Nunes et al., 2021). Furthermore, tropical moist forests, which tend to have denser vegetation, suffer greater carbon losses at edges than tropical dry forests (Chaplin-Kramer et al., 2015). Sites which have been more heavily exploited in the past probably also contain fewer large trees prior to fragmentation, as these would have been extracted during logging operations (Lindenmayer et al., 2012), therefore these sites may simply have had less AGC to lose.

4.6.3 Edge effects worsen over time

Carbon stocks in tropical forest edges are known to degrade over time (Ordway and Asner, 2020; Silva Junior et al., 2020), and we found a negative effect of edge age on forest edge AGC, irrespective of adjacent matrix structure (Table 4.1; Figure 4.4). We anticipated that the benefits of a low-contrast matrix would be more pronounced (i.e. a stronger effect of matrix AGC on edge forest AGC) in younger edges, when regrowth has not yet ‘sealed’ the forest edge (Camargo and Kapos, 1995; Murcia, 1995) and the buffering effect of a low-contrast matrix may therefore be most beneficial. However, we found no significant interaction between age effects and matrix effects, indicating that the impacts of matrix structure are consistent across age categories. We expect that this is probably due to the time delay between edge creation (i.e. forest clearance) and the subsequent planting and growth of vegetation in the adjacent matrix (Luskin and Potts, 2011; Gaveau et al., 2016), thereby offsetting the potential extra benefits of a low-contrast matrix in young edges. Given the limited availability of remotely-sensed data on AGC, our study only provides a single snapshot of matrix structure and forest edge carbon, limiting our ability to address this question. The increasing availability of high-resolution remotely-sensed data on forest carbon (Dubayah et al., 2020; Dubayah et al., 2022) may allow for future time-series studies to examine this further and elucidate potential interactions between age effects and matrix effects.

We found that carbon stocks were lowest in edges over eight years old, but that there was no difference in AGC between intermediate (8-16 years) and old (16+ years) edges. This indicates that most reductions in AGC occur within approximately 8 years following edge creation, but that AGC levels in older edges show no signs of recovery to pre-fragmentation levels. Our results correspond with research showing that AGC stocks at tropical forest edges reach a post-disturbance equilibrium within 6 - 15 years, with AGC levels consistently lower than core forest (Silva Junior et al., 2020). This equilibrium reflects the ongoing abiotic disturbance (e.g. wind penetration (D'Angelo et al., 2004) and fire (Cochrane, 2003)), high turnover rates (Qie et al., 2017), and time-lagged degradation of carbon stocks in standing dead trees near edges, which are only partly compensated by the increased growth of pioneer trees (Nascimento and Laurance, 2004). The localised loss of late-successional tree species, as well as the slow growth rates of large trees, likely also contributed to the persistent long-term depression of AGC we observed here. Unlike the edges in our study, carbon losses in some edges in this landscape do not stabilize until around 20 years post-edge creation (Ordway and Asner, 2020). Thus, there is considerable variability in the temporal dynamics of edge effects even within the same region. It is possible that replanting events in adjacent land-uses (e.g. oil palm plantations (Luskin and Potts, 2011)) may increase structural contrast at some older edge sites, thus contributing to this temporal variability and causing further AGC losses in some older edges, such as those studied by Ordway and Asner (2020). However, a lack of data on replanting events limits our capacity to study these effects. Temporal variability in AGC losses may also be driven by local variation in extreme weather events and natural disasters; significant temporal variability has been observed in Amazonian forest edges, where biomass recovery in some forest edges is hampered by frequent exposure to localised fires, whilst edges exposed to fire less frequently can recover biomass to pre-fragmentation levels in around two decades (Almeida et al., 2019; Silva Junior et al., 2020). Approximately one third of the sites we studied were under eight years old. Thus, carbon stocks may continue to degrade in these edges, with significant implications for the future integrity of these forest sites.

4.6.4 Management implications for fragmented tropical landscapes

We found that carbon losses at forest edges are roughly halved when the adjacent matrix is low-contrast (e.g. mature tree or palm plantations) rather than high-contrast (e.g. pasture). Management activities to reduce the structural contrast of land-uses bordering forest remnants may therefore help to protect forest carbon stocks in fragmented tropical landscapes. Increasing the amount of tree cover in the matrix, particularly near forest remnants, should help reduce AGC losses by dampening abiotic edge effects, and also has co-benefits for landscape connectivity and biodiversity (Arroyo-Rodríguez et al., 2020; Maeda et al., 2023). Where possible, the planting of perennial rather than annual crops in close proximity to forest edges is also preferable, although significant carbon losses still occur at these edges (Ordway and Asner, 2020; Anderson et al., 2022), therefore matrix management is likely to be beneficial in these land uses also. For example, permanently preserving mature crop strips directly adjacent to forest edges may be beneficial when crop replanting takes place. Alternatively, the planting of diverse agroforestry buffers adjacent to forest remnants in oil palm plantations, as previously recommended (Koh et al., 2009), may also buffer edge effects. Future studies should seek to determine the optimal width of these buffer zones for the protection of AGC stocks, as well as potential trade-offs with yield. In the absence of such data we suggest a buffer width of 100m, given that edge effects on AGC are typically strongest within this range (chapter 2). Staggered replanting regimes may also limit matrix contrast without reducing crop cover or net yield (Luskin and Potts, 2011). These approaches are also likely to have wider co-benefits unrelated to edge effects, such as the preservation of biodiversity within plantations, increased landscape connectivity, and a more consistent revenue stream over the rotational period (Luskin and Potts, 2011; Kurz et al., 2016; Ashton-Butt et al., 2019).

In addition to management activities aimed at reducing structural contrast of the adjacent matrix, our results also show that management targeted at protecting and promoting forest quality at a site level is necessary for the protection of carbon stocks. Carbon losses are most severe at the edge of high quality sites, which is particularly concerning given that forest fragmentation is increasing throughout the tropics (Fischer et al., 2021) and there are few large tracts of primary forest remaining (Hansen et al., 2020). Furthermore, oil palm plantations have been increasingly expanding into carbon-rich forests (Xu et al., 2022). The protection of primary forest sites from fragmentation is therefore critical. Management activities aimed at boosting site-level AGC, such as active forest restoration (Philipson et al., 2020), are likely to be beneficial for core forest which is not subject to edge influence. However, the benefits of restoration in highly fragmented forests may be limited by the ongoing abiotic disturbance near edges (Scriven et al., 2022), particularly if the aim is to restore communities of late-successional trees. Restoration success in fragmented forests may therefore be improved when combined with matrix management strategies to reduce edge contrast, thereby minimizing abiotic disturbance and facilitating the re-establishment of large and late-successional tree communities, and associated carbon stocks, near edges.

4.7 References

Almeida, D.R.A., Stark, Scott C, Schietti, Juliana, Camargo, Jose L C, Amazonas, Nino T, Gorgens, Eric B, … Silva, C A 2019. Persistent effects of fragmentation on tropical rainforest canopy structure after 20 yr of isolation. *Ecological Applications*. **29**(6), p.e01952.

Anderson, J.A., McClean, C.J., Sim, S., Pettorelli, N., Jelling, A., Tangah, J., & Hill, J.K. 2022. Weak edge effects on trees in Bornean rainforest remnants bordering oil palm. *Biotropica*. **54**(4), pp.921–932.

Arroyo-Rodríguez, V., Fahrig, L., Tabarelli, M., Watling, J.I., Tischendorf, L., Benchimol, M., … Tscharntke, T. 2020. Designing optimal human-modified landscapes for forest biodiversity conservation. *Ecology Letters*. **23**(9), pp.1404–1420.

Arroyo-Rodríguez, V., Saldaña-Vázquez, R.A., Fahrig, L., & Santos, B.A. 2017. Does forest fragmentation cause an increase in forest temperature? *Ecological Research*. **32**(1), pp.81–88.

Ashton-Butt, A., Willcock, S., Purnomo, D., Suhardi, Aryawan, A.A.K., Wahyuningsih, R., … Snaddon, J.L. 2019. Replanting of first-cycle oil palm results in a second wave of biodiversity loss. *Ecology and Evolution*. **9**(11), ece3.5218.

Asner, G.P., Brodrick, P.G., Philipson, C., Vaughn, N.R., Martin, R.E., Knapp, D.E., … Coomes, D.A. 2018. Mapped aboveground carbon stocks to advance forest conservation and recovery in Malaysian Borneo. *Biological Conservation*. **217**, pp.289–310.

Barlow, J., Lennox, G.D., Ferreira, J., Berenguer, E., Lees, A.C., Nally, R. Mac, … Gardner, T.A. 2016. Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. *Nature*. **535**(7610), pp.144–147.

Berenguer, E., Ferreira, J., Gardner, T.A., Aragão, L.E.O.C., De Camargo, P.B., Cerri, C.E., … Barlow, J. 2014. A large-scale field assessment of carbon stocks in human-modified tropical forests. *Global Change Biology*. **20**(12), pp.3713–3726.

Berry, N.J., Phillips, O.L., Lewis, S.L., Hill, J.K., Edwards, D.P., Tawatao, N.B., … Hamer, K.C. 2010. The high value of logged tropical forests: Lessons from northern Borneo. *Biodiversity and Conservation*. **19**(4), pp.985–997.

Briant, G., Gond, V., & Laurance, S.G.W. 2010. Habitat fragmentation and the desiccation of forest canopies: A case study from eastern Amazonia. *Biological Conservation*. **143**(11), pp.2763–2769.

Brinck, K., Fischer, R., Groeneveld, J., Lehmann, S., Dantas De Paula, M., Pütz, S., … Huth, A. 2017. High resolution analysis of tropical forest fragmentation and its impact on the global carbon cycle. *Nature Communications*. **8**(Article no:14855).

Bryan, J.E., Shearman, P.L., Asner, G.P., Knapp, D.E., Aoro, G., & Lokes, B. 2013. Extreme Differences in Forest Degradation in Borneo: Comparing Practices in Sarawak, Sabah, and Brunei. *PLOS ONE*. **8**(7), p.e69679.

Camargo, J.L., & Kapos, V. 1995. Complex edge effects on soil moisture and microclimate in central Amazonian forest. *Journal of Tropical Ecology*. **11**(2), pp.205–221.

Campbell, R.E., Harding, J.S., Ewers, R.M., Thorpe, S., & Didham, R.K. 2011. Production land use alters edge response functions in remnant forest invertebrate communities. *Ecological Applications*. **21**(8), pp.3147–3161.

Chaplin-Kramer, R., Ramler, I., Sharp, R., Haddad, N.M., Gerber, J.S., West, P.C., … King, H. 2015. Degradation in carbon stocks near tropical forest edges. *Nature Communications*. **6**(Article no: 10158).

Chapman, S., Syktus, J., Trancoso, R., Salazar, A., Thatcher, M., Watson, J.E.M., … Mcalpine, C.A. 2020. Compounding impact of deforestation on Borneo's climate during El Niño events. *Environmental Research Letters*. **15**(8), p.084006.

Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M.S., Delitti, W.B.C., … Vieilledent, G. 2014. Improved allometric models to estimate the aboveground biomass of tropical trees. *Global Change Biology*. **20**(10), pp.3177–3190.

Cochrane, M.A. 2003. Fire science for rainforests. *Nature 2003 421:6926*. **421**(6926), pp.913–919.

Curtis, P.G., Slay, C.M., Harris, N.L., Tyukavina, A., & Hansen, M.C. 2018. Classifying drivers of global forest loss. *Science*. **361**(6407), pp.1108–1111.

D'Angelo, S.A., Andrade, A.C.S., Laurance, S.G., Laurance, W.F., & Mesquita, R.C.G. 2004. Inferred causes of tree mortality in fragmented and intact Amazonian forests. *Journal of Tropical Ecology*. **20**, pp.243–246.

Davies-Colley, R.J., Payne, G.W., & Elswijk, M. van 2000. Microclimate gradients across a forest edge. *New Zealand Journal of Ecology*. **24**(2), pp.111–121.

Driscoll, D.A., Banks, S.C., Barton, P.S., Lindenmayer, D.B., & Smith, A.L. 2013. Conceptual domain of the matrix in fragmented landscapes. *Trends in Ecology and Evolution*. **28**(10), pp.605–613.

Dubayah, R., Armston, J., Healey, S.P., Bruening, J.M., Patterson, P.L., Kellner, J.R., … Luthcke, S. 2022. GEDI launches a new era of biomass inference from space. *Environmental Research Letters*. **17**(9), p.095001.

Dubayah, R., Blair, J.B., Goetz, S., Fatoyinbo, L., Hansen, M., Healey, S., … Silva, C. 2020. The Global Ecosystem Dynamics Investigation: High-resolution laser ranging of the Earth's forests and topography. *Science of Remote Sensing*. **1**, p.100002.

Fischer, R., Taubert, F., Müller, M.S., Groeneveld, J., Lehmann, S., Wiegand, T., & Huth, A. 2021. Accelerated forest fragmentation leads to critical increase in tropical forest edge area. *Science Advances*. **7**(37).

Fleiss, S., Waddell, E.H., Bala Ola, B., Banin, L.F., Benedick, S., Bin Sailim, A., … Hill, J.K. 2020. Conservation set-asides improve carbon storage and support associated plant diversity in certified sustainable oil palm plantations. *Biological Conservation*. **248**(Article no: 108631).

Gaveau, D.L.A., Locatelli, B., Salim, M.A., Yaen, H., Pacheco, P., & Sheil, D. 2019. Rise and fall of forest loss and industrial plantations in Borneo (2000–2017). *Conservation Letters*. **12**(3), p.e12622.

Gaveau, D.L.A., Sheil, D., Husnayaen, Salim, M.A., Arjasakusuma, S., Ancrenaz, M., … Meijaard, E. 2016. Rapid conversions and avoided deforestation: examining four decades of industrial plantation expansion in Borneo. *Scientific Reports*. **6**(Article no: 32017).

Gaveau, D.L.A., Sloan, S., Molidena, E., Yaen, H., Sheil, D., Abram, N.K., … Meijaard, E. 2014. Four Decades of Forest Persistence, Clearance and Logging on Borneo. *PLoS One*. **9**(7), p.e101654.

Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., … Townshend, J.R. 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances*. **1**(2).

Hansen, M.C., Potapov, P. V, Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., … Townshend, J.R.G. 2013. High-resolution global maps of 21st-century forest cover change. *Science (New York, N.Y.)*. **342**(6160), pp.850–3.

Hansen, M.C., Wang, L., Song, X.P., Tyukavina, A., Turubanova, S., Potapov, P. V., & Stehman, S. V. 2020. The fate of tropical forest fragments. *Science Advances*. **6**(11), pp.8574–8585.

Hardwick, S.R., Toumi, R., Pfeifer, M., Turner, E.C., Nilus, R., & Ewers, R.M. 2015. The relationship between leaf area index and microclimate in tropical forest and oil palm plantation: Forest disturbance drives changes in microclimate. *Agricultural and Forest Meteorology*. **201**, pp.187–195.

Harper, K.A., Macdonald, S.E., Burton, P.J., Chen, J., Brosofske, K.D., Saunders, S.C., … Esseen, P.A. 2005. Edge Influence on Forest Structure and Composition in Fragmented Landscapes. *Conservation Biology*. **19**(3), pp.768–782.

Hatfield, J.H., Barlow, J., Joly, C.A., Lees, A.C., Parruco, C.H. de F., Tobias, J.A., … Banks-Leite, C. 2020. Mediation of area and edge effects in forest fragments by adjacent land use. *Conservation Biology*. **34**(2), pp.395–404.

Jucker, T., Asner, G.P., Dalponte, M., Brodrick, P.G., Philipson, C.D., Vaughn, N.R., … Coomes, D.A. 2018. Estimating aboveground carbon density and its uncertainty in Borneo's structurally complex tropical forests using airborne laser scanning. *Biogeosciences*. **15**(12), pp.3811–3830.

Jucker, T., Hardwick, S.R., Both, S., Elias, D.M.O., Ewers, R.M., Milodowski, D.T., … Coomes, D.A. 2018. Canopy structure and topography jointly constrain the microclimate of human-modified tropical landscapes. *Global Change Biology*. **24**(11), pp.5243–5258.

Koh, L.P., Levang, P., & Ghazoul, J. 2009. Designer landscapes for sustainable biofuels. *Trends in Ecology & Evolution*. **24**(8), pp.431–438.

Kurz, D.J., Turner, E.C., Aryawan, A.A., Barkley, H.C., Caliman, J.-P., Konopik, O., … Foster, W.A. 2016. Replanting reduces frog diversity in oil palm. *Biotropica*. **48**(4), pp.483–490.

Lapola, D.M., Pinho, P., Barlow, J., Aragão, L.E.O.C., Berenguer, E., Carmenta, R., … Walker, W.S. 2023. The drivers and impacts of Amazon forest degradation. *Science*. **379**(6630).

Laurance, W.F., Camargo, J.L.C., Fearnside, P.M., Lovejoy, T.E., Williamson, G.B., Mesquita, R.C.G., … Laurance, S.G.W. 2018. An Amazonian rainforest and its fragments as a laboratory of global change. *Biological Reviews*. **93**(1), pp.223–247.

Laurance, W.F., Camargo, J.L.C., Luizão, R.C.C., Laurance, S.G., Pimm, S.L., Bruna, E.M., … Lovejoy, T.E. 2011. The fate of Amazonian forest fragments: A 32-year investigation. *Biological Conservation*. **144**(1), pp.56–67.

Laurance, W.F., & Curran, T.J. 2008. Impacts of wind disturbance on fragmented tropical forests: A review and synthesis. *Austral Ecology*. **33**(4), pp.399–408.

Laurance, W.F., Delamônica, P., Laurance, S.G., Vasconcelos, H.L., & Lovejoy, T.E. 2000. Rainforest fragmentation kills big trees. *Nature*. **404**, p.836.

Laurance, W.F., Lovejoy, T.E., Vasconcelos, H.L., Bruna, E.M., Didham, R.K., Stouffer, P.C., … Sampaio, E. 2002. Ecosystem decay of Amazonian forest fragments: a 22-year investigation. *Conservation Biology*. **16**(3), pp.605–618.

Laurance, W.F., Nascimento, H.E.M., Laurance, S.G., Andrade, A., Ewers, R.M., Harms, K.E., … Ribeiro, J.E. 2007. Habitat fragmentation, variable edge effects, and the landscape-divergence hypothesis. *PLoS ONE*. **2**(10), p.e1017.

Lewis, S.L., Edwards, D.P., & Galbraith, D. 2015. Increasing human dominance of tropical forests. *Science*. **349**(6250), pp.827–32.

Lindenmayer, D.B., Laurance, W.F., & Franklin, J.F. 2012. Global decline in large old trees. *Science*. **338**(6112), pp.1305–1306.

Luskin, M.S., & Potts, M.D. 2011. Microclimate and habitat heterogeneity through the oil palm lifecycle. *Basic and Applied Ecology*. **12**(6), pp.540–551.

Maeda, E.E., Aragão, L.E.O.C., Baker, J.C.A., Balbino, L.C., de Moura, Y.M., Nobre, A.D., … dos Reis, J.C. 2023. Land use still matters after deforestation. *Communications Earth & Environment 2023 4:1*. **4**(1), pp.1–4.

Magnago, L.F.S., Rocha, M.F., Meyer, L., Martins, S.V., & Meira-Neto, J.A.A. 2015. Microclimatic conditions at forest edges have significant impacts on vegetation structure in large Atlantic forest fragments. *Biodiversity and Conservation*. **24**(9), pp.2305–2318.

Mahmood, R., Pielke, R.A., Hubbard, K.G., Niyogi, D., Dirmeyer, P.A., Mcalpine, C., … Fall, S. 2014. Land cover changes and their biogeophysical effects on climate. *International Journal of*

Climatology. **34**(4), pp.929–953.

Malcolm, J.R., Valenta, K., & Lehman, S.M. 2017. Edge effects in tropical dry forests of Madagascar: additivity or synergy? *Landscape Ecology*. **32**(2), pp.327–341.

Malhi, Y., Gardner, T.A., Goldsmith, G.R., Silman, M.R., & Zelazowski, P. 2014. Tropical forests in the anthropocene. *Annual Review of Environment and Resources*. **39**, pp.125–159.

Marín-Spiotta, E., Ostertag, R., & Silver, W.L. 2007. Long-term patterns in tropical reforestation: Plant community composition and aboveground biomass accumulation. *Ecological Applications*. **17**(3), pp.828–839.

Matricardi, E.A.T., Skole, D.L., Costa, O.B., Pedlowski, M.A., Samek, J.H., & Miguel, E.P. 2020. Long-term forest degradation surpasses deforestation in the Brazilian Amazon. *Science*. **369**(6509), pp.1378–1382.

Maxwell, S.L., Evans, T., Watson, J.E.M., Morel, A., Grantham, H., Duncan, A., … Malhi, Y. 2019. Degradation and forgone removals increase the carbon impact of intact forest loss by 626%. *Science Advances*. **5**(10).

McMorrow, J., & Talip, M.A. 2001. Decline of forest area in Sabah, Malaysia: Relationship to state policies, land code and land capability. *Global Environmental Change*. **11**(3), pp.217–230.

Melito, M., Metzger, J.P., & de Oliveira, A.A. 2018. Landscape-level effects on aboveground biomass of tropical forests: A conceptual framework. *Global Change Biology*. **24**(2), pp.597–607.

Mesquita, R.C.G., Delamônica, P., & Laurance, W.F. 1999. Effect of surrounding vegetation on edge-related tree mortality in Amazonian forest fragments. *Biological Conservation*. **91**(2–3), pp.129–134.

Mills, M.B., Malhi, Y., Ewers, R.M., Kho, L.K., Teh, Y.A., Both, S., … Riutta, T. 2023. Tropical forests post-logging are a persistent net carbon source to the atmosphere. *Proceedings of the National Academy of Sciences of the United States of America*. **120**(3), p.e2214462120.

Ministry of Agriculture and Fisheries 2017. *Third Sabah Agricultural Policy (SAP3)* [Online]. [Accessed 15 March 2023]. Available from: https://skn.sabah.gov.my/dokumen/dasar/sabah-agricultural-policy.pdf.

Mitchard, E.T.A. 2018. The tropical forest carbon cycle and climate change. *Nature*. **559**(7715), pp.527–534.

Murcia, C. 1995. Edge effects in fragmented forests: implications for conservation. *Trends in Ecology & Evolution*. **10**(2), pp.58–62.

Nascimento, H.E.M., & Laurance, W.F. 2004. Biomass dynamics in amazonian forest fragments. *Ecological Applications*. **14**(4 SUPPL.).

Newbold, T., Hudson, L.N., Hill, S.L.L., Contu, S., Lysenko, I., Senior, R.A., … Purvis, A. 2015. Global effects of land use on local terrestrial biodiversity. *Nature*. **520**(7545), pp.45–50.

Nunes, C.A., Berenguer, E., França, F., Ferreira, J., Lees, A.C., Louzada, J., … Barlow, J. 2022. Linking land-use and land-cover transitions to their ecological impact in the Amazon. *Proceedings of the National Academy of Sciences of the United States of America*. **119**(27), p.e2202310119.

Nunes, M.H., Jucker, T., Riutta, T., Svátek, M., Kvasnica, J., Rejžek, M., … Coomes, D.A. 2021. Recovery of logged forest fragments in a human-modified tropical landscape during the 2015-16 El Niño. *Nature Communications*. **12**(Article no: 1526).

Ordway, E.M., & Asner, G.P. 2020. Carbon declines along tropical forest edges correspond to heterogeneous effects on canopy structure and function. *Proceedings of the National Academy of Sciences of the United States of America*. **117**(14), pp.7863–7870.

de Paula, M.D., Costa, C.P.A., & Tabarelli, M. 2011. Carbon storage in a fragmented landscape of Atlantic forest: the role played by edge-affected habitats and emergent trees. *Tropical Conservation Science*. **4**(3), pp.349–358.

Permana, G., Marliana, S.N., Susandarini, R., & Addaha, H. 2022. Sustaining rainforest remnants in plantation landscapes: degree of oil palm stand-induced edge effects on forest microclimate and regeneration. *CERNE*. **28**(1).

Pfeifer, M., Lefebvre, V., Peres, C.A., Banks-Leite, C., Wearn, O.R., Marsh, C.J., … Ewers, R.M. 2017. Creation of forest edges has a global impact on forest vertebrates. *Nature*. **551**, pp.187–191.

Philipson, C.D., Cutler, M.E.J., Brodrick, P.G., Asner, G.P., Boyd, D.S., Costa, P.M., … Burslem, D.F.R.P. 2020. Active restoration accelerates the carbon recovery of human-modified tropical forests. *Science*. **369**(6505), pp.838–841.

Pillay, R., Hua, F., Loiselle, B.A., Bernard, H., & Fletcher, R.J. 2018. Multiple stages of tree seedling recruitment are altered in tropical forests degraded by selective logging. *Ecology and Evolution*. **8**(16), pp.8231–8242.

Pinard, M., Howlett, B., & Davidson, D. 1996. Site Conditions Limit Pioneer Tree Recruitment After

Logging of Dipterocarp Forests in Sabah, Malaysia. *Biotropica*. **28**(1), p.2.

Pyles, M.V., Silva Magnago, L.F., Maia, V.A., Pinho, B.X., Pitta, G., de Gasper, A.L., … Lima, R.A.F. 2022. Human impacts as the main driver of tropical forest carbon. *Science Advances*. **8**(24), p.7968.

Qie, L., Lewis, S.L., Sullivan, M.J.P., Lopez-Gonzalez, G., Pickavance, G.C., Sunderland, T., … Phillips, O.L. 2017. Long-term carbon sink in Borneo's forests halted by drought and vulnerable to edge effects. *Nature Communications*. **8**(Article no: 1966).

R Core Team 2022. R: A language and environment for statistical computing.

Reynolds, G., Payne, J., Sinun, W., Mosigil, G., & Walsh, R.P.D. 2011. Changes in forest land use and management in Sabah, Malaysian Borneo, 1990-2010, with a focus on the Danum Valley region. *Philosophical Transactions of the Royal Society B: Biological Sciences*. **366**(1582), pp.3168–3176.

Ries, L., Murphy, S.M., Wimp, G.M., & Fletcher, R.J. 2017. Closing persistent gaps in knowledge about edge ecology. *Current Landscape Ecology Reports*. **2**, pp.30–41.

Riutta, T., Kho, L.K., Teh, Y.A., Ewers, R., Majalap, N., & Malhi, Y. 2021. Major and persistent shifts in below-ground carbon dynamics and soil respiration following logging in tropical forests. *Global Change Biology*. **27**(10), pp.2225–2240.

Santos-Barrera, G., & Urbina-Cardona, J.N. 2011. The role of the matrix-edge dynamics of amphibian conservation in tropical montane fragmented landscapes. *Revista mexicana de biodiversidad*. **82**(2), pp.679–687.

Schwartz, N.B., Uriarte, M., Defries, R., Bedka, K.M., Fernandes, K., Gutiérrez-Vélez, V., & Pinedo-Vasquez, M.A. 2017. Fragmentation increases wind disturbance impacts on forest structure and carbon stocks in a western Amazonian landscape. *Ecological Applications*. **27**(6), pp.1901–1915.

Scriven, S.A., Waddell, E.H., Sim, S., King, H., Reynolds, G., Yeong, K.L., & Hill, J.K. 2022. Supporting decision-making by companies in delivering their climate net-zero and nature recovery commitments: Synthesising current information and identifying research priorities in rainforest restoration. *Global Ecology and Conservation*. **40**, p.e02305.

Silva Junior, C.H.L., Aragão, L.E.O.C., Anderson, L.O., Fonseca, M.G., Shimabukuro, Y.E., Vancutsem, C., … Saatchi, S.S. 2020. Persistent collapse of biomass in Amazonian forest edges following deforestation leads to unaccounted carbon losses. *Science Advances*. **6**(40), p.eaaz8360.

Silvério, D. V., Brando, P.M., Bustamante, M.M.C., Putz, F.E., Marra, D.M., Levick, S.R., & Trumbore, S.E. 2019. Fire, fragmentation, and windstorms: A recipe for tropical forest degradation. *Journal of Ecology*. **107**(2), pp.656–667.

Slik, J.W.F., Aiba, S.I., Brearley, F.Q., Cannon, C.H., Forshed, O., Kitayama, K., … van Valkenburg, J.L.C.H. 2010. Environmental correlates of tree biomass, basal area, wood specific gravity and stem density gradients in Borneo's tropical forests. *Global Ecology and Biogeography*. **19**(1), pp.50–60.

Slik, J.W.F., Paoli, G., Mcguire, K., Amaral, I., Barroso, J., Bastian, M., … Zweifel, N. 2013. Large trees drive forest aboveground biomass variation in moist lowland forests across the tropics. *Global Ecology and Biogeography*. **22**(12), pp.1261–1271.

Stride, G., Thomas, C.D., Benedick, S., Hodgson, J.A., Jelling, A., Senior, M.J.M., & Hill, J.K. 2018. Contrasting patterns of local richness of seedlings, saplings, and trees may have implications for regeneration in rainforest remnants. *Biotropica*. **50**(6), pp.889–897.

Taubert, F., Fischer, R., Groeneveld, J., Lehmann, S., Müller, M.S., Rödig, E., … Huth, A. 2018. Global patterns of tropical forest fragmentation. *Nature*. **554**, pp.519–522.

Thomas, R., Lello, J., Medeiros, R., Pollard, A., Robinson, P., Seward, A., … Vaughan, I. 2017. *Data analysis with R statistical software*.

Tyukavina, A., Baccini, A., Hansen, M.C., Potapov, P. V., Stehman, S. V., Houghton, R.A., … Goetz, S.J. 2015. Aboveground carbon loss in natural and managed tropical forests from 2000 to 2012. *Environmental Research Letters*. **10**(7), p.074002.

Xu, Y., Yu, L., Ciais, P., Li, W., Santoro, M., Yang, H., & Gong, P. 2022. Recent expansion of oil palm plantations into carbon-rich forests. *Nature Sustainability 2022 5:7*. **5**(7), pp.574–577.

Zhu, L., Li, W., Ciais, P., He, J., Cescatti, A., Santoro, M., … Wang, J. 2023. Comparable biophysical and biogeochemical feedbacks on warming from tropical moist forest degradation. *Nature Geoscience 2023 16:3*. **16**(3), pp.244–249.

Chapter 5 - **General Discussion**

Emergent tree in a lowland dipterocarp rainforest

5.1 Summary of thesis findings

The main aims of my thesis were to (1) investigate the impacts of edge creation on forest trees and carbon stocks in oil palm landscapes, in order to better understand the environmental impacts of oil palm agriculture, and (2) provide new information on the drivers of edge effect variability in order to inform management strategies to ameliorate detrimental edge impacts. I used field data collected in Sabah, Malaysian Borneo, to quantify edge effects on forest structure, above ground carbon (AGC) stocks, microclimate and tree community composition and richness, in forest edges bordering mature oil palm plantations. I found that deleterious edge effects on large trees caused a significant reduction in AGC near edges, but that edge influence was relatively weak overall; there were no effects on most variables I studied and a large amount of variation in forest structure and AGC was not explained by edge proximity. I used remotely-sensed data to examine the influence of multiple edges on forest AGC in Sabah. I determined that proximity to multiple edges causes a substantial reduction in AGC, and that a metric which accounts for multiple edges explains more variation in AGC in fragmented forests than a metric which only accounts for distance to the nearest edge. Finally, I used remotely-sensed data to investigate the impact of the adjacent non-forest matrix structure on AGC at forest edges. I found that carbon stocks were lower in edges bordering high-contrast matrices (e.g. pasture) than in edges bordering low-contrast matrices (e.g. mature palm and tree plantations), and that edge age and local core forest AGC also mediate AGC losses at edges. In this final discussion chapter, I summarise the key findings of each chapter in relation to their main objectives, discuss the contribution of my results for understanding trends, mechanisms and variability of rainforest edge effects, and draw conclusions about the relative importance of edge effects in Sabah's fragmented forests. I also discuss the wider implications of my research for conservation and management in oil palm landscapes, and for understanding AGC dynamics in fragmented tropical forests more generally. Finally, I offer suggestions for future research and put forward my final conclusions.

Chapter 2: Weak edge effects on trees in Bornean rainforest remnants bordering oil palm

Main objectives:

(1) Quantify the influence of edge proximity on forest structure (canopy density, number and size of stems ≥10 cm diameter), microclimate (air temperature and light intensity) and AGC stocks in 0.2 ha plots placed at increasing distances from forest edges bordering mature oil palm plantations, in 10 lowland rainforest remnants in Sabah (57 plots in total)

(2) In the same 10 sites, quantify the influence of edge proximity on the composition (taxonomic and functional) and diversity (taxonomic) of forest tree communities, both at a plot level and across sites

In this chapter, I investigated local plot-scale changes in forest structure, microclimate, tree communities and AGC stocks in forests bordering mature oil palm plantations. I established that forest remnants in Sabah are highly heterogeneous, particularly in terms of their local AGC stocks, tree genus richness, and community composition. I found that edge proximity caused a significant reduction in maximum tree size, with the trunks of the largest trees up to 21% thinner and 26% shorter near edges, and that this loss of large trees caused a reduction in plot-level AGC of up to 30% (30% reduction at 50m from edge), with most effects occurring within approximately 300m of edges. However, there was no effect of edge proximity on most of the components of forest structure that I measured (i.e. canopy density, stem number, average stem size), and only a weak effect on microclimate. There was also no evidence of a reduction in plot-level tree diversity (genus richness) near edges, or of the loss of any genera at edges, and edge communities were neither taxonomically nor functionally distinct from forest interior communities. Furthermore, the significant edge effects I observed on forest structure and AGC were relatively weak in the context of existing AGC variation, with distance-from-edge explaining <13% of the total variability in maximum tree size or carbon. I conclude that these relatively weak edge effects probably reflect low structural contrast between forest and mature oil palm, as well as limited invasion of pioneer trees from plantations, combined with the high heterogeneity of forest remnants. The highlights of this chapter are as follows:

- In forest adjacent to oil palm, edge effects on large trees cause AGC loss (30% AGC reduction at 50m from edge, losses occur up to 300m from edge)
- Overall, edge effects are relatively weak (no effects on mature tree composition or diversity, large amount of unexplained AGC variation)
- Mature palms may buffer forest edges, and dipterocarp forests appear to be resilient to fragmentation effects

Chapter 3: Proximity to multiple edges reduces carbon stocks in fragmented tropical rainforests

Main objectives:

(1) Develop a metric of forest ‘edginess’, which accounts for both the amount and proximity of nearby edges, and use the metric to map edginess throughout Sabah’s fragmented forests

(2) Quantify reductions in AGC in forest areas which are influenced by multiple edges, using the information on edginess in combination with remotely-sensed data on AGC
(3) Test whether the metric of edginess explains more variation in AGC than the more commonly used measure of ‘distance to nearest edge’

In chapter 2, I found a significant reduction in AGC at forest edges bordering oil palm plantations, but observed that overall edge effects were fairly weak. I explored these findings in more detail by examining whether edge AGC was lower in forests that were close to multiple edges, where tree communities are likely to be exposed to increased levels of abiotic disturbance. I also tested whether a metric that accounts for effects from multiple edges explains more variation in edge-affected features such as AGC. I produced a map of natural forest cover for Sabah, and applied a heat-diffusion model to generate a state-wide map of forest edginess, integrating both the proximity and number of nearby edges. From my edginess map, I estimated that almost half of Sabah’s remaining forest area is likely edge-affected, with approximately a quarter of this edge-affected forest influenced by multiple edges. I quantified the relationship between edginess and AGC for a stratified sample of 600,000 forest pixels, and found that AGC was significantly lower in proximity to multiple edges. Specifically, model-fitted AGC was 23% lower in the edgiest forest areas than in forest adjacent to a single edge, and over 60% lower than in the forest core. Furthermore, a model of AGC using my edginess metric was superior to a model which used ‘distance to nearest edge’, though a considerable amount of unexplained AGC variation still remained. I conclude that proximity to multiple edges greatly reduces forest AGC, probably because of increased abiotic disturbance within the forest, therefore forest reserves should be designed to minimize edge:area ratios. I also conclude that accounting for multiple edges is important for understanding how edge effects impact AGC, and that ignoring the impacts of multiple edges may lead to an underestimation of carbon emissions from forest fragmentation. The highlights of this chapter are as follows:

- Forest AGC is lower in proximity to multiple edges (AGC 23% lower near multiple edges *vs* single edge, and 60% lower than core forest)
- A metric which accounts for multiple edges explains more AGC variation than a ‘distance to nearest edge’ metric (R^2 = 18% *vs* 15% within 1km of edge, 11% *vs* 1.5% within 100m)
- Accounting for multiple edges is key for accurate estimates of edge-related carbon emissions
- Reserve designs should account for multiple edge effects, to preserve AGC

Chapter 4: Carbon stocks at rainforest edges are mediated by adjacent habitat structure

Main objectives:

1. Examine how structure of the adjacent land-use matrix (i.e. structural contrast with the forest) influences AGC at forest edges throughout Sabah, using remotely-sensed data on AGC
2. Determine the influence of edge age on forest edge AGC, and whether the effects of matrix contrast are mediated by the age of the edge as well as local core forest AGC

In this chapter, I analysed the remotely-sensed data which I used in chapter 3, in order to examine additional factors which may mediate edge effects on AGC. I focused on the influence of the vegetation structure of adjacent matrix, and studied 902 forest edge sites throughout Sabah. These sites bordered a variety of matrix types including mature palm and tree plantations (low-contrast edges), and pasture and annual crops (high-contrast edges). I demonstrated that edge effects on AGC were most severe at high-contrast edges, with an average model-fitted loss of 21% AGC in high-contrast edges compared to losses of 10% in low-contrast edges. I also found that AGC in edges declines over time irrespective of matrix structure, primarily within around 8 years following edge creation, and shows no sign of recovery in older edges. Whilst adjacent matrix structure was an important determinant of edge carbon (mean forest AGC within 120m of edge), I found that the amount of carbon in the nearby forest core has a greater impact. Low-carbon forest sites tended to have the lowest carbon stocks at edges, but high-carbon sites suffered the greatest proportional carbon losses, with around 1.5 times more AGC lost at edges of high-carbon sites compared to average-carbon sites. I conclude that the most severe AGC losses are predicted to occur at sites with high forest core AGC bordering high-contrast matrices. Management activities to reduce edge contrast, such as the creation of matrix buffer habitats, may be important to protect carbon stocks in fragmented agricultural landscapes. The highlights of this chapter are as follows:

- AGC loss at forest edges is mediated by adjacent land-use structure
- High-contrast edges have double AGC loss of low-contrast edges (21% *vs* 10% loss)
- Edge AGC declines over time, but stabilises within eight years of edge creation
- High-carbon forests suffer the greatest AGC losses at edges (1.5 times greater loss than average-carbon forests)
- Management strategies to buffer edge contrast may preserve forest edge AGC

5.2 Edge effect trends and causes of variability

Edge effects on forest carbon

Throughout this thesis I examined edge effects on trees and AGC in fragmented tropical rainforests, as well as factors which mediate these effects. Until recently, there have been relatively few studies which quantify AGC losses at rainforest edges, therefore the ubiquity of edge effects on AGC has been questioned (Melito et al., 2018). Indeed, studies in some tropical systems have found no evidence of AGC losses near edges (Phillips et al., 2006; Schedlbauer et al., 2007; Numata et al., 2017), whilst others have found considerable variation in AGC declines (Melito et al., 2018). In chapter 2, I conducted the first field assessment of edge effects on forest trees and AGC stocks in an oil palm landscape, and found evidence of AGC losses of up to 30% in edges bordering oil palm plantations (30% reduction at 50m from edge), with most effects occurring within 300m of the edge. These losses were primarily driven by edge effects on large trees, which are known to be highly sensitive to abiotic disturbances near edges (Laurance et al., 2000; de Paula et al., 2011). The magnitude and depth of this AGC loss is broadly consistent with the effects reported in other tropical studies; AGC generally appears to decline by between 10% - 50%, with the greatest effects observed within 100m - 500m from edges (Laurance et al., 1997; de Paula et al., 2011; Chaplin-Kramer, Ramler, et al., 2015 a; Ordway and Asner, 2020; Silva Junior et al., 2020; Zhao et al., 2021), although losses of up to 70% can sometimes occur (Magnago et al., 2017). Thus, it appears that AGC losses at tropical forest edges are common across many tropical study systems, even if the exact size of the effect is variable. My results provide the first field evidence of AGC losses at edges in an oil palm landscape, indicating that edge effects are a significant source of carbon emissions in these tropical agricultural landscapes. Around 30% of the remaining tropical forest area is within 100m of an edge (Fischer et al., 2021). Within this approximate distance, I observed an average reduction in AGC of around 10% relative to the forest core (chapter 4). If the trends observed here are representative of edge effects throughout the tropics, this suggests that edge effects have caused a reduction of at least 3% of total pantropical forest AGC (30% of forest experiencing 10% AGC loss). The actual amount of AGC lost is likely to be even greater, given that AGC is further reduced in proximity to multiple edges (chapter 3) and high-contrast land-uses (chapter 4), and reductions can occur at scales greater than 100m (e.g. 300m effect observed in chapter 2). However, even a loss of 3% throughout the tropics poses an important challenge for the conservation of global forest carbon.

Edge effects are notoriously variable in strength and depth, which has often limited our capacity to make large-scale predictions about their impacts (Ries et al., 2004; Laurance et al., 2007; Ries et al., 2017). My research provides valuable information on the drivers of variability in AGC losses at edges, thereby improving our understanding of AGC dynamics in fragmented forests throughout the tropics and improving our conceptual understanding of edge processes. In chapters 3 and 4, I demonstrated that edge effects on AGC (and thus, the underlying tree communities) are mediated by proximity to multiple edges, and by structural contrast with the adjacent matrix. I found that AGC losses rose to over 60% in forest areas close to multiple edges (chapter 3), and that high-contrast edges (e.g. bordering pasture) lost twice as much carbon (21% loss vs 10% loss) as low-contrast edges (e.g. bordering mature palms or trees; chapter 4). Though increased severity of edge effects has been observed on a variety of taxa in proximity to multiple edges (Porensky and Young, 2013; Laurance et al., 2018) and in edges adjacent to high-contrast matrices (Mesquita et al., 1999; Campbell et al., 2011; Hatfield et al., 2020), different taxa often respond to disturbances in distinct ways (Harper et al., 2005), and my findings are the first time that these patterns have been documented in AGC (and thus, in mature trees). Given that edge effects on trees are largely driven by abiotic gradients (Harper et al., 2005; Magnago et al. 2015 a; Magnago et al., 2017), greater AGC losses near multiple edges and high-contrast matrices are probably due to strengthened abiotic disturbances. Indeed, wind disturbance is typically greatest in forest areas close to multiple edges (Laurance and Curran, 2008; Schwartz et al., 2017), and modelling studies have demonstrated that edgier forest areas are likely exposed to higher temperatures and more severe fires (Malcolm, 1998; LaCroix et al., 2008). Temperatures are also increased at edges bordering high-contrast matrices (Arroyo-Rodríguez et al., 2017), as is wind speed (Davies-Colley et al., 2000; Laurance and Curran, 2008). Thus, variation in matrix contrast and edginess probably contributes to much of the reported variation in edge effects on trees and AGC in the literature. In chapter 4, I also found evidence of temporal variability in AGC losses, and a mediating influence of local core forest carbon. I observed a reduction in forest edge AGC over time, with most losses occurring within approximately eight years following edge creation, and no evidence of AGC recovery in older edges, indicating that many fragmented tropical landscapes will experience long-term depletions in AGC. I found that carbon losses were greatest in forests with higher core AGC; forest sites with core AGC similar to protected primary forests (207 Mg C ha^{-1}) were estimated to lose around 1.5 times more AGC at the edge than sites with core AGC typical of logged forests (98.3 Mg C ha^{-1}). This difference is probably because forests with taller, denser canopies (and thus, higher AGC) will have greater structural contrast with adjacent matrices, resulting in stronger abiotic disturbances at edges (Harper et al., 2005), which may also explain why edge effects on canopy height growth are more pronounced in primary forest than in disturbed forest (Nunes et al., 2021). It is also possible that historic exploitation of the large tree stand in most forests in Sabah, via commercial selective logging (Lindenmayer et al., 2012), may already have eliminated the largest trees which are most vulnerable to edge effects, thus acting as a type of extinction filter (Betts et al., 2019). My thesis provides new information on the factors which drive variability in edge effects (multiple edges, matrix contrast, edge age and local core forest structure), particularly with regard to edge effects on AGC, and therefore contributes to an improved understanding of edge effect dynamics. My results provide empirical support of conceptual models on the drivers of AGC in fragmented tropical forests (Melito et al., 2018), and if my results are generalizable to other fragmented agricultural landscapes throughout the tropics, then it is possible to make predictions about where edge effects are likely to cause the greatest reductions in AGC. Integrating my findings from all three chapters, I conclude that the most severe edge-related carbon losses are likely to occur in forest areas with a high-contrast adjoining matrix, high core forest AGC, and in close proximity to multiple edges, and that carbon losses will worsen over time.

Edge effects on tree composition and diversity

Unlike many studies in other tropical landscapes, my field survey data showed that AGC losses can occur independently of compositional shifts in the underlying tree communities (chapter 2). Typically, tree communities near edges become dominated by disturbance-adapted pioneers, to the detriment of late-successional trees with high wood densities (Oliveira et al., 2004; Michalski et al., 2007; Laurance et al., 2011; de Paula et al., 2011), and this compositional shift to low wood-density species contributes to AGC losses (de Paula et al., 2011; Qie et al., 2017; Melito et al., 2018). However, I observed no changes in either taxonomic or functional composition of tree communities near edges at my Sabah study sites, and declines in AGC appear to be solely driven by declines in maximum tree size. I also observed no change in the taxonomic diversity of tree communities at edges, contrary to the general trend of cross-taxa diversity losses at tropical forest edges documented by a recent meta-analysis (Willmer et al., 2022). However, relatively few studies have examined edge effects on the taxonomic diversity of tropical tree communities, which limits our capacity to draw any general patterns. Willmer et al. (2022) concluded that matrix contrast can mediate edge effects on species richness. Thus, as my field study was conducted in forest edges adjacent to mature oil palm plantations, it is possible that this relatively low-contrast matrix may have buffered forest edges against abiotic disturbances which typically drive changes in tree composition and diversity. As discussed in chapter 2, other aspects of the oil palm matrix (i.e. its management and extent) may also have minimised compositional shifts in forest edges, by preventing the dispersal of disturbance-adapted trees into edges, because many trees in this region have short dispersal distances (Corlett, 2009). Some forests are known to be more resilient to edge effects than others (Phillips et al., 2006; Numata et al., 2017), therefore it is also possible that certain characteristics of these Southeast Asian forests may make them more resilient to edge effects. Borneo forests are dominated by dipterocarp trees which are wind-dispersed rather than vertebrate-dispersed (Corlett, 2019), and so the recruitment of these trees is unlikely to be affected by changes in vertebrate abundance near edges, e.g. from defaunation or in response to abiotic disturbance (Peres, 2001; Pfeifer et al., 2017), although changes in the abundance of some seed predators could still influence seedling establishment (Curran et al., 1999; Luskin et al., 2017). Defaunation has been shown to have little to no impact on carbon stocks in Southeast Asian forests, because there are more abiotically-dispersed tree species in these forests (Osuri et al., 2016), though it can result in losses of local tree diversity over time (Harrison et al., 2013). The community-wide mast-fruiting events in these forests can often lead to significant time-lags in tree community responses to disturbance (e.g. Slik et al., 2011; Stride et al., 2018), because of the irregular timing of these events (Appanah, 1993). Thus, it is also possible that changes in tree composition and diversity may not yet be detectable in the mature tree cohorts (> 10cm diameter) which I studied, if there is a time-lagged response. Indeed, edge effects on younger cohorts can often occur independently of effects on adult trees (Slik et al., 2011; Luskin et al., 2017; Krishnadas et al., 2019), as can other fragmentation effects such as area and isolation effects in Southeast Asian rainforests (Stride et al., 2018).

Overall, with the exception of large trees and associated AGC stocks (chapter 2; Ordway and Asner, 2020), adult tree communities appear to be largely resilient to edge effects in this oil palm-dominated landscape. I therefore conclude that compositional shifts and diversity losses do not occur in all tropical forest edges. In these Southeast Asian rainforests, this weak edge influence may be due to the nature of the oil palm matrix (i.e. its structure, composition and extent), as well as specific characteristics of the dipterocarp forests themselves, such as community-wide mast-fruiting events and the dominance of wind-dispersed trees.

Contextualising edge influence in Sabah's forests

In many fragmented tropical landscapes, edge effects are the primary driver of ecological change (Berenguer et al., 2014; Benchimol and Peres, 2015; Laurance et al., 2018; Püttker et al., 2020). However, in addition to a lack of edge effects on tree composition, diversity and most components of forest structure in this study (chapter 2), I also found that edge effects explained a relatively small amount of variation in forest structure and AGC. The results of my field study showed that distance-from-edge explained <13% of the total variation in maximum tree size or AGC, whereas site-level differences explained considerably more variation (40% of variation in maximum diameter, and 22% of variation in AGC). In my analysis of remotely-sensed data on AGC stocks throughout Sabah (chapter 3), I found that a metric of edge influence which accounted for the effects of multiple edges still only explained around 20% of variation in AGC, and in chapter 4 I found that local core carbon had the strongest influence on AGC at edges. Thus, edge effects on tree communities and AGC appear to be relatively weak in these Southeast Asian rainforests, when contextualised against the high levels of AGC heterogeneity within forests. Contextualising edge influence against variation within a system is essential, in order to judge the biological significance of edge effects (Harper et al., 2005). However, many studies do not report key statistics such as R^2 values, which limits our capacity to draw conclusions about the relative importance of edge effects or to make comparisons among systems. Furthermore, one of the most highly cited studies on fragmentation impacts, the Biological Dynamics of Forest Fragments Project (BDFFP; Laurance et al., 2002; Laurance et al., 2011; Laurance et al., 2018) is in an experimentally fragmented landscape, where fragments are largely protected from disturbances such as logging, fire and cattle encroachment. Thus, our understanding of edge and other fragmentation effects in more typical fragmented tropical forests exposed to additional disturbances from logging has been limited (Berenguer et al., 2014; Fleiss et al., 2020), despite the fact that over 25% of tropical forests have been logged at least once (Edwards et al., 2019). As discussed in chapter 4, the majority of Sabah's forests have been selectively logged (Reynolds et al., 2011). Logging results in considerable variability in AGC stocks, both in this landscape (Asner et al., 2018; Fleiss et al., 2020) and in other tropical regions (Berenguer et al., 2014; Nunes et al., 2022). I therefore conclude that fragmentation effects on trees in Borneo forests are largely dwarfed by existing heterogeneity, and that historic disturbances such as commercial selective logging have likely driven much of this variation. However, whilst edge effects appear to be contextually quite weak, AGC losses are nevertheless significant, particularly in proximity to multiple edges and when edges are adjacent to high-contrast matrices. Thus, these edge effects should be factored into landscape management decisions aimed at preserving carbon stocks of remaining forest areas.

5.3 Conservation and management implications for oil palm landscapes

The oil palm industry is a major driver of deforestation in Southeast Asia, with over 17.5 Mha of land now converted to plantations (Descals et al., 2021). Fragmented landscapes dominated by oil palm plantations, such as my Sabah study system, are therefore common (Gaveau et al., 2016; Meijaard et al., 2020), and the growing demand for vegetable oils is likely to drive further expansion of oil palm (Butler and Laurance, 2009; Searchinger et al., 2018; Meijaard et al., 2020). This expansion has a number of direct environmental impacts relating to forest clearance and peatland drainage (Meijaard et al., 2020), and my research demonstrates that there are also significant indirect impacts via edge effects, with AGC losses of up to 30% in forest edges adjacent to oil palm plantations (30% AGC reduction at 50m from edge; chapter 2) driven by the loss of large trees. A number of initiatives have been developed to reduce the environmental impacts of oil palm agriculture, such as zero-deforestation commitments and voluntary sustainability certification schemes (Austin et al., 2021), however these schemes largely focus on reducing or mitigating direct impacts from deforestation. The Roundtable on Sustainable Palm Oil (RSPO) is a non-profit, industry-led certification scheme founded in 2004, which aims to improve the sustainability of the palm oil industry (Laurance et al., 2010; RSPO, 2018), for example via the identification and protection of High Conservation Value (HCV) and High Carbon Stock (HCS) forest reserves within plantations (P&C 7; Rosoman et al., 2017; RSPO, 2018). However, the HCV and HCS approach has historically had little scientific input (Edwards et al., 2012; Senior et al., 2015), and these HCV-HCS reserves are often too small to contain core forest areas (i.e. areas free of edge effects; Scriven et al., 2019). The results of this thesis highlight the importance of ensuring that forest remnants contain core forest areas, in order to maintain AGC stocks within oil palm landscapes. The results of chapter 3 demonstrate the importance of remnant size and shape recommendations underlying the HCV and HCS approach, because proximity to multiple edges is shown to reduce AGC by a further 23% and I found that edginess is greater in small, geometrically-complex fragments. Indeed, the AGC levels I observed in the edgiest forest pixels are similar to those found in small HCV remnants in a field study by Fleiss et al. (2020). The edginess metric I developed in chapter 3 may therefore be beneficial for planning reserve designs to maximise AGC stocks. Furthermore, the results of chapter 2 indicate that a 100m edge penetration depth, as is commonly assumed in core area models (e.g. Lucey et al., 2017), may not suffice to preserve carbon stocks. I observed a reduction in AGC up to 300m from edges, and so core area models currently used in these HCV and HCS approaches should be adjusted to account for this increased penetration depth, to preserve carbon stocks and associated biodiversity within plantations.

In chapter 3, I mapped forest cover and edginess throughout Sabah, and found that almost half (41%) of the remaining forest area is within 300m of an edge. Whilst the remaining forests in Sabah are protected (Williams et al., 2020) and further fragmentation is therefore unlikely, management strategies to reduce influence from existing edges are important, both within HCV-HCS remnants and in other protected forest areas which are adjacent to plantations. My results in chapter 4 indicate that management activities to reduce structural contrast of plantations bordering forest remnants may help to preserve forest AGC. There are a number of ways in which this could be accomplished. For example, the preservation of mature palm buffers (Pashkevich et al., 2022) directly adjacent to forest edges may be beneficial, because oil palm replanting is likely to increase structural contrast at edges. Increasing the complexity of understorey vegetation within plantations may also help to reduce contrast, because this provides a cooler and more stable microclimate within plantations (Luskin and Potts, 2011) and the increased AGC loss I observed at high-contrast edges (chapter 4) was likely driven by stronger abiotic gradients. Increasing the amount of tree cover within plantations, either through the preservation of natural forest remnants (Rosoman et al., 2017; RSPO, 2018) or through agroforestry practices (Bhagwat and Willis, 2008; Zemp et al., 2019) may also be beneficial for the same purpose. However, it is important that trade-offs with crop yield are considered if these management strategies compromise yield (Koh et al., 2009; Foster et al., 2011; Padfield et al., 2019; Hamer et al., 2021), damaging livelihoods and potentially encouraging additional land clearance to compensate for reduced yield. Other edge buffering strategies which may not compromise yield include staggered replanting regimes (Luskin and Potts, 2011), which would minimize structural contrast with adjacent forest stands during palm replanting, and the planting of diverse agroforestry buffers adjacent to forest edges. If trade-offs with yield remain, then prioritising the placement of buffers around the corners of forest remnants (i.e. the edgiest forest areas) may provide the greatest benefits, by protecting the forest from multiple edge effects (chapter 3) whilst minimising any reductions in the planted area. These strategies could be implemented via the RSPO's Principles and Criteria, or via the guidelines of other sustainability schemes such as the Malaysian Sustainable Palm Oil (MSPO) and Indonesian Sustainable Palm Oil (ISPO) schemes. When used alongside best management practices to maximise yield within the planted area (Donough et al., 2009), strategies such as these may help to preserve forest carbon stocks without significantly compromising yield, thus improving the sustainability of oil palm agriculture. These recommendations are likely to apply to oil palm landscapes in other regions too, for example in Sub-Saharan Africa (Ordway et al., 2019).

5.4 Wider implications for carbon emissions

The global climate is changing rapidly, due to anthropogenic activities which release greenhouse gases (IPCC, 2021). Tropical forests are a key component of the terrestrial carbon sink and play a key role in global climate regulation (Le Quéré et al., 2017), however the impacts of degradation on tropical forest carbon are poorly understood (Mitchard, 2018). This knowledge gap is because it is difficult to map the extent of forest degradation (IPCC, 2019), and because much of our understanding of forest carbon dynamics comes from intact forest landscapes (Smith et al., 2018), whilst degradation impacts are highly variable (see reviews in Houghton, 2005; Bustamante et al., 2016; Mitchard, 2018). Of all the drivers of tropical forest AGC degradation, edge effects have the largest physical footprint (Zhu et al., 2023). Thus, by quantifying AGC declines near forest edges in a poorly-studied tropical system, my research contributes to an improved understanding of the impacts of degradation, via fragmentation and edge effects, on tropical forest carbon stocks. My results highlight the threat that tropical agricultural expansion and associated forest fragmentation pose to carbon stocks (AGC losses of up to 60% observed in forest exposed to multiple edges; chapter 3), which is particularly concerning given that the total pantropical edge area is projected to nearly double by 2050 (Fischer et al., 2021).

Importantly, my results demonstrate that AGC losses are highly variable depending upon local contextual factors, such as matrix contrast and the number of nearby edges. Yet, as noted by Melito et al. (2018), most estimates of carbon emissions resulting from edge effects are based on simulations from a few single-edge field studies in Neotropical forests (Pütz et al., 2014; Brinck et al., 2017; Fischer et al., 2021), which may therefore be misleading in terms of global impacts. The influence of multiple edges is an important finding of my thesis, because many fragmented forests are in close proximity to multiple edges (Taubert et al., 2018) and so studies which estimate carbon emissions based on assumptions of single-edge effects (e.g. Brinck et al., 2017; Fischer et al., 2021) will underestimate emissions. The edginess metric I developed in chapter 3 is a promising approach for improving predictions of edge-related emissions and it would be relatively straightforward to modify this metric to account for other important factors, such as the structure of nearby land-uses. By improving the understanding of factors which drive variability in AGC losses near edges, my results will benefit efforts to estimate emissions from tropical land-use change (Chaplin-Kramer et al., 2017; Lam et al., 2019), and have the potential to improve predictions of future changes in the tropical carbon sink (Mitchard, 2018).

An improved understanding of factors which mediate AGC losses at edges, as well as an improved capacity to estimate and map these losses, will likely improve the accuracy of national and global carbon budgets. This could aid governments in their efforts to meet emissions-reduction targets (Silva Junior et al., 2021), and will also be beneficial for ecosystem service assessments (e.g. for carbon storage). These assessments typically do not consider the influence of landscape-level processes such as fragmentation and edge effects (Metzger, Villarreal-Rosas, et al., 2021), which leads to inaccurate assessments and hinders strategies to manage ecosystem services (Chaplin-Kramer, Sharp, et al., 2015; Metzger, Fidelman, et al., 2021). As demonstrated by my thesis, edge-affected forest can comprise a large part of tropical agricultural landscapes (e.g. almost half of the remaining forest in Sabah is within 300m of an edge; chapter 3), and edge effects can contribute significantly to landscape-level variation in AGC (approximately 20% of AGC variation throughout

Sabah is explained by edge effects; chapter 3). Accounting for edge influence on AGC is therefore crucial for accurate estimates of emissions and ecosystem services. These improvements are also important for carbon finance systems, such as the Reducing Emissions from Deforestation and Forest Degradation framework (REDD+). REDD+ is a financial incentive for countries with carbon-rich forests, particularly in the tropics, to reduce emissions arising from forest exploitation. These carbon finance systems rely heavily on accurate estimates of carbon emissions (Goetz et al., 2015) and uncertainties in emissions arising from forest degradation have been a major constraint in the implementation of REDD+ mechanisms (Gibbs et al., 2007; Bustamante et al., 2016). Approaches by which to map these losses (e.g. the edginess metric developed in chapter 3) could help improve the robustness of these kinds of carbon finance schemes, thus leading to greater success in the future.

5.5 Recommendations for future work

My field study of edge effects focused on mature tree communities, with a minimum 10cm diameter size threshold. Thus, whilst I am able to draw conclusions about the impacts of edge effects on adult trees, my field data provides no information on younger cohorts (i.e. seedlings and saplings) or on regeneration processes. Other studies have shown that fragmentation impacts younger cohorts in the absence of any impacts on adult trees established pre-fragmentation (Slik et al., 2011; Stride et al., 2018; Krishnadas et al., 2019), and so future studies should seek to determine whether there are time lags in compositional shifts and diversity losses at forest edges in Sabah. Support for this line of future research comes from a recent study in a Sumatran oil palm landscape, which revealed some weak compositional shifts among seedlings, with a slight decline in late-successional species observed near forest edges, but found no effects on seedling species richness (Permana et al., 2022). Given that edges are likely to become more common as global demand for biofuel and vegetable oil grows (Corley, 2009; Searchinger et al., 2019), there is an urgent need for further studies, both on tree communities and also on additional plant and animal taxa at forest edges in oil palm landscapes.

The edginess metric which I developed in chapter 3 offers an improvement over the more commonly used ‘distance to nearest edge’ metric. This metric could be adapted further by adjusting the parameters of the heat-diffusion model to give greater weighting to the influence of high-contrast matrices than low-contrast ones. Whilst I tested the impacts of matrix contrast on edge AGC after controlling for the influence of multiple edges, it would be interesting to examine how these two factors interact with one another. I tested the capacity of this metric to explain variability in AGC throughout an entire landscape, but additional testing at a fragment level would be beneficial, to determine whether the effect of edginess on AGC is consistent across spatial scales.

An important topic which I was unable to address in this thesis is the impact that replanting of oil palm plantations may have on forest edges. Replanting occurs every 20-30 years, once palms have passed their peak yields (Corley and Tinker, 2015). The process is highly destructive, causing heavy soil disturbance and the disruption of hydrological systems (Snaddon et al., 2013), as well as declines in the diversity of multiple taxa within plantations (Kurz et al., 2016; Ashton-Butt et al., 2019; Pashkevich et al., 2021). The impact of replanting on edges has not been studied, but it is likely to result in greater disturbance in adjacent forest due to the ensuing increase in structural contrast (Luskin and Potts, 2011). However, a barrier to such studies is the limited availability of high resolution remotely-sensed time-series data. Temporal studies of edge effect dynamics have typically had to rely on space-for-time designs (e.g. chapter 4; Ordway and Asner, 2020) or have been relatively limited in their scope, studying only small areas which can be repeatedly surveyed in the field (e.g. Laurance et al., 2018). The increasing availability of high-resolution remotely-sensed data at large scales (e.g. Dubayah et al., 2020; Dubayah et al., 2022) offers opportunities to study oil palm replanting, and drone-based lidar technology (e.g. Almeida et al., 2019) offers a cost-effective means to repeatedly survey forest edges over smaller scales (Tang and Shao, 2015). Repeat field surveys could ground-truth these remotely-sensed assessments, whilst also measuring changes in tree community composition and diversity which cannot be assessed with remotely-sensed data. This research is important because large areas of mature palm plantations throughout Southeast Asia have been replanted at least once, with many more likely to be replanted in the near future.

Much of the existing edge effect literature has focused on quantifying impacts, because edge effects are a remarkably diverse set of phenomena which scientists are keen to understand better (Ries et al., 2004; Harper et al., 2005; Ries et al., 2017). Overall, edge effects in tropical forests are detrimental for many taxa and endangered species (Magnago et al. 2015 b; Pfeifer et al., 2017; Willmer et al., 2022) and for carbon storage (Chaplin-Kramer, Ramler, et al., 2015; Ordway and Asner, 2020; Silva Junior et al., 2020; Anderson et al., 2022; Zhao et al., 2021). However, there is a lack of research into management strategies to reduce edge impacts, therefore this should be a key focus of future research. The findings of chapter 4 indicate that the use of vegetative buffers adjacent to forest edges may reduce edge effects on tree communities and AGC, by minimizing abiotic disturbances within the forest. Enrichment planting of late-successional trees in edges may also help to reverse losses observed in some systems, when used in combination with strategies such as vegetative buffers to limit abiotic disturbances and within-forest management, such as liana cutting, to promote seedling regeneration (Philipson et al., 2020; Scriven et al., 2022). Based on the findings of my thesis, a buffer width of 300m would likely suffice given that edge effects occur up to this distance (chapter 2), however even buffers of 100m would likely provide significant benefits, given that edge effects are strongest within this distance (chapter 2; chapter 3). Future studies could seek to determine optimal buffer widths, optimal composition of buffers, trade-offs with crop yields, and whether different taxa and ecosystem functions respond similarly. Edge effects are likely to have long-term detrimental impacts and so by developing effective management interventions, it may be possible to reverse some of their impacts and improve the integrity of fragmented forests into the future.

5.6 Conclusions

The expansion of tropical agriculture, such as oil palm, drives fragmentation of tropical rainforests, and edge effects threaten the integrity of many fragmented forests. In oil palm landscapes in Southeast Asia, I showed that edge effects on large trees drive significant declines in forest carbon, but that edges have no observable impact on the composition or diversity of mature tree communities, and effects on forest structure and microclimate are limited. Furthermore, edge effects on forest carbon are relatively weak compared to high levels of variation in carbon in surrounding forest areas. However, my research also showed that carbon losses increase in the presence of multiple edges, indicating that forest areas experiencing high levels of 'edginess' (e.g. in small or irregularly shaped fragments) suffer high levels of disturbance from edge effects. Consideration of the impacts of multiple edges is therefore important when quantifying carbon emissions from forest fragmentation, and a metric which accounts for multiple edges improves our ability to explain variation in forest carbon in fragmented landscapes. I also found that carbon losses are greater when forest is adjacent to high-contrast matrices (e.g. pasture or annual crops), compared to relatively low-contrast matrices (e.g. mature palm or tree plantations), particularly in forests with high local core carbon. There is evidence that carbon stocks decline over time in edges, with no signs of recovery in older edges. There are a number of practical and management recommendations arising from the results of this thesis, which are summarised in Table 5.1. For example, management interventions to reduce edge contrast, such as the use of vegetative buffer habitats, as well as efforts to reduce edge:area ratios of remnant forest reserves, will help to maintain forest carbon stocks in the face of continued agricultural expansion in tropical regions.

Table 5.1 – Key recommendations (management and practical) based on the findings of this thesis.

Recommendation	**Evidence**
Environmental footprinting of products containing palm oil should account for edge effects	Forest edges adjacent to oil palm plantations have reduced AGC (30% reduction at 50m from edge, losses detectable up to 300m from edge)
Forest reserve designs (e.g. HCV & HCS reserves within oil palm plantations) should minimize edge:area ratios to preserve AGC stocks	AGC stocks are lowest in forest with high 'edginess' (additional 23% AGC loss *vs* single edge). Edginess is greatest in small, geometrically complex fragments (with high edge:area ratios)
Core area models used in these approaches should assume 300m edge effect depth	Edge effects on AGC detectable up to 300m from edge
Non-forest management (e.g. vegetative buffers, increased tree cover, increased understorey complexity) should reduce contrast with adjacent forest, to preserve forest AGC	High-contrast edges have double AGC loss of low-contrast edges (21% loss *vs* 10% loss)
Vegetative buffers (e.g. mature palms, diverse agroforestry) should be at least 100m wide, or ideally 300m wide	Edge effects on AGC are most severe within 100m of edges, but occur up to 300m
Buffer placement around forest fragment corners should be prioritised	AGC losses are greatest in 'edgier' forest, e.g. fragment corners
High-carbon forests should be protected from fragmentation	High-carbon forests suffer 1.5 times greater AGC loss at edges than average-carbon forests
Carbon emissions estimates and ecosystem service assessments should account for multiple edge effects, using an edginess metric (e.g. the metric developed in chapter 3)	AGC stocks are lowest in forest with high 'edginess' (additional 23% AGC loss *vs* single edge) An edginess metric explains more variation in AGC than a 'nearest edge' metric (R^2 = 18% *vs* 15% within 1km of edge, 11% *vs* 1.5% within 100m)

5.7 References

Almeida, D.R.A., Broadbent, E.N., Zambrano, A.M.A., Wilkinson, B.E., Ferreira, M.E., Chazdon, R., … Brancalion, P.H.S. 2019. Monitoring the structure of forest restoration plantations with a drone-lidar system. *International Journal of Applied Earth Observation and Geoinformation*. **79**, pp.192–198.

Appanah, S. 1993. Mass flowering of dipterocarp forests in the aseasonal tropics. *J. Biosci*. **18**(4), pp.457–474.

Arroyo-Rodríguez, V., Saldaña-Vázquez, R.A., Fahrig, L., & Santos, B.A. 2017. Does forest fragmentation cause an increase in forest temperature? *Ecological Research*. **32**(1), pp.81–88.

Ashton-Butt, A., Willcock, S., Purnomo, D., Suhardi, Aryawan, A.A.K., Wahyuningsih, R., … Snaddon, J.L. 2019. Replanting of first-cycle oil palm results in a second wave of biodiversity loss. *Ecology and Evolution*. **9**(11), ece3.5218.

Asner, G.P., Brodrick, P.G., Philipson, C., Vaughn, N.R., Martin, R.E., Knapp, D.E., … Coomes, D.A. 2018. Mapped aboveground carbon stocks to advance forest conservation and recovery in Malaysian Borneo. *Biological Conservation*. **217**, pp.289–310.

Austin, K.G., Heilmayr, R., Benedict, J.J., Burns, D.N., Eggen, M., Grantham, H., … Carlson, K.M. 2021. Mapping and Monitoring Zero-Deforestation Commitments. *BioScience*. **71**(10), pp.1079–1090.

Benchimol, M., & Peres, C.A. 2015. Edge-mediated compositional and functional decay of tree assemblages in Amazonian forest islands after 26 years of isolation. *Journal of Ecology*. **103**(2), pp.408–420.

Berenguer, E., Ferreira, J., Gardner, T.A., Aragão, L.E.O.C., De Camargo, P.B., Cerri, C.E., … Barlow, J. 2014. A large-scale field assessment of carbon stocks in human-modified tropical forests. *Global Change Biology*. **20**(12), pp.3713–3726.

Betts, M.G., Wolf, C., Pfeifer, M., Banks-Leite, C., Arroyo-Rodríguez, V., Ribeiro, D.B., … Ewers, R.M. 2019. Extinction filters mediate the global effects of habitat fragmentation on animals. *Science*. **366**(6470), pp.1236–1239.

Bhagwat, S.A., & Willis, K.J. 2008. Agroforestry as a Solution to the Oil-Palm Debate. *Conservation Biology*. **22**(6), pp.1368–1369.

Brinck, K., Fischer, R., Groeneveld, J., Lehmann, S., Dantas De Paula, M., Pütz, S., … Huth, A. 2017. High resolution analysis of tropical forest fragmentation and its impact on the global carbon cycle. *Nature Communications*. **8**(Article no:14855).

Bustamante, M.M.C., Roitman, I., Aide, T.M., Alencar, A., Anderson, L.O., Aragão, L., … Vieira, I.C.G. 2016. Toward an integrated monitoring framework to assess the effects of tropical forest degradation and recovery on carbon stocks and biodiversity. *Global Change Biology*. **22**(1), pp.92–109.

Butler, R.A., & Laurance, W.F. 2009. Is oil palm the next emerging threat to the Amazon? *Tropical*

Conservation Science. **2**(1), pp.1–10.

Campbell, R.E., Harding, J.S., Ewers, R.M., Thorpe, S., & Didham, R.K. 2011. Production land use alters edge response functions in remnant forest invertebrate communities. *Ecological Applications*. **21**(8), pp.3147–3161.

Chaplin-Kramer, R., Ramler, I., Sharp, R., Haddad, N.M., Gerber, J.S., West, P.C., … King, H. 2015. Degradation in carbon stocks near tropical forest edges. *Nature Communications*. **6**(Article no: 10158).

Chaplin-Kramer, R., Sharp, R., Mandle, L., Sim, S., Johnson, J., Butnar, I., … Kareiva, P.M. 2015. Spatial patterns of agricultural expansion determine impacts on biodiversity and carbon storage. *Proceedings of the National Academy of Sciences of the United States of America*. **112**(24), pp.7402–7407.

Chaplin-Kramer, R., Sim, S., Hamel, P., Bryant, B., Noe, R., Mueller, C., … Daily, G. 2017. Life cycle assessment needs predictive spatial modelling for biodiversity and ecosystem services. *Nature Communications*. **8**, p.15065.

Corlett, R.T. 2009. Seed dispersal distances and plant migration potential in tropical East Asia. *Biotropica*. **41**(5), pp.592–598.

Corlett, R.T. 2019. *The Ecology of Tropical East Asia* Third Edit. Oxford, UK: Oxford University Press.

Corley, R.H.V. 2009. How much palm oil do we need? *Environmental Science & Policy*. **12**(2), pp.134–139.

Corley, R.H.V., & Tinker, P.B. 2015. *The Oil Palm* [Online] Fifth Edition. John Wiley & Sons. [Accessed 26 March 2023]. Available from: https://onlinelibrary.wiley.com/doi/book/10.1002/9781118953297.

Curran, L.M., Caniago, I., Paoli, G.D., Astianti, D., Kusneti, M., Leighton, M., … Haeruman, H. 1999. Impact of El Nino and logging on canopy tree recruitment in Borneo. *Science*. **286**(5447), pp.2184–2188.

Davies-Colley, R.J., Payne, G.W., & Elswijk, M. van 2000. Microclimate gradients across a forest edge. *New Zealand Journal of Ecology*. **24**(2), pp.111–121.

Descals, A., Wich, S., Meijaard, E., Gaveau, D.L.A., Peedell, S., & Szantoi, Z. 2021. High-resolution global map of smallholder and industrial closed-canopy oil palm plantations. *Earth System Science Data*. **13**(3), pp.1211–1231.

Donough, C.R., Witt, C., & Fairhurst, T. 2009. Yield Intensification in Oil Palm Plantations through Best Management Practice Smallholder Oil Palm Handbook View project Oil Palm Field Handbooks View project. *Better Crops*. **93**(1), pp.12–14.

Dubayah, R., Armston, J., Healey, S.P., Bruening, J.M., Patterson, P.L., Kellner, J.R., … Luthcke, S. 2022. GEDI launches a new era of biomass inference from space. *Environmental Research Letters*. **17**(9), p.095001.

Dubayah, R., Blair, J.B., Goetz, S., Fatoyinbo, L., Hansen, M., Healey, S., … Silva, C. 2020. The Global

Ecosystem Dynamics Investigation: High-resolution laser ranging of the Earth’s forests and topography. *Science of Remote Sensing*. **1**, p.100002.

Edwards, D.P., Fisher, B., & Wilcove, D.S. 2012. High Conservation Value or high confusion value? Sustainable agriculture and biodiversity conservation in the tropics. *Conservation Letters*. **5**(1), pp.20–27.

Edwards, D.P., Socolar, J.B., Mills, S.C., Burivalova, Z., Koh, L.P., & Wilcove, D.S. 2019. Conservation of Tropical Forests in the Anthropocene. *Current Biology*. **29**(19), pp.R1008–R1020.

Fischer, R., Taubert, F., Müller, M.S., Groeneveld, J., Lehmann, S., Wiegand, T., & Huth, A. 2021. Accelerated forest fragmentation leads to critical increase in tropical forest edge area. *Science Advances*. **7**(37).

Fleiss, S., Waddell, E.H., Bala Ola, B., Banin, L.F., Benedick, S., Bin Sailim, A., … Hill, J.K. 2020. Conservation set-asides improve carbon storage and support associated plant diversity in certified sustainable oil palm plantations. *Biological Conservation*. **248**(Article no: 108631).

Foster, W.A., Snaddon, J.L., Turner, E.C., Fayle, T.M., Cockerill, T.D., Farnon Ellwood, M.D., … Yusah, K.M. 2011. Establishing the evidence base for maintaining biodiversity and ecosystem function in the oil palm landscapes of South East Asia. *Philosophical Transactions of the Royal Society B: Biological Sciences*. **366**(1582), pp.3277–3291.

Gaveau, D.L.A., Sheil, D., Husnayaen, Salim, M.A., Arjasakusuma, S., Ancrenaz, M., … Meijaard, E. 2016. Rapid conversions and avoided deforestation: examining four decades of industrial plantation expansion in Borneo. *Scientific Reports*. **6**(Article no: 32017).

Gibbs, H.K., Brown, S., Niles, J.O., & Foley, J.A. 2007. Monitoring and estimating tropical forest carbon stocks: making REDD a reality. *Environ. Res. Lett*. **2**, p.13.

Goetz, S.J., Hansen, M., Houghton, R.A., Walker, W., Laporte, N., & Busch, J. 2015. Measurement and monitoring needs, capabilities and potential for addressing reduced emissions from deforestation and forest degradation under REDD+. *Environmental Research Letters*. **10**(12), p.123001.

Hamer, K.C., Sasu, M.A., Ofosuhene, L., Asare, R., Ossom, B., Parr, C.L., … Hill, J.K. 2021. Proximity to forest mediates trade-offs between yields and biodiversity of birds in oil palm smallholdings. *Biotropica*. **53**(6), pp.1498–1509.

Harper, K.A., Macdonald, S.E., Burton, P.J., Chen, J., Brosofske, K.D., Saunders, S.C., … Esseen, P.A. 2005. Edge Influence on Forest Structure and Composition in Fragmented Landscapes. *Conservation Biology*. **19**(3), pp.768–782.

Harrison, R.D., Tan, S., Plotkin, J.B., Slik, F., Detto, M., Brenes, T., … Davies, S.J. 2013. Consequences of defaunation for a tropical tree community. *Ecology Letters*. **16**(5), pp.687–694.

Hatfield, J.H., Barlow, J., Joly, C.A., Lees, A.C., Parruco, C.H. de F., Tobias, J.A., … Banks-Leite, C. 2020. Mediation of area and edge effects in forest fragments by adjacent land use. *Conservation Biology*. **34**(2), pp.395–404.

Houghton, R.A. 2005. Aboveground Forest Biomass and the Global Carbon Balance. *Global Change Biology*. **11**(6), pp.945–958.

IPCC 2021. *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* (V. Masson-Delmotte, P. Zhai, A. Pirani, S. L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M. I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J. B. R. Matthews, T. K. Maycock, T. Waterfield, O. Yelekçi, R. Yu, & B. Zhou, eds.). Cambridge, United Kingdom and New York, NY, USA: Cambridge University Press.

IPCC 2019. Land Degradation *In*: L. Olsson, Humberto Barbosa, Suruchi Bhadwal, J. Manuel Moreno, C. Vera, A. Salisu Barau, H Barbosa, S Bhadwal, A. Cowie, K. Delusca, D. Flores-Renteria, K. Hermans, E. Jobbagy, W. Kurz, D. Li, P. Shukla, J. Skea, E. Calvo Buendia, V. Masson-Delmotte, H. Pörtner, D. C. Roberts, P. Zhai, R. Slade, S. Connors, R. van Diemen, M. Ferrat, E. Haughey, S. Luz, S. Neogi, M. Pathak, J. Petzold, J. Portugal Pereira, P. Vyas, E. Huntley, K. Kissick, M. Belkacemi and J. Malley, eds. *Climate Change and Land: an IPCC special report on climate change, desertification, land degradation, sustainable land management, food security, and greenhouse gas fluxes in terrestrial ecosystems* [Online]. Available from: https://www.ipcc.ch/site/assets/uploads/sites/4/2022/11/SRCCL_Chapter_4.pdf.

Koh, L.P., Levang, P., & Ghazoul, J. 2009. Designer landscapes for sustainable biofuels. *Trends in Ecology & Evolution*. **24**(8), pp.431–438.

Krishnadas, M., Kumar, A.N., & Comita, L.S. 2019. Edge effects reduce α-diversity but not β-diversity during community assembly in a human-modified tropical forest. *Ecological Applications*. **29**(8), p.e01996.

Kurz, D.J., Turner, E.C., Aryawan, A.A., Barkley, H.C., Caliman, J.-P., Konopik, O., … Foster, W.A. 2016. Replanting reduces frog diversity in oil palm. *Biotropica*. **48**(4), pp.483–490.

LaCroix, J.J., Li, Q., Chen, J., Henderson, R., & John, R. 2008. Edge effects on fire spread in a disturbed Northern Wisconsin landscape. *Landscape Ecology*. **23**(9), pp.1081–1092.

Lam, W.Y., Kulak, M., Sim, S., King, H., Huijbregts, M.A.J., & Chaplin-Kramer, R. 2019. Greenhouse gas footprints of palm oil production in Indonesia over space and time. *Science of the Total Environment*. **688**, pp.827–837.

Laurance, W., Koh, L., Butler, R., Sodhi, N., Corey, J., Neidel, J., … Vega, J. 2010. Improving the performance of the roundtable on sustainable palm oil for nature conservation. *Conservation Biology*. **24**(2), pp.377–381.

Laurance, W.F., Camargo, J.L.C., Fearnside, P.M., Lovejoy, T.E., Williamson, G.B., Mesquita, R.C.G., … Laurance, S.G.W. 2018. An Amazonian rainforest and its fragments as a laboratory of global change. *Biological Reviews*. **93**(1), pp.223–247.

Laurance, W.F., Camargo, J.L.C., Luizão, R.C.C., Laurance, S.G., Pimm, S.L., Bruna, E.M., … Lovejoy, T.E. 2011. The fate of Amazonian forest fragments: A 32-year investigation. *Biological Conservation*. **144**(1), pp.56–67.

Laurance, W.F., & Curran, T.J. 2008. Impacts of wind disturbance on fragmented tropical forests: A review and synthesis. *Austral Ecology*. **33**(4), pp.399–408.

Laurance, W.F., Delamônica, P., Laurance, S.G., Vasconcelos, H.L., & Lovejoy, T.E. 2000. Rainforest fragmentation kills big trees. *Nature*. **404**, p.836.

Laurance, W.F., Laurance, S.G., Ferreira, L. V., Rankin-de Merona, J.M., Gascon, C., & Lovejoy, T.E. 1997. Biomass collapse in Amazonian forest fragments. *Science*. **278**(5340), pp.1117–1118.

Laurance, W.F., Lovejoy, T.E., Vasconcelos, H.L., Bruna, E.M., Didham, R.K., Stouffer, P.C., … Sampaio, E. 2002. Ecosystem decay of Amazonian forest fragments: a 22-year investigation. *Conservation Biology*. **16**(3), pp.605–618.

Laurance, W.F., Nascimento, H.E.M., Laurance, S.G., Andrade, A., Ewers, R.M., Harms, K.E., … Ribeiro, J.E. 2007. Habitat fragmentation, variable edge effects, and the landscape-divergence hypothesis. *PLoS ONE*. **2**(10), p.e1017.

Lindenmayer, D.B., Laurance, W.F., & Franklin, J.F. 2012. Global decline in large old trees. *Science*. **338**(6112), pp.1305–1306.

Lucey, J.M., Palmer, G., Yeong, K.L., Edwards, D.P., Senior, M.J.M., Scriven, S.A., … Hill, J.K. 2017. Reframing the evidence base for policy-relevance to increase impact: a case study on forest fragmentation in the oil palm sector. *Journal of Applied Ecology*. **54**(3), pp.731–736.

Luskin, M.S., Brashares, J.S., Ickes, K., Sun, I.F., Fletcher, C., Wright, S.J., & Potts, M.D. 2017. Cross-boundary subsidy cascades from oil palm degrade distant tropical forests. *Nature Communications*. **8**(Article no: 2231).

Luskin, M.S., & Potts, M.D. 2011. Microclimate and habitat heterogeneity through the oil palm lifecycle. *Basic and Applied Ecology*. **12**(6), pp.540–551.

Magnago, L.F.S., Magrach, A., Barlow, J., Schaefer, C.E.G.R., Laurance, W.F., Martins, S.V., & Edwards, D.P. 2017. Do fragment size and edge effects predict carbon stocks in trees and lianas in tropical forests? *Functional Ecology*. **31**, pp.542–552.

Magnago, Luiz Fernando S., Magrach, A., Laurance, W.F., Martins, S. V., Meira-Neto, J.A.A., Simonelli, M., & Edwards, D.P. 2015. Would protecting tropical forest fragments provide carbon and biodiversity cobenefits under REDD+? *Global Change Biology*. **21**(9), pp.3455–3468.

Magnago, Luiz Fernando Silva, Rocha, M.F., Meyer, L., Martins, S.V., & Meira-Neto, J.A.A. 2015. Microclimatic conditions at forest edges have significant impacts on vegetation structure in large Atlantic forest fragments. *Biodiversity and Conservation*. **24**(9), pp.2305–2318.

Malcolm, J.R. 1998. A model of conductive heat flow in forest edges and fragmented landscapes. *Climatic Change*. **39**(2–3), pp.487–502.

Meijaard, E., Brooks, T.M., Carlson, K.M., Slade, E.M., Garcia-Ulloa, J., Gaveau, D.L.A., … Sheil, D. 2020. The environmental impacts of palm oil in context. *Nature Plants*. **6**, pp.1418–1426.

Melito, M., Metzger, J.P., & de Oliveira, A.A. 2018. Landscape-level effects on aboveground biomass of tropical forests: A conceptual framework. *Global Change Biology*. **24**(2), pp.597–

607.

Mesquita, R.C.G., Delamônica, P., & Laurance, W.F. 1999. Effect of surrounding vegetation on edge-related tree mortality in Amazonian forest fragments. *Biological Conservation*. **91**(2–3), pp.129–134.

Metzger, J.P., Fidelman, P., Sattler, C., Schröter, B., Maron, M., Eigenbrod, F., … Rhodes, J.R. 2021. Connecting governance interventions to ecosystem services provision: A social-ecological network approach. *People and Nature*. **3**(2), pp.266–280.

Metzger, J.P., Villarreal-Rosas, J., Suárez-Castro, A.F., López-Cubillos, S., González-Chaves, A., Runting, R.K., … Rhodes, J.R. 2021. Considering landscape-level processes in ecosystem service assessments. *Science of The Total Environment*. **796**, p.149028.

Michalski, F., Nishi, I., & Peres, C.A. 2007. Disturbance-mediated drift in tree functional groups in Amazonian forest fragments. *Biotropica*. **39**(6), pp.691–701.

Mitchard, E.T.A. 2018. The tropical forest carbon cycle and climate change. *Nature*. **559**(7715), pp.527–534.

Numata, I., Silva, S.S., Cochrane, M.A., & d'Oliveira, M. V. 2017. Fire and edge effects in a fragmented tropical forest landscape in the southwestern Amazon. *Forest Ecology and Management*. **401**, pp.135–146.

Nunes, C.A., Berenguer, E., França, F., Ferreira, J., Lees, A.C., Louzada, J., … Barlow, J. 2022. Linking land-use and land-cover transitions to their ecological impact in the Amazon. *Proceedings of the National Academy of Sciences of the United States of America*. **119**(27), p.e2202310119.

Nunes, M.H., Jucker, T., Riutta, T., Svátek, M., Kvasnica, J., Rejžek, M., … Coomes, D.A. 2021. Recovery of logged forest fragments in a human-modified tropical landscape during the 2015-16 El Niño. *Nature Communications*. **12**(Article no: 1526).

Oliveira, M.A., Grillo, A.S., & Tabarelli, M. 2004. Forest edge in the Brazilian Atlantic forest: Drastic changes in tree species assemblages. *Oryx*. **38**(4), pp.389–394.

Ordway, E.M., & Asner, G.P. 2020. Carbon declines along tropical forest edges correspond to heterogeneous effects on canopy structure and function. *Proceedings of the National Academy of Sciences of the United States of America*. **117**(14), pp.7863–7870.

Ordway, E.M., Naylor, R.L., Nkongho, R.N., & Lambin, E.F. 2019. Oil palm expansion and deforestation in Southwest Cameroon associated with proliferation of informal mills. *Nature Communications 2019 10:1*. **10**(1), pp.1–11.

Osuri, A.M., Ratnam, J., Varma, V., Alvarez-Loayza, P., Hurtado Astaiza, J., Bradford, M., … Sankaran, M. 2016. Contrasting effects of defaunation on aboveground carbon storage across the global tropics. *Nature Communications*. **7**(1), p.11351.

Padfield, R., Hansen, S., Davies, Z.G., Ehrensperger, A., Slade, E.M., Evers, S., … Struebig, M.J. 2019. Co-producing a Research Agenda for Sustainable Palm Oil. *Frontiers in Forests and Global Change*. **2**, p.33.

Pashkevich, M.D., Aryawan, A.A.K., Luke, S.H., Dupérré, N., Waters, H.S., Caliman, J., … Turner, E.C. 2021. Assessing the effects of oil palm replanting on arthropod biodiversity M. Struebig, ed. *Journal of Applied Ecology*. **58**(1), pp.27–43.

Pashkevich, M.D., Luke, S.H., Aryawan, A.A.K., Waters, H.S., Caliman, J.P., Dupérré, N., … Turner, E.C. 2022. Riparian buffers made of mature oil palms have inconsistent impacts on oil palm ecosystems. *Ecological Applications*. **32**(4), p.e2552.

de Paula, M.D., Costa, C.P.A., & Tabarelli, M. 2011. Carbon storage in a fragmented landscape of Atlantic forest: the role played by edge-affected habitats and emergent trees. *Tropical Conservation Science*. **4**(3), pp.349–358.

Peres, C.A. 2001. Synergistic Effects of Subsistence Hunting and Habitat Fragmentation on Amazonian Forest Vertebrates. *Conservation Biology*. **15**(6), pp.1490–1505.

Permana, G., Marliana, S.N., Susandarini, R., & Addaha, H. 2022. Sustaining rainforest remnants in plantation landscapes: degree of oil palm stand-induced edge effects on forest microclimate and regeneration. *CERNE*. **28**(1).

Pfeifer, M., Lefebvre, V., Peres, C.A., Banks-Leite, C., Wearn, O.R., Marsh, C.J., … Ewers, R.M. 2017. Creation of forest edges has a global impact on forest vertebrates. *Nature*. **551**, pp.187–191.

Philipson, C.D., Cutler, M.E.J., Brodrick, P.G., Asner, G.P., Boyd, D.S., Costa, P.M., … Burslem, D.F.R.P. 2020. Active restoration accelerates the carbon recovery of human-modified tropical forests. *Science*. **369**(6505), pp.838–841.

Phillips, O.L., Rose, S., Mendoza, A.M., & Vargas, P.N. 2006. Resilience of southwestern Amazon forests to anthropogenic edge effects. *Conservation Biology*. **20**(6), pp.1698–1710.

Porensky, L.M., & Young, T.P. 2013. Edge-Effect Interactions in Fragmented and Patchy Landscapes. *Conservation Biology*. **27**(3), pp.509–519.

Püttker, T., Crouzeilles, R., Almeida-Gomes, M., Schmoeller, M., Maurenza, D., Alves-Pinto, H., … Prevedello, J.A. 2020. Indirect effects of habitat loss via habitat fragmentation: A cross-taxa analysis of forest-dependent species. *Biological Conservation*. **241**, p.108368.

Pütz, S., Groeneveld, J., Henle, K., Knogge, C., Martensen, A.C., Metz, M., … Huth, A. 2014. Long-term carbon loss in fragmented Neotropical forests. *Nature Communications*. **5**(1), p.5037.

Qie, L., Lewis, S.L., Sullivan, M.J.P., Lopez-Gonzalez, G., Pickavance, G.C., Sunderland, T., … Phillips, O.L. 2017. Long-term carbon sink in Borneo's forests halted by drought and vulnerable to edge effects. *Nature Communications*. **8**(Article no: 1966).

Le Quéré, C., Andrew, R.M., Friedlingstein, P., Sitch, S., Pongratz, J., Manning, A.C., … Zhu, D. 2017. Global Carbon Budget 2017. *Earth System Science Data Discussions*., pp.1–79.

Reynolds, G., Payne, J., Sinun, W., Mosigil, G., & Walsh, R.P.D. 2011. Changes in forest land use and management in Sabah, Malaysian Borneo, 1990-2010, with a focus on the Danum Valley region. *Philosophical Transactions of the Royal Society B: Biological Sciences*. **366**(1582), pp.3168–3176.

Ries, L., Fletcher, R.J., Battin, J., & Sisk, T.D. 2004. Ecological responses to habitat edges: mechanisms, models, and variability explained. *Annual Review of Ecology, Evolution, and*

Systematics. **35**, pp.491–522.

Ries, L., Murphy, S.M., Wimp, G.M., & Fletcher, R.J. 2017. Closing persistent gaps in knowledge about edge ecology. *Current Landscape Ecology Reports*. **2**, pp.30–41.

Rosoman, G., Sheun, S.S., Opal, C., Anderson, P., & Trapshah (Eds.), R. 2017. The HCS Approach Toolkit. Available from: http://highcarbonstock.org/wp-content/uploads/2017/05/HCSA-Toolkit-v2.0-Module-1-Introduction-190917-web.pdf.

RSPO 2018. *Roundtable on Sustainable Palm Oil Principles & Criteria for Sustainable Palm Oil* [Online]. Available from: https://rspo.org/resources/certification/rspo-principles-criteria-certification.

Schedlbauer, J.L., Finegan, B., & Kavanagh, K.L. 2007. Rain Forest Structure at Forest-Pasture Edges in Northeastern Costa Rica. *Biotropica*. **39**(5), pp.578–584.

Schwartz, N.B., Uriarte, M., Defries, R., Bedka, K.M., Fernandes, K., Gutiérrez-Vélez, V., & Pinedo-Vasquez, M.A. 2017. Fragmentation increases wind disturbance impacts on forest structure and carbon stocks in a western Amazonian landscape. *Ecological Applications*. **27**(6), pp.1901–1915.

Scriven, S.A., Carlson, K.M., Hodgson, J.A., McClean, C.J., Heilmayr, R., Lucey, J.M., & Hill, J.K. 2019. Testing the benefits of conservation set-asides for improved habitat connectivity in tropical agricultural landscapes M. Struebig, ed. *Journal of Applied Ecology*. **56**(10), pp.2274–2285.

Scriven, S.A., Waddell, E.H., Sim, S., King, H., Reynolds, G., Yeong, K.L., & Hill, J.K. 2022. Supporting decision-making by companies in delivering their climate net-zero and nature recovery commitments: Synthesising current information and identifying research priorities in rainforest restoration. *Global Ecology and Conservation*. **40**, p.e02305.

Searchinger, T., Waite, R., Hanson, C., Ranganathan, J., & Matthews, E. 2019. *Creating a Sustainable Food Future* [Online]. [Accessed 27 March 2023]. Available from: https://www.wri.org/research/creating-sustainable-food-future.

Searchinger, T.D., Wirsenius, S., Beringer, T., & Dumas, P. 2018. Assessing the efficiency of changes in land use for mitigating climate change. *Nature 2018 564:7735*. **564**(7735), pp.249–253.

Senior, M.J.M., Brown, E., Villalpando, P., & Hill, J.K. 2015. Increasing the Scientific Evidence Base in the “High Conservation Value” (HCV) Approach for Biodiversity Conservation in Managed Tropical Landscapes. *Conservation Letters*. **8**(5), pp.361–367.

Silva Junior, C.H.L., Aragão, L.E.O.C., Anderson, L.O., Fonseca, M.G., Shimabukuro, Y.E., Vancutsem, C., … Saatchi, S.S. 2020. Persistent collapse of biomass in Amazonian forest edges following deforestation leads to unaccounted carbon losses. *Science Advances*. **6**(40), p.eaaz8360.

Silva Junior, C.H.L., Carvalho, N.S., Pessôa, A.C.M., Reis, J.B.C., Pontes-Lopes, A., Doblas, J., … Aragão, L.E.O.C. 2021. Amazonian forest degradation must be incorporated into the COP26 agenda. *Nature Geoscience 2021 14:9*. **14**(9), pp.634–635.

Slik, J.W.F., van Beek, M., Bernard, C., Bongers, F., Breman, F.C., Cannon, C.H., & Sidiyasa, K. 2011. Limited edge effects along a burned-unburned Bornean forest boundary seven years after disturbance. *Biotropica*. **43**(3), pp.288–298.

Smith, I.A., Hutyra, L.R., Reinmann, A.B., Marrs, J.K., & Thompson, J.R. 2018. Piecing together the fragments: elucidating edge effects on forest carbon dynamics. *Frontiers in Ecology and the Environment*. **16**(4), pp.213–221.

Snaddon, J.L., Willis, K.J., & Macdonald, D.W. 2013. Oil-palm replanting raises ecology issues. *Nature 2013 502:7470*. **502**(7470), pp.170–171.

Stride, G., Thomas, C.D., Benedick, S., Hodgson, J.A., Jelling, A., Senior, M.J.M., & Hill, J.K. 2018. Contrasting patterns of local richness of seedlings, saplings, and trees may have implications for regeneration in rainforest remnants. *Biotropica*. **50**(6), pp.889–897.

Tang, L., & Shao, G. 2015. Drone remote sensing for forestry research and practices. *Journal of Forestry Research*. **26**(4), pp.791–797.

Taubert, F., Fischer, R., Groeneveld, J., Lehmann, S., Müller, M.S., Rödig, E., … Huth, A. 2018. Global patterns of tropical forest fragmentation. *Nature*. **554**, pp.519–522.

Williams, S.H., Scriven, S.A., Burslem, D.F.R.P., Hill, J.K., Reynolds, G., Agama, A.L., … Brodie, J.F. 2020. Incorporating connectivity into conservation planning for the optimal representation of multiple species and ecosystem services. *Conservation Biology*. **34**(4), pp.934–942.

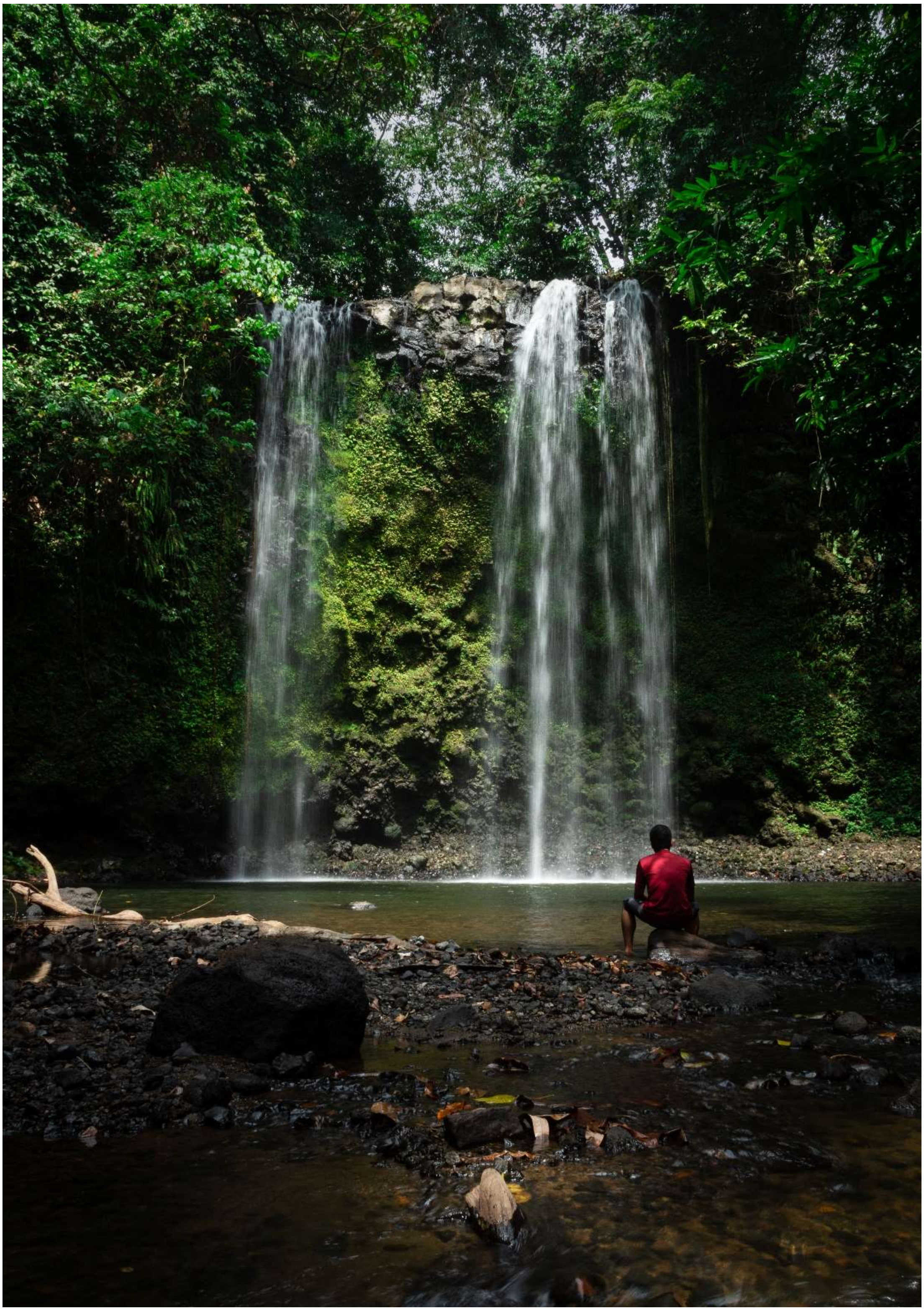
Willmer, J.N.G., Püttker, T., & Prevedello, J.A. 2022. Global impacts of edge effects on species richness. *Biological Conservation*. **272**, p.109654.

Zemp, D.C., Gérard, A., Hölscher, D., Ammer, C., Irawan, B., Sundawati, L., … Kreft, H. 2019. Tree performance in a biodiversity enrichment experiment in an oil palm landscape M. Isaac, ed. *Journal of Applied Ecology*. **56**(10), pp.2340–2352.

Zhao, Z., Li, W., Ciais, P., Santoro, M., Cartus, O., Peng, S., … Wang, J. 2021. Fire enhances forest degradation within forest edge zones in Africa. *Nature Geoscience 2021 14:7*. **14**(7), pp.479–483.

Zhu, L., Li, W., Ciais, P., He, J., Cescatti, A., Santoro, M., … Wang, J. 2023. Comparable biophysical and biogeochemical feedbacks on warming from tropical moist forest degradation. *Nature Geoscience 2023 16:3*. **16**(3), pp.244–249.

Appendices



Taking a break during field work

Appendix 1 – **Supporting information for Chapter 2**

Supplementary Information: Weak edge effects on trees in Bornean rainforest remnants bordering oil palm

Chapter 2 abstract translated into Malay –

Sebahagian besar kawasan hutan tropika dipelopori oleh habitat pinggir, yang turut mempengaruhi struktur kanopi hutan, stok karbon dan kepelbagaian biologi. Walau bagaimanapun, kesan habitat pinggir seperti ini sentiasa bergolak mengikut keadaan semasa, dan kajian seumpamanya dikawasan yang bersempadan dengan ladang kelapa sawit masih kurang. Di hutan tanah pamah Borneo, kami telah memilih 10 kawasan kajian habitat pinggir di kawasan hutan yang bersempadan dengan ladang kelapa sawit. Tinjauan dilakukan melalui penubuhan 0.2 ha plot-plot kajian di sepanjang transek habitat pinggir bersebelahan ladang sawit (i.e., 1.6 km transek; 5-6 plot bagi setiap transek; 57 jumlah plot). Kami mengkaji bagaimana kesan habitat pinggir diperingkat plot akan mempengaruhi struktur kanopi hutan (penutup kanopi, bilangan dan saiz batang ⩾ 10 cm diameter), stok karbon atas tanah, iklim mikro (suhu udara dan keamatan cahaya), dan komposisi komuniti pokok dan kekayaan spesis. Jumlah pokok terbesar jauh lebih kecil (sehingga 21% diameter dan semakin berkurangan) di plot berhampiran habitat pinggir dan karbon di peringkat plot juga adalah sehingga 30% lebih rendah (purata model-dipasang = 64.7 Mg ha-1 pada 50 m dari habitat pinggir, berbanding 92.3 Mg ha-1 pada 1600 m), dengan kesan ketara dalam lingkungan 300 m daripada jarak habitat pinggir. Walau bagaimanapun, kesan ketara habitat pinggir ini agak kecil dalam konteks variasi yang sedia ada, dimana terdapat <13% daripada jumlah kebolehubahan dalam saiz pokok maksimum atau karbon. Secara amnya tiada kesan habitat pinggir terhadap mana-mana komponen lain, struktur hutan, seperti, komposisi atau kepelbagaian, dan hanya terdapat kesan iklim mikro yang sangat kecil. Kami berpendapat bahawa kesan habitat pinggir yang terhad dalam kajian ini mungkin boleh mengambarkan perbezaan struktur fungsi yang rendah antara hutan dan ladang kelapa sawit yang matang, dimana penyesaran pokok perintis di ladang kelapa sawit adalah terhad. Keadaan ini turut mempengaruhi habitat pinggir dalam struktur hutan hujan tropika yang pelbagai.

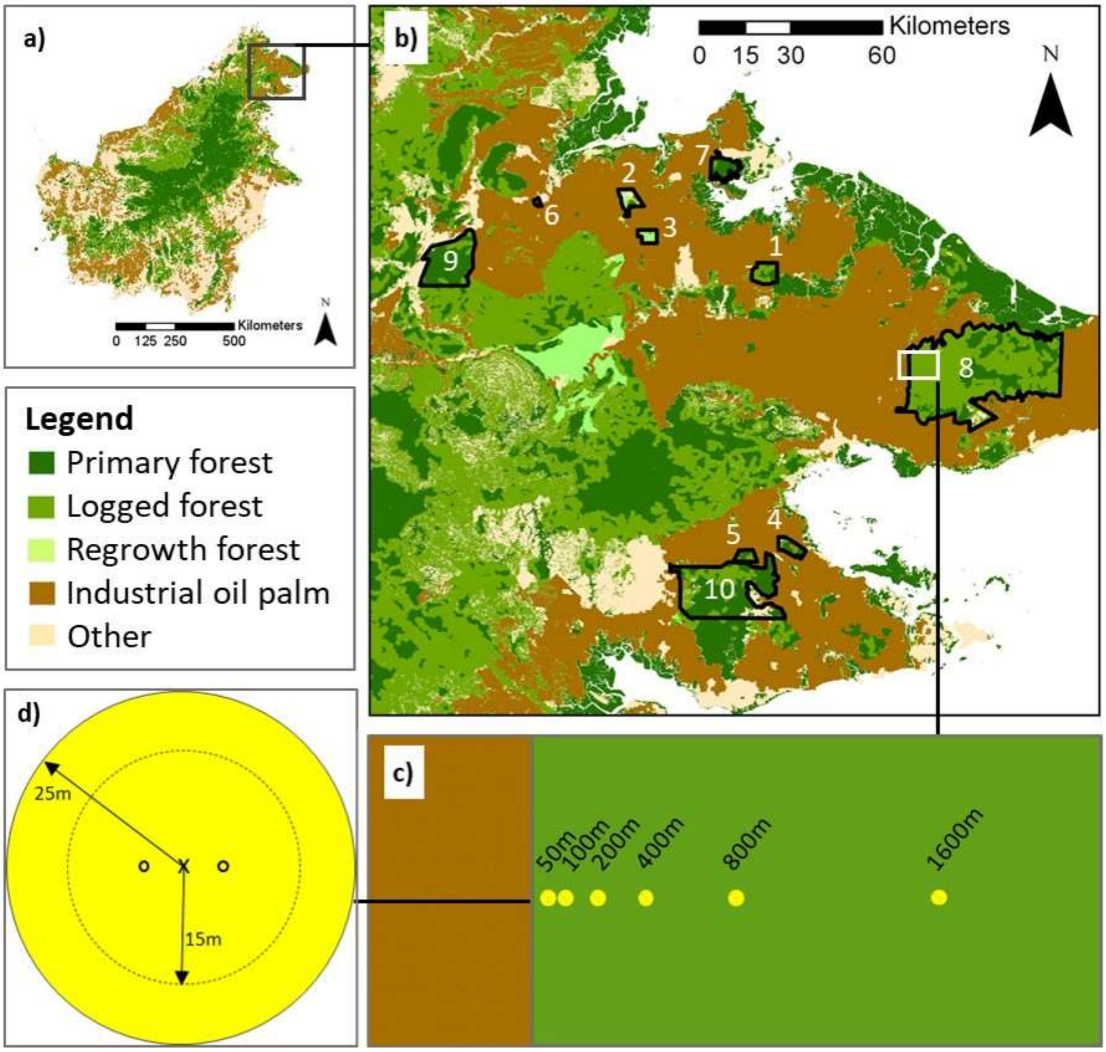


Figure S1. Clockwise from left: (**a**) Location of study area in Sabah, Malaysian Borneo and (**b**) location of the 10 forest remnant sites (see Table S1 for information on each). Maps of forest cover and oil palm plantations were obtained from CIFOR (Gaveau et al., 2014; Gaveau et al., 2016), reserve outlines were downloaded from the World Database of Protected Areas (WDPA; http://www.protectedplanet.net). (**c**) Transects ran perpendicular from the edge and contained five or six 0.2 ha circular plots, with plot centres at 50 m, 100 m, 200 m, 400 m, 800 m and (in seven sites) 1600 m from the edge. (**d**) Nested sampling plot design. We inventoried live stems ≥25 cm dbh in the main plot of 25 m radius (0.2 ha), and live stems ≥10 cm and <25 cm dbh in the subplot of 15 m radius (0.07 ha). Canopy density was measured in 4 compass directions from the plot centre, and microclimate data loggers were placed 5 m to the East and West of the plot centre (hollow circles), 1.8 m from the ground.

Table S1. Locations and descriptions of study sites. Levels of protection of sites are Sabah Government Classifications. All sites are Class I, VI or VII forest reserves, which are protected for the purposes of environmental safeguarding, nature conservation and scientific research (McMorrow and Talip, 2001) and typically have the most protected forest carbon stocks and biological diversity in Sabah (Asner et al., 2018). All edge ages are for 2019 (when the field study was conducted) and were obtained from CIFOR (Gaveau et al., 2014; Gaveau et al., 2016). Edge age is not available for Site 6, but is likely 20-49 years, based on patterns of deforestation in the surrounding landscape. *Edge creation at Site 4 appears to have taken place 49 years prior to the study, however there may have been additional expansion (approx. 50m) of the plantation into the forest 19 years ago.

Site	Site name	Transect start (edge) lat/long	Protection classification	Transect length (m)	Edge age (years)	Palm height (m)
1	Gomantong	5.5361/118.1083	I	1600	19	15
2	Lungmanis North	5.734733/117.648167	VI	1600	46	16
3	Lungmanis South	5.632233/117.756517	VI	1600	46	7
4	Madai-Baturong 1	4.728533/118.113517	VI	1600	49*	10
5	Madai-Baturong 2	4.689667/118.042783	VI	1600	29	10
6	Sapi	5.736883/117.409	VI	800	-	10
7	Sepilok	5.86695/117.929183	VI	800	49	11
8	Tabin	5.259867/118.496133	VII	1600	19	16
9	Tawai	5.621233/117.21605	I	1600	19	18
10	Ulu Kalumpang	4.653533/118.058467	I	800	49	11

Microclimate measurements

We measured air temperature (°C) and light intensity (lum/ft^2) within each plot using two Hobo$^®$ loggers (Figure S1d), which took readings every 20 minutes for 1-5 days. Sampling periods were consistent across all plots within a site, but sites were sampled on different days. Mean daily temperature (24hr) and mean daytime (0600 - 1800 h) light intensity were calculated at the plot-level by averaging measurements from the two loggers. For one plot, measurements were calculated from a single logger as the second was removed by wildlife.

Carbon stock estimation

Wood density (g/cm^3) values were assigned using the Global Wood Density Database (Zanne et al., 2009; Chave et al., 2009), at the finest taxonomic level available, after checking identifications against a taxonomic database (The Plant List, 2013). Densities were assigned to 12.9% of stems at species level, 82.4% at genus level and 4.6% at family level. Mean plot-level wood density was assigned to one unidentified individual (0.04% of all stems). We used the R BIOMASS package (Rejou-Mechain et al., 2017) to estimate tree biomass, using a pantropical allometric equation that incorporates tree dbh, height and wood density (Chave et al., 2014), which is the preferred equation when these measurements are available (Labrière et al., 2016; Fleiss et al., 2020), and used a mixed-species model for palms (using stem height, dbh and dry mass fraction set at 0.37) (Goodman et al., 2013). Assuming a carbon content of 47.1% (Thomas and Martin, 2012), we converted biomass estimates to plot-level AGC (Mg C ha^{-1}).

Generating an 'expected' abundance-based distribution of genera amongst distance classes

Having pooled all data from the 10 sites into 3 distance classes: 'edge' (50m + 100m plots), 'intermediate' (200m + 400m plots) and 'core' (800m + 1600m plots), we used a randomisation approach to generate an expected random distribution of genera among each possible combination of classes (e.g. 'edge only', 'edge + intermediate', 'edge + core' etc. and 'all classes'; *n* = 7 categories in total), based on the abundance of each genus in the entire dataset (number of occurrences) and observed stem counts in each of the three distance classes. We repeated randomised draws 1000 times and calculated the mean number of genera found in each of the 7 categories, to serve as our 'expected' values in our chi-square goodness-of-fit test.

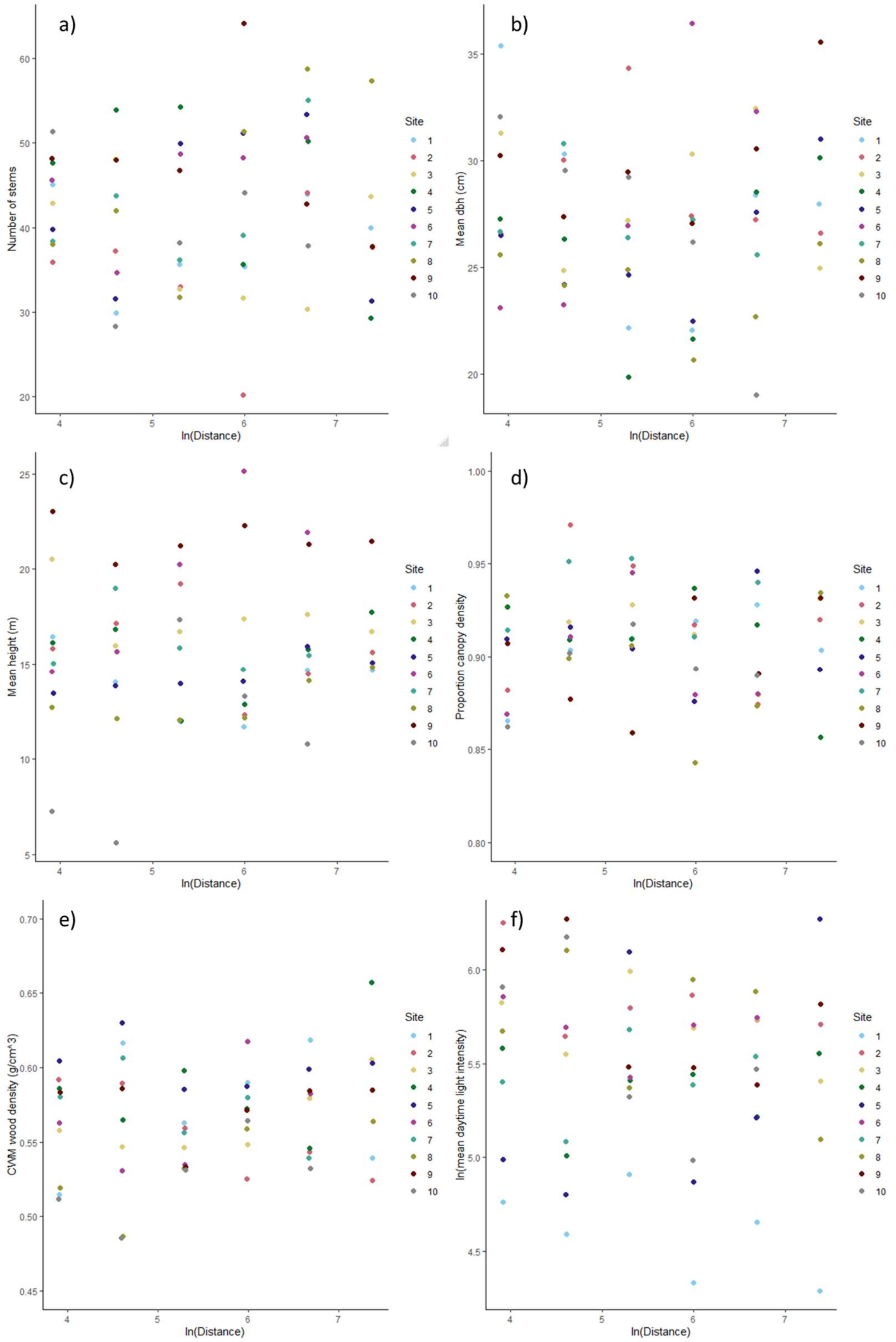


Figure S2. No effect of edge proximity (ln-transformed) on (**a**) number of stems, (**b**) mean dbh (cm), (**c**) mean height (m), (**d**) proportion canopy density, (**e**) community-weighted mean wood density (g/cm^3) or (**f**) mean daytime light intensity (lum/ft^2; ln-transformed). Minor jitter applied to all figures to aid visualisation of overlapping data points. See Table 1 in main text for model structures, coefficients and significance values.

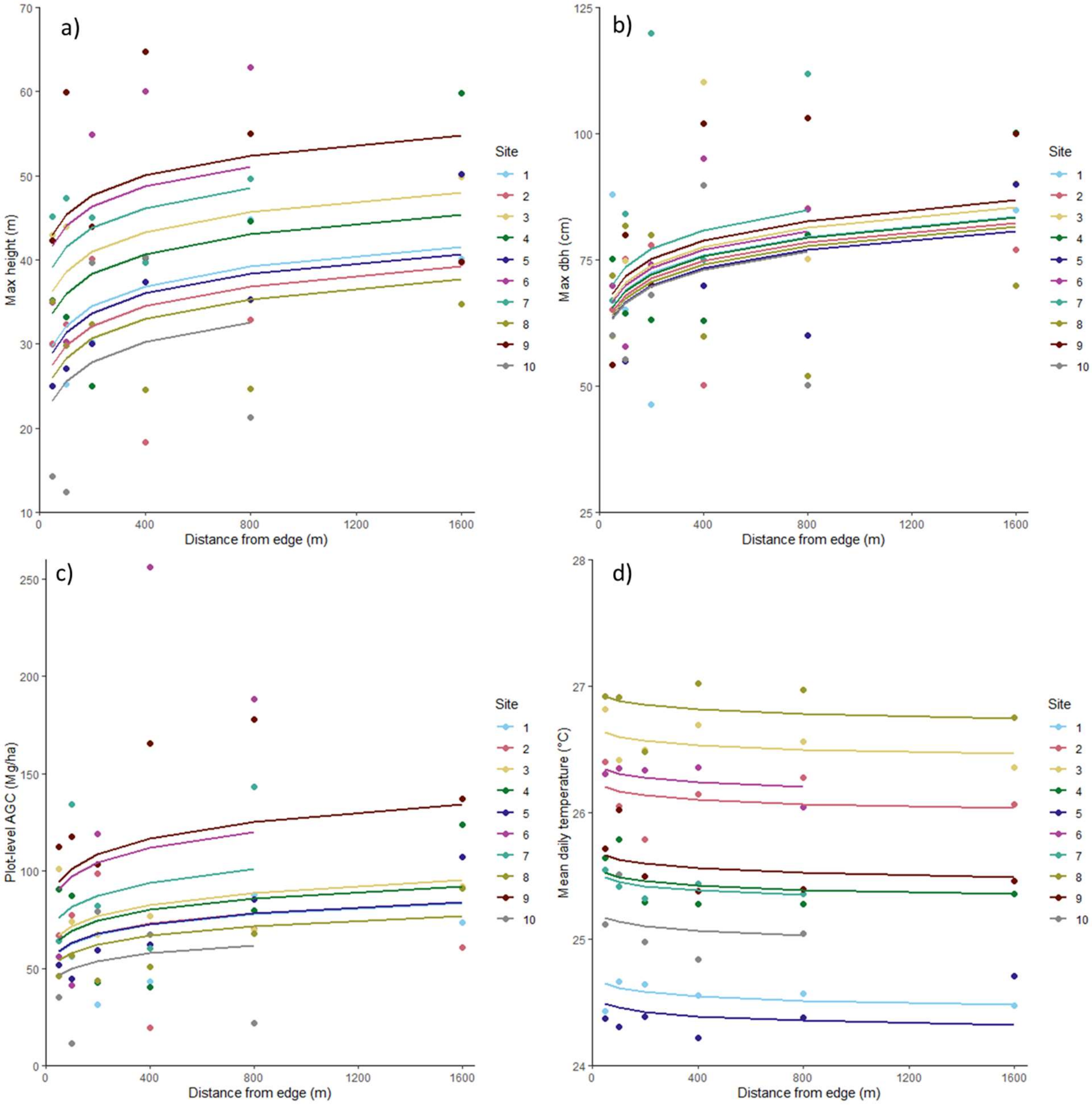


Figure S3. Significant effect of edge proximity (ln-transformed) on (**a**) maximum height (m), (**b**) maximum dbh (cm), (**c**) AGC (Mg ha^{-1}) and (**d**) mean daily temperature (°C), with random site intercept shown (individual trend lines for each site, from model-fitted values). Relationships are plotted against untransformed distance in order to visualise the non-linear edge effect. Maximum dbh was ln-transformed prior to analysis, therefore the exponents of predicted values were taken to make results more interpretable. Minor jitter applied to all figures to aid visualisation of overlapping data points. See Table 1 in main text for model structures, coefficients and significance values.

Taxonomic sensitivity analyses

To confirm that our results are robust to the taxonomic resolution of our data, which are primarily at genus level, we repeated all analyses of diversity and composition using higher-resolution subsets of our data, using the same analytical methods described in the main text. Firstly, we calculated community-weighted mean (CWM) wood density (g/cm^3) for each plot using only the stems for which we had species-level trait values (12.9% of our stems), which excluded six plots that contained no species-level values. Re-analysis of these scores for the remaining 51 plots (mixed-effects model, random site intercept) gave the same qualitative result as we originally reported of no effect of distance on CWM wood density ($\beta = 0.01$, $p = 0.25$; Figure S4a).

Secondly, our original analysis of CWM wood density included some data at family level, and so we re-calculated CWM values using only those stems for which we had either species- or genus-level wood density values (95.3% of stems). Previously this analysis had been non-significant, but re-analysis of these scores indicated a significant but weak effect of distance on CWM wood density ($N = 57$, $\beta = 0.008$, $p = 0.035$; Figure S4b). However, model residual plots indicated a clear outlier - a plot with an exceptionally low CWM value. Repeating the analysis with this plot excluded resulted in our original conclusion of no significant edge effect ($N = 56$, $\beta = 0.007$, $p = 0.059$), indicating that the significant effect was being driven by this single outlier plot. This outlier plot had a large number of stems with family-level trait data (43% of stems vs average 5% stems in other plots) and so the removal of stems with family-level trait values had an exceptionally large influence on this plot, further justifying its removal from this analysis. The removal of another plot with a disproportionate number of family-level data (57% of stems), also highlighted as a possible outlier in residual plots, confirmed our original finding of no edge effects on CWM wood density (with two outlier plots removed; $\beta = 0.008$, $p = 0.186$). Our original analysis reported in the main text revealed a non-significant 3% decline in CWM wood density from 1600m to 50m from the edge, and this new analysis excluding family-level data reports a similarly small effect size of a 5% decline in CWM wood density (with or without the two outlier plots included).

We also repeated our analyses of taxonomic composition (NMDS ordination & PERMANOVA analysis) and diversity (mixed-effect model of distance-from-edge on richness) using only stems with species-level identifications (23.1% of our stems), which excluded one plot that contained no species-level stems. These analyses support our original findings of no edge effects on plot-level composition (no clustering by distance in species-level NMDS ordination analysis, Figure S4c; no effect of distance on species composition in the PERMANOVA: $R^2 = 0.08$, $p = 0.85$) or richness (no effect of distance-from-edge on species richness, $\beta = 0.086$, $p = 0.11$; Figure S4d).

Finally, we repeated our randomisation analysis on data pooled into three distance classes (edge, intermediate and core), using species-level stems (23.1% of our stems). In contrast to our original analysis, the chi-square goodness-of-fit test using pooled species-level data revealed fewer species shared between all three distance classes, more species shared between the intermediate and core distances, and more species unique to the core distance, than expected by chance ($\chi^2(6) = 24.9$, $p = 0.0004$; Table S2), indicative of a possible edge effect. However, there was no evidence of fewer species shared between the edge and core classes than expected by chance, and no evidence of more unique species at the edge. Additionally, species that were absent from the edge category but were either unique to the core or present in both the intermediate and core classes (i.e. those that were driving the significant effect), were rare species (average <1 individual/ha in our dataset) which can confound species-level compositional analyses (Laurance et al., 2006; Ewers et al., 2017).

Overall, sensitivity analyses show that our results are robust to the taxonomic resolution of our data, with no qualitative change in most results. A minority of analyses did give significant results, but these were biologically weak and were driven entirely by outlier plots or rare species. These analyses therefore support our conclusion that edge effects are weak in this study.

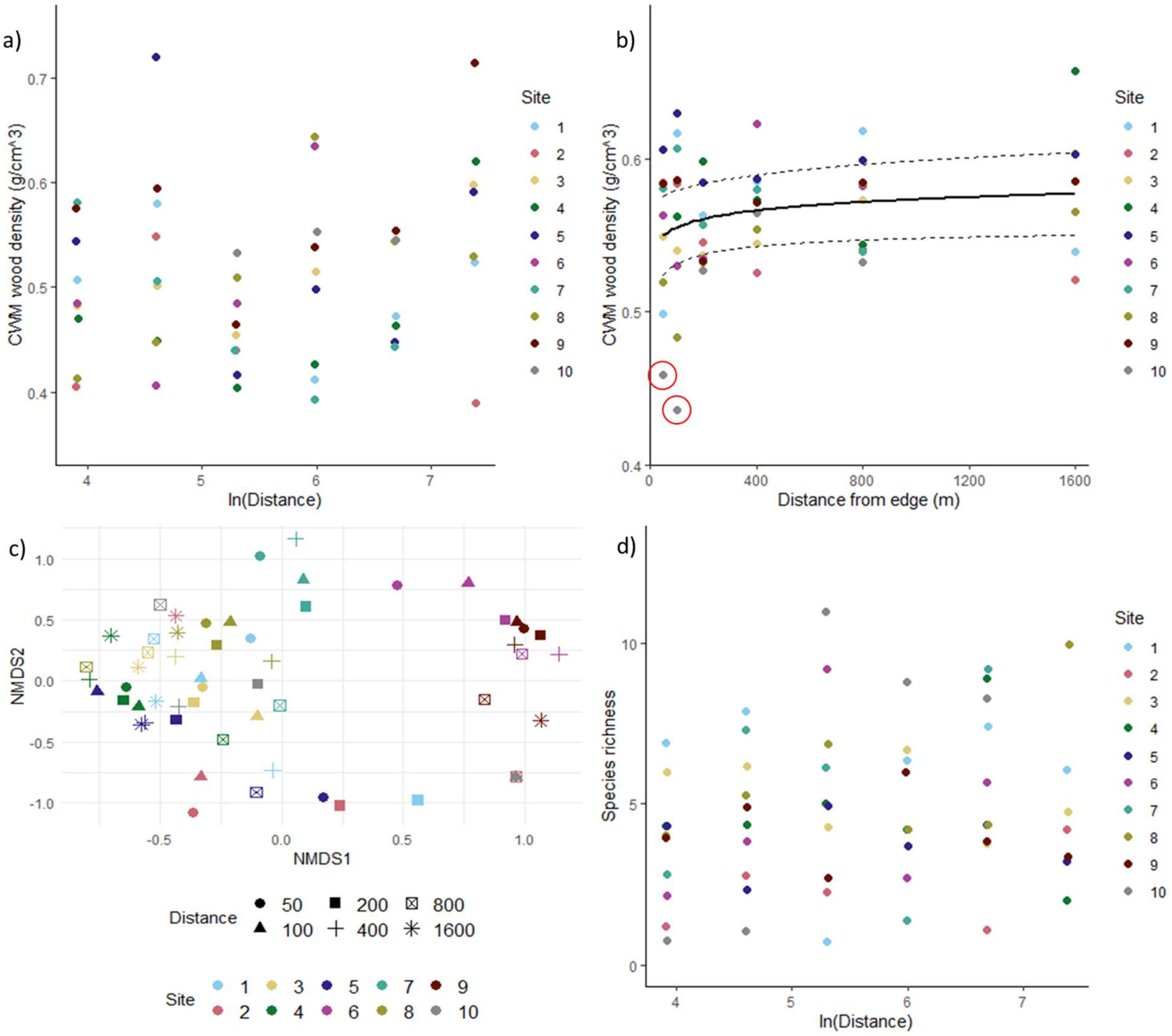


Figure S4. (**a**) No effect of edge proximity (ln-transformed distance-from-edge) on community-weighted mean wood density (g/cm^3) calculated from species-level wood density estimates only (N = 51, β = 0.01, p = 0.25), but a significant effect on (**b**) Community-weighted mean wood density (g/cm^3) calculated from species- and genus-level wood density estimates only (N = 57, β = 0.008, p = 0.035), with relationship plotted against untransformed distance to visualise the non-linear effect, and with 95% confidence intervals. However, this effect is driven by 2 outlier plots (circled) that experienced a disproportionate loss of data when family-level wood density values were removed, and the effect disappears when these plots are excluded from the analysis (N = 55, β = 0.008, p = 0.186). (**c**) Non-metric multidimensional scaling (NMDS) of plot species composition (N = 56) using Bray–Curtis index scores based on relative abundances (stress = 0.26), (**d**) No effect of edge proximity (ln-transformed) on plot-level species richness (*N* = 56, *β* = 0.086, *p* = 0.11). Minor jitter applied to all figures to aid visualisation of overlapping data points.

Table S2. Observed and expected numbers of species in each combination of distance classes, from pooled species-level data (23.1% of our stems). 'Edge' (**E**) = 50m + 100m plots, 'Intermediate' (**I**) = 200m + 400m plots and 'Core' (**C**) = 800m + 1600m plots. Expected values were generated using randomised abundance-based draws. A chi-square goodness-of-fit test showed a significant difference between the expected and observed distribution of species amongst distance classes ($\chi^2(6) = 24.9$, $p = 0.0004$). Post hoc two-tailed z-tests (parameterised from the same randomisation approach) were used to identify where these significant differences were (denoted in **bold**) based on a critical value of $z = 1.96$.

	E + I + C	**I + C**	**E + C**	**E + I**	**C only**	**I only**	**E only**
Observed	17	13	6	6	10	11	6
Expected	28.8	4.9	5.8	8.2	5.6	7.3	8.4
Z	**-5.34**	**4.2**	0.08	-0.97	**2.17**	1.72	-1.04

Figure S5. Emergent *Koompassia excelsa* at the edge of a rainforest remnant bordering an oil palm plantation in Sabah, Borneo, with palms in the foreground. Large emergent trees such as this are the most vulnerable to edge effects, as evidenced by the findings of our study. Photo credit: J Anderson (author).

Table S3. Genera and species sampled in this study, along with abundance (number of occurrences) across the entire dataset.

Taxa	**Abundance**
Actinodaphne spp.	3
Aglaia spp.	39
Alangium spp.	21
Alangium javanicum	2
Albizia spp.	1
Allophylus spp.	1
Alstonia spp.	9
Anisophyllea spp.	9
Anisoptera costata	1
Antidesma spp.	4
Aporosa spp.	10
Aporosa elmeri	2
Aquilaria spp.	1
Archidendron spp.	33
Ardisia spp.	1
Artocarpus spp.	20
Baccaurea spp.	23
Barringtonia spp.	38
Barringtonia lanceolata	1
Beilschmiedia spp.	15
Blumeodendron spp.	2
Bridelia glauca	1
Brownlowia spp.	11
Brownlowia peltata	2
Buchanania spp.	7
Callicarpa spp.	14
Calophyllum spp.	4
Canarium spp.	35

Carallia spp.	2
Caryota spp.	7
Castanopsis spp.	2
Chionanthus spp.	9
Chisocheton spp.	44
Chisocheton sarawakanus	5
Cleistanthus spp.	17
Crateva spp.	1
Crateva magna	1
Croton spp.	40
Croton argyratus	4
Cryptocarya spp.	7
Dasymaschalon spp.	4
Decaspermum spp.	1
Dehaasia spp.	34
Dendrocnide spp.	7
Dillenia spp.	8
Dillenia excelsa	4
Dimocarpus spp.	12
Dimorphocalyx spp.	1
Diospyros spp.	65
Dipterocarpus caudiferus	19
Dipterocarpus confertus	1
Dipterocarpus gracilis	2
Dipterocarpus lowii	2
Dipterocarpus stellatus	9
Dracontomelon spp.	2
Dracontomelon costatum	1
Dryobalanops beccarii	38
Dryobalanops lanceolata	33
Drypetes spp.	89
Drypetes longifolia	3

Duabanga spp.	1
Duabanga moluccana	1
Durio spp.	17
Dysoxylum spp.	27
Elaeis guineensis	35
Elaeocarpus spp.	2
Endospermum spp.	23
Erythroxylum spp.	1
Eusideroxylon spp.	74
Fagraea spp.	13
Ficus spp.	32
Fordia spp.	2
Garcinia spp.	14
Gironniera spp.	22
Glochidion spp.	45
Gluta spp.	6
Gluta wallichii	3
Gmelina spp.	1
Gonystylus spp.	3
Guioa spp.	3
Helicia spp.	20
Heynea spp.	2
Homalium spp.	12
Hopea ferruginea	2
Hopea nervosa	14
Hopea pentanervia	8
Hopea sangal	9
Hydnocarpus spp.	24
Hydnocarpus borneensis	4
Ixora spp.	4
Kibatalia arborea	1
Knema spp.	22

Koilodepas spp.	3
Koompassia spp.	1
Koompassia excelsa	5
Koordersiodendron spp.	1
Koordersiodendron pinnatum	1
Lansium spp.	10
Leucaena spp.	1
Lithocarpus spp.	31
Litsea spp.	42
Lophopetalum spp.	9
Ludekia spp.	9
Macaranga spp.	18
Macaranga conifera	1
Macaranga gigantea	5
Macaranga hypoleuca	10
Madhuca spp.	7
Magnolia spp.	6
Mallotus spp.	33
Mallotus peltatus	19
Mangifera spp.	2
Meiogyne spp.	2
Melanochyla auriculata	2
Melicope spp.	2
Memecylon spp.	1
Microcos spp.	43
Monoon spp.	4
Myristica spp.	7
Nauclea spp.	50
Neesia spp.	6
Neo-uvaria spp.	1
Neolamarckia spp.	30
Neolamarckia cadamba	12

Neolitsea spp.	1
Neoscortechinia spp.	1
Nephelium spp.	2
Nephelium ramboutanake	2
Ochanostachys spp.	2
Ochanostachys amentacea	2
Octomeles sumatrana	24
Palaquium spp.	29
Pangium spp.	1
Paracroton spp.	1
Paranephelium spp.	36
Paraserianthes spp.	1
Parashorea spp.	1
Parashorea malaanonan	4
Parashorea tomentella	96
Parishia spp.	1
Payena spp.	1
Pentace spp.	57
Pentace laxiflora	2
Planchonia spp.	1
Pleiocarpidia spp.	25
Pleiocarpidia sandahanica	8
Polyalthia spp.	37
Polyalthia sumatrana	1
Psydrax spp.	13
Pternandra spp.	12
Pterocymbium spp.	1
Pterospermum spp.	111
Quercus spp.	1
Ryparosa spp.	2
Sageraea spp.	1
Santiria spp.	15

Saraca declinata	1
Scaphium spp.	31
Scleropyrum pentandrum	1
Scorodocarpus spp.	1
Shorea acuminatissima	6
Shorea agamii	4
Shorea beccariana	6
Shorea falciferoides	6
Shorea fallax	10
Shorea gibbosa	6
Shorea guiso	3
Shorea johorensis	23
Shorea laxa	8
Shorea leprosula	21
Shorea leptoderma	2
Shorea macroptera	6
Shorea mecisopteryx	1
Shorea multiflora	2
Shorea ovalis	7
Shorea parvifolia	22
Shorea seminis	3
Shorea smithiana	5
Shorea superba	1
Sindora spp.	6
Sloanea spp.	1
Stemonurus spp.	7
Symplocos spp.	2
Symplocos fasciculata	1
Syzygium spp.	71
Tabernaemontana spp.	4
Teijsmanniodendron spp.	16
Terminalia spp.	5

Urophyllum spp.	1
Vatica oblongifolia	4
Vatica sarawakensis	3
Walsura pinnata	2
Xanthophyllum spp.	6

References

Asner, G.P., Brodrick, P.G., Philipson, C., Vaughn, N.R., Martin, R.E., Knapp, D.E., … Coomes, D.A. 2018. Mapped aboveground carbon stocks to advance forest conservation and recovery in Malaysian Borneo. *Biological Conservation*. **217**, pp.289–310.

Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G., & Zanne, A.E. 2009. Towards a worldwide wood economics spectrum. *Ecology Letters*. **12**(4), pp.351–366.

Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M.S., Delitti, W.B.C., … Vieilledent, G. 2014. Improved allometric models to estimate the aboveground biomass of tropical trees. *Global Change Biology*. **20**(10), pp.3177–3190.

Ewers, R.M., Andrade, A., Laurance, S.G., Camargo, J.L., Lovejoy, T.E., & Laurance, W.F. 2017. Predicted trajectories of tree community change in Amazonian rainforest fragments. *Ecography*. **40**(1), pp.26–35.

Fleiss, S., Waddell, E.H., Bala Ola, B., Banin, L.F., Benedick, S., Bin Sailim, A., … Hill, J.K. 2020. Conservation set-asides improve carbon storage and support associated plant diversity in certified sustainable oil palm plantations. *Biological Conservation*. **248**(Article no: 108631).

Gaveau, D.L.A., Sheil, D., Husnayaen, Salim, M.A., Arjasakusuma, S., Ancrenaz, M., … Meijaard, E. 2016. Rapid conversions and avoided deforestation: examining four decades of industrial plantation expansion in Borneo. *Scientific Reports*. **6**(Article no: 32017).

Gaveau, D.L.A., Sloan, S., Molidena, E., Yaen, H., Sheil, D., Abram, N.K., … Meijaard, E. 2014. Four Decades of Forest Persistence, Clearance and Logging on Borneo. *PLoS One*. **9**(7), p.e101654.

Goodman, R.C., Phillips, O.L., Del Castillo Torres, D., Freitas, L., Cortese, S.T., Monteagudo, A., & Baker, T.R. 2013. Amazon palm biomass and allometry. *Forest Ecology and Management*. **310**, pp.994–1004.

Labrière, N., Locatelli, B., Vieilledent, G., Kharisma, S., Basuki, I., Gond, V., & Laumonier, Y. 2016. Spatial congruence between carbon and biodiversity across forest landscapes of northern Borneo. *Global Ecology and Conservation*. **6**, pp.105–120.

Laurance, W.F., Nascimento, H.E.M., Laurance, S.G., Andrade, A., Ribeiro, J.E.L.S., Giraldo, J.P., … D'Angelo, S. 2006. Rapid decay of tree-community composition in Amazonian forest fragments. *Proceedings of the National Academy of Sciences of the United States of America*. **103**(50), pp.19010–19014.

McMorrow, J., & Talip, M.A. 2001. Decline of forest area in Sabah, Malaysia: Relationship to state policies, land code and land capability. *Global Environmental Change*. **11**(3), pp.217–230.

Rejou-Mechain, M., Tanguy, A., Piponiot, C., Chave, J., & Herault, B. 2017. BIOMASS : an {R} package for estimating above-ground biomass and its uncertainty in tropical forests. *Methods in Ecology and Evolution*. **8**(9).

The Plant List 2013. The Plant List Version 1.1. *The Plant List Version 1.1*. [Online]. [Accessed 1 March 2020]. Available from: http://www.theplantlist.org/.

Thomas, S.C., & Martin, A.R. 2012. Carbon Content of Tree Tissues: A Synthesis. *Forests*. **3**(2), pp.332–352.

Zanne, A.E., Lopez-Gonzalez, G., Coomes, D.A., Ilic, J., Jansen, S., Lewis, S.L., … Chave, J. 2009. Global wood density database. Available from: https://doi.org/10.5061/dryad.234.

Appendix 2 – **Supporting information for Chapter 3**

Supplementary Information: Proximity to multiple edges reduces carbon stocks in fragmented tropical rainforests

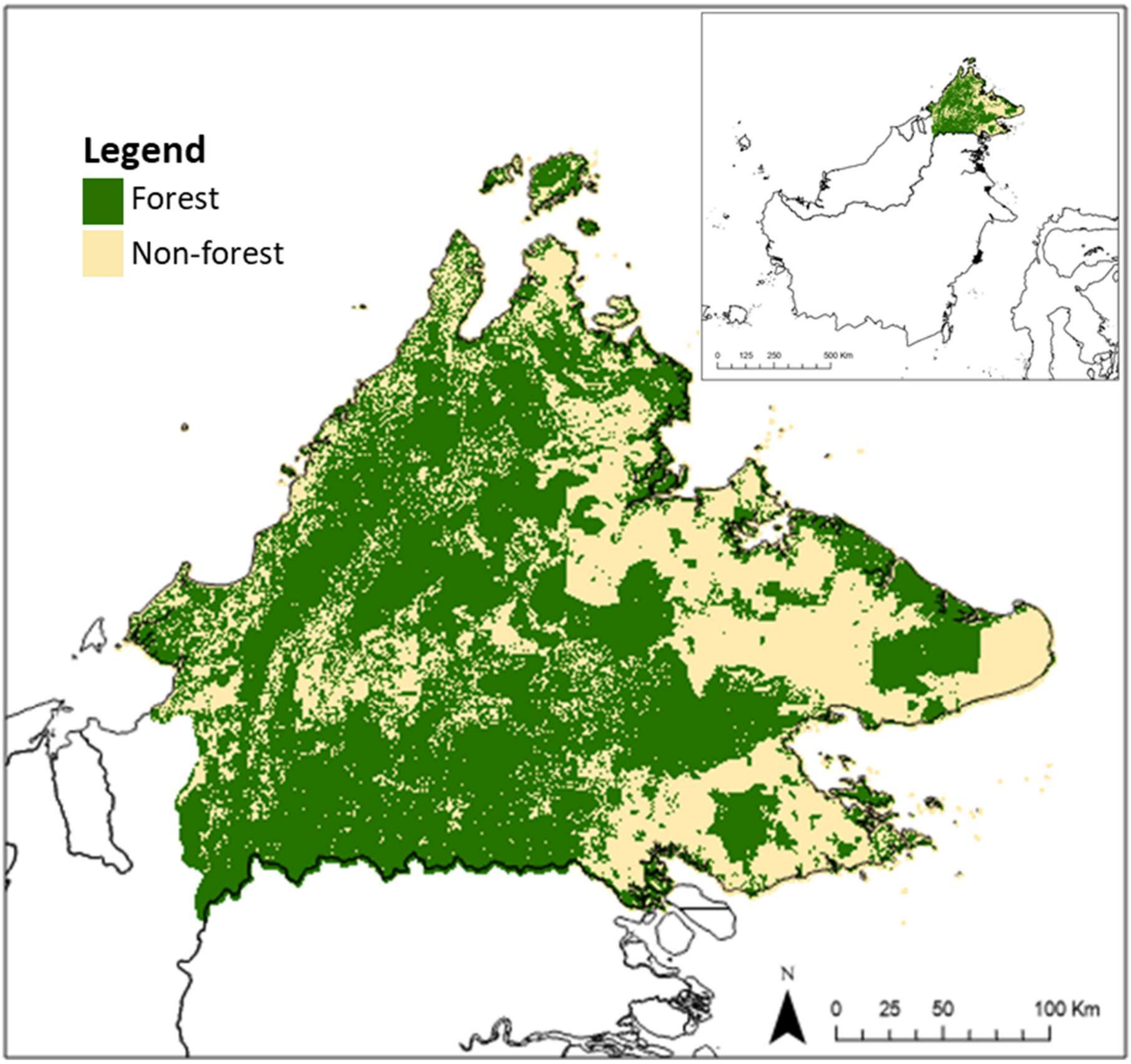
Generating a map of forest edginess for Sabah

In order to generate a map of edginess for forest pixels throughout Sabah, we adapted the heat-diffusion code provided by Malcolm et al. (2017), which allows for the parameterisation of multiple edge effects according to known edge gradients. Thus, modelling parameters were developed in a single-edge dummy landscape raster, given that the relationship between edge proximity and aboveground carbon is well studied in single edges (Ordway and Asner, 2020; Anderson et al., 2022). As recommended by Malcolm et al., we specified a constant temperature of 35 for all non-forest pixels (T_{max} = 35), a starting temperature of 20 for all forest pixels (T_{min} = 20), and an α value of 0.24 (proportionality constant specifying the proportion of heat transferred between neighbouring pixels with each iteration). The diffusion proceeds iteratively, with heat permeating inwards from non-forest into adjacent forest in a stepwise manner, therefore the number of iterations determines the depth of edge influence parameterised. Thus, after each iteration we extracted the modelled temperatures (a proxy for edge influence) of forest pixels in our dummy landscape, and ran a segmented regression (Muggio, 2008) of temperature against distance to edge, to identify the depth of the modelled edge effect. In this way, we identified the 103rd iteration (i = 103) as the one which parameterised a 300m edge effect. We then applied the heat-diffusion model to our binary land cover raster for Sabah in 2016, using these parameters (T_{max} = 35, T_{min} = 20, α = 0.24, i = 103), to generate our map of forest edginess. Because the model is additive, the modelled temperatures in areas of edge intersection represent the summed influence of all nearby edges that are close enough to have an influence. Heat diffusion is not adjusted based on the identity of the neighbouring non-forest, given that the influence of matrix identity on edge effects is not well quantified. Finally, we scaled the temperature values to between 0-1, based on the full range of values present, to improve metric interpretability and produce our final edginess metric. This metric of edginess offers advantages over alternatives such as ‘edge density’ (Ries et al., 2017) or the ‘point edge effect’ (Malcolm, 1994; Fernández et al., 2002), which do not capture the non-linear influence of edges and give unrealistic estimates in small fragments (Malcolm et al., 2017; Ries et al., 2017). For full details of the heat diffusion model, including model equations, see Malcolm et al. (2017).

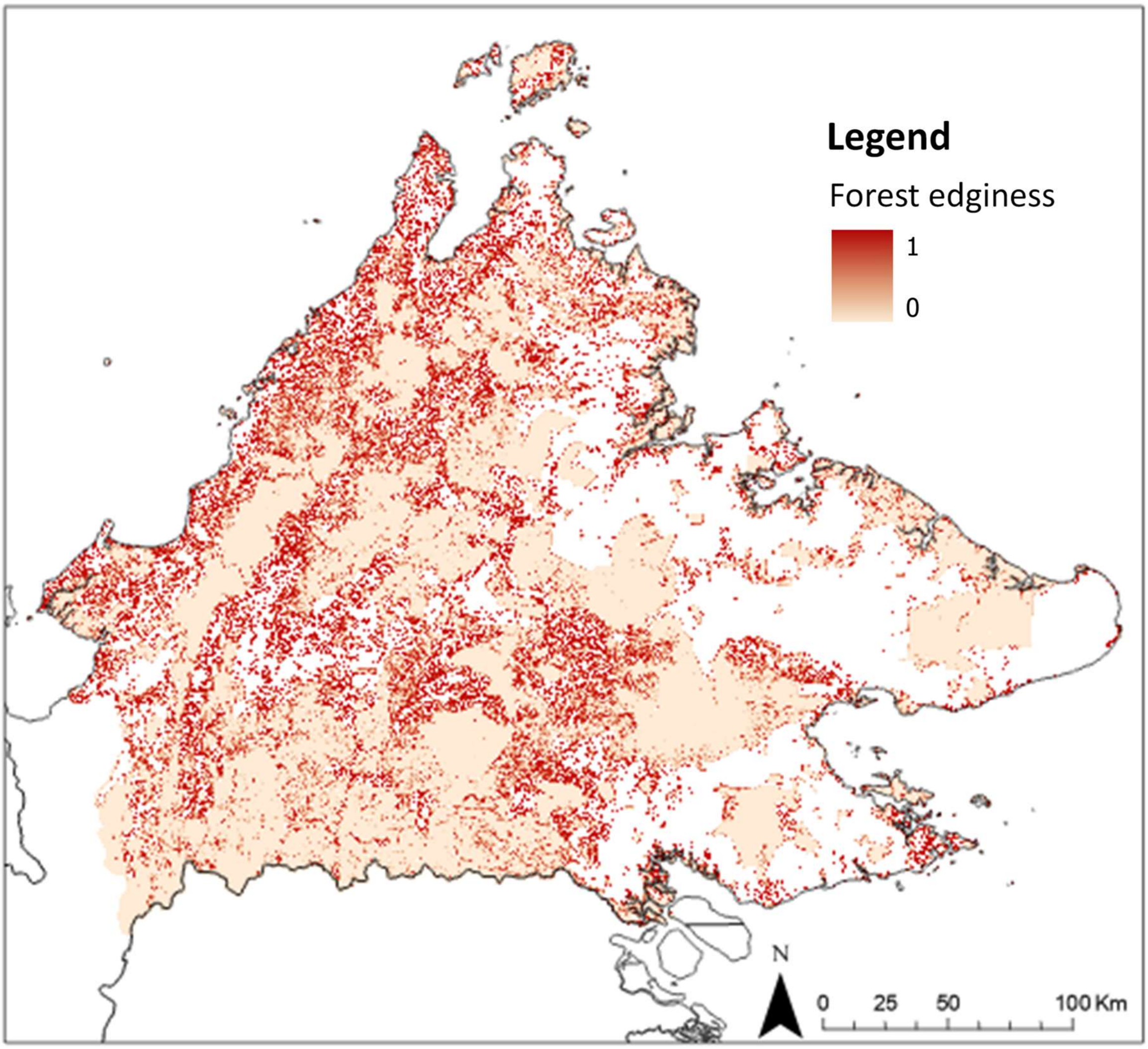
Spatial autocorrelation

Correlograms revealed evidence of spatial autocorrelation in model residuals, therefore we constructed additional spatial regressions to ensure that our results are robust to this autocorrelation. Given the unreasonably large computation times associated with spatial analysis of large datasets (Beale et al., 2010), we partitioned our landscape and constructed spatial regressions for a 17,000 ha sub-region which contained a similar distribution of edginess values as in the full landscape. For the 2275 sampled pixels in this sub-region, we constructed models using standard Ordinary Least Squares (OLS) methods as in the main text (non-spatial regressions), then compared results to those from models constructed using Generalized Least Squares (GLS) methods (as recommended by Dormann et al. (2007) and Beale et al. (2010)), which accounted for spatial autocorrelation using a Gaussian autocorrelation structure.

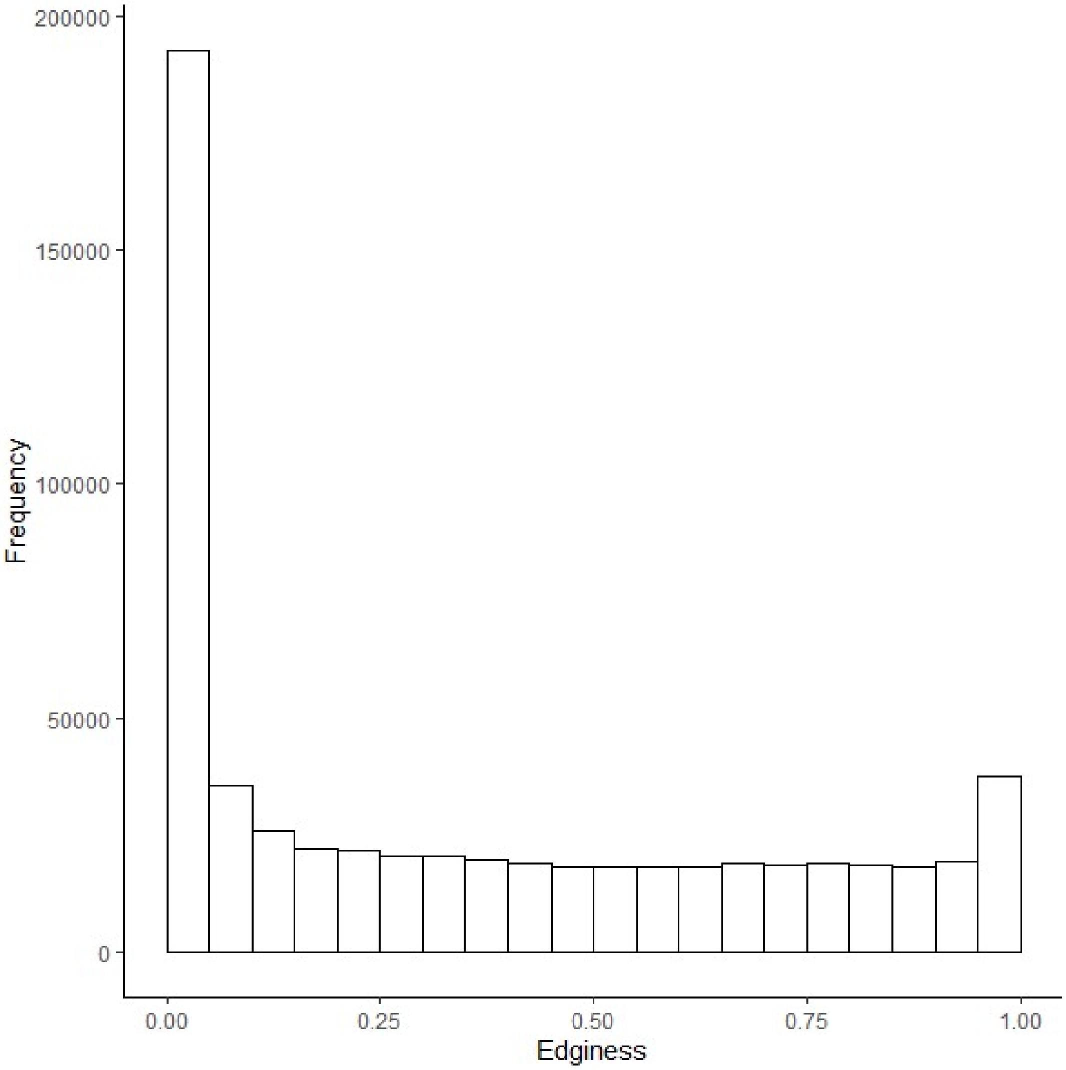
Results of the OLS models for the sub-region are qualitatively the same as those reported for the full landscape in the main text, with only a small change in model parameters. There is a significant negative effect of edginess on sqrt-transformed AGC (β = -4.32, p <0.0001) and a significant positive effect of Euclidean distance ($\log_{10}$ transformed) on sqrt-transformed AGC (β = 2.88, p < 0.0001), with the edginess model outperforming the Euclidean distance model (ΔAIC = 251). Results of the GLS models give qualitatively the same results after accounting for spatial autocorrelation, with a significant negative effect of edginess on sqrt-transformed AGC (β = -4.2, p <0.0001), a significant positive effect of Euclidean distance ($\log_{10}$ transformed) on sqrt-transformed AGC (β = 2.53, p < 0.0001), and with the edginess model outperforming the Euclidean distance model (ΔAIC = 192). Thus, we conclude that our original model results are robust to spatial autocorrelation, and that this autocorrelation did not influence our main conclusions.



SI Figure 1 - Binary land cover map (forest, non-forest) produced at 30m resolution for Sabah, 2016, with location shown inset.



SI Figure 2 - Forest edginess map produced at 30m resolution for Sabah, 2016. Only forest areas are coloured; white signifies area of non-interest (i.e. non-forest or external landscape).



SI Figure 3 - Frequency histogram of edginess values in our sample of 600,000 forest pixels.

References

Anderson, J.A., McClean, C.J., Sim, S., Pettorelli, N., Jelling, A., Tangah, J., & Hill, J.K. 2022. Weak edge effects on trees in Bornean rainforest remnants bordering oil palm. *Biotropica*. **54**(4), pp.921–932.

Beale, C.M., Lennon, J.J., Yearsley, J.M., Brewer, M.J., & Elston, D.A. 2010. Regression analysis of spatial data. *Ecology Letters*. **13**(2), pp.246–264.

F. Dormann, C., M. McPherson, J., B. Araújo, M., Bivand, R., Bolliger, J., Carl, G., … Wilson, R. 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography*. **30**(5), pp.609–628.

Fernández, C., Acosta, F.J., Abellá, G., López, F., & Díaz, M. 2002. Complex edge effect fields as additive processes in patches of ecological systems. *Ecological Modelling*. **149**(3), pp.273–283.

Malcolm, J.R. 1994. Edge Effects in Central Amazonian Forest Fragments. *Ecology*. **75**(8), pp.2438–2445.

Malcolm, J.R., Valenta, K., & Lehman, S.M. 2017. Edge effects in tropical dry forests of Madagascar: additivity or synergy? *Landscape Ecology*. **32**(2), pp.327–341.

Muggio, V.M. 2008. segmented: an R Package to Fit Regression Models with Broken-Line Relationships.

Ordway, E.M., & Asner, G.P. 2020. Carbon declines along tropical forest edges correspond to heterogeneous effects on canopy structure and function. *Proceedings of the National Academy of Sciences of the United States of America*. **117**(14), pp.7863–7870.

Ries, L., Murphy, S.M., Wimp, G.M., & Fletcher, R.J. 2017. Closing persistent gaps in knowledge about edge ecology. *Current Landscape Ecology Reports*. **2**, pp.30–41.