

Title

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

Authors

Charlotte C. Smith¹

Fernando Del Bon Espírito-Santo²

John R. Healey³

Paul J. Young^{1,4}

Gareth D. Lennox¹

Joice Ferreira⁵

Jos Barlow^{1,6}

Institutions

1. Lancaster Environment Centre, Lancaster University, UK

2. Leicester Institute of Space and Earth Observation, Centre for Landscape and Climate Research, School of Geography, Geology and Environment, University of Leicester, University Road, Leicester LE1 7RH, UK

3. School of Natural Sciences, College of Environmental Sciences and Engineering, Bangor University, Bangor, LL57 2DG, UK

4. Centre of Excellence for Environmental Data Science, Lancaster University, UK

5. Embrapa Amazônia Oriental, Trav. Eneas Pinheiro, S/N, Marco, CP 48, Belém, 66017-970, Brazil

6. Federal University of Lavras, Minas Gerais, 37200-000, Brazil

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 MapBiomass 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 km² of secondary forest in the Brazilian Amazon stored 0.33±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.

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, Asner and Field, 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 km² to 4,571 km²), 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 km² of forest by 2030 and is supported by the New York Declaration on Forests (2014) and by the UN Decade of 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 km² 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.*, 2019). 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, Elliott and Lichstein, 2016; Chazdon *et al.*, 2016). Locally, secondary forests growing on abandoned pasture accumulate carbon more slowly than on abandoned cropland (Fearnside and Guimarães, 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 MapBiomass 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?

Methods

Assessing secondary forests and deforestation

We used MapBiomass 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 MapBiomass 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 MapBiomass is also comparable to that of PRODES (2020; Figure S1).

Secondary forest extent

Our study focused on the Brazilian Amazon, a 4.27 million km² 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 - 2017 using the MapBiomass 3.1 land cover dataset and a change-detection algorithm (Supporting Information). We initially reclassified the MapBiomass schema into four classes:

old-growth forest, cropland, pasture, and other (Table 1; Figure S2). 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.

Table 1: Reclassification of MapBiomass schema

MapBiomass ID	MapBiomass 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

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 km² 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 interannual variability.

Above-ground biomass in secondary forest

Requena Suarez et al. (2019) estimate biomass accumulation rates for young (≤ 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 ($\sim 91.8\%$), tropical moist forest ($\sim 7.8\%$) and tropical montane forest ($\sim 0.2\%$). For these ecozones, Requena Suarez et al. (2019) estimate above-ground biomass accumulation rates (mean \pm 95% CI) of, respectively, 5.9 ± 0.8 Mg ha⁻¹ yr⁻¹, 4.4 ± 1.3 Mg ha⁻¹ yr⁻¹ and 5.2 ± 1 Mg ha⁻¹ yr⁻¹ for young secondary forest, and 2.3 ± 0.3 Mg ha⁻¹ yr⁻¹, 1.8 ± 0.8 Mg ha⁻¹ yr⁻¹ and 2.7 ± 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).

Deforestation emissions

Using the change in old-growth forest extent captured by our analysis of MapBiomass, 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 km² 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 MapBiomass 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 Van 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 also 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).

174 **Factors mediating secondary forest recovery**

175 Climatic

176 Rainfall, rainfall seasonality and climatic water deficit have been found to be the best climatic indicators of absolute
177 biomass recovery potential in the Neotropics (Poorter et al., 2016). Using these same measures, with mean annual
178 rainfall and rainfall seasonality from WorldClim (variable 'BIO12' and 'BIO15', respectively; Hijmans *et al.*, 2005) and
179 climatic water deficit from Chave *et al.* (2014), we compared the climate of secondary forests with that of the whole
180 Brazilian Amazon. This allowed us to determine if secondary forests are situated in climatic contexts relatively more or
181 less favourable for biomass recovery than the biome average. To do so, we randomly sampled the distribution of each
182 climate indicator for both secondary forest and the whole Brazilian Amazon, then used the Wilcoxon Rank Sum test to
183 assess whether the samples were drawn from different distributions. We repeated this process 10,000 times and
184 recorded the mean p-value. We undertook these analyses with a variety of sample sizes. However, results were
185 insensitive to sample size (Table S5), and we report results for $n = 1000$.

186

187 Variation in local climate is known to influence carbon sequestration in secondary forest (Elias *et al.*, 2019). However,
188 accounting for it involves a number of spatial and temporal issues. For example, local climate is altered drastically by
189 deforestation (e.g. Spracklen et al., 2018; Spracklen and Garcia-Carreras, 2015), and accounting for this would require
190 climate data to be updated in near real-time. Moreover, there are no large-scale assessments of the sensitivity of
191 secondary forests to these changes.

192

193 Landscape

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

198

199 Local

200 For the period 1985 - 2017, the change-detection algorithm records total clearance events as the number of times a
201 pixel transitions from 'forest' to 'non-forest'. Our two measures of prior agricultural land use (time as cropland and
202 time as pasture) were recorded as the number of years spent as cropland or pasture between the most recent
203 clearance event and the pixel returning to 'forest'.

204

205 **Associations between factors influencing biomass accumulation**

206 Using Spearman's Rank-Order Correlation and a sample of secondary forest pixels ($n = 1000$), we tested the association
207 between each of the climatic, landscape and local variables. To enhance the dispersal of selected pixels across the
208 Brazilian Amazon, we used stratified sampling with replacement such that 25% of pixels were situated in each quadrant
209 of the Amazon biome, while within-quadrant selection was random. We repeated this process 10,000 times, recording
210 the mean correlation coefficient. Results were similar from a spatially unconstrained selection process (Figure S4).
211 Given the large number of repeated tests ($n = 10^4$) and the relatively large sample size ($n = 1000$), we used a more
212 conservative significance threshold of 0.01 for this analysis.

Results

Secondary forest extent and age

We find a near-continuous expansion in the extent of secondary forest from 1985 onwards (Figure 2a), resulting in a total of 129,361 km² of secondary forest in the Brazilian Amazon in 2017. When averaged across the time series, the yearly increase in secondary forest extent was $8.61 \pm 10.96\%$ (mean \pm 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 km². 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 1a). Our results show that in 2017, 111,023 km² (85.8%) of secondary forests were less than 20 years old, with a median age of seven years. Very young secondary forests (≤ 5 years old) accounted for 42.08% (Figure 1c). From 1995, these very young forests consistently represent almost half of total secondary forest extent ($48.0 \pm 4.5\%$).

Old-growth deforestation emissions offset by secondary forest growth

Old-growth deforestation emissions: Between 1985 and 2017, MapBiomas detects the clearance of 512,473 km² 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 CO₂ (Figure 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 CO₂ (mean \pm 95% CI; Figure 1d) and more than a quarter (26.9%) of the total carbon stock was stored in forests ≤ 10 years old. Gross secondary forest carbon sequestration increased considerably over the time series, from 10.38 ± 1.6 million Mg CO₂ in 1986 to 66.12 ± 9.7 million Mg CO₂ in 2017 (mean \pm 95% CI; Figure 2b). The accumulation of carbon in secondary forests was slowed by clearance, with an average $6,410 \pm 2007$ km² of secondary forest cleared annually (Figure 2a). Of all the secondary forest mapped during our time series, 60.6% (198,688 km²) 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 CO₂ in emissions (mean \pm 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 \pm 95% CI).

Deforestation emissions offset: Our findings show that between 1985 and 2017, approximately 9.37% (1.20 ± 0.18 billion Mg CO₂, mean \pm 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 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, $10.29 \pm 6.8\%$ 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.

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 3a), and where there is greater rainfall seasonality (secondary forest: 70%, Brazilian Amazon: 57%, Figure 3b) and a greater climatic water deficit (secondary forest: -375.5 mm yr⁻¹, Brazilian Amazon: -259 mm yr⁻¹ Figure 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 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 S6). Therefore, 17.2% of all secondary forests had a surrounding landscape that was almost entirely forested ($\geq 95\%$ total forest cover; Figure 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 4a; Figure 4c). 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 S6). Thus, secondary forests in landscapes with $< 10\%$ total forest cover are in the minority (2.4%; Figure 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.

Local

Across all secondary forests present in 2017, the median time spent as agriculture (cropland and pasture) prior to abandonment was 4 years (Figure 4b). The majority of secondary forest (85.4 %, 110,522 km²) had experienced just one type of agricultural use, with median usage times of 2 years for cropland (39.2%, 50,692 km²) and 5 years for pasture (46.3%, 59,830 km²; Figure 4d). For the portion of secondary forests that had experienced multiple use types (14.6%, 18,838 km²), 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 4f). However, much had been subjected to more than one clearance event during the time series (33.2%, 42,958 km²) and thus experienced additional land use in previous cycles.

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 S5). 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 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 5; Figure S5). The number of clearance events was positively associated with secondary forest cover ($p < 0.01$; Figure 5; Figure S5). 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 5; Figure S5). 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 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 5; Figure S5). 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 5; Figure S5). 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 5; Figure S5).

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.*, 2016). The MapBiomass 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 Nunes *et al.*, 2020 and Almeida *et al.*, 2016). Crucially, if these secondary forests have followed the 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 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 S3). 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.

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; Elias *et al.*, 2019; Requena Suarez *et al.*, 2019). Recent estimates suggest a 32-year-old secondary forest, the maximum age detectable with MapBiomass, would hold a maximum of $68.4 \pm 9.2 \text{ Mg C ha}^{-1}$, which is just $59 \pm 8\%$ of the average for old-growth forest ($115.2 \text{ Mg C ha}^{-1}$; 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.*, 2019). Moreover, these maximum values are rarely attained because high rates of secondary forest clearance (6,410 km² yr⁻¹) impose an age distribution that is highly skewed towards young age classes (Figure 1c; see also Chazdon *et al.*, 2016). 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 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 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.*, 2017). 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).

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 (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 1a, Figure S7a-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 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 S3). 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.*, 2018; Spracklen and Garcia-Carreras, 2015) and higher temperatures (Silva, Pereira and da Rocha, 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.*, 2019). 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

364 density (Phillips *et al.*, 2009; Uriarte *et al.*, 2016). Conversely, if the slow shift towards species associated with dry
365 environments that is seen in old-growth forest (Esquivel-Muelbert *et al.*, 2019) is also occurring in secondary forests,
366 then the latter may become more resilient to drought. However, secondary forests are often found in regions with little
367 surrounding old-growth forest cover (e.g. Elias *et al.* 2020), and compositional changes may be limited by seed
368 availability.

369

370 Landscape factors

371 Agricultural land abandonment is a complex phenomenon primarily driven by socioeconomic factors such as migration
372 (Benayas *et al.*, 2007). As a result, although Amazon-wide secondary forest covered approximately 20% of deforested
373 land, this figure varied greatly between regions. The greatest proportional recovery occurred in the highly forested
374 areas of the western Amazon, where headwater abandonment and rural-to-urban migration are enabling secondary
375 forest growth (Figure 1b, Parry *et al.*, 2010). As surrounding forest cover has positive effects on biomass recovery
376 (Jakovac *et al.*, 2015; Toledo *et al.*, 2020), secondary forests growing in these relatively intact landscapes were
377 positioned favourably for carbon sequestration. However, across the Brazilian Amazon, we find such forests to be in the
378 minority: just 13% of all secondary forest was in landscapes with $\geq 80\%$ old-growth forest (Figure 4a). Most secondary
379 forest was found along the highly deforested agricultural frontier, where it may suffer the negative impacts of
380 fragmentation, isolation, and edge effects (Ewers and Didham, 2005; Magnago *et al.*, 2017). Consequently, these
381 forests likely have considerably lower carbon-accumulation potential than those in regions with more intact forest
382 landscapes (Chazdon, 2003; Bihn, Gebauer and Brandl, 2010). Finally, although surrounding forest cover is important
383 for carbon accumulation, the role of the type and condition of the surrounding forest requires further research. Recent
384 findings indicate that high surrounding of secondary forest cover is advantageous for forest growth in the early stages
385 of succession (Toledo *et al.*, 2020). However, it is likely that proximity to old-growth forest will be more important later
386 in succession, as they are essential for providing the diverse seed sources required to establish resilient, biodiverse and
387 high-biomass secondary forests (e.g. Hawes *et al.* 2020). Furthering our understanding these relationships will be key to
388 designing effective restoration programmes within landscapes where there is little old-growth forest remaining.

389

390 Local factors

391 Incorporating measures of prior land use has previously been suggested as a mechanism for improving the accuracy of
392 biomass estimates in secondary forest (Wandelli and Fearnside, 2015), as studies have found that higher land use
393 intensity leads to slower biomass recovery (e.g. Jakovac *et al.*, 2015). Our assessment provides a mixed evaluation of
394 the favourability of local land use intensity factors for secondary forest carbon accumulation. We find the majority
395 (66.8%) of secondary forests in 2017 were in the favourable position of only having experienced one agricultural cycle.
396 However, this alone does not adequately represent land use intensity, as the type and length of land use within a single
397 cycle vary greatly. Secondary forests accumulate carbon more slowly on abandoned pasture than on abandoned
398 cropland (Fearnside and Guimarães, 1996). We find 46.3% of secondary forests in 2017 to be growing on land that was
399 previously pasture and a further 14.6% on land that was pasture at some point during the most recent land use cycle
400 (Figure 4d), placing the majority of secondary forests on unfavourable ground for carbon accumulation. Although
401 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 and Fearnside, 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 and Ostertag, 2001; Jakovac *et al.*, 2015; Martínez-Ramos *et al.*, 2016). Although providing some insight into the variety of secondary forest land use histories, the MapBiomass 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 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 experienced 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 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.*, 2019) may be representative of far greater areas of Amazonia's secondary forests, highlighting the urgent need to expand sampling efforts.

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; Brien *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, Mitchard and Gloor, 2014)(Elias *et al.*, 2019). 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⁻¹yr⁻¹ in Paragominas and Santarém-Belterra (Lennox *et al.*, 2018), 1.08 ha⁻¹yr⁻¹ in Bragança (Elias *et al.*, 2019) or as low as 0.89 Mg ha⁻¹yr⁻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, 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.*, 2019).

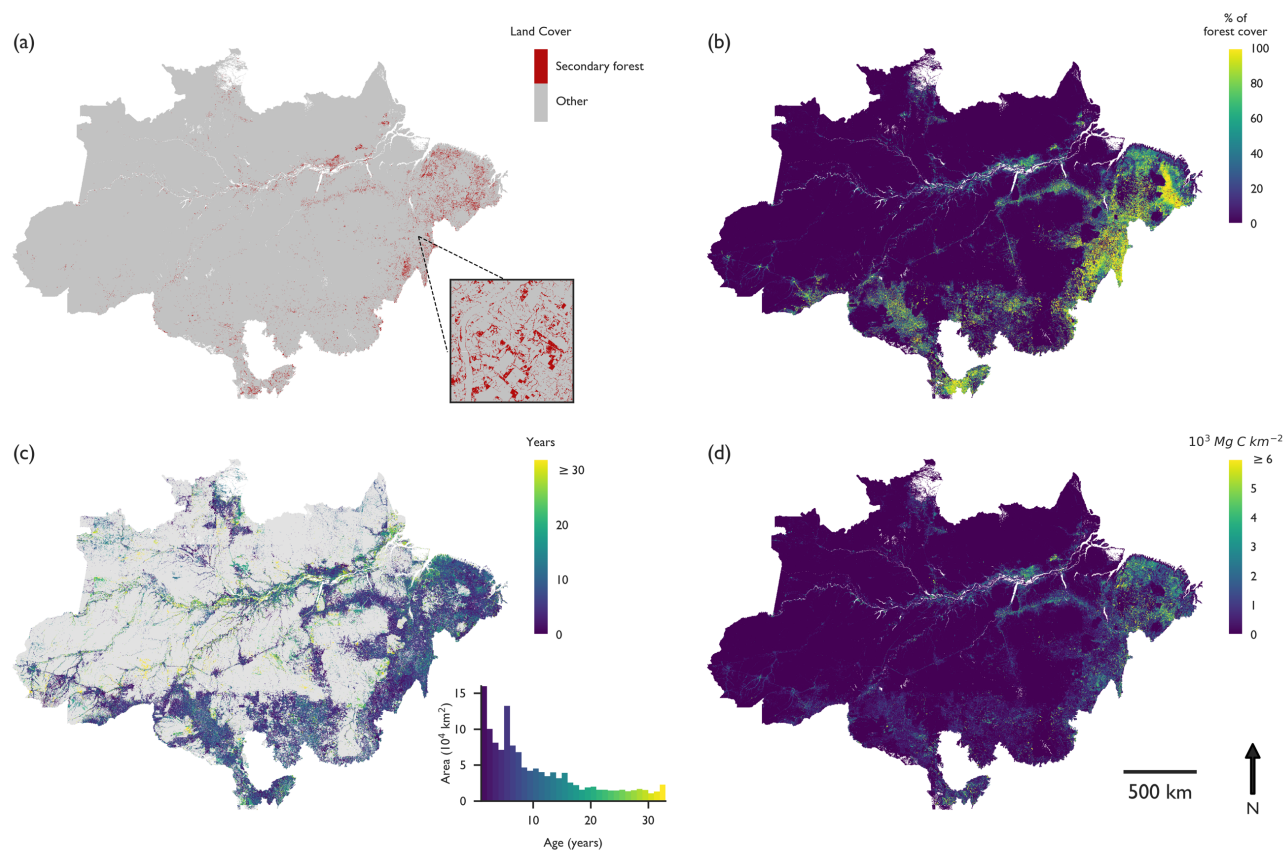
Conclusion

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

477 to remain minimal. With 10,000 km² of old-growth forest cleared in the Brazilian Amazon in 2019 (PRODES, 2020), this
478 is unlikely to change in the near future. We have also shown that there is likely to be much more geographical variation
479 in secondary forest recovery rates than is incorporated in current estimates. Future policies relying on secondary forest
480 growth will require a much better understanding of the factors determining recovery to ensure different secondary
481 forests are treated appropriately, with protection focused on those of greatest long-term carbon storage potential
482 (Gren and Aklilu, 2016). More accurate quantification of carbon stocks and recovery rates in secondary forests will
483 support the production of appropriate management proposals (Wandelli and Fearnside, 2015) and will be critical if
484 carbon-based payments for ecosystem services (e.g. REDD+) are to be successfully implemented. Moreover, increasing
485 our knowledge of secondary forests is crucial to our understanding of tropical forest responses to environmental
486 stressors, and the resilience of one of the world's most important biomes.

487

488 **Figures**
489



490
491

492 **Figure 1: The extent, age, and carbon stock of secondary forest in the Brazilian Amazon.**

493 **(A)** The spatial distribution of secondary forest (red). Inset reveals the level of detail available with 30-m resolution data
494 **(B)** The proportion of total forest cover made up of secondary forest **(C)** Median secondary forest age per 1 km² with
495 inset of the secondary forest age distribution **(D)** Total above-ground carbon stock in secondary forests, calculated
496 using accumulation rates estimated by Requena Suarez et al. (2019).

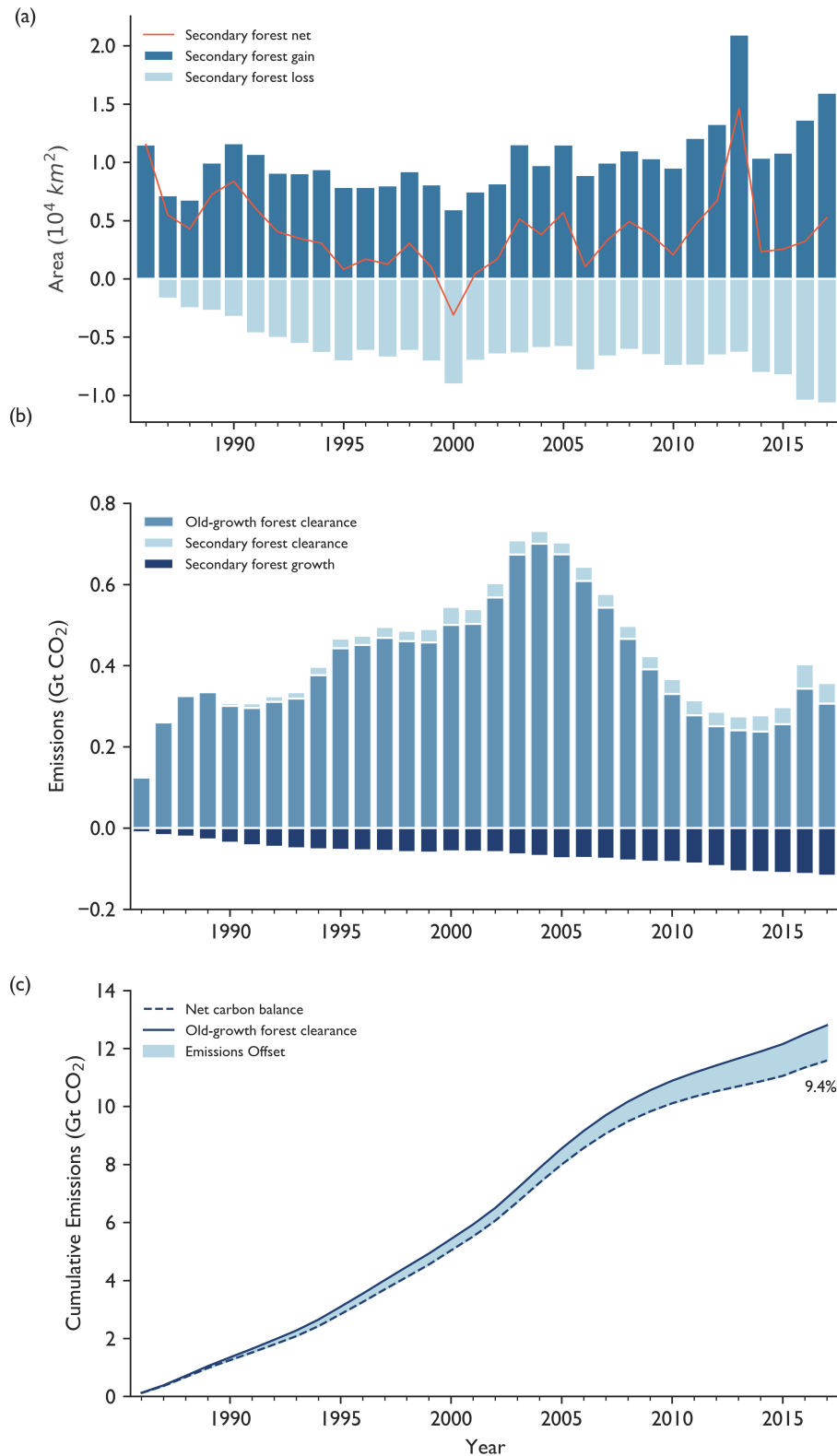


Figure 2: Forest cover change and associated emissions in the Brazilian Amazon from 1985 to 2017

(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).

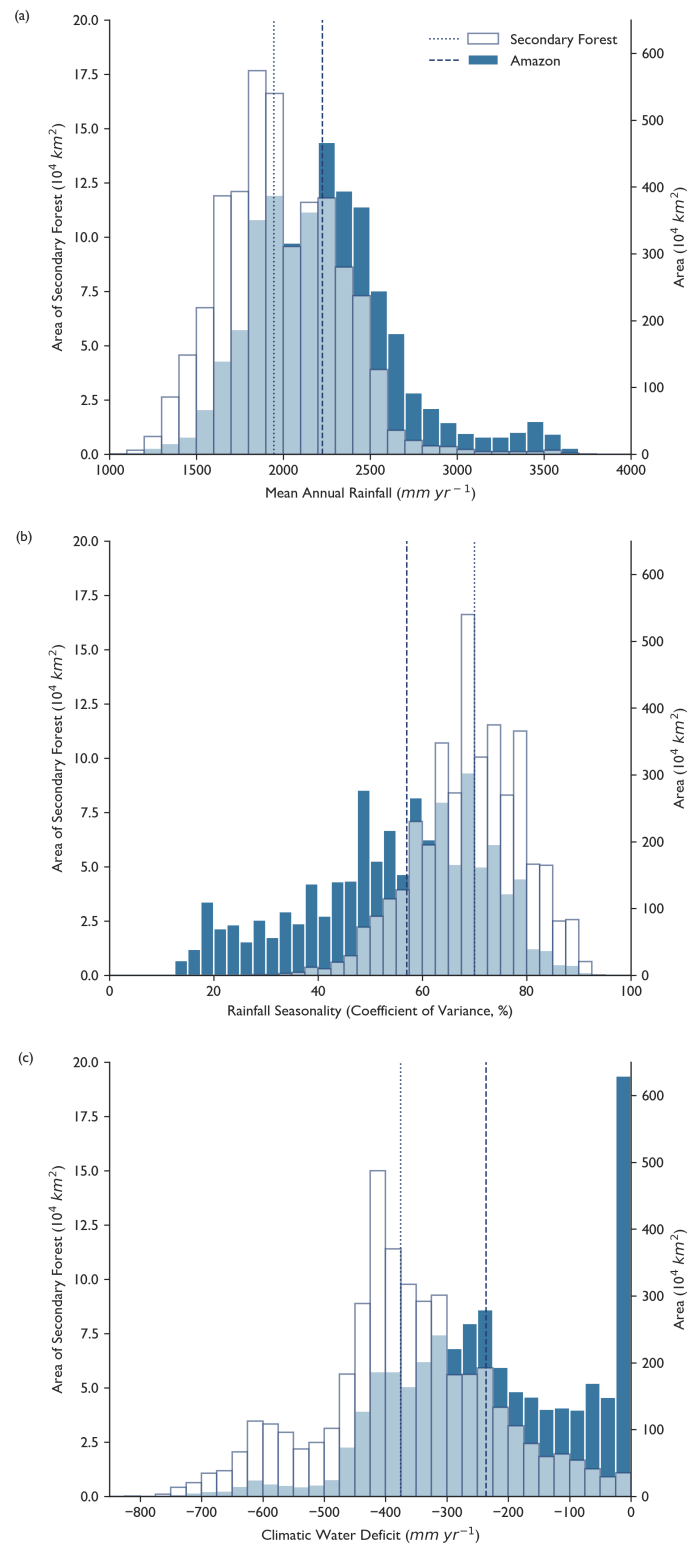


Figure 3: The climatic context of secondary forest in the Brazilian Amazon in 2017

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.

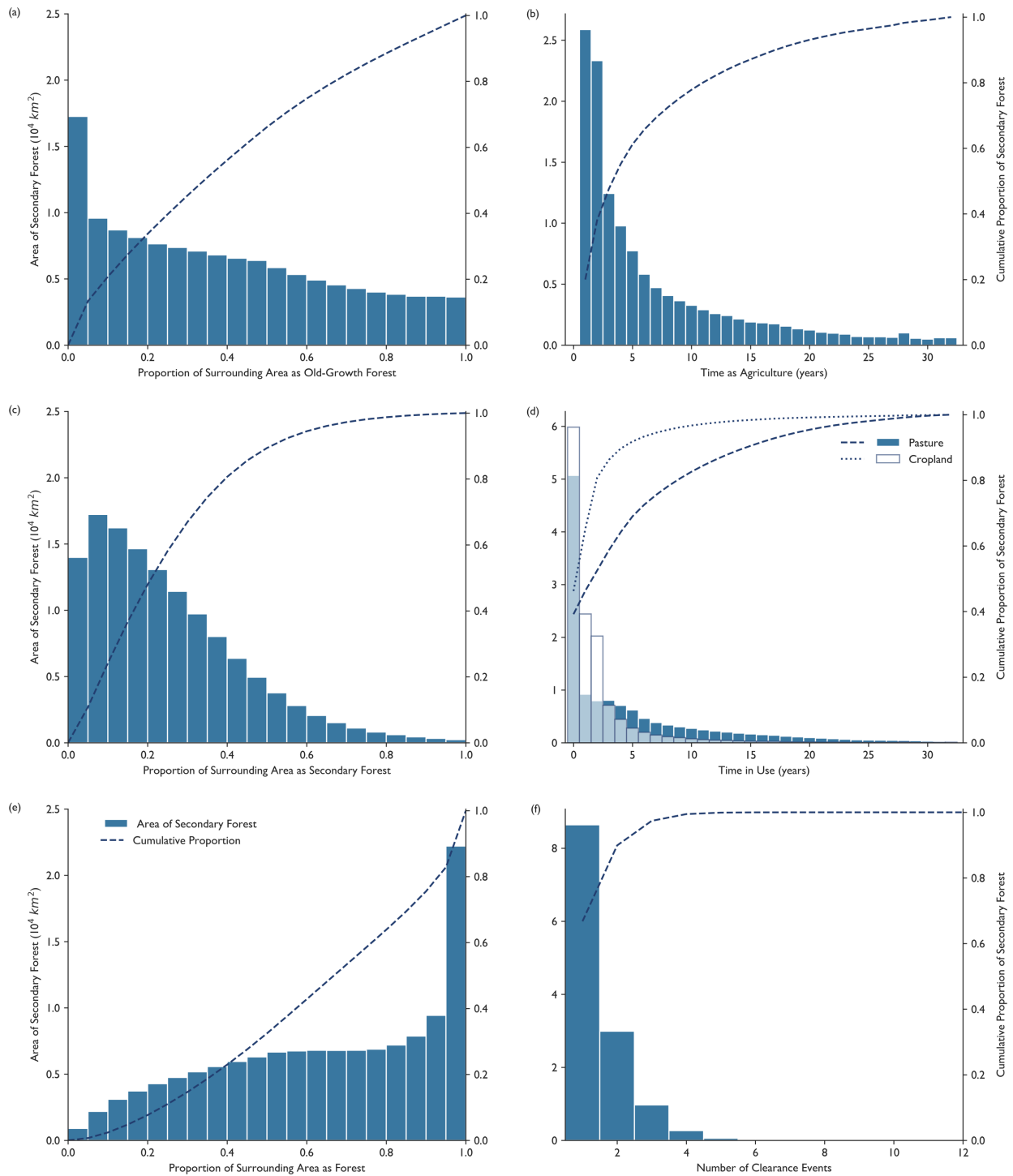
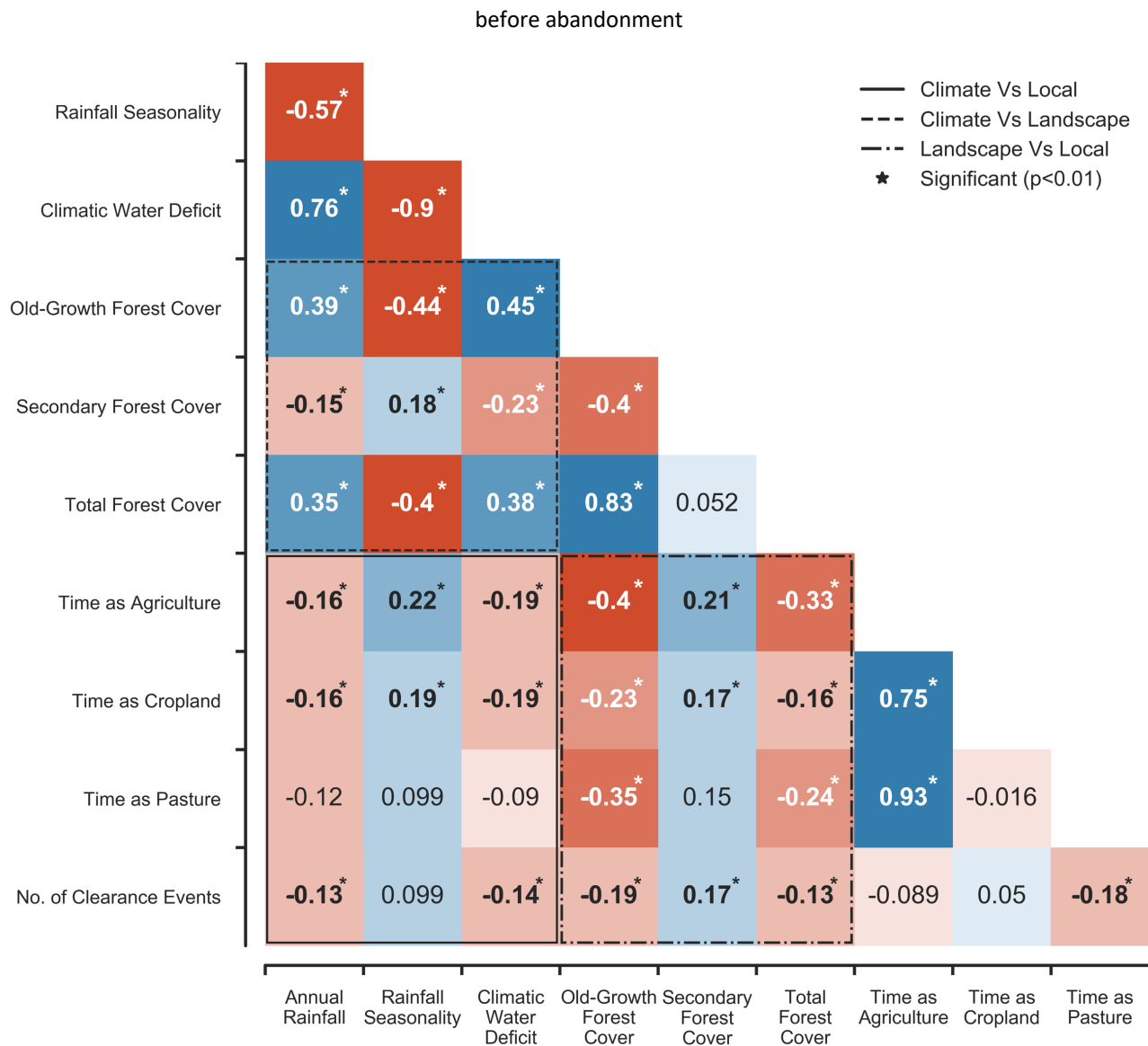


Figure 4: Landscape and local contexts of secondary forest in the Brazilian Amazon in 2017

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

517



518

519

520

521 **Figure 5: Spatial correlations between climatic, landscape and local context of secondary forest in the Brazilian**
522 **Amazon in 2017**

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

527

528

References

- Achard, F. *et al.* (2002) 'Determination of deforestation rates of the world's humid tropical forests.', *Science (New York, N.Y.)*. American Association for the Advancement of Science, 297(5583), pp. 999–1002. doi: 10.1126/science.1070656.
- Aide, T. M. *et al.* (2013) 'Deforestation and Reforestation of Latin America and the Caribbean (2001-2010)', *Biotropica*. John Wiley & Sons, Ltd (10.1111), 45(2), pp. 262–271. doi: 10.1111/j.1744-7429.2012.00908.x.
- Almeida, C. A. de *et al.* (2016) 'High spatial resolution land use and land cover mapping of the Brazilian Legal Amazon in 2008 using Landsat-5/TM and MODIS data', *Acta Amazonica*. SciELO Brasil, 46(3), pp. 291–302.
- Almeida, D. R. A. *et al.* (2019) 'The effectiveness of lidar remote sensing for monitoring forest cover attributes and landscape restoration', *Forest Ecology and Management*, 438, pp. 34–43. doi: <https://doi.org/10.1016/j.foreco.2019.02.002>.
- Avitabile, V. *et al.* (2016) 'An integrated pan-tropical biomass map using multiple reference datasets', *Global Change Biology*. John Wiley & Sons, Ltd (10.1111), 22(4), pp. 1406–1420. doi: 10.1111/gcb.13139.
- Baccini, A. *et al.* (2012) 'Estimated carbon dioxide emissions from tropical deforestation improved by carbon-density maps', *Nature Climate Change*. Nature Publishing Group, 2(3), pp. 182–185. doi: 10.1038/nclimate1354.
- Baker, T. R. *et al.* (2004) 'Variation in wood density determines spatial patterns in Amazonian forest biomass', *Global Change Biology*. John Wiley & Sons, Ltd, 10(5), pp. 545–562. doi: 10.1111/j.1365-2486.2004.00751.x.
- Benayas, J. M. R. *et al.* (2007) 'Abandonment of agricultural land: an overview of drivers and consequences', *CAB reviews: Perspectives in agriculture, veterinary science, nutrition and natural resources*, 2(57), pp. 1–14.
- Berenguer, E. *et al.* (2014) 'A large-scale field assessment of carbon stocks in human-modified tropical forests', *Global Change Biology*. John Wiley & Sons, Ltd (10.1111), 20(12), pp. 3713–3726. doi: 10.1111/gcb.12627.
- Bihn, J. H., Gebauer, G. and Brandl, R. (2010) 'Loss of functional diversity of ant assemblages in secondary tropical forests', *Ecology*. John Wiley & Sons, Ltd, 91(3), pp. 782–792. doi: 10.1890/08-1276.1.
- Bonn Challenge (2011) *Bonn Challenge*. Available at: <https://www.bonnchallenge.org> (Accessed: 10 January 2020).
- Brienen, R. J. W. *et al.* (2015) 'Long-term decline of the Amazon carbon sink', *Nature*. Nature Publishing Group, 519(7543), pp. 344–348. doi: 10.1038/nature14283.
- Bullock, E. L. *et al.* (2020) 'Satellite-based estimates reveal widespread forest degradation in the Amazon', *Global Change Biology*. John Wiley & Sons, Ltd, 26(5), pp. 2956–2969. doi: 10.1111/gcb.15029.
- Caughlin, T. T., Elliott, S. and Lichstein, J. W. (2016) 'When does seed limitation matter for scaling up reforestation from patches to landscapes?', *Ecological Applications*. doi: 10.1002/eap.1410.
- Chave, J. *et al.* (2014) 'Improved allometric models to estimate the aboveground biomass of tropical trees', *Global Change Biology*. John Wiley & Sons, Ltd (10.1111), 20(10), pp. 3177–3190. doi: 10.1111/gcb.12629.
- Chave, J. *et al.* (2020) 'Slow rate of secondary forest carbon accumulation in the Guianas compared with the rest of the Neotropics', *Ecological Applications*. John Wiley & Sons, Ltd, 30(1). doi: 10.1002/eap.2004.
- Chazdon, R. L. (2003) 'Tropical forest recovery: legacies of human impact and natural disturbances', *Perspectives in Plant Ecology Evolution and Systematics*. Urban & Fischer, 6(December 2003), pp. 51–71. doi: 10.1078/1433-8319-00042.

Chazdon, R. L. (2014) *Second growth : the promise of tropical forest regeneration in an age of deforestation*. University of Chicago Press. Available at:
<https://books.google.co.uk/books?hl=en&lr=&id=EYhFAwAAQBAJ&oi=fnd&pg=PR7&dq=Second+Growth:+The+Promise+of+Tropical+Forest+Regeneration+in+an+Age+of+Deforestation&ots=7OPBsqlGk9&sig=G-12JkIVx6756ZMWzipi5h1JylE#v=onepage&q=Second+Growth%3A+The+Promise> (Accessed: 3 September 2019).

Chazdon, R. L. *et al.* (2016) 'Carbon sequestration potential of second-growth forest regeneration in the Latin American tropics', *Science Advances*, 2(5). doi: 10.1126/sciadv.1501639.

Crouzeilles, R. *et al.* (2017) 'Ecological restoration success is higher for natural regeneration than for active restoration in tropical forests', *Science Advances*. American Association for the Advancement of Science, 3(11), p. e1701345. doi: 10.1126/sciadv.1701345.

Eggleston, H. S. *et al.* (eds) (2006) *2006 IPCC Guidelines for National Greenhouse Gas Inventories*. Japan: IGES. Available at: https://www.ipcc-nggip.iges.or.jp/public/2006gl/pdf/4_Volume4/V4_00_Cover.pdf.

Elias, F. *et al.* (2019) 'Assessing the growth and climate sensitivity of secondary forests in highly deforested Amazonian landscapes', *Ecology*. Wiley Online Library, p. e02954.

Esquivel-Muelbert, A. *et al.* (2019) 'Compositional response of Amazon forests to climate change', *Global Change Biology*. John Wiley & Sons, Ltd, 25(1), pp. 39–56. doi: 10.1111/gcb.14413.

Eva, H. D. *et al.* (2012) 'Forest cover changes in tropical south and Central America from 1990 to 2005 and related carbon emissions and removals', *Remote Sensing*. doi: 10.3390/rs4051369.

Ewers, R. M. and Didham, R. K. (2005) 'Confounding factors in the detection of species responses to habitat fragmentation', *Biological Reviews*. Cambridge University Press, 81(01), p. 117. doi: 10.1017/S1464793105006949.

FAO (2012) *Global ecological zones for FAO forest reporting: 2010 Update*. Rome, Italy. Available at: <http://www.fao.org/3/a-ap861e.pdf>.

Fearnside, P. M. (1990) 'The Rate and Extent of Deforestation in Brazilian Amazonia', *Environmental Conservation*, 17(3). doi: 10.1017/S0376892900032355.

Fearnside, P. M. (2005) 'Deforestation in Brazilian Amazonia: History, rates, and consequences', *Conservation Biology*. Blackwell Science Inc, 19(3), pp. 680–688. doi: 10.1111/j.1523-1739.2005.00697.x.

Fearnside, P. M. and Guimarães, W. M. (1996) 'Carbon uptake by secondary forests in Brazilian Amazonia', *Forest Ecology and Management*. Elsevier, 80(1–3), pp. 35–46. doi: 10.1016/0378-1127(95)03648-2.

Fernandes Neto, J. G. *et al.* (2019) 'Alternative functional trajectories along succession after different land uses in central Amazonia', *Journal of Applied Ecology*. Edited by J. Moore, 56(11), pp. 2472–2481. doi: 10.1111/1365-2664.13484.

Fu, R. *et al.* (2013) 'Increased dry-season length over southern Amazonia in recent decades and its implication for future climate projection.', *Proceedings of the National Academy of Sciences of the United States of America*. National Academy of Sciences, 110(45), pp. 18110–5. doi: 10.1073/pnas.1302584110.

Fujisaka, S. *et al.* (1996) 'Slash-and-burn agriculture, conversion to pasture, and deforestation in two Brazilian Amazon colonies', *Agriculture, Ecosystems & Environment*. Elsevier, 59(1–2), pp. 115–130. doi: 10.1016/0167-8809(96)01015-8.

604 Grace, J., Mitchard, E. and Gloor, E. (2014) 'Perturbations in the carbon budget of the tropics', *Global Change Biology*.
605 John Wiley & Sons, Ltd (10.1111), 20(10), pp. 3238–3255. doi: 10.1111/gcb.12600.

606 Grassi, G. *et al.* (2017) 'The key role of forests in meeting climate targets requires science for credible mitigation',
607 *Nature Climate Change*. Nature Publishing Group, 7(3), pp. 220–226. doi: 10.1038/nclimate3227.

608 Gren, I.-M. and Aklilu, A. Z. (2016) 'Policy design for forest carbon sequestration: A review of the literature', *Forest*
609 *Policy and Economics*. Elsevier, 70, pp. 128–136. doi: 10.1016/J.FORPOL.2016.06.008.

610 Griscom, B. W. *et al.* (2017) 'Natural climate solutions.', *Proceedings of the National Academy of Sciences of the United*
611 *States of America*. National Academy of Sciences, 114(44), pp. 11645–11650. doi: 10.1073/pnas.1710465114.

612 Guariguata, M. R. and Ostertag, R. (2001) 'Neotropical secondary forest succession: changes in structural and functional
613 characteristics', *Forest Ecology and Management*. Elsevier, 148(1–3), pp. 185–206. doi: 10.1016/S0378-
614 1127(00)00535-1.

615 Hansen, M. C. *et al.* (2013) 'High-resolution global maps of 21st-century forest cover change', *Science*, 342(6160), pp.
616 850–853. doi: 10.1126/science.1244693.

617 Harris, N. L. *et al.* (2012) 'Baseline map of carbon emissions from deforestation in tropical regions', *Science*. American
618 Association for the Advancement of Science, 336(6088), pp. 1573–1576. doi: 10.1126/science.1217962.

619 Hijmans, R. J. *et al.* (2005) 'Very high resolution interpolated climate surfaces for global land areas', *International*
620 *Journal of Climatology*. John Wiley & Sons, Ltd, 25(15), pp. 1965–1978. doi: 10.1002/joc.1276.

621 Houghton, R. A. *et al.* (2000) 'Annual fluxes of carbon from deforestation and regrowth in the Brazilian Amazon',
622 *Nature*. Nature Publishing Group, 403(6767), pp. 301–304. doi: 10.1038/35002062.

623 Hubau, W. *et al.* (2020) 'Asynchronous carbon sink saturation in African and Amazonian tropical forests', *Nature*.
624 Nature Publishing Group, 579(7797), pp. 80–87. doi: 10.1038/s41586-020-2035-0.

625 *Initiative 20x20* (2014). Available at: <https://initiative20x20.org/> (Accessed: 5 May 2020).

626 Jakovac, C. C. *et al.* (2015) 'Loss of secondary-forest resilience by land-use intensification in the Amazon', *Journal of*
627 *Ecology*. doi: 10.1111/1365-2745.12298.

628 Van Leeuwen, T. T. *et al.* (2014) 'Biomass burning fuel consumption rates Biomass burning fuel consumption rates: a
629 field measurement database Biomass burning fuel consumption rates', *Biogeosciences Discuss*, 11, pp. 8115–
630 8180. doi: 10.5194/bgd-11-8115-2014.

631 Lennox, G. D. *et al.* (2018) 'Second rate or a second chance? Assessing biomass and biodiversity recovery in
632 regenerating Amazonian forests', *Global Change Biology*. John Wiley & Sons, Ltd (10.1111), 24(12), pp. 5680–
633 5694. doi: 10.1111/gcb.14443.

634 Loarie, S. R., Asner, G. P. and Field, C. B. (2009) 'Boosted carbon emissions from Amazon deforestation', *Geophys. Res.*
635 *Lett.*, 36. doi: 10.1029/2009GL037526.

636 Luyssaert, S. *et al.* (2007) 'CO2 balance of boreal, temperate, and tropical forests derived from a global database',
637 *Global Change Biology*. Blackwell Publishing Ltd, 13(12), pp. 2509–2537. doi: doi:10.1111/j.1365-
638 2486.2007.01439.x.

639 Magnago, L. F. S. *et al.* (2017) 'Do fragment size and edge effects predict carbon stocks in trees and lianas in tropical
640 forests?', *Functional Ecology*. John Wiley & Sons, Ltd (10.1111), 31(2), pp. 542–552. doi: 10.1111/1365-
641 2435.12752@10.1111/(ISSN)2041-210X.NATIONALTREEWEEK2016.

642 Markesteijn, L. *et al.* (2011) 'Hydraulics and life history of tropical dry forest tree species: coordination of species'
 643 drought and shade tolerance', *New Phytologist*. John Wiley & Sons, Ltd, 191(2), pp. 480–495. doi:
 644 10.1111/j.1469-8137.2011.03708.x.

645 Martínez-Ramos, M. *et al.* (2016) 'Natural forest regeneration and ecological restoration in human-modified tropical
 646 landscapes', *Biotropica*. John Wiley & Sons, Ltd (10.1111), 48(6), pp. 745–757. doi: 10.1111/btp.12382.

647 Morton, D. C. *et al.* (2008) 'Agricultural intensification increases deforestation fire activity in Amazonia', *Global Change
 648 Biology*. John Wiley & Sons, Ltd, 14(10), pp. 2262–2275. doi: 10.1111/j.1365-2486.2008.01652.x.

649 Nepstad, D. C. *et al.* (1994) 'The role of deep roots in the hydrological and carbon cycles of Amazonian forests and
 650 pastures', *Nature*, 372(6507), pp. 666–669. doi: 10.1038/372666a0.

651 New York Declaration on Forests (2014) *New York Declaration on Forests*. Available at: <https://forestdeclaration.org>
 652 (Accessed: 10 January 2020).

653 Nunes, S. *et al.* (2020) 'Unmasking secondary vegetation dynamics in the Brazilian Amazon', *Environmental Research
 654 Letters*. Available at: <http://iopscience.iop.org/10.1088/1748-9326/ab76db>.

655 Pan, Y. *et al.* (2011) 'A large and persistent carbon sink in the world's forests.', *Science (New York, N.Y.)*. American
 656 Association for the Advancement of Science, 333(6045), pp. 988–93. doi: 10.1126/science.1201609.

657 Parry, L. *et al.* (2010) 'Drivers of rural exodus from Amazonian headwaters', *Population and Environment*. Springer
 658 Netherlands, 32(2–3), pp. 137–176. doi: 10.1007/s11111-010-0127-8.

659 Phillips, O. L. *et al.* (2009) 'Drought Sensitivity of the Amazon Rainforest', *Science*, 323(5919), pp. 1344 LP – 1347. doi:
 660 10.1126/science.1164033.

661 Poorter, L. *et al.* (2016) 'Biomass resilience of Neotropical secondary forests', *Nature*. Nature Publishing Group,
 662 530(7589), pp. 211–214. doi: 10.1038/nature16512.

663 Powers, J. S. *et al.* (2011) 'Geographic bias of field observations of soil carbon stocks with tropical land-use changes
 664 precludes spatial extrapolation.', *Proceedings of the National Academy of Sciences of the United States of
 665 America*. National Academy of Sciences, 108(15), pp. 6318–22. doi: 10.1073/pnas.1016774108.

666 PRODES (2020) *PRODES*. Available at:
 667 http://terrabrasilis.dpi.inpe.br/app/dashboard/deforestation/biomes/legal_amazon/rates (Accessed: 5 April
 668 2018).

669 Quesada, C. A. *et al.* (2011) 'Soils of Amazonia with particular reference to the RAINFOR sites', *Biogeosciences*, 8, pp.
 670 1415–1440. doi: 10.5194/bg-8-1415-2011.

671 Quesada, C. A. *et al.* (2012) 'Basin-wide variations in Amazon forest structure and function are mediated by both soils
 672 and climate', *Biogeosciences*. doi: 10.5194/bg-9-2203-2012.

673 Requena Suarez, D. *et al.* (2019) 'Estimating aboveground net biomass change for tropical and subtropical forests:
 674 Refinement of IPCC default rates using forest plot data', *Global Change Biology*. John Wiley & Sons, Ltd
 675 (10.1111), p. gcb.14767. doi: 10.1111/gcb.14767.

676 Rogelj, J. *et al.* (2018) 'Mitigation Pathways Compatible with 1.5°C in the Context of Sustainable Development.', in
 677 *Global Warming of 1.5°C. An IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial
 678 levels and related global greenhouse gas emission pathways, in the context of strengthening the global response
 679 to the threat of climate change.*

680 Saatchi, S. S. *et al.* (2011) 'Benchmark map of forest carbon stocks in tropical regions across three continents.',
681 *Proceedings of the National Academy of Sciences of the United States of America*. National Academy of Sciences,
682 108(24), pp. 9899–904. doi: 10.1073/pnas.1019576108.

683 Schwartz, N. B. *et al.* (2017) 'Land-use dynamics influence estimates of carbon sequestration potential in tropical
684 second-growth forest', *Environmental Research Letters*. IOP Publishing, 12(7), p. 074023. doi: 10.1088/1748-
685 9326/aa708b.

686 Silva, M. E. S., Pereira, G. and da Rocha, R. P. (2016) 'Local and remote climatic impacts due to land use degradation in
687 the Amazon "Arc of Deforestation"', *Theoretical and Applied Climatology*, 125(3), pp. 609–623. doi:
688 10.1007/s00704-015-1516-9.

689 Skole, D. L. *et al.* (1994) 'Physical and Human Dimensions of Deforestation in Amazonia', *BioScience*, 44(5), pp. 314–322.
690 doi: 10.2307/1312381.

691 Spracklen, D. V *et al.* (2018) 'The Effects of Tropical Vegetation on Rainfall', *Annual Review of Environment and*
692 *Resources*. Annual Reviews, 43(1), pp. 193–218. doi: 10.1146/annurev-environ-102017-030136.

693 Spracklen, D. V and Garcia-Carreras, L. (2015) 'The impact of Amazonian deforestation on Amazon basin rainfall',
694 *Geophysical Research Letters*. John Wiley & Sons, Ltd, 42(21), pp. 9546–9552. doi: 10.1002/2015GL066063.

695 Toledo, R. M. *et al.* (2020) 'Restoring tropical forest composition is more difficult, but recovering tree-cover is faster,
696 when neighbouring forests are young', *Landscape Ecology*. Springer, pp. 1–14. doi: 10.1007/s10980-020-01023-
697 7.

698 *UN Decade on Restoration* (2019). Available at: <https://www.decadeonrestoration.org/> (Accessed: 5 May 2020).

699 Uriarte, M. *et al.* (2016) 'Impacts of climate variability on tree demography in second growth tropical forests: the
700 importance of regional context for predicting successional trajectories', *Biotropica*. John Wiley & Sons, Ltd,
701 48(6), pp. 780–797. doi: 10.1111/btp.12380.

702 Vera-Diaz, M. del C. *et al.* (2008) 'An interdisciplinary model of soybean yield in the Amazon Basin: The climatic,
703 edaphic, and economic determinants', *Ecological Economics*. Elsevier, 65(2), pp. 420–431. doi:
704 10.1016/J.ECOLECON.2007.07.015.

705 Wandelli, E. V. and Fearnside, P. M. (2015) 'Secondary vegetation in central Amazonia: Land-use history effects on
706 aboveground biomass', *Forest Ecology and Management*, 347, pp. 140–148. doi: 10.1016/j.foreco.2015.03.020.

707 Wang, Y. *et al.* (2020) 'Upturn in secondary forest clearing buffers primary forest loss in the Brazilian Amazon', *Nature*
708 *Sustainability*. Nature Publishing Group, 3(4), pp. 290–295. doi: 10.1038/s41893-019-0470-4.

709