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

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## Abstract\*\*

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Secondary forests (SFs) growing on previously cleared land could be a low-cost 23 climate change mitigation strategy due to their potential to sequester CO<sub>2</sub>. 24 However, given widespread changes in climate and land-use in the Amazon in the 25 past 20 years, it is not clear whether current rates of carbon uptake by SFs reflect 26 estimates based on dividing the carbon stock by the estimated age of the forest. 27 28 This is important, as differences between methodological approaches could lead to important discrepancies in estimates of carbon accumulation. Furthermore, we 29 know little about how carbon uptake rates of secondary forests vary across some 30 of the most deforested regions of the Amazon, where reforestation actions are 31 most needed. Here, we compare the rates of carbon accumulation estimated over 32 the lifetime of a stand (by stand age) with the contemporary rates estimated by 33 recensus data, based on 28 permanent SFs plots distributed across four regions. 34 Then, we compare how carbon uptakes rates vary across regions and how they 35 compare to previous studies. The average rates of contemporary (1.23 ±0.57 Mg C 36 ha<sup>-1</sup> yr<sup>-1</sup>) and lifetime (1.14 ±0.63 Mg C ha<sup>-1</sup> yr<sup>-1</sup>) carbon accumulation were 37 strongly correlated (r = 0.78) and similar between regions. Overall, our carbon 38 39 accumulation rates were much lower than other estimates of Amazonian SFs, which suggests that regions with the greatest opportunities for large-scale 40 implementation of SFs have some of the slowest rates of carbon accumulation. 41 Contrary to predictions from chronosequence analysis, the lack of difference 42 between lifetime and contemporary rates of carbon accumulation suggests forests 43 are maintaining a consistent rate of growth in the first decades after abandonment. 44

- These results combined with the high rates of ongoing environmental change -
- 46 highlight the importance of continuing to monitor the rate of carbon accumulation in
- 47 secondary forests. This is necessary to support the implementation and monitoring
- of large-scale passive restoration in the highly-deforested Amazon.
- 49 Keywords: Aboveground biomass, natural regeneration, nature based-solutions,
- 50 UN restoration decade
  - \*\* The abstract in Portuguese is available in the Supplementary Material.

## 1. Introduction

Secondary forests are one of the most important nature-based solutions to climate change (Griscom et al., 2017; Melo et al., 2020) 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), 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 CO<sub>2</sub>, 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).

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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 CO<sub>2</sub> 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 CO<sub>2</sub> fertilisation will have a marked impact on growth young forests (DeLucia, 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 & 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 recensuses)? 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 1970s (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 x 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).

## 2.2 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 Santarem, it was defined through an analysis of biannual Landsat Images from 1988-2010 (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 ranged from 9 to 58 years at the time of the last census (Table SM 2).

#### 2.3 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,  $\rho$  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.

## 2.4 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 'Ismeans' 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 ± 0.57 Mg C ha<sup>-1</sup> yr<sup>-1</sup>) or lifetime (1.14 ± 0.63 Mg C ha<sup>-1</sup> yr<sup>-1</sup>) 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 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).

#### 3. 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.

# 3.1 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 & Santos, 2005) evidence. Sigmoidal growth could mask changes if the faster and slower parts of the sigmoidal curve are balancing each other out over the assessed timescales. 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 CO<sub>2</sub> fertilisation. It seems likely that increases in CO<sub>2</sub> would have a strong positive effect in tropical secondary vegetation, as (i) CO<sub>2</sub> enrichment experiments show an important fertilisation effect in young and early successional temperate forests (DeLucia, 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 CO<sub>2</sub> 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 forest responses to CO<sub>2</sub> (Lapola & Norby, 2014), there is no comparable experiment assessing secondary forests.

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Methodological implications for assessing carbon accumulation rates in secondary forests

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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).

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# 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.

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# References

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

- 364 92(1), 326–340. doi: 10.1111/brv.12231
- Avila-Diaz, A., Benezoli, V., Justino, F., Torres, R., & Wilson, A. (2020). Assessing
- 366 current and future trends of climate extremes across Brazil based on
- reanalyses and earth system model projections. *Climate Dynamics*, *55*(5–6),
- 368 1403–1426. doi: 10.1007/s00382-020-05333-z
- Baker, J. C. A., & Spracklen, D. V. (2019). Climate Benefits of Intact Amazon
- Forests and the Biophysical Consequences of Disturbance. Frontiers in
- Forests and Global Change, 2(August), 1–13. doi: 10.3389/ffgc.2019.00047
- Barlow, J., Gardner, T. A., Araujo, I. S., Avila-Pires, T. C., Bonaldo, A. B., Costa, J.
- E., ... Peres, C. A. (2007). Quantifying the biodiversity value of tropical
- primary, secondary, and plantation forests. *Proceedings of the National*
- 375 Academy of Sciences, 104(47), 18555–18560. doi: 10.1073/pnas.0703333104
- Barlow, J., Sist, P., Almeida, R., Arantes, C. C., Berenguer, E., Caron, P., ...
- Valentim, J. F. (2021). Restoration Options for the Amazon. In *Science Panel*
- for the Amazon Amazon Assessment Report 2021 (p. 31).
- Batterman, S. A., Hedin, L. O., Van Breugel, M., Ransijn, J., Craven, D. J., & Hall,
- J. S. (2013). Key role of symbiotic dinitrogen fixation in tropical forest
- 381 secondary succession. *Nature*, *502*(7470), 224–227. doi:
- 382 10.1038/nature12525
- 383 BRASIL. (2019). REDD+ and Brazil's Nationally Determined Contribution.
- 384 Ministério do Meio Ambiente.
- Bretfeld, M., Ewers, B. E., & Hall, J. S. (2018). Plant water use responses along
- secondary forest succession during the 2015–2016 El Niño drought in

- Panama. New Phytologist, 219(3), 885–899. doi: 10.1111/nph.15071
- Carreiras, J. M. B., Jones, J., Lucas, R. M., & Shimabukuro, Y. E. (2017). Mapping
- major land cover types and retrieving the age of secondary forests in the
- 390 Brazilian Amazon by combining single-date optical and radar remote sensing
- data. Remote Sensing of Environment, 194, 16–32. doi:
- 392 10.1016/j.rse.2017.03.016
- Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M. S., Delitti,
- W. B. C., ... Vieilledent, G. (2014). Improved allometric models to estimate the
- aboveground biomass of tropical trees. Global Change Biology, 20(10), 3177–
- 396 3190. doi: 10.1111/gcb.12629
- 397 Chazdon, R. L. (2014). Second Growth. In Second Growth (Vol. 32). doi:
- 398 10.7208/chicago/9780226118109.001.0001
- 399 Crouzeilles, R., Ferreira, M. S., Chazdon, R. L., Lindenmayer, D. B., Sansevero, J.
- B. B., Monteiro, L., ... Strassburg, B. B. N. (2017). Ecological restoration
- success is higher for natural regeneration than for active restoration in tropical
- 402 forests. *Science Advances*, 3(11), 1–8. doi: 10.1126/sciadv.1701345
- 403 DeLucia, E. H. (1999). Net Primary Production of a Forest Ecosystem with
- Experimental CO2 Enrichment. Science, 284(5417), 1177–1179. doi:
- 405 10.1126/science.284.5417.1177
- 406 Elias, F., Ferreira, J., Lennox, G. D., Berenguer, E., Ferreira, S., Schwartz, G., ...
- Barlow, J. (2020). Assessing the growth and climate sensitivity of secondary
- forests in highly deforested Amazonian landscapes. *Ecology*, 101(3). doi:
- 409 10.1002/ecy.2954

- Fearnside, P. M. (2018). Brazil's Amazonian forest carbon: the key to Southern
- 411 Amazonia's significance for global climate. Regional Environmental Change,
- 412 18(1), 47–61. doi: 10.1007/s10113-016-1007-2
- ForestPlots.net, Blundo, C., Carilla, J., Grau, R., Malizia, A., Malizia, L., ... Tran, H.
- D. (2021). Taking the pulse of Earth's tropical forests using networks of highly
- distributed plots. *Biological Conservation*, 260(October 2020), 108849. doi:
- 416 10.1016/j.biocon.2020.108849
- Fleischer, K., Rammig, A., De Kauwe, M. G., Walker, A. P., Domingues, T. F.,
- Fuchslueger, L., ... Lapola, D. M. (2019). Amazon forest response to CO2
- fertilization dependent on plant phosphorus acquisition. Nature Geoscience,
- 420 12(9), 736–741. doi: 10.1038/s41561-019-0404-9
- 421 Gardner, T. A., Ferreira, J., Barlow, J., Lees, A. C., Parry, L., Guimarães Vieira, I.
- 422 C., ... Zuanon, J. (2013). A social and ecological assessment of tropical land
- uses at multiple scales: The Sustainable Amazon Network. *Philosophical*
- Transactions of the Royal Society B: Biological Sciences, 368(1619). doi:
- 425 10.1098/rstb.2012.0166
- 426 Garrett, R. D., Niles, M. T., Gil, J. D. B., Gaudin, A., Chaplin-Kramer, R., Assmann,
- 427 A., ... Valentim, J. (2017). Social and ecological analysis of commercial
- integrated crop livestock systems: Current knowledge and remaining
- 429 uncertainty. Agricultural Systems, 155, 136–146. doi:
- 430 10.1016/j.agsy.2017.05.003
- 431 Gatti, L. V., Basso, L. S., Miller, J. B., Gloor, M., Domingues, L. G., Cassol, H. L.
- G., ... Neves, R. A. L. (2021). Amazonia as a carbon source linked to

- deforestation and climate change. *Nature*, *595*(July). doi: 10.1038/s41586-
- 434 021-03629-6
- Gilroy, J. J., Woodcock, P., Edwards, F. A., Wheeler, C., Baptiste, B. L. G., Medina
- Uribe, C. A., ... Edwards, D. P. (2014). Cheap carbon and biodiversity co-
- benefits from forest regeneration in a hotspot of endemism. *Nature Climate*
- 438 *Change*, 4(6), 503–507. doi: 10.1038/nclimate2200
- Gloor, M., Barichivich, J., Ziv, G., Brienen, R., Schöngart, J., Peylin, P., ... Baker,
- J. (2015). Recent Amazon climate as background for possible ongoing and
- future changes of Amazon humid forests. Global Biogeochemical Cycles,
- 442 29(9), 1384–1399. doi: 10.1002/2014GB005080
- 443 Griscom, B. W., Adams, J., Ellis, P. W., Houghton, R. A., Lomax, G., Miteva, D. A.,
- ... Fargione, J. (2017). Natural climate solutions. *Proceedings of the National*
- Academy of Sciences of the United States of America, 114(44), 11645–11650.
- 446 doi: 10.1073/pnas.1710465114
- Heinrich, V. H. A., Dalagnol, R., Cassol, H. L. G., Rosan, T. M., de Almeida, C. T.,
- Silva Junior, C. H. L., ... Aragão, L. E. O. C. (2021). Large carbon sink
- 449 potential of secondary forests in the Brazilian Amazon to mitigate climate
- 450 change. *Nature Communications*, 12(1), 1785. doi: 10.1038/s41467-021-
- 451 22050-1
- Hubau, W., Lewis, S. L., Phillips, O. L., Affum-Baffoe, K., Beeckman, H., Cuní-
- Sanchez, A., ... Zemagho, L. (2020). Asynchronous carbon sink saturation in
- 454 African and Amazonian tropical forests. *Nature*, 579(7797), 80–87. doi:
- 455 10.1038/s41586-020-2035-0

- 456 IPCC. (2021). Climate Change 2021: The Physical Science Basis. Contribution of
- Working Group I to the Sixth Assessment Report of the Intergovernmental
- Panel on Climate Change [Masson-Delmotte, V., P. Zhai, A. Pirani, S. L.
- Connors, C. Péan, S. Berger, N. Caud, Y. Chen, Cambridge University Press,
- 460 (In Press), 3949. Retrieved from
- https://www.ipcc.ch/report/ar6/wg1/downloads/report/IPCC\_AR6\_WGI\_Full\_R
- 462 eport.pdf
- 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. doi: 10.1111/1365-2745.12298
- 466 Johnson, E. A., & Miyanishi, K. (2008). Testing the assumptions of
- chronosequences in succession. *Ecology Letters*, 11(5), 419–431. doi:
- 468 10.1111/j.1461-0248.2008.01173.x
- Lapola, D. M., & Norby, R. J. (2014). AMAZON FACE, Assessing the effects of
- increased atmospheric CO2 on the ecology and resilience of the Amazon
- 471 *forest*. Retrieved from
- https://amazonface.inpa.gov.br/pdf/AmazonFACE Science Plan & Implemen
- 473 tation Strategy.pdf
- Lavelle, P., Dolédec, S., de Sartre, X. A., Decaëns, T., Gond, V., Grimaldi, M., ...
- Velasquez, J. (2016). Unsustainable landscapes of deforested Amazonia: An
- analysis of the relationships among landscapes and the social, economic and
- environmental profiles of farms at different ages following deforestation. *Global*
- 478 Environmental Change, 40, 137–155. doi: 10.1016/j.gloenvcha.2016.04.009

- Lennox, G. D., Gardner, T. A., Thomson, J. R., Ferreira, J., Berenguer, E., Lees, A.
- 480 C., ... Barlow, J. (2018). Second rate or a second chance? Assessing biomass
- and biodiversity recovery in regenerating Amazonian forests. *Global Change*
- 482 *Biology*, 24(12), 5680–5694. doi: 10.1111/gcb.14443
- Lenth, R. V. (2016). Least-Squares Means: The R Package Ismeans. Journal of
- 484 Statistical Software, 69(1). doi: 10.18637/jss.v069.i01
- Lopez-Gonzalez, G., Lewis, S. L., Burkitt, M., & Phillips, O. L. (2011).
- ForestPlots.net: A web application and research tool to manage and analyse
- tropical forest plot data. *Journal of Vegetation Science*, 22(4), 610–613. doi:
- 488 10.1111/j.1654-1103.2011.01312.x
- Maeda, E. E., Abera, T. A., Siljander, M., Aragão, L. E. O. C., Moura, Y. M. de, &
- Heiskanen, J. (2021). Large-scale commodity agriculture exacerbates the
- 491 climatic impacts of Amazonian deforestation. *Proceedings of the National*
- 492 Academy of Sciences, 118(7), e2023787118. doi: 10.1073/pnas.2023787118
- Melo, F. P. L., Parry, L., Brancalion, P. H. S., Pinto, S. R. R., Freitas, J., Manhães,
- 494 A. P., ... Chazdon, R. L. (2020). Adding forests to the water-energy-food
- 495 nexus. *Nature Sustainability*, (September). doi: 10.1038/s41893-020-00608-z
- 496 Mu, Y., Biggs, T. W., & De Sales, F. (2021). Forests mitigate drought in an
- agricultural region of the Brazilian Amazon: Atmospheric moisture tracking to
- 498 identify critical source areas. Geophysical Research Letters, n/a(n/a),
- 499 e2020GL091380. doi: 10.1029/2020GL091380
- N'Guessan, A. E., N'dja, J. K., Yao, O. N., Amani, B. H. K., Gouli, R. G. Z.,
- Piponiot, C., ... Hérault, B. (2019). Drivers of biomass recovery in a secondary

- forested landscape of West Africa. Forest Ecology and Management,
- 433(September 2018), 325–331. doi: 10.1016/j.foreco.2018.11.021
- Neeff, T., & Dos Santos, J. R. (2005). A growth model for secondary forest in
- Central Amazonia. Forest Ecology and Management, 216(1–3), 270–282. doi:
- 506 10.1016/j.foreco.2005.05.039
- Ngo, K. M., Turner, B. L., Muller-Landau, H. C., Davies, S. J., Larjavaara, M., Nik
- Hassan, N. F. bin, & Lum, S. (2013). Carbon stocks in primary and secondary
- tropical forests in Singapore. Forest Ecology and Management, 296, 81–89.
- 510 doi: 10.1016/j.foreco.2013.02.004
- Oberleitner, F., Egger, C., Oberdorfer, S., Dullinger, S., Wanek, W., & Hietz, P.
- 512 (2021). Recovery of aboveground biomass, species richness and composition
- in tropical secondary forests in SW Costa Rica. Forest Ecology and
- *Management*, 479(July 2020), 118580. doi: 10.1016/j.foreco.2020.118580
- 515 Phillips, O. L., & Brienen, R. J. W. (2017). Carbon uptake by mature Amazon
- forests has mitigated Amazon nations' carbon emissions. *Carbon Balance and*
- 517 *Management*, 12(1), 1. doi: 10.1186/s13021-016-0069-2
- Poorter, L., Bongers, F., Aide, T. M., Almeyda Zambrano, A. M., Balvanera, P.,
- Becknell, J. M., ... Rozendaal, D. M. A. (2016). Biomass resilience of
- Neotropical secondary forests. *Nature*, 530(7589), 211–214. doi:
- 521 10.1038/nature16512
- Quinn, G. P., & Keough, M. J. (2002). Experimental Design and Data Analysis for
- 523 *Biologists*. Cambridge: Cambridge University Press.
- R Core Team. (2020). R: A Language and Environment for Statistical Computing.

- 525 R Foundation for Statistical Computing. Vienna, Austria.
- 526 Réjou-Méchain, M., Tanguy, A., Piponiot, C., Chave, J., & Hérault, B. (2017).
- 527 Biomass: an R Package for Estimating Above-Ground Biomass and Its
- 528 Uncertainty in Tropical Forests. *Methods in Ecology and Evolution*, 8(9),
- 529 1163–1167. doi: 10.1111/2041-210X.12753
- 530 Requena-Suarez, D., Rozendaal, D. M. A. A., De Sy, V., Phillips, O. L.,
- Alvarez-Dávila, E., Anderson-Teixeira, K., ... 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. doi: 10.1111/gcb.14767
- Rocha-Santos, L., Pessoa, M. S., Cassano, C. R., Talora, D. C., Orihuela, R. L. L.,
- Mariano-Neto, E., ... Cazetta, E. (2016). The shrinkage of a forest:
- Landscape-scale deforestation leading to overall changes in local forest
- structure. *Biological Conservation*, 196, 1–9. doi:
- 539 10.1016/j.biocon.2016.01.028
- 540 Saldarriaga, J. G., West, D. C., Tharp, M. L., & Uhl, C. (1988). Long-Term
- Chronosequence of Forest Succession in the Upper Rio Negro of Colombia
- and Venezuela. *The Journal of Ecology*, 76(4), 938. doi: 10.2307/2260625
- SEMAS. (2020). Plano Estadual Amazônia Agora, Decreto 941, 3 de Agosto 2020.
- Retrieved September 20, 2020, from Diário Oficial do Estado do Pará, Portal
- Legislativo da Secretaria de Estado de Meio Ambiente e Sustentabilidade
- website: https://www.semas.pa.gov.br/legislacao/publico/view/8457
- 547 Smith, C. C., Espírito-Santo, F. D. B., Healey, J. R., Young, P. J., Lennox, G. D.,

- Ferreira, J., & Barlow, J. (2020). Secondary forests offset less than 10% of
- deforestation-mediated carbon emissions in the Brazilian Amazon. *Global*
- 550 Change Biology, 26(12), 7006–7020. doi: 10.1111/gcb.15352
- 551 Smith, C. C., Healey, J. R., Berenguer, E., Young, P. J., Taylor, B., Elias, F., ...
- Barlow, J. (2021). Old-growth forest loss and secondary forest recovery across
- 553 Amazonian countries. *Environmental Research Letters*, 16(8). doi:
- 554 10.1088/1748-9326/ac1701
- 555 Sullivan, M. J. P., Lewis, S. L., Hubau, W., Qie, L., Baker, T. R., Banin, L. F., ...
- Phillips, O. L. (2018). Field methods for sampling tree height for tropical forest
- biomass estimation. *Methods in Ecology and Evolution*, 9(5), 1179–1189. doi:
- 558 10.1111/2041-210X.12962
- Tucker, J. M., Brondizio, E. S., & Morán, E. F. (1998). Rates of forest regrowth in
- Eastern Amazônia: A comparison of Altamira and Bragantina regions, pará
- state, Brazil. *Interciencia*, 23(2), 64–73.
- van Kuijk, M., Anten, N. P. R., Oomen, R. J., van Bentum, D. W., & Werger, M. J.
- A. (2008). The limited importance of size-asymmetric light competition and
- growth of pioneer species in early secondary forest succession in Vietnam.
- 565 *Oecologia*, 157(1), 1–12. doi: 10.1007/s00442-008-1048-4
- Vanclay, J. K. (1994). Modelling forest growth and yield: applications to mixed
- tropical forests. In *CAB International*. Wallingford UK.
- Walker, A. P., De Kauwe, M. G., Bastos, A., Belmecheri, S., Georgiou, K., Keeling,
- R. F., ... Zuidema, P. A. (2021). Integrating the evidence for a terrestrial
- carbon sink caused by increasing atmospheric CO 2. New Phytologist, 229(5),

571	2413–2445. doi: 10.1111/nph.16866
572	Walker, A. P., De Kauwe, M. G., Medlyn, B. E., Zaehle, S., Iversen, C. M., Asao,
573	S., Norby, R. J. (2019). Decadal biomass increment in early secondary
574	succession woody ecosystems is increased by CO2 enrichment. Nature
575	Communications, 10(1), 454. doi: 10.1038/s41467-019-08348-1
576	WRI - World Resources Institute. (2020). CAIT Climate Data Explorer. Retrieved
577	September 20, 2020, from CAIT Historical - Explore Historic Greenhouse Gas
578	Emissions website: http://cait.wri.org/
579	

# **Figures**

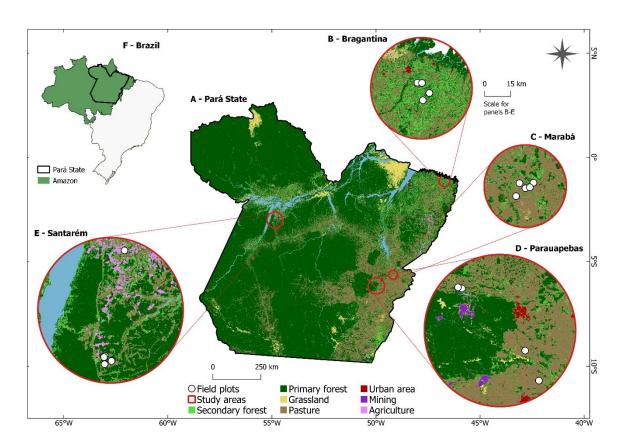


Figure 1. Location of our four study regions in the state of Pará, in the Brazilian Amazon. The main land-uses in the state are old-growth forest (dark green), secondary forest (light green), pasture (brown) and agriculture (pink).

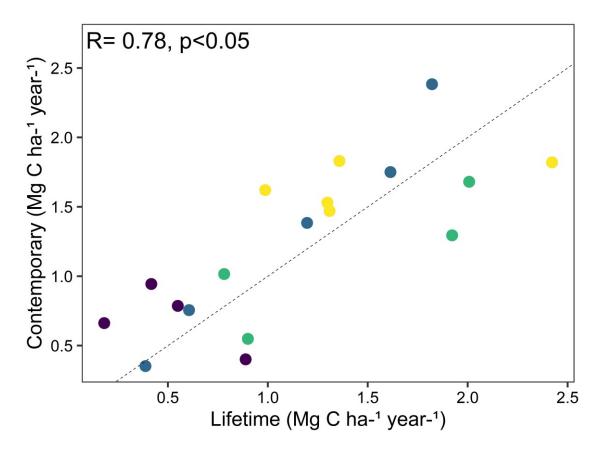


Figure 2. Pearson's correlations between contemporary and lifetime carbon accumulation rates in secondary forests. The regions are represented by purple (Bragantina), blue (Marabá), green (Parauapebas) and yellow points (Santarém). Dashed line represents the 1:1 ratio.

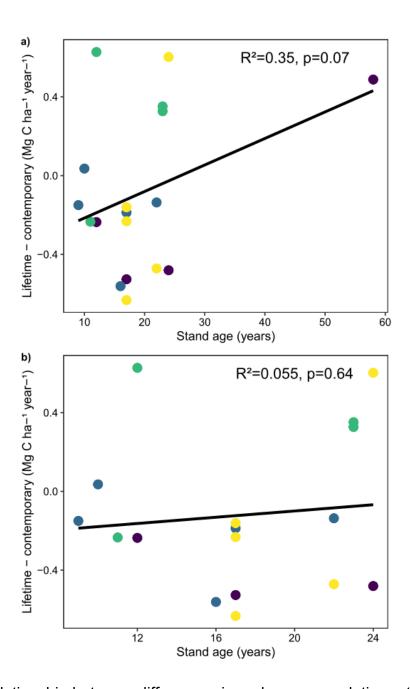


Figure 3. Relationship between differences in carbon accumulation rates (lifetime - contemporary) and stand age of secondary forests with the insertion (a) and removal of age outliers (b). The regions are represented by purple (Bragantina), blue (Marabá), green (Parauapebas) and yellow points (Santarém).

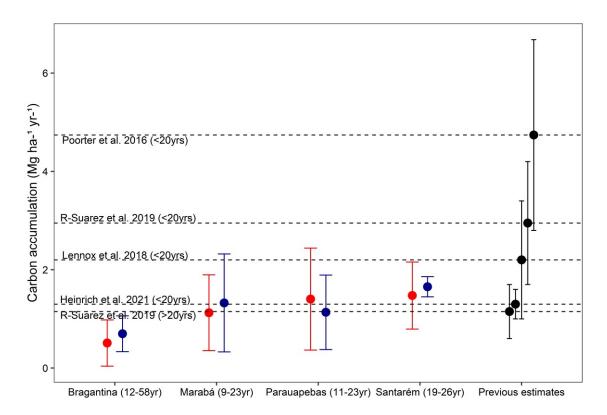


Figure 4. Comparisons of contemporary (darkblue) and lifetime (red) carbon accumulation rates of secondary forests across regions and with others estimates (black) for the Eastern Amazon (Poorter et al., 2016; Lennox et al., 2018, Heinrich et al., 2021) and South America (Requena-Suarez et al., 2019). Points represent the average rates (±95% CI).