Climate-sensitivity of secondary forests

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

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Abstract

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

are unlikely to return to their original levels on politically meaningful timescales.

Keywords

Amazon, Bragantina region, biodiversity, carbon, climate change, secondary forests

Introduction

Secondary forests regenerating after land clearance represent > 50% of all tropical forests (Chazdon et al. 2009), and there is hope that they can cost-effectively mitigate climate change and biodiversity loss (Chazdon 2014, Lewis et al. 2019) – two of the defining crises of the Anthropocene (Malhi et al. 2014). For example, secondary forest carbon uptake is estimated to be 11 times higher than that of Neotropical primary forests (Poorter et al. 2016), providing an estimated global carbon sink of 130 Pg between 2016 and 2100 (Houghton and Nassikas 2018). Secondary forests can also provide important biodiversity co-benefits in landscapes otherwise devoid of primary forests or with high levels of deforestation (Vieira and Gardner 2012, Lennox et al. 2018, Matos et al. 2019). However, to realize their potential to mitigate climate change and biodiversity loss, tropical secondary forests must be able to recover under novel climatic conditions.

Global climate change is affecting the humid tropics through higher temperatures and levels of atmospheric CO_2 (Malhi et al. 2014), increases in dry-season length (Fu et al. 2013) and the frequency and intensity of climate extremes (Brando et al. 2019). These climate changes may be exacerbated by declines in precipitation and increases in temperature linked to regional deforestation (Spracklen et al. 2018, Baker and Spracklen 2019). Three types of evidence suggest tropical secondary forests will be sensitive to these changes. First, primary forest estimates show a decrease in the carbon sink during extreme droughts (Brienen et al. 2015). Second, large-scale studies of secondary forests indicate a strong effect of climate on the recovery rates of carbon and biodiversity (Anderson-Teixeira et al. 2013, Poorter et al. 2016, Rozendaal et al. 2019). Third, longitudinal studies have revealed how droughts modulate recovery speed, increase mortality and reduce recruitment and growth (Chazdon et al. 2005, Maza-Villalobos et al. 2013, Martínez-Ramos et al. 2018), due to the negative effects on the water balance and photosynthetic rates of trees, especially in the earlier stages of succession (Bretfeld et al. 2018).

While these studies provide a useful knowledge base, there are some important limitations. First, secondary forests are likely to be even more sensitive than primary forests to changes in precipitation (Uriarte et al. 2016) because pioneer species are more vulnerable to embolism (Markesteijn et al. 2011). Second, the large-scale studies that have inferred temporal trends from spatial data (i.e. the chronosequence approach) are complicated by factors such as species turnover and natural variation between samples (Johnson and Miyanishi 2008, Norden et al. 2015, França et al. 2016) and idiosyncratic determinants of recovery (Chazdon et al. 2007, Arroyo-Rodríguez et al. 2017). Third, most longitudinal studies focus on short-term assessments restricted to a single drought event (Chazdon et al. 2005, Maza-Villalobos et al. 2013, Bretfeld et al. 2018, Martínez-Ramos et al. 2018), which cannot detect responses to longer-term increases in temperature or post-drought growth compensation (Berenguer et al. 2018). Furthermore, the few longer-term studies relating secondary forest carbon dynamics to climate focus on tropical dry forests (e.g., Álvarez-Yépiz et al. 2018, Martínez-Ramos et al. 2018), meaning there is a lack of research in humid tropical regions where species may be even more sensitive to drought (Esquivel-Muelbert et al. 2019).

Initiatives such as the Bonn Challenge highlight two additional knowledge gaps linked to management. It seems likely that the increase in landscape-scale restoration will also increase secondary forest permanence, moving beyond the current situation where secondary forests are often cleared again within 5-20 years (Aguiar et al. 2016, Reid et al. 2018). Although our current understanding of younger forests is good (Poorter et al. 2015, 2016, 2019, Martínez-Ramos et al. 2018, Villa et al. 2018, Rozendaal et al. 2019), and the non-linear response of forest recovery over time is well established (Poorter et al. 2016, Ferreira et al. 2018, Lennox et al. 2018, Requena Suarez et al. 2019, Rozendaal et al. 2019), there is far too much variation in the relationship to use young forests to accurately predict recovery rates in older forests. Moreover, the relative recovery rates of carbon and biodiversity are unclear. While some regional assessments report a tight coupling at all stages of succession (Lennox et al. 2018), continent-scale assessments suggest a much faster recovery of biodiversity: plots recovered 80% of tree species richness 20 years after abandonment (Rozendaal et al. 2019) and only 27% of the carbon stock (Poorter et al. 2016). As recovery of both carbon and biodiversity are mediated by factors such as stand age and landscape and local conditions (Jakovac et al. 2015, Magnago et al. 2017, Villa et al. 2018, Ferreira et al. 2018, Lennox et al. 2018, Matos et al. 2019), it is not clear how these rates compare in heavily deforested landscapes.

Here, we address these knowledge gaps by investigating secondary forest recovery in the Bragantina region, the oldest deforestation frontier in the Brazilian Amazon (Almeida et al. 2010). We undertook 10 repeated censuses of 3 ha of older secondary forests (~60 years) over 18 years and addressed four questions: 1) What are the recovery rates of carbon stocks and tree species richness, and what is the relationship between these measures? 2) Does variation in seasonal temperature, water stress and landscape context influence carbon dynamics? 3) How does carbon recovery in the Bragantina region compare to estimates from other tropical regions? 4) What is the timeframe for carbon to return to typical primary forest levels?

Methods

Study area and landscape context

Our study focused on the eastern-Amazonian municipality of Bragança (Appendix S1: Fig. S1). This municipality has lost 90.2% of its native forests and mangrove areas. Secondary forest covers 28.8% of the landscape, accounting for 67.5% of the total forest cover (including mangrove areas) (Appendix S1: Fig. S1). Primary and secondary forests (established post-1985) are situated in small, isolated, and selectively logged fragments (~30 to 60 hectares; MapBiomas 2019).

We established three study-plot classes. In 1999, we began inventories in 12 secondary forest plots (50 x 50 m = 0.25 ha; Appendix S1: Fig. S1, Table S1; hereafter, "*long-term plots*"). These plots were separated by a mean distance of 265 m (range 70-590 m). In 2017, we established an additional four secondary forest plots (250 x 10 m = 0.25 ha; hereafter, "*extra plots*") in different fragments of the Bragança municipality. In 2017, we also established three plots in primary forests (250 x 10 m 0.25 ha; Appendix S1: Fig. S1; hereafter "*primary forest plots*").

Both long-term and extra secondary forest plots were abandoned after successive cycles of slash-and-burn agriculture (for manioc, maize, and rice cultivation). There was no record of wildfires after agricultural abandonment at our plots. Given that undisturbed primary forests are extremely rare in the region, to select primary forest plots we conducted interviews with local people to identify sites that retain the structural characteristics of Amazonian old-growth forests; nonetheless, it is likely that selective logging and edge effects have already altered our primary forest plots. All plots were located in *terra-firme* areas. The predominant soils across all plots are oxisols with low fertility and 15-35% clay in the superficial layers (Da Silva Castro et al. 2013). Plots were flat, and average elevation was 35 m (range: 30-66 m).

Age of secondary forests

We used two approaches to evaluate secondary forest age. The long-term plots are older than the existing satellite record and were provisionally aged by interviews conducted by the researchers who established them in 1999. The estimated age in 2017 was c. 48-58 years old. Unfortunately, Landsat 1 images from the region (1974) were also too cloudy to support these interviews. We therefore estimated ages by back casting the non-linear growth trajectories (Question 4). For the extra plots recovering post 1985, we used the MapBiomas 3.1 dataset to estimate their ages (details in Appendix S1; MapBiomas 2019).

Tree censuses

The long-term secondary forest plots were established with a full tree census in 1999, with repeated surveys taking place annually between 2000-2004 then subsequently in 2006, 2011, 2014 and 2017, while a full tree census was undertaken in the extra and primary forest plots when they were established in 2017. In all plots, we measured all trees ≥ 10 cm diameter at breast height (DBH). In the last census, we also estimated tree height by visual assessment. Plant identification was conducted in the field and when necessary botanical samples were collected for comparisons from the Herbário IAN (Embrapa Amazônia Oriental) collection. Tree census data are available at ForestPlots.net (Lopez-Gonzalez et al. 2011).

Estimation of carbon stocks and tree species richness

We used three approaches to estimate the above-ground biomass (AGB) of individual stems. First, we calculated AGB using the allometric equation: $AGB = 0.637 \times (\rho D^2 H)^{0.976}$

where ρ represents tree wood density (g cm^{-3}), D represents stem DBH (cm) and H represents stem height (Chave et al. 2014). Stem wood densities were taken from the Global Wood Density Database (Chave et al. 2009). We subset the data to entries for South America and used the mean wood density across entries at the lowest available taxonomic level (e.g. where no data was available for a species, we used the genus average).

To estimate the height of stems for censuses prior to 2017, we used non-linear least-squares to determine height-DBH relationships at each study plot. Using the 2017 height and DBH values as training data, we assumed a functional relationship described by the Michaelis-Menten model: $H = \frac{a \times D}{b \times D}$, where a and b are estimated from the training data. Second, due to potential errors in the tree height sample caused by our visual assessment approach, we applied correction functions to the 2017 stem heights then determined pre-2017 tree heights as described above. The height-correction functions were derived from large primary and second secondary forest tree samples (c. 500 individuals in both forest types) from the eastern Brazilian Amazon for which visual and laser-based heights were estimated. These data suggest that visual assessments tend to underestimate stem height, especially stems < 15 m tall in secondary forests (Appendix S1: Fig. S2). Finally, we also estimated stem biomass using the following allometric equation that does not include a height parameter: $AGB = exp\,[-1.803 - 0.976E + 0.976\,ln\,(\rho) + 2.673\,ln\,(D) - 0.299\,ln\,(D)^2]$, where E is a measure of environmental stress, defined by cumulative water deficit and temperature and precipitation seasonality (Chave et al. 2014).

Results across these approaches suggest that use of the uncorrected values of stem height values underestimates plot-level carbon by around 10-20%, so we do not report results from this approach. In the main text, we focus on results from the height-corrected estimation technique because including height is known to improve AGB estimates (Sullivan et al. 2018). However, the height-corrected approach returned highly similar carbon estimates to those obtained using the allometric equation that does not include height (mean root square difference < 1.5 Mg C ha^{-1}). The results for this latter approach can be found in Appendix S1: Fig. S6. We assumed that the carbon content of the individuals represents 50% of the AGB. Tree species richness (of individuals > 10 cm DBH) in each plot was assessed by rarefying richness to 100 individuals, the minimum abundance in the sampled plots.

Climatological and landscape predictors of carbon dynamics

Monthly precipitation and temperature for each census year were determined using data collected at a local meteorological station (INMET 2018; Appendix S1: Fig. S1). These data show that the study region has annual precipitation of 1,850 mm, with a rainy season from December to July (222 mm month^{-1}) and a dry season from August to November (19.5 mm month^{-1}).

We calculated three climatological predictors of carbon dynamics: the Standardized Precipitation Evapotranspiration Index (SPEI; Vicente-Serrano et al. 2010), the Maximum Climatological Water Deficit (MCWD; Malhi et al. 2009), and the maximum dry season temperature (MDST). SPEI is a measure of water stress based on the difference between monthly precipitation and potential evapotranspiration expressed as a standardized index, with negative values representing drier periods over the timescale considered relative to median values for a long-term reference time-series. To account for medium-term water deficit, we estimated monthly SPEI values for a 12-month moving window from May to April. MCWD is the most negative accumulated value of the climatological water deficit (CWD) over each one-year period (between May and April; 1973-2017). CWD is defined as monthly precipitation, minus evapotranspiration, minus the CWD of the previous month (Malhi et al. 2009). MDST was measured as the highest monthly temperature value during the dry season (i.e., between August and November). Finally, we used edge distance as our predictor of landscape context effects on carbon dynamics. For each secondary forest plot, edge distance was calculated as the distance from the plot centroid to the nearest forest edge using images from Google Earth 7.1.7.2600 (earth.google.com).

Carbon anomalies

We calculated the amount of carbon incorporated by growth (G) and recruitment (R), as well as that lost by mortality (M) for each census interval, thus obtaining periodic carbon balance (B = G + R - M). We used anomalies to subtract the expected natural carbon accumulation that occurs through time. Censuses occurred at varying intervals (1, 2, 3 and 5 years). Let $i \in 1, 2, \ldots, 9$ be one of the intervals, let T_{-i} be the total length of the time series minus the length of interval i, let C_{-i} be the change in carbon balance or one of its components over all intervals not including i, let n_i be the number of years in interval i, and let a_i be the observed change C in interval i. Therefore, the expected change in C in interval i is $E(C_i) = \frac{n_i \times C_{-i}}{T_{-i}}$, and the anomaly is $a_t - E(C_t)$.

Statistical analysis

We used Bayesian piecewise linear splines to estimate i) carbon recovery with time; ii) tree species richness recovery with time; and iii) the relationship between carbon and tree species richness recovery (Question 1). Bayesian model comparison with reversible jump Markov Chain Monte Carlo simulations (Lunn et al. 2009) was used to average multiple piecewise-linear models to produce smoothed curvilinear relationships (Thomson et al. 2010). The number and location of change-points were assigned hierarchical prior distributions that included zero changepoints as a possibility. In each simulation, the spline function was comprised of up to $k = 6$ linear coefficients (i.e., between zero and six) and $k - 1$ corresponding changepoints. The resulting posterior distributions yielded model-averaged parameter estimates and 95% credible intervals that account for uncertainties about model structure. The model for long-term secondary forest recovery included plot-level random effects to account for expected similarities between plots.

To explore whether variation in maximum dry season temperature, water stress (SPEI and MCWD) and landscape context (edge distance) influence tree growth, recruitment, mortality and carbon dynamics (Question 2), we used Bayesian variable selection with nonlinear covariate effects (Thomson et al. 2010). We used the lowest recorded value of MCWD in a given period as our measure of one-off drought severity (see also Esquivel-Muelbert et al. 2019). We used SPEI values (Vicente-Serrano et al. 2010) as a measure of the longer-term (here 12-month) water balance, which is known to be significant for tree growth (Greenwood et al. 2017). The relative importance of an explanatory variable was assessed by the posterior probability of a non-zero effect. We considered posterior probabilities > 0.75 to be indicative of a statistical association.

We compared the average carbon accumulation rates of our secondary forest plots (both long-term and extra plots) to estimates of carbon accumulation from leading tropical and global assessments (Bonner et al. 2013, Poorter et al. 2016, Lennox et al. 2018, Requena Suarez et al. 2019) and pan-Amazonian estimates in old-growth and logged primary forests (Brienen et al. 2015, Rutishauser et al. 2015) (Question 3). To investigate secondary forest recovery timeframes (Question 4), we fit monotonically increasing and marginally decreasing rational functions, based on third-order polynomials as the numerator and second-order polynomials as the denominator, to the median and lower and upper bounds of the 95% credible intervals for carbon levels in the long-term plots (Fig. 1A).

Results

Climate variation over the time-series (1972-2017)

The maximum dry season temperature increased by 0.1 °C per decade across our time series (Appendix S1: Fig. S5). Water stress (MCWD and SPEI values) was highly variable, declined weakly, and was highest (lowest values of MCWD and SPEI) in strong El-Niño years. MCWD and SPEI were only weakly related ($r = 0.44$ across the 1973-2017 time series; $r = 0.19$ during census years – Appendix S1: Fig. S3).

Carbon and tree species richness recovery

The average carbon stock in 2017 was 141.7 (±16.3 SE), 58.3 (±2.7) and 4.27 (±1.19) Mg ha^{-1} in, respectively, the primary forest, long-term, and extra plots, whereas rarefied richness was 60.05 (±4.07), 41.2 (±1.4) and 33.9 (±3.5) (Appendix S1: Table S1). In the long-term secondary forest plots, the recovery of carbon and rarefied richness showed different trajectories among census (Fig. 1A-B). The mean accumulation of carbon in our long-term plots was 1.08 Mg ha^{-1} yr^{-1} between 1999 and 2017. Carbon and time were associated at the 0.07 level (i.e., 93% of the R^2 posterior mass was greater than zero). Rarefied richness displayed a much weaker relationship with time, being associated only at the 0.33 level and with a mean trend of 0.21 species yr^{-1}. Carbon stock in the long-term secondary forest plots reached only 41.1% of the average primary forest level in 2017, while rarefied richness recovered to 56%. Above-ground carbon stocks and plant diversity were not related to each other over time (Fig. 1).

Influence of climate and edge distance on carbon anomalies

Carbon balance was positively related to SPEI in the long-term plots. These changes were driven by variation in stem growth, with lower than average carbon accumulation in drier periods (Fig. 2). Although the maximum dry season temperature did not affect the overall carbon balance, it had countervailing effects on carbon growth and recruitment: growth was highest and recruitment lowest in the warmest years and vice versa. Carbon loss from mortality was not associated with any of the predictors (Fig 2), and edge distance and MCWD were not associated with any of the carbon anomalies (Appendix S1: Fig. S7).

Comparison between carbon recovery rates

The carbon recovery rate in the long-term plots was lower than most estimates of secondary forest recovery from the Amazon or across the tropics, and our younger extra plots had even lower recovery rates than the older long-term plots (Fig. 3). Recovery rates at our study plots were also below Amazon-wide estimates of primary forest recovery after selective logging and were only slightly higher than the average carbon uptake rate of tropical primary forests (Fig. 3).

Extrapolating carbon recovery timeframes

Our backwards extrapolation (to zero) gives approximate ages for the long-term secondary forests of 39 and 48 years in 2017 (Fig. 4), which is marginally lower but generally consistent with the ages reported during interviews (c. 48-58 years old in 2017). As a consequence of the low carbon recovery rates of the long-term plots, our extrapolation of future carbon levels — aimed at providing a rough estimate of a plausible recovery window under present-day conditions — suggests that it will take at least another century (c. 150 years since abandonment) until the site regains carbon levels similar to local primary forests (Fig. 4).

Discussion

Influence of climate on carbon recovery in secondary forests

Our results show for the first time that secondary forest carbon accumulation in the Amazon can be influenced by periods of water deficit. This suggests that the role of water availability in regulating carbon uptake observed in humid primary forests (e.g., Phillips et al. 2009, Anderson et al. 2018), dry primary (Mendivelso et al. 2014, Álvarez-Yépiz et al. 2018) and dry secondary forests (Maza-Villalobos et al. 2013, Martínez-Ramos et al. 2018) also extends to humid secondary forests. The generality of this finding is consistent with the strong link between the evapotranspiration index SPEI and spatial variation in carbon recovery in tropical forests (Schwalm et al. 2017). Indeed, secondary forests in the humid tropics may be even more sensitive than those in tropical dry regions given that the former show longer recovery times in the face of seasonal water availability (Poorter et al. 2019). Despite the similarity of the findings across forest types, our results also suggest that different mechanisms may underpin the sensitivity of the carbon balance to water deficit. Drought-mediated changes in primary forest carbon balance are driven by increased mortality (Phillips et al. 2009, Anderson et al. 2018), while the changes in the carbon balance observed in this study were primarily driven by reduced growth (Fig. 2).

Although the maximum dry season temperature (MDST) had no influence on the carbon balance of the studied secondary forests, increasing MDST increased the growth of established stems while reducing recruitment. The mechanistic explanation for such contrasting results requires further investigation. However, it might indicate a differential temperature effect between stems size classes. For example, higher temperatures exacerbate the physiological consequences of acute water stress (Lloyd and Farquhar 2008, Markesteijn et al. 2011), and shallow-rooted smaller stems (<10cm DBH) may be more sensitive to drought effects than the medium-sized stems (10-30 cm DBH) (Elias et al. 2018). The increase in growth also suggests that established stems that can cope with higher temperatures may also benefit from factors associated with hotter years, such as better light conditions (Bentos et al. 2017) or faster litter decomposition rates and nutrient cycling (Eichenberg et al. 2013).

The positive relationship between temperature and growth in the assessed secondary forest contrasts with findings in tropical primary forests, where negative relationships (e.g. Feeley et al 2007) and a lack of any relationship (e.g. Rowland et al. 2014) have been detected. This difference may be explained by the dominance in secondary forests of fast growing, heliophilic species (Vieira et al. 1994, Chazdon 2014), which tend to show relatively high optimum temperature points (Slot et al. 2014). A more complete understanding of secondary forest temperature responses is crucial given their importance as a climate change mitigation technology.

Carbon recovery

Carbon accumulation rates in our long-term study plots (48-58 years old) were low compared to most other studies (Fig. 3), and only around twice that recorded in Amazonia's primary forests. Although this rate of carbon accumulation is comparable to recent continental-scale estimates of biomass recovery in older (20-80 years old) tropical secondary rainforests in the Americas (Requena Suarez et al. 2019; Fig. 3), this similarity masks one important difference: our long-term plots had a much lower lifetime recovery rate than the same continent-scale estimates (Fig. 4B). Combining the mean < 20- and 20-80-year-old accumulation rates of Requena Suarez et al. (2019) suggests that a typical American tropical secondary rainforest will accumulate the median carbon seen at our study site (Fig. 1) in just 20-21 years, less than half the site's estimated age (Fig 4B). Moreover, even the lower bound of the Requena Suarez et al. (2019) 95%

accumulation rate confidence intervals suggests that American tropical secondary rainforests should attain our site's median carbon in 28 years.

The low lifetime recovery rate and equivalent rates of recovery over the last two decades can only be reconciled if forests in the Bragantina region have a very slow rate of early forest succession (Fig 4B). This is supported by the four younger extra secondary forest plots, which displayed even lower recovery rates than the long-term plots and are far below the predictions of Requena Suarez et al. (2019) for age-equivalent plots (Fig. 3). Furthermore, our backward extrapolation of growth tended to underestimate the secondary forest age when compared to interview data – if we assume the interview-based dates are correct, this would be consistent with slower than predicted growth rates when the forests were younger.

Such slow early-successional recovery rates could reduce the effectiveness of climate mitigation strategies in regions that have a long history of human occupation, have lost most of the original forest cover, and have suffered the widespread defaunation of large-bodied vertebrates through hunting (Almeida et al. 2010, Moura et al. 2014). These factors reduce the dispersal and colonization of forest tree species (Hooper et al. 2005), reduce carbon stocks (Bello et al. 2015) and increase recovery times (Jakovac et al. 2015, Chazdon 2014, Villa et al. 2018). Moreover, it is important to note that these measures of carbon recovery were observed under the climatic and landscape conditions over the lifetimes of the secondary forest plots. Future recovery could be slower if the last forest remnants are lost, further decreasing forest connectivity (Aguiar et al. 2016, Reid et al. 2018, Matos et al. 2019), if the frequency of farm-fallow cycles increases (Jakovac et al. 2015, Villa et al. 2018), or if deforestation and climate change further increase water deficits (Fu et al. 2013, Spracklen et al. 2018).

Interesting insights can be drawn from the two predictors – the Maximum Climatological

Water Deficit (MCWD) and edge distance – that had no discernible impact on carbon balance. First, MCWD is one of the most frequently used measures of water deficit in studies of tropical forests (e.g., Malhi et al. 2009, Anderson et al. 2018, Berenguer et al. 2018, Esquivel-Muelbert et al. 2017, 2019), but it appears that longer-term measures such as the 12-month SPEI index can reveal ecological processes that are not influenced by inter-period water deficit maximums. Second, edge effects have been detected in a wide range of contexts, including in secondary forests (e.g. Magnago et al. 2017); the lack of any effect in our study could be due to the limited range of distance-to-edge (62-266 m) or the possibility that all long-term study plots were under some form of edge influence in this highly deforested landscape.

The recovery of biodiversity

Although rarefied richness exhibited greater convergence to primary forest levels (56%) than carbon (41.1%), there was a near-zero increase in secondary forest rarefied richness between 1999 and 2017. Richness therefore responds differently to carbon recovery, as tree diversity appears to have increased quickly in the initial stages of succession (see also Lennox et al. 2018) before reaching a state of impeded or arrested succession (Arroyo-Rodríguez et al. 2017). This slowdown could be due to the absence of diverse seed inputs and the slow generation time of trees limiting the recruitment of older-growth species. It also suggests that the strong carbon-biodiversity relationships observed in recovering forests elsewhere (Gilroy et al. 2014, Ferreira et al. 2018, Lennox et al. 2018) may not occur in older secondary forests or in highly deforested landscapes. Finally, it is also likely that we are overestimating the relative recovery of biodiversity: although we rarefied richness by 100 stems, which is two to five times higher than previous studies assessing biodiversity recovery (Rozendaal et al. 2019), the absolute difference between primary and secondary forest would likely be much greater if we considered larger plots that capture more of the high beta diversity of primary forest (e.g., Solar et al. 2015).

Conclusion

The capacity of regenerating tropical secondary forests to sequester carbon and provide habitat for tropical species has profound implications for global climate change and biodiversity conservation. Our study is among the first to utilize data collected over two decades through periodic resampling and finds that the ability of secondary forests to mitigate climate change and limit biodiversity loss are likely to be negatively affected by increases in the rate of tropical deforestation and ongoing climate change. Understanding the generality and future climate sensitivity of these responses will require further investment in long term studies in human modified tropical forests.

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Figure Legends

Figure 1: The recovery of secondary forests in Bragança. Carbon (A) and rarefied species richness (B) and the relationship between carbon and rarefied richness (C) between 1999 and 2017 in the twelve long-term study plots. Points show results at each census. Points and lines are color-coded

by plot. The black line shows the median trend. The grey band shows the 95% credible interval.

Figure 2: Climate and secondary forest carbon dynamics. The marginal effect of the standardized precipitation-evapotranspiration index (SPEI; A, C, E, G) and the maximum dry season temperature (Max temperature; B, D, F, H) on carbon balance (A-B), growth (C-D), mortality (E-F) and recruitment (G-H) in the twelve long-term secondary forest study plots. Lines show the median relationship. Bands show the 95% credible interval. A statistical association was assumed for posterior probabilities of a non-zero effect (*Pr(>0)*) > 0.75.

Figure 3: Estimates of carbon accumulation rates from previous studies compared to those from the twelve long-term and four extra secondary forest study plots. Bars show median values (or the mean where the median was unavailable). Error bars show 95% confidence/credible intervals. The Poorter et al. (2016) tropical secondary forest estimate uses only Neotropical plots. For the Requena Suarez et al. (2016) study, we used their estimates from tropical rainforests in the Americas. The Rutishauser et al. (2015) and Brienen et al. (2015) studies are from the Amazon.

Figure 4. (A) Extrapolation of past and future carbon levels for the 12 long-term study plots. The white line shows median carbon; the grey band shows a possible range. These estimates were derived by fitting rational functions to the median and 95% credible lower and upper bounds of carbon recovery shown in Fig. 1A. The inset shows the data. Points shows carbon levels at each census. Points and lines are color coded by plot. The black dashed line shows mean primary forest carbon. (B) Comparison of carbon recovery trajectories from the present study and Requena Suarez et al. (2019). For this comparison, we used the Requena Suarez et al. (2019) 95% confidence interval carbon accumulation rates for <20- and >20-year-old tropical American secondary rainforests. For the present study, we assumed the 12 long-term study plots were 50

years old, meaning that the first census occurred (in 1999) at age 32 (shown by the vertical dashed line). Carbon recovery rates post this age were taken from the 95% credible lower and upper bounds (Fig. 1A). Rates prior to this age were extrapolated linearly from the 32-year-old 95% credible lower and upper bound values.