



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

Fernando Elias^{a,b,*}, Joice Ferreira^{a,b}, Angélica F. Resende^b, Erika Berenguer^{c,d}, Filipe França^e, Charlotte C. Smith^d, Gustavo Schwartz^b, Rodrigo O. Nascimento^{a,b}, Matheus Guedes^b, Liana Chesini Rossi^f, Marina Maria Moraes de Seixas^a, Carolina Melo da Silva^{a,g}, Jos Barlow^d

^a Universidade Federal do Pará, Instituto de Ciências Biológicas, Programa de Pós-Graduação em Ecologia, Campus Guamá, 66075-110, Belém, PA, Brazil

^b Embrapa Amazônia Oriental, Rede Amazônia Sustentável, 66095-903, Belém, PA, Brazil

^c Environmental Change Institute, University of Oxford, Oxford OX1 3QY, UK

^d Lancaster Environment Centre, Lancaster University, Lancaster LA1 4YQ, UK

^e School of Biological Sciences, University of Bristol, Bristol BS8 1QU, UK

^f Universidade Estadual Paulista, Departamento de Ecologia, 13506-900, Rio Claro, SP, Brazil

^g Universidade Federal Rural da Amazônia, Campus Capitão Poço, 68650-000, Capitão Poço, PA, Brazil

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ABSTRACT

Secondary forests (SFs) growing on previously cleared land could be a low-cost climate change mitigation strategy due to their potential to sequester CO₂. However, given widespread changes in climate and land-use in the Amazon in the past 20 years, it is not clear whether current rates of carbon uptake by SFs reflect estimates based on dividing the carbon stock by the estimated age of the forest. This is important, as differences between methodological approaches could lead to important discrepancies in estimates of carbon accumulation. Furthermore, we know little about how carbon uptake rates of secondary forests vary across some of the most deforested regions of the Amazon, where reforestation actions are most needed. Here, we compare the rates of carbon accumulation estimated over the lifetime of a stand (by stand age) with the contemporary rates estimated by recensus data, based on 28 permanent SFs plots distributed across four regions. Then, we compare how carbon uptakes rates vary across regions and how they compare to previous studies. The average rates of contemporary ($1.23 \pm 0.57 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$) and lifetime ($1.14 \pm 0.63 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$) carbon accumulation were strongly correlated ($r = 0.78$) and similar between regions. Overall, our carbon accumulation rates were much lower than other estimates of Amazonian SFs, which suggests that regions with the greatest opportunities for large-scale implementation of SFs have some of the slowest rates of carbon accumulation. Contrary to predictions from chronosequence analysis, the lack of difference between lifetime and contemporary rates of carbon accumulation suggests forests are maintaining a consistent rate of growth in the first decades after abandonment. These results—combined with the high rates of ongoing environmental change - highlight the importance of continuing to monitor the rate of carbon accumulation in secondary forests. This is necessary to support the implementation and monitoring of large-scale passive restoration in the highly-deforested Amazon.

1. Introduction

Secondary forests are one of the most important nature-based solutions to climate change (Griscom et al., 2017; Melo et al., 2021) and are fundamental to the commitments of many tropical forest countries under the 2015 Paris agreement. Although high rates of deforestation make Brazil is the world's sixth highest emitter of greenhouse gases (WRI, 2020), it also provides a great potential for carbon sequestration

via forest restoration (Smith et al., 2021). To date, this potential has not been realised beyond broad commitments to restore 12 million hectares of forest by 2030 (BRASIL, 2019). Assuming this goes ahead, a large part of this restoration will likely occur in the Amazon, where restoration already forms a key part of regional government policy to attain carbon neutrality (SEMAS, 2020).

The cheapest and most effective method of restoring deforested areas in the Amazon is 'passive' natural regeneration (Crouzeilles et al., 2017),

* Corresponding author.

E-mail address: felias@ufpa.br (F. Elias).

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which gives rise to secondary forests (defined here as forests growing on land that had been previously cleared for agriculture). The area of natural regeneration in the Amazon has grown steadily over the last 30 years even without policy interventions (Smith et al., 2020), as agricultural abandonment is a direct consequence of the low profitability and unsustainability of many of the prevalent farming systems (Garrett et al., 2017; Lavelle et al., 2016). Currently, approximately 148,764 km² in the Amazon are occupied by secondary forests (Smith et al., 2020). This area represents c. 20–23% of the deforested areas in the region (Smith et al. 2020; INPE, 2020). Although these secondary forests are not ecologically equivalent to primary forests (Barlow et al., 2007; Lennox et al., 2018), they play an important socioeconomic and ecological role in maintaining ecosystem services and protecting the remaining biodiversity (Chazdon, 2014). Crucially, by sequestering CO₂, they are helping to mitigate climate change: between 1985 and 2017, secondary forests in the Brazilian Amazon could have accumulated c. 0.33 billion Mg C, offsetting ~ 10% of the deforestation that occurred in the same period (Smith et al., 2020, 2021).

Despite the potential importance of Amazonian secondary forests as a nature-based solution to climate change, there is much uncertainty about their carbon accumulation rates in some of the most deforested regions, where secondary forests are most prevalent, the potential for large-scale restoration is greatest, and actions are more urgent (Smith et al., 2020, 2021). There are three broad reasons for the uncertainty. First, many of the studies assessing carbon accumulation in secondary forests have focussed on the wetter and less seasonal Amazonian regions (Smith et al., 2020), where carbon accumulation rates are likely to be higher (Poorter et al., 2016; Requena Suarez et al., 2019; Heinrich et al., 2021).

The second uncertainty relates to the age of the forests and the time when studies were carried out. Many of the studies underpinning recent assessments of secondary forest growth are decades old, involving stands that started growing before 1985 (Poorter et al., 2016; Requena Suarez et al., 2019). Conditions may have been more favourable for carbon accumulation in these older assessments as (i) the abandoned land may have undergone fewer agricultural cycles prior to abandonment, with less depletion of soil resources that negatively impact forest recovery (Jakovac et al., 2015); (ii) the cumulative area of deforestation in the Amazon was much lower, meaning older secondary forests were in more favourable landscape with higher levels of primary forest cover and more seed sources (Oberleitner et al., 2021; Rocha-Santos et al., 2016); and (iii) the Amazon was less affected by climate change caused by greenhouse gas emissions or regional deforestation (Fearnside, 2018; Baker & Spracklen, 2019). Increases in temperature and dry seasons lengths (Gloor et al., 2015; Gatti et al., 2021) and the number of extreme droughts (Avila-Diaz et al., 2020) could slow down carbon accumulation rates by increasing tree mortality (Phillips & Brienen, 2017) or by reducing growth due to their negative effects on water balance and photosynthetic capacity (Bretfeld et al., 2018; Elias et al., 2020). In contrast, higher atmospheric CO₂ concentrations may counter these factors, or even encourage faster carbon accumulation rates (Fleischer et al., 2019; Hubau et al., 2020; Walker et al., 2021). Evidence from temperate zones suggests CO₂ fertilisation will have a marked impact on growth young forests (DeLucia et al., 1999; Walker et al., 2019).

The third reason for uncertainty relates to the methodological approaches that have been used in previous studies, which are mostly based on chronosequence data (Poorter et al., 2016; Lennox et al., 2018; Requena Suarez et al., 2019). These approaches can only estimate an average rate of carbon accumulation over the entire lifetime of the stand. Thus, they cannot detect recent changes in the growth rate of forests that result from (i) the sigmoidal shape of successional development that forms the basis of the Bertalanffy-Chapman-Richards forest growth models (Vanclay, 1994) and is supported by empirical data from the Amazon (N'Guessan et al., 2019; Neeff and Dos Santos, 2005), or (ii) recent changes in environmental conditions, such as deforestation or climate change (Carreiras et al., 2017; Johnson & Miyanishi, 2008).

Furthermore, lifetime estimates are reliant on stand age, which is used as the denominator in the calculation. Thus, any inaccuracies in the age of secondary forests estimated by remote sensing or interviews will influence carbon accumulation rates.

Here, we investigate the spatial, temporal and methodological knowledge gaps of carbon accumulation rates in Amazonian secondary forests, increasing the representation of regions where large-scale restoration opportunities are greatest. We use data from 28 permanent plots distributed across four regions in Pará, the Brazilian state with the largest area of deforested land, highest secondary forest coverage (Smith et al., 2021), and where nature-based solutions configure as a top government priority—Pará has committed to restore > 7 million ha of forests by 2035 (SEMAS, 2020; Barlow et al., 2021). We ask (1) do chronosequence approaches to assessing carbon accumulation rates in secondary forests (based on lifetime assessments using each stand's estimated age) reflect contemporary rates (based on recent censuses)? If secondary forests are slowing down their growth rates in response to growth-age functions or environmental change, we would expect lifetime rates to be higher than contemporary rates. We then ask (2) whether our estimates differ across the four survey regions and compare these rates with previous studies. We expect growth rates in our study regions to be significantly lower than many previous estimates, given that our study regions have experienced severe land-use and climatic changes (Elias et al., 2020; Smith et al., 2021).

2. Methods

2.1. Study region

We focused on four regions in the state of Pará—Bragantina (including the municipalities of Bragança and Viseu), Marabá, Parauapebas (Parauapebas and Canaã dos Carajás) and Santarém (Santarém, Belterra, and Mojuí dos Campos). These regions have different histories of colonization and land-use change, which have resulted in their current day forest cover (Fig. 1). The Bragantina region is the oldest agricultural frontier in the Amazon, whereas Marabá, Parauapebas, and Santarém are more recent agricultural frontiers with deforestation ongoing since the 1970 s (Tucker et al., 1998). We provide additional details about landscape context for each region in the Supplementary material (Fig. SM 1; Table SM 1).

2.2. Tree censuses

We established 28 permanent secondary forest plots sampled between 1999 and 2019. We sampled 15 plots in the Bragantina region, five in Marabá, four in Parauapebas and five in Santarém (See Table SM 2 for more details). The older plots in the Bragantina region (plot codes: MHO-01/02) were established in the same small fragment and, therefore, we used the average values in the analyses (Table SM 2). All plots were 0.25 ha (250 × 10 m) and located on *terra-firme* forests. Within each region, plots were separated from each other by at least 1.5 km to minimize spatial dependence. Sampling was standardized across all plots—we measured and identified to species level all trees ≥ 10 cm in diameter at breast height (DBH).

2.3. Defining the stand age

Secondary forest age was defined as the number of years since land abandonment (i.e., the age of first regrowth). The stand age of secondary forests varied across sites. In Santarém, it was defined through an analysis of biannual Landsat Images from 1988 to 2010 (Gardner et al., 2013; Lennox et al., 2018). In the other regions, where some sites were older than remote-sensing record, it was estimated through interviews with landowners at the time of the first census (e.g., Elias et al., 2020), which is the standard approach in many studies (e.g., Gilroy et al., 2014; Poorter et al., 2016). The estimated ages of our secondary forest plots

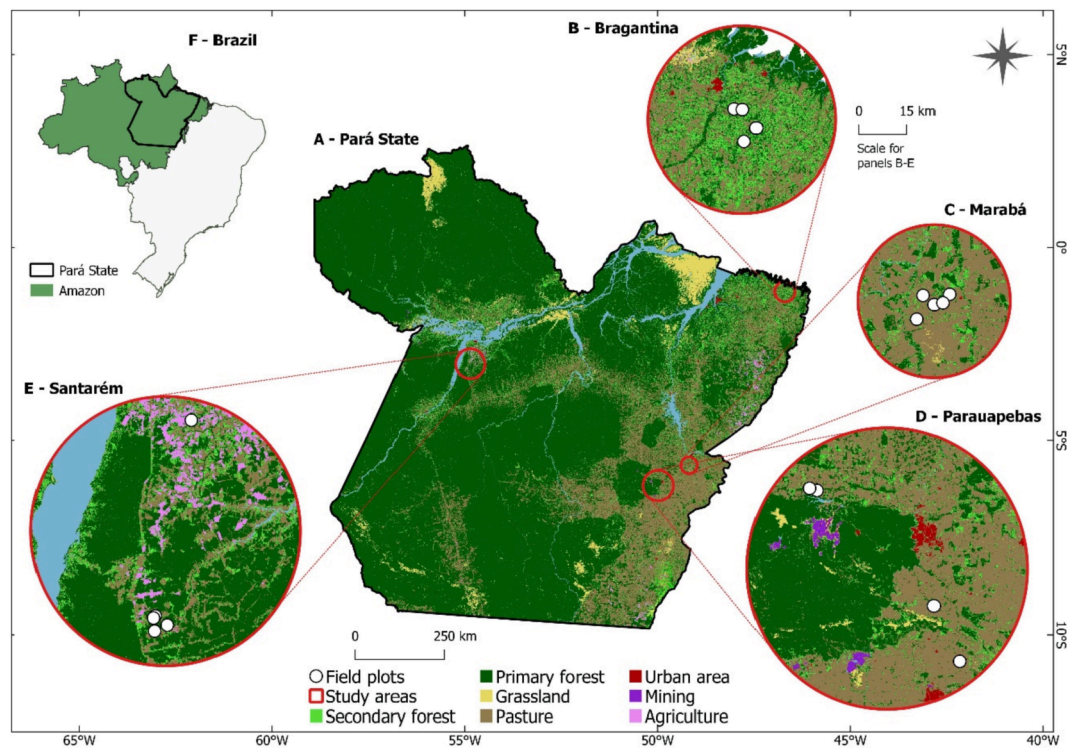


Fig. 1. Location of our four study regions in the state of Pará, in the Brazilian Amazon. The main land-uses in the state are old-growth forest (dark green), secondary forest (light green), pasture (brown) and agriculture (pink). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

ranged from 9 to 58 years at the time of the last census (Table SM 2).

2.4. Carbon stock and accumulation estimates

We calculate the aboveground biomass (AGB) of each stem using the equation $AGB = 0.673 \times (\rho D^2 H)^{0.976}$ (Chave et al., 2014) performed in the 'BIOMASS' package (Réjou-Méchain et al., 2017). Where, ρ is wood density extracted from the Global Wood Density Database; D is diameter at breast height (cm); and H is total height (m) estimated by height-diameter models at region-level (Sullivan et al., 2018). We assumed carbon stocks to represent 50% of AGB (Ngo et al., 2013). We calculate plot-level carbon stock as the sum of the carbon stock of all individuals in a plot.

To calculate lifetime carbon accumulation rates, we divided each plot's carbon stocks by the age since land abandonment. To calculate contemporary carbon accumulation rates, we subtracted, from the last census, the carbon stocks from the prior census, dividing by the number of years in the interval between both censuses.

2.5. Statistical analyses

All statistical analyses were performed in software R version 4.0.3 (R Core Team, 2020). We used Pearson's Linear Correlation analysis to assess the similarity of lifetime and contemporary carbon accumulation rates. To compare carbon accumulation rates between regions we used Linear Models (LM) performed by 'lsmeans' package (Lenth, 2016). In addition, we graphically compared the percentage differences in the average carbon accumulation rates of our plots with the carbon accumulation estimates from 1) Poorter et al. (2016) for SF < 20 years old in eastern Pará (East Pará 1–3); 2) Lennox et al. (2018) for SF < 20 years in the Santarém region; 3) Heinrich et al. (2021) for SF < 20 years in the Eastern Amazon (*sensu lato*); and Requena Suarez et al. (2019) for SF < 20 and > 20 years across tropical South America. We also used LM to examine whether stand age predicted any difference between the

lifetime and contemporary carbon accumulation rates. The models' assumptions were checked by the graphical analysis (Quinn & Keough, 2002). We tested the spatial autocorrelation using the Durbin Watson test and found no spatial dependence on the models' residuals (p -value > 0.05).

We compared the last 20 years (1990–2020) variation in annual rainfall between our secondary forest plots with previous studies used in the Fig. 4, except for Heinrich et al. (2021) and Requena Suarez et al. (2019) whose estimates of carbon accumulation are not site based and include large-scale regions (secondary forests in Eastern Amazonia and South America, respectively). From the geographical coordinates of the plots (ours and those found in previous studies), we extracted from the CHIRPS database the annual rainfall values between the years 1990 and 2020. We then calculated and plotted the average and confidence interval (95%) in a biplot (Fig. SM 2). The original CHIRPS rainfall data is available in: <https://edcintl.cr.usgs.gov/downloads/sciweb1/shared/fews/web/global/monthly/chirps/final/downloads/monthly/>.

3. Results

Lifetime and contemporary carbon accumulation rates were strongly and positively correlated ($r = 0.78$, $p < 0.05$; Fig. 2), and stand age did not explain the difference between contemporary and lifetime rates (Fig. 3). We also found no difference between contemporary ($1.23 \pm 0.57 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$) or lifetime ($1.14 \pm 0.63 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$) approaches to estimating carbon accumulation within the regions evaluated ($p > 0.05$; Table SM 3).

Despite the variation in carbon accumulation in previous studies in Amazonian secondary forests, both of our estimates of carbon accumulation rates (i.e., lifetime and contemporary) were much lower than the estimates of Poorter et al. (2016) and the younger secondary forests of Requena Suarez et al. (2019) (Fig. 4). For example, Poorter et al.'s (2016) rates for secondary forests up to 20 years old in Eastern Amazon were 49% and 92% higher than our highest and lowest contemporary

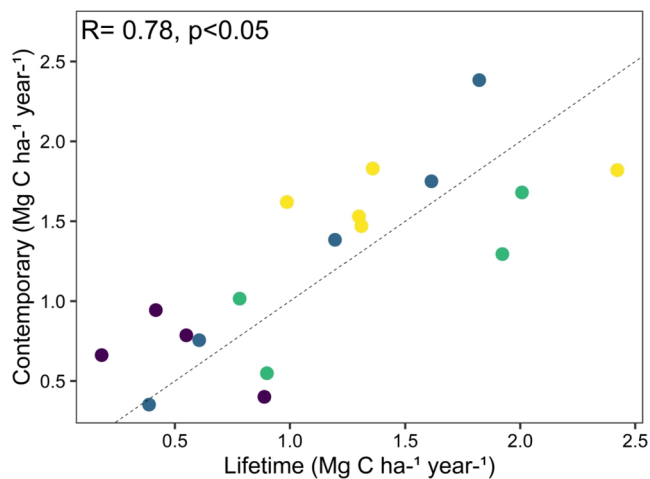


Fig. 2. Pearson's correlations between contemporary and lifetime carbon accumulation rates in secondary forests. The regions are represented by purple (Bragantina), blue (Marabá), green (Parauapebas) and yellow points (Santarém). Dashed line represents the 1:1 ratio. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

rates, and 48% and 96% of our lifetime carbon accumulation rates, respectively. Our rates were also much lower than Requena Suarez et al.'s (2019) estimates for similar aged secondary forests in South America, and are more in line with their much slower rate estimated for older forests. Overall, the estimates of Heinrich et al. (2021) are more similar to our estimates, but the rates from the Bragantina region were lower than even these (Fig. 4).

4. Discussion

We report results from the first large-scale study of contemporary carbon accumulation rates of Amazonian secondary forests. These findings provide robust insights into carbon accumulation rates in regions where deforestation has been extensive and where have the largest areas available for large-scale restoration. We provide comparisons between contemporary and lifetime rates and discuss about their methodological implications for a better understanding of interregional patterns of carbon accumulation in secondary forests.

4.1. Assessing the successional trajectory of carbon accumulation

There are many reasons why secondary forest growth rates would slow over time. The attenuation of growth with stand age has been identified in many chronosequence studies (Saldarriaga et al., 1988; Poorter et al., 2016; N'Guessan et al., 2019; Requena Suarez et al., 2019; Heinrich et al., 2021), while the loss of forest cover and climate changes in the past 40 years (e.g., Gatti et al. 2021) could lead to theoretically slower growth (Elias et al., 2020). Yet, the evidence here did not meet this expectation for forest stands with the age range we examined (9–58 years), as (i) there was a strong positive correlation between lifetime and contemporary rates, and (ii) their overall rates were similar. Furthermore, although the differences were not significant, the direction of the trends actually puts contemporary above lifetime rates in three of the four regions (Fig. 3) and 67% of plots (Fig. 2).

There are two possible explanations for these findings. First, models assuming a decrease in secondary forest growth rates over time, such as those used by Requena Suarez et al. (2019) and Heinrich et al. (2021), are almost certainly an oversimplification of sigmoidal growth curve that is supported by both theoretical (Vanclay, 1994) and empirical (N'Guessan et al., 2019; Neeff and Dos Santos, 2005) evidence. Sigmoidal growth could mask changes if the faster and slower parts of

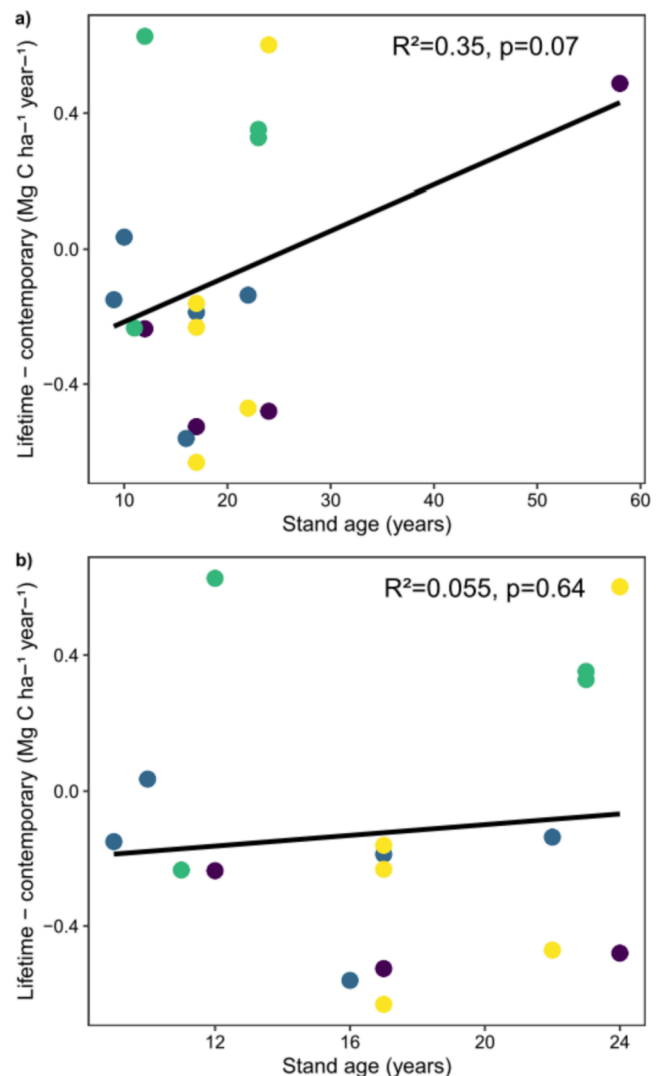


Fig. 3. Relationship between differences in carbon accumulation rates (lifetime - contemporary) and stand age of secondary forests with the insertion (a) and removal of age outliers (b). The regions are represented by purple (Bragantina), blue (Marabá), green (Parauapebas) and yellow points (Santarém). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the sigmoidal curve are balancing each other out over the assessed time-scales. However, if this was the case, we would also expect a significant negative relationship between stand age and the difference between contemporary and lifetime rates—which was not supported (Fig. 3).

A second possibility is that the expected reduction in secondary forest carbon accumulation with stand age are being offset by environmental change such as CO₂ fertilisation. It seems likely that increases in CO₂ would have a strong positive effect in tropical secondary vegetation, as (i) CO₂ enrichment experiments show an important fertilisation effect in young and early successional temperate forests (DeLucia et al., 1999; Walker et al., 2019), and (ii) early successional growth is less constrained by competition (van Kuijk et al., 2008) and/or (iii) the high prevalence of nitrogen-fixing legumes could help overcome constraints from nutrients (Batterman et al., 2013). Although our observational data do not prove an effect, they form the basis for developing hypotheses, and suggest that a better understanding of secondary forest responses to CO₂ fertilisation could be key to determining their effectiveness as a nature-based solution to climate change. Although the Amazon-FACE experiment will provide interesting insights into forest responses to CO₂ (Lapola & Norby, 2014), there is no comparable

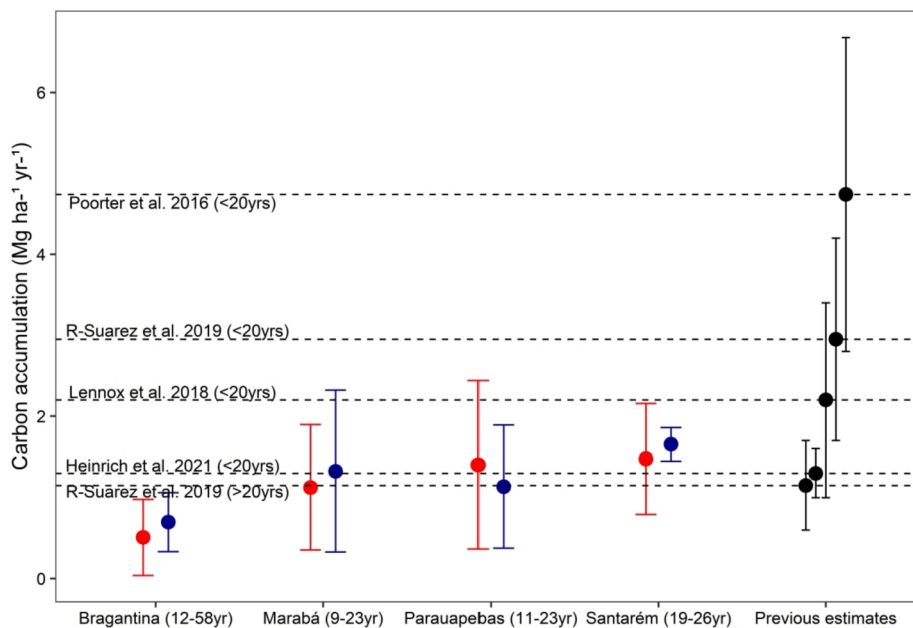


Fig. 4. Comparisons of contemporary (darkblue) and lifetime (red) carbon accumulation rates of secondary forests across regions and with others estimates (black) for the Eastern Amazon (Poorter et al., 2016; Lennox et al., 2018; Heinrich et al., 2021) and South America (Requena Suarez et al., 2019). Points represent the average rates ($\pm 95\%$ CI). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

experiment assessing secondary forests.

4.2. Methodological implications for assessing carbon accumulation rates in secondary forests

Although the idiosyncratic processes that occur during forest succession challenge carbon recovery predictions in secondary forests (Arroyo-Rodríguez et al., 2017), our results indicate that rates of contemporary and lifetime carbon accumulation in secondary forests are convergent. Contemporary carbon accumulation rates can be predicted—at c. 78%—by using a single assessment of the carbon stock and stand age. These results are encouraging from a scientific point of view, as most existing data comes from one off surveys. However, there are some important limitations to this positive correlation. First, our results do not include all stages of succession, as they are restricted to secondary forests up to 58 years old. Therefore, longer-term extrapolations of carbon accumulation remain less certain (c.f. Requena Suarez et al., 2019). Second, although we did not detect changes in secondary forest growth rates over time, this does not mean that they will have not or will not occur. Such changes are key to understanding forest responses to climate change arising from global greenhouse gas emission (IPCC, 2021) or regional changes in the climate brought about by deforestation, agricultural intensification, or large-scale reforestation (e.g., Maeda et al., 2021; Mu et al., 2021). Continuous monitoring of the carbon dynamics of secondary forests is fundamental for effectively assessing the resilience of tropical forests in an era of rapid environmental change, and would provide a valuable additional contribution to the large-scale understanding gained from plot networks in intact forests (Lopez-Gonzalez et al., 2011; ForestPlots.net et al., 2021).

4.3. Implications for large-scale restoration of eastern Amazon

Secondary forests are a strategic nature-based solution to climate change, and accurate assessments of their carbon balance are vital to track their growth rates over time and their responses to environmental changes. The high convergence between lifetime and contemporaneous carbon accumulation rates supported by our data is an important methodological finding, which supports efforts to predict the regional variation in carbon accumulation using data from chronosequences.

However, we also found that carbon recovery rates are lower in much of the eastern Amazon, emphasizing the need for more data from drier and more deforested regions in these assessments. Finally, these slower rates should not be used to discourage restoration efforts in the drier and more deforested regions of the Amazon. First, our results suggest that recovery rates of secondary forests are not slowing down in the first decades of regrowth, which bode well for large-scale passive restoration. Second, carbon accumulation per hectare is only one consideration when implementing restoration, and a broad suite of costs and benefits should be evaluated.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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