Using big data to understand carbon recovery and habitat availability in the Amazon biome.

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A thesis submitted for the degree of

Doctor of Philosophy

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Abstract

The scale of information required to inform global climate change and biodiversity initiatives goes beyond traditional environmental monitoring and into the realms of big data. Halting deforestation and restoring the world's forests is key to the success of such initiatives and there is growing recognition of the potential of large-scale restoration in the Amazon as a "nature-based solution" for both climate change and biodiversity loss. But our understanding of forest loss and recovery in the Amazon is incomplete. In this thesis I use MapBiomas, a 30-m resolution annual timeseries of Amazonian landcover from 1985 to 2020, to address knowledge gaps surrounding secondary forests and their role in carbon accumulation and habitat provisioning. Chapter 2 maps the extent, age, and carbon stocks of secondary forest in the Brazilian Amazon and explores their distribution relative to key variables known to influence secondary forest carbon accumulation. The findings show that, in 2017, despite occupying 20% of deforested land, secondary forests had offset less than 10% of deforestation emissions. Furthermore, they were typically situated in contexts that are less favourable for carbon accumulation. These results demonstrate that old-growth forest loss remains the most important factor determining the carbon balance of the Brazilian Amazon. Chapter 3 evaluates spatial and temporal trends in forest loss and recovery across all nine Amazonian countries. The findings reveal a strong, negative spatial relationship between old-growth forest loss and recovery by secondary forests, showing that regions with the greatest area available for large-scale restoration are also those that currently have the lowest recovery. This chapter also highlights the variation between countries; Brazil has both the highest percentage of deforestation and the lowest percentage of secondary forest recovery. Chapter 4 explores the co-location of old-growth and secondary forests. It finds that while 41% and 94% of secondary forests are adjacent or connected to old-growth forests, these values decline to 20% and 57% when considering adjacency and connectivity with structurally intact and extensive old-growth forest. It also reveals that secondary forests buffer over 40% of old-growth forest edges and reduce the number of isolated old-growth fragments by ~2 million. Chapter 5 explores the impact of deforestation, disturbance, and regeneration on habitat availability for species with different tolerances for disturbance. It reveals that, although old-growth forest cover has only reduced by 8.6%, there has been a 40% decline in biome-wide habitat for disturbance-sensitive species since 1985, with 79% of the loss due to changes in forest condition rather than extent. Overall, this thesis provides new insights into changes in forest cover and condition in the Amazon biome and demonstrates the power of big data for answering environmental questions at large spatial scales.

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Declaration

I declare that the work presented in this thesis is, to the best of my knowledge and belief, original and my own work. The material has not been submitted, either in whole or in part, for a degree at this, or any other university. Excerpts of this thesis have been published in journals, as indicated within. This thesis does not exceed the maximum permitted word length of 80,000 words including appendices and footnotes, but excluding the bibliography. Estimated word count: 33,149.

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Preface

This thesis has been written as standalone research papers for publication in peer-reviewed journals. They are logically connected on the theme of using big data to explore changing forest cover in the Amazon biome. As a result of being prepared for publication, there is some overlap in the information provided by each data chapter. Inconsistencies in chapter formatting are the result of the different requirements of the target journals.

The work presented in this thesis is my own, completed under the guidance of my principal supervisor Professor Jos Barlow and my wider supervisory team – Professor John R. Healey, Dr Paul J. Young, Dr Fernando Espírito-Santo, and Professor Naomi B. Schwartz – all of whom provided invaluable feedback on the design, analysis and writing. Further contributions were made by Dr Gareth Lennox, who provided advice on statistical analysis; Dr Erika Berenguer, Professor Alexander C. Lees, Dr Jack Shutt, and Dr Oliver C. Metcalf who provided advice on analysis; and Dr Ben Taylor, who provided advice on computational efficiency.

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Smith C.C., Healey J.R., Berenguer E.B., Young P.J., Taylor B., Elias F., Espírito-Santo F.D.B., Barlow J. Old-growth forest loss and secondary forest recovery across Amazonian countries. *Environmental Research Letters*

In review

Smith C.C., Healey J.R., Lees A.C., Shutt J., Metcalf O.C., Carvalho R., Resende A.F., Taylor B., Young P.J., Ferreira J., Barlow J. Deforestation and disturbance drive a 40% decline in habitat availability for Amazonian species. *Nature*

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Associated Publications

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Berenguer E.B., Lennox G.D., Ferreira J., Malhi Y., Aragão L.E.O.C., Rodrigues Barreto J., Espírito-Santo F.D.B., Figueiredo A.E.S., França F., Gardner T.A., Joly C.A., Palmeira A.F., Quesada C.A., Rossi L.C., Marina Moraes de Seixas M., **Smith C.C.,** Withey K., Barlow J. Tracking the impacts of El Niño drought and fire in human-modified Amazonian forests. *Proceedings of the National Academy of Sciences*

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In review

Barlow J., Berenguer, E.B., Carvalho N.S., França, F., Lees A.C., Metcalf, O.C., Shutt, J., **Smith, C.C.** Improving our understanding of fire impacts on tropical forest biodiversity *Nature*

Chapter 1

Introduction

Humanity is altering the planet at an unprecedented rate and anthropogenic climate change is now unavoidable (Masson-Delmotte et al., 2021). In response, a number of international agreements and initiatives have been developed to mitigate the effects of climate change and tackle biodiversity loss (e.g. Bonn Challenge, 2011; UN Decade on Restoration, 2019). Halting deforestation and restoring the world's forests is key to the success of many climate change and biodiversity targets (e.g. United Nations, 2021). The scale of the data required to advise on the implementation of such initiatives, to monitor the resulting actions, and hold governments accountable for their commitments, goes beyond traditional environmental monitoring into the realms of *big data* (See Section 1.3). In this thesis I demonstrate how *big data* can be used to expand our understanding of environmental change across whole biomes by exploring forest loss and recovery in the Amazon. The following chapters contribute a new understanding of the distribution of secondary forests and their role in the Amazonian carbon balance, as well as the first biome-wide assessment of habitat availability for species based on their disturbance tolerance.

1.1 Tropical forests

Concentrated in the Amazon Basin, the Congo Basin, and southeast Asia, tropical forests occupy ~18.3 million km^2 (FAO et al., 2020) and are essential to the provisioning of numerous ecosystem services (Assessment, 2005; Malhi et al., 2014). Tropical forests store upwards of 190 billion Mg of above-ground carbon (Saatchi et al., 2011) and provide approximately half of the world's terrestrial carbon sink (Malhi, 2010; Pan et al., 2011). They are fundamental to the global carbon budget both as a means for capturing atmospheric carbon (Chazdon et al., 2016a; Poorter et al., 2016) and as a source of emissions when they are degraded or destroyed. Tropical forests are also the most biodiverse and ecologically complex ecosystems on the planet, providing habitat for two thirds of all terrestrial species (Myers et al., 2000; Gardner et al., 2009, 2010), including over 60% of the planet's vertebrates (Pillay et al., 2021) and 67% of tree species (Gatti et al., 2022). However, widespread deforestation and forest disturbance are jeopardising the existence of species that depend upon tropical forests as habitat (Barlow et al., 2016; Giam, 2017).

1.1.1 Deforestation in tropical forests

The world's tropical, forests are under immense anthropogenic pressure and conversion of old-growth forest to agriculture remains the largest form of land use change globally (Eva et al., 2012; Hansen et al., 2013). It is estimated that as much as 5 million km^2 of tropical forest has been cleared (Rainforest Foundation Norway, 2021) and human-modified landscapes now dominate much of the tropics (Gardner et al., 2009). Tropical deforestation is driven largely by agricultural expansion and its occurrence is therefore strongly influenced by an area's agricultural suitability, as determined by a suite of economic, climatic, and edaphic conditions (Carmen Vera-Diaz et al., 2008). In Amazonia, forest conversion is primarily for pasture and soy (Barona et al., 2010), whilst in Southeast Asia the predominant crop is oil palm (Austin et al., 2019). Almost half of deforestation resulting from agricultural expansion can be attributed to crops cultivated for export to the European Union, China, and North America (Lawson et al., 2014; Hoang et al., 2021). Other drivers of deforestation include immigration, expansion of transport networks, and increases in industrial logging and mining in response to global demand for commodities (Andersen, 1996; Harding et al., 2021).

Tropical deforestation eliminates a safe, natural, and irreplaceable carbon sink that is responsible for sequestering as much 1.3±0.4 Pg C annually (Pan et al., 2011). It also generates 0.8–1.1 billion Mg of carbon emissions annually (Baccini et al., 2012; Harris et al., 2012), releasing carbon stocks that have accumulated in trees and soil over decades or centuries (Gatti et al., 2021). Across the world, tropical deforestation represents 8-12% of all anthropogenic emissions, while deforestation and land-use change combined contribute the majority of carbon emissions in most tropical forest countries (Edenhofer et al., 2014; Le Quéré et al., 2016; Seymour et al., 2016; Mitchard, 2018). These changes in the carbon balance risk tropical regions becoming a net source of carbon emissions (Mitchard, 2018), increasing the likelihood that global warming will exceed 1.5℃ (Brienen et al., 2015; Maxwell et al., 2019; Masson-Delmotte et al., 2021) – an important benchmark for climate change.

Deforestation also has severe impacts for biodiversity through the destruction and fragmentation of habitat. Continued clearance of old-growth forests will lead to irreversible biodiversity loss (Wearn et al., 2012; Moura et al., 2014). It is difficult to assess the true impact of forest loss on biodiversity as many tropical species remain undescribed or insufficiently documented. Furthermore, delayed biodiversity loss due to extinction debt (Wearn et al., 2012) may be causing species declines to be underestimated. Deforestation also impacts both biodiversity and carbon stocks through changes in local climatic conditions and the introduction of edge effects that alter the forest microclimate. The removal of forest cover results in reduced rainfall (Spracklen et al., 2015, 2018) and higher temperatures (Silva et al., 2016), leading to increased evapotranspiration and drought stress. Drought is known to affect tree species composition and lead to biomass reductions in old-growth forest (Phillips et al., 2009; Esquivel-Muelbert et al., 2019).

1.1.2 Tropical secondary forests

Although deforestation is the principal environmental narrative in tropical regions, it is not the end of the story. The abandonment of agriculture on previously deforested land – a typical land use change in the tropics – is resulting in the expansion of secondary forests (Aide et al., 2013; Chazdon, 2014). Defined in this thesis as forests growing after complete old-growth forest clearance, secondary forests are an increasingly prominent feature of human-modified tropical landscapes. Compared to old-growth forests, secondary forests are relatively species-poor and store smaller quantities of carbon (Gibson et al., 2011; Berenguer et al., 2014; Lennox et al., 2018). Nonetheless, they are a vital resource in deforested landscapes (Chazdon et al., 2009; Gardner et al., 2009; Letcher et al., 2009). When left undisturbed secondary forests can provide many of the ecosystem services of old-growth forests and have the potential to be an important tool for both biodiversity conservation (Barlow et al., 2007a; Chazdon et al., 2009; Rozendaal et al., 2019) and climate change mitigation (Martin et al., 2013; Matos et al., 2020; Heinrich et al., 2021).

In addition to reducing carbon emissions, recapturing atmospheric carbon is essential for mitigating climate change (Edenhofer et al., 2014; Houghton et al., 2015; Griscom et al., 2017). As such, promoting carbon sequestration through secondary forest growth is considered an efficient and cost-effective ‘nature-based solution’ to climate change (Griscom et al., 2017; Rogelj et al., 2018; Cook-Patton et al., 2020; Lubowski et al., 2020). However, not all secondary forests are equal in their ability to sequester carbon (Elias et al., 2020). The trajectory of secondary forest growth is influenced by numerous factors, with rates of carbon accumulation ranging from 0.89 Mg (Chave et al., 2020) to 7.6 Mg per hectare per year (Requena Suarez et al., 2019). For example, carbon accumulation is known to be slower in regions with longer, more intense dry seasons, and lower annual rainfall (Poorter et al., 2016). The positioning of secondary forests within the landscape also influences growth rates: surrounding forest cover has positive effects on biomass recovery (Jakovac et al., 2015; Toledo et al., 2020) and secondary forests growing in relatively intact landscapes are likely to have considerably higher carbon accumulation potential than those in highly deforested areas (Chazdon, 2003; Bihn et al., 2010). Studies have also found that higher land use intensity prior to abandonment leads to slower biomass recovery (e.g. Jakovac et al., 2015) and secondary forests growing on abandoned pasture are known to accumulate carbon more slowly compared to those on abandoned cropland (Fearnside et al., 1996; Jakovac et al., 2021). Nonetheless, even in regions with high growth rates, it takes many decades for secondary forests to recovery the quantity of biomass present in old-growth forests (Poorter et al., 2021) and frequent clearance (Schwartz et al., 2020; Wang et al., 2020), particularly of young forests (Schwartz et al., 2017a), undermines their value as a long-term carbon store (Poorter et al., 2021). Protecting secondary forests from clearance is key if they are to be used to meet climate change mitigation goals (Grassi et al., 2017).

Despite the structure and microclimate of secondary forests being very different from old-growth forest (Guariguata et al., 2001), they do provide habitat for many species (Lennox et al., 2018). Species richness in secondary forests increases over time (Barlow et al., 2007a; Barlow et al., 2007b; Moura et al., 2016) but it takes upwards of 50 years to recover the species richness of old-growth forest (Rozendaal et al., 2019; Poorter et al., 2021) and some specialist species may never return (Moura et al., 2013). Recent findings indicate that high surrounding old-growth forest cover is advantageous for secondary forest growth in the early stages of succession (Toledo et al., 2020). It is also likely that proximity to old-growth forest will also be important later in succession, as they are essential for providing the diverse seed sources required to establish resilient, biodiverse and high-biomass secondary forests (e.g. Caughlin et al., 2016; Hawes et al., 2020).

1.1.3 Disturbance in tropical forests

Forest disturbance has received increasing scientific attention in recent years as studies have begun to reveal the scale of its impact in tropical regions (e.g. Bullock et al., 2020; Matricardi et al., 2020). Disturbance can dramatically alter the composition of a forest ecosystem (Moura et al., 2016), driving local biodiversity loss (Gibson et al., 2011; Barlow et al., 2016; Withey et al., 2018; Marco et al., 2019). Disturbed forests typically have more heterogeneous and open canopies, with dense understories that make them unsuitable as habitat for many forest species, although some species may eventually return if further disturbances are avoided (Mestre et al., 2013a; Mollinari et al., 2019). Furthermore, the carbon respired or burned during forest disturbance generates large quantities of carbon dioxide emissions, comparable to deforestation (Pearson et al., 2017; Aragão et al., 2018; Silva Junior et al., 2020a).

Selective logging, both legal and illegal, is amongst the most widespread forms of forest disturbance (Asner et al., 2005; Foley et al., 2007; Brancalion et al., 2018). Even best-practice reduced-impact logging can have significant detrimental impact on forest structure (Boltz et al., 2003; Sist et al., 2021), leaving increased canopy openness and higher abundance of lianas (Gerwing, 2002). Fire is also a major driver of forest disturbance (Aragão et al., 2007; Barlow et al., 2020), impacting huge areas of forest. For example, fires relating to the 2015 El Niño event burnt 1 million ha of forest in the Santarém region of Brazil (Withey et al., 2018; Barlow et al., 2020). Fire does not occur naturally in tropical regions, however, logging, edge effects, and droughts can create conditions in which fire can take hold within standing forests (Brando et al., 2012; Barlow et al., 2020), usually from anthropogenic sources of ignition. As tropical species have not co-evolved with fire, they are extremely vulnerable to it (Barlow et al., 2003a; Brando et al., 2012) and even a small understorey forest fire can increase tree mortality by 50% (Barlow et al., 2003b; Brando et al., 2014; Silva et al., 2018). Reductions in forest biomass may last decades after a fire event (Silva et al., 2018), with potentially permanent alterations in forest structure (Barlow et al., 2008; Prestes et al., 2020). As global warming exacerbates El Niño events and creates increasingly warmer and drier conditions, the regularity, intensity, and extent of wildfires are only likely to increase (Silva et al., 2018; Brando et al., 2020). Disturbance can also occur naturally as a result of drought and windthrow, which are both estimated to generate large carbon losses (e.g. Schwartz et al., 2017b). However, even these seemingly natural disturbances may also have underlying anthropogenic causes. For example, climate change made the probability of the 2015-16 El Niño drought four times more likely (Ribeiro et al., 2021). As much as 17% of remaining old-growth forest in the Amazon is estimated to have been impacted by some form of disturbance (Bullock et al., 2020), causing a carbon loss of 0.1 Pg per year (Bullock et al., 2021).

Fragmentation, caused by deforestation and by the networks of roads and tacks created to facilitate access for logging and mining (Arima et al., 2005), is an additional source of forest disturbance. The expansion of forest edges exposes more forest to increased light, heat, and wind, leading to reduced humidity and hydrological inconsistency (Paula et al., 2015). These changes in microclimate are known as edge effects and drastically impact the structure and functioning of the forest, causing its carbon stock to decrease over time due to increased tree mortality and shifting species assemblages (Laurance et al., 2002; Magnago et al., 2017). The most severe ecological and physical edge effects occur in the first 100 m, but other impacts have been recorded hundreds of metres into the forest (Laurance et al., 2002), including reductions in the abundance of forest species, which have been reported to extend 200 - 400 m from edges (Pfeifer et al., 2017). Remote sensing studies have begun to map edge effects in tropical forests across large spatial scales (e.g. Silva Junior et al., 2020a) and estimate that carbon losses from edge effects may contribute an additional 36% of emissions relative to those occurring directly from forest clearance (Silva Junior et al., 2020b). Fragmentation also reduces the size of forest patches, with severe implications for biodiversity. Area effects are well known drivers of species richness and population persistence (Ferraz et al., 2007). Species dependent on old-growth forest are more sensitive to fragment size than species able to survive in secondary forest and forest edge habitat (Lees et al., 2006). Reduction in fragment size also increases its accessibility to people and consequently increases its vulnerability to additional anthropogenic pressures such as hunting (Parry et al., 2009; Andrade Melo et al., 2015).

1.2 The Amazon

The Amazon biome is the largest remaining expanse of tropical forest in the world. Encompassing nine South American countries, it occupies 6.5 million km^2 of land and is estimated to be storing 86 Pg of carbon (Saatchi et al., 2007). From influencing rainfall patterns across the Americas (Spracklen et al., 2018) to regulating local climate, the Amazon is fundamental to the provision of vital ecosystem services across multiple scales (Malhi et al., 2014). However, it also has some of the highest rates of forest clearance globally (Hansen et al., 2013), accounting for over 50% of all tropical forest cover loss in the last two decades (World Resources Institute, 2020).

Forest loss in the Amazon has been concentrated mainly in the south and east of the biome – a region known as the *‘arc of deforestation’* that was once the world’s most active deforestation frontier (Hansen et al., 2010; Barlow et al., 2011). Amazonian deforestation slowed dramatically from 2004 to 2012, which is largely attributed to highly effective implementation of Brazil’s forest code and a drop in global soybean prices. However, many of Brazil’s environmental protections have since been dismantled – notably following the election of Jair Bolsonaro in 2018 – leading to a rise in deforestation rates and a surge in illegal armed incursions onto Indigenous reserves. As such, the 13,235 km^2 cleared in 2021 marked a 15-year high in Amazonian deforestation (PRODES, 2021). Deforestation is not the only environmental disaster in the Amazon. Much of the remaining forest has suffered disturbance (Peres et al., 2006; Tyukavina et al., 2017; Bullock et al., 2020), reducing its viability as habitat and generating large quantities of carbon emissions (Barlow et al., 2016; Bullock et al., 2021). Global climate change is also causing the Amazon to become drier and is increasing the dry season length by as much as 6.5 days per decade in some regions (Fu et al., 2013). Longer, drier and hotter dry seasons increase the risk of forests fires (Le Page et al., 2017), which have long lasting effects on the forest (Silva et al., 2018; Berenguer et al., 2021).

Despite these ongoing environmental catastrophes, there is growing international recognition of the potential of large-scale forest restoration in the Amazon as a *'nature-based solution'* to climate change. Compared with other tropical regions, the Amazon could be ideal for forest restoration as it has low population densities (Cunningham et al., 2018), extensive areas of unproductive or unprofitable agricultural systems (Garrett et al., 2017, 2021), and moderate to high carbon sequestration rates (Requena Suarez et al., 2019).

1.3 Big data in environmental science

Increasing availability of large-scale data (*big data*) and the growing need to examine and resolve major environmental problems, is driving a shift towards *big science*. Although there is little consensus on what constitute *big data* (Graham et al., 2013; Kitchin et al., 2016), it is generally used to refer to massive volumes of data that cannot readily be handled by the usual tools or practises (Snijders et al., 2012). Across academia, industry, and government, *big data* presents opportunities for increasing our understanding of complex systems and optimizing decision making (Wamba et al., 2015). However, it has only recently entered mainstream use in ecology and environmental science. These fields have historically been dominated by research conducted over limited spatial and temporal scales – largely due to time, accessibility, and financial constraints preventing large-scale field data collection (Heidorn, 2008). However, the *big data* revolution is changing the way we produce and analyse data, opening new possibilities for research and completely transforming the scales at which we can quantify the natural world and our impact on it.

Despite being relatively new to environmental science, increasing availablity of large datasets and long time series mean that *big data* has already been used to study a range of environmental phenomena, from glacial melt (Ye et al., 2017) and pollution (Apte et al., 2017) to flood risk (Pollard et al., 2018) and wildfires (Dutta et al., 2016). In the environmental and geophysical sciences, sensors are the principal source of *big data*. For example, the Wildlife Insights platform holds over 12 million camera trap records (Wildlife Insights, 2020), and the Landsat satellites add ~1500 new 30-million-pixel images to their 48-year dataset daily; with every point on earth photographed every 8 days (USGS, 2020). Citizen science is another major source of big environmental data – eBird, the online platform for aggregating the sightings of birdwatchers, has become one of the world's largest biodiversity-related datasets, with more than 100 million bird sightings contributed annually (eBird, 2021). Quantification of the natural world at these scales will provide unprecedented insights into the patterns and predictors of complex environmental and anthropogenic systems, paving the way for a new era of data-informed policy.

Big data presents innumerable opportunities to explain the past, describe the present, and project the future of our planet. As a well-studied region, with an increasing number of large, high-resolution geospatial datasets becoming available (e.g. Bullock et al., 2020; MapBiomas, 2021), the Amazon makes an ideal case study for using *big data* to explore environmental change.

1.4 Thesis objectives

In this thesis, I use *big data* to address four key knowledge gaps for the Amazon. First, despite increasing dependency on secondary forest growth in climate change mitigation strategies, there is limited high-resolution data on their current extent, location, temporal dynamics (i.e. longevity, clearance cycles) and their contribution to the carbon balance. Second, Amazonian research typically focuses on the Brazilian Amazon, failing to account for 40% of the biome. As a result, key information on the rates of forest loss and recovery, and their associated implications for carbon stocks, are missing for the majority of Amazonian countries and the biome as a whole. Third, although research indicates that the benefits of forest restoration are strongly influenced by a number of spatially variable factors, the location of secondary forests within the landscape has not been quantified at scale. Forth, there have been no biome-wide assessments of how deforestation and anthropogenic disturbances are driving habitat loss. Specifically, I aim to answer the following questions.

1. What is the current extent and carbon stock of secondary forests? What is their contribution to the tropical carbon balance? (Chapter 2 - Secondary forests offset less than 10% of deforestation-mediated carbon emissions in the Brazilian Amazon)

2. What are the spatial patterns in the extent of forest loss and recovery in the Amazon? How do carbon emissions and accumulation vary across the biome? (Chapter 3 - Old-growth forest loss and secondary forest recovery across Amazonian countries)

3. Where are secondary forests growing in relation to old-growth forests? How do secondary forests change old-growth forest edge exposure and fragmentation? (Chapter 4 – The proximity of secondary forests to old-growth forests reduces forest fragmentation and buffers edges in the Amazon)

4. How have deforestation, disturbance and secondary forest growth impacted habitat availability in the Amazon? (Chapter 5 - Deforestation and degradation drive 40% declines in habitat availability for Amazonian species)

1.5 Thesis structure

The four data chapters in this thesis have been written for publication. Chapter 2 is published in Global Change Biology; Chapter 3 is published in Environmental Research Letters; Chapter 4 in is preparation for submission to Global Change Biology; and Chapter 5 is in review for Nature. These chapters are stand-alone pieces of work logically connected on the theme of using *big data* to understand broad-scale environmental change in relation to Amazonian tropical forests. As a result of being prepared for publication, there is overlapping information between chapters – notably in their introductions and methodologies. However, each chapter provides a novel contribution to the field. Inconsistencies in chapter formatting are the result of differing requirements of the target journals. Chapter 6 provides a summary of the thesis findings and discusses their importance for science and future environmental policies in the Amazon region. It also highlights future research needs. The appendices provide the supplementary material published alongside each chapter, as well as the abstracts for other research output produced using data created for this thesis.

Chapter 2

Secondary forests offset less than 10% of deforestation-mediated carbon emissions in the Brazilian Amazon

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Conceptualization: CCS, JB, JRH, EB; Data curation: CCS; Formal Analysis: CCS; Methodology: CCS, JB, JRH, BT; Resources & Software: CCS; Supervision: JB, JRH, PJY; Visualization: CCS; Writing: CCS, JB, JRH; Editing: All authors

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Abstract

Secondary forests are increasing in the Brazilian Amazon and have been cited as an important mechanism for reducing net carbon emissions. However, our understanding of the contribution of secondary forests to the Amazonian carbon balance is incomplete, and it is unclear to what extent emissions from old-growth deforestation have been offset by secondary forest growth. Using MapBiomas 3.1 and recently refined IPCC carbon sequestration estimates, we mapped the age and extent of secondary forests in the Brazilian Amazon and estimated their role in offsetting old-growth deforestation emissions since 1985. We also assessed whether secondary forests in the Brazilian Amazon are growing in conditions favourable for carbon accumulation in relation to a suite of climatic, landscape, and local factors. In 2017, the 129,361 km^2 of secondary forest in the Brazilian Amazon stored 0.33$\pm$0.05 billion Mg of above-ground carbon but had offset just 9.37% of old-growth emissions since 1985. However, we find that the majority of Brazilian secondary forests are situated in contexts that are less favourable for carbon accumulation than the biome average. Our results demonstrate that old-growth forest loss remains the most important factor determining the carbon balance in the Brazilian Amazon. Understanding the implications of these findings will be essential for improving estimates of secondary forest carbon sequestration potential. More accurate quantification of secondary forest carbon stocks will support the production of appropriate management proposals that can efficiently harness the potential of secondary forests as a low-cost, nature-based tool for mitigating climate change.

2.1 Introduction

Tropical forests are an enormous reservoir of carbon, storing upwards of 190 billion Mg of above-ground carbon (Saatchi et al., 2011). However, this critical carbon store is threatened by deforestation (Eva et al., 2012; Hansen et al., 2013), which is responsible for 0.81–1.14 billion Mg of carbon emissions annually (Baccini et al., 2012; Harris et al., 2012). The rate of global deforestation has prompted the establishment of several international initiatives intended to reduce the rate of forest loss and its associated consequences (e.g. Reducing emissions from deforestation and forest degradation). The Amazon basin is the largest remaining tropical carbon stock (Saatchi et al., 2011). However, it also has the highest rates of forest clearance (Hansen et al., 2013), with carbon losses directly related to deforestation estimated to be 0.16–0.67 billion Mg C yr^{-1} (Achard et al., 2002; Loarie et al., 2009). Approximately 20% of old-growth forest in the Brazilian Amazon has already been cleared, and since the dramatic slowdown in deforestation from 2004 to 2012 (27,772 km^2 to 4,571 km^2) the rate of forest loss has been increasing, with 2019 marking a 10-year high (PRODES, 2020).

The abandonment of agriculture on previously deforested land – a typical land use change in the tropics – is resulting in the expansion of secondary forests (Aide et al., 2013; Chazdon, 2014). Secondary forests, defined here as forest growing after complete land clearance, rapidly store large quantities of carbon (Poorter et al., 2016; Requena Suarez et al., 2019), making them a potentially important mechanism for reducing net carbon emissions (Pan et al., 2011; Griscom et al., 2017; Rogelj et al., 2018). Secondary forests have long been recognised as important for offsetting deforestation emissions (Skole et al., 1994) and in recent years, promoting secondary forest growth has been included in a number of key global policies as a readily available and cost effective strategy for reducing net carbon emissions and mitigating climate change. For example, the Bonn Challenge (2011) aims to restore 3.5 million km^2 of forest by 2030 and is supported by the New York Declaration on

Forests (2014) and by the UN Decade on Restoration (2019), which recognises the need to reverse ecosystem degradation in order to achieve the UN Sustainable Development Goals. In South America, these schemes are reinforced on a regional scale in several countries by agreements such as Initiative 20x20 (2014), which aimed to restore 200,000 km^2 of degraded land by 2020. Within Brazil, secondary forests are supported by the Forest Code, which mandates that properties within the Legal Amazon hold up to 80% forest cover, of either primary and secondary vegetation. However, whilst secondary forest is known to be increasing in the Brazilian Amazon (Nunes et al., 2020), it is also subject to widespread clearance (Wang et al., 2020), which undermines its effectiveness as a carbon store.

Our understanding of the contribution of secondary forests to the tropical carbon balance is incomplete. First, despite studies estimating deforestation-mediated emissions (e.g. Harris et al., 2012), it is not clear to what extent these emissions have been offset by secondary forest growth or how this has varied over time. The value of secondary forests as a carbon store needs to be assessed within a context of dynamic land use, with old-growth forests still being lost and secondary forests reconverted to agriculture. With the promotion of secondary forest growth being suggested as an important climate change mitigation strategy (Pan et al., 2011; Griscom et al., 2017; Rogelj et al., 2018), the need to improve our understanding grows more pressing. Second, the trajectory and rate of secondary forest growth are influenced by numerous climatic, landscape, and local factors, which contribute to a ten fold difference in estimates of carbon sequestration rates across the tropics (Elias et al., 2020). Carbon accumulation in secondary forests is strongly linked to climatic conditions, with longer, more intense dry seasons, and lower annual rainfall known to slow accumulation (Poorter et al., 2016). At the landscape scale, secondary forest growth is slower when there is less old-growth forest cover to act as a seed source (Caughlin et al., 2016; Chazdon et al., 2016a). Locally, secondary forests growing on abandoned pasture accumulate carbon more slowly than on abandoned cropland (Fearnside et al., 1996) and growth is slower where the number of previous swidden cycles, also known as slash-and-burn or shifting cultivation, is higher (Jakovac et al., 2015). The status of the majority of secondary forests in relation to these climatic, landscape, and local variables is not known. Establishing the location of secondary forests will provide insights into whether they are growing in contexts that are more or less favourable to rapid carbon accumulation.

Here we address these knowledge gaps, using the MapBiomas 3.1 landcover dataset (1985-2017) and the Avitabile et al. (2016) pan tropical biomass map to provide the first spatially explicit estimate of the role of secondary forests in offsetting deforestation emissions in the Brazilian Amazon. We calculate the age, extent and carbon stock of secondary forests and estimate the initial carbon stock of old-growth forest, asking (1) what has been the potential role of secondary forests in offsetting old-growth deforestation emissions since 1985? We then explore (2) how secondary forests are distributed in relation to a broad suite of climatic, landscape, and local factors that are known to affect carbon accumulation. Finally, as a first step in identifying the potential for interacting effects, (3) how are these variables correlated spatially within the existing range of secondary forests?

2.2 Methods

2.2.1 Assessing secondary forests and deforestation

We used MapBiomas to define deforestation and forest recovery. We opted to use it over other alternatives such as TerraClass (see Wang et al., 2020) as it provides a longer temporal series (1985-2017 rather than 2004-2014) and has undergone an extensive two-stage validation process: first a comparative analysis with existing land cover maps and second a visual analysis of 30,000 sample pixels. While there is a low level of agreement (33.8%) between the secondary forest map derived from MapBiomas and that of the most recent TerraClass product at the pixel level (both for 2014), the two datasets broadly agree in terms of spatial distribution (see supplementary information). The temporal pattern of deforestation captured by MapBiomas is also comparable to that of (PRODES, 2020, Figure A.1,).

Table 2.1 Initial reclassification of MapBiomas schema.

MapBiomas ID	MapBiomas Classification	Reclassification
1	1. Forest	Old-growth Forest
2	1.1. Natural Forest	Old-growth Forest
3	1.1.1. Forest Formation	Old-growth Forest
4	1.1.2. Savannah Formation	Old-growth Forest
5	1.1.3. Mangrove	Old-growth Forest
9	1.2. Forest Plantation	Cropland
10	2. Non-Forest Natural Formation	Other/Water
11	2.1. Wetland	Other/Water
12	2.2. Grassland Formation	Other/Water
32	2.3. Salt Flat	Other/Water
13	2.3. Other Non-Forest Natural Formation	Other/Water
14	3. Farming	Cropland
15	3.1. Pasture	Pasture
18	3.2. Agriculture	Cropland
21	3.3. Mosaic of Agriculture and Pasture	Cropland
22	4. Non-Vegetated Area	Other/Water
23	4.1. Beach and Dune	Other/Water
24	4.2. Urban Infrastructure	Other/Water
29	4.3. Rocky Outcrop	Other/Water
30	4.4. Mining	Other/Water
25	4.5. Other Non-Vegetated Area	Other/Water
26	5. Water	Other/Water
33	5.1. River, Lake and Ocean	Other/Water
31	5.2. Aquaculture	Other/Water
27	6. Non-Observed	NA

2.2.2 Secondary forest extent

Our study focused on the Brazilian Amazon, a 4.27 million km^2 expanse covering almost a quarter of the South American landmass and constituting 60% of the total Amazon forest. We produced 30-m resolution annual maps of secondary forest cover for the Brazilian Amazon from 1986 to 2017 using the MapBiomas 3.1 land cover dataset and a change-detection algorithm (Supporting Information). We initially reclassified the MapBiomas schema into four classes: old-growth forest, cropland, pasture, and other (Table 2.1; Figure A.2). The secondary forest class was introduced during the change detection process. Pixels were classified as secondary forest when they returned to 'forest' following a period being classified as 'non forest'. We applied a spatial filter restricting 'forest' to 'non forest' transitions to a minimum of 0.36 ha (4 contiguous pixels), unless directly adjacent to a pre-existing non forest area of 4 or more pixels. This filter was used to limit the influence of natural canopy opening events (e.g. small tree falls) and changes resulting from georeferencing issues from being incorrectly recorded as anthropogenic clearances, whilst also being small enough to capture the activities of all land use change including by small landholders, who typically clear just 2-3 ha yr^{-1} (Fujisaka et al., 1996). Averaged over the time series, this resulted in an Amazon wide reduction in calculated secondary forest area of 0.82±0.31% (n = 32, mean±SD) compared with the same analysis conducted without the spatial filter.

2.2.3 Secondary forest age

Using our annual maps of secondary forest extent, we calculated secondary forest age as the number of consecutive years that a pixel was classified as secondary forest. The first year in our time series is 1985, meaning the maximum age of secondary forests is 32 years. We assumed all forest existing in 1985 to be old-growth forest. As large scale deforestation began in the 1970s, this old-growth mask included some secondary forest. However, only a proportion of the ~140,000 km^2 of the land deforested before 1985 (Fearnside, 1990) would have returned to secondary forest (Almeida et al., 2016; Nunes et al., 2020) and much of that secondary forest is likely to have been cleared again during our time series. As such, we believe this old-growth forest mask is unlikely to have had major impacts on our more recent estimates of secondary forest extent and age. Where reporting forest extent or age, results are reported as mean ± the temporal standard deviation in order to capture inter-annual variability.

2.2.4 Above-ground biomass in secondary forest

Requena Suarez et al. (2019) estimate biomass accumulation rates for young ($\leq$20 years) and old (21 to 100 years) secondary forest in tropical and subtropical ecozones (FAO, 2012). Three of these ecozones intersect our study area: tropical rainforest (~91.8%), tropical moist forest (~7.8%) and tropical montane forest (~0.2%). For these ecozones, Requena Suarez et al. (2019) estimate above-ground biomass accumulation rates (mean$\pm$95% CI) of, respectively, 5.9$\pm$0.8 Mg ha^{-1} yr^{-1}, 4.4$\pm$1.3 Mg ha^{-1} yr^{-1} and 5.2$\pm$1 Mg ha^{-1} yr^{-1} for young secondary forest, and 2.3$\pm$0.3 Mg ha^{-1} yr^{-1}, 1.8$\pm$0.8 Mg ha^{-1} yr^{-1} and 2.7$\pm$0.8 Mg ha^{-1} yr^{-1} for old secondary forest. We applied these refined estimates across our map of secondary forest age to calculate the total above-ground biomass of secondary forest in the Brazilian Amazon.

We converted these above-ground biomass values to carbon stock by multiplying them by the Intergovernmental Panel on Climate Change (IPCC) conversion factor of 0.47 (Eggleston et al., 2006). As this is just one estimate of carbon accumulation in secondary forest, we explore the representativeness of the underlying plot network in the supplementary information. Below-ground carbon may contribute an additional 25% to the total stored carbon (Luyssaert et al., 2007). However, assessing below-ground carbon is not within the scope of this study (Powers et al., 2011).

2.2.5 Deforestation emissions

Using the change in old-growth forest extent captured by our analysis of MapBiomas, we calculated deforestation emissions using above-ground biomass estimates produced by Avitabile et al. (2016), which fuse the Saatchi et al. (2011) and Baccini et al. (2012) datasets to produce a 1-km resolution pan-tropical above-ground biomass map for the early 2000s. Much of the deforestation captured by our algorithm occurred before the most recent datasets used by Avitabile et al. (2016). Therefore, we infilled the biomass of areas deforested before 2010 with the mean above-ground biomass from the surrounding 10 km^2 using the ArcGIS Pro Focal Statistics tool. As the Avitabile et al. (2016) estimates include degraded forests, we may be under-estimating emissions from old-growth deforestation. A further limitation of the Avitabile et al. (2016) dataset is its 1-km resolution, which we downscaled to match the 30-m resolution MapBiomas land cover data. We assigned above-ground biomass values to each old-growth forest pixel using its centroid. To calculate annual emissions, we apply an exponential decay rate of 0.49, based on the combustion rate reported by Leeuwen et al. (2014), to extend emissions from a deforestation event over several years. Repeated fires increase combustion completeness to nearly 100% for cropland deforestation and up to 90% for pasture deforestation (Morton et al., 2008). This exponential decline is a reasonable expectation as pasture management practices often involve fire for several years after deforestation. It is also consistent with the loss of all above-ground biomass in deforested land in longer-term assessments (e.g. Berenguer et al., 2014). Results were similar when we assumed all above-ground carbon was emitted in the year of deforestation (see supplementary information).

We estimated emissions from secondary forest clearance using our map of secondary forest above-ground biomass, calculated using the Requena Suarez et al. (2019) accumulation rates. We convert above-ground biomass to carbon stock using a conversion factor of 0.47 and apply an exponential decay rate of 0.49 to emissions, as above. We report variation in secondary forest emissions using the 95% confidence interval of estimates in Requena Suarez et al. (2019).

2.2.6 Factors mediating secondary forest recovery

Climatic

Rainfall, rainfall seasonality, and climatic water deficit have been found to be the best climatic indicators of absolute biomass recovery potential in the Neotropics (Poorter et al., 2016). Using these same measures, with mean annual rainfall and rainfall seasonality from WorldClim (variable ‘BIO12’ and ‘BIO15’, respectively; Hijmans et al., 2005) and climatic water deficit from Chave et al. (2014), we compared the climate of secondary forests with that of the whole Brazilian Amazon. This allowed us to determine if secondary forests are situated in climatic contexts relatively more or less favourable for biomass recovery than the biome average. To do so, we randomly sampled the distribution of each climate indicator for both secondary forest and the whole Brazilian Amazon, then used the Wilcoxon Rank Sum test to assess whether the samples were drawn from different distributions. We repeated this process 10,000 times and recorded the mean p-value. We undertook these analyses with a variety of sample sizes. However, results were insensitive to sample size (Table A.4), and we report results for n = 1000.

Variation in local climate is known to influence carbon sequestration in secondary forest (Elias et al., 2020). However, accounting for it involves a number of spatial and temporal issues. For example, local climate is altered drastically by deforestation (e.g. Spracklen et al., 2015, 2018), and accounting for this would require climate data to be updated in near real-time. Moreover, there are no large-scale assessments of the sensitivity of secondary forests to these changes.

Landscape

We calculated the proportion of the landscape within 1 km of each secondary forest pixel that was occupied by old-growth forest, secondary forest, and total forest (either old-growth or secondary). We created a 1-km buffer for each pixel using the Python package Shapely and calculated the area of each forest type within the buffer using the zonal_stats function from the Python package rasterstats. All Python packages are freely available.

Local

For the period 1985 – 2017, the change-detection algorithm records total clearance events as the number of times a pixel transitions from either old-growth or secondary forest to a non-forest class. Our two measures of prior agricultural land use (time as cropland and time as pasture) were recorded as the number of years spent as cropland or pasture between the most recent clearance event and the pixel returning to ‘forest’.

2.2.7 Associations between factors influencing biomass accumulation

Using Spearman’s Rank Order Correlation and a sample of secondary forest pixels (n = 1000), we tested the association between each of the climatic, landscape, and local variables. To enhance the dispersal of selected pixels across the Brazilian Amazon, we used stratified sampling with replacement such that 25% of pixels were situated in each quadrant of the Amazon biome, while within quadrant selection was random. We repeated this process 10,000 times, recording the mean correlation coefficient. Results were similar from a spatially unconstrained selection process (Figure A.4). Given the large number of repeated tests (n = 104) and the relatively large sample size (n = 1000), we used a more conservative significance threshold of 0.01 for this analysis.

2.3 Results

2.3.1 Secondary forest extent and age

We find a near continuous expansion in the extent of secondary forest from 1985 onwards (Figure 2.2a), resulting in a total of 129,361 km^2 of secondary forest in the Brazilian Amazon in 2017. When averaged across the time series, the yearly increase in secondary forest extent was 8.61±10.96% (mean±SD; hereafter unless stated) and in 2017 these forests accounted for approximately 3.8% of the total forest cover. The year 2000 is the only exception to this upward trend, with a decline in secondary forest area of 3,089 km^2. We find that secondary forests were not distributed uniformly across the basin but were concentrated along the ‘arc of deforestation’, waterways and major highways (e.g. Trans Amazonian highway; Figure 2.1a). Our results show that in 2017, 111,023 km^2 (85.8%) of secondary forests were less than 20 years old, with a median age of seven years. Very young secondary forests ($\leq$ 5 years old) accounted for 42.08% (Figure 2.1c). From 1995, these very young forests consistently represent almost half of total secondary forest extent (48.0±4.5%).

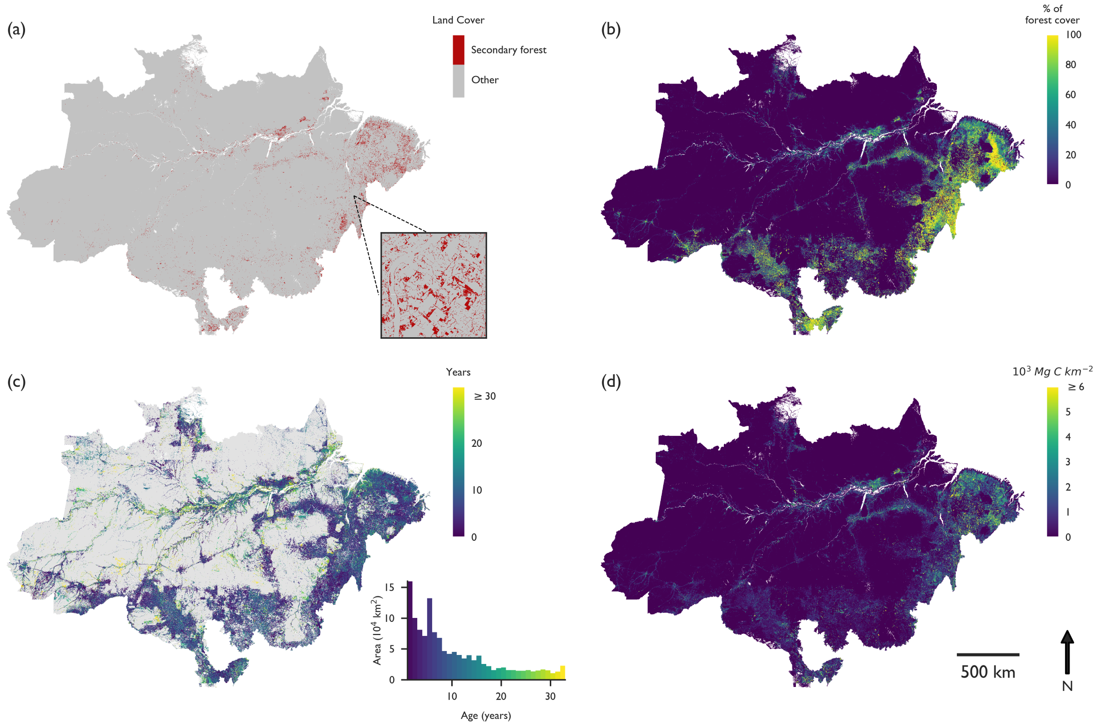


Figure 2.1: The extent, age, and carbon stock of secondary forest in the Brazilian Amazon. (a) The spatial distribution of secondary forest (red). Inset reveals the level of detail available with 30-m resolution data **(b)** The proportion of total forest cover made up of secondary forest **(c)** Median secondary forest age per 1 km^2 with inset of the secondary forest age distribution **(d)** Total above-ground carbon stock in secondary forests, calculated using accumulation rates estimated by Requena Suarez et al. (2019).

2.3.2 Old-growth deforestation emissions offset by secondary forest growth

Old-growth deforestation emissions

Between 1985 and 2017, MapBiomas detects the clearance of 512,473 km^2 of old-growth forest. We estimate that this resulted in a gross carbon loss of 3.49 billion Mg

C, emitting the equivalent of 12.80 billion Mg CO_2 Figure (2.2c).

Secondary forest sequestration

We estimate that in 2017, secondary forests in the Brazilian Amazon stored 0.33±0.05 billion Mg C, equivalent to 1.20±0.18 billion Mg CO_2 (mean±95% CI; Figure 2.1d) and more than a quarter (26.9%) of the total carbon stock was stored in forests $\leq$ 10 years old. Gross secondary forest carbon sequestration increased considerably over the time series, from 10.38±1.6 million Mg CO_2 in 1986 to 66.12±9.7 million Mg CO_2 in 2017 (mean±95% CI; Figure 2.2b). The accumulation of carbon in secondary forests was slowed by clearance, with an average 6,410±2007 km^2 of secondary forest cleared annually (Figure 2.2a). Of all the secondary forest mapped during our time series, 60.6% (198,688 km^2) had been cleared again by 2017, resulting in the gross loss of 0.23±0.03 billion Mg C, equivalent to 0.83±0.12 billion Mg CO_2 in emissions (mean±95% CI). However, averaged across the time series, secondary forests were a net carbon sink of 6.75±1 million Mg C yr^{-1} (mean±95% CI).

Deforestation emissions offset

Our findings show that between 1985 and 2017, approximately 9.37% (1.20±0.18 billion Mg CO_2, mean±95% CI) of old-growth deforestation emissions had been offset by secondary forest growth, once the loss of carbon from secondary forest clearance had been subtracted (Figure 2.2c). For much of the time series (1986 2004), old-growth deforestation emitted carbon at 16.95±4.6 times the rate of net secondary forest sequestration. However, following the rapid decline in old-growth deforestation after the 2004 peak, emissions dropped to 4.97±1.1 times annual secondary forest net sequestration (2010 – 2017). When averaged across the time series, 10.29±6.8% of old-growth emissions were offset by net secondary forest sequestration annually (1986 – 2017). The proportion of old-growth deforestation emissions offset by net secondary forest sequestration varied across the time series, dropping from 8.51% in 1993 to 5.48% in 2003 and then peaking at 25.59% in 2013.

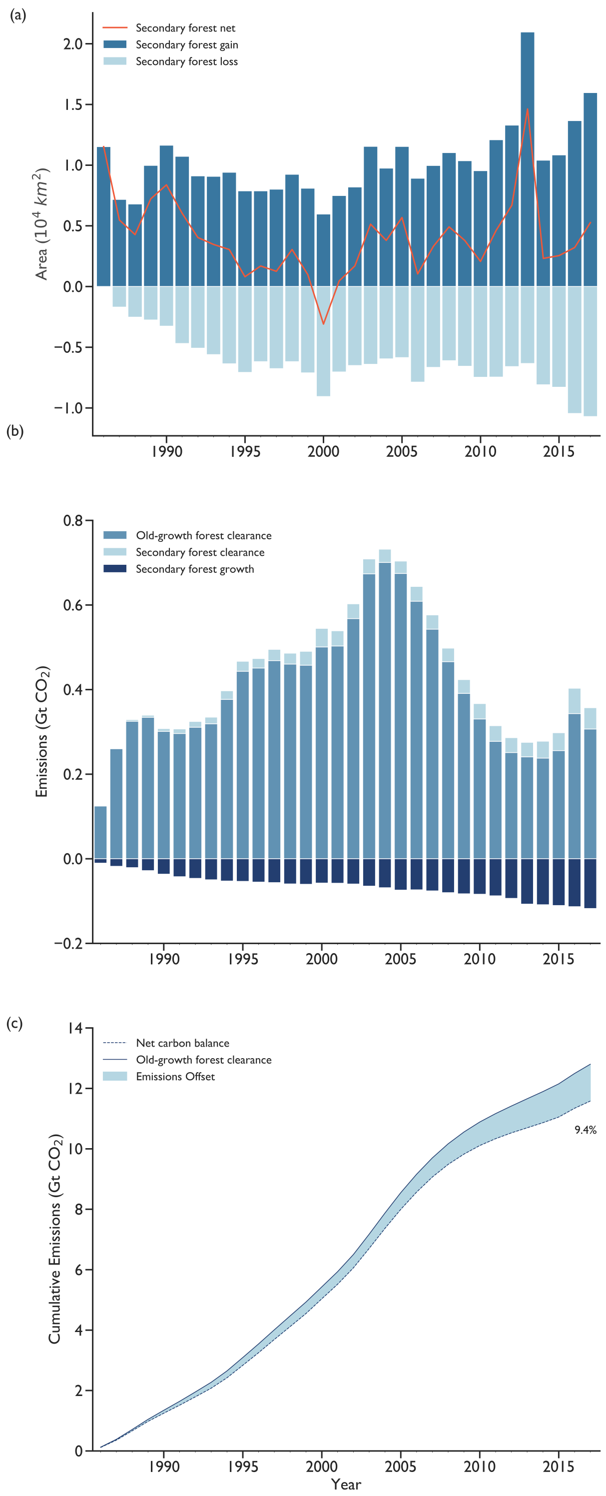


Figure 2.2: Forest cover change and associated emissions in the Brazilian Amazon from 1985 to 2017. (a) Net annual change in secondary forest extent (red) with gross annual new growth (dark) and clearance (light) **(b)** Gross annual emissions from old-growth clearance (medium), secondary forest clearance (light) and secondary forest growth (dark) **(c)** Cumulative old-growth deforestation emissions (solid) and net carbon balance (dashed) after offset by secondary forest emissions (shaded).

2.3.3 Factors influencing secondary forest carbon sequestration

Climatic

In 2017, there was an important spatial congruence between climate and secondary forests. Most secondary forests were located in regions where annual rainfall is lower than the biome average (secondary forest: 1945 mm, Brazilian Amazon: 2224 mm, Figure 2.3a), and where there is greater rainfall seasonality (secondary forest: 70%, Brazilian Amazon: 57%, Figure 2.3b) and a greater climatic water deficit (secondary forest: 375.5 mm yr^{-1}, Brazilian Amazon: 259 mm yr^{-1} Figure 2.3c). We can be highly confident ($p < 0.01$) in meaningful differences between these distributions (Wilcoxon rank sum; climatic water deficit: $W = -16.71$, $p < 0.01$, rainfall: $W = -14.49$, $p < 0.01$, seasonality: $W = 20.25$, $p < 0.01$).

Landscape

The majority (98.9%) of secondary forests in 2017 were within 1 km of old-growth forest, with 28.9% having more than half of the surrounding landscape (1 km radius) occupied by old-growth forest (Figure 2.4a). Where the proportion of old-growth forest cover in the surrounding landscape was high ($\geq$70%), secondary forest typically occupied the majority of the deforested area (median: 83%; Figure A.6). Therefore, 17.2% of all secondary forests had a surrounding landscape that was almost entirely forested ($\geq$95% total forest cover; Figure 2.4e); despite very little secondary forest having such high surrounding forest cover when considering old-growth and secondary forest cover separately (2.8% and 0.2%, respectively; Figure 2.4a,c). Where the proportion of old-growth forest cover in the surrounding landscape was very low (<10%), secondary forest typically occupied 26.0% (median) of the deforested area (Figure A.6). Thus, secondary forests in landscapes with < 10% total forest cover are in the minority (2.4%; Figure 2.4e). The median proportion of the surrounding landscape occupied by each forest type was 34% for old-growth forest, 20% for secondary forest and 66% for total forest.

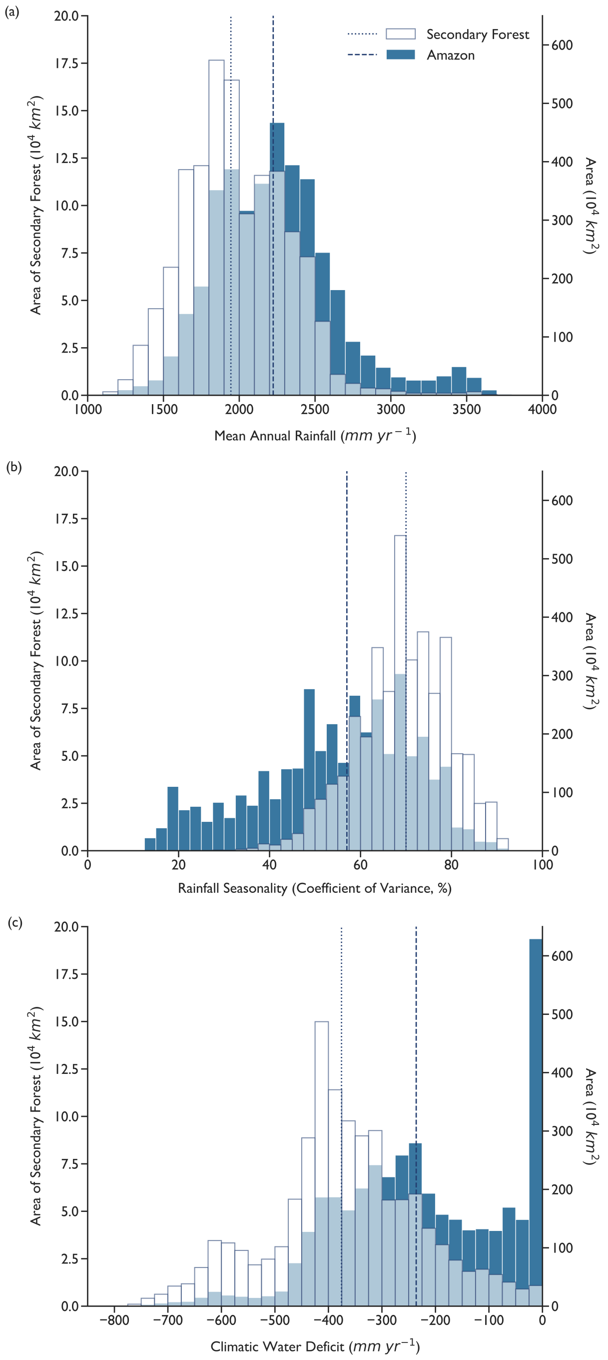


Figure 2.3: The climatic context of secondary forest in the Brazilian Amazon in 2017. The distribution of **(a)** annual rainfall (mm yr^{-1}), **(b)** rainfall seasonality (% difference in wet and dry season rainfall) and **(c)** climatic water deficit (mm yr^{-1}) of secondary forest in the Brazilian Amazon (white, left). The distributions of all three variables were significantly different to the distributions for the entire Brazilian Amazon (blue, right) ($p < 0.01$). Medians for secondary forest (dots) and Amazon-wide (dashed) indicated by vertical lines.

Local

Across all secondary forests present in 2017, the median time spent as agriculture (cropland and pasture) prior to abandonment was 4 years (Figure 2.4b). The majority of secondary forest (85.4%, 110,522 km^2) had experienced just one type of agricultural use, with median usage times of 2 years for cropland (39.2%, 50,692 km^2) and 5 years for pasture (46.3%, 59,830 km^2; Figure 2.4d). For the portion of secondary forests that had experienced multiple use types (14.6%, 18,838 km^2), median land use time was 2 years for cropland, 8 years for pasture and 12 years for total use time. The majority (66.8%) of secondary forest in 2017 was growing on land that had only been cleared of forest once (Figure 2.4f). However, much had been subjected to more than one clearance event during the time series (33.2%, 42,958 km^2) and thus experienced additional land use in previous cycles.

2.3.4 Associations between factors that influence biomass accumulation

Climatic versus Landscape

All our climatic (climatic water deficit, annual rainfall and rainfall seasonality) and landscape (old-growth forest cover, secondary forest cover, total forest cover) variables were significantly correlated ($p < 0.01$; Figure A.5). These correlations show that secondary forests set in low forest cover landscapes also tend to be in regions with drier and more seasonal climates (Figure 2.5).

Landscape versus Local

The proportion of the surrounding landscape occupied by secondary forest was positively correlated with all our measures of prior use (time as agriculture, time as pasture, time as cropland). The strength of the correlation with time as pasture was weaker than the others and statistically marginal given the sample sizes and the number of tests ($p = 0.02$; Figure 2.5; Figure A.5). The number of clearance events was positively associated with secondary forest cover ($p < 0.01$; Figure 2.5; Figure

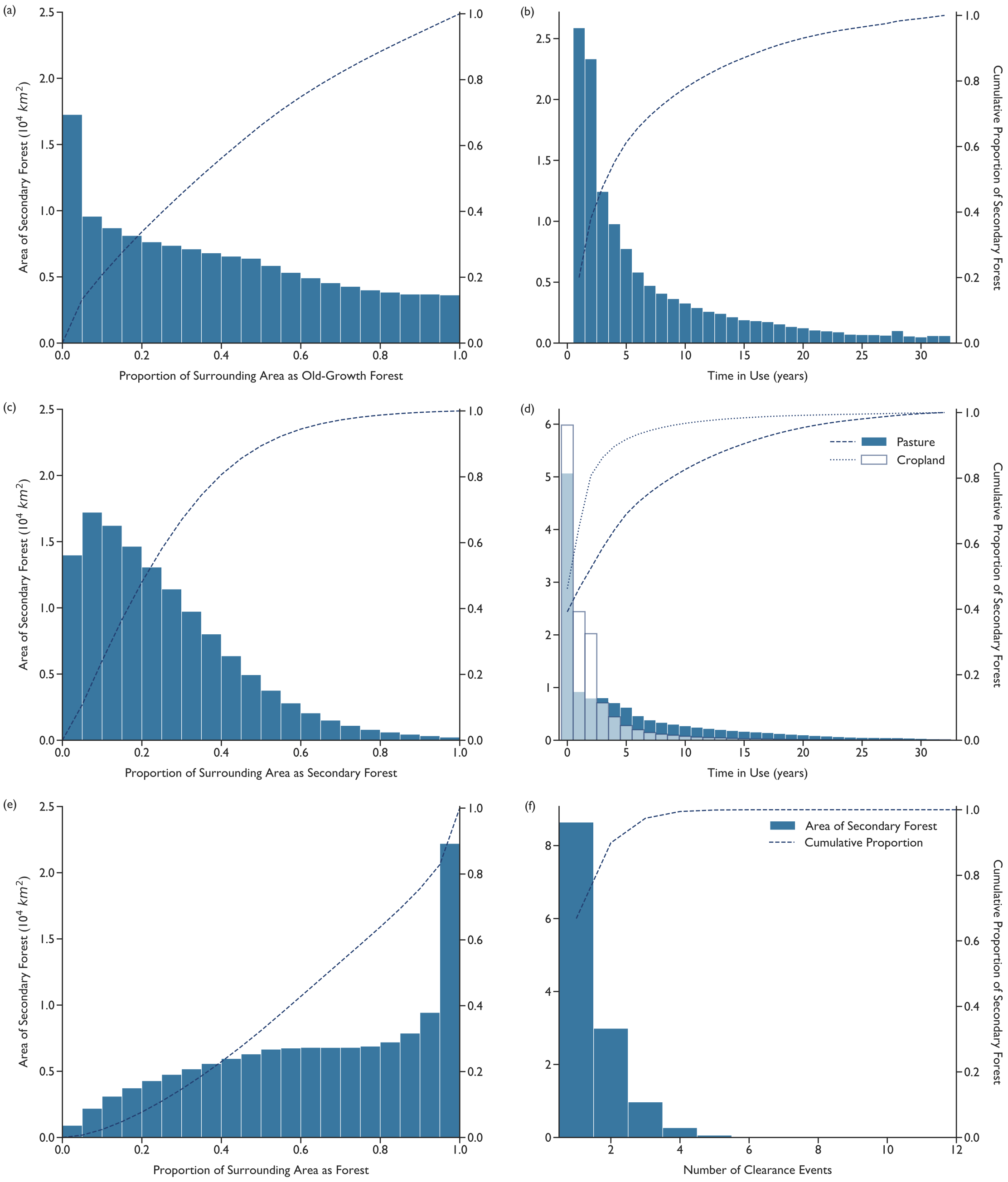


Figure 2.4: Landscape and local contexts of secondary forest in the Brazilian Amazon in 2017. The distribution of landscape **(a, c, e)** and local **(b, d, f)** factors known to influence carbon accumulation for secondary forest in the Brazilian Amazon in 2017. Landscape factors: the proportion of land cover within 1 km of a secondary forest pixel that was classified as **(a)** old-growth forest, **(c)** secondary forest, and **(e)** total forest. Local factors: **(b)** the number of clearance cycles, and the number of years a secondary forest pixel spent as **(d)** cropland or **(f)** pasture before abandonment.

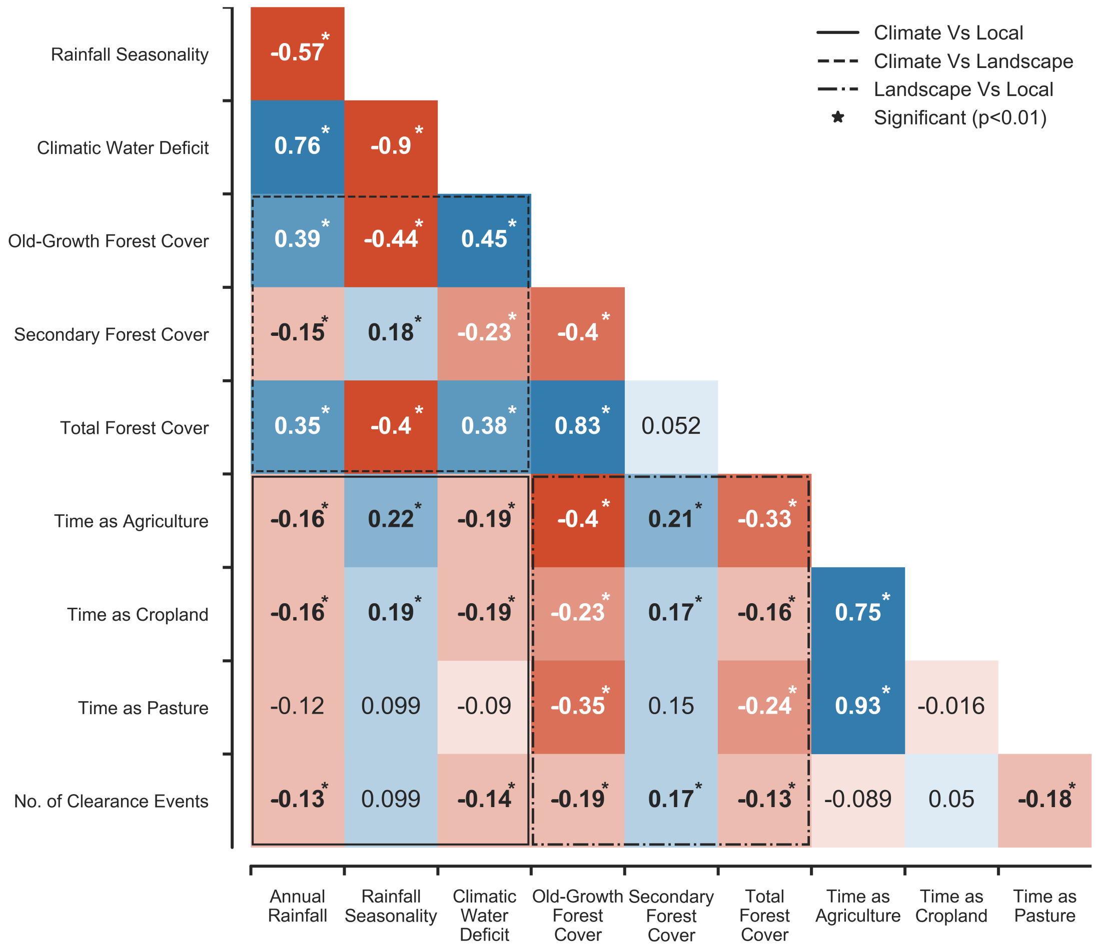
A.5). These associations were reversed for old-growth forest cover and total forest cover, which have negative correlations with all our local factors ($p < 0.01$; Figure 2.5; Figure A.5). Taken together, we find longer use times and more agricultural cycles in landscapes with lower overall forest cover and where secondary forests represent a larger proportion of total forest cover (Figure 2.5).

Climatic versus Local

Climatic water deficit and annual rainfall were both negatively correlated with number of clearance events, time as agriculture and time as cropland ($p < 0.01$; Figure 2.5; Figure A.5). Rainfall seasonality was positively correlated with these same factors, although the association with number of clearance events was weaker. We found similar correlations between climatic variables and time as pasture, albeit with lower confidence in the associations ($p > 0.01$; Figure 2.5; Figure A.5). Taken together, these findings show that secondary forests in regions with drier climates also experienced a higher frequency of agricultural cycles and more prolonged use times ($p < 0.01$; Figure 2.5; Figure A.5).

2.4 Discussion

Inaccurate estimates of forest age and low resolution images, leading to an overestimation of secondary forest extent, have been two of the greatest limitations of previous attempts to estimate secondary forest carbon stocks at large scale (Chazdon et al., 2016a). The MapBiomas land cover data has allowed us to overcome both of these challenges. Using annual data, we found that in 2017 secondary forests occupied 20% of the deforested land in the Brazilian Amazon (also see Almeida et al., 2016; Nunes et al., 2020). Crucially, if these secondary forests have followed the



	Annual Rainfall	Rainfall Seasonality	Climatic Water Deficit	Old-Growth Forest Cover	Secondary Forest Cover	Total Forest Cover	Time as Agriculture	Time as Cropland	Time as Pasture
Rainfall Seasonality	**-0.57***								
Climatic Water Deficit	**0.76***	**-0.9***							
Old-Growth Forest Cover	**0.39***	**-0.44***	**0.45***						
Secondary Forest Cover	**-0.15***	**0.18***	**-0.23***	**-0.4***					
Total Forest Cover	**0.35***	**-0.4***	**0.38***	**0.83***	0.052				
Time as Agriculture	**-0.16***	**0.22***	**-0.19***	**-0.4***	**0.21***	**-0.33***			
Time as Cropland	**-0.16***	**0.19***	**-0.19***	**-0.23***	**0.17***	**-0.16***	**0.75***		
Time as Pasture	-0.12	0.099	-0.09	**-0.35***	0.15	**-0.24***	**0.93***	-0.016	
No. of Clearance Events	**-0.13***	0.099	**-0.14***	**-0.19***	**0.17***	**-0.13***	-0.089	0.05	**-0.18***

Figure 2.5: Spatial correlations between climatic, landscape, and local context of secondary forest in the Brazilian Amazon in 2017. Mean correlation co efficient of the spatial associations between the climatic, landscape, and local contexts of secondary forest in the Brazilian Amazon. The tests used 10,000 iterations of Spearman's Rank Order Correlation on samples of secondary forest pixels (n = 1000) and a significance (*) threshold of $p < 0.01$. Samples were selected such that 25% of points were situated in each quadrant of the Amazon biome.

regrowth trajectories calculated by Requena Suarez et al. (2019), we show that by 2017 their total carbon stock had offset less than 10% of the emissions resulting from the loss of old-growth forest (Figure 2.2c). This is much lower than the 20% offset calculated by Houghton et al. (2000), despite secondary forests now covering an area almost the size of England. Nonetheless, our estimate may be high, given the climatic conditions of secondary forest compared to the network of plots on which the carbon accumulation rates are modelled (Figure A.3). We explore these issues below, first examining why secondary forest carbon stocks are so low, and then exploring what climatic, landscape, and local factors indicate about the recovery potential of secondary forests in the Brazilian Amazon.

2.4.1 High rates of forest conversion limit secondary forest carbon stocks

Within the Amazon, there is clear evidence that the carbon stock of secondary forests is related to their age (Poorter et al., 2016; Lennox et al., 2018; Requena Suarez et al., 2019; Elias et al., 2020). Recent estimates suggest a 32-year-old secondary forest, the maximum age detectable with MapBiomas, would hold a maximum of 68.4±9.2 Mg C ha^{-1}, which is just 59±8% of the average for old-growth forest (115.2 Mg C ha^{-1}; Avitabile et al., 2016). Furthermore, some secondary forests recover at much slower rates still, reaching just 34.6 Mg C ha^{-1} at 32 years (Elias et al., 2020). Moreover, these maximum values are rarely attained because high rates of secondary forest clearance (6,410 km^2 yr^{-1}) impose an age distribution that is highly skewed towards young age classes (Figure 2.1c)(also see Chazdon et al., 2016a). We find only 16% of secondary forests were aged between 20 and 32 years in 2017, whereas forests less than 5 years old, which store just 12±2% of the carbon of old-growth forest, comprised 50% of all secondary forests.

The carbon balance of secondary forests was undermined by continued clearance (Figure 2.2a-b). Over the time series, almost as much carbon as was stored by secondary forest in 2017 (0.33±0.05 billion Mg C), was released back into the atmosphere through secondary forest clearance (0.25±0.4 billion Mg C, Figure 2.2b). The ephemeral nature of secondary forests seems unlikely to change as younger secondary forests, which constitute the majority (84%), are also more susceptible to clearance (Schwartz et al., 2017a). Furthermore, the increasing proportion of total forest loss accounted for by secondary forest indicates they are being cleared preferentially (Wang et al., 2020). Protecting secondary forests from clearance is key if they are to be used to meet climate change mitigation goals (Grassi et al., 2017). Yet, any such policies also need to consider their contribution to swidden agriculture and examine whether their clearance helps to reduce old-growth forest loss (Wang et al., 2020).

2.4.2 Could the climatic, landscape, and local context of secondary forests be affecting their carbon accumulation potential?

Climatic factors

The occurrence of deforestation is strongly influenced by an area's agricultural suitability, which in turn is determined by a suite of economic, climatic, and edaphic conditions (Carmen Vera-Diaz et al., 2008). This has resulted in the more seasonal regions of the Brazilian Amazon experiencing the most extensive land use change (Figure 2.1a, Figure A.7a-c). Consequently, in 2017, the distribution of secondary forests within the Amazon's climatic range was also skewed towards these drier and more seasonal conditions (Figure 2.3), which are likely to be less favourable for secondary forest growth (Poorter et al., 2016). Crucially, our understanding of secondary forest growth in these drier regions is also limited – the plots underpinning the most recent basin-wide estimates of secondary forest carbon accumulation rate (Requena Suarez et al., 2019) are located in significantly wetter regions of the Amazon than secondary forests generally (Figure A.3). This climatic distribution of secondary forests means they could be more sensitive to climate change resulting from global greenhouse gas emissions and regional changes in forest cover. On a local scale, deforestation results in reduced rainfall (e.g. Spracklen et al., 2015, 2018) and higher temperatures (Silva et al., 2016), leading to increased evapotranspiration and drought stress. Over longer time scales, these changes are likely to be intensified by global climate change, which is causing the Amazon to become drier and increasing the dry season length – by as much as 6.5 days per decade in some regions (Fu et al., 2013). Drought is known to affect tree species composition and lead to biomass reductions in old-growth forest (Phillips et al., 2009; Esquivel-Muelbert et al., 2019) and there is evidence that such changes could reduce secondary forest recovery rates (Elias et al., 2020). We could reasonably expect secondary forests to be even more susceptible to these drought stresses as they may lack the deep roots known to support old-growth forests (Nepstad et al., 1994), pioneer tree species have lower water use efficiency (Markesteijn et al., 2011), and mortality from droughts is linked to lower wood density (Phillips et al., 2009; Uriarte et al., 2016). Conversely, if the slow shift towards species associated with dry environments that is seen in old-growth forest (Esquivel-Muelbert et al., 2019) is also occurring in secondary forests, then the latter may become more resilient to drought. However, secondary forests are often found in regions with little surrounding old-growth forest cover (e.g. Elias et al., 2020), and compositional changes may be limited by seed availability.

Landscape factors

Agricultural land abandonment is a complex phenomenon primarily driven by socioeconomic factors such as migration (Benayas et al., 2007). As a result, although Amazon-wide secondary forest covered approximately 20% of deforested land, this figure varied greatly between regions. The greatest proportional recovery occurred in the highly forested areas of the western Amazon, where headwater abandonment and rural-to-urban migration are enabling secondary forest growth (Figure 2.1b) (Parry et al., 2010). As surrounding forest cover has positive effects on biomass recovery (Jakovac et al., 2015; Toledo et al., 2020), secondary forests growing in these relatively intact landscapes were positioned favourably for carbon sequestration. However, across the Brazilian Amazon, we find such forests to be in the minority: just 13% of all secondary forest was in landscapes with $\geq$80% old-growth forest (Figure 2.4a). Most secondary forest was found along the highly deforested agricultural frontier, where it may suffer the negative impacts of fragmentation, isolation, and edge effects (Ewers et al., 2005; Magnago et al., 2017). Consequently, these forests likely have considerably lower carbon-accumulation potential than those in regions with more intact forest landscapes (Chazdon, 2003; Bihn et al., 2010). Finally, although surrounding forest cover is important for carbon accumulation, the role of the type and condition of the surrounding forest requires further research. Recent findings indicate that high surrounding of secondary forest cover is advantageous for forest growth in the early stages of succession (Toledo et al., 2020). However, it is likely that proximity to old-growth forest will be more important later in succession, as they are essential for providing the diverse seed sources required to establish resilient, biodiverse and high-biomass secondary forests (e.g. Hawes et al., 2020). Furthering our understanding these relationships will be key to designing effective restoration programmes within landscapes where there is little old-growth forest remaining.

Local factors

Incorporating measures of prior land use has previously been suggested as a mechanism for improving the accuracy of biomass estimates in secondary forest (Wandelli et al., 2015), as studies have found that higher land use intensity leads to slower biomass recovery (e.g. Jakovac et al., 2015). Our assessment provides a mixed evaluation of the favourability of local land use intensity factors for secondary forest carbon accumulation. We find the majority (66.8%) of secondary forests in 2017 were in the favourable position of only having experienced one agricultural cycle. However, this alone does not adequately represent land use intensity, as the type and length of land use within a single cycle vary greatly. Secondary forests accumulate carbon more slowly on abandoned pasture than on abandoned cropland (Fearnside et al., 1996). We find 46.3% of secondary forests in 2017 to be growing on land that was previously pasture and a further 14.6% on land that was pasture at some point during the most recent land use cycle (Figure 2.4d), placing the majority of secondary forests on unfavourable ground for carbon accumulation. Although secondary forest pixels were on average in use for just 4 years, almost 25% had 10 or more years of use before being abandoned. Extended use periods are more characteristic of pasture (median: 5 years), which typically had a longer use period than cropland (median: 2 years). This short-term cropland use suggests that most of the secondary forests growing on former cropland may be part of farm-fallow swidden land use practises, on which secondary forests grow more quickly than on abandoned pasture (Wandelli et al., 2015) or mechanised croplands. These conditions are more favourable for carbon accumulation. However, the land is an inherent component of a cyclical agricultural system that supports local livelihoods, thus cannot be relied upon for long-term carbon storage. The impact of land use on carbon accumulation rate is complex, with many interacting variables determining the fate of the subsequent forest (Guariguata et al., 2001; Jakovac et al., 2015; Martinez-Ramos et al., 2016). Although providing some insight into the variety of secondary forest land use histories, the MapBiomas classifications of pasture and cropland mask important details about specific land use practises which may be key to fully understanding the influence of local factors on secondary forest growth.

Interactions between predictors of secondary forest recovery

While each of these climatic, landscape, and local factors are important in their own right, they do not act independently (Figure 2.5), giving rise to the possibility that interactions between factors that may be influencing carbon accumulation in secondary forests. Some of the variables are so influential that they may overwhelm the effect of others; for example, higher previous land use intensity can restrict carbon recovery even in very high forest-cover landscapes (Fernandes Neto et al., 2019). Therefore, the longer land use periods found in high forest cover areas suggests that the benefits of a favourable landscape context experiences by many secondary forests could be reduced by their land use history.

Other associations between factors known to affect carbon accumulation may act together to limit secondary forest recovery. For example, secondary forests in drier, less favourable climatic contexts are also more likely to have lower surrounding forest cover and a greater proportion of the landscape comprising secondary rather than old-growth forest (Figure 2.5). These secondary forests are not only suffering the consequence of limited water availability (Poorter et al., 2016) but may also be subject to edge and isolation effects, reduced tree seed sources and the changes in local climate that result from high levels of deforestation (Fu et al., 2013; Magnago et al., 2017; Spracklen et al., 2018). The association between these factors suggests that the very low biomass accumulation rates found in one region in the eastern Amazon (Elias et al., 2020) may be representative of far greater areas of Amazonia's secondary forests, highlighting the urgent need to expand sampling efforts.

2.4.3 Uncertainty in the role of secondary forests as a carbon sink

While the carbon balance of undisturbed forests has been well studied (Pan et al., 2011; Saatchi et al., 2011; Brienen et al., 2015; Hubau et al., 2020), estimates of the rate of carbon sequestration in secondary forests remain highly variable (Pan et al., 2011; Saatchi et al., 2011; Grace et al., 2014; Elias et al., 2020; Heinrich et al., 2021). Requena Suarez et al. (2019) have made huge advances in refining our understanding of secondary forest carbon accumulation. However, there are uncertainties associated with applying their rates universally in order to produce large-scale estimates. Chiefly, the estimates we used are based on a plot network that, despite being the most wide-spread available, does not fully represent conditions influencing secondary forest growth. This network is over-representing the accumulation rates in regions that are wetter and less seasonal than the majority of secondary forests in the Brazilian Amazon (see supplementary information). This disparity in climate may even be greater than reported here, as we have potentially underestimated the climatic range of secondary forests by using WorldClim data, which may no longer be representative of true climate on the ground, given the impact of deforestation on local climates (Spracklen et al., 2018). Many of the plots (~60%) also began growing before 1985 (Requena Suarez et al., 2019), when large-scale deforestation had not yet substantially reduced forest cover (Fearnside, 2005) and before mechanised agriculture had intensified land use. Recent studies from other regions have shown much lower carbon accumulation rates of 2.25 Mg ha^{-1} yr^{-1} in Paragominas and Santarém-Belterra (Lennox et al., 2018), 1.08 ha^{-1} yr^{-1} in Bragança (Elias et al., 2020) or as low as 0.89 Mg ha^{-1} yr^{-1} in the Guiana Shield

(Chave et al., 2020).

Further uncertainty is introduced by the inability to account for the different drivers of secondary forest growth, which we show may be associated in ways that could result in important interacting effects on carbon accumulation. Forest degradation contributes yet more uncertainty to large-scale estimates of carbon stock. This often unaccounted for source of carbon emissions affects 17% of the forest area in the Amazon (Bullock et al., 2020), meaning that we are under-estimating emissions from old-growth forests and over-estimating secondary forest carbon stock. The intricacies of local soil variation present another source of uncertainty when estimating secondary forest carbon stock across large regions and requires further research before we can begin to understand its impact on secondary forest carbon accumulation rates (Quesada et al., 2011; Quesada et al., 2012).

Some of these limitations may be overcome by improvements in LiDAR technology and our capacity to analyse the resulting data (Almeida et al., 2019). Nevertheless, these new remote sensing techniques cannot capture several key measures that are essential for understanding the impact of biogeographic factors on carbon accumulation, notably wood density (Baker et al., 2004). In order to overcome this, investment is needed to develop a distributed secondary forest plot network that captures the full range of factors known to affect recovery, with a design that allows studies to assess interactions between factors, and includes local measures of soil and other land use histories that cannot be resolved from space. Repeated samples of the same plot will also provide advantages over chronosequence approaches, allowing biomass responses to climatic variation to be included in models (Elias et al., 2020).

2.5 Conclusion

With properly implemented policy, secondary forests could provide an effective, low-cost, nature-based tool for mitigating climate change (Crouzeilles et al., 2017) and for reaching national and international ecosystem restoration targets (e.g. Bonn Challenge, UN Decade for Restoration). If just 80% of Brazil's 12 million ha reforestation target took place in the Amazon, with the accumulation rates reported by Requena Suarez et al. (2019), it could store as much 1.1±0.2 billion Mg C if left undisturbed 20 years. Yet, despite a fifth of deforested land now being covered by secondary forest, in more than 30 years, secondary forest growth has at most offset less than 10% of deforestation emissions. Without halting old-growth forest loss, the importance of secondary forest for the carbon balance of Amazonia is likely to remain minimal. With 10,000 km^2 of old-growth forest cleared in the Brazilian Amazon in 2019 (PRODES, 2020), this is unlikely to change in the near future. We have also shown that there is likely to be much more geographical variation in secondary forest recovery rates than is incorporated in current estimates. Future policies relying on secondary forest growth will require a much better understanding of the factors determining recovery to ensure different secondary forests are treated appropriately, with protection focused on those of greatest long-term carbon storage potential (Gren et al., 2016). More accurate quantification of carbon stocks and recovery rates in secondary forests will support the production of appropriate management proposals (Wandelli et al., 2015) and will be critical if carbon-based payments for ecosystem services (e.g. REDD+) are to be successfully implemented. Moreover, increasing our knowledge of secondary forests is crucial to our understanding of tropical forest responses to environmental stressors, and the resilience of one of the world's most important biomes.

Chapter 3

Old-growth forest loss and secondary forest recovery across Amazonian countries

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Abstract

There is growing recognition of the potential of large-scale forest restoration in the Amazon as a “nature-based solution” to climate change. However, our knowledge of forest loss and recovery beyond Brazil is limited, and carbon emissions and accumulation have not been estimated for the whole biome. Combining a 33-year land cover dataset with estimates of above-ground biomass and carbon sequestration rates, we evaluate forest loss and recovery across nine Amazonian countries and at a local scale. We also estimate the role of secondary forests in offsetting old-growth deforestation emissions and explore the temporal trends in forest loss and recovery. We find secondary forests across the biome to have offset just 9.7% of carbon emissions from old-growth deforestation, despite occupying 23.7% of deforested land. However, these numbers varied between countries ranging from 7.7% in Brazil to 23.8% in Guyana for carbon offsetting, and 20.1% in Brazil to 56.9% in Ecuador for forest area recovery. We reveal a strong, negative spatial relationship between old-growth forest loss and recovery by secondary forests, showing that regions with the greatest potential for large-scale restoration are also those that currently have the lowest recovery (e.g. Brazil dominates deforestation and emissions but has the lowest recovery). In addition, a temporal analysis of the regions that were >80% deforested in 1997 shows a continued decline in overall forest cover. Our findings identify three important challenges: (1) incentivising large-scale restoration in highly deforested regions, (2) protecting secondary forests without disadvantaging landowners who depend on farm-fallow systems, and (3) preventing further deforestation. Combatting all these successfully is essential to ensuring that the Amazon biome achieves its potential in mitigating anthropogenic climate change.

3.1 Introduction

Deforestation is a major and ongoing threat, with an estimated 4.2 million km^2 of global forests cleared since 1990 (FAO et al., 2020). Across the world tropical deforestation represents around 8% of all anthropogenic emissions (Seymour et al., 2016), while deforestation and land-use change combined contribute the majority of carbon emissions in most tropical forest countries. However, tropical forests are fundamental to the world's climate crisis not only as a source of emissions, but also as a means for capturing atmospheric carbon. Secondary forests growing on previously deforested land are rapidly sequestering carbon and providing refuge for many forest dependant species. While old-growth forests are undeniably more valuable than secondary forests, both in terms of biodiversity and carbon storage (Gibson et al., 2011; Berenguer et al., 2014), there is growing recognition of the potential of large-scale tropical forest restoration as a “nature-based solution” to climate change mitigation (UN Decade on Restoration, 2019) and of its importance for meeting the ambitious emissions targets of the Paris agreement (Grassi et al., 2021).

The Amazon biome has been recognised by researchers and policymakers alike for its key role in future climate policy for two main reasons. First, the Amazon biome stores an estimated 86 Pg of carbon (Saatchi et al., 2007), making it one of the world's largest carbon strongholds (Saatchi et al., 2011). Unchecked, deforestation could convert much of this carbon stock into emissions (Gatti et al., 2021), significantly accelerating climate change. The Brazilian Amazon has witnessed amongst the highest absolute rates of deforestation in the tropics, with a notable increase in recent years (PRODES, 2020), placing Brazil in the top 10 emitters in the world (World Resources Institute, 2021). Second, compared with other tropical regions, the Amazon could be ideal for forest restoration as it has low population densities (Cunningham et al., 2018), extensive areas of unproductive or unprofitable agricultural systems (Garrett et al., 2017, 2021), and moderate to high carbon sequestration rates

(Requena Suarez et al., 2019). However, patterns of forest loss and recovery, and their impact on the carbon balance have not been estimated for the whole biome. Our understanding has previously focused on Brazil (e.g. Smith et al., 2020), which only makes up 60% of the Amazon biome. The contribution of the other seven countries (Bolivia, Colombia, Ecuador, Guyana, Peru, Suriname, Venezuela) and the French overseas territory (French Guiana; henceforth included in the collective ‘countries’) is much less well understood. With recent studies showing increasing occurrences of deforestation hotspots outside Brazil (Kalamandeen et al., 2018), the need to expand our knowledge beyond Brazil grows more critical. Furthermore, forest recovery also varies greatly over space and time (Chave et al., 2020; Smith et al., 2020), making it crucial to understand where forests are already recovering and how this recovery differs both across political units and on finer spatial scales, so that active restoration efforts and novel policy incentives can be targeted effectively. Despite restoration offering a growing opportunity to mitigate anthropogenic emissions (Chazdon et al., 2016b, 2020; Matos et al., 2020), to date, we are not aware of any analysis examining patterns of forest loss and recovery across Amazonia at both national and subnational level, which are the relevant scales for policy interventions promoting restoration..

Here, we combine a 33-year land cover dataset (MapBiomas Amazonia 2; 1985-2018) with estimates of above-ground biomass (AGB; Avitabile et al., 2016) and forest regrowth potential (Requena Suarez et al., 2019) to evaluate the distribution of forest loss and recovery across the nine countries and nine Brazilian states that intersect the Amazon biome. We ask three questions. (1) What is the current (2017) extent of old-growth deforestation and forest recovery, and their associated impact on the Amazonian carbon balance? We estimate carbon emissions from forest loss and carbon accumulation from secondary forest growth (i.e. forest growing on previously deforested land) across the Amazon biome and its major political units. (2) What is the geographic relationship between old-growth deforestation and secondary forest recovery? We examine this at the country- and state-level, and then at a finer resolution using a ~60 km^2 grid. (3) How have the rates of old-growth deforestation and secondary forest recovery varied over the last two decades? We discuss our results in light of the challenges of avoiding further deforestation and achieving large-scale forest restoration across Amazonia.

3.2 Methods

3.2.1 Old-growth and secondary forest extent

We use the MapBiomas Amazonía 2 dataset to assess deforestation and SF extent for the Amazon Biome (Appendix B.4). By using the MapBiomas dataset we were able to exclude forestry plantations, which is important for evaluating changes in SF extent. We reclassify the MapBiomas schema into: forest, pasture, cropland and other, then use a change detection algorithm to produce annual maps of the extent of OG and SF cover across the Amazon biome (Appendix B.4). Any pixel (900 m^2) classified as ‘forest’ in the first year of the time series (1985) was considered to be OG until it transitioned to ‘non-forest’. Pixels that transitioned from ‘non-forest’ to ‘forest’ were classified as SF. As the MapBiomas time series begins in 1985, any SF that began growing before this date is included in our OG class (Appendix B.4). Our method is based on the approach previously described by Smith et al. (2020).

3.2.2 Secondary forest age and residence time

We measured SF age as the number of consecutive years a pixel was classified as SF in our annual maps of forest cover. Due to incomplete data coverage in some regions this should be considered a “minimum” age estimate rather than a precise measure (Appendix B.4). We measured SF residence time as the age of SF at clearance. We conducted Kruskal-Wallis tests to determine if SF age or residence time (for SF cleared 1997 to 2017) differs between countries and Brazilian states. To avoid assigning significance to small effect sizes due to large samples, we used a sample size of 100. We repeated this process 10,000 times and recorded the mean p-value. Brazil was excluded from the analysis in favour of its component states to avoid pseudo-replication. Where the Kruskal-Wallis test was significant, we conducted Dunn's post-hoc tests to identify which pairs of countries or states had different distributions. We do not explore the dynamics of repeated clearances or "third-growth" forests in this study as less than 0.04% of deforested pixels had been cleared multiple times during the study period.

3.2.3 Calculating above-ground carbon

Old-growth forest

We calculated AGB in OG using the Avitabile et al. (2016) 1-km resolution pan-tropical AGB map, which we downscaled to match the 30-m resolution MapBiomas land cover data. For areas deforested before 2010, prior to the most recent dataset used by Avitabile et al. (2016), we interpolate AGB using the KNNImputer function from the Python package sklearn, which infills missing values with the mean of a pixel's twenty nearest neighbours. We converted AGB to carbon stock using the Intergovernmental Panel on Climate Change (IPCC) conversion factor of 0.47 g C (g biomass)$^{-1}$ (Eggleston et al., 2006). For the purposes of this study, we assume above-ground carbon to be static as, although OG are accumulating carbon, it is at a very slow rate (~1 Mg ha^{-1} year^{-1}; Requena Suarez et al, 2019). Due to the complexity of mapping the intensity of disturbance in OG over large spatial scales, accounting for the impact of degradation on carbon stocks was beyond the scope of this study. Therefore, we may be over-estimating carbon emissions from deforestation. Below-ground carbon is estimated to contribute an additional 25% to tropical forest carbon stocks (Luyssaert et al., 2007), but its assessment was also beyond the scope of this study.

Secondary forest

We estimate SF AGB using our maps of SF age in conjunction with the Requena Suarez et al. (2019) biomass accumulation rates for old ($\geq$20 years) and young (<20 years) SF. We converted AGB values to carbon stock as above (conversion factor: 0.47). Carbon accumulation rates can vary greatly in response to local climatic, environmental, and disturbance factors (Poorter et al., 2016; Elias et al., 2020), but to date analyses calculating local scale accumulation rates have been limited to the Brazilian Amazon (Heinrich et al., 2021). As our study encompasses the entire Amazon biome, we opted to use the baseline carbon accumulation rates calculated by (Requena Suarez et al., 2019) for the FAO Ecozones (FAO, 2012). Four ecozones intersect our study area: tropical rainforest (~61.7%), tropical moist forest (~25.6%), tropical montane forest (~11.7%), and tropical dry forest (~1.0%).

3.2.4 Deforestation extent and emissions

Using the change in forest cover captured by our analysis of MapBiomas, we calculated the annual extent of OG and SF deforestation and the associated carbon emissions. For each forest type, we applied an exponential decay of 0.49 (Leeuwen et al., 2014) to our estimate of the pixel's above-ground carbon in order to extend emissions from a deforestation event over several years, as is seen in long-term assessments of AGB loss on deforested land (e.g. Berenguer et al., 2014). Above-ground carbon was converted to carbon dioxide equivalent using the conversion factor 3.67. For pixels classified as cropland or pasture in the first year of our time series (1985), we calculate emissions as if the pixels were cleared in 1984. While this means that some of the pixels are assumed to have been cleared more recently than they actually were, the impact of this on our estimates of OG deforestation emissions is negligible as, by the most recent year of our anaylsis (2017), more than 99.99% of the carbon they contained is accounted for. We report variation in SF emissions using the 95% confidence interval of estimates of Requena Suarez et al. (2019). While some deforested timber is harvested and utilized long-term – meaning not all above-ground carbon is transferred to the atmosphere – we believe the impact of this on our estimate of carbon emissions to be small as: (i) our map of old-growth above-ground carbon includes degraded forest, so much of the carbon loss associated with timber removal is already accounted for; (ii) timber offtake rates are generally low (e.g. Sist et al., 2021), (iii) the efficiencies of turning natural timber to long-lifespan products are also very low (Alice-Guier et al., 2020).

3.2.5 Relationship between deforestation and recovery

Political scale

We use the term forest area recovery to mean the percentage of the total area of OG deforestation occupied by SF, and the term carbon recovery to mean the percentage of total OG deforestation emissions offset by carbon accumulated in SF. We use Akaike information criterion (AIC) model selection to find best-fit models (Nally et al., 2018) for the relationships between the percentage of OG deforestation (relative to original OG extent; see above) and forest area recovery, and between the percentage of OG carbon emissions (relative to original carbon stock; see above) and SF carbon recovery. We conducted this analysis across political units, comparing the AIC score of five difference models: null, linear and broken-stick (up to three segments). This analysis was conducted using the *stats* (R Core Team 2021) and *segmented* (Muggeo, 2017) R-packages. The assumptions of the models were checked by graphical analysis (Quinn et al., 2002).

Local scale

We repeated the above analysis at a local scale by dividing the Amazon biome into a regular grid of ~58.9 km^2 cells (65,536 pixels; pixel size: 0.0009 km^2; size determined by computational efficiency). Cells with >99% of pixels classified as ‘other’ (i.e. where less than 1% of the cell area is capable of being forest) were excluded from the grid level analysis. Cells with $\leq$0.1% deforestation were considered to have experienced no deforestation and were excluded from the analysis. To understand how recovery in highly deforested landscapes has changed over time, we selected cells that had lost more than 80% of their OG cover by 1997 (Figure B.7) and calculated the change in their percentage OG, SF and total forest cover from 1997 to 2017.

3.2.6 Temporal trend analysis

To explore how OG deforestation, SF extent and their associated carbon emissions have changed over time, we used the AIC model selection method described above using AICc; a small-sample-size corrected version of AIC. We conduct this analysis between 1997 and 2017 to avoid assigning significance to ‘trends’ that are an artifact of SF older than 33-years being included in our OG class.

3.3 Results

3.3.1 Old-growth deforestation extent and carbon emissions

By 2017, we found that 813,944 km^2 of old-growth forest (OG) in the Amazon biome had been cleared (Table 3.1). Brazil has seen the greatest loss in OG area both in absolute terms (689,451 km^2; 3.1a) and proportional to its Amazonian extent (17.6%; 3.1b). Two-thirds of Brazil’s nine Amazonian states have an absolute area of deforestation exceeding that of any of the other countries (3.1a); the deforested area in Pará state alone is more than double that of all other countries combined (Pará: 262,869 km^2; other countries: 124,493 km^2; 3.1a). By 2017, OG deforestation across the Amazon biome had resulted in the loss of 6.33 Pg C from AGB, emitting the equivalent of 23.22 Pg CO$_2$ (Table 3.1). Brazil contributed 79.9% of all OG deforestation emissions (5.06 Pg C; Figure B.1). Ecuador had the greatest percentage loss of carbon relative to its original OG above-ground carbon stock (12.3%), but this represents just 2.2% of total emissions. The Brazilian states of Pará, Mato Grosso and Rondônia exceed the emissions of any other individual Amazonian country (Table 3.1).

Table 3.1 Old-growth deforestation, secondary forest growth and their associated carbon emissions in the Amazon biome in 2017.

Region	**Amazon biome (%)**	**OG loss (km^2)**	**OG loss (%)**	**OG carbon loss (Tg C)**	**OG carbon loss (%)**	**SF area (km^2)**	**Total forest (% SF)**	**Forest area recovery (%)**	**SF carbon (Tg)**	**SF carbon 95% CI (Tg)**	**Carbon recovery (%)**	**Carbon recovery 95% CI (%)**
Brazil	61.9%	689,451	17.6%	5,057.7	15.8%	138,287	4.1%	20.1%	391.5	65.7	7.7%	1.3%
Amazonas	*23.6%*	*37,403*	*2.5%*	*337.1*	*1.9%*	*16,462*	*1.1%*	*44.0%*	*59.4*	*9.3*	*17.6%*	*2.7%*
Pará	*18.4%*	*262,869*	*22.7%*	*2,060.4*	*15.1%*	*58,800*	*6.2%*	*22.4%*	*165.3*	*27.3*	*8.0%*	*1.3%*
Mato Grosso	*7.3%*	*170,288*	*37.0%*	*1,175.3*	*29.3%*	*21,541*	*6.9%*	*12.6%*	*59.2*	*10.1*	*5.0%*	*0.9%*
Rondonia	*3.6%*	*92,835*	*41.4%*	*712.5*	*32.7%*	*8,909*	*6.4%*	*9.6%*	*24.3*	*4.0*	*3.4%*	*0.6%*
Roraima	*2.7%*	*12,029*	*7.0%*	*96.3*	*5.2%*	*4,588*	*2.8%*	*38.1%*	*12.1*	*2.4*	*12.5%*	*2.5%*
Acre	*2.6%*	*22,756*	*13.7%*	*207.9*	*10.7%*	*3,851*	*2.6%*	*16.9%*	*11.1*	*1.8*	*5.3%*	*0.9%*
Amapá	*1.8%*	*4,606*	*4.0%*	*44.1*	*2.2%*	*3,182*	*2.8%*	*69.1%*	*11.8*	*1.8*	*26.9%*	*4.0%*
Maranhão	*1.6%*	*66,832*	*66.7%*	*348.0*	*54.7%*	*17,280*	*34.2%*	*25.9%*	*38.4*	*7.2*	*11.1%*	*2.1%*
Tocantins	*0.4%*	*19,833*	*82.9%*	*76.0*	*80.4%*	*3,674*	*47.2%*	*18.5%*	*9.9*	*1.8*	*13.0%*	*2.4%*
Peru	11.5%	49,852	6.9%	630.7	7.3%	25,579	3.7%	51.3%	73.8	15.4	11.7%	2.4%
Colombia	7.4%	35,393	7.6%	267.5	5.3%	11,055	2.5%	31.2%	31.5	5.5	11.8%	2.1%
Venezuela	6.1%	7,996	2.1%	54.6	1.3%	3,528	0.9%	44.1%	9.3	1.9	17.0%	3.5%
Bolivia	5.2%	10,592	3.2%	93.1	2.7%	3,049	1.0%	28.8%	9.7	2.4	10.4%	2.5%
Guyana	3.0%	5,558	3.0%	57.2	1.9%	3,046	1.6%	54.8%	13.6	2.5	23.8%	4.4%
Suriname	2.1%	2,816	2.1%	27.0	1.3%	1,344	1.0%	47.7%	6.0	1.2	22.3%	4.5%
Ecuador	1.5%	12,160	12.7%	139.7	12.3%	6,922	7.7%	56.9%	16.4	3.7	11.7%	2.6%
French Guiana	1.3%	126	0.2%	1.3	0.1%	57	0.1%	45.0%	0.1	0.0	10.1%	1.5%
Amazon	100.0%	813,944	13.4%	6,328.8	8.6%	192,867	3.4%	23.7%	616.3	111.3	9.7%	1.8%

3.3.2 Secondary forest extent, age, residence time and carbon accumulation

In 2017, secondary forests (SF) covered 192,867 km^2 of land in the Amazon biome, accounting for approximately 3.4% of the total forest cover (Table 3.1). 71.7% of Amazonian SF was in Brazil (138,287 km^2; 3.1c), with 13.3% in Peru (25,579 km^2; 3.1c), and 5.7% in Colombia (11,055 km^2; 3.1c). Making up 4.1%, 3.7% and 2.5% of each country's total forest cover respectively (Table 3.1). The majority (78.2%) of all SF was less than 20 years old and the median age was 8 years (Figure B.2). Very young SF ($\leq$5 years old) accounted for 35.9% of all cover. This skewed age distribution was apparent in the majority of countries (Figure B.3). Guyana and Suriname were the only countries with significantly different age distributions with large spikes in 18 to 24-year-old SF (Dunn's post-hoc test: $P<0.05$; Figure B.5a), although this could be an artifact of poor temporal data availability in these countries (Appendix B.2). As our time series began in 1985, the maximum detectable age of SF is 32 years. However, the skewed distribution of forest ages suggests that very little forest would have exceeded this maximum detectable age (Figure B.3). Across the Amazon biome, during the period 1997-2017, the majority (70.0%) of SF cleared was 5-years old or less and the median residence time (from the start of SF regrowth to clearance) was just 2 years. There were no significant differences in the distribution of residence times across countries or states (Figure B.5b). SF present in 2017 had accumulated 0.62±0.11 Pg C, equivalent to 2.26±0.41 Pg CO_2. SF deforestation has resulted in the loss of 38.9% (391.65±94.62 Tg C) of all carbon accumulated by SF between 1985 and 2017.

3.3.3 Spatial relationships between deforestation and recovery

In 2017, carbon accumulated in SF had offset less than 30% of OG deforestation emissions in every Amazonian country or Brazilian state we assessed (Table 3.1). Across the Amazon biome as a whole just 9.7±1.8% of carbon emissions had been

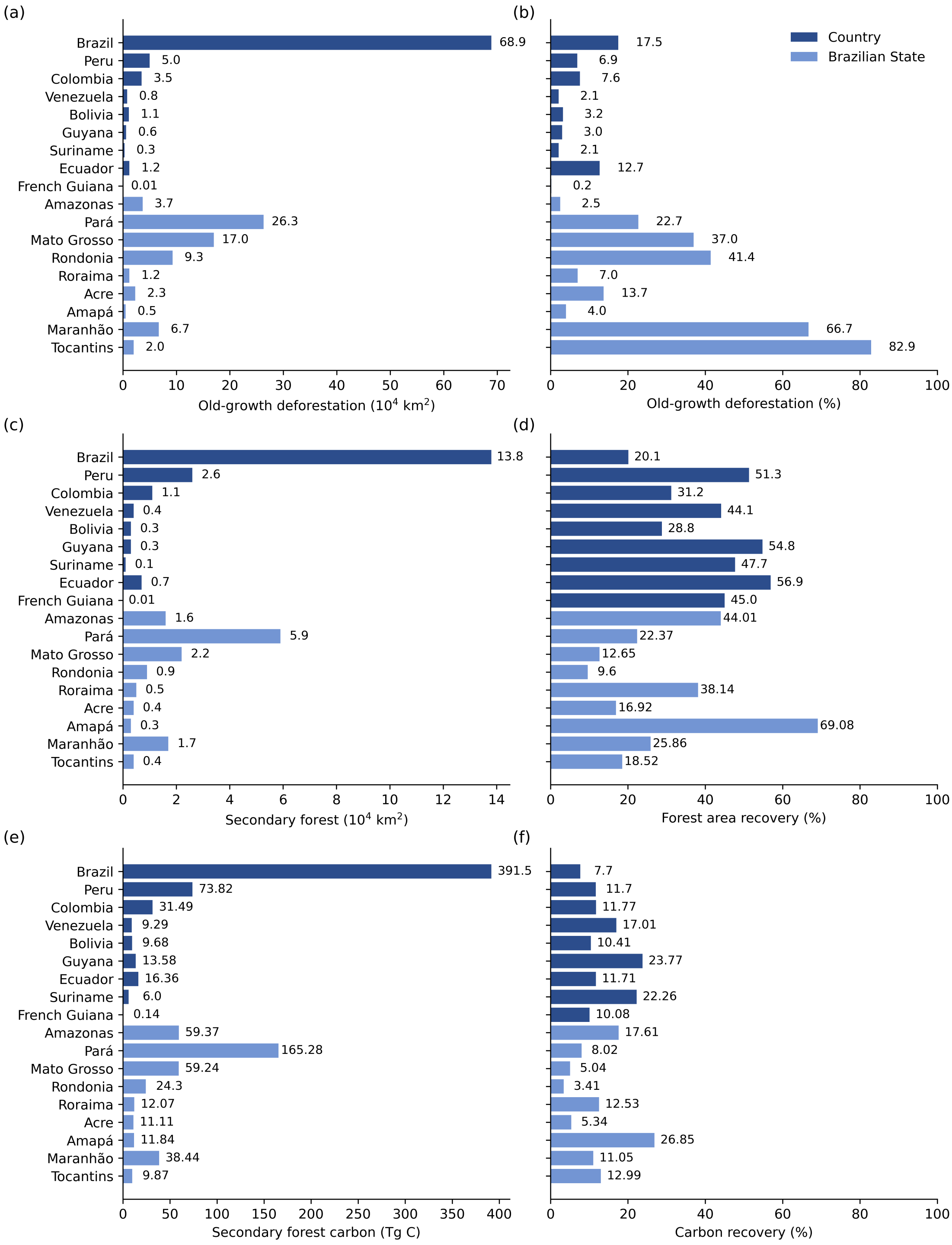

Figure 3.1: OG deforestation, SF extent and SF carbon recovery in Amazonian countries and Brazilian states in 2017. The **(a)** area of OG deforestation, **(c)** area of SFs, and **(e)** SF carbon stock for Amazonian countries (dark) and Brazilian states (light) in 2017. Proportional values (right) are measured as **(b)** the percentage of original OG forest extent (measured as the total area capable of supporting forest) that has been deforested, **(d)** the percentage of deforested land occupied by SF, and (f) the percentage of OG deforestation emissions offset by carbon sequestration in SFs. Countries and states are ordered by the area of the Amazon they contain.

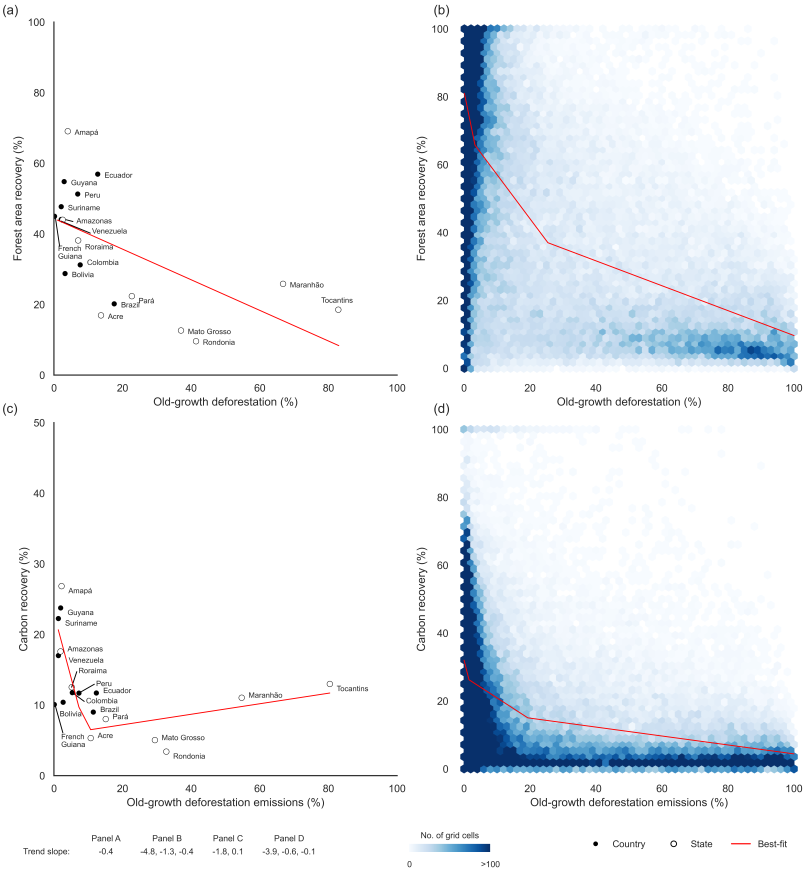

Figure 3.2: Proportional recovery of SF in the Amazon biome in 2017. The relationship between SF recovery, measured as the percentage of cleared land occupied by SF and deforestation as a percentage of total land within the Amazon basin **(a,b)**. The relationship between emissions offset by SF carbon accumulation and deforestation emissions as a percentage of original above-ground carbon **(c, d)**. For **(a, c)** Amazonian countries (.) and Brazilian states (o); and **(b, d)** the Amazon basin gridded at ~59.8 km^2. The best-fit models (where AICc $\geq$ 2) are shown in red: generalised linear model for panel **(a)**; and broken stick for panels **(b-d)**. Brazil was excluded from the calculation of the best-fit models for panels **(a)** and **(c)** in favour of its component states. Note the y-axis is different on panel **(c)**.

offset, despite 23.7% of deforested land being occupied by SF. Forest area recovery (defined here as the percentage of deforested land occupied by SF) varied across countries and Brazilian states. Brazil had the lowest forest area recovery (20.1%) of any Amazon country, while Ecuador and Amapá state had the greatest forest area recovery, with SF occupying 56.9% and 69.1% of deforested land, respectively (Figure 3.2a). Carbon recovery (defined here as the percentage of emissions from OG deforestation offset by carbon accumulation in SF) also varied greatly between countries, with the lowest in Brazil (7.7%) and the highest in Guyana (23.8%; Figure 3.2c).

Across countries and states, there were significant negative relationships between deforestation and recovery, which followed linear or L-shaped trends (Figure 3.2a,c; Table B.3; see Methods). As such, countries or states with a high percentage loss of OG typically have a low forest area recovery, while those which have lost less OG have a higher forest area recovery (Figure 3.2a). For example, Ecuador, which was 12.7% deforested in 2017, had the greatest forest area recovery (56.9%), while Brazil, which was 17.6% deforested, had the lowest forest area recovery (20.1%; Figure 3.2a). The extremes are more accentuated across Brazilian states: Tocantins had 82.9% OG deforestation and just 18.5% forest area recovery, while Amapá had 4.0% OG deforestation and 69.1% forest area recovery (Figure 3.2a). These spatial patterns of loss and recovery were even more pronounced for losses and gains of above-ground carbon stocks (Figure 3.2c).

These relationships between OG deforestation and SF recovery (and their resulting carbon balance) were also spatially linked at a local scale. A gridded analysis revealed strong negative, non-linear relationships that were well described by broken-stick regression with two segments (Figure 3.2b,d; Table B.4). Of the cells that had experienced some OG deforestation (>0.01% forest loss), the majority (62.8%) were characterised by low deforestation (<50% forest loss) with high forest area recovery ($\geq$50% of deforested area), and just 1.1% of cells exhibit both high deforestation

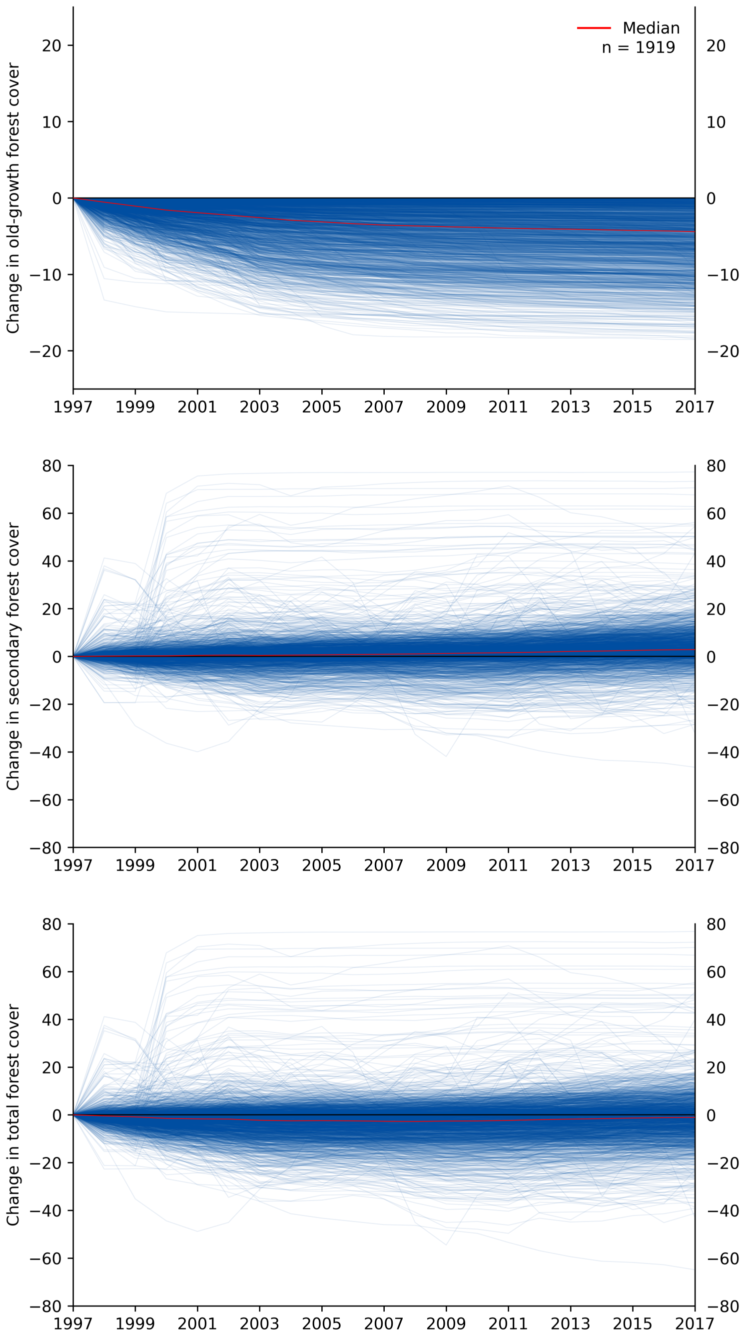

Figure 3.3: Temporal changes in forest cover in highly deforested Amazonian landscapes. The change in **(a)** old-growth forest, **(b)** secondary forest, and **(c)** total forest cover in highly deforested Amazonian landscapes from 1997 to 2017. The Amazon biome was gridded at ~58.9 km^2, and each line represents a grid cell where old-growth deforestation was $\geq$80% in 1997. Change in forest cover is measured as the difference in the percentage of a grid cell occupied by each forest type compared to its percentage cover in 1997. The median change across all the highly deforested cells is shown in red.

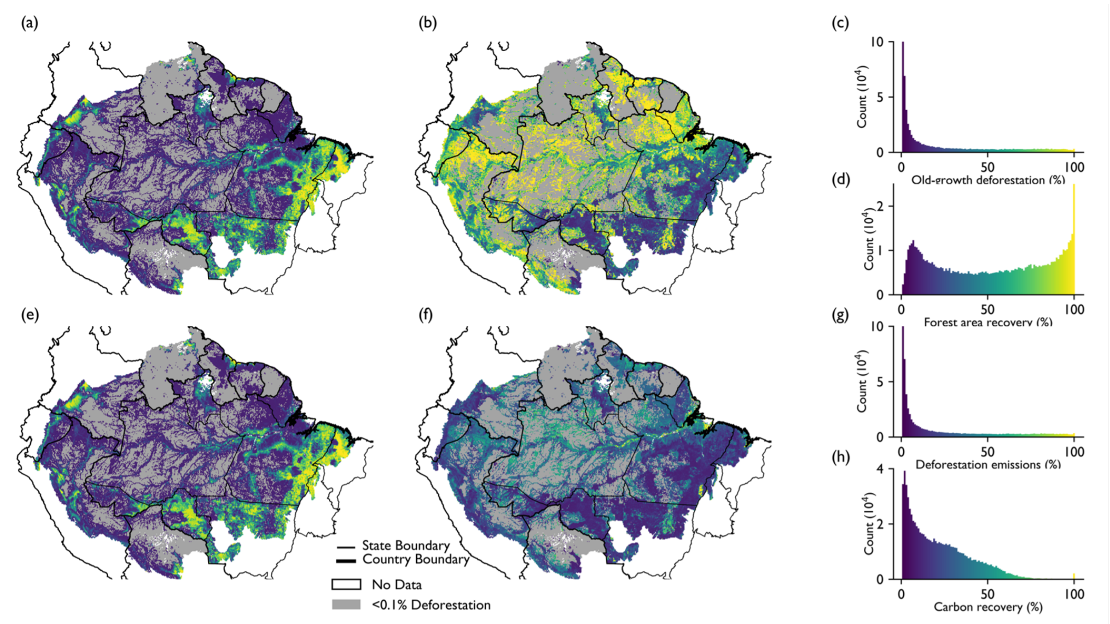

Figure 3.4: Old-growth deforestation, secondary forest recovery, carbon emissions and carbon accumulation in the Amazon biome in 2017. The spatial distribution of **(a)** old-growth deforestation, **(b)** secondary forest recovery, **(e)** carbon emissions from old-growth deforestation and **(f)** carbon accumulation in secondary forest for the Amazon biome in 2017. Values were calculated over a regular grid of ~59.8 km^2 cells. Old-growth deforestation is measured as the percentage of the cell area cleared of forest. Secondary forest recovery is measured as the percentage of deforested land occupied by secondary forest. Old-growth deforestation emissions are measured as the percentage of the original old-growth above-ground carbon lost to deforestation. Carbon recovery is measured as secondary forest carbon stock as a percentage of old-growth deforestation emissions. The distribution of cell values for each variable is shown in panels **c, d, g,** and **h**, respectively, which also define the colours used in panels **a, b, e** and **f**.

($\geq$50%) and high forest area recovery ($\geq$50%; Figure 3.2b; Figure 3.4c-d). Moreover, cells with very high deforestation in 1997 ($\geq$80%; n=1919) typically did not show increased recovery over time (1997-2017; Figure 3.3) with a median change in total forest cover of -1.0%. Over half (56.2%) of these cells saw further decline in total forest cover, while those that did increase (n=843) only did so by an average of 4.6% (median). Finally, any small increases in secondary forest cover were more than offset by the continues loss of old-growth forest. These trends were even more pronounced for carbon, with high carbon recovery only occurring in cells with the smallest losses from OG deforestation (Figure 3.2d; Figure 3.4g-h). Mapping these data revealed clear patterns in the distribution of the percentage of both OG loss and SF recovery (Figure 3.4). As expected, the highest levels of OG deforestation were concentrated in the south and east, forming the well-characterised ‘arc of deforestation’ (Figure 3.4). This contrasted with the spatial patterns for SF, where recovery of extent and carbon stocks was highest in areas of low deforestation or low carbon losses (Figure 3.4e-f).

3.3.4 Temporal trends in deforestation and recovery

The annual trend in OG deforestation between 1997 and 2017 was best described by a broken-stick regression with three segments (Table B.1); the most recent of which (2009-2017) showed an increase in the annual rate of deforestation from a low of 9,918 km^2 in 2013 to 11,899 km^2 in 2017 (Figure 3.5a). This reversed the previous trend in which annual OG loss declined by more than half from 29,806 km^2 in 2002.

We found no temporal trend in the area of new SF from 1997 to 2017, which was on average 22,882±2,247 km^2 per year (mean±SD; Figure 3.5c). In contrast, the extent of SF deforestation has increased over time, from 15,775 km^2 in 1997 to 17,750 km^2 in 2017, and is well described by a linear trend (Figure 3.5c; Table B.1). However, there was no temporal trend in the net change in SF area (Table B.1), which fluctuated between plus 10,263 km^2 and minus 1,961 km^2 with a mean of plus 5490 km^2.

OG deforestation emissions decreased from 0.82 Pg CO_2 in 2004, to a low of 0.40 Pg CO_2 in 2010, before increasing to 0.56 Pg CO_2 in 2017 (Figure 3.5b); best described by a broken-stick model with two segments (Table B.2). Annual carbon accumulation from the expansion and growth of SF increased from 1997 to 2017 and is well described by a linear trend (Table B.2). It was typically 2.42±0.3 times (mean±sd) the carbon emitted by SF deforestation each year (Figure 3.5d), which was best described by a broken stick model with two segments. SF net annual carbon accumulation increased linearly from 65.91 Tg CO_2 in 1997 to 103.91 Tg CO_2 in 2017 (Figure 3.5d, Table B.2). The trend in annual OG deforestation emissions offset by net annual secondary forest carbon accumulation (i.e. carbon recovery) was described by a broken stick regression with three segments (Table B.2). It remained below 15% until 2007, then peaked at 26.1% in 2013 before declining again.

3.4 Discussion

We conduct the first comparison of forest loss and recovery across national and sub-national political boundaries in Amazonia, analysing its impact on the carbon balance and exploring recent temporal trends. We found that, across the biome, SF offset just 9.7% of carbon emissions from OG deforestation despite occupying 23.7% of deforested land. We also reveal a strong, negative spatial relationship between OG deforestation extent and recovery by SF, with high recovery unlikely where a greater percentage of OG has been cleared, even decades after deforestation. These findings show there are clear barriers to recovery in landscapes that have been highly deforested, likely reflecting both biophysical limitations and socio-economic drivers (Curtis et al., 2018; Crouzeilles et al., 2020). Interestingly, the lack of increase in forest cover in highly deforested landscapes suggests Amazonian forest-agriculture dynamics are very different from those in the Brazilian Atlantic forest, where distance to closest forest was an important predictor of natural regeneration from 1995-2016 (Crouzeilles et al., 2020). Building upon recent work in the Brazilian Amazon (Nunes et al., 2020; Silva Junior et al., 2020b; Smith et al., 2020), we use the newly expanded MapBiomas land cover dataset to look beyond changes in Brazil and examine trends across the entire Amazon biome.

By providing measures of OG deforestation and SF recovery specific to each Amazonian country, our study reveals high variation across political boundaries. Some countries, such as Ecuador, demonstrate much greater levels of recovery than the Amazon biome as a whole, while in other countries and Brazilian states recovery is much lower. As expected, we find that Brazil is dominating Amazonian deforestation

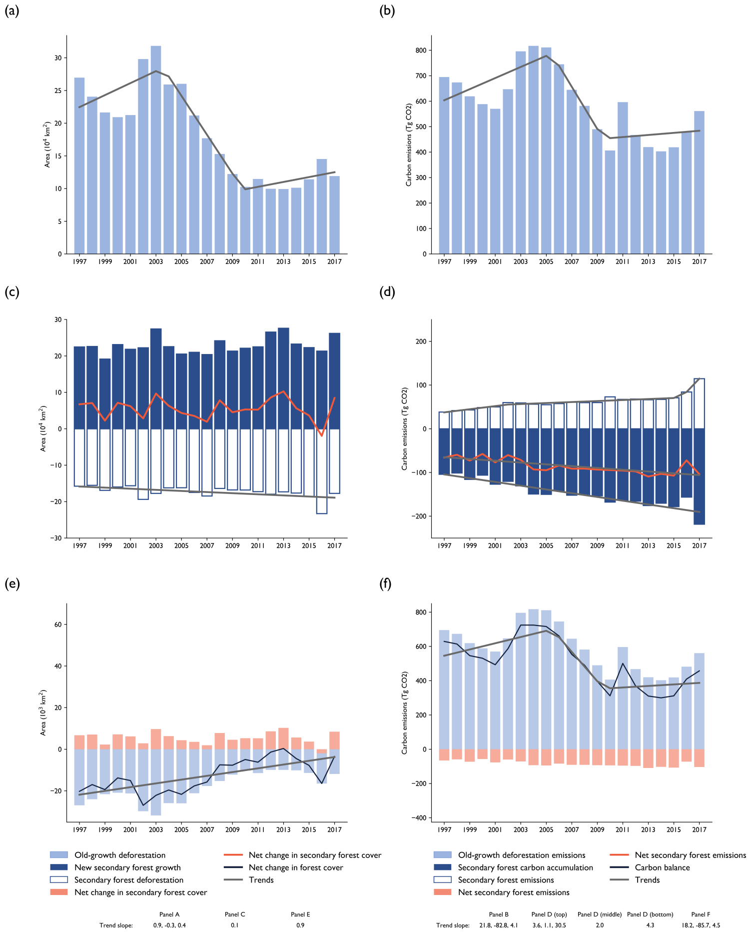

Figure 3.5: Annual change and temporal trends in forest cover and carbon emissions in the Amazon biome from 1997 to 2017. (a) The annual change in the extent of old-growth deforestation and **(b)** its associated carbon emissions. **(c)** The annual change in secondary forest extent comprising new secondary forest growth (dark), secondary forest clearance (white) and the net change in secondary forest extent (red line). **(d)** The annual carbon balance of secondary forests, comprising carbon accumulation from new and existing secondary forests (dark), carbon emissions from secondary forest clearance (white) and net change in secondary forest carbon (red). **(e)** The annual balance of forest extent with old-growth deforestation (blue), net change in secondary forest extent (red) and the net change in total forest cover (dark blue line). **(f)** The annual balance in carbon emissions with old-growth deforestation emissions (blue), net change in secondary forest carbon (red) and the net carbon emissions from old-growth deforestation after offset by secondary forest carbon accumulation (dark blue line). The best-fit models (where AICc ≥ 2) for temporal trends are shown in grey: broken stick for old-growth deforestation extent and emissions, secondary forest gross carbon emissions, and net emissions from forest cover change; and generalised linear model for secondary forest clearance, carbon accumulation and net carbon emissions, and the net change in total forest cover.

and emissions (85.4%; 79.9%), but its dominance also goes beyond that expected by the portion of the Amazon biome it contains. For example, Pará state alone has contributed more deforestation than that of all other Amazonian countries combined. Furthermore, Brazil has the lowest forest area recovery, with just 20.1% of deforested land occupied by SF, compared to 23.7% for the Amazon biome as a whole and a range of 28.8 - 56.9% amongst the other countries. These trends were even more marked when we analysed the percentage of carbon emissions resulting from OG deforestation that have been offset by SF carbon accumulation. Despite growing awareness of deforestation in other Amazonian countries (Kalamandeen et al., 2018), these findings make it clear that combating land-use change in Brazil remains fundamental to efforts to mitigate global climate change. However, the Brazilian Amazon's high deforestation rates – including the recent uptick in deforestation that was not covered by the time series we analysed (PRODES, 2020) – and its low percentage of restoration also suggest that there are major institutional and social barriers to overcome (Arima et al., 2014). These are exacerbated by issues of governance, with the current Brazilian administration being accused of encouraging deforestation by weakening policies, undermining forest monitoring, cutting resources for environmental law enforcement (Barlow et al., 2020; Vale et al., 2021) and censoring scientific publications (Escobar, 2021).

Our findings show that OG deforestation emissions are outstripping SF carbon accumulation across the Amazon biome, with less than a third of emissions offset in every country or state we assess and less than 10% for the biome as a whole. These findings confirm the need to prioritise halting deforestation and to preserve remaining OG. However, it is widely accepted that in order to mitigate climate change reducing emissions is not enough, and we must also recapture carbon from the atmosphere (Edenhofer et al., 2014; Houghton et al., 2015; Griscom et al., 2017), with SF growth suggested as an efficient and cost-effective method to do so (Rogelj et al., 2018; Lubowski et al., 2020). Our analysis provides some important insights into the challenges of large-scale forest restoration.

First, the negative relationship between OG deforestation and forest area recovery demonstrates the difficulty of increasing SF cover in low-OG cover landscapes, despite them having the greatest potential for large-scale recovery of forest cover. The scale of the challenge is clear from our assessment of landscapes with $\geq$80% deforestation in 1997; which show no evidence of forest recovery over time. Many of these highly-deforested landscapes were in Brazil (see S.I. map), showing that the National Vegetation Protection Law (and the previous Forest Code) has not helped enhance forest cover in these regions. These findings highlight the importance of new incentives and targeted policy interventions for increasing SF in low-OG cover landscapes. Policies must be targeted locally and regionally as well as nationally, and could build on some of the ambitious state-level plans for achieving carbon neutrality, such as Pará's State Plan for the Amazon Now (Plano Estadual Amazônia Agora, Decree nº 941, 03/08/2020). Although SF growth rates may be lower in these highly deforested regions than those proposed by Requena Suarez et al. (2019) (e.g. Elias et al., 2020; Heinrich et al., 2021), restoration in these regions could also delivers important co-benefits, such as regulating local temperatures and stream flows as well as providing habitat for a number of species (Lennox et al., 2018) including some of the most threatened in the Amazon such as the Critically Endangered Belém curassow (*Crax [fasciolata] pinima)*, black-winged trumpeter (*Psophia obscura*), and the Kaapori capuchin (*Cebus kaapori*). Furthermore, assisted natural regeneration could help encourage forest recovery where natural regeneration is limited by a lack of seed dispersal from adjacent forests or the intensity of previous land uses (Chazdon et al., 2020; Shono et al., 2020; Jakovac et al., 2021).

Second, the young SF age and low carbon offsets found across the biome highlight the importance of addressing the high turnover rates and low residence times of SF (Jakovac et al., 2017; Schwartz et al., 2020), which result in the loss of huge quantities of carbon annually (Tyukavina et al., 2017; Smith et al., 2020; Wang et al., 2020). Implementing and enforcing policies to protect SF from deforestation could substantially increase their effectiveness as long-term carbon stores (Chazdon et al., 2016b). For example, following the accumulation rates reported by Requena Suarez et al. (2019), preserving the 2017 extent of SF (192,867 km^2) would result in the accumulation of 3.3±0.5 Pg C by 2050. However, any such policy needs to be carefully implemented as the use of forests as fallows is crucial for the livelihoods of many Amazonian smallholders and traditional peoples (Porro et al., 2015) and some SF clearance may buffer against further OG loss (Wang et al., 2020). Furthermore, the temporal consistency of the net increase in SF indicates that it is less sensitive to socio-economic events than OG deforestation, suggesting that instigating change may be difficult.

This study used three up-to-date resources to quantify forest cover dynamics and their resulting effects on carbon balance (Methods). Yet important uncertainties remain. First, while this study focuses on emissions from deforestation, it is important to note that forest degradation, which affects up to 17% of forest cover (Bullock et al., 2020), is also resulting in huge losses of carbon from OG (Bullock et al., 2021). As our biomass map was from the early 2000s, the carbon emissions from OG deforestation reported in this study may be over-estimated as some of the above-ground carbon will have already been lost to prior disturbance. Recent advances in assessing forest disturbance (e.g. Matricardi et al., 2020; Qin et al., 2021) are restricted to the Brazilian Amazon, but demonstrate the importance – and complexity (Silva Junior et al., 2020b) - of estimating it across decadal time-scales. Second, we used above-ground biomass accumulation rates from Requena Suarez et al. (2019) to estimate the SF carbon accumulation. However, this is likely to over-estimate recovery in the more deforested and drier regions of the 'arc of deforestation' (e.g. Elias et al., 2020; Heinrich et al., 2021). As such, Brazil's contribution to carbon recovery may be over-estimated in our analysis, increasing its contribution to net carbon emissions.

Although our analysis shows a pan-Amazonian uptick in deforestation in recent years, it also helps highlight moments in space and time that can be used to guide more positive actions. For example, the huge reduction in Brazilian OG deforestation from an all-time high in 2004 to an all-time low in 2012 is a demonstration of what can be achieved with well-implemented policy (Boucher et al., 2013; PRODES, 2020; Saraiva et al., 2020). Furthermore, although instigating change in Brazil will be key to restoration efforts within the Amazon biome, an understanding of what is enabling other countries to achieve greater levels of recovery could also help guide policy interventions across the Amazon biome (Latawiec et al., 2014). For example, the high levels of recovery in Ecuador and Amapá demonstrates that there are contexts where recovery is occurring, and there may be valuable lessons to be learned from previous and ongoing success. However, future research needs to go beyond mapping forest cover change and examine the socio-economic conditions which are key to restoration success (Grau et al., 2003; Aide et al., 2013; Rudel et al., 2016). Quantifying the role of policy as driver of the relationships outlined in this study would be a valuable next step and should be a priority for future research in this field. Finally, the strong negative patterns of recovery found consistently across geographic scales show that the regions with the greatest potential for large-scale restoration are also those that currently have the least amount of recovery. The new challenge facing policy makers is how to incentivise large-scale restoration in these regions in order to break this trend. Doing so successfully is essential to ensuring that the Amazon biome achieves its potential in mitigating anthropogenic climate change.

Chapter 4

The proximity of secondary forests to old-growth forests reduces forest fragmentation and buffers edges in the Amazon

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Abstract

Restoration of tropical forests is crucial for climate change mitigation and offers co-benefits for biodiversity. However, secondary forest position within the landscape could influence the strength of these benefits. Research has shown carbon and biodiversity recovery in secondary forests is enhanced by proximity to old-growth forests. But old-growth forests may also benefit from secondary forests in return through buffering of edge effects and reduced fragmentation. To date there has been no biome wide assessment of secondary forest location relative to old-growth forests. We mapped Amazonian secondary forests and explored their proximity to old-growth forests of different conditions. We also calculated the extent to which secondary forests buffer old-growth forest edges and the influence of secondary forests on fragmentation. In 2020, 41.2% of Amazonian secondary forests were directly adjacent to old-growth forest and 94.1% was in a fragment connected to old growth; however, adjacency and connectedness fell to 20.1% and 57.4%, respectively, when only considering structurally-intact old-growth forest. Secondary forests buffered 43.1% of old-growth forest edges, reduced the total number of old-growth fragments by 2 million, and doubled the median amount of old-growth forest in a contiguous fragment. Our results reveal the importance of understanding spatial context when examining the potential benefits of forest restoration. A greater understanding of the benefits of locating secondary forests next to old-growth forests could support the development of more effective climate change mitigation and conservation strategies.

4.1 Introduction

Restoring forests, especially on deforested land in the moist tropics, has a key role to play in achieving global climate change mitigation objectives (Cook-Patton et al., 2020; Strassburg et al., 2020; Poorter et al., 2021). Although tropical secondary forests store less carbon than old-growth forests, they rapidly remove carbon dioxide from the atmosphere with estimates ranging from 0.89 Mg (Chave et al., 2020) to 7.6 Mg of carbon per hectare per year (Requena Suarez et al., 2019). Restoration in tropical regions also offers important co-benefits for the provisioning of other ecosystem services (Matos et al., 2020), including the preservation of biodiversity (Lennox et al., 2018), improving water quality (Chavarria et al., 2021), and regulating water flow (Buytaert et al., 2007; Meerveld et al., 2021).

Understanding where secondary forests exist at present, their temporal dynamics under current policies and practices, and the potential benefits of sustaining or increasing their extent is fundamental to the success of large-scale restoration (Hobbs et al., 2014). These questions have been addressed in increasing detail in recent years, with studies revealing that secondary forests are growing on as much as 20% of deforested land in the Amazon (Smith et al., 2021) and that safeguarding existing secondary forests in Brazil could achieve as much as 5.5% of the national emissions reduction target (Heinrich et al., 2021). However, secondary forests are often short lived and are typically cleared within the first 5 years (Schwartz et al., 2017a; Reid et al., 2019; Smith et al., 2020), which limits their usefulness as a long-term carbon store (Chazdon et al., 2016a). Other studies have refined our understanding of secondary forest growth rates, showing that they vary considerably based on climatic conditions (Poorter et al., 2016; Elias et al., 2020) and previous land use (Jakovac et al., 2015; Cook-Patton et al., 2020). Nonetheless, most studies agree that if secondary forests are maintained long-term, they have the potential to store large quantities of carbon and provide habitat for a diverse range of species. With the potential benefits of forest restoration well-established, we must now determine how future restoration efforts can maximise environmental benefits, especially in terms of forest location (Brancalion et al., 2019). Understanding the current position of secondary forests at the landscape scale, specifically in relation to old-growth forests, could be instrumental in achieving this goal.

4.1.1 Influence of proximity to old-growth forests on secondary forest recovery

The position of secondary forests within the wider landscape influences growth rates and biodiversity (Figure 4.1). Landscape context dictates the diversity of source communities and plays a critical role in determining community recovery (Chazdon et al., 2009; Arasa-Gisbert et al., 2021). Low surrounding forest cover has been linked to sharp declines in biodiversity and it has been suggested that landscapes with more than 50% forest cover are required for successful conservation of forest dwelling species in the tropics (Arroyo-Rodriguez et al., 2020; Arasa-Gisbert et al., 2021). Surrounding forest cover also has positive effects on biomass recovery (Martinez-Ramos et al., 2016; Toledo et al., 2020) and secondary forests growing in relatively intact landscapes are likely to have higher carbon accumulation potential than those in highly deforested landscapes (Chazdon, 2003; Bihn et al., 2010). Recent findings indicate that proximity to old-growth forest is advantageous throughout succession, supporting greater forest growth and 30% more species diversity in the early stages (Jakovac et al., 2015; Toledo et al., 2020), as well as providing the diverse seed sources required to establish resilient, biodiverse and high-biomass secondary forests later (Hawes et al., 2020).

The quality of surrounding old-growth forest may also be important for species recruitment in secondary forests. Structural disturbance events (e.g. forest fires, selective logging) alter the composition of old-growth forests, leaving the area in a forested but degraded state, which renders it unsuitable as habitat for many forest species (Mestre et al., 2013b; Barlow et al., 2016; Moura et al., 2016). Species occupancy in old-growth forests is also impacted by fragmentation. Smaller fragments will not hold many of the large vertebrates that could support the movement of large-seeded plant species into adjacent secondary forests (Laurance et al., 2002; Lees et al., 2006) and connectivity to extensive areas of old-growth forest is a key determinant of species richness in secondary forests (Mayhew et al., 2019). These relationships indicate that secondary forests may benefit considerably from proximity to large areas of structurally-intact old-growth, whereas development of secondary forests in landscapes with highly fragmented old-growth forest cover or extensive forest disturbance is likely to be limited by lack of seed sources (Matos et al., 2020).

4.1.2 Benefits of secondary forest cover for old-growth forest

Secondary forests could provide additional environmental benefits if they help buffer old-growth forests against edge effects (Figure 4.1). Edge effects are a well-documented phenomenon that drastically impact the structure and functioning of a forest through changes in microclimate, leading to reduced carbon stock and altered species assemblages (see review by Laurance et al., 2002). Field studies have demonstrated that the ecological and physical impacts of edge-effects extend hundreds of metres into the forest (Laurance et al., 2002), while remote sensing studies have revealed their substantial impact on carbon emissions across large spatial scales (Silva Junior et al., 2020a). However, these impacts may be mitigated by secondary forest growth adjacent to old-growth forest edges. Secondary forest buffers may significantly reduce edge-related tree mortality (Mesquita et al., 1999), faunal edge avoidance (Stouffer et al., 1995) and the intensity of changes in microclimate (Didham et al., 1999). However, the benefits of secondary forest buffers are likely to be influenced by the temporal relationship between edge exposure and regeneration. As much as 90% of edge-induced carbon loss occurs within five years of exposure (Silva Junior et al., 2020a), but it takes time for secondary forests to reach a level of structural maturity at which they may begin to offer protection from abiotic changes or offer habitat to core-forest species (Laurance et al., 2002). Nonetheless, landscape-wide increases in the occupancy and abundance of specialist species have been found following regeneration by secondary forests (Rocha et al., 2018).

Secondary forests may also benefit old-growth forests by increasing fragment connectivity (Figure 4.1; Newmark et al., 2017). Even small breaks in forest cover can present impassable barriers to some species (Lees et al., 2009) and fragment isolation has been found to explain more variation in species composition than either forest type or forest age (Mayhew et al., 2019). By connecting old-growth forest fragments, secondary forests could mitigate isolation effects by supporting the movement of animals between old-growth forest fragments, even if the secondary forest is not necessarily habitat for those species (Newmark et al., 2017).

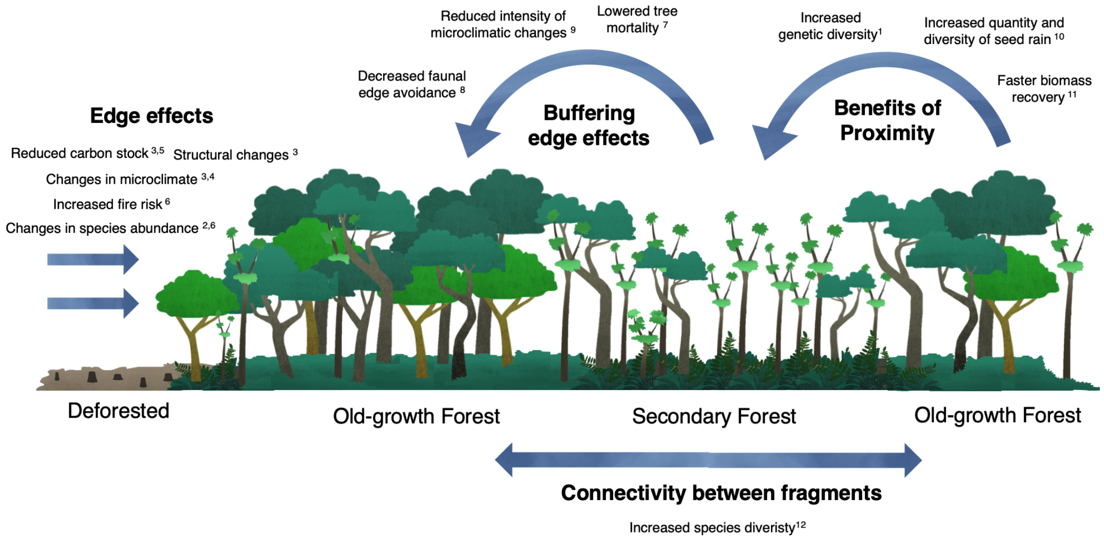

Figure 4.1: Conceptual diagram of the benefits of secondary forest proximity to old-growth. **[1]** Senzen et. al, Ecology (2007) **[2]** Pfeifer et. al, Nature (2017) **[3]** Magnago et. al, Functional Ecology (2016) **[4]** Schwartz et. al, Ecological Applications (2017) **[5]** Silva Junior et. al Science Advances (2020) **[6]** Laurance et al. Conservation Biology (2002) **[7]** Mesquita et al. Biological Conservation (1999) **[8]** Stouffer & Bierregaard Ecology (1995) **[9]** Didham & Lawton Biotropica (1999) **[10]** Cramer et al, Biological Conservation (2007) **[11]** Martínez-Ramos et al. Biotropica (2016) **[12]** Mayhew et al, Biotropica (2019)

While previous studies have demonstrated trends in the location of secondary forests relative to old-growth forests at the landscape level (Schwartz et al., 2017a; Smith et al., 2020, 2021), to date there has been no large-scale analysis directly addressing this issue. Here, we make the first biome-wide assessment of the location of secondary forests in relation to old-growth forests. We do this for the Amazon, the world's largest remaining expanse of tropical forest and a region of critical importance in mitigating climate change. We explore the positioning of secondary forests within the landscape, asking (1) Where are secondary forests located in relation to old-growth forests of different quality? (2) To what extent do secondary forests buffer old-growth forest edges? And (3) how do secondary forests affect the fragmentation of old-growth forests? We investigate the exposure time of old-growth forest edges, as well as the age of secondary forests acting as buffers or connecting fragments, to provide insights into the potential benefits of their proximity. Enhancing our understanding of the spatial and temporal relationships between old-growth edges and secondary forests would help to refine our estimates of edge-related carbon emissions and habitat loss and could aid in the design of effective restoration programmes.

4.2 Methods

4.2.1 Mapping forest cover

We assessed old-growth and secondary forest cover in the Amazon biome using the MapBiomas Amazonia Collection 3.0 dataset (MapBiomas, 2021), which provides annual 30-m resolution land cover maps from 1985 to 2020. We reduced the MapBiomas schema to two classes (forest and non-forest) and then applied a change detection algorithm to identify which forest pixels were secondary forests. Following the method of Smith et al. (2021), any pixel (900 m^2) in the 'forest' class in the first year of the time series (1985) was considered old-growth forest until it transitioned to 'non-forest'. Pixels that transitioned from 'non-forest' to 'forest' were labelled as secondary forest.

As the MapBiomas time series begins in 1985, any secondary forest that began growing before this date is classified as old-growth forest and the maximum age of secondary forests detectable with this method is 34 years. As such, our method may be overestimating old-growth forest extent and underestimating secondary forest extent. However, we believe the impact of this on our results to be small as secondary forests typically have low residence times and high turnover rates (Schwartz et al., 2020; Smith et al., 2020), so it is unlikely that much of the pre-1985 secondary forest remains in 2020. Furthermore, as the earliest reliable satellite imagery covering the whole Amazon is from 1985, MapBiomas provides the best available map of historic forest cover.

4.2.2 Assessing old-growth forest quality

We created 3 classes of old-growth forest quality based on structural disturbance and fragment size: (1) any old-growth forest, (2) structurally-intact old-growth forest, and (3) extensive (> 50 km^2) structurally-intact old-growth forest. These classes are intended primarily as a proxy for the availability of faunal seed dispersers and seed rain diversity.

Bullock et al. (2020) provide a spatially explicit dataset of degradation from 1995 to 2017. They defined degradation as a natural or anthropogenic disturbance that does not change a pixel's land cover category – including fire, windthrow, selective logging, and damage to standing forests during expansion of roads or development. We resampled the condensed Bullock et al. (2020) dataset to align with MapBiomas, then identified structurally-intact old-growth forest as those pixels that had not experienced a disturbance event in the last ten years (relative to 2020). We selected a ten-year threshold as forests recover over time (Rutishauser et al., 2015; Silva et al., 2018) and some species may eventually be able to return if further disturbances are avoided (Mestre et al., 2013b; Mollinari et al., 2019). While the Bullock et al. (2020) dataset is the most recent map of forest degradation currently available for the Amazon, there are two limitations to its use in this study that may mean we are underestimating the extent of structural disturbance. First, it does not extend to our study year (2020) so we cannot account for the three most recent years of structural disturbance. Second, Bullock et al. (2020) conducted their analysis for the Amazon EcoRegion as defined by Olson et al. (2001) meaning a small proportion of our study area (the RAISG-defined Amazon biome) is not included.

We measured the size of forest fragments in our 2020 land cover map as the number of contiguous pixels classified as each forest type. Fragment size was calculated using the Accounting tool from the Guidos Toolbox software. We applied 8-way connectivity and identified 'extensive' forest as those fragments over 50 km^2.

4.2.3 Assessing the proximity of secondary forests to old-growth forests

Distance to nearest old-growth forest

We calculated the distance between secondary forests and their closest old-growth forest fragment. We did so by applying the Guidos Toolbox Distance tool to a binary map of old-growth forest cover to calculate the Euclidean distance from every pixel to the nearest old-growth forest edge. We repeated this analysis for the three classes of old-growth forest cover defined above: any, structurally-intact, and extensive structurally-intact.

Landscape context

We measured the landscape context of secondary forests as the proportion of the surrounding landscape that was occupied by each old-growth forest class. This analysis was conducted using the Guidos Toolbox Landscape Mosaic tool for a 0.99 km radius, the nearest value to 1 km available for 30 m pixels. For each secondary forest pixel, this tool provided the percentage of the surrounding landscape that was occupied by old-growth forest to the nearest 10%.

Identifying old-growth forest edges

To map old-growth forest edges, we calculated the Euclidean distance from every old-growth pixel to the nearest old-growth forest edge using the Guidos Toolbox Distance tool. Any pixel within 120 m of an edge was marked as edge forest. The most intense edges effects occur within 100 m of an edge (Laurance et al., 2002), 120 m is the closest distance measurable using 30-m resolution pixels. We repeated this analysis for all forest cover (old-growth and secondary forest combined). Any old-growth forest pixels that were no longer in the edge zone after the inclusion of secondary forests were identified as buffered edges, while those that remained in the edge zone were considered exposed edges. We conducted this analysis for every year in the time series to produce annual maps of forest edge exposure (1986-2020). From these annual maps we calculated the age of old-growth forest edges in 2020 and the total time they had been exposed or buffered. Edges present in 1985 were excluded from the analysis as we could not determine their age or duration of exposure. Excluding these edges also serves to remove natural edges from our analysis.

4.2.4 Measuring changes to connectivity

We measure the influence of secondary forests on old-growth forests connectivity by calulating the change in the number of isolated fragments and the fragment size. First, we used the Guidos Toolbox Accounting tool to identify individual old-growth forest fragments and determined their area. To measure the change in fragmentation, we then repeated this analysis for three secondary forest age groups: all secondary forest, secondary forests >5 years old, and secondary forests >15 years old. Fragments consisting of only secondary forest were excluded.

4.3 Results

4.3.1 Proximity of secondary forests to old-growth forests

In 2020, there were 189,451 km^2 of secondary forests in the Amazon biome (Figure 4.2); comprising over 5.3 million fragments that ranged in size from 4,500 m^2 (the smallest area detectable by our analysis) to 125 km^2. 41.2% of all secondary forest (78,059 km^2) was directly adjacent to an old-growth forest (measured as secondary forest pixels occurring next to an old-growth pixel), while 94.1% of secondary forest was within a fragment connected to an old-growth forest fragment. These figures were slightly lower for structurally-intact old-growth forests, with 33.2% of secondary forest directly adjacent and 92.6% within a connected fragment. However, the area of secondary forest directly adjacent to extensive structurally intact old-growth forest (20.1%) was less than half that directly adjacent to any old growth forest. The amount of secondary forest within a fragment connected to extensive structurally-intact old-growth forest (57.4%) was also much smaller. The median (inter-quartile range; IQR) distance from a secondary forest pixel to old-growth forest of each condition group was 30 m (30-120), 60 m (30-210), and 1,110 m (30-8010) for old-growth forest, structurally-intact old-growth forest, and extensive structurally-intact old-growth forest, respectively (Figure 4.2).

Across the biome, less than half of secondary forests were within 1 km of extensive structurally-intact old-growth forest (48.9%; 92,674 km^2), but the majority were within 1 km for any old-growth forest or structurally-intact old-growth forest (98.6% and 96.8% respectively; Figure 4.2)). Less than half of secondary forest pixels had a surrounding landscape (0.99 km radius) of >50% old-growth forest (45.5%; 85,759 km^2) and 21.7% (40,907 km^2) had <10% surrounding old-growth forest cover. Restricting the analysis to structurally-intact old-growth forest, 33.0% (62,604 km^2) of secondary forests had >50% surrounding old-growth forest cover, while 30.8% (58,271 km^2) had <10% surrounding old-growth forest cover. With further restriction to

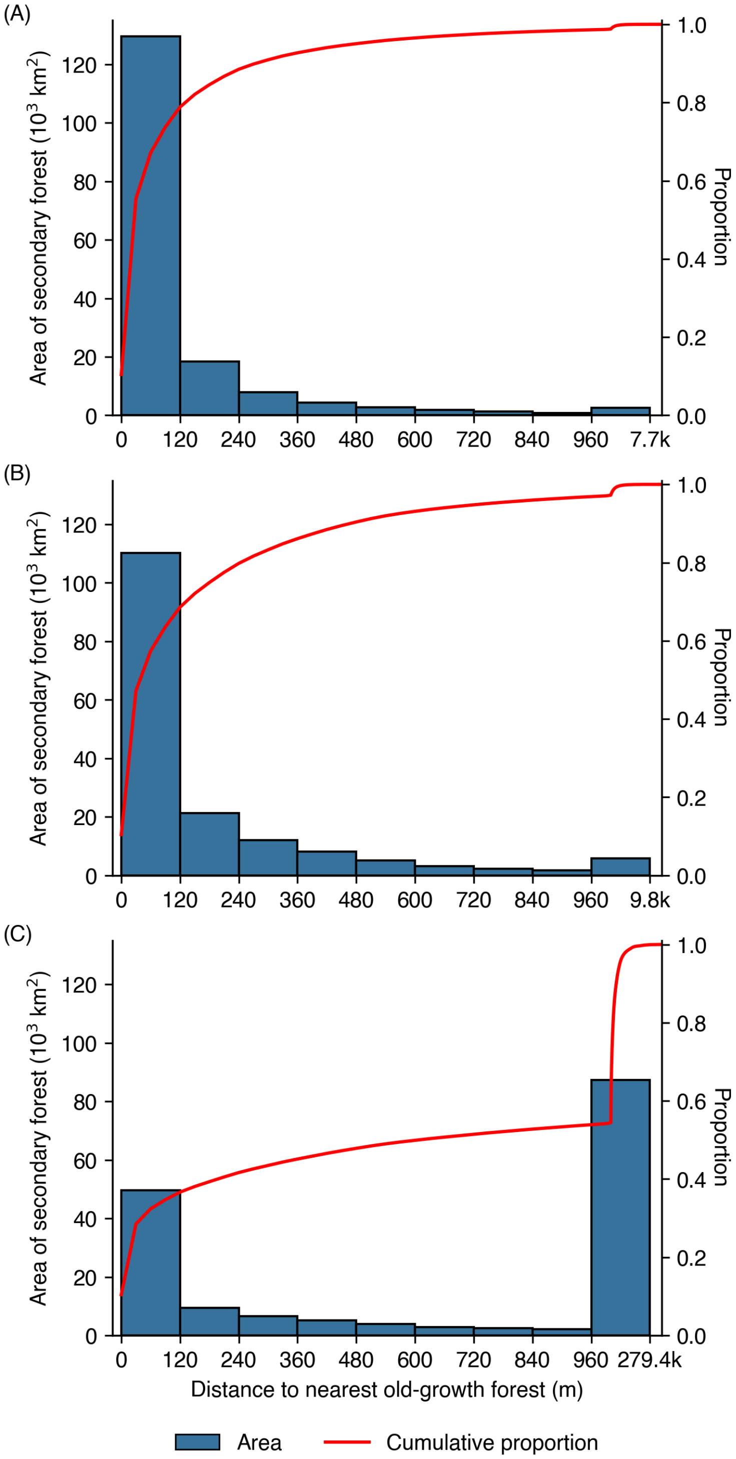

Figure 4.2: The distance from secondary forests to old-growth forests in the Amazon biome in 2020. The distance from secondary forests to old-growth forests in the Amazon biome in 2020. The distance from the centre of a secondary forest pixel to the centre of the nearest pixel of **(a)** any old-growth forest, **(b)** structurally-intact old-growth forest, and **(c)** extensive (>50 km^2) structurally-intact old-growth forest. The cumulative proportion of all secondary forests is indicated by the red line. For each old-growth forests class, the secondary forests pixels more than 960 m from an old-growth forest are group into the final bar.

extensive structurally-intact old-growth forest, only 23.0% (43,545 km^2) of secondary forests had >50% surrounding old-growth forest cover, and 63.2% (119,666 km^2) had <10% surrounding old-growth forest cover.

4.3.2 Old-growth forest edges buffered by secondary forests

In 2020, 6.4% (348,903 km^2) of old-growth forest in the Amazon biome was within 120 m of an anthropogenic edge created after 1985. However, 41.1% (143,392 km^2) of these old-growth edges were buffered by secondary forests of any age (Figure 4.3). To buffer all old-growth edges would require a further 182,773 km^2 of secondary forest, in addition to the 141,189 km^2 already acting as a buffer. The extent of buffering reduced to 32.2% (112,448 km^2) when restricted to secondary forests more than 5 years old, and 22.9% (79,902 km^2) for secondary forests more than 15 years old. Secondary forests acting as a buffer for old-growth forest edges were older than those not acting as a buffer (median (IQR); buffering: 11 years (4-21) not-buffering: 5 years (2-12)). Old-growth forest edges present in 2020 had a median (IQR) exposure time of 6 years (2-14) and 36.9% of edges had never been buffered by secondary forest (Figure 4.3).

Of the 681,027 km^2 of old-growth forest edges created during our time series (1986-2020), almost half (48.8%) had been deforested prior to 2020 and the median (IQR) age at which an edge was cleared was 4 years (2-9). 7.3% of edges were buffered by secondary forest when they were cleared and buffered edges were typically older at clearance compared to exposed edges (median (IQR); buffered: 9 years (6-15); exposed: 4 years, (1-8)). The age of old-growth forest edges present in 2020 was evenly distributed (median (IQR): 19 years (8-27)), but buffered edges were typically older (median (IQR): 23 years, (15-29)) than exposed edges (median (IQR): 14 years (4-24)). Old-growth forests within 120 m of a 1-year-old edge (i.e. an edge created in 2020) accounted for almost double any other annual age class (1-year-old edges: 25,769 km^2; older edges: 6,472-15,114 km^2).

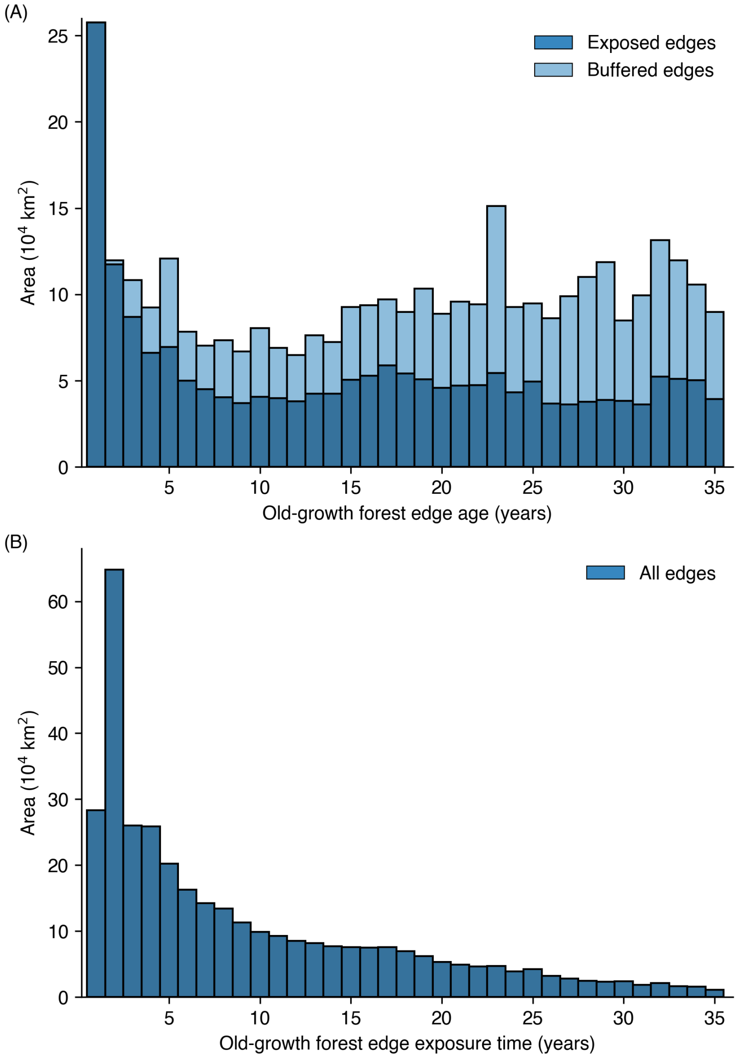

Figure 4.3: The distribution age and exposure time of old-growth forest edges in the Amazon in 2020. (a) The area of old-growth forest within 120 m of anthropogenic edges created between 1986 and 2020, for edges adjacent to non-forest landcover (exposed; dark blue) and edges buffered by secondary forests (light blue). **(b)** The area of old-growth edge forest with different durations of exposure (total time in years that a pixel was part of an expose edge).

4.3.3 Old-growth forest fragmentation

In 2020, there were 3.3 million old-growth forest fragments in the Amazon biome (Figure 4.5), with a median (IQR) fragment size of 4,500 m^2 (1,800 - 13,500; Figure 4.4). Allowing any secondary forest to act as a bridge between old-growth fragments reduced the total to 1.3 million fragments (excluding those that were comprised of only secondary forests; Figure 4.5) and almost doubled median (IQR) fragment area (8,100 m^2, 3,600 - 26,100; the area of old-growth forest within a mixed-forest fragments) and reduced the area of old-growth forest in small fragments (<50 km^2) by 31.2% (77,456 km^2; Figure 4.4). When applying a minimum age (of either 5 or 15 years) for secondary forest bridges, the effect of secondary forest on fragmentation was reduced but still pronounced (Figure 4.4).

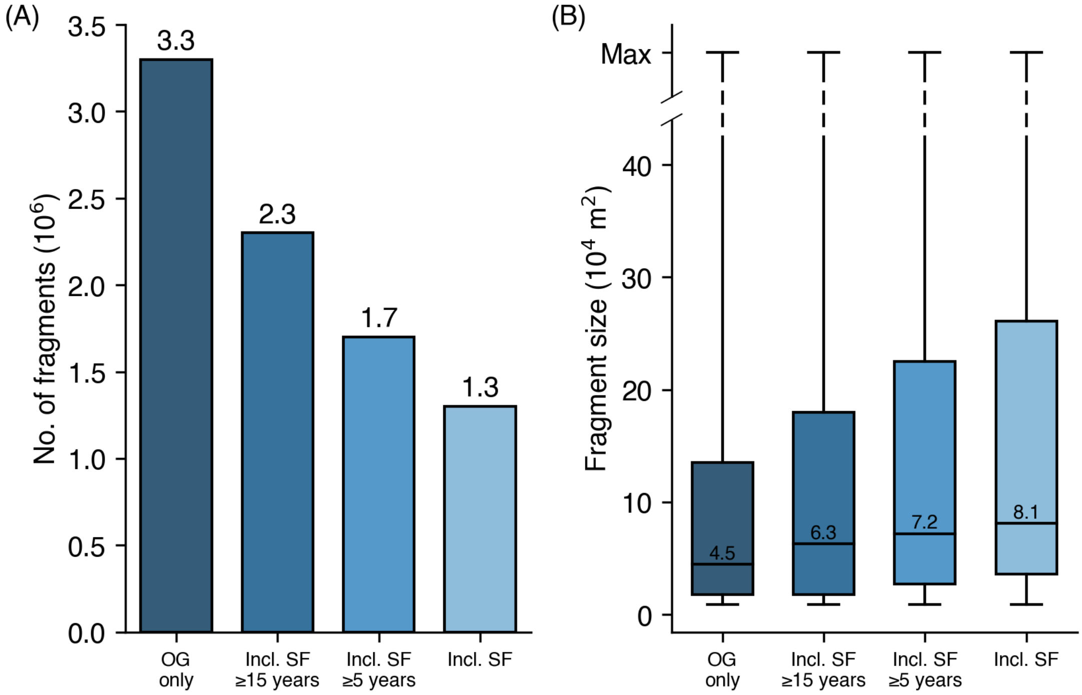

Figure 4.4: Old-growth forest fragmentation in the Amazon in 2020. The **(a)** total number and **(b)** size distribution of old-growth forest fragments for old-growth forest cover only (OG) and when including bridges of secondary forest (SF) of different ages ($\geq$15 years old, $\geq$5 years, and all ages). For old-growth forest fragments connected by secondary forest bridges, size was measured as the total area of old-growth forest within the mixed-forest fragment. Fragments consisting of only secondary forest were excluded. The total number of fragments and the median area for each group are annotated. The error bars show the full range of fragment sizes, with the maximum fragment size for each group ~137,000 km^2.

4.4 Discussion

We conduct the first biome-wide assessment of the location of secondary forests in relation to old-growth forests. We expand upon recent works that have produced

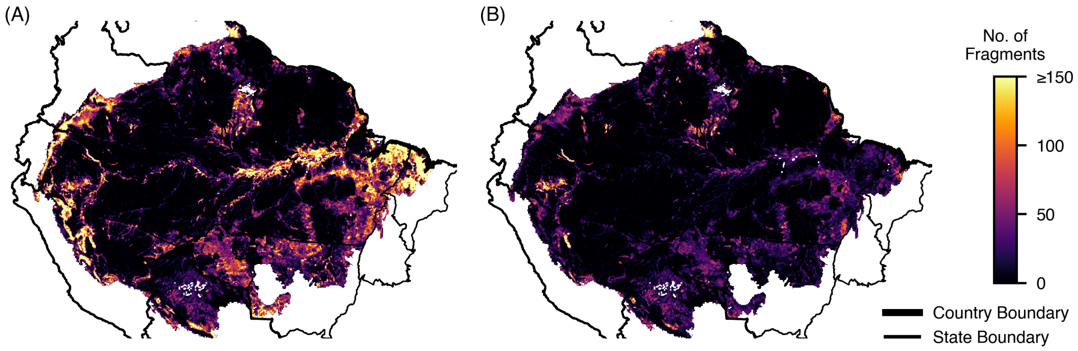

Figure 4.5: A comparison of old-growth forest fragmentation with and without connectivity by secondary forests across the Amazon biome in 2020. The number of old-growth forest fragments in the Amazon when considering **(a)** only old-growth forest and **(b)** when allowing secondary forest to connected fragments. Data is presented across a ~56.2 km^2 grid. Fragment count was calculated as the number of fragments intersecting each grid cell and fragment size is the median size of fragments intersecting each cell.

high-resolution maps of secondary forest extent (Nunes et al., 2020; Silva Junior et al., 2020b; Smith et al., 2020, 2021), to explore their position within the landscape and how this could be influencing the environmental benefits of forest recovery across the biome. In 2020, most secondary forests were positioned favourably for beneficial effects from proximity to old-growth forests. The position of secondary forests may also provide important benefits to old-growth forests: they substantially reduce the number of isolated old-growth forest fragments, and buffer more than half of old-growth forest edges. These findings show that secondary forests are a valuable feature of human-modified landscapes, potentially exerting an influence that goes far beyond their immediate extent.

4.4.1 Conserving old-growth forest extent and integrity could support secondary forest succession

In 2020, almost half the total area of Amazonian secondary forest was growing directly adjacent to old-growth forest, which, all else being equal, is the best location for fast biomass recovery and formation of diverse ecosystems (Jakovac et al., 2015; Mayhew et al., 2019). Recent findings indicate that surrounding forest cover is advantageous for secondary forest development in the early stages of succession (Toledo et al., 2020). It is likely that proximity to old-growth forest will also be important later in succession, as they provide the diverse seed sources required to establish resilient, biodiverse, and high-biomass secondary forests (Martinez-Ramos et al., 2016; Hawes et al., 2020). However, structural disturbance and small patch area reduce the quality of old-growth forest fragments: when old-growth forest condition was taken into account secondary forest adjacency declined by as much as 64%. These findings highlight an additional, hitherto unaddressed, benefit of preventing further deforestation and disturbance of old-growth forest: enabling more secondary forests to achieve higher species richness and rates of carbon sequestration. However, further research is needed as we do not currently have a sufficient understanding of the influence of the type and condition of surrounding forest on secondary forest succession. As old-growth forests become increasingly fragmented (Montibeller et al., 2020; Fischer et al., 2021) and structural disturbance continues to spread (Bullock et al., 2020; Matricardi et al., 2020), furthering our understanding of these relationships will be integral to designing effective restoration programmes, especially in landscapes where little old-growth forest remains (Crouzeilles et al., 2019).

4.4.2 The benefits of secondary forest growth for old-growth forest condition

The close proximity of the majority of secondary forests to old-growth forests indicates they could have a substantial role as buffers to edge effects: 43.1% of old-growth edges were buffered by secondary forests. However, there is scope for improvement, as over half (56.9%) of all old-growth forest edges are not buffered. Carbon losses at exposed forest edges are rapid, with declines of over 20% within 1 year of edge creation (Silva Junior et al., 2020a). Based on the edge exposure times found in this study and the 15-year carbon decay curve reported by Silva Junior et al. (2020a) for old-growth forest within 120 m of an edge, as much as 33.4% of the carbon stock in old-growth forest edges ($\leq$15 years old) may have already been lost – a substantial figure considering old-growth forest edges represent an area larger than the United Kingdom. The role of secondary forests as buffers is also relevant for biodiversity conservation. Changes in microclimate and structure at forest edges (Laurance et al., 2002) mean that for many species, the amount of habitat available in landscapes with highly fragmented forest is considerably smaller than the total forest cover. Our findings show that across the biome 6.4% of remaining old-growth forest cover is within 120 m of an edge, meaning core-forest species may have lost as much as 348,903 km^2 of habitat in addition to that already lost to widespread deforestation. Secondary forest buffers may be mitigating the microclimatic changes along almost half of old-growth forest edges, potentially increasing habitat availability for some species.

The potential benefits of secondary forests as buffers for old-growth forest edges are numerous, but we do not currently have a thorough understanding of these processes. Some studies have indicated responses such as reduced edge-related tree mortality (Mesquita et al., 1999), but considerably more research is needed to quantify the mechanisms through which such responses occur. With 63% of edges in 2020 having been buffered at some point, one important question is whether secondary forest buffering simply prevents further degradation or enables old-growth forest edges to recover some of their ecological integrity, such as leaf area (e.g. Almeida et al., 2019). Equally, the increase in height, leaf area, and canopy complexity of secondary forests during succession (Peña-Claros, 2003; Feldpausch et al., 2005) suggests that the age of a secondary forest would strongly influence its effectiveness as a buffer. Given the proportion of buffered edges drops from 41% to 22% when restricting buffers to secondary forests $\geq$ 15-years-old, the impacts of an age-related relationship would not be insubstantial. The effectiveness of a secondary forest buffer could also vary with its width, which may be important in determining its mitigation of the penetration of different edge effects into the old-growth forest (Laurance et al., 2002). However, we lack data to demonstrate the form of these relationships and if any thresholds could be used to guide management. A more comprehensive understanding of how secondary forests influence old-growth forest edges could help improve estimates of carbon emissions and guide conservation planning for some of the world's most vulnerable species.

4.4.3 Secondary forests reduce old-growth forest fragmentation

In addition to their role as edge buffers, the considerable reduction in old-growth fragment isolation resulting from secondary forest bridges further demonstrates the value of secondary forests beyond the ~190,000 km^2 of additional forest cover they provide. These secondary forest bridges could act as corridors for those species able to move through them, linking together valuable habitat remnants in highly fragmented landscapes, restoring genetic diversity, and alleviating the risk of extinction in fragments that are too small to support long-term viable populations (Metzger et al., 2009; Newmark et al., 2017). Connectivity within landscapes and between protected areas is receiving increasing attention in global policy (Juffe-Bignoli et al., 2018; Ward et al., 2020), However, there are still many unknowns to be answered before we can rigorously quantify the benefits of these effects. Research is needed into the parameters of what makes a viable forest bridge for different species groups. For example, species differ in their ability to move through secondary forests of different ages (Powell et al., 2013, 2015a). Our analysis highlights the importance of understanding these details, as there were an additional ~400,000 isolated fragments of old-growth forest when we restricted viable bridges to secondary forests $\geq$ 5 years old. Furthermore, the length and width of a secondary forest may also be critical to determining its suitability as a bridge. Width is important as edge effects will be altering the abiotic conditions (Laurance et al., 2002), especially in very narrow bridges that may suffer from additive edge effects (Porensky et al., 2013). Length is important as some species that can disperse through secondary forest, but cannot use it as their permanent habitat, may have maximum dispersal distances that they will not move beyond (Paim et al., 2015). Research is especially needed into the role of secondary forest permanence and configuration in mitigating fragmentation effects on species of conservation concern.

4.4.4 Improving the accuracy of methods used to record spatial and temporal shifts in secondary forests

In satellite imagery, pixels at the intersection of different land cover types may contain a mixture of land covers and hence are liable to temporal variations in classification. Our method of identifying secondary forests through change detection means that if a mixed-pixel was misclassified as a deforestation event, it would subsequently be classed as secondary forest by our algorithm if it appeared to ‘return’ to a forested state in future years. As such, some of our adjacent secondary forest pixels may actually contain exposed old-growth forest edge. As a result, we may be overestimating the extent of secondary forest and its role in buffering edges. The surge in buffered edges in 1998 and 2016 also suggests that some misclassification may have occurred due to fires and drought during the 1997-1998 and 2015-2016 El Niño events. However, the MapBiomas dataset undergoes a rigorous validation process (MapBiomas, 2021) and so the impact of such misclassifications on our results is likely to be limited. As more advanced biomass products become available (e.g. GEDI), it may be possible to further reduce misclassifications of this kind in future, by validating new secondary forest growth against high-resolution biomass estimates. Future large-scale studies should endeavour to combine historic land cover data with newly available remote sensing technologies to reduce uncertainties in land cover maps.

4.4.5 Implementation challenges

Expanding forest restoration is essential for achieving to global targets on climate change mitigation and biodiversity conservation. The longevity of those restoration efforts is, however, key to unlocking the additional benefits considered in this study. Unfortunately, with Amazonian deforestation on the rise (PRODES, 2021; Smith et al.,

2021) and trends of low residence time and high turnover rates for secondary forests (Nunes et al., 2020; Schwartz et al., 2020; Smith et al., 2020), even just maintaining the existing extent of secondary forests will be a major challenge. Nonetheless, the preservation and expansion of secondary forest must remain a priority in order to realise the important benefits it can provide.

If secondary forest are going to help avoid the rapid decay of carbon at old-growth forest edges (Silva Junior et al., 2020a) they need to establish soon after deforestation, at the newest edges. Unfortunately, this is likely to be difficult to achieve in practice, as new edges are created in regions of active deforestation where forest loss rather than land abandonment dominate. Furthermore, regions of active deforestation are characterised by corruption and inadequate land tenure arrangements (Geist et al., 2002); the opposite of what is required for encouraging restoration. Yet in regions where deforestation has been stopped, and governance is reinstated, incentivising natural regeneration along edges would be a sensible strategy (Chazdon et al., 2016b), and a potential double win for conservation.

Connectivity between forest fragments is important for maintaining habitats that are sufficiently large to support viable long-term populations (Michalski et al., 2007) and connection to extensive old-growth forests has been shown to strongly influence the species that inhabit a fragment (Mayhew et al., 2019). Using restoration efforts to increase landscape connectivity could therefore offer major benefits for biodiversity. However, identifying where to increase functional connectivity between forest fragments is not a simple task and the criteria used for planning has a considerable influence on which areas are proposed for restoration (Sousa Miranda et al., 2021). Our ability to estimate the benefits of different connectivity scenarios is also inhibited by a lack of empirical data on movement behaviour in tropical species, although it is noteworthy that at least one of Amazonia's critically endangered species, the Ka'apor capuchin monkey (*Cebus kaapori*), is able to use secondary forest (De Oliveira et al., 2014). Furthermore, planning must also take future climate into account: areas offering suitable habitat are likely to shift (Chen et al., 2011) meaning the most beneficial fragment networks now may be of less value later.

An additional challenge is determining the landscapes in which to focus restoration efforts to gain the greatest return on investment. Natural, spontaneous regeneration is more likely in landscapes that have suffered little deforestation (Crouzeilles et al., 2019), and greater surrounding old-growth forest cover offers a greater diversity of seed sources that will enable biomass and species richness to recover more rapidly (Martinez-Ramos et al., 2016; Hawes et al., 2020; Toledo et al., 2020). Conversely, highly deforested landscapes tend to have lower carbon accumulation in regenerating forests (Chazdon, 2003; Bihn et al., 2010) and reduced species diversity (Arasa-Gisbert et al., 2021). Yet, the remaining old-growth forest could benefit greatly from edge-buffering, which may preserve irreplaceable carbon stocks and habitats (Gibson et al., 2011). Species in highly deforested landscapes could also gain much from the reconnection of remnant old-growth forest habitats through secondary forest bridges (Newmark et al., 2017). This is especially true for endemic species in regions such as Belém, where the little forest that remains is highly fragmented (Chapter 5). Further complication is introduced by the fact that highly deforested landscapes have historically displayed limited recovery even decades after clearance (Smith et al., 2021) and have more variation in restoration success (Crouzeilles et al., 2019), meaning restoration in these landscapes is likely to entail a greater financial cost.

4.5 Conclusion

In a bid to reach net-zero emissions, many ambitious global forest restoration targets have been set (e.g. Bonn Challenge, 2011). However, while forest restoration benefits both carbon and biodiversity (Lennox et al., 2018), how these benefits are influenced by spatial context has yet to be fully quantified. Improving our understanding of the mechanisms driving variation in forest recovery at the landscape scale and the potential benefits of secondary forest as buffers will enable us to refine current estimates of forest carbon stocks and emissions. Forest restoration is undoubtedly a valuable conservation tool (Chazdon et al., 2016b; Chazdon et al., 2019) and is already providing substantial benefits to deforested landscapes across the tropics. However, a systematic approach is needed to maximise the benefits of expanding secondary forest cover, whilst minimising the cost of achieving restoration targets (Crouzeilles et al., 2020). Future policies must be applied at a landscape scale, aligning restoration with old-growth forest edges and increasing fragment connectivity. Doing so could generate important co-benefits by both increasing recovery rates in regenerating secondary forests and improving conservation of biodiversity and carbon stocks in remaining old-growth forest.

Chapter 5

Deforestation and disturbance drive a 40% decline in habitat availability for Amazonian species

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Abstract

As the largest remaining expanse of tropical rainforest on Earth, the Amazon is of critical importance for biodiversity conservation (Pillay et al., 2021; Cazzolla Gatti et al., 2022). However, it is also undergoing widespread deforestation (PRODES, 2021; Smith et al., 2021) and much of the remaining forest has been subject to disturbance events (Bullock et al., 2020; Matricardi et al., 2020). It is well-documented that both deforestation and disturbance have severe consequences for biodiversity, with the latter rendering standing forests unsuitable as habitat for many species (Barlow et al., 2016). Yet, while the impacts of deforestation are closely monitored, the role of forest disturbance as a driver of habitat loss has not been assessed at large-spatial scales. Here we show that the combined impact of deforestation and disturbance has reduced potential habitat by 40% for disturbance-sensitive bird species, despite the Amazon retaining 83% of its forest extent. 79% of this loss was due to changes in forest condition. The situation in some regions is critical: despite retaining more than half its forest cover, the Belém Area of Endemism could have just 9% of its habitat remaining for disturbance-sensitive bird species. Our results provide the first biome-wide assessment of habitat loss for forest-dwelling Amazonian species, highlighting the critical importance of monitoring forest condition and the urgent need to protect the remaining areas of high-quality forest.

5.1 Background, Results and Interpretation

Deforestation of old-growth forest is often the metric used to assess the degree of human-impact on tropical landscapes. Yet doing so results in a focus on changing forest quantity, while ignoring the quality of the forest that remains. Disturbances such as logging, fire, and edge effects significantly alter forest condition without changing the land cover type, but still drive local biodiversity loss (Gibson et al., 2011; Barlow et al., 2016; Marco et al., 2019) and generate carbon dioxide emissions (Pearson et al., 2017; Silva Junior et al., 2020a). By not explicitly including forest condition, the 2021 United Nations Declaration on Forests and Land Use from COP26 in Glasgow may fail to properly safeguard the world's most carbon-rich and biodiverse regions. While relationships between forest disturbance and carbon loss are increasingly well studied (Maxwell et al., 2019), impacts on biodiversity are less well understood and have been poorly assessed at the large spatial scales required to inform conservation policy and practise.

Disturbance and other anthropogenic pressures are particularly damaging for the hyper-diverse biota of the humid tropics (Betts et al., 2019), which account for around 60% of the world's terrestrial species (Pillay et al., 2021). Tropical forest species are especially sensitive to disturbance (Betts et al., 2019) and many species are unable to persist in human-modified forests, including old-growth forests disturbed by human actions and secondary forests growing on previously cleared land (Gibson et al., 2011; Pfeifer et al., 2017). Changes in forest condition can be as important as deforestation in driving biodiversity loss (Barlow et al., 2016). Consequently, national commitments and international declarations relating solely to forest extent provide an imprecise measure of habitat availability, as they do not account for the sensitivity of tropical forests species' to edge effects (Pfeifer et al., 2017), structural disturbance such as from logging or fires (Barlow et al., 2006), species' ability to use secondary forests at different stages of recovery (Lennox et al., 2018) or the minimum habitat area required to avoid anthropogenic pressures associated with accessibility (e.g.

hunting; Parry et al., 2009; Andrade Melo et al., 2015).

Here we undertake a heuristic exercise to estimate the extent of habitat that is potentially available for forest-dwelling bird species across Amazonia, the world's largest tropical forest. Given the lack of comprehensive data describing species' actual distributions and their sensitivity to disturbance, we base our estimates of habitat extent on six response groups that represent broad groups of bird species with similar habitat preferences. The response groups range from disturbance-tolerant to disturbance-sensitive, developing plausible response types using site-specific studies and expert knowledge of Amazonian birds, the best-studied taxonomic group in terms of distribution and disturbance sensitivity (see Methods). To map forest cover and deforestation (defined here as the complete removal of forest cover), we obtained annual land cover data from MapBiomas (1985 – 2020; MapBiomas, 2021) and masked out wetlands using a combination of data sources (Hess et al., 2015; Gumbricht et al., 2017). We quantified forest condition in four ways. (i) We applied a change-detection method to the MapBiomas dataset to identify and age secondary forests (Smith et al., 2021). (ii) Structural disturbances (defined as natural or anthropogenic disturbance that does not change a pixel's land cover category, including fire, windthrow, and selective logging) were identified using Bullock et al. (2020). (iii) Old-growth forests subject to edge effects were mapped using the Guidos Distance tool (Soille et al., 2009). (iv) The area of habitat available within individual forest fragments was calculated using the Guidos Accounting tool (Soille et al., 2009). Species within the most disturbance-tolerant response group would be able to use all available forests with a minimum habitat area of 0.01 km^2. In contrast, species within the most disturbance-sensitive group would avoid all secondary forest, forest within 300 m of an edge, forest that experienced structural disturbance in the last 20 years, and also required a minimum habitat area of 50 km^2 (see methods). We report habitat loss as the area of potential habitat for each response group in 2020 relative to total extent of old-growth forest in 1985.

We found that in 2020, the Amazon biome contained 5.1 million km^2 of terra firma forest (old-growth forests: 4,976,600 km^2; secondary forests: 169,677 km^2). For the most-disturbance tolerant response group, which can use almost any forest, habitat has decreased by 8.5% (477,541 km^2) since 1985. However, estimates of potential habitat loss increased sharply with increasing disturbance sensitivity. The most disturbance-sensitive group has lost 39.8% of its potential habitat since 1985, with 79% of this loss due to changes in forest condition rather than extent (Figure 5.1). These results were insensitive to major changes in response group parameters (see Methods; Figure C.1). The reduction in potential habitat for the most disturbance-sensitive groups (Figure 5.1) emphasises the importance of avoiding further deforestation and disturbance across the basin and protecting wilderness areas (Marco et al., 2019).

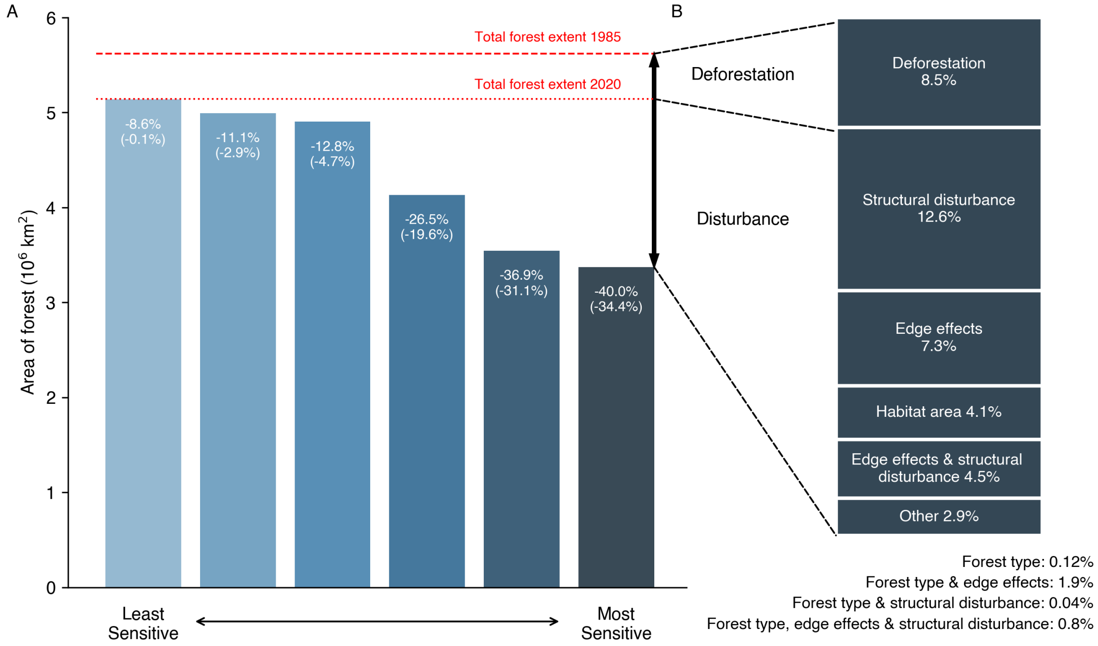

Figure 5.1: Estimated habitat availability for disturbance response groups in the Amazon biome. (a) The area of habitat available for each disturbance response group across the Amazon biome in 2020. The percentage change relative to total forest extent in 1985 is shown within each bar; loss from disturbance is shown in brackets. **(b)** The individual and combined drivers of habitat loss for the most disturbance sensitive response group compared to total forest extent in 1985. Drivers that are too small to be displayed are annotated below. See supplementary material for response group definitions.

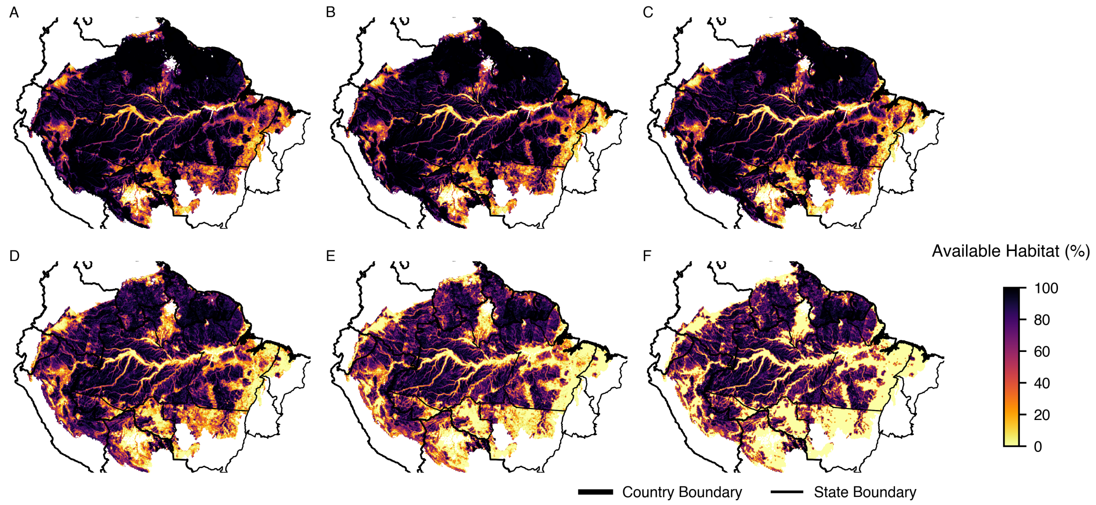

Figure 5.2: Spatial distribution of estimated habitat availability for disturbance response groups in the Amazon biome. (a-f) The spatial distribution of habitat available to six disturbance response groups across the Amazon biome in 2020; measured as the percentage of a ~60 km^2 grid cell that is habitat. Groups increase in sensitivity to disturbance from **(a)** the least sensitive to **(f)** the most sensitive. See supplementary material for response group definitions.

Amazonia's many large rivers act as barriers to dispersal and have driven allopatric speciation (Smith et al., 2014) and the development of distinct areas of endemism over the last 5 million years – especially for vertebrates such as birds and primates (Ribas et al., 2012). To explore how the potential habitat available to each response group varies across these biogeographic provinces, we calculated habitat extent within the ten widely accepted major areas of endemism (Borges et al., 2012, Figure 5.3a). Potential habitat declined with increasing disturbance sensitivity across all areas of endemism, but the degree of change was far greater in the south and east of the Amazon (the Rondônia, Tapajós, Xingu and Belém areas of endemism; Figure 5.3b). The importance of considering habitat availability is exemplified by the Belém Area of Endemism where extensive forest disturbance has left just 14,833 km^2 of potential habitat for the most disturbance-sensitive group (9.1% of its 1985 extent), despite the region containing 110,420 km^2 of forest in 2020 (67.5% of its 1985 extent). Our assessment of potential habitat is validated by the Critically Endangered status of some of the region's vertebrates that are restricted to a few remaining areas of the eastern Amazon, such as the Black-winged Trumpeter *Psophia obscura*, Belém

Curassow *Crax pinima*, and the Kaapori Capuchin *Cebus kaapori*. The dramatic loss of potential habitat in the south and east contrast with the six areas of endemism in the north and west, which have all retained enough high-quality, old-growth forests to have >75% of their 1985 habitat remaining for the most disturbance-sensitive response group.

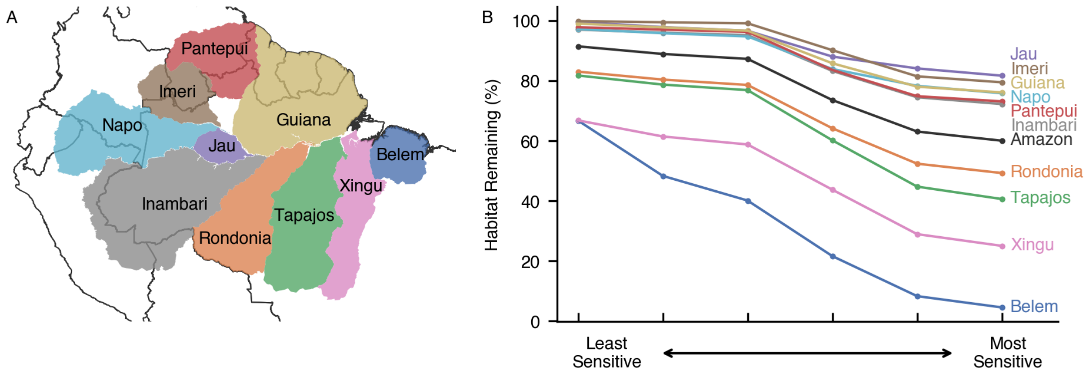

Figure 5.3: Estimated habitat availability for disturbance response groups in areas of endemism in the Amazon biome. (a) A map of areas of endemism in the Amazon biome and **(b)** the proportion of habitat remaining in each area of endemism in 2020 relative to the 1985 forest extent, for six response groups with increasing sensitivity to disturbance. See supplementary material for response group definitions. Lines are to aid interpretation only and do not represent continuous data.

We explored the unique and combined contribution of different factors in reducing potential habitat for the most disturbance-sensitive group (Figure 5.1). Across the biome, deforestation alone (i.e. without associated edge effects) reduced potential habitat by 8.4% between 1985 and 2020. This was exceeded by the unique contribution of structural disturbances, which led to a reduction of 13.6%, over 60% more than has been lost to deforestation. The role of structural disturbances in reducing potential habitat increased to 18% when including areas that also experienced other forms of disturbance (combined contribution). The combined contribution of structural disturbance caused the largest reduction in potential habitat across all areas of endemism, except for Belém and Xingu where it was exceeded by edge effects and deforestation, respectively. Edge effects were responsible for the third-largest biome-wide reduction in potential habitat (unique: 5.8%; combined: 14.5%), comparable with deforestation itself. Excepting Xingu, habitat loss from the combined contribution of edge effects exceeded deforestation in every area of endemism, with the greatest disparity in the least deforested north and east regions. Forest type (old-growth, young/old secondary) had less impact on potential habitat, reducing it by 0.12% alone or by an additional 2.8% in combination with other factors. This modest biome-wide contribution is unsurprising as secondary forests represent a small proportion of total forest cover in the Amazon (young secondary forests: 2.1%; old secondary forests: 1.1% Smith et al., 2021).

Protected areas are an important tool for safeguarding forests (Gray et al., 2016). Crucially, they also represent one of the best opportunities to retain the high-quality forest cover that is essential for many species (Watson et al., 2018). However, laws governing private lands – such as the Native Vegetation Protection Law in Brazil (Federal Law no. 12,651/2012) – focus only on forest extent, and do not consider forest condition (Barlow et al., 2016). To explore the importance of protected areas across the biome, we calculated the extent of potential habitat falling within the boundaries of protected areas listed in the World Database on Protected Areas. We find that almost half (49.5%) of existing forest cover in the Amazon biome is within a protected area, leaving up to 2.6 million km^2 with elevated risks of future clearance or disturbance (Geldmann et al., 2019). Protected areas are already a critical last refuge for the most disturbance-sensitive response group in areas of endemism in the south and east of the biome, where they hold between 70% and 84% of the group's potential habitat (Figure 5.4). For the most disturbance-sensitive group, 28% of potential habitat loss across the biome has occurred inside protected areas. This will likely increase as unprotected forests dwindle and buffer zones are eroded (Curran et al., 2004). An insight into this future can already be seen in the highly deforested areas of endemism in south-east Amazonia, which exhibit the highest relative losses of potential habitat from inside protected areas. Importantly, protected areas are not immune to deforestation and disturbance, which could have occurred before the protected area was established and, in some cases, may still be ongoing either legally (i.e. in sustainable use zones) or illegally (Geldmann et al., 2019).

Improved estimates of habitat availability could be used to revise species' threat status. The IUCN classifies a species as Critically Endangered when more than 80% of its habitat is lost in 10 years or three generations. Furthermore, evidence-based conservation interventions will be more effective if they are informed by real data on species occurrences and threats. Our results can help this by revealing priority areas for research and conservation: for example, we estimate there are 3,483 km^2 of high-quality habitat outside of protected areas in the Belém Area of Endemism. The recent rediscovery of the Belém Curassow *Crax pinima* in the eastern Amazon (Alteff et al., 2019), and the proximity of these sightings to our estimates of remaining habitat (Figure C.2), shows the importance of scaling up biodiversity assessments in the last remaining patches of high-quality habitat.

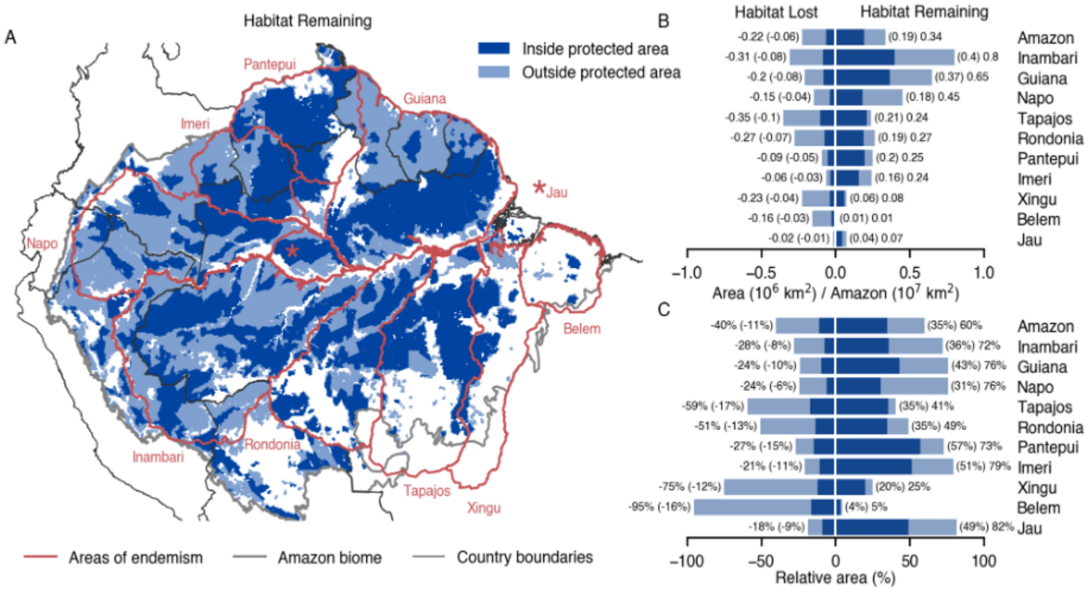

Figure 5.4: Estimated habitat availability for the most disturbance-sensitive response group inside and outside of protected areas in the Amazon biome. **(a)** Habitat inside (dark blue) and outside (light blue) protected areas in 2020 for the most disturbance-sensitive response group. The **(b)** absolute and **(c)** relative (to 1985 forest extent) area of habitat loss and habitat remaining in 2020 inside and outside protected areas in the whole Amazon biome and each area of endemism. Total values are shown by each bar, with the values for inside protected areas shown in brackets. See methods for response group definition.

Our results highlight four key points for conservation policy and practice. First, the remaining forests that provide habitat for the most disturbance-sensitive species need urgent protection. Many of the measures required to achieve this are well known (Nobre et al., 2021) and include supporting the autonomy and land rights of indigenous peoples, creation of new protected areas, renewed investment in existing protected areas, and avoiding damaging infrastructure. Second, novel policies and interventions are needed to prevent structural disturbances, such as illegal logging (Brancalion et al., 2018) and forest fires (Barlow et al., 2020), as these are by far the most important drivers of habitat loss for disturbance-sensitive species across the Amazon. Third, restoration efforts, many of which are aimed at sequestering carbon dioxide, should be located strategically to buffer old-growth forests against edge effects. This would help to mitigate one of the leading drivers of habitat loss, particularly in the most deforested regions of the Amazon (Figure 5.2), which have the largest amount of land available for restoration (Smith et al., 2021). Finally, action must be taken now. World leaders may have committed to “no new deforestation by 2030”, but significant habitat loss can occur over a short period of time, especially when disturbance and deforestation are considered together, and the rate of change for disturbances such as fire could worsen under climate change (Brando et al., 2020).

5.2 Materials and Methods

5.2.1 Study Area

The Amazon biome spans 6.7 million km^2 and is the largest remaining expanse of tropical forest on earth. This study focuses on upland terra firma forests (92% of total forest cover), as wetland forests are quite different structurally and in their species assemblages. Any pixels classified as wetland by Hess et al. (2015) or Gumbricht et al. (2017) are excluded from our forest classes.

5.2.2 Assessing deforestation

We assessed deforestation in the Amazon biome using the MapBiomas Amazonia Collection 3.0 dataset (MapBiomas, 2021), comparing old-growth forest extent in 1985 and 2020 to calculate the total loss of old-growth forest. As large-scale deforestation in the Amazon began in the 1970s, our approach underestimates long-term old-growth deforestation. Previous estimates suggest that ~140,000 km^2 of forest in the Brazilian Amazon may have been cleared prior to 1985 (Fearnside, 1990). However, as the earliest reliable satellite imagery covering the whole Amazon is from 1985, MapBiomas (2021) provides the best available map of historic forest cover. Secondary forests that began growing after 1985 were excluded from the old-growth forest mask using the change detection algorithm outlined below.

5.2.3 Assessing forest condition and configuration

Old-growth forest vs secondary forest

Secondary forests are defined in this study as forest growing on previously cleared land. Although secondary forests may rapidly come to resemble old-growth forest – especially in terms of spectral reflectance in satellite imagery – they remain structurally very different for many years, particularly in earlier stages of succession (Guariguata et al., 2001). Species richness in secondary forests increases over time (Lennox et al., 2018), but although some forest species can make use of older secondary forest (Barlow et al., 2007a; Barlow et al., 2007b; Moura et al., 2016; Lennox et al., 2018), the composition remains very different from old-growth forest and many specialist species avoid secondary forests altogether (Moura et al., 2013). Forest type is therefore a critical factor in determining a forest's suitability as habitat.

In this study we used three forest classes: old-growth, old secondary (>15 years), and young secondary ($\leq$15 years). To create masks of these classes, we applied a change detection algorithm to the MapBiomas Amazonia Collection 3.0 dataset

(MapBiomas, 2021) to produce annual maps of the extent of old-growth and secondary forest cover from 1985 to 2020, following the method of Smith et al. (2021). Any pixel (900 m^2) in the 'forest' class in the first year of the time series (1985) was considered old-growth forest until it transitioned to 'non-forest' (any land cover class in the MapBiomas schema that is not a natural forest formation). Pixels that transitioned from 'non-forest' to 'forest' were labelled as secondary forest. We then measured secondary forest age as the number of consecutive years a pixel was classified as secondary forest. As the MapBiomas time series begins in 1985, any secondary forest that began growing before this date is included in our old-growth forest class and the maximum age of secondary forest detectable with this method is 34 years. However, the low residence time and high turnover rate of secondary forests means we are unlikely to have substantially underestimated secondary forest extent (Smith et al., 2020).

Edge effects

Fragmentation introduces edge effects that drastically alter the microclimate of the forest by exposing it to increased wind, light, and temperature, whilst also reducing humidity and hydrological consistency. The most severe impacts occur within the first 100 m, but others can penetrate hundreds of metres into the forest (Laurance et al., 2002). These changes render forest edges unsuitable as habitat for many species, reducing the abundance of forest core species 200 - 400 m from edges (Pfeifer et al., 2017).

To identify anthropogenic forest edges (natural edges such as those along a river are considered undisturbed), we calculated the Euclidean distance from every old-growth pixel to the nearest old-growth forest edge using the Guidos Toolbox Distance tool (Soille et al., 2009). We then created as mask of pixels that were within 60m and 300m of an edge. Pixels that were classified as edge forest in both 1985 and 2020 were considered natural edges and were excluded from the masks.

Structural disturbance

Structural disturbance from events such as forest fires or selective logging can dramatically alter the composition of a forest ecosystem (Moura et al., 2016) and only a small proportion of the affected areas are subsequently deforested (Bullock et al., 2020). The resulting forests take decades to recover (Rutishauser et al., 2015; Silva et al., 2018), and their more heterogeneous and open canopies and dense understories make them unsuitable as habitat for many forest species. However, even some of the more disturbance-sensitive species may eventually be able to return if further disturbances are avoided (Mestre et al., 2013a; Mollinari et al., 2019).

Bullock et al. (2020) provides a spatially explicit dataset of degradation and natural disturbance from 1995 to 2017. They defined degradation as a natural or anthropogenic disturbance that does not change a pixel's land cover category – including fire, windthrow, selective logging, and damage to standing forests during expansion of roads or development. We use this dataset as our pan-Amazonian measure of structural disturbance and create three classes: undisturbed, disturbed more than 20 years ago, and disturbed more than 10 years ago (relative to 2020). We resampled the condensed Bullock et al. (2020) dataset to align with MapBiomas (2021).

The Bullock et al. (2020) dataset is the most recent map of forest degradation currently available for the Amazon and we found it to be very effective at capturing the well-studied burn scar from the 2015/2016 forest fires in the Santarém region (Figure C.3). However, there are two limitations to its use in this study that mean we may be underestimating potential habitat loss resulting from structural disturbance. First, it does not extend to our study year (2020) so we cannot account for the three most recent years of structural disturbance. Second, Bullock et al. (2020) conducted their analysis for the Amazon EcoRegion as defined by Olson et al. (2001) meaning a small proportion of our study area (the RAISG-defined Amazon biome) is not included. We also recognise that the Bullock et al. (2020) dataset includes natural disturbances. Although this study is primarily concerned with identifying habitat loss resulting from anthropogenic interference, we consider the inclusion of disturbances classed as natural by Bullock et al. (2020) to be acceptable as the change in canopy openness would still render the forest unsuitable as habitat for the relevant response groups. Furthermore, many of these natural disturbances occurred along river edges, which are naturally more open and dynamic, and will have been masked out by our wetlands layer. It is also possible that some of these “natural” disturbances could also have underlying anthropogenic causes. For example, climate change made the probability of the 2015-16 El Niño drought four times more likely (Ribeiro et al., 2021) providing a direct link between anthropogenic actions and excess tree mortality seen during climate extremes (Berenguer et al., 2021).

Area effects

Area effects are well known drivers of species richness and population persistence across the world and in the Amazon (Ferraz et al., 2007). Species dependent on old-growth forest are more sensitive to fragment size than species able to survive in secondary forest and forest edge habitat (Lees et al., 2006). The size of a habitat fragment is also indicative of its accessibility to people and so can act as a proxy for other anthropogenic pressures such as hunting, which is predominantly carried out on foot with a range of ~5.4 km (Parry et al., 2009; Andrade Melo et al., 2015).

To account for area effects, we masked out forest pixels that did not meet the habitat criteria for forest type, minimum distance from edge, and structural disturbance, then used the Guidos Toolbox *Accounting* tool to calculate the size of the remaining habitat fragments. We masked out habitat fragments below the minimum size threshold for each response group. It is important to note that this provides a measure of remaining habitat within a forest fragment once the other habitat criteria have been met and is not the total size of the forest fragment. Due to the computational complexity of assessing fragment isolation, we also assumed that species in all groups are not capable of moving between habitat fragments and therefore a small habitat fragment cannot be supplemented by proximity to a larger fragment. This decision is also supported by the finding that area effects are more important and consistent predictors of patch occupancy of birds than isolation effects (Ferraz et al., 2007). The principle aim of our area thresholds is to explore the short-term habitat availability for our response groups, and we are not projecting future survival, source-sink dynamics, nor considering minimum viable populations.

5.2.4 Disturbance response groups

We assess the impact of deforestation and disturbance (including anthropogenic pressures such as hunting that do not immediately alter forest structure) on habitat availability across the Amazon biome for six disturbance response groups (see below). These hypothetical groups are based on site-specific studies and expert knowledge of real habitat preferences seen in Amazonian birds. Expert opinion was guided by co-authors AL and JB; both have worked on disturbance impacts on Amazonian birds for over two decades, and AL is a member of the IUCN Species Survival Commission Bird Red List Authority (IUCN, 2020). We use birds as a proxy for other fauna, as they are the best-known taxon in terms of species-level responses to disturbance, and their biogeography is also relatively well known. Our results are likely to reflect other vertebrates that align with areas of endemism (e.g. primates; Paim et al., 2015), but may be less accurate for plants which have different biogeographical patterns (Nobre et al., 2021).

It is important to recognise that these response groups are a heuristic exercise, intended to be a proxy for broader species responses to disturbance. We use response groups as there are three major limitations in our current understanding of species distributions and species-specific responses to disturbance for the >1400 Amazonian bird species. First, insufficient data means that range estimates for species with few recent recorded sightings are highly uncertain. For example, the range estimate for the Critically Endangered Black-winged Trumpeter *Psophia* *obscura* is based on its historical range, covering the entire Belém Area of Endemism (BirdLife International, 2022) and not its current range, which is limited to just a few locations (Figure C.2). Second, in terms of species-specific responses, studies on Amazonian birds tend to focus on responses to a specific disturbance in a single location and biogeographic region, and at a single time point, but species can response idiosyncratically to disturbances across different regions (Moura et al., 2016). Third, there is the difficulty of collecting sufficient data on the habitat preferences of the rarest species, which are rare precisely because of their sensitivity to disturbance (Banks-Leite et al., 2014). Taken together, there is insufficient data to develop a comprehensive assessment of species' present-day distributions and their responses to disturbance across the biome.

We define suitable habitat for each response group based on four variables that describe forest condition: forest type, minimum distance from edge, structural disturbance, and habitat fragment size. These response groups range from disturbance-tolerant species that can inhabit any forest to highly disturbance-sensitive species.

Group 1

The most disturbance-tolerant group. This response group represents species that can use both old-growth and secondary forests of any age. They do not avoid forest edges or areas with structural disturbance and require a minimum habitat fragment of 0.01 km^2. This group is representative for species such as the Coraya Wren (*Pheugopedius coraya*) and Moustached Wren (*Pheugopedius genibarbis*) which are common in variably-aged secondary forests (Barlow et al., 2007b; Moura et al., 2013) and use some of the smallest habitat fragments (Stouffer et al., 1995; Lees et al., 2008).

Group 2

This group represents species that can use old-growth forests and secondary forests that are >15 years old. They do not avoid forest edges or areas with structural disturbance, but do require a minimum habitat fragment of 0.1 km^2. This group is representative of species such as the Forest Elaenia (*Myiopagis gaimardii*) and the Wedge-billed Woodcreeper (*Glyphorynchus spirurus*) – for example, the latter uses all old-growth forests including once-burned sites (Barlow et al., 2004), as well as edges (Powell et al., 2015b), and inhabits older secondary forests (Barlow et al., 2007b), but avoids the youngest secondary forests (Moura et al., 2013; Powell et al., 2015b).

Group 3

This group represents species that can only use old-growth forests. They do not avoid forest edges or areas with structural disturbance and require a minimum habitat fragment of 0.5 km^2. This group is representative of species such as the Amazonian Barred-Woodcreeper (*Dendrocolaptes certhia*) and the Bright-rumped Attila (*Attila spadiceus*). Both species are found in older secondary forests (Barlow et al., 2007b; Moura et al., 2013) and most fragments of over 50 ha (Lees et al., 2009).

Group 4

This group represents species that can only use old-growth forests. They avoid secondary forests of any age, forest within 60 m of an edge and areas where structural disturbance has occurred in the last 10 years (after 2010). They require a minimum habitat fragment of 0.5 km^2. This group is representative of species such as the Pará Foliage-gleaner (*Automolus paraensis*) and the Chestnut-belted Gnateater (*Conopophaga aurita*). The latter was never recorded in secondary forest in the study of Barlow et al. (2007b), was sensitive to the isolation of fragments 1-100 ha in size (Stouffer et al., 1995) and was only encountered in old-growth forests without a recent history of disturbance (Moura et al., 2013). The Pará Foliage-gleaner avoids habitat patches of under 50 ha (Lees et al., 2009) and forests subject to any disturbance (Moura et al., 2016).

Group 5

This group also represents species that can only use old-growth forests, avoid secondary forests of any age and areas where structural disturbance has occurred in the last 10 years (after 2010). In addition, they avoid forest within 300 m of an edge and require a minimum habitat fragment of 1 km^2. This group is representative of species such as the Ringed Antpipit (*Corythopis torquatus*) and the Striated Antthrush (*Chamaeza nobilis*). The former disappeared from fragments of under 100 ha (Stratford et al., 1999) and is absent from secondary forests and recently disturbed old-growth forests (Moura et al., 2013). The latter is very uncommon seemingly everywhere and has only been recorded from large intact habitat blocks around Alta Floresta (Lees et al., 2009).

Group 6

This is the most disturbance-sensitive group. It represents species that can only use old-growth forests and avoids secondary forests of any age, forest within 300 m of an edge, and areas where structural disturbance has occurred in the last 20 years (after 2000). They require a minimum habitat fragment of 50 km^2. This group is representative of species such as trumpeters (*Psophia spp*), which are unable to persist in regions with low forest cover, such that the last record of Black-winged Trumpeter (*Psophia obscura*) in the Belém metropolitan area was 1922, with an estimated date of extirpation of 1935 (Moura et al., 2014). Similarly, a large-scale ecological survey showed it to be restricted to large undisturbed forests remnants (Moura et al., 2016).

For response group 6, we varied the value of each forest condition parameter and found the results to be insensitive to major changes (Figure C.1). Reducing minimum fragment size, distance to edge, and time since structural disturbance by 50%

reduced habitat loss by 0.7%, 4.8%, and 2.5%; respectively. Increasing these parameters by 50% increased habitat loss by 0.4%, 2.5% and 2%. Allowing any forest type reduces habitat loss by 3.1%. Parameters were varied individually, with the other three held constant at the value used for group 6.

5.2.5 Areas of endemism

Amazonia's many large rivers act as barriers to dispersal for many organisms and have led to speciation and the development of distinct areas of endemism over the last 5 million years (Ribas et al., 2012). Furthermore, the spatially heterogeneous rate of deforestation and disturbance across the Amazon means that different endemism zones face different levels of threat. As such, species within the same habitat response group may have very different habitat availability depending on how their range is restricted by endemism. We explore this phenomenon across ten widely recognised areas of endemism: Belém, Guiana, Imeri, Inambari, Jau, Napo, Pantepui, Rondônia, Tapajós, Xingu (Borges et al., 2012).

5.2.6 Protected areas

To explore how much of the habitat available to the most disturbance-sensitive response group is within protected areas, we used data from the World Database on Protected Areas (IUCN et al., 2021), which is the most comprehensive global database of marine and terrestrial protected areas. We used the February 2021 version to the dataset and restricted our use to protected areas that were instated in or before 2020.

Chapter 6

Conclusion

In this thesis I used big data, in the form of large-scale and long-term remote sensing data, to derive new insights on a globally relevant environmental issue. Changing forest cover offered an interesting case study for doing so as it presents both problem and solution. Forest loss is contributing to two of the greatest environmental challenges of our time, climate change and biodiversity loss, while forest regeneration offers one of our greatest hopes for mitigating these catastrophes through nature-based solutions. This balance of forest loss and restoration is crucial to the future of the Amazon, where deforestation is once again on the rise, but secondary forest growth also has huge potential environmental benefits.

6.1 Thesis Summary

6.1.1 Secondary forests in the Brazilian Amazon (Chapter 2)

Motivating Questions: *What is the current extent and carbon stock of secondary forests? What is their contribution to the tropical carbon balance?*

Chapter 2 delivers high-resolution, spatially explicit estimates of secondary forest extent and accumulated carbon in the Brazilian Amazon. Using the MapBiomas Brazil Collection 3 dataset (MapBiomas, 2019), I mapped the extent and age of secondary forests, then combined these maps with estimates of carbon accumulation rates from Requena Suarez et al. (2019) to calculate secondary forest carbon stock. I found that in 2017 secondary forests occupied 20% of deforested land within the Brazilian Amazon, representing 4% of total forest cover. They had accumulated 0.33±0.05 billion Mg of above-ground carbon and offset 9.37% of emissions from deforestation. I also explored the spatial variation in climatic, landscape, and local factors that may impede secondary forest carbon sequestration. My findings revealed that secondary forests were typically located in areas that are unfavourable for carbon accumulation, making it likely that my estimate of carbon emissions offset by secondary forest growth is optimistic. Overall, this chapter contributes a new understanding of the extent, location, and dynamics of secondary forests in Brazil and their relative importance for the region's carbon balance. This chapter is published in Global Change Biology (Smith et al., 2020) and was shortlisted for the MapBiomas Award.

6.1.2 Forest loss and recovery in the Amazon (Chapter 3)

Motivating Questions: *What are the spatial patterns in the extent of forest loss and recovery in the Amazon? How do carbon emissions and accumulation vary across the biome?*

Chapter 3 expands the dataset I created in Chapter 2 to incorporate all Amazonian countries. It explores the geographic distribution of forest cover and carbon stocks across the Amazon biome, exploring how forest loss and recovery differ across political boundaries and at a local scale. Using the method developed for Chapter 2, I combined the 33-year MapBiomas Amazonia Collection 2 land cover dataset (MapBiomas, 2021) with estimates of above-ground biomass (Avitabile et al., 2016) and secondary forest carbon accumulation rates (Requena Suarez et al., 2019).

I found that Brazil has contributed disproportionally to old-growth forest loss, with Pará State alone responsible for more deforestation than the other eight countries combined. The analysis also revealed a negative spatial relationship between old-growth forest loss and recovery by secondary forests, both in terms of forest extent and carbon stock, showing that regions with the greatest potential for large-scale restoration are also those with the lowest forest cover recovery. I also found that highly deforested landscapes are not regaining forest cover, even after 20 years. Overall, this chapter contributes a new understanding of changing Amazonian forest cover and the first biome-wide estimates of carbon accumulation and emissions at this spatial resolution (30 m). This chapter is published in Environmental Research Letters (Smith et al., 2021).

6.1.3 Secondary forest position within the landscape (Chapter 4)

Motivating Questions: *Where are secondary forests growing in relation to old-growth forests in the Amazon? To what extent do secondary forests buffer old-growth forests edge?*

Chapter 4 updated the forest cover data produced in Chapter 3 to examine the spatial context of secondary forest growth in relation to remaining old-growth forests in 2020. I used annual maps of forest cover to establish the extent and age of old-growth forest edges and to quantify the proximity of secondary forests to these edges. My results revealed that although 94.1% secondary forests are part of a fragment that is connected to old-growth forest, less than half of secondary forests (48.9%) are within 1 km of a structurally intact old-growth forest fragment of more than 50 km^2. I also found that ~350,000 km^2 of old-growth forests were within 120 m of an anthropogenic edge, with secondary forests potentially buffering edge effects for less than half of these edges (41.1%). However, allowing secondary forests bridges reduced the total number of isolated old-growth forest fragments by up to 2 million. Overall, this chapter contributes the first quantification of secondary forest proximity to old-growth forests for the entire Amazon biome and demonstrates the importance of accounting for spatial context when examining the potential benefits of forest restoration. This chapter is in preparation for submission to Global Change Biology.

6.1.4 Habitat loss in the Amazon biome (Chapter 5)

Motivating Questions: *How have deforestation, disturbance, and secondary forest growth impacted habitat availability in the Amazon?*

Chapter 5 explores the implications of the findings of Chapter 4 from the perspective of habitat loss. To look beyond binary measures of forest cover, I combined maps of forest extent with data on forest degradation from Bullock et al. (2020), to highlight the perilous state of habitat availability in the Amazon. I found that the habitat available for disturbance-sensitive species has fallen by 40% since 1985, with 79% of this loss due to changes in forest condition rather than extent. Furthermore, I found that species endemism compounds these habitat losses. In the Belém area of endemism, fragmentation, edge-effects, and structural disturbance may have reduced habitat for disturbance-sensitive species by 91%, despite the region retaining 67% of its forest cover. Overall, this chapter contributes the first biome-wide estimates of habitat availability for Amazonian species based on their tolerance to disturbance and demonstrates the critical importance of monitoring forest condition as well as extent. This chapter is in preparation for submission to Nature Ecology and Evolution.

6.2 Key messages

As a whole, this thesis demonstrates the power of using big data to address environmental questions over large spatial scales. By combining very large datasets with high-performance computing, I have quantified spatial and temporal relationships between forest loss and recovery on a continental scale, whilst maintaining a resolution that can detect local scale change. More specifically, I address changing forest cover in the Amazon, with a particular focus on the role of secondary forests in offseting carbon emissions and providing refuge for biodiversity. While each data chapter focuses on a different aspect of this wider topic, there are four important messages that are consistent across all chapters.

Halting deforestation and degradation must be prioritised.

Deforestation in the world's tropical regions is without doubt one of the greatest environmental catastrophises of the last century. In the Amazon, over ~800,000 km^2 of old-growth forest has already been cleared (Smith et al., 2021), but the implications of deforestation reach beyond its immediate extent, by way of edge effects (Magnago et al., 2015, 2017), fragmentation (Fischer et al., 2021), and exposure to additional sources of degradation (Bullock et al., 2020; Matricardi et al., 2020). Together, deforestation and forest degradation cause huge disruption to tropical ecosystems (Barlow et al., 2016) and generate large quantities of carbon emissions (Qin et al., 2021). Although secondary forests may mitigate some of these impacts, the findings of this thesis highlight several important reasons why preventing further forest loss and degradation must remain the priority.

First, although secondary forests are increasing in extent (Smith et al., 2020, 2021), the rate at which they accumulate carbon (Requena Suarez et al., 2019; Elias et al., 2020, 2022) and the time frame over which they recuperate ecosystem composition (Poorter et al., 2021), means they cannot keep pace with the loss of intact old-growth forest that the Amazon is currently experiencing (Matricardi et al., 2020; Smith et al., 2020, 2021). Chapter 3 shows that to date, they have offset just 9.7% of carbon emissions from deforestation (Smith et al., 2021), a figure that would almost halve if also considering emissions from forest degradation (Bullock et al., 2021). Second, old-growth forests are key to supporting recovery in secondary forests (Chazdon et al., 2009; Arroyo-Rodriguez et al., 2020; Arasa-Gisbert et al., 2021). Old-growth forests are critical seed sources (Hawes et al., 2020) and connection to old-growth forests may be fundamental to the recovery of community composition (Mayhew et al., 2019). High surrounding forest cover has been shown to be important in the early stages of succession (Toledo et al., 2020), which is particularly prevalent given that 35.9% of secondary forests are currently $\leq$5 years old (Smith et al., 2021). Third, secondary forests do not provide habitat for all species (Barlow et al., 2007a). Chapter 5 reveals a 40% decline in habitat for species relying on extensive areas of structural-intact old-growth forests. Recovery by secondary forests cannot replace these old-growth forest habitats (Gibson et al., 2011) and preventing further deforestation and degradation is the only way to secure the future of these vulnerable species.

Although Amazonian deforestation rates are currently on the rise (PRODES, 2021), looking at the history of forest loss in the biome shows us that bringing an end to large-scale deforestation is not an impossibility. Through a combination of well-enforced policy and favourable economic conditions (Boucher et al., 2013; Tacconi et al., 2019; Heilmayr et al., 2020), Brazil was able to reduce its rate of deforestation by 79% in less than a decade (2004-2012; PRODES, 2021). As a result, we already have a viable pathway for ending forest loss in the Amazon, if those with the power to generate change take action. World leaders recently committed to “no new deforestation by 2030” (United Nations, 2021), it is critical that they make good on that promise.

Secondary forests are not reaching their full potential for carbon accumulation or biodiversity preservation.

Secondary forests have the potential to help mitigate both carbon emissions and biodiversity loss (Chazdon et al., 2009, 2016a; Lennox et al., 2018; Cook-Patton et al., 2020). However, a defining theme of my thesis is that the location of existing secondary forests is far from optimal maximizing carbon storage or biodiversity conservation. Foremost, Chapters 2 and 3 demonstrate that secondary forests are threatened by clearance (Schwartz et al., 2020; Smith et al., 2020; Wang et al., 2020; Smith et al., 2021). This ephemerality undermines their ability to act as a long-term carbon store and interrupts succession, preventing them from developing into complex and resilient ecosystems (Chazdon, 2014). There is also a growing body of research showing that secondary forest recovery trajectories vary considerably due to differences in climate, previous land use, and landscape context (Jakovac et al., 2015; Poorter et al., 2016; Mayhew et al., 2019; Elias et al., 2020, 2022). In exploring the location of secondary forests across the biome and within landscapes, this thesis shows that many secondary forests are aligned with conditions that are less favourable for recovery (Smith et al., 2020, Chapter 4). Chapter 2 shows that secondary forests are typically located in drier, more seasonable regions, as well as on land that has previously been intensely cultivated (Smith et al., 2020). Both climate and land use intensity are well-studied drivers of reduced recovery in secondary forests (Jakovac et al., 2015; Poorter et al., 2016; Elias et al., 2020; Jakovac et al., 2021; Elias et al., 2022). However, Chapter 4 reveals that 40% of secondary forests are growing directly adjacent to old-growth forests, the benefits of which may help compensate for the negative impacts of other unfavourable biophysical and socio-economic factors (Mayhew et al., 2019).

It is clear from the findings of this thesis that the environmental benefits of secondary forests could be enhanced. Data-informed policies that strategically target restoration efforts could ensure secondary forests are of maximum benefit to tropical landscapes and global environmental goals. For example, encouraging regeneration adjacent to old-growth forests, particularly on the 56.9% of old-growth edges that are currently exposed to open land use (Chapter 4), could be a double win for the environment by enhancing secondary forest recovery rates and protecting old-growth forests from further degradation. It is also clear from the findings of Chapter 3, that secondary forests are not recovering in highly deforested landscapes (Smith et al., 2021). New interventions – such as tree islands or enrichment planting (Alves et al., 2022) – specifically targeting these regions could help to initiate restoration in areas that have the greatest available space. Finally, inclusion of secondary forests in monitoring programmes and improved definitions of what consitutes a secondary forest would be important first steps in securing their longevity. Permanence is critical to the success of any restoration efforts. Future research projecting the outcomes of different approaches to promoting secondary forest recovery will be essential for planning effective policy interventions.

Further research is essential to achieving maximum environmental benefits from forest regeneration.

Maximising the environmental benefits of regeneration depends on our ability to identify where secondary forest growth will be most effective. In this thesis I have explored the distribution of existing secondary forests in relation to factors that are linked to variation in recovery rates (Chapter 4; Smith et al., 2020). However, there are critical gaps in our understanding of the processes that drive this variation. For example, although we know that surrounding old-growth forest cover influences secondary forest recovery (Mayhew et al., 2019; Arroyo-Rodriguez et al., 2020; Arasa-Gisbert et al., 2021), we do not know how this is affected by the condition of the surround forest. Chapter 4 demonstrates the scale at which this may be influencing recovery success: while 98.6% of secondary forests are within 1 km of any old-growth forest, this drops to just 48.9% for extensive structurally-intact old-growth forest. We also do not know how different drivers of secondary forest recovery rate might interact (Crouzeilles et al., 2021; Prieto et al., 2021). Chapter 2 finds correlations between many of the climatic, landscape, and local factors that were explored (Smith et al., 2020). The influence of some variables may overwhelm the effect of others – intense prior land use restricts carbon recovery even in high forest-cover landscapes (Fernandes Neto et al., 2019) – but others may be additive. We also have very limited research on the benefits secondary forests may provide to old-growth forest through buffering of edge effects and reduction in fragmentation. Secondary forest may be buffering as much as 41.1% of old-growth forest edges (Chapter 4). But there are many unknowns, including the age at which secondary forests become viable buffers and whether buffers facilitate recovery in the adjacent old-growth forest. In Chapter 4, introducing an age threshold of $\geq$15 years reduced edge buffering by 56%.

The governance of secondary forests is notoriously challenging yet doing so successfully is essential to ensuring that they achieve their full potential for carbon sequestration and biodiversity conservation. If we can fully understand the mechanism driving variation in secondary forest recovery, we can develop restoration strategies that achieve the greatest environmental gain from the limited space and funds that are available for restoration. This thesis demonstrates that while much of the ecological data is already available, many questions remain. Furthermore, in practice, selecting areas for restoration is fraught with additional social and economic complexities, such as land ownership, food security, and the importance of forests fallows for traditional peoples. Effective policy will also need to incorporate these social and economic variables in order to balance the needs of people and nature.

Field data is fundamental to the success of big data analysis.

Advances in big data and increasing access to high-performance computing is enabling unprecedented environmental analysis, transforming the scale at which we can study the natural world. This thesis offers a perfect example of how the rapidly changing big data landscape can transform research over a relatively short time frame. The release of the MapBiomas Brazil dataset (MapBiomas, 2019) expanded this thesis from what was initially intended to be a small-scale analysis of secondary forest dynamics, into an assessment of all secondary forests in the Brazilian Amazon (Smith et al., 2020). The subsequent release of the Amazon-wide MapBiomas collections (MapBiomas, 2021) in the following years expanded this again, enabling high-resolution, biome-wide analyses of changing forest cover for the first time (Smith et al., 2021). However, it is important to remember that in the context of this thesis, big data is a tool to amplify findings initially provided by field studies. Thus, while the expansion of the study area was facilitated by the availability of big data, many of the findings are underpinned by traditional field data and almost all the future research requirements highlighted in this thesis require studies to be conducted in the field. Therefore, although big data presents exciting new possibilities for research, collection of field data is still intrinsic to the study of ecological processes and the impact of human activity upon them.

6.3 Limitations and uncertainties

While the datasets and methods that underpin this thesis were the best available at the time of writing, there are limitations that are important to note. Here I provide an overview of the three key sources of uncertainty for my thesis as a whole – the implications of these for my findings are detailed in the relevant data chapters.

First, across all four data chapters, I have relied on the MapBiomas (2019, 2021) datasets to map changing forest cover. MapBiomas is built from the Landsat archive and is the first edge-to-edge map of annual land cover in the Amazon. Although MapBiomas is ground-breaking in its spatial and temporal resolution, it is not without limitations. As a tropical region, the Amazon has exceptionally high cloud cover for much of the year, which renders many Landsat images useless. This is particularly prevalent in the northeast of the biome, where a chronic lack of cloud-free images reduces the accuracy of the land cover classifications, as documented on the MapBiomas website. The main implication of this inaccuracy is that my estimates of secondary forest cover and secondary forest age in these areas may not truly represent historic changes in land cover.

Second, my estimates of secondary forest carbon stocks are based upon a single model for carbon sequestration from Requena Suarez et al. (2019). While the chosen model made huge advances in refining our understanding of secondary forest carbon accumulation, there are uncertainties associated with having applied it universally across all secondary forests. These uncertainties are discussed in detail in Chapter 2, but primarily arise from the huge variation in carbon accumulation estimates for

Amazonian secondary forests (Elias et al., 2020; Heinrich et al., 2021; Elias et al., 2022) and the fact that the underlying field plot network has a location bias towards regions where climatic conditions are favourable for rapid carbon accumulation (Smith et al., 2020). As such I may be over estimating carbon stocks within secondary forests and therefore their role in offsetting carbon emissions from deforestation. Future studies may improve upon this by making use of soon to be available datasets from new satellites such as the NASA GEDI mission (Hancock et al., 2019) or the European Space Agency Biomass mission (Quegan et al., 2019).

Finally, many tropical species are insufficiently documented and more still have yet to be identified. Our limited knowledge of the behaviour and ranges of Amazonian species, also limits the extent to which the value of secondary forests for biodiversity can be extrapolated across large areas. For example, estimates of habitat availability in Chapter 5, are based on expert knowledge, rather than upon empirical data on habitat preferences of individual species. With substantial declines in habitat predicted for species world-wide (Powers et al., 2019), identifying habitat loss is key to enabling targeted, knowledge-based conservation solutions. Therefore, refining our understanding of Amazonian species and the specifics of their habitat loss across different landscapes should remain a research priority.

6.4 Final remarks

In this thesis I used big data to further our understanding of changing forest cover in the Amazon, a globally important biome. I address key knowledge gaps surrounding the extent, distribution, and dynamics of secondary forest, as well as the spatial and temporal relationships between old-growth forest loss and secondary forest expansion. My findings demonstrate that secondary forests are not mitigating the impacts of forest loss and that bringing an end to deforestation remains critical for reaching net zero carbon emissions and preserving biodiversity. However, I also show that secondary forests could play an important role in future if we can increase their permanence withing the landscape and encourage further regeneration where secondary forests can act as a buffer for old-growth edges or increase connectivity between forest fragments. Two important next steps are to implement policy to maximise the benefits of existing secondary forest and to identify where to encourage regeneration in order to achieve the highest returns on investment. This thesis is testament to the advances that are possible with open-access, big datasets such as MapBiomas (2021). As new datasets become available, big data analysis will become an increasingly important tool for environmental science and we can expect exciting new research across a range of fields in the near future.

Appendix A

Supplementary material for Chapter 2

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A.1 MapBiomas

A.1.1 Background

This study makes use of land cover data produced by MapBiomas (MapBiomas, 2019), a multi-institutional initiative that used the Landsat archive to produce 30-m resolution annual land cover maps for Brazil from 1985 to 2017, applying automatic classification processes. These maps are the highest spatial and temporal resolution time series of land cover that is currently available for the Brazilian Amazon. The data are open-access and can be downloaded from Google Earth Engine using the MapBiomas Toolkit. This study uses MapBiomas version 3.1. A full description of the MapBiomas project can be found at: `http://mapbiomas.org`.

A.1.2 MapBiomas vs TerraClass

The TerraClass Project was created in 2008 to map land use and land cover within the deforested areas of the Brazilian Legal Amazon (Almeida et al., 2016). The most recent report (2014) estimates 158,072 km^2 of secondary forest, 36% more than the 116,587 km^2 found by our approach using MapBiomas data for the same year. Generally, the two maps follow the same overall spatial pattern, however, the TerraClass patches are typically much larger and just 33.8% of the pixels classified as secondary forest by our study were also marked as secondary forest by TerraClass. These disparities may largely be due to methodological differences. Although it is the same resolution as our map (30-m), by only analysing pixels within the PRODES deforestation mask (Almeida et al., 2016), TerraClass is limited to secondary forest growing in deforested areas of more than 6.25 ha, which is the minimum clearance detected by PRODES. TerraClass also records secondary forest that began growing before 1985. However, as abandoned land begins to resemble primary forest in satellite images after just a few years, it is unlikely that the visual inspection method used in TerraClass is catching much of this pre-1985 regeneration. Additionally, as largescale deforestation did not begin until the 1970s it is unlikely that there are significant amount of secondary forest lying outside our time series, with some estimating there was as little as 30,000 km^2 by 1980 (e.g. Aguiar et al., 2016) of which some would have been cleared again since then and identified by our algorithm.

A.1.3 MapBiomas Vs PRODES

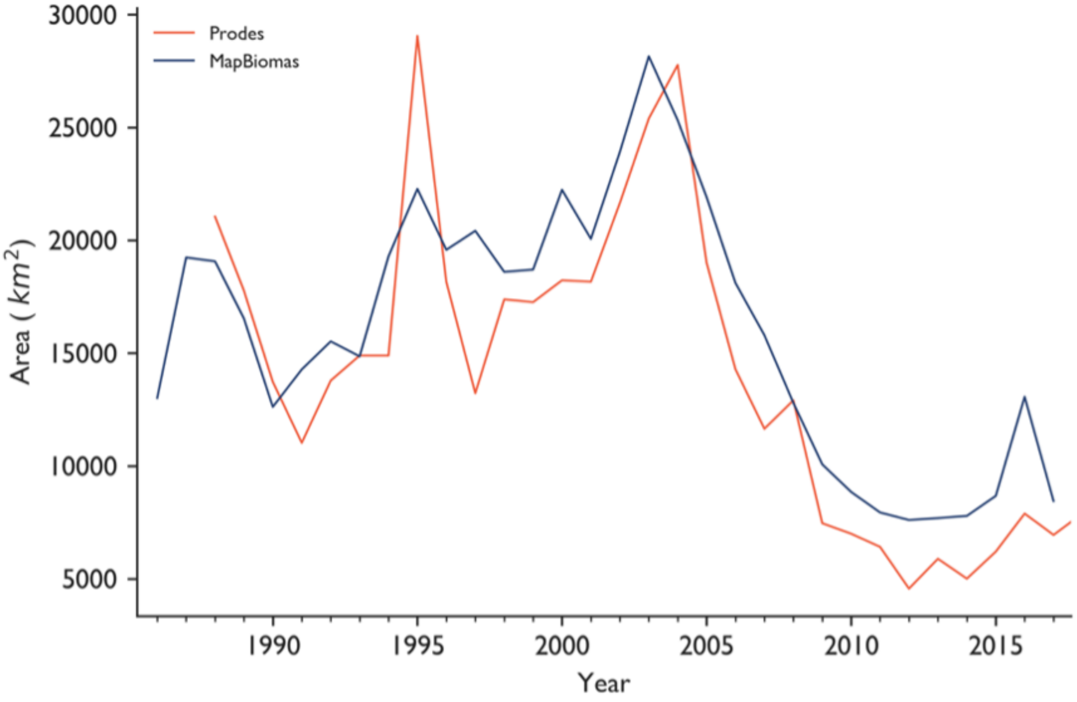


Figure A.1: Comparison of the extent of old-growth deforestation reported by PRODES and MapBiomas. The annual extent of old-growth deforestation as identified by PRODES (red) and MapBiomas (blue). Due to methodological difference, notably the size threshold for clearance (our analysis: 0.36 ha, PRODES: 6.25 ha), there are undoubtedly differences in the spatial distribution between the old-growth forest masks of the two datasets. However, the temporal trends are comparable. The deforestation mask provided by our analysis is considered to be more accurate as the clearance threshold is small enough to capture the activities of all land use change including that carried out by small landholders, who typically clear just 2 - 3 ha yr^{-1}, which is liable to be missed by the larger PRODES threshold.

A.2 Data processing

A.2.1 Water masking

Following reclassification, a temporal filter was applied to create a uniform water mask to be used across the time series. The land cover data were analysed in three-year increments such that if a pixel remained as water for a single year before returning to the previous year's land cover type, the middle year was reclassified to match the others. For example, if a pixel follows the trajectory Forest – Water – Forest it becomes Forest – Forest – Forest. MapBiomas applies similar rules during its classification process (MapBiomas, 2019). We then applied the maximum extent of water across the time series.

A.2.2 Change detection

Change detection was conducted at the pixel level to produce a comprehensive history of change for the entire Brazilian Amazon at 30-m resolution. Following reclassification, pixels were given the arbitrary value 0, 1, 4 or 9, representing water/other, cropland, pasture and old-growth forest, respectively. Transitions were calculated by subtracting the classification value of the current year from that of the same pixel in the previous year, generating a unique value for each possible transition (Table A.2).

The transition values were used to calculate the following disturbance variables for each pixel: age, time as cropland, time as pasture and number of clearance events. For the first year in the time series a standard value is assigned to each variable based on land cover type (Table A.1). These standard values assume that all forest in the first year is old-growth forest, that all non-forest pixels have only undergone one clearance event and that the land cover in each pixel is 1-year-old.

For subsequent years, the disturbance variables are calculated using the transition value of the current year and the disturbance variables from the previous year (Table A.3). MapBiomas does not separate secondary forest in its classification, thus, at this stage, secondary forest is introduced as an additional land cover class (4). Any pixel classified as 'forest' that has undergone a clearance event is marked by the algorithm as 'secondary forest'.

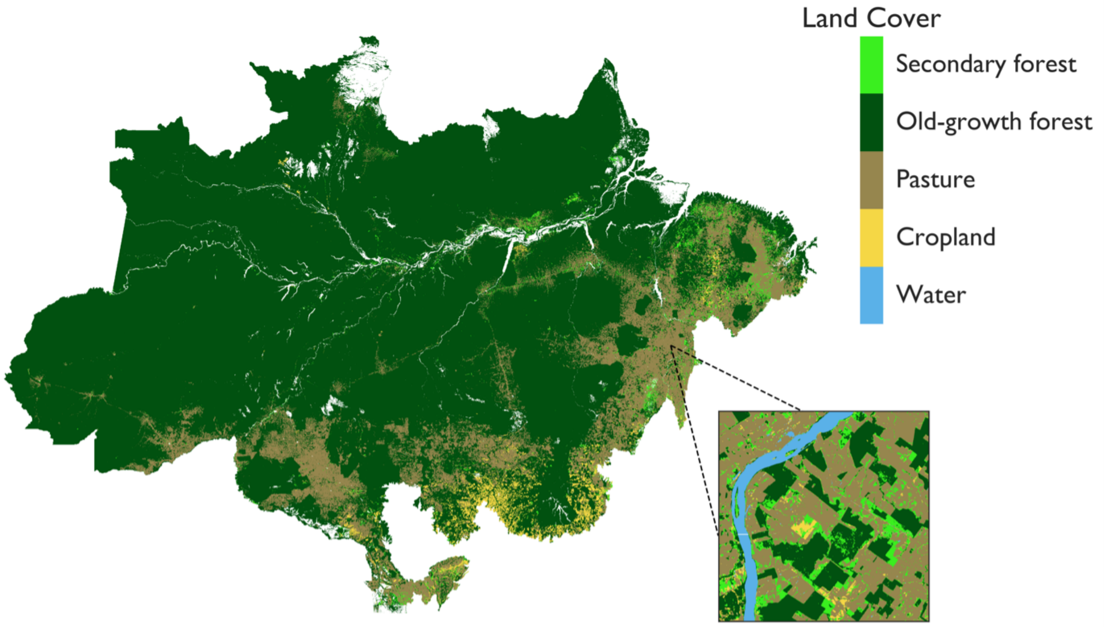


Figure A.2: Landcover in the Brazilian Amazon in 2017. A map of the extent of old-growth forest (dark green), secondary forest (light green), pasture (brown) and cropland (yellow) in the Brazilian Amazon in 2017 produced from the MapBiomas dataset. The inset demonstrates the detail available from 30-m resolution data.

Table A.1 Values assigned to pixel disturbance variables in first year of time series.

Current Classification	Land Cover	Time as Cropland	Time as Pasture	No. of Clearance Events	Age
Forest	3	*0*	*0*	*0*	0
Pasture	2	*0*	*1*	*1*	0
Cropland	1	*1*	*0*	*1*	0
Water/Other	*0*	*N/A*	*N/A*	*N/A*	*N/A*

Table A.2 Possible land cover transitions.

Transition Value	From	To
-9	Water/Other	Old-growth forest
-8	Cropland	Old-growth forest
-5	Pasture	Old-growth forest
-4	Water/Other	Pasture
-3	Cropland	Pasture
-1	Water/Other	Cropland
0	No Change	
1	Cropland	Water/Other
3	Pasture	Cropland
4	Pasture	Water/Other
5	Old-growth forest	Pasture
8	Old-growth forest	Cropland
9	Old-growth forest	Water/Other

Table A.3 Pixel disturbance variable calculations.

Transition Value	Land Cover	Time as Cropland	Time as Pasture	No. of Clearance Events	Age
-8 (C to OG)	4	*n*	*n*	*n*	1
-5 (P to OG)	4	*n*	*n*	*n*	1
-3 (C to P)	2	*n*	*n+1*	*n*	1
0 (OG to OG)	*n*	*n*	*n*	*n*	*n+1*
0 (SF to SF)	4	*n*	*n*	*n*	*n+1*
0 (C to C)	*n*	*n+1*	*n*	*n*	*n+1*
0 (P to P)	*n*	*n*	*n+1*	*n*	*n+1*
3 (P to C)	1	*n+1*	*n*	*n*	1
5 (OG to P)	2	0	1	*n+1*	1
5 (SF to P)	2	0	1	*n+1*	1
8 (OG to C)	1	1	0	*n+1*	1
8 (OG to C)	1	1	0	*n+1*	1

n = value from the previous year Transition Value: OG=Old-Growth Forest, C=Cropland, P=Pasture, SF=Secondary Forest

A.3 Representativeness of the secondary forest plot network

A.3.1 Methodology

Rainfall, rainfall seasonality and climatic water deficit have been found to be the best climatic indicators of absolute biomass recovery potential in the Neotropics (Poorter et al., 2016). Using these same measures, with mean annual rainfall and rainfall seasonality from WorldClim (variable ‘BIO12’ and ‘BIO15’, respectively; Hijmans et al., 2005) and climatic water deficit from Chave et al. (2014), we tested whether the secondary forest plot network used by Requena Suarez et al. (2019) is representative of secondary forest climatic contexts within the Brazilian Amazon. To do so, we took a random sample equal to the number of forest plots (n = 30) from each climatic variable’s distribution across all secondary forests. We then used the Wilcoxon Rank Sum test to assess the evidence that the sample and the plot network values were drawn from different distributions. We repeated this process 10,000 times and recorded the mean p value. The procedure allowed us to test whether the plot network climate was significantly different from the expected climate for a sample of cardinality equal to the number of plots.

A.3.2 Results

The Brazilian secondary forest plot network (Requena Suarez et al., 2019) is not evenly distributed, with plots concentrated in the far east and near Manaus. Climatic water deficit and annual rainfall are both more favourable for forest growth at the plot network sites than for secondary forests generally. The former are lower (plot network median: 249.0 mm yr^{-1}; secondary forest median: 375.5 mm yr^{-1}; Wilcoxon rank sum: W = 2.35, p = 0.035; Figure 2.3c) and the latter higher (plot network median: 2236 mm yr^{-1}; secondary forest median: 1945 mm yr^{-1}; Wilcoxon rank sum: W = 2.82, p = 0.019; Figure 2.3a). There is less confidence in the difference in rainfall seasonality (plot network: 60%; secondary forest: 70%; Wilcoxon rank sum: W = 2.01, p = 0.057; Figure 2.3b).

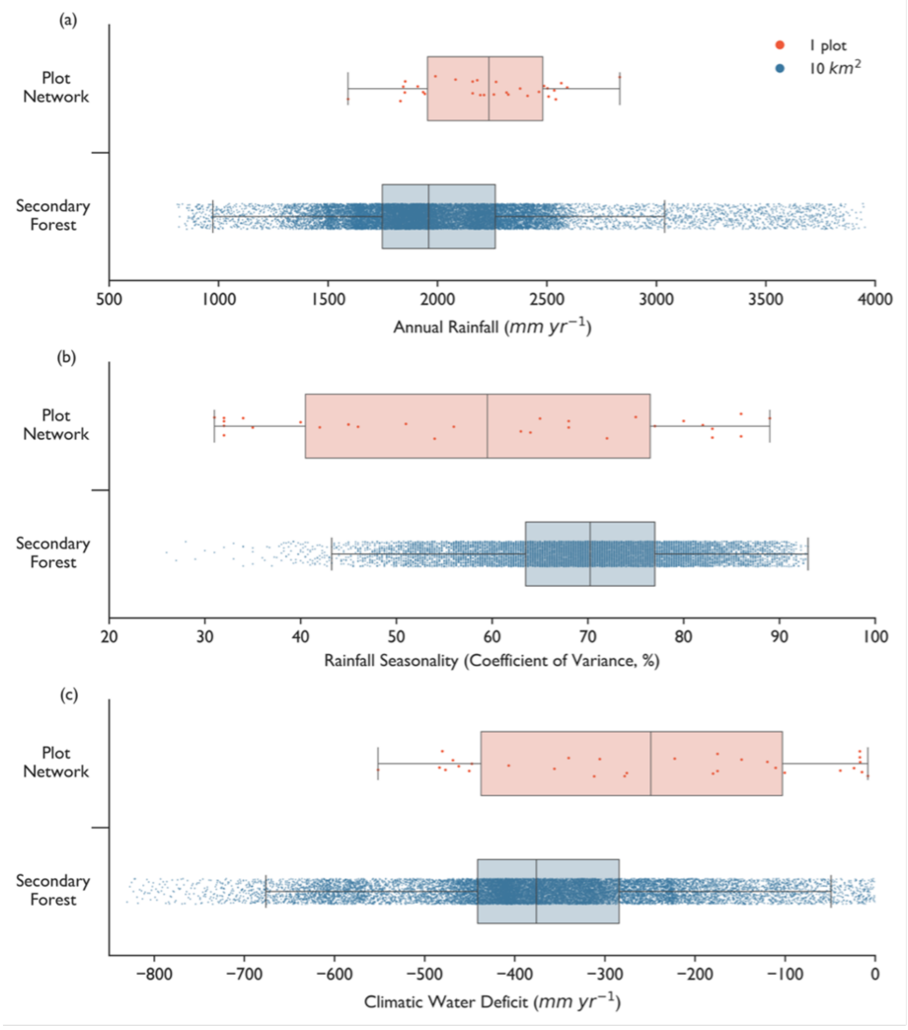


Figure A.3: Comparison of the climatic distributions of secondary forest in the Brazilian Amazon and the secondary forest plot network. The **(a)** annual rainfall (mm yr^{-1}), **(b)** rainfall seasonality (% difference in wet and dry season rainfall) and **(c)** climatic water deficit (mm yr^{-1}) of secondary forests in the Brazilian Amazon (blue) in comparison to the Brazilian plot network (red) used by Requena Suarez et al. (2019) to estimate secondary forest carbon accumulation rates. Box plots show median, quartiles and standard deviation (estimated as 1.5*Inter Quartile Range). Climatic water deficit of the plot network is significantly less than for secondary forest and annual rainfall was significantly greater ($p < 0.05$). The difference in rainfall seasonality is not significant ($p > 0.05$). Annual rainfall and rainfall seasonality were obtained from WorldClim (BIO12; BIO15) and climatic water deficit from Chave et al. (2014)

A.4 Associations between factors influencing biomass accumulation

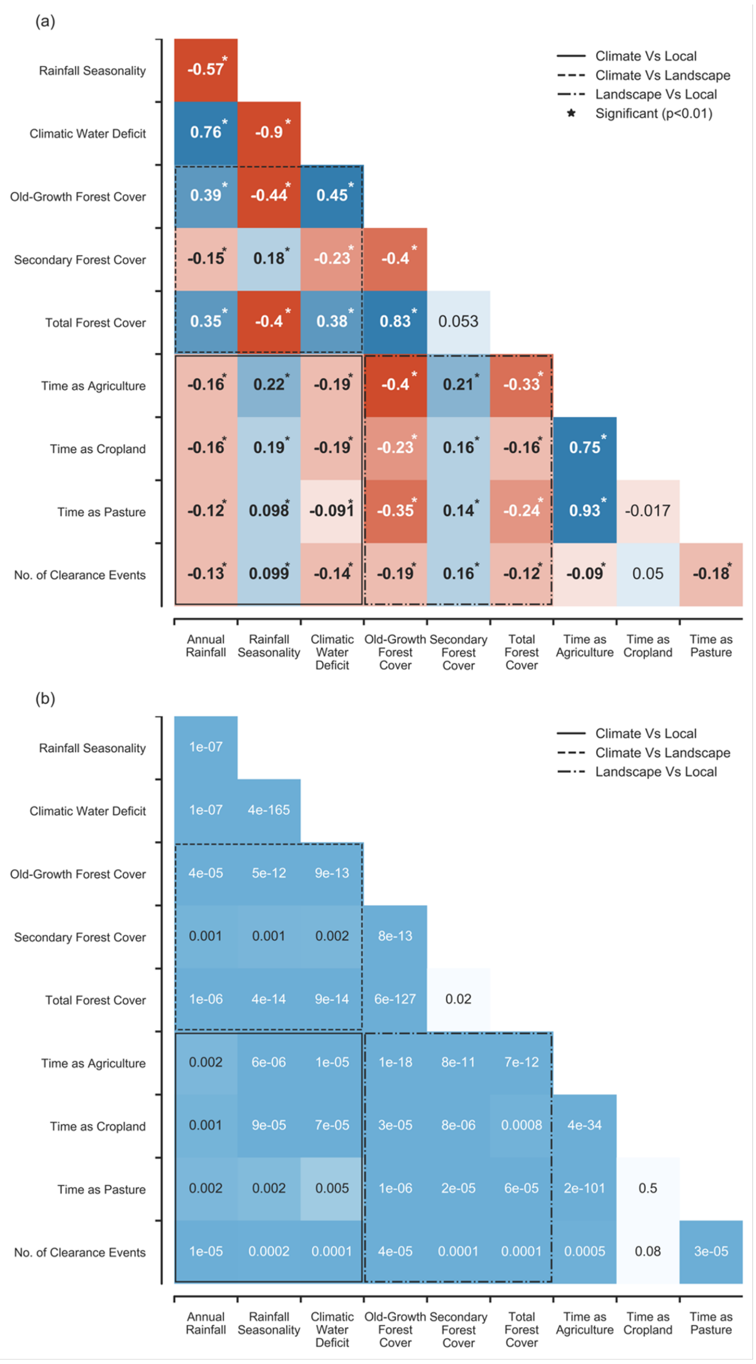
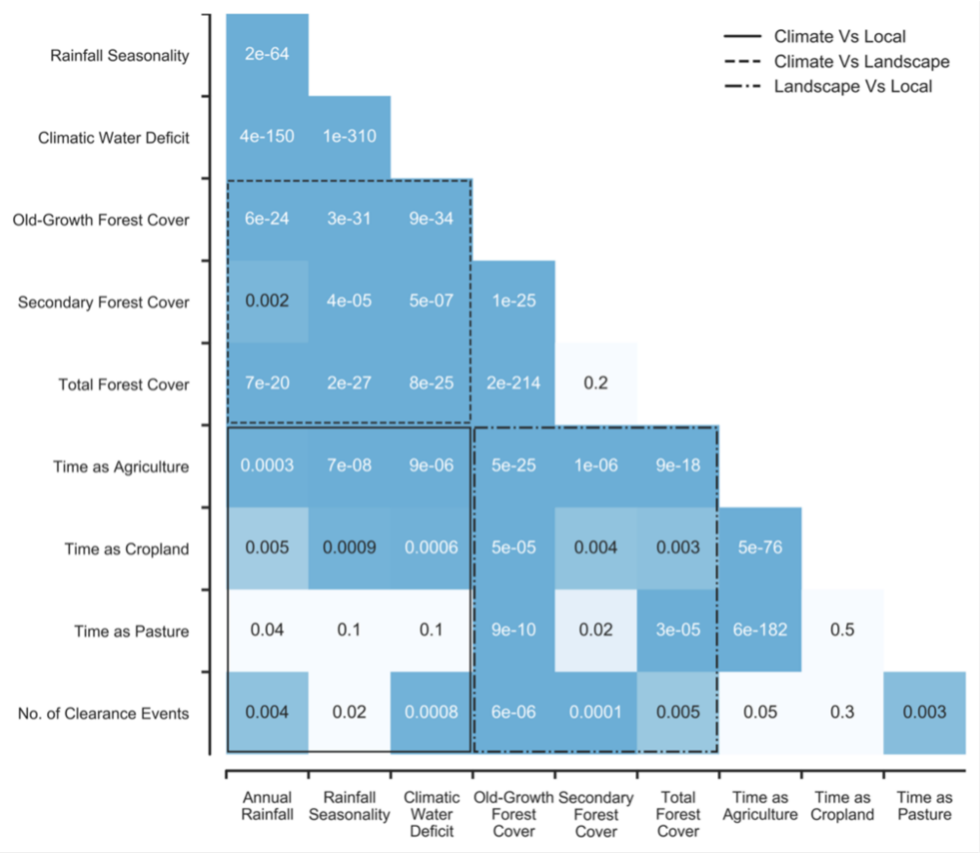


Figure A.4: Correlations between climatic, landscape and local context of secondary forest in the Brazilian Amazon in 2017. Mean correlation co efficient **(a)** and significance **(b)** of the spatial associations between the climatic, landscape and local contexts of secondary forest in the Brazilian Amazon. This was tested using 10,000 iterations of Spearman's Rank Order Correlation on samples of secondary forest pixels (n = 1000) and a significance threshold of p < 0.01 (blue). Samples were selected randomly across entire Brazilian Amazon.



	Annual Rainfall	Rainfall Seasonality	Climatic Water Deficit	Old-Growth Forest Cover	Secondary Forest Cover	Total Forest Cover	Time as Agriculture	Time as Cropland	Time as Pasture
Rainfall Seasonality	2e-64								
Climatic Water Deficit	4e-150	1e-310							
Old-Growth Forest Cover	6e-24	3e-31	9e-34						
Secondary Forest Cover	0.002	4e-05	5e-07	1e-25					
Total Forest Cover	7e-20	2e-27	8e-25	2e-214	0.2				
Time as Agriculture	0.0003	7e-08	9e-06	5e-25	1e-06	9e-18			
Time as Cropland	0.005	0.0009	0.0006	5e-05	0.004	0.003	5e-76		
Time as Pasture	0.04	0.1	0.1	9e-10	0.02	3e-05	6e-182	0.5	
No. of Clearance Events	0.004	0.02	0.0008	6e-06	0.0001	0.005	0.05	0.3	0.003

Figure A.5: Significance of correlations between climatic, landscape and local context of secondary forest in the Brazilian Amazon in 2017. Mean significance of the spatial associations between the climatic, landscape and local contexts of secondary forest in the Brazilian Amazon. This was tested using 10,000 iterations of Spearman's Rank Order Correlation on samples of secondary forest pixels (n = 1000) and a significance threshold of $p < 0.01$ (blue). Samples were elected such that 25% of points were situated in each quadrant of the Amazon biome.

A.5 Emissions from deforestation and secondary forest clearance

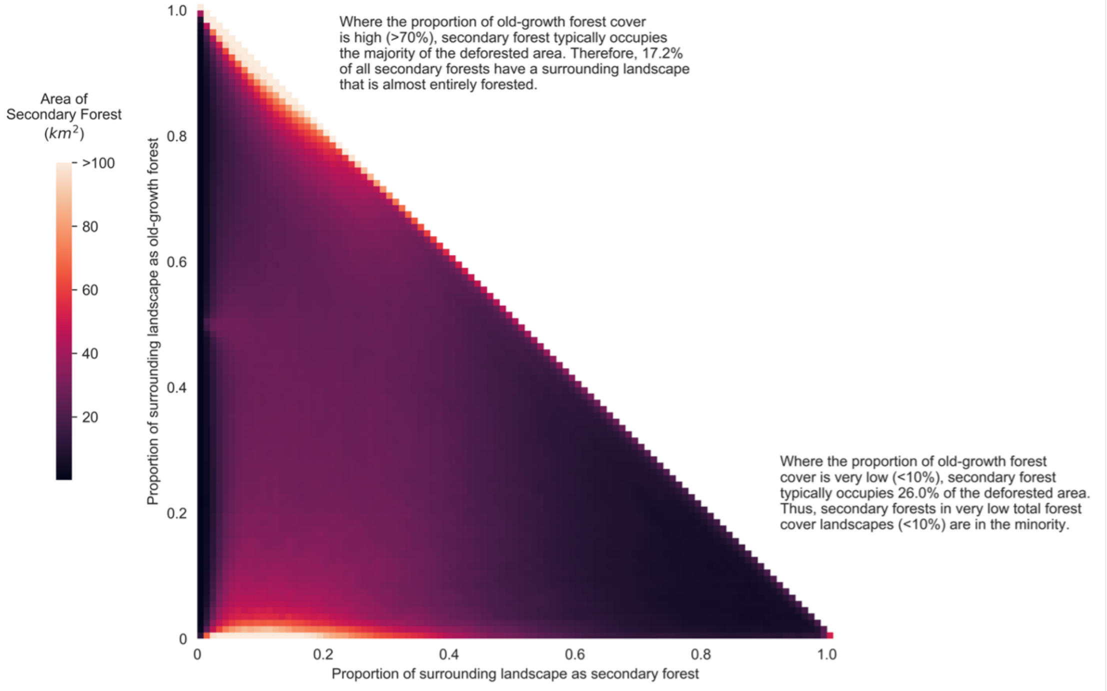
When we assumed all above-ground carbon was emitted in the year of deforestation, we estimate that old-growth clearance resulted in a gross carbon loss of 3.71 billion Mg C, emitting the equivalent of 13.63 billion Mg CO_2, with approximately 8.79% of these emissions offset by secondary forest growth. Gross loss of carbon from secondary forest clearance with this same assumption is 0.25±0.04 billion Mg C, equivalent to 0.91±0.14 billion Mg CO_2 (mean±95% CI).

A.6 Factors influencing secondary forest carbon sequestration

Table A.4 Sample size analysis for secondary forest and entire Brazilian Amazon climate comparison.

Climatic Variable	n	W	p-value
Climatic Water Deficit	100	-16.712762	4.97E-43
Climatic Water Deficit	1000	-16.693106	4.98E-45
Climatic Water Deficit	10000	-16.695283	2.64E-42
Climatic Water Deficit	500	-16.693944	3.37E-46
Climatic Water Deficit	5000	-16.711775	7.10E-45
Rainfall Seasonality	100	20.2465559	1.48E-70
Rainfall Seasonality	1000	20.2495723	4.49E-69
Rainfall Seasonality	10000	20.2487432	7.96E-72
Rainfall Seasonality	500	20.2462727	1.80E-69
Rainfall Seasonality	5000	20.2559599	4.42E-70
Annual Rainfall	100	-14.504375	2.33E-32
Annual Rainfall	1000	-14.472156	3.54E-31
Annual Rainfall	10000	-14.493542	8.66E-32
Annual Rainfall	500	-14.465979	1.24E-33
Annual Rainfall	5000	-14.482788	1.59E-31

n = sample size; W = Wilcoxon Rank-Sum test statistic



Where the proportion of old-growth forest cover is high (>70%), secondary forest typically occupies the majority of the deforested area. Therefore, 17.2% of all secondary forests have a surrounding landscape that is almost entirely forested.

Where the proportion of old-growth forest cover is very low (<10%), secondary forest typically occupies 26.0% of the deforested area. Thus, secondary forests in very low total forest cover landscapes (<10%) are in the minority.

Figure A.6: Landscape configuration of secondary forest in the Brazilian Amazon. The proportion of the landscape (1 km radius) surrounding secondary forest pixels (900 m^2) that is occupied by old-growth and secondary forest. Lighter colour represents a greater area of secondary forest with a given landscape configuration.

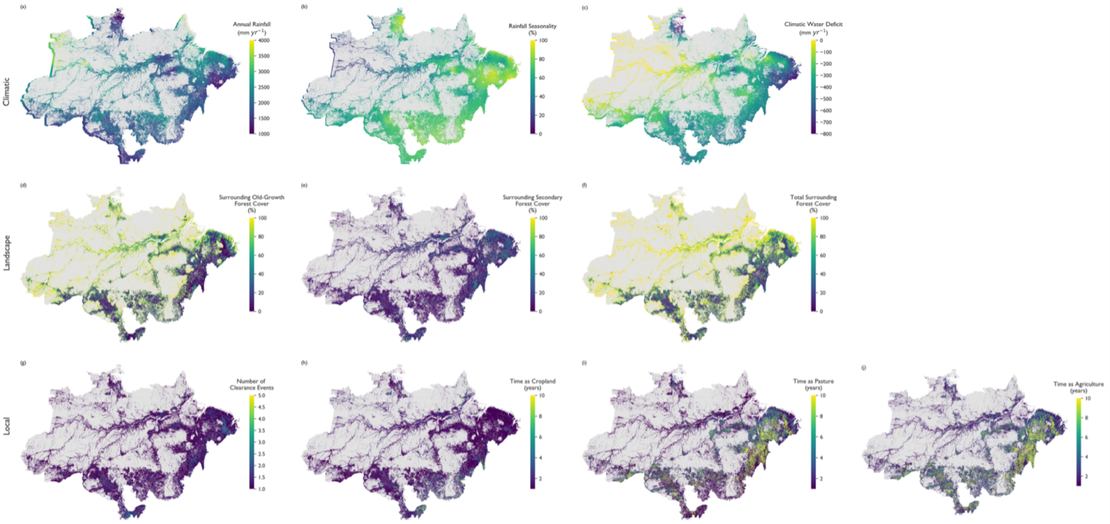


Figure A.7: Climatic, landscape and local contexts of secondary forest in the Brazilian Amazon in 2017. Maps of secondary forest in relation to **(a, b, c)** climatic, **(d, e, f)** landscape and **(g, h, i, j)** local factors known to influence carbon accumulation rate. Maps show the median value for secondary forest pixels (0.009 km^2) in a 1 km^2 grid of the Amazon biome. Climatic: **(a)** annual rainfall, **(b)** rainfall seasonality and **(c)** climatic water deficit. Landscape: proportion of the land cover within 1 km^2 of a secondary forest pixel as **(d)** old-growth forest, **(e)** secondary forest and **(f)** total forest. Local: **(g)** the number of clearance cycles, the number of years a secondary forest pixel spent as **(h)** cropland or **(i)** pasture prior to abandonment, and **(j)** the total time in use prior to abandonment.

Appendix B

Supplementary material for Chapter 3

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B.1 Old growth deforestation emissions

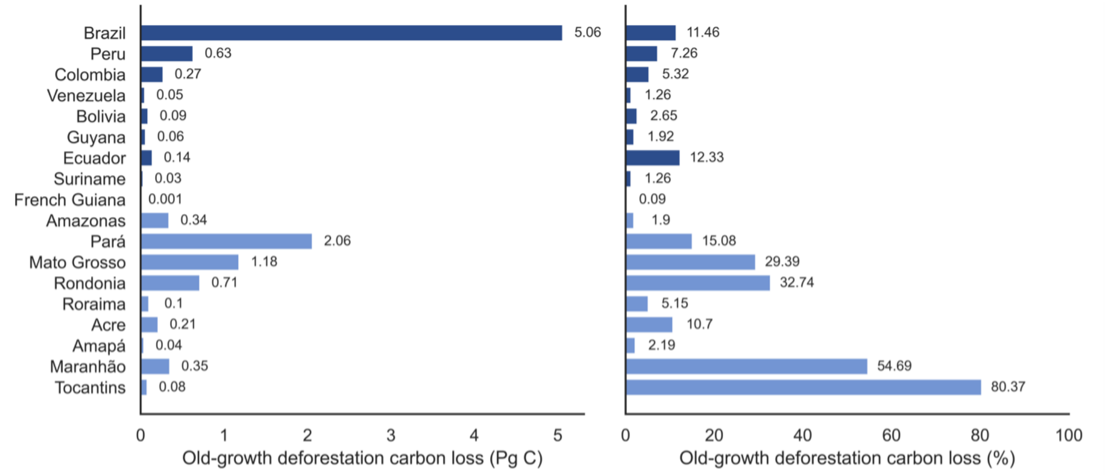

Figure B.1: Carbon loss from old-growth deforestation in Amazonian countries and Brazilian States in Amazonian countries and Brazilian states in 2017. The **(a)** carbon lost from old-growth deforestation and **(b)** the proportion of original old-growth forest carbon stock lost to deforestation for Amazonian countries (dark) and Brazilian states (light) in 2017. Countries and states are ordered by the area of the Amazon they contain.

B.2 Secondary forest age and residence time

B.2.1 Secondary forest age

The age distribution of secondary forest in the majority of Amazon countries is highly skewed towards young forests (Figure B.3). Bolivia, Guyana and Suriname are the exceptions. Bolivia shows a largely bimodal distribution, with fewer mid-age forests than either young or old. While Guyana and Suriname, both exhibit a skew towards old forests and large spikes in 31-year-old and 18 to 22-year-old secondary forests respectively. While all Brazilian states show a skew toward younger secondary forest, Acre, Amapa and Tocantins all exhibit similar large spikes in 16-year-old secondary forest (Figure B.4). Kruskal-Wallis tests indicated significant differences in the distribution of secondary forest age between countries and states (Kruskal–Wallis Chi square = 174.4, P < 0.01, df = 16), but post-hoc Dunn's test reveal that Guyana and Suriname are the only political units with significantly different age distributions

(Figure B.5). The anomalous distributions of Guyana, Suriname and the three Brazilian States are likely due to these regions having persistently limited cloud-free Landsat image cover over much of the time series (see MapBiomas data availability

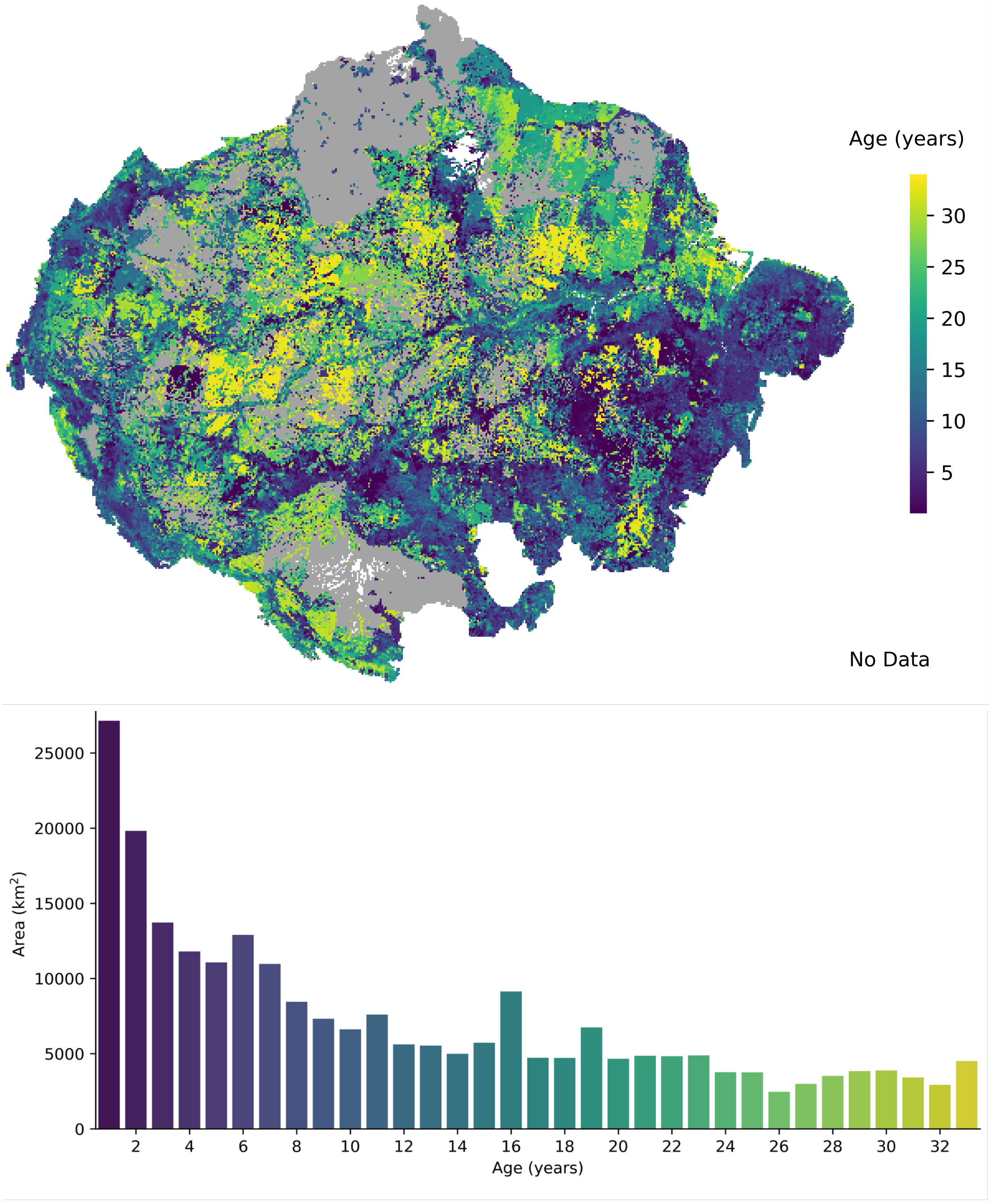

Figure B.2: Secondary forest age in the Amazon Biome. (a) Spatial variation in median secondary forest age across the Amazon, plotted on an ~60 km^2 grid. Cells which have experienced no deforestation are shown in grey and those where < 1% of the cell is capable of supporting forest are omitted. **(b)** The distribution in secondary forest age for all secondary forest in the Amazon.

layer).

B.2.2 Secondary forest residency time

Across the Amazon, the majority (70.03%) of secondary forest cleared since 1997 was 5 years old or less at clearance and the median residency time was just 2 years. This skew towards the clearance of young forests is seen in every Amazonian country, with median residency time ranging from 2 years in Brazil and French Guiana, to 5 years in Ecuador and Suriname. While Kruskal-Wallis tests indicated significant differences in the distribution of secondary forest age between countries and states (Kruskal–Wallis Chi square = 48.2, $P < 0.01$, df = 16), post-hoc Dunn's test reveal that there are no significant differences between political units (Figure B.5).

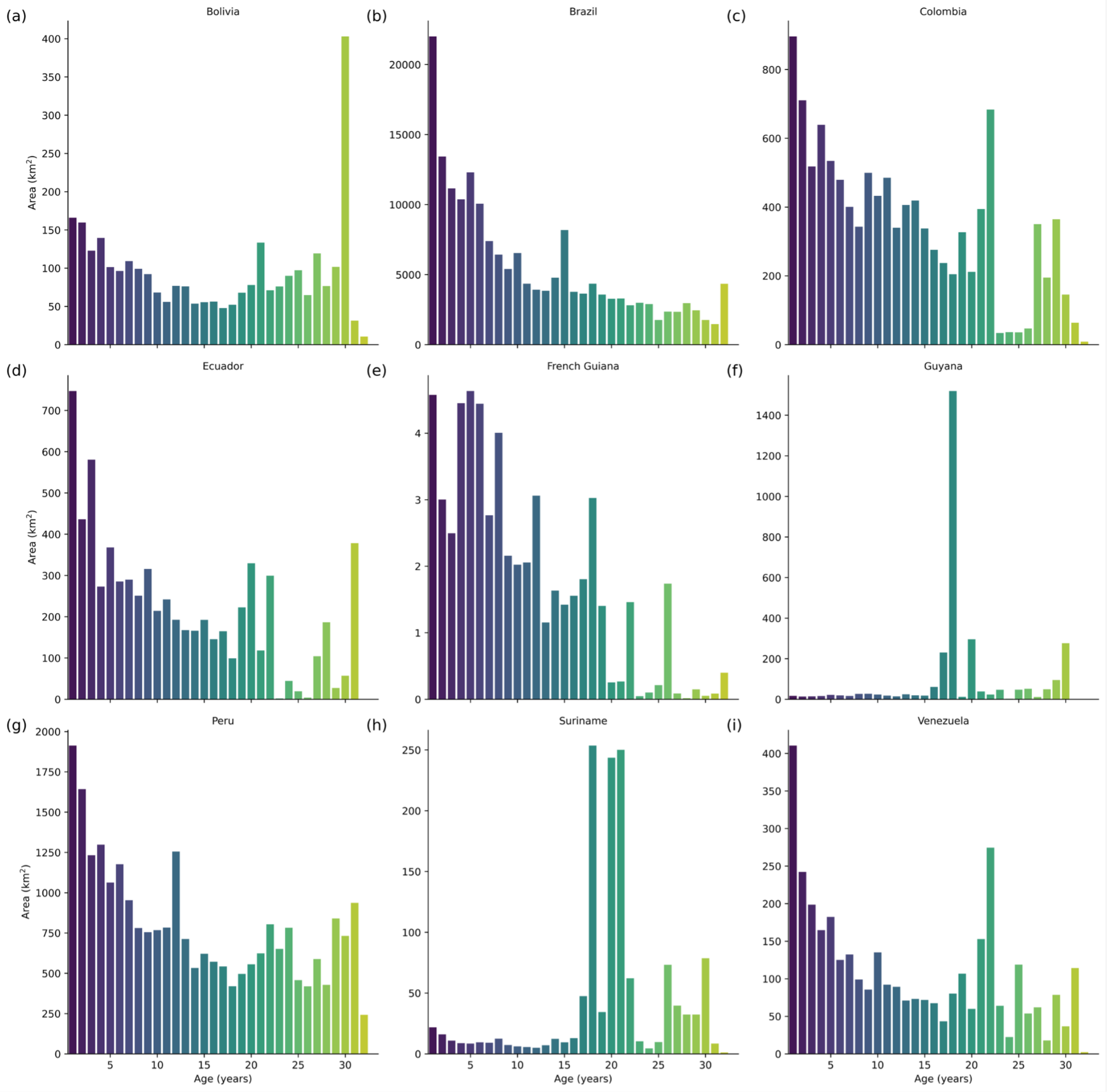

Figure B.3: The age distribution of secondary forest in Amazonian countries. The distribution of secondary forest age in **(a)** Bolivia, **(b)** Brazil, **(c)** Colombia, **(d)** Ecuador, **(e)** French Guiana, **(f)** Guyana, **(g)** Peru, **(h)** Suriname and **(i)** Venezuela

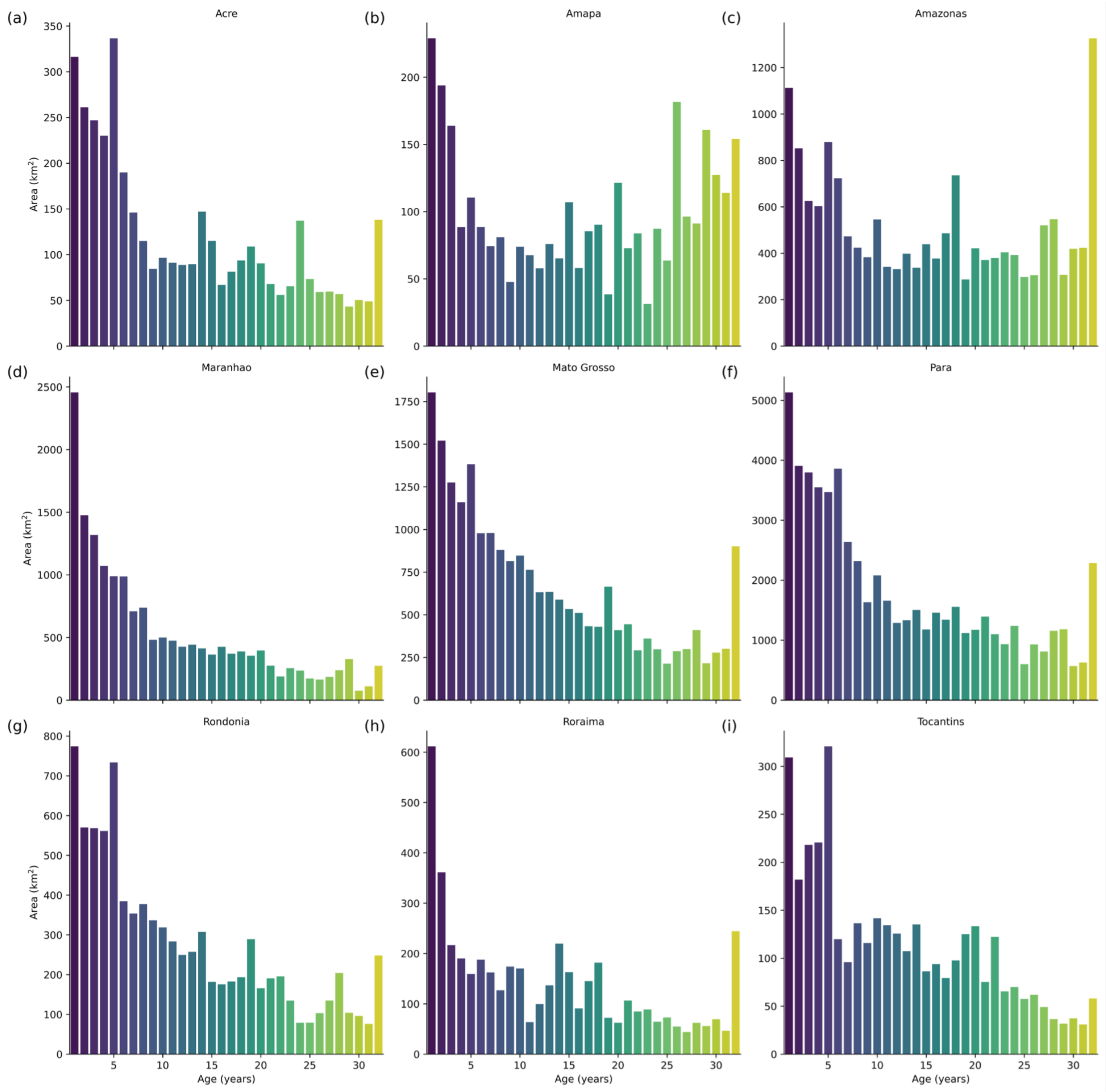

Figure B.4: The age distribution of secondary forest in Brazilian States. The distribution of secondary forest age in **(a)** Acre, **(b)** Amapa, **(c)** Amazonas, **(d)** Maranhao, **(e)** Mato Grosso, **(f)** Para, **(g)** Rondonia, **(h)** Roraima and **(i)** Tocantins

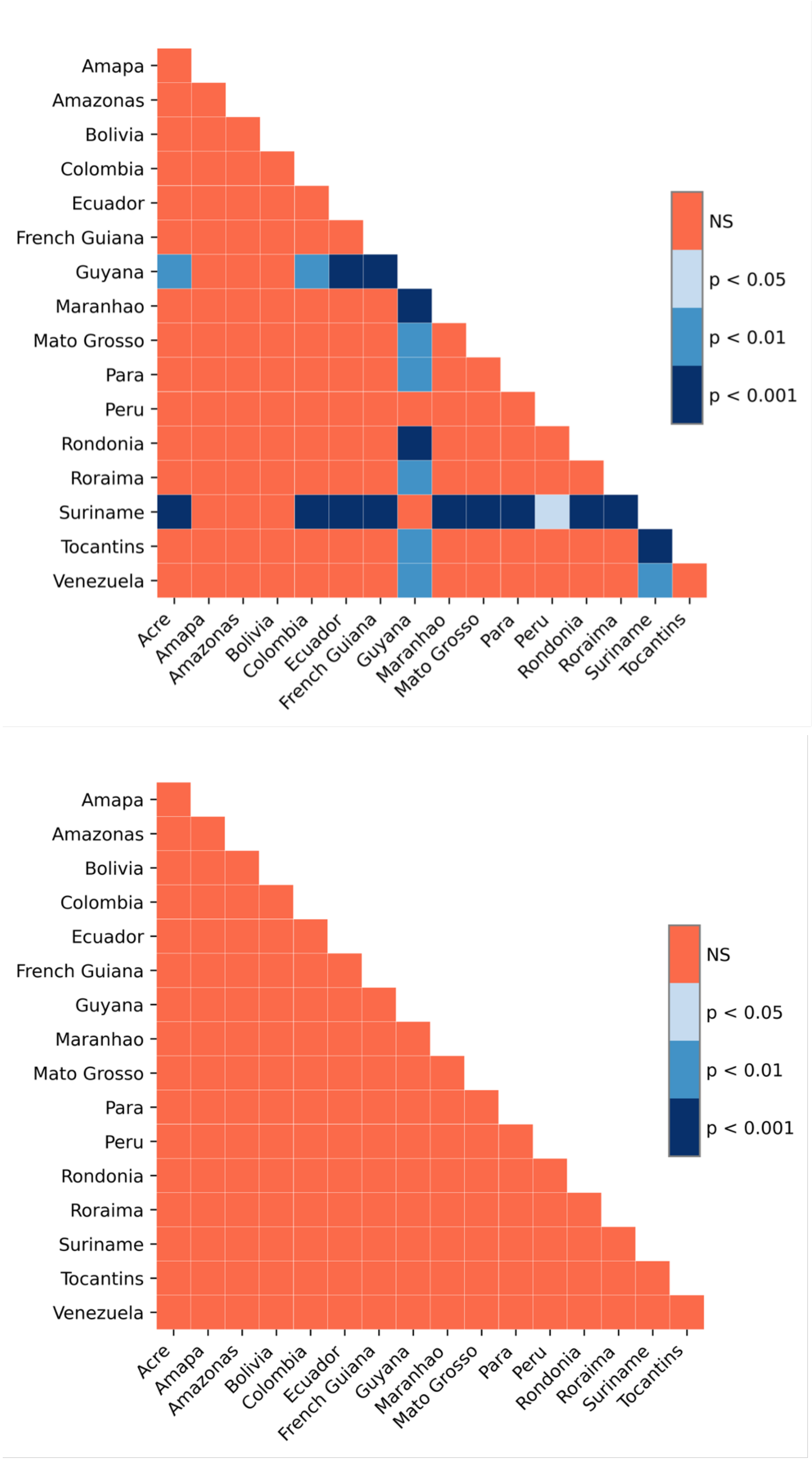

Figure B.5: Differences in secondary forest age and residence time across political units in the Amazon. The significance of post-hoc Dunn's test for differences in **(a)** secondary forest age and **(b)** secondary forest residence time between Amazonian countries and Brazilian states.

B.3 Temporal trends in deforestation and recovery

Table B.1 Best-fit models (ΔAICc ≤ 2; in bold) for the temporal trends in changes in old-growth and secondary forest cover in the Amazon biome.

	M$_i$	**AICc**	**Δ_iAICc**	**W$_i$**	***P***
Area of old-growth deforestation	**NON-LINEAR (2)**	**116.77**	**0.00**	**0.98**	**–**
	LINEAR	126.94	10.17	0.01	0.99
	NON-LINEAR (3)	127.92	11.15	0.00	1.00
	NON-LINEAR (1)	130.03	13.26	0.00	1.00
	NULL	146.27	29.50	0.00	1.00
Area of secondary forest deforestation	**LINEAR**	**80.53**	**0.00**	**0.45**	**–**
	NON-LINEAR (1)	84.81	4.28	0.05	0.89
	NULL	85.62	5.08	0.04	0.93
	NON-LINEAR (2)	91.49	10.95	0.00	1.00
	NON-LINEAR (3)*	–	–	–	–
Area of new secondary forest	**NULL**	**98.28**	**0.00**	**0.38**	**–**
	LINEAR	98.72	0.45	0.30	0.56
	NON-LINEAR (1)	104.66	6.38	0.02	0.96
	NON-LINEAR (2)	112.70	14.42	0.00	1.00
	NON-LINEAR (3)	118.75	20.47	0.00	1.00
Net change in secondary forest area	**NULL**	**107.80**	**0.00**	**0.64**	**–**
	LINEAR	110.43	2.64	0.17	0.79
	NON-LINEAR (1)	115.90	8.10	0.01	0.98
	NON-LINEAR (2)	123.81	16.02	0.00	1.00
	NON-LINEAR (3)	133.18	25.39	0.00	1.00
Net change in forest cover	**LINEAR**	**137.24**	**0.00**	**0.22**	**–**
	NON-LINEAR (2)	135.51	-1.73	0.52	0.30
	NON-LINEAR (1)	140.33	3.09	0.05	0.82
	NON-LINEAR (3)	146.14	8.90	0.00	0.99
	NULL	149.67	12.43	0.00	1.00

M$_i$ = model; Δ_i (AIC) = [AIC$_i$ – min(AIC)]; W$_i$ = the rounded Akaike weights
P = the normalised probability that the best-fit model is preferred to M$_i$
$*$ = did not converge

Table B.2 Best-fit models (ΔAICc ≤ 2; in bold) for the temporal trends in changes in old-growth and secondary forest emissions in the Amazon biome.

	M$_i$	**AICc**	**Δ_iAICc**	**W$_i$**	***P***
Old-growth deforestation emissions	**NON-LINEAR (2)**	**256.15**	**0.00**	**0.73**	**–**
	NON-LINEAR (1)	260.03	3.87	0.11	0.87
	LINEAR	260.53	4.38	0.08	0.90
	NON-LINEAR (3)	264.01	7.86	0.01	0.98
	NULL	268.82	12.67	0.00	1.00
Secondary forest deforestation emissions	**NON-LINEAR (2)**	**125.02**	**0.00**	**0.81**	**–**
	NON-LINEAR (1)	127.95	2.93	0.19	0.81
	LINEAR	156.02	31.00	0.00	1.00
	NULL	180.61	55.59	0.00	1.00
	NON-LINEAR (3)*	–	–	–	–
Secondary forest carbon accumulation	**LINEAR**	**166.68**	**0.00**	**0.33**	**0.50**
	NON-LINEAR (1)	171.89	5.21	0.02	0.93
	NULL	204.44	37.75	0.00	1.00
	NON-LINEAR (2)*	–	–	–	–
	NON-LINEAR (3)*	–	–	–	–
Net secondary forest emissions	**LINEAR**	**164.29**	**0.00**	**0.26**	**–**
	NON-LINEAR (1)	164.80	0.51	0.20	0.56
	NON-LINEAR (2)	173.25	8.96	0.00	0.99
	NULL	180.76	16.47	0.00	1.00
	NON-LINEAR (3)*	–	–	–	–
Net emissions from changes in forest cover	**NON-LINEAR (2)**	**256.11**	**0.00**	**0.77**	**–**
	LINEAR	260.20	4.09	0.10	0.89
	NON-LINEAR (1)	260.64	4.53	0.08	0.91
	NON-LINEAR (3)	263.28	7.17	0.02	0.97
	NULL	271.23	15.12	0.00	1.00

M$_i$ = model; Δ_i (AIC) = [AIC$_i$ – min(AIC)]; W$_i$ = the rounded Akaike weights
P = the normalised probability that the best-fit model is preferred to M$_i$
$*$ = did not converge

B.4 Data processing

We opted to use the MapBiomas dataset over other alternatives due to its high-resolution (30 m), longer temporal series (1985–2018) and extensive validation process (MapBiomas, 2021) (MapBiomas, 2020). The geographic limit of MapBiomas Amazonía is defined by Red Amazónica de Información Socioambiental

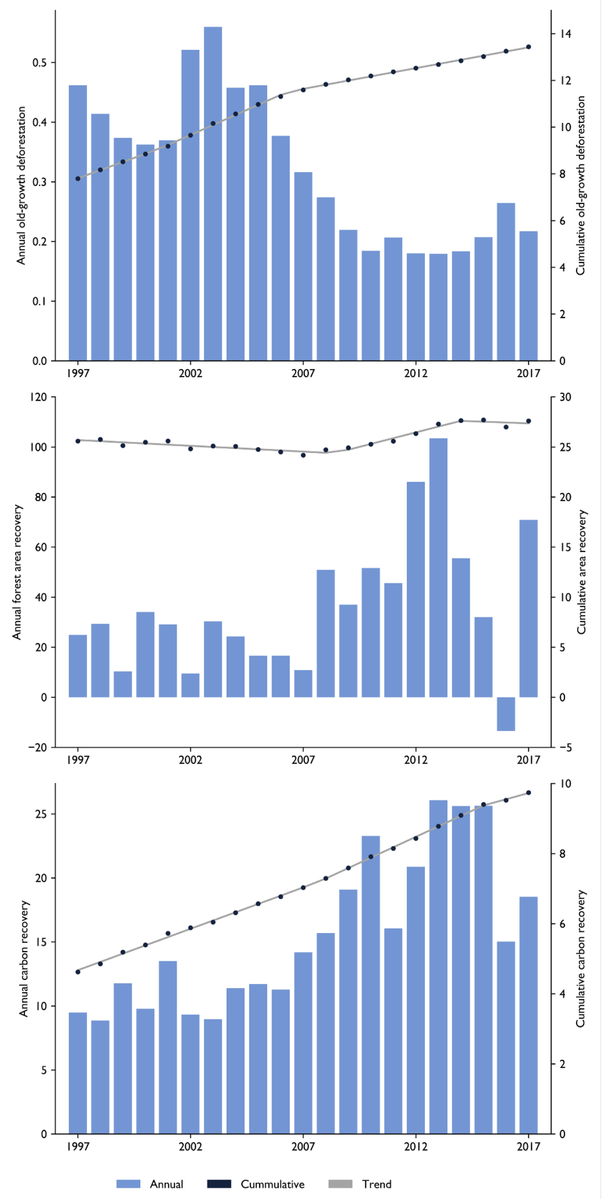

Figure B.6: Temporal trends in old-growth deforestation and secondary forest recovery. (a) Deforestation measured as the percentage of remaining old-growth forest cleared annually (bars) and the percentage of original old-growth forest cleared (points). The temporal trend in cumulative deforestation (line) is well-described by a broken-stick regression with two segments. **(b)** Forest area recovery measured as the percentage of the area deforested each year offset by the net change in secondary forest extent that year (bars) and the percentage of the total deforested area offset by the total secondary forest extent (points). The temporal trend in forest area recovery (line) is well-described by a broken-stick regression with three segments. **(c)** Carbon recovery measured as the percentage of annual old-growth deforestation emissions offset by the net carbon balance of secondary forest that year (bars) and the percentage of cumulative old-growth deforestation emissions offset by the total accumulated carbon for all secondary forest (points). The temporal trend in cumulative carbon recovery (line) is well-described by a broken-stick regression with two segments.

Table B.3 Best-fit models ($\triangle$AICc $\leq$ 2; in bold) for the relationship between deforestation and recovery across Amazonian countries.

	M$_i$	**AICc**	**Δ_iAICc**	**W$_i$**	***P***
Forest Area	**LINEAR**	**143.69**	**0.00**	**0.38**	**–**
	NON-LINEAR (1)	144.95	1.27	0.20	0.65
	NULL	148.85	5.16	0.03	0.93
	NON-LINEAR (2)	154.90	11.22	0.00	1.00
Carbon Emissions	**NON-LINEAR (1)**	**104.02**	**0.00**	**0.96**	**–**
	LINEAR	111.22	7.21	0.03	0.97
	NON-LINEAR (2)	113.09	9.08	0.01	0.99
	NULL	116.15	12.14	0.00	1.00

M$_i$ = model; Δ_i (AIC) = [AIC$_i$ – min(AIC)]; W$_i$ = the rounded Akaike weights
P = the normalised probability that the best-fit model is preferred to M$_i$
$*$ = did not converge

Table B.4 Best-fit models ($\triangle$AICc $\leq$ 2; in bold) for the relationship between deforestation and recovery across the Amazon biome.

	M$_i$	**AICc**	**Δ_iAICc**	**W$_i$**	***P***
Forest Area	**NON-LINEAR (2)**	**704100**	**0.00**	**1.00**	**–**
	NON-LINEAR (1)	704591	490.21	0.00	1.00
	LINEAR	711351	7250.95	0.00	1.00
	NULL	753395	49294.99	0.00	1.00
Carbon Emissions	**NON-LINEAR (2)**	**638038**	**0.00**	**1.00**	**–**
	NON-LINEAR (1)	638313	274.24	0.00	1.00
	LINEAR	641272	3233.39	0.00	1.00
	NULL	657814	19775.82	0.00	1.00

M$_i$ = model; Δ_i (AIC) = [AIC$_i$ – min(AIC)]; W$_i$ = the rounded Akaike weights
P = the normalised probability that the best-fit model is preferred to M$_i$
$*$ = did not converge

Georreferenciada (RAISG) and incorporates six biomes (Amazonia, Andes, Cerrado, Chaco-Chiquitano, Panantal, Tucumano-Boliviano). For this study we use the RAISG defined ‘Amazonia’ biome. This dataset is freely available to download: https://amazonia.mapbiomas.ord/downloads/. We conduct our analysis for 2017 as the MapBiomas filtering method means the land cover classification is likely to be more accurate than for 2018. We simplify the MapBiomas schema by reclassifying it into four broader classes: forest, pasture, cropland and other (Table B.5).

Table B.5 Reclassification of MapBiomas schema.

MapBiomas ID	MapBiomas Classification	Reclassification
1	1. Forest	Old-growth Forest
2	1.1. Natural Forest	Old-growth Forest
3	1.1.1. Forest Formation	Old-growth Forest
4	1.1.2. Open Forest	Old-growth Forest
5	1.1.3. Mangrove	Old-growth Forest
6	1.1.4 Flooded Forest	Old-growth Forest
9	1.2. Forest Plantation	Cropland
10	2. Non-Forest Natural Formation	Other/Water
11	2.1. Wetland	Other/Water
12	2.2. Grassland Formation	Other/Water
13	2.4. Other Non-Forest Natural Formation	Other/Water
14	3. Agriculture	Cropland
15	3.1. Pasture	Pasture
16	3.1.1 Pasture in Natural Fields	Pasture
17	3.1.2 Other Pastures	Pasture
18	3.2. Agriculture	Cropland
19	3.2.1 Annual Perennial Use	Cropland
20	3.2.1 Semi-Perennial Use	Cropland
28	3.2.3 Mixed Crop	Cropland
21	3.3. Mosaic of Agriculture and Pasture	Cropland
22	4. Non-Vegetated Area	Other/Water
23	4.1. Beach and Dune	Other/Water
24	4.2. Urban Infrastructure	Other/Water
29	4.3. Rocky Outcrop	Other/Water
30	4.4. Mining	Other/Water
25	4.5. Other Non-Vegetated Area	Other/Water
26	5. Water	Other/Water
33	5.1. River, Lake and Ocean	Other/Water
31	5.2. Aquaculture	Other/Water
34	5.3 Glacier	Other/Water
27	6. Non-Observed	NA

B.4.1 Water masking

Following reclassification, a temporal filter was applied to create a uniform water mask to be used across the time series. The land cover data were analysed in three-year increments such that if a pixel remained as water for a single year before returning to the previous year's land cover type, the middle year was reclassified to match the others. For example, if a pixel follows the trajectory Forest – Water – Forest it becomes Forest – Forest – Forest. MapBiomas applies similar rules during its classification process. We then applied the maximum extent of water across the time series.

B.4.2 Change detection

Change detection was conducted at the pixel level to produce a comprehensive history of change for the entire Amazon Biome at 30-m resolution. Following reclassification, pixels were given the arbitrary value 0, 1, 4 or 9, representing water/other, cropland, pasture and old-growth forest, respectively. Transitions were calculated by subtracting the classification value of the current year from that of the same pixel in the previous year, generating a unique value for each possible transition (Table B.6). MapBiomas does not separate secondary forest in its classification, thus, at this stage, secondary forest is introduced as an additional land cover class. Any pixel which transitions from 'non-forest' to 'forest' is marked by the algorithm as secondary forest. For the first year in the time series, we assuming all forest is old-growth forest.

B.5 Highly deforested landscapes in 1997

Table B.6 Possible land cover transitions.

Transition Value	From	To
-9	Water/Other	Old-growth forest
-8	Cropland	Old-growth forest
-5	Pasture	Old-growth forest
-4	Water/Other	Pasture
-3	Cropland	Pasture
-1	Water/Other	Cropland
0	No Change	
1	Cropland	Water/Other
3	Pasture	Cropland
4	Pasture	Water/Other
5	Old-growth forest	Pasture
8	Old-growth forest	Cropland
9	Old-growth forest	Water/Other

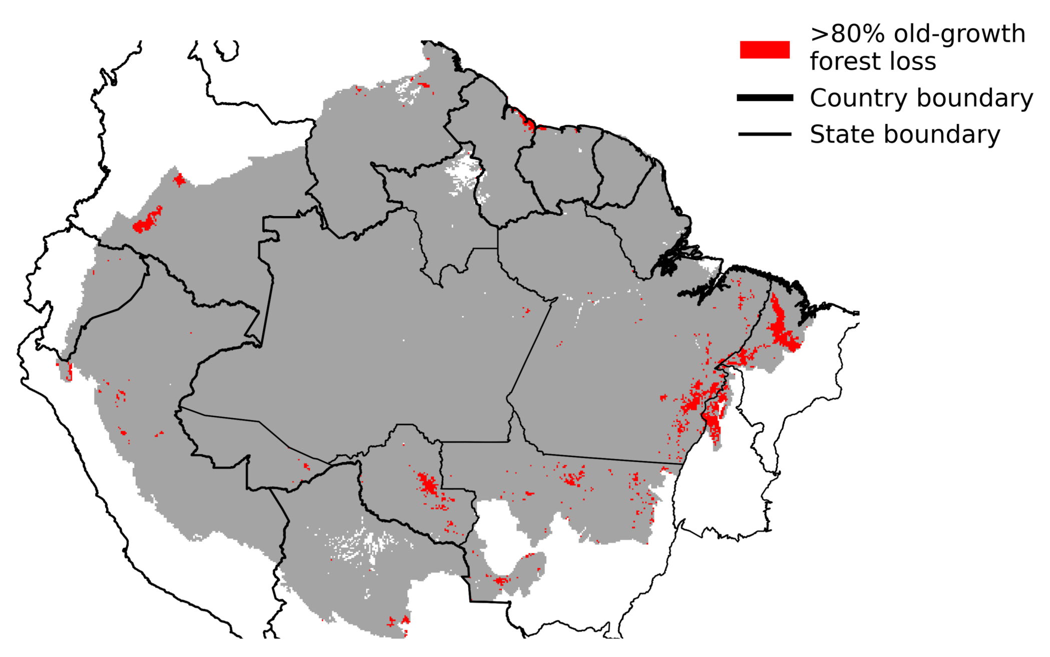

Figure B.7: Highly deforested landscapes in the Amazon biome in 1997. The Amazon biome gridded at ~60 km^2. Cells with $\geq$ 80% old-growth deforestation in 1997 are shown in red. The Amazon biome is shown in grey.

Appendix C

Supplementary material for Chapter 5

Charlotte C. Smith[1] , John R. Healey[2] , Alexander C. Lees[3] , Jack D. Shutt[3] , Oliver C. Metcalf[3] , Raquel Carvalho[4] , Angelica F. Resende[5] , Ben Taylor[6] , Paul J. Young[1,7,8] , Joice Ferreira[4] , Jos Barlow[1]

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Author contributions
Conceptualization: CCS, JB, JRH; Data curation: CCS, JDS, RC, AFR; Formal Analysis: CCS; Methodology: CCS, JB, JRH, ACL, OCM, JDS, BT; Resources & Software: CCS; Supervision: JB, JRH, PJY; Visualization: CCS; Writing: CCS, JB, JRH; Editing: All authors

Article in preparation for submission to Nature Ecology and Evolution.

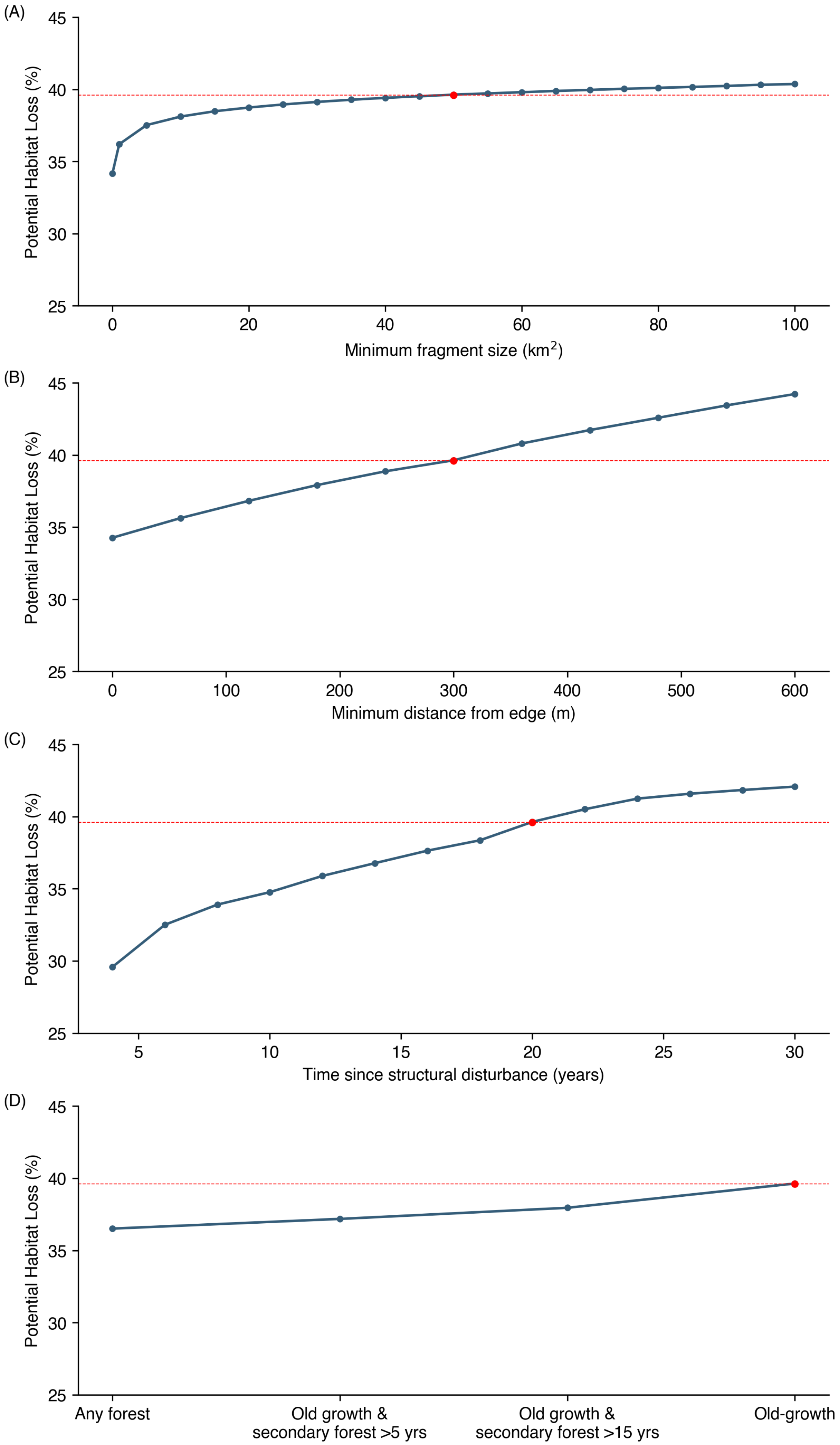

Figure C.1: Sensitivity of estimated habitat extent to forest condition parameters. The percentage of habitat loss for the most disturbance-sensitive response group (selected parameters shows in red) when varying requirements for the **(a)** minimum habitat fragment size, **(b)** minimum distance from edge, **(c)**

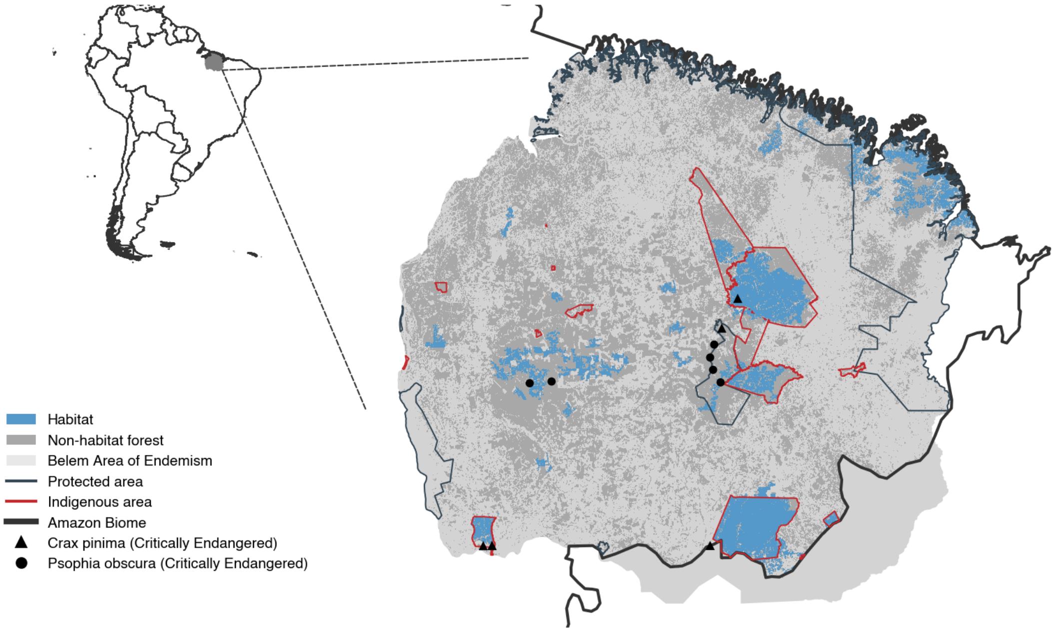

Figure C.2: Locations of recent sightings of two highly threatened bird species in the Belém Area of Endemism in relation to estimated habitat for the most disturbance-sensitive response group. The recorded locations of two Critically Endangered species – *Crax pinima* (triangle) and *Psophia obscura* (circle) – in relation to forest cover meeting the requirements of our most disturbance-sensitive response group. Locations of bird sighting were extracted from eBird (Sullivan et al., 2014) and Alteff et al. (2019). To protect these critically endangered species, the precise sighting locations are obscured. eBird sightings are georeferenced to the start points of submitted checklists, and as such are only approximate indicators of the location of the sighting.

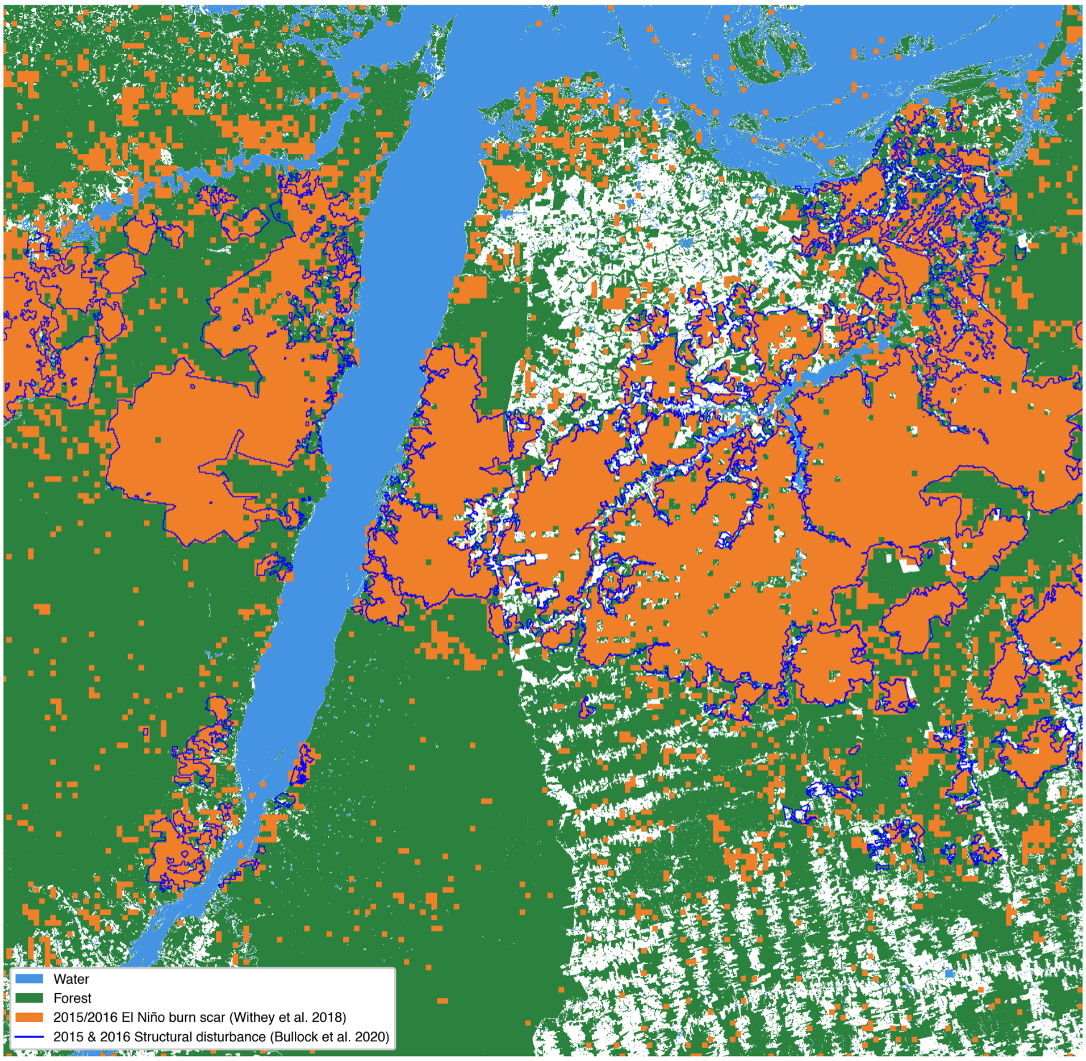

Figure C.3: Comparison of mapped structural disturbance and burn scars in the Santarém region. The Bullock et al. (2020) map of structural disturbance occurring in 2015 and 2016 (orange) is very effective at capturing the well-studied 2015/2016 El Niño burn scar (blue) in the Santarém region of Para, Brazil. Burn scar data from Withey et al. (2018).

Appendix D

Associated publications

Assessing the growth and climate sensitivity of secondary forests in highly deforested Amazonian landscapes

Authors

Elias F., Ferreira J., Lennox G.D., Berenguer E.B., Ferreira S., Schwartz G., de Oliveira Melo L., Reis Junior D.N., Nascimento R.O., Nascimento Ferreira F., Espírito-Santo F.D.B., **Smith C.C.,** Barlow J.

Abstract

Tropical forests hold 30% of Earth's terrestrial carbon and at least 60% of its terrestrial biodiversity, but forest loss and degradation are jeopardizing these ecosystems. Although the regrowth of secondary forests has the potential to offset some of the losses of carbon and biodiversity, it remains unclear if secondary regeneration will be affected by climate changes such as higher temperatures and more frequent extreme droughts. We used a data set of 10 repeated forest inventories spanning two decades (1999–2017) to investigate carbon and tree species recovery and how climate and landscape context influence carbon dynamics in an older secondary forest located in one of the oldest post-Columbian agricultural frontiers in the Brazilian Amazon. Carbon accumulation averaged 1.08 Mg ha^{-1} yr^{-1}, and species richness was effectively constant over the studied period. Moreover, we provide evidence that secondary forests are vulnerable to drought stress: Carbon balance and growth rates were lower in drier periods. This contrasts with drought responses in primary forests, where changes in carbon dynamics are driven by increased stem mortality. These results highlight an important climate change–vegetation feedback, whereby the increasing dry-season lengths being observed across parts of Amazonia may reduce the effectiveness of secondary forests in sequestering carbon and mitigating climate change. In addition, the current rate of forest regrowth in this region was low compared with previous pan-tropical and Amazonian assessments—our secondary forests reached just 41.1% of the average carbon and 56% of the tree diversity in the nearest primary forests—suggesting that these areas are unlikely to return to their original levels on politically meaningful time scales.

Tracking the impacts of El Niño drought and fire in human-modified Amazonian forests.

Authors

Berenguer E.B., Lennox G.D., Ferreira J., Malhi Y., Aragão L.E.O.C., Rodrigues Barreto J., Espírito-Santo F.D.B., Figueiredo A.E.S., França F., Gardner T.A., Joly C.A., Palmeira A.F., Quesada C.A., Rossi L.C., Marina Moraes de Seixas M., **Smith C.C.,** Withey K., Barlow J.

Abstract

With humanity facing an unprecedented climate crisis, the conservation of tropical forests has never been so important – their vast terrestrial carbon stocks can be turned into emissions by climatic and human disturbances. However, the duration of these effects is poorly understood, and it is unclear whether impacts are amplified in forests with a history of previous human disturbance. Here, we focus on the Amazonian epicenter of the 2015–16 El Niño, a region that encompasses 1.2% of the Brazilian Amazon. We quantify, at high temporal resolution, the impacts of an extreme El Niño (EN) drought and extensive forest fires on plant mortality and carbon loss in undisturbed and human-modified forests. Mortality remained higher than pre-El Niño levels for 36 mo in EN-drought–affected forests and for 30 mo in EN-fire–affected forests. In EN-fire–affected forests, human disturbance significantly increased plant mortality. Our investigation of the ecological and physiological predictors of tree mortality showed that trees with lower wood density, bark thickness and leaf nitrogen content, as well as those that experienced greater fire intensity, were more vulnerable. Across the region, the 2015–16 El Niño led to the death of an estimated 2.5 ± 0.3 billion stems, resulting in emissions of 495 ± 94 Tg CO2. Three years after the El Niño, plant growth and recruitment had offset only 37% of emissions. Our results show that limiting forest disturbance will not only help maintain carbon stocks, but will also maximize the resistance of Amazonian forests if fires do occur.

Drivers and Ecological Impacts of Deforestation and Forest Degradation.

Authors

Berenguer E.B., Armenteras D., Alencar A., Almeida C., Aragão L., Barlow J., Bilbao B., Brando P., Bynoe P., Fearnside P., Finer M., Flores B.M., Jenkins C.N., Silva Junior C.H.L, Lees A.C., **Smith C.C.,** Souza C., García-Villacorta R.

Abstract

Deforestation, the complete removal of an area's forest cover; and forest degradation, the significant loss of forest structure, functions, and processes; are the result of the interaction between various direct drivers, often operating in tandem. By 2018, the Amazon biome had lost approximately 870,000 km^2 of its original forest cover, mainly due to agricultural expansion. Other direct drivers of forest loss include the opening of new roads, construction of hydroelectric dams, exploitation of minerals and oil, and urbanization. Impacts of deforestation range from local to global, including local changes in landscape configuration, climate, and biodiversity; regional impacts on hydrological cycles; and global increase of greenhouse gas emissions. Of the remaining Amazonian forests, 17% are degraded, corresponding to approximately 1,036,080 km^2. Various anthropogenic drivers, including understory fires, edge effects, selective logging, hunting, and climate change can cause forest degradation. Degraded forests have significantly different structure, microclimate, and biodiversity as compared to undisturbed ones. These forests tend to have higher tree mortality, lower carbon stocks, more canopy gaps, higher temperatures, lower humidity, higher wind exposure, and exhibit compositional and functional shifts in both fauna and flora. Degraded forests can come to resemble their undisturbed counterparts, but this depends on the type, duration, intensity, and frequency of the disturbance event. In some cases, this may prohibit the return to a historic baseline. Avoiding further loss and degradation of Amazonian forests is crucial to ensure they continue to provide valuable and life-supporting ecosystem services.

Comparing contemporary and lifetime rates of carbon accumulation from secondary forests in the eastern Amazon.

Authors

Elias, F., Ferreira J., Resende A.F., Berenguer, E.B., França F., **Smith C.C.,** Schwartz G., Nascimento R.O., Guedes M., Rossi L.C., Seixas M.M.M., Silva C.M., Barlow J.

Abstract

Secondary forests (SFs) growing on cleared land could be a low-cost climate change mitigation strategy due to their potential to sequester CO_2. However, given widespread changes in climate and land-use in the Amazon in the past 20 years, it is not clear whether current rates of carbon uptake by SFs reflect estimates based on dividing the carbon stock by the estimated age of the forest. Differences between methodological approaches could lead to important discrepancies in estimates of carbon accumulation. Furthermore, we know little about how carbon uptake rates of secondary forests vary across some of the most deforested regions of the Amazon, where reforestation actions are most needed. Here, we compare the rates of carbon accumulation estimated over the lifetime of a stand (by stand age) with the contemporary rates estimated by recensus data, based on 28 permanent SFs plots distributed across four regions. Then, we compare how carbon uptakes rates vary across regions and how they compare to previous studies. The average rates of contemporary (1.23±0.57 Mg C ha^{-1} yr^{-1}) and lifetime (1.14±0.63 Mg C ha^{-1} yr^{-1}) carbon accumulation were strongly correlated (r=0.78) and similar between regions. Overall, our carbon accumulation rates were much lower than other estimates of Amazonian SFs, which suggests that regions with the greatest opportunities for large-scale implementation of SFs have some of the slowest rates of carbon accumulation. Contrary to predictions from chronosequence analysis, the lack of difference between lifetime and contemporary rates of carbon accumulation suggests forests are maintaining a consistent rate of growth in the first decades after abandonment. These results, combined with the high rates of ongoing environmental change, highlight the importance of continuing to monitor the rate of carbon accumulation in secondary forests. This is necessary to support the implementation and monitoring of large-scale passive restoration in the highly-deforested Amazon.

Linking land-use and land-cover transitions to their ecological impact on tropical forest ecosystems.

Authors

Nunes C.A., Berenguer E.B., França F., Ferreira J., Lees A.C., Louzada J., Sayer, E.J., Solar R.R.C., **Smith C.C.,** Aragão L., Braga D.D.L., Camargo P.B., Cerri Junior C.E.P., Oliveira Junior R.C., Durigan M., Moura N., Oliveira V.H.F., Ribas C., Vaz-de-Mello F., Vieira I., Zanetti R., Barlow J.

Abstract

Human activities pose a major threat to tropical forest biodiversity and ecosystem services. Although the impacts of deforestation are well studied, multiple land-use and land-cover transitions (LUCTs) occur in tropical landscapes, and we do not know how LUCTs differ in their rates or impacts on key ecosystem components. Here, we quantified the impacts of 18 LUCTs on three ecosystem components (biodiversity, carbon, soil), based on 18 variables collected from 310 sites in the Brazilian Amazon. Across all LUCTs, biodiversity was the most affected ecosystem component, followed by carbon stocks, but the magnitude of change differed widely among LUCTs and individual variables. Forest clearance for pasture was the most prevalent and high-impact transition, but we also identified other LUCTs with high impact but lower prevalence (e.g., forest to agriculture). Our study demonstrates the importance of considering multiple ecosystem components and LUCTs to understand the consequences of human activities in tropical landscapes.

Improving our understanding of fire impacts on tropical forest biodiversity

Authors

Barlow J., Berenguer, E.B., Carvalho N.S., França, F., Lees A.C., Metcalf, O.C., Shutt, J., **Smith, C.C.**

Abstract

Deforestation and human disturbances, such as forest fires, threaten Amazonian biodiversity. Efforts to understand their impacts at scale are important, but remain challenging. Nonetheless, we are concerned that some of the approaches of Feng et al. 2021 (the authors, hereafter) confuse instead of clarify fire impacts. To improve future analysis, we outline six key limitations and considerations.

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