



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

Charlotte C. Smith¹ | Fernando D. B. Espírito-Santo² | John R. Healey³ | Paul J. Young^{1,4} | Gareth D. Lennox¹ | Joice Ferreira⁵ | Jos Barlow^{1,6}

¹Lancaster Environment Centre, Lancaster University, Lancaster, UK

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

³School of Natural Sciences, College of Environmental Sciences and Engineering, Bangor University, Bangor, UK

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

⁵Embrapa Amazônia Oriental, Belém, Brazil

⁶Federal University of Lavras, Minas Gerais, Brazil

Correspondence

Charlotte C. Smith, Lancaster Environment Centre, Lancaster University, Lancaster, UK. Email: charlottesmith0308@outlook.com

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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 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.

KEYWORDS

carbon sequestration, climate change, forest regeneration, human-modified landscapes, negative emissions, secondary vegetation, tropical forests

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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/year (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 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 (Griscom et al., 2017; Pan et al., 2011; Rogelj et al., 2018). Secondary forests have long been recognized 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 recognizes 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 or 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 (Griscom et al., 2017; Pan et al., 2011; 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 10-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 et al., 2016; Chazdon et al., 2016). Locally, secondary forests growing on abandoned pasture accumulate carbon more slowly than on abandoned cropland (Fearnside & 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 land cover data set (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 (a) what has been the potential role of secondary forests in offsetting old-growth deforestation emissions since 1985? We then explore (b) 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; (c) how are these variables correlated spatially within the existing range of secondary forests?

2 | METHODS

2.1 | Assessing secondary forests and deforestation

We used MapBiomass to define deforestation and forest recovery. We opted to use this dataset 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 data sets broadly agree in terms of spatial distribution

(see Data S1). The temporal pattern of deforestation captured by MapBiomass is also comparable to that of PRODES (2020; Figure S1).

2.2 | 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 to 2017 using the MapBiomass 3.1 land cover data set and a change-detection algorithm (Data S1). 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 (four contiguous pixels), unless directly adjacent

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	2.4. 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

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/year (Fujisaka et al., 1996). Averaged over the time series, this resulted in an Amazon-wide reduction in calculated secondary forest area of $0.82 \pm 0.31\%$ ($n = 32$, mean \pm SD) compared with the same analysis conducted without the spatial filter.

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 km² of the land deforested before 1985 (Fearnside, 1990) would have returned to secondary forest (de 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 \pm the temporal standard deviation in order to capture interannual variability.

2.4 | Above-ground biomass in secondary forest

Requena Suarez et al. (2019) estimate biomass accumulation rates for young (≤ 20 years) and old (21–100 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 ± 0.8 , 4.4 ± 1.3 and 5.2 ± 1 Mg ha⁻¹ year⁻¹ for young secondary forest, and 2.3 ± 0.3 , 1.8 ± 0.8 and 2.7 ± 0.8 Mg ha⁻¹ year⁻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 Data S1. 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).

2.5 | 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) data sets 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 data sets 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 underestimating emissions from old-growth deforestation. A further limitation of the Avitabile et al. (2016) data set 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 Data S1).

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).

2.6 | Factors mediating secondary forest recovery

2.6.1 | 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 S5) and we report results for $n = 1,000$.

Variation in local climate is known to influence carbon sequestration in secondary forest (Elias et al., 2019). 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., 2018; Spracklen & Garcia-Carreras, 2015), 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.

2.6.2 | 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.

2.6.3 | Local

For the period 1985–2017, the change-detection algorithm records total clearance events as the number of times a pixel transitions from 'forest' to 'non-forest'. 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'.

2.7 | Associations between factors influencing biomass accumulation

Using Spearman's Rank-Order Correlation and a sample of secondary forest pixels ($n = 1,000$), 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 S4). Given the large

number of repeated tests ($n = 10^4$) and the relatively large sample size ($n = 1,000$), we used a more conservative significance threshold of 0.01 for this analysis.

3 | RESULTS

3.1 | 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 7 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 ($48.0 \pm 4.5\%$).

3.2 | Old-growth deforestation emissions offset by secondary forest growth

3.2.1 | Old-growth deforestation emissions

Between 1985 and 2017, MapBiomass 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).

3.2.2 | 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

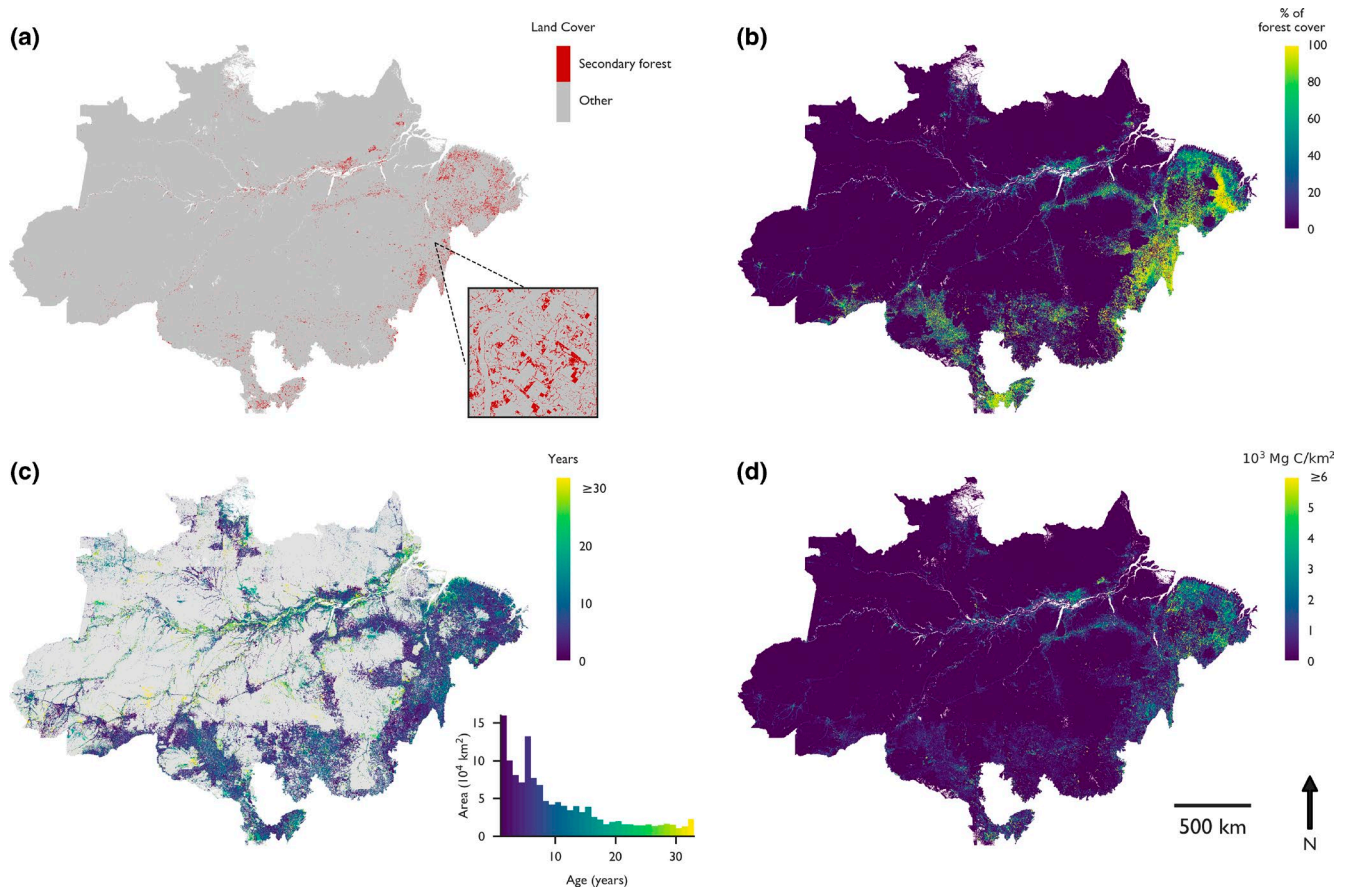


FIGURE 1 The extent, age and carbon stock of secondary forest in the Brazilian Amazon. (a) The spatial distribution of secondary forest (red). Inset reveals the level of detail available with 30 m resolution data. (b) The proportion of total forest cover made up of secondary forest. (c) Median secondary forest age per 1 km², 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)

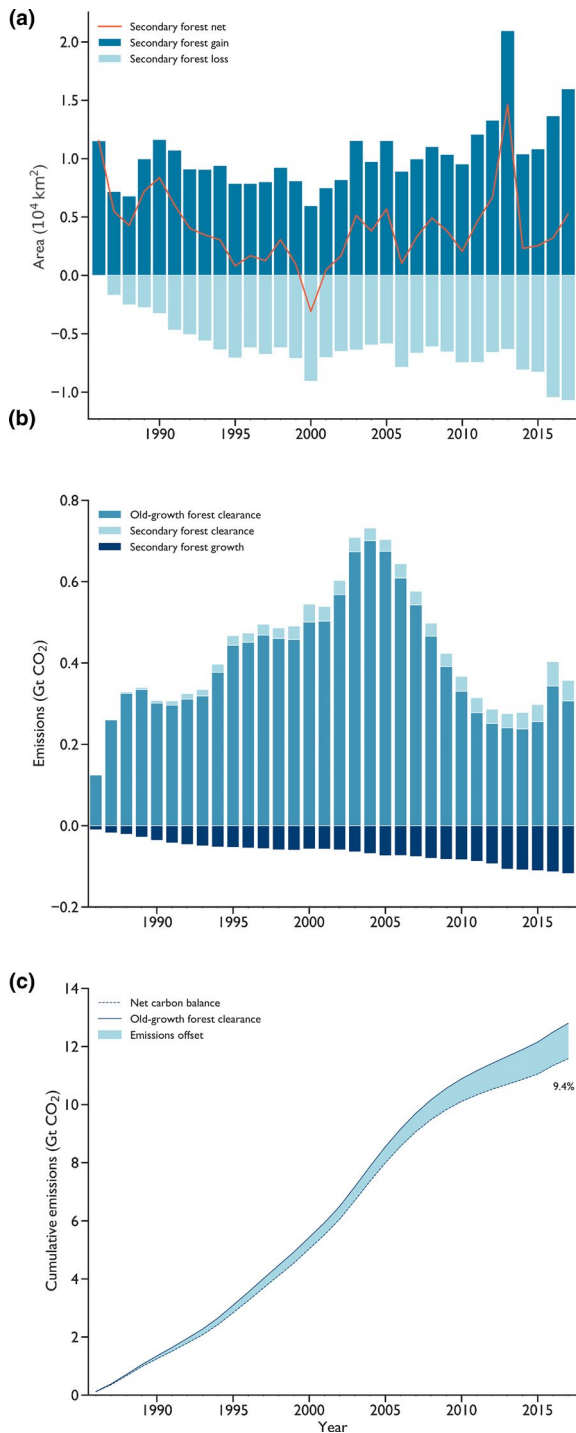


FIGURE 2 Forest cover change and associated emissions in the Brazilian Amazon from 1985 to 2017. (a) Net annual change in secondary forest extent (red) with gross annual new growth (dark) and clearance (light). (b) Gross annual emissions from old-growth clearance (medium), secondary forest clearance (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)

Mg CO_2 (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 CO_2 in 1986 to 66.12 ± 9.7 million Mg CO_2 in 2017 (mean \pm 95% CI; Figure 2b). The accumulation of carbon in secondary forests was slowed by clearance, with an average $6,410 \pm 2,007 \text{ km}^2$ of secondary forest cleared annually (Figure 2a). Of all the secondary forest mapped during our time series, 60.6% ($198,688 \text{ km}^2$) 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 \pm 95% CI). However, averaged across the time series, secondary forests were a net carbon sink of 6.75 ± 1 million $\text{Mg C}/\text{year}$ (mean \pm 95% CI).

3.2.3 | Deforestation emissions offset

Our findings show that between 1985 and 2017, approximately 9.37% (1.20 ± 0.18 billion Mg CO_2 , 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 the 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.

3.3 | Factors influencing secondary forest carbon sequestration

3.3.1 | 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: 1,945 mm, Brazilian Amazon: 2,224 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: $-375.5 \text{ mm}/\text{year}$, Brazilian Amazon: $-259 \text{ mm}/\text{year}$, Figure 3c). We can be highly confident ($p < .01$) in meaningful differences between these distributions (Wilcoxon rank sum; climatic water deficit: $W = -16.71$, $p < .01$, rainfall: $W = -14.49$, $p < .01$, seasonality: $W = 20.25$, $p < .01$).

3.3.2 | 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

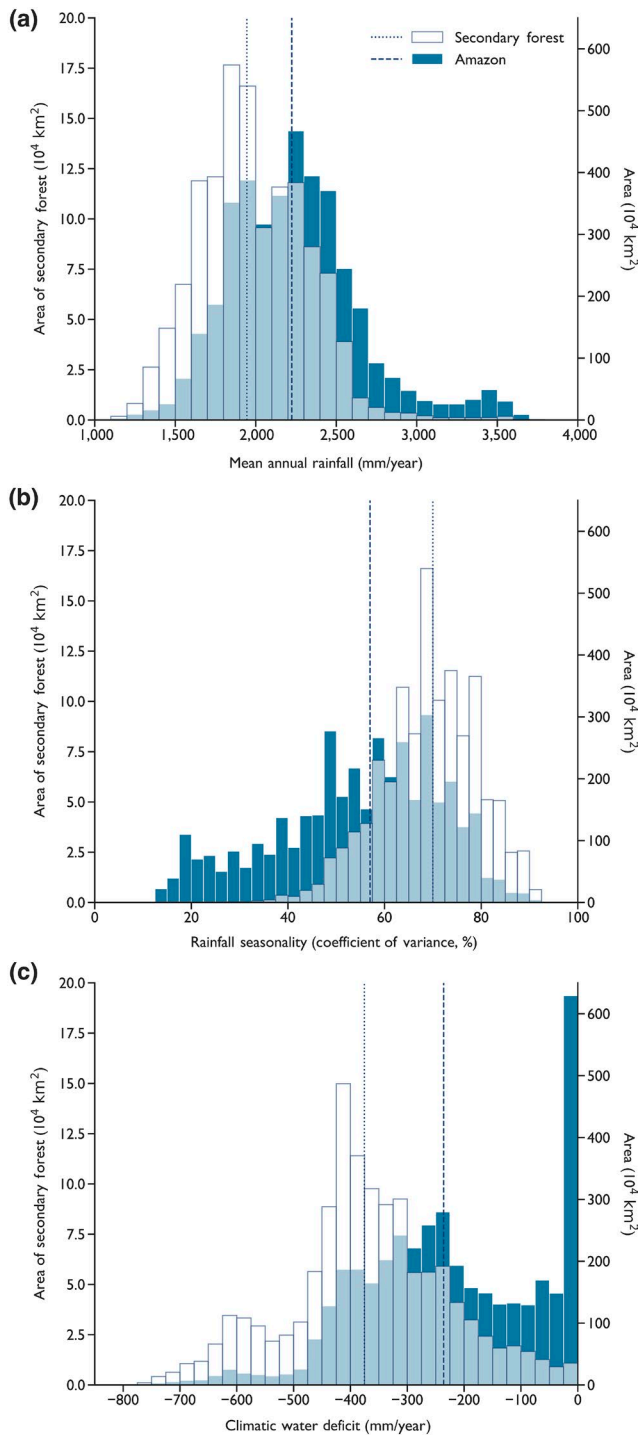


FIGURE 3 The climatic context of secondary forest in the Brazilian Amazon in 2017. The distribution of (a) annual rainfall (mm/year), (b) rainfall seasonality (% difference in wet and dry season rainfall) and (c) climatic water deficit (mm/year) of secondary forest in the Brazilian Amazon (white, left). The distributions of all three variables were significantly different to the distributions for the entire Brazilian Amazon (blue, right; $p < .01$). Medians for secondary forest (dots) and Amazon-wide (dashed) are indicated by vertical lines

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,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 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.

3.3.3 | 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.

3.4 | Associations between factors that influence biomass accumulation

3.4.1 | 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 ($p < .01$; 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).

3.4.2 | 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

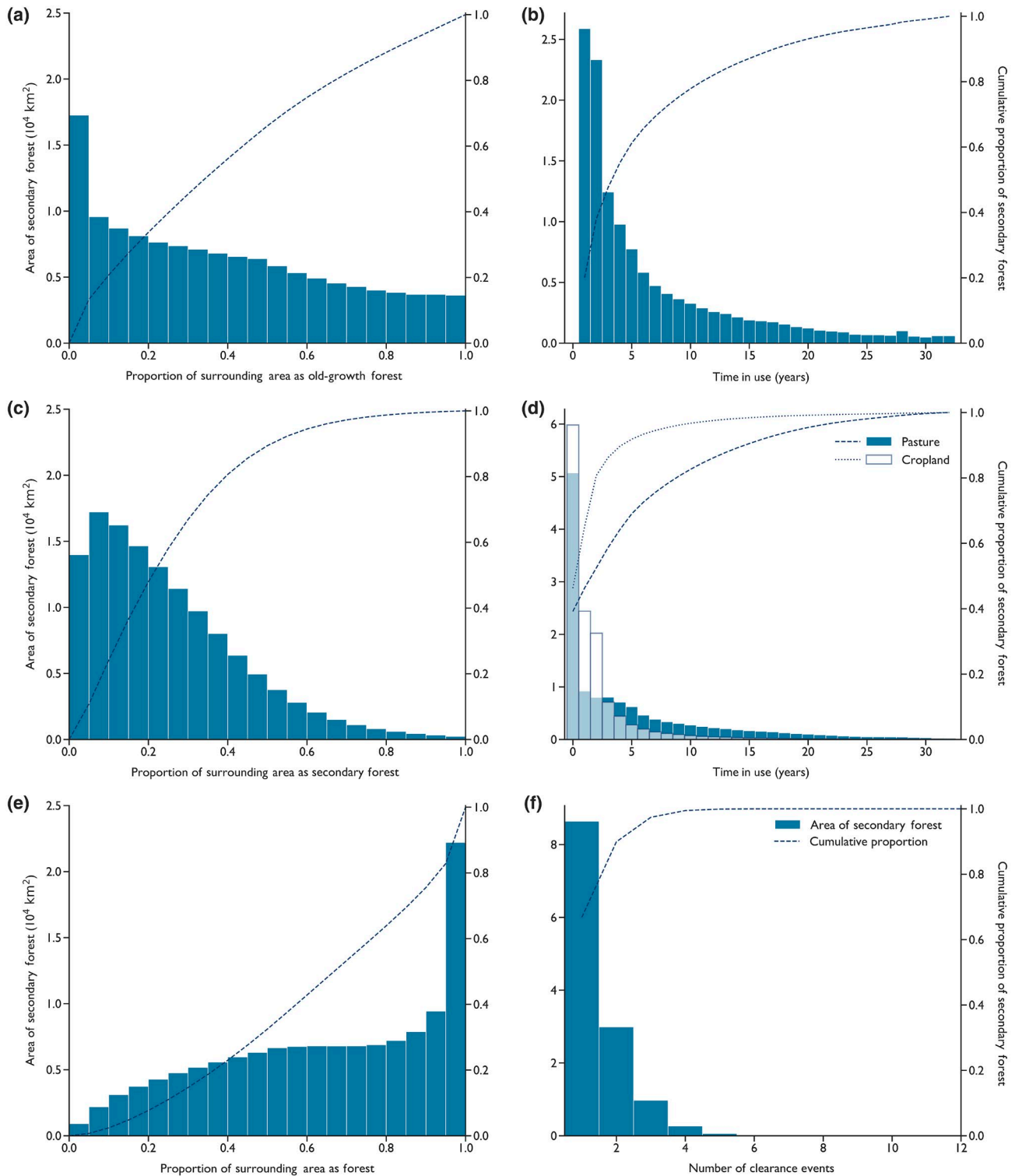


FIGURE 4 Landscape and local contexts of secondary forest in the Brazilian Amazon in 2017. The distribution of landscape (a, c, e) and local (b, d, f) factors known to influence carbon accumulation for secondary forest in the Brazilian Amazon in 2017. Landscape factors: the proportion of land cover within 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, d) the number of years a secondary forest pixel spent as agriculture before abandonment and (f) the number of clearance cycles

the others and statistically marginal given the sample sizes and the number of tests ($p = .02$; Figure 5; Figure S5). The number of clearance events was positively associated with secondary forest cover

($p < .01$; 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 ($p < .01$; Figure 5; Figure S5).

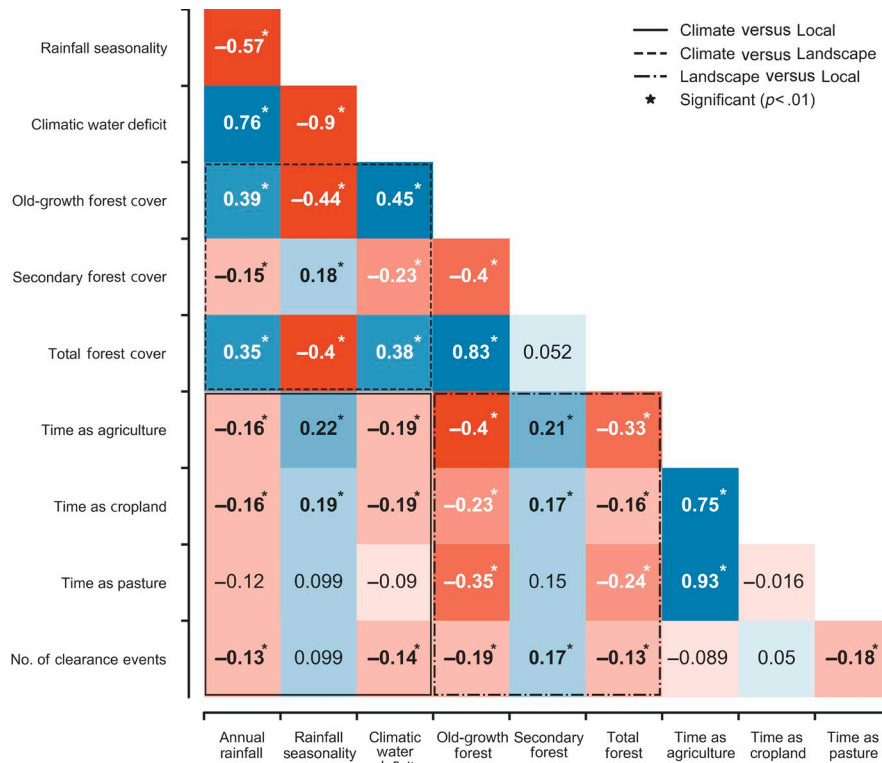


FIGURE 5 Spatial correlations between climatic, landscape and local context of secondary forest in the Brazilian Amazon in 2017. Mean correlation co-efficient of the spatial associations between the climatic, landscape and local contexts of secondary forest in the Brazilian Amazon. The tests used 10,000 iterations of Spearman's Rank-Order Correlation on samples of secondary forest pixels ($n = 1,000$) and a significance (*) threshold of $p < .01$. Samples were selected such that 25% of points were situated in each quadrant of the Amazon biome

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).

3.4.3 | 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 ($p < .01$; Figure 5; Figure S5). Rainfall seasonality was positively correlated with the 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 ($p > .01$; 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 ($p < .01$; Figure 5; Figure S5).

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., 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 (see also Almeida et al., 2016; Nunes et al., 2020). 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. Furthermore, 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.

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 (Elias et al., 2019; Lennox et al., 2018; Poorter et al., 2016; 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 ± 9.2 Mg C/ha, which is just $59 \pm 8\%$ of the average for old-growth forest (115.2 Mg C/ha; Avitabile et al., 2016). Furthermore, some secondary forests recover at much slower rates still, reaching just 34.6 Mg C/ha at 32 years (Elias et al., 2019). Moreover, these maximum values are rarely attained because high rates of secondary forest clearance (6,410 km²/year) 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 $12 \pm 2\%$ of the carbon of old-growth forest, comprised almost 50% of all secondary forests.

The carbon balance of secondary forests is 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 young 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).

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

4.2.1 | 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 & Garcia-Carreras, 2015) and higher temperatures (Silva et al., 2016), leading to increased evapotranspiration and drought stress. Over longer timescales, 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 (Esquivel-Muelbert et al., 2019; Phillips et al., 2009) 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), with pioneer tree species having lower water use efficiency (Markesteijn et al., 2011) and mortality from droughts being 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.

4.2.2 | 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 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 4a). Most secondary forests were found along the highly deforested agricultural frontier, where they may suffer the negative impacts of fragmentation, isolation and edge effects (Ewers & Didham, 2005; Magnago et al., 2017). Consequently, these forests likely have considerably lower carbon accumulation potential than those in regions with more intact forest landscapes (Bihn et al., 2010; Chazdon, 2003). 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 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.

4.2.3 | 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 & Fearnside, 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 to be 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 & Guimarães, 1996). We find 46.3% of secondary forests in 2017 to be growing on land that was previously a pasture and a further 14.6% on land that was pasture at some point during the most recent land use cycle (Figure 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 & Fearnside, 2015) or mechanized 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 & 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.

4.2.4 | 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 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 suggest 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 consequences 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.

4.3 | Uncertainty in the role of secondary forests as a carbon sink

While the carbon balance of undisturbed forests has been well studied (Brienen et al., 2015; Hubau et al., 2020; Pan et al., 2011; Saatchi et al., 2011), estimates of the rate of carbon sequestration in secondary forests remain highly variable (Elias et al., 2019; Grace et al., 2014; Pan et al., 2011; Saatchi et al., 2011). 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 overrepresenting the accumulation rates of regions that are wetter and less seasonal than the majority of secondary forests in the Brazilian Amazon (see Data S1). 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 mechanized agriculture had intensified land use. Recent studies from other regions have shown much lower carbon accumulation rates of 2.25 Mg ha⁻¹ year⁻¹ in Paragominas and Santarém-Belterra (Lennox et al., 2018), 1.08 Mg ha⁻¹ year⁻¹ in Bragança (Elias et al., 2019) or as low as 0.89 Mg ha⁻¹ year⁻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 the source of carbon emissions affects 17% of the forest area in the Amazon (Bullock et al., 2020), meaning that

we are underestimating emissions from old-growth forests and overestimating 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 plots will also provide advantages over chronosequence approaches, allowing biomass responses to climatic variation to be included in models (Elias et al., 2019).

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 km² 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 & Aklilu, 2016). More accurate quantification of carbon stocks and recovery rates in secondary forests will support the production of appropriate management proposals (Wandelli & Fearnside, 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.

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DATA AVAILABILITY STATEMENT

This study makes use of the following publicly available data sets: MapBiomass Brazil v3.1 (<https://mapbiomas.org>), Avitabile et al. (2016; https://www.wur.nl/en/Research-Results/Chair-groups/Environmental-Sciences/Laboratory-of-Geo-information-Science-and-Remote-Sensing/Research/Integrated-land-monitoring/Forest_Biomass.htm), WorldClim (<https://www.worldclim.org>) and Chave et al. (2014; http://chave.ups-tlse.fr/pantropical_allometry). All codes used to run change detection are available here: <https://github.com/charlottesmith0308/amazon-secondary-forest>.

ORCID

Charlotte C. Smith  <https://orcid.org/0000-0002-3767-6587>

Gareth D. Lennox  <https://orcid.org/0000-0002-4285-0551>

REFERENCES

- Achard, F., Eva, H. D., Stibig, H.-J., Mayaux, P., Gallego, J., Richards, T., & Malingreau, J.-P. (2002). Determination of deforestation rates of the world's humid tropical forests. *Science*, 297(5583), 999–1002. <https://doi.org/10.1126/science.1070656>
- Aide, T. M., Clark, M. L., Grau, H. R., López-Carr, D., Levy, M. A., Redo, D., Bonilla-Moheno, M., Riner, G., Andrade-Núñez, M. J., & Muñiz, M. (2013). Deforestation and reforestation of Latin America and the Caribbean (2001–2010). *Biotropica*, 45(2), 262–271. <https://doi.org/10.1111/j.1744-7429.2012.00908.x>
- Almeida, D. R. A., Stark, S. C., Chazdon, R., Nelson, B. W., Cesar, R. G., Meli, P., Gorgens, E. B., Duarte, M. M., Valbuena, R., Moreno, V. S., Mendes, A. F., Amazonas, N., Gonçalves, N. B., Silva, C. A., Schiatti, J., & Brancalion, P. H. S. (2019). The effectiveness of lidar remote sensing for monitoring forest cover attributes and landscape restoration. *Forest Ecology and Management*, 438, 34–43. <https://doi.org/10.1016/j.foreco.2019.02.002>
- Avitabile, V., Herold, M., Heuvelink, G. B. M., Lewis, S. L., Phillips, O. L., Asner, G. P., Armston, J., Ashton, P. S., Banin, L., Bayol, N., Berry, N. J., Boeckx, P., de Jong, B. H. J., DeVries, B., Girardin, C. A. J., Kearsley, E., Lindsell, J. A., Lopez-Gonzalez, G., Lucas, R., ... Willcock, S. (2016). An integrated pan-tropical biomass map using multiple reference datasets. *Global Change Biology*, 22(4), 1406–1420. <https://doi.org/10.1111/gcb.13139>
- Baccini, A., Goetz, S. J., Walker, W. S., Laporte, N. T., Sun, M., Sulla-Menashe, D., Hackler, J., Beck, P. S. A. A., Dubayah, R., Friedl, M. A., Samanta, S., & Houghton, R. A. (2012). Estimated carbon dioxide emissions from tropical deforestation improved by carbon-density maps. *Nature Climate Change*, 2(3), 182–185. <https://doi.org/10.1038/nclimate1354>
- Baker, T. R., Phillips, O. L., Malhi, Y., Almeida, S., Arroyo, L., Di Fiore, A., Erwin, T., Killeen, T. J., Laurance, S. G., Laurance, W. F., Lewis, S. L., Lloyd, J., Monteagudo, A., Neill, D. A., Patiño, S., Pitman, N. C. A., Silva, M., Natalino, J., & Vásquez Martínez, R. (2004). Variation in wood density determines spatial patterns in Amazonian

- forest biomass. *Global Change Biology*, 10(5), 545–562. <https://doi.org/10.1111/j.1365-2486.2004.00751.x>
- Benayas, J. M. R., Martins, A., Nicolau, J. M., & Schulz, J. J. (2007). Abandonment of agricultural land: An overview of drivers and consequences. *CAB Reviews: Perspectives in Agriculture, Veterinary Science, Nutrition and Natural Resources*, 2(57), 1–14. <https://doi.org/10.1079/PAVSNNR20072057>
- Berenguer, E., Ferreira, J., Gardner, T. A., Aragão, L. E. O. C., De Camargo, P. B., Cerri, C. E., Durigan, M., De Oliveira, R. C., Vieira, I. C. G., & Barlow, J. (2014). A large-scale field assessment of carbon stocks in human-modified tropical forests. *Global Change Biology*, 20(12), 3713–3726. <https://doi.org/10.1111/gcb.12627>
- Bihn, J. H., Gebauer, G., & Brandl, R. (2010). Loss of functional diversity of ant assemblages in secondary tropical forests. *Ecology*, 91(3), 782–792. <https://doi.org/10.1890/08-1276.1>
- Bonn Challenge. (2011). *Bonn Challenge*. <https://www.bonnchallenge.org>
- Brienen, R. J. W., Phillips, O. L., Feldpausch, T. R., Gloor, E., Baker, T. R., Lloyd, J., Lopez-Gonzalez, G., Monteagudo-Mendoza, A., Malhi, Y., Lewis, S. L., Vásquez Martínez, R., Alexiades, M., Álvarez Dávila, E., Alvarez-Loayza, P., Andrade, A., Aragão, L. E. O. C., Araujo-Murakami, A., Arets, E. J. M. M., Arroyo, L., ... Zagt, R. J. (2015). Long-term decline of the Amazon carbon sink. *Nature*, 519(7543), 344–348. <https://doi.org/10.1038/nature14283>
- Bullock, E. L., Woodcock, C. E., Souza, C., & Olofsson, P. (2020). Satellite-based estimates reveal widespread forest degradation in the Amazon. *Global Change Biology*, 26(5), 2956–2969. <https://doi.org/10.1111/gcb.15029>
- Caughlin, T. T., Elliott, S., & Lichstein, J. W. (2016). When does seed limitation matter for scaling up reforestation from patches to landscapes? *Ecological Applications*, 26(8), 2439–2450. <https://doi.org/10.1002/eap.1410>
- Chave, J., Piconiot, C., Maréchaux, I., Foresta, H., Larpin, D., Fischer, F. J., Derroire, G., Vincent, G., & Hérault, B. (2020). Slow rate of secondary forest carbon accumulation in the Guianas compared with the rest of the Neotropics. *Ecological Applications*, 30(1), <https://doi.org/10.1002/eap.2004>
- Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M. S., Delitti, W. B. C., Duque, A., Eid, T., Fearnside, P. M., Goodman, R. C., Henry, M., Martínez-Yrizar, A., Mugasha, W. A., Muller-Landau, H. C., Mencuccini, M., Nelson, B. W., Ngomanda, A., Nogueira, E. M., Ortiz-Malavassi, E., ... Vieilledent, G. (2014). Improved allometric models to estimate the aboveground biomass of tropical trees. *Global Change Biology*, 20(10), 3177–3190. <https://doi.org/10.1111/gcb.12629>
- Chazdon, R. L. (2003). Tropical forest recovery: legacies of human impact and natural disturbances. *Perspectives in Plant Ecology Evolution and Systematics*, 6(December 2003), 51–71. <https://doi.org/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. <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=7OPBsqliGk9&sig=G-I2JklVx6756ZMWzipi5h1JylE#v=onepage&q=SecondGrowth%3AThePromise>
- Chazdon, R. L., Broadbent, E. N., Rozendaal, D. M. A., Bongers, F., Zambrano, A. M. A., Aide, T. M., Balvanera, P., Becknell, J. M., Boukili, V., Brancalion, P. H. S., Craven, D., Almeida-Cortez, J. S., Cabral, G. A. L., De Jong, B., Denslow, J. S., Dent, D. H., DeWalt, S. J., Dupuy, J. M., Durán, S. M., ... Poorter, L. (2016). Carbon sequestration potential of second-growth forest regeneration in the Latin American tropics. *Science Advances*, 2(5). <https://doi.org/10.1126/sciadv.1501639>
- Crouzeilles, R., Ferreira, M. S., Chazdon, R. L., Lindenmayer, D. B., Sansevero, J. B. B., Monteiro, L., Iribarrem, A., Latawiec, A. E., & Strassburg, B. B. N. (2017). Ecological restoration success is higher for natural regeneration than for active restoration in tropical forests. *Science Advances*, 3(11), e1701345. <https://doi.org/10.1126/sciadv.1701345>
- de Almeida, C. A., Coutinho, A. C., Esquerdo, J. C. D. M., Adami, M., Venturieri, A., Diniz, C. G., Dessay, N., Durieux, L., & Gomes, A. R. (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*, 46(3), 291–302. <https://doi.org/10.1590/1809-4392201505504>
- Eggleston, H. S., Buendia, L., Miwa, K., Ngara, T., & Tanabe, K. (Eds.). (2006). *2006 IPCC guidelines for national greenhouse gas inventories*. IGES. https://www.ipcc-nggip.iges.or.jp/public/2006gl/pdf/4_Volum_e4/V4_00_Cover.pdf
- Elias, F., Ferreira, J., Lennox, G. D., Berenguer, E., Ferreira, S., Schwartz, G., Melo, L. D. O., Reis Júnior, D. N., Nascimento, R. O., Ferreira, F. N., Espirito-Santo, F., Smith, C. C., & Barlow, J. (2020). Assessing the growth and climate sensitivity of secondary forests in highly deforested Amazonian landscapes. *Ecology*, 101(3), <https://doi.org/10.1002/ecy.2954>
- Esquivel-Muelbert, A., Baker, T. R., Dexter, K. G., Lewis, S. L., Brienen, R. J. W., Feldpausch, T. R., Lloyd, J., Monteagudo-Mendoza, A., Arroyo, L., Álvarez-Dávila, E., Higuchi, N., Marimon, B. S., Marimon-Junior, B. H., Silveira, M., Vilanova, E., Gloor, E., Malhi, Y., Chave, J., Barlow, J., ... Phillips, O. L. (2019). Compositional response of Amazon forests to climate change. *Global Change Biology*, 25(1), 39–56. <https://doi.org/10.1111/gcb.14413>
- Eva, H. D., Achard, F., Beuchle, R., de Miranda, E., Carboni, S., Seliger, R., Vollmar, M., Holler, W. A., Oshiro, O. T., Arroyo, V. B., & Gallego, J. (2012). Forest cover changes in tropical south and Central America from 1990 to 2005 and related carbon emissions and removals. *Remote Sensing*, 4(5), 1369–1391. <https://doi.org/10.3390/rs4051369>
- Ewers, R. M., & Didham, R. K. (2005). Confounding factors in the detection of species responses to habitat fragmentation. *Biological Reviews*, 81(01), 117. <https://doi.org/10.1017/S1464793105006949>
- FAO. (2012). *Global ecological zones for FAO forest reporting: 2010 update*. <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), 213–226. <https://doi.org/10.1017/S0376892900032355>
- Fearnside, P. M. (2005). Deforestation in Brazilian Amazonia: History, rates, and consequences. *Conservation Biology*, 19(3), 680–688. <https://doi.org/10.1111/j.1523-1739.2005.00697.x>
- Fearnside, P. M., & Guimarães, W. M. (1996). Carbon uptake by secondary forests in Brazilian Amazonia. *Forest Ecology and Management*, 80(1–3), 35–46. [https://doi.org/10.1016/0378-1127\(95\)03648-2](https://doi.org/10.1016/0378-1127(95)03648-2)
- Fernandes Neto, J. G., Costa, F. R. C., Williamson, G. B., & Mesquita, R. C. G. (2019). Alternative functional trajectories along succession after different land uses in central Amazonia. *Journal of Applied Ecology*, 56(11), 2472–2481. <https://doi.org/10.1111/1365-2664.13484>
- Fu, R., Yin, L., Li, W., Arias, P. A., Dickinson, R. E., Huang, L., Chakraborty, S., Fernandes, K., Liebmann, B., Fisher, R., & Myneni, R. B. (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*, 110(45), 18110–18115. <https://doi.org/10.1073/pnas.1302584110>
- Fujisaka, S., Bell, W., Thomas, N., Hurtado, L., & Crawford, E. (1996). Slash-and-burn agriculture, conversion to pasture, and deforestation in two Brazilian Amazon colonies. *Agriculture, Ecosystems & Environment*, 59(1–2), 115–130. [https://doi.org/10.1016/0167-8809\(96\)01015-8](https://doi.org/10.1016/0167-8809(96)01015-8)
- Grace, J., Mitchard, E., & Gloor, E. (2014). Perturbations in the carbon budget of the tropics. *Global Change Biology*, 20(10), 3238–3255. <https://doi.org/10.1111/gcb.12600>
- Grassi, G., House, J., Dentener, F., Federici, S., den Elzen, M., & Penman, J. (2017). The key role of forests in meeting climate targets requires

- science for credible mitigation. *Nature Climate Change*, 7(3), 220–226. <https://doi.org/10.1038/nclimate3227>
- Gren, I.-M., & Aklilu, A. Z. (2016). Policy design for forest carbon sequestration: A review of the literature. *Forest Policy and Economics*, 70, 128–136. <https://doi.org/10.1016/j.FORPOL.2016.06.008>
- Griscom, B. W., Adams, J., Ellis, P. W., Houghton, R. A., Lomax, G., Miteva, D. A., Schlesinger, W. H., Shoch, D., Siikamäki, J. V., Smith, P., Woodbury, P., Zganjar, C., Blackman, A., Campari, J., Conant, R. T., Delgado, C., Elias, P., Gopalakrishna, T., Hamsik, M. R., ... Fargione, J. (2017). Natural climate solutions. *Proceedings of the National Academy of Sciences of the United States of America*, 114(44), 11645–11650. <https://doi.org/10.1073/pnas.1710465114>
- Guariguata, M. R., & Ostertag, R. (2001). Neotropical secondary forest succession: Changes in structural and functional characteristics. *Forest Ecology and Management*, 148(1–3), 185–206. [https://doi.org/10.1016/S0378-1127\(00\)00535-1](https://doi.org/10.1016/S0378-1127(00)00535-1)
- Hansen, M. C., Potapov, P. V., Moore, R., Hancher, M., Turubanova, S. A., Tyukavina, A., Thau, D., Stehman, S. V., Goetz, S. J., Loveland, T. R., Kommareddy, A., Egorov, A., Chini, L., Justice, C. O., & Townshend, J. R. G. (2013). High-resolution global maps of 21st-century forest cover change. *Science*, 342(6160), 850–853. <https://doi.org/10.1126/science.1244693>
- Harris, N. L., Brown, S., Hagen, S. C., Saatchi, S. S., Petrova, S., Salas, W., Hansen, M. C., Potapov, P. V., & Lotsch, A. (2012). Baseline map of carbon emissions from deforestation in tropical regions. *Science*, 336(6088), 1573–1576. <https://doi.org/10.1126/science.1217962>
- Hawes, J. E., Vieira, I. C. G., Magnago, L. F. S., Berenguer, E., Ferreira, J., Aragão, L. E. O. C., Cardoso, A., Lees, A. C., Lennox, G. D., Tobias, J. A., Waldron, A., & Barlow, J. (2020). A large-scale assessment of plant dispersal mode and seed traits across human-modified Amazonian forests. *Journal of Ecology*, 108, 1373–1385. <https://doi.org/10.1111/1365-2745.13358>
- Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, 25(15), 1965–1978. <https://doi.org/10.1002/joc.1276>
- Houghton, R. A., Skole, D. L., Nobre, C. A., Hackler, J. L., Lawrence, K. T., & Chomentowski, W. H. (2000). Annual fluxes of carbon from deforestation and regrowth in the Brazilian Amazon. *Nature*, 403(6767), 301–304. <https://doi.org/10.1038/35002062>
- Hubau, W., Lewis, S. L., Phillips, O. L., Affum-Baffoe, K., Beeckman, H., Cuní-Sánchez, A., Daniels, A. K., Ewango, C. E. N., Fauset, S., Mukinzi, J. M., Sheil, D., Sonké, B., Sullivan, M. J. P., Sunderland, T. C. H., Taedoumg, H., Thomas, S. C., White, L. J. T., Abernethy, K. A., Adu-Bredu, S., ... Zemagho, L. (2020). Asynchronous carbon sink saturation in African and Amazonian tropical forests. *Nature*, 579(7797), 80–87. <https://doi.org/10.1038/s41586-020-2035-0>
- Initiative 20x20. (2014). <https://initiative20x20.org/>
- Jakovac, C. C., Peña-Claros, M., Kuyper, T. W., & Bongers, F. (2015). Loss of secondary-forest resilience by land-use intensification in the Amazon. *Journal of Ecology*, 103(1), 67–77. <https://doi.org/10.1111/1365-2745.12298>
- Lennox, G. D., Gardner, T. A., Thomson, J. R., Ferreira, J., Berenguer, E., Lees, A. C., Mac Nally, R., Aragão, L. E. O. C., Ferraz, S. F. B., Louzada, J., Moura, N. G., Oliveira, V. H. F., Pardini, R., Solar, R. R. C., Vaz-de Mello, F. Z., Vieira, I. C. G., & Barlow, J. (2018). Second rate or a second chance? Assessing biomass and biodiversity recovery in regenerating Amazonian forests. *Global Change Biology*, 24(12), 5680–5694. <https://doi.org/10.1111/gcb.14443>
- Loarie, S. R., Asner, G. P., & Field, C. B. (2009). Boosted carbon emissions from Amazon deforestation. *Geophysical Research Letters*, 36(14). <https://doi.org/10.1029/2009GL037526>
- Luyssaert, S., Inglima, I., Jung, M., Richardson, A. D., Reichstein, M., Papale, D., Piao, S. L., Schulze, E.-D.-D., Wingate, L., Matteucci, G., Aragao, L., Aubinet, M., Beer, C., Bernhofer, C., Black, K. G., Bonal, D., Bonnefond, J.-M.-M.-M., Chambers, J., Ciais, P., ... Janssens, I. A. (2007). CO₂ balance of boreal, temperate, and tropical forests derived from a global database. *Global Change Biology*, 13(12), 2509–2537. <https://doi.org/10.1111/j.1365-2486.2007.01439.x>
- Magnago, L. F. S., Magrach, A., Barlow, J., Schaefer, C. E. G. R., Laurance, W. F., Martins, S. V., & Edwards, D. P. (2017). Do fragment size and edge effects predict carbon stocks in trees and lianas in tropical forests? *Functional Ecology*, 31(2), 542–552. <https://doi.org/10.1111/1365-2435.12752>
- Markesteyn, L., Poorter, L., Bongers, F., Paz, H., & Sack, L. (2011). Hydraulics and life history of tropical dry forest tree species: Coordination of species' drought and shade tolerance. *New Phytologist*, 191(2), 480–495. <https://doi.org/10.1111/j.1469-8137.2011.03708.x>
- Martínez-Ramos, M., Pingarrón, A., Rodríguez-Velázquez, J., Toledo-Chelala, L., Zermeno-Hernández, I., & Bongers, F. (2016). Natural forest regeneration and ecological restoration in human-modified tropical landscapes. *Biotropica*, 48(6), 745–757. <https://doi.org/10.1111/btp.12382>
- Morton, D. C., Defries, R. S., Randerson, J. T., Gigilo, L., Schroeder, W., & Van Der Werf, G. R. (2008). Agricultural intensification increases deforestation fire activity in Amazonia. *Global Change Biology*, 14(10), 2262–2275. <https://doi.org/10.1111/j.1365-2486.2008.01652.x>
- Nepstad, D. C., de Carvalho, C. R., Davidson, E. A., Jipp, P. H., Lefebvre, P. A., Negreiros, G. H., da Silva, E. D., Stone, T. A., Trumbore, S. E., & Vieira, S. (1994). The role of deep roots in the hydrological and carbon cycles of Amazonian forests and pastures. *Nature*, 372(6507), 666–669. <https://doi.org/10.1038/372666a0>
- New York Declaration on Forests. (2014). *New York Declaration on Forests*. <https://forestdeclaration.org>
- Nunes, S., Oliveira, L., Siqueira, J., Morton, D. C., & Souza, C. M. (2020). Unmasking secondary vegetation dynamics in the Brazilian Amazon. *Environmental Research Letters*, 15(3). <https://doi.org/10.1088/1748-9326/ab76db>
- Pan, Y., Birdsey, R. A., Fang, J., Houghton, R., Kauppi, P. E., Kurz, W. A., Phillips, O. L., Shvidenko, A., Lewis, S. L., Canadell, J. G., Ciais, P., Jackson, R. B., Pacala, S. W., McGuire, A. D., Piao, S., Rautiainen, A., Sitch, S., & Hayes, D. (2011). A large and persistent carbon sink in the world's forests. *Science*, 333(6045), 988–993. <https://doi.org/10.1126/science.1201609>
- Parry, L., Day, B., Amaral, S., & Peres, C. A. (2010). Drivers of rural exodus from Amazonian headwaters. *Population and Environment*, 32(2–3), 137–176. <https://doi.org/10.1007/s11111-010-0127-8>
- Phillips, O. L., Aragão, L. E. O. C., Lewis, S. L., Fisher, J. B., Lloyd, J., López-González, G., Malhi, Y., Monteagudo, A., Peacock, J., Quesada, C. A., van der Heijden, G., Almeida, S., Amaral, I., Arroyo, L., Aymard, G., Baker, T. R., Bánki, O., Blanc, L., Bonal, D., ... Torres-Lezama, A. (2009). Drought sensitivity of the Amazon rainforest. *Science*, 323(5919), 1344–1347. <https://doi.org/10.1126/science.1164033>
- Poorter, L., Bongers, F., Aide, T. M., Almeyda Zambrano, A. M., Balvanera, P., Becknell, J. M., Boukili, V., Brancalion, P. H. S., Broadbent, E. N., Chazdon, R. L., Craven, D., de Almeida-Cortez, J. S., Cabral, G. A. L., de Jong, B. H. J., Denslow, J. S., Dent, D. H., DeWalt, S. J., Dupuy, J. M., Durán, S. M., ... Rozendaal, D. M. A. (2016). Biomass resilience of Neotropical secondary forests. *Nature*, 530(7589), 211–214. <https://doi.org/10.1038/nature16512>
- Powers, J. S., Corre, M. D., Twine, T. E., & Veldkamp, E. (2011). Geographic bias of field observations of soil carbon stocks with tropical land-use changes precludes spatial extrapolation. *Proceedings of the National Academy of Sciences of the United States of America*, 108(15), 6318–6322. <https://doi.org/10.1073/pnas.1016774108>
- PRODES. (2020). PRODES. http://terrabrasilis.dpi.inpe.br/app/dashbord/deforestation/biomes/legal_amazon/rates
- Quesada, C. A., Lloyd, J., Anderson, L. O., Fyllas, N. M., Schwarz, M., & Czimczik, C. I. (2011). Soils of Amazonia with particular reference to the RAINFOR sites. *Biogeosciences*, 8, 1415–1440. <https://doi.org/10.5194/bg-8-1415-2011>

- Quesada, C. A., Phillips, O. L., Schwarz, M., Czimczik, C. I., Baker, T. R., Patiño, S., Fyllas, N. M., Hodnett, M. G., Herrera, R., Almeida, S., Alvarez Dávila, E., Arneeth, A., Arroyo, L., Chao, K. J., Dezzeo, N., Erwin, T., di Fiore, A., Higuchi, N., Honorio Coronado, E., ... Lloyd, J. (2012). Basin-wide variations in Amazon forest structure and function are mediated by both soils and climate. *Biogeosciences*, 9(6), 2203–2246. <https://doi.org/10.5194/bg-9-2203-2012>
- Requena Suarez, D., Rozendaal, D. M. A., De Sy, V., Phillips, O. L., Alvarez-Dávila, E., Anderson-Teixeira, K., Araujo-Murakami, A., Arroyo, L., Baker, T. R., Bongers, F., Brienen, R. J. W., Carter, S., Cook-Patton, S. C., Feldpausch, T. R., Griscom, B. W., Harris, N., Hérault, B., Honorio Coronado, E. N., Leavitt, S. M., ... Herold, M. (2019). Estimating aboveground net biomass change for tropical and subtropical forests: Refinement of IPCC default rates using forest plot data. *Global Change Biology*, 25(11), 3609–3624. <https://doi.org/10.1111/gcb.14767>
- Rogelj, J., Shindell, D., Jiang, K., Fifita, S., Forster, P., Ginzburg, V., Handa, C., Khesghi, H., Kobayashi, S., Kriegler, E., Mundaca, L., Séférian, R., & Vilariño, M. V. (2018). Mitigation pathways compatible with 1.5°C in the context of sustainable development. In V. Masson-Delmotte, P. Zhai, H. O. Pörtner, D. Roberts, J. Skea, P. R. Shukla, A. Pirani, W. Moufouma-Okia, C. Péan, R. Pidcock, S. Connors, J. B. R. Matthews, Y. Chen, X. Zhou, M. I. Gomis, E. Lonnoy, T. Maycock, M. Tignor, & T. Waterfield (Eds.), *Global warming of 1.5°C. An IPCC special report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change* (93–174). IPCC.
- Saatchi, S. S., Harris, N. L., Brown, S., Lefsky, M., Mitchard, E. T. A., Salas, W., Zutta, B. R., Buermann, W., Lewis, S. L., Hagen, S., Petrova, S., White, L., Silman, M., & Morel, A. (2011). Benchmark map of forest carbon stocks in tropical regions across three continents. *Proceedings of the National Academy of Sciences of the United States of America*, 108(24), 9899–9904. <https://doi.org/10.1073/pnas.1019576108>
- Schwartz, N. B., Uriarte, M., DeFries, R., Gutierrez-Velez, V. H., & Pinedo-Vasquez, M. A. (2017). Land-use dynamics influence estimates of carbon sequestration potential in tropical second-growth forest. *Environmental Research Letters*, 12(7), 074023. <https://doi.org/10.1088/1748-9326/aa708b>
- Silva, M. E. S., Pereira, G., & da Rocha, R. P. (2016). Local and remote climatic impacts due to land use degradation in the Amazon "Arc of Deforestation". *Theoretical and Applied Climatology*, 125(3), 609–623. <https://doi.org/10.1007/s00704-015-1516-9>
- Skole, D. L., Chomentowski, W. H., Salas, W. A., & Nobre, A. D. (1994). Physical and human dimensions of deforestation in Amazonia. *BioScience*, 44(5), 314–322. <https://doi.org/10.2307/1312381>
- Spracklen, D. V., Baker, J. C. A., Garcia-Carreras, L., & Marsham, J. H. (2018). The effects of tropical vegetation on rainfall. *Annual Review of Environment and Resources*, 43(1), 193–218. <https://doi.org/10.1146/annurev-environ-102017-030136>
- Spracklen, D. V., & Garcia-Carreras, L. (2015). The impact of Amazonian deforestation on Amazon basin rainfall. *Geophysical Research Letters*, 42(21), 9546–9552. <https://doi.org/10.1002/2015GL066063>
- Toledo, R. M., Perring, M. P., Verheyen, K., Martini, A. M. Z., Ferreira, M. P., & Santos, R. F. (2020). Restoring tropical forest composition is more difficult, but recovering tree-cover is faster, when neighbouring forests are young. *Landscape Ecology*, 35(6), 1403–1416. <https://doi.org/10.1007/s10980-020-01023-7>
- UN Decade on Restoration. (2019). <https://www.decadeonrestoration.org/>
- Uriarte, M., Schwartz, N., Powers, J. S., Marin-Spiotta, E., Liao, W., & Werden, L. K. (2016). Impacts of climate variability on tree demography in second growth tropical forests: The importance of regional context for predicting successional trajectories. *Biotropica*, 48(6), 780–797. <https://doi.org/10.1111/btp.12380>
- van Leeuwen, T. T., van der Werf, G. R., Hoffmann, A. A., Detmers, R. G., Rücker, G., French, N. H. F., Archibald, S., Carvalho, J. A., Cook, G. D., de Groot, W. J., Hély, C., Kasischke, E. S., Kloster, S., McCarty, J. L., Pettinari, M. L., Savadogo, P., Alvarado, E. C., Boschetti, L., Manuri, S., ... Trollope, W. S. W. (2014). Biomass burning fuel consumption rates: A field measurement database. *Biogeosciences Discussions*, 11, 8115–8180. <https://doi.org/10.5194/bgd-11-8115-2014>
- Vera-Diaz, M. D. C., Kaufmann, R. K., Nepstad, D. C., & Schlesinger, P. (2008). An interdisciplinary model of soybean yield in the Amazon Basin: The climatic, edaphic, and economic determinants. *Ecological Economics*, 65(2), 420–431. <https://doi.org/10.1016/J.ECOLECON.2007.07.015>
- Wandelli, E. V., & Fearnside, P. M. (2015). Secondary vegetation in central Amazonia: Land-use history effects on aboveground biomass. *Forest Ecology and Management*, 347, 140–148. <https://doi.org/10.1016/j.foreco.2015.03.020>
- Wang, Y., Ziv, G., Adami, M., de Almeida, C. A., Antunes, J. F. G., Coutinho, A. C., Esquerdo, J. C. D. M., Gomes, A. R., & Galbraith, D. (2020). Upturn in secondary forest clearing buffers primary forest loss in the Brazilian Amazon. *Nature Sustainability*, 3(4), 290–295. <https://doi.org/10.1038/s41893-019-0470-4>

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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