



Degradation exposure scenario in the Brazilian Amazon: Edge effect on hyperdominant C-cycle tree species

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ABSTRACT

The Amazon basin strongly influences the global carbon cycle, storing billions of tonnes of carbon in a relatively small number of 'hyperdominant' tree species. However, the Amazon carbon stock is threatened by land-use change. In the remaining forest patches, trees close to the forest border bear various physical and biotic edge effects that alter plant growth and survival. To assess how edge effects influence tree mortality and carbon storage, we investigated the occurrence of hyperdominant tree species in the Brazilian Amazon between 1988 and 2021. Evaluating tree records from a network of permanent plots and herbarium collections, we found that 22 % of tree occurrence records were in deforested areas, 35% within 1 km of the forest edge, and 43 % in continuous forest. At the local scale in Central Amazonia, tree monitoring data over 30 years revealed that forest fragments hyperdominant trees had twice the mortality rate of continuous forest ones due to edge effects during the 15 years following edge establishment. Although trees in fragments had higher initial growth, this pattern declined over the years and eventually resulted in significant carbon loss, mainly from tree mortality. Edge effects have led to annual declines in the biomass of forest remnants, suggesting that hyperdominant species are also susceptible to disturbances that lead to degradation and forest losses. Conservation of the Amazon forests requires an approach that considers the effects of local disturbances on carbon stocks in the region.

1. Introduction

The Amazon rainforest plays a crucial role in regulating the global carbon (C) cycle due to its capacity for C fixation and biomass storage (Melillo et al. 1993; Dixon et al. 1994; Pan et al. 2011). Most of this C in biomass is stored above ground, notably concentrated within a small fraction of tree species, just 1% of tree species in Amazonia store half of the C (Fauset et al. 2015). The disproportionate accumulation is driven by parameters related to the hyperdominance of certain species in the biome, with just 2% of the species representing half of the trees in tropical forests worldwide (ter Steege et al. 2013; Cooper et al. 2024). Hyperdominance is expressively influenced by functional traits such as large size, growth rate, and wood density (Fyllas et al. 2009). The amount of C stored as biomass or transferred to necromass is governed by the rates of tree growth and mortality, which, in turn, are influenced by fluctuations in water availability and temperature variations, shaping

the forest dynamic (Roebroek et al. 2020).

However, the rising levels of atmospheric CO₂ associated with high deforestation rates, and increasingly frequent climate fluctuations have undermined the notion of the Amazon as a significant C sink (Schimel, 2015; Hubau et al. 2020; Zhao & Running, 2010). Land-use changes have accounted for over 70% of Brazil's greenhouse gas emissions recently (SEEG, 2021). Currently, the Southeastern region of the biome has transitioned from a C sink to a source due to significant deforestation and the subsequent increase in forest fires (Gatti et al. 2021; Rosan et al. 2023). Furthermore, National Institute for Space Research (2023) reports that approximately 18% of the Brazilian Amazon's original forest cover has been lost in forested areas where all vegetation has been converted into pasture or cropland. Vegetation removal raises the risk of wildfires in regions where they would not naturally occur due to humidity, leading to the emission of stored carbon from both living and dead biomass. (Nepstad et al. 1999; Pan et al. 2011).

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We refer to 'deforestation' as the complete removal of forest cover within a short period, followed by its subsequent replacement with other land uses. On the other hand, 'forest degradation' refers to anthropogenic disturbances significantly impacting forest structure, such as logging, fires, and forest fragmentation (INPE, 2008; Matricardi et al. 2020; Berenguer et al. 2021). This study focuses on degradation caused by fragmentation related to deforestation.

Deforestation in the Amazon rainforest exhibits significant spatial and temporal variation, mainly driven by agricultural expansion. The process of agricultural and livestock expansion stems from a history of public policies and is often associated with illegal practices (Margulis, 2003; Becker, 2005). In the 1970s, a government project in the eastern Amazon implemented a series of measures, including building infrastructure such as roads, hydroelectric dams, and communication networks. Settlement projects were also initiated, providing tax incentives to attract migrants from other regions of Brazil, who would subsequently arrive and occupy the area (Becker, 2009). Large and small landowners settled in the area, and the expansion extended into the Central Amazon through the highways established for agribusiness expansion, a significant factor in the region's devastation (Becker, 2004). The expansion of the agricultural frontier was mainly enabled by the greater accessibility resulting from the official construction of highways and the substantial illegal opening of secondary roads (Brandão et al. 2006; Haddad et al. 2015).

Converting continuous forests into agricultural and livestock areas leads to losing the initial forest habitat and forest fragmentation. Consequently, the landscape is spatially reconfigured, and the exposure extent of forest edges to non-forest matrices is increased (Laurance et al. 1997; Bennett et al. 2006; Berenguer et al. 2021). Forests close to the edge of forest fragments experience adverse environmental conditions, including exposure to higher solar radiation, increased wind intensity, and subsequent desiccation, which affect tree growth and survival. These environmental conditions are known as edge effects and significantly impact vegetation dynamics up to 300 m within a forest fragment or any forested edge (Laurance, 2004).

The impacts of edge effects vary among the tree species, and big trees are more susceptible to physiological complications caused by desiccation, which increases their likelihood of dying (Laurance et al. 2000). The higher frequency of mortality of large trees (>60 cm diameter at breast height) significantly reduces the local C stock, especially within the first 100 m from the edge. The loss of biomass that will be transformed in necromass or at different paces into atmospheric carbon without any quick replacement mechanism can lead to the local collapse of the carbon stock (Laurance et al. 1997; Lutz et al. 2018).

The fall of large trees leads to subsequent canopy opening, favoring the growth and establishment of pioneer trees that sequester less C. This significantly modifies the potential storage of C in the edge arboreal community (Laurance et al. 1998a, 1998b, 2000; Stephenson et al. 2014). Albiero-Junior et al. (2019) observed a reduction in the growth rate of *Scleronema micranthum*, a common Amazonian large-sized species, in individuals located on the edges over ten years after forest fragmentation. This large-scale phenomenon, occurring within the biome, can affect C stocks at forest edges (Albiero-Junior et al. 2019, 2021).

Given the relevance of tree species in regulating the C cycle and the magnitude of deforestation in the Amazon, we investigated the effects of environmental degradation through edge effects on the C stock dynamics of hyperdominant tree species. In doing so, we ask: (1) How much of the known occurrence of hyperdominant species was lost in the Brazilian Amazon biome between 1988 and 2021¹? Of the remaining hyperdominant tree species records, (2) what proportion are located in forest edges? (3) How does the edge effect affect mortality and C accumulation in the species populations? We hypothesize that exposure to the edge effect due to deforestation alters the dynamics and C stock in populations of hyperdominant species. Thus, we expect an increase in the mortality rate of the tree populations investigated and a decrease in

growth rate as a negative response to edge effects or, conversely, an increase in growth rate favored by an environment with greater light availability. The study aims to assess the impact of forest fragmentation on key hyperdominant species, exploring the C balance based on losses and gains represented by mortality and growth rates.

¹The period defined for this study corresponds to the Brazilian official monitoring data on deforestation in the Brazilian Amazon.

2. Material and methods

2.1. Study area

In this study, we analyzed databases covering two spatial scales. To address questions 1 and 2, we used a regional scale corresponding to the Brazilian Amazon biome with deforestation data generated by the Satellite Deforestation Monitoring Project in Legal Amazon – PRODES (INPE, 2022) (Fig. 1).

To answer the third question raised, we focused on a local study area using tree monitoring data from the Biological Dynamics of Forest Fragments Project (BDFFP), located approximately 80 km North of Manaus in the Central Amazon. The BDFFP is the longest-running project monitoring biodiversity and assessing the consequences of forest fragmentation in tropical forests (Laurance et al. 2018). The experimental area established in 1979 covers 1 000 km², with forest areas of different sizes within continuous mature forests and remaining forest fragments represented by samples of permanent forest plots of 1 ha (100 × 100 m). Isolated plots were initially surrounded by a matrix of pasture created by clear-cutting techniques and, subsequently, after being abandoned, a matrix of secondary forest (Lovejoy, 1986; Laurance, 2002). Every five years, a strip of 100 m surrounding the forest fragments was cut to keep them isolated. With data from these two different environments, we could comparatively assess the consequences of forest edge effects on mortality rates and C accumulation in selected tree species populations.

For the Biome scale study, we used a subdivision of the Brazilian Amazon proposed by Becker (2004), which divides it into three macro-regions. The regionalization considers the different historical patterns of local settlements, aiding in discussing the Amazon spatial and temporal heterogeneity related to human occupation and forest loss and its effects in the species occurrence patterns within the biome. The Densely Populated Arc region consists mainly of Maranhão, Tocantins, Mato Grosso, and Rondônia states. The Central Amazon corresponds to most of Pará, Amapá, and the Eastern part of Amazonas state. Finally, the Western region includes the states of Roraima, the remaining part of Amazonas, and part of Acre (Fig. 2A).

2.2. Database and sampling design

We focused on the list of hyperdominant species as presented by Fauset and colleagues (2015), based on a dataset from 530 permanent plots distributed throughout the Amazon biome, maintained and organized by the RAINFOR and ForestPlots.net projects (Lopez-Gonzalez et al. 2011). From this list, we selected 182 tree species responsible for storing 50% of the forest biomass in the monitored plots. We then excluded from the list palm species and tree species occurring exclusively outside the Brazilian Amazon, resulting in a final selection of 146 tree species.

To compile the known occurrence points of the selected species, we checked the information from Amazon Tree Diversity Network permanent plots database (ATDN, 2019) and online herbarium platforms: Botanical Information and Ecological Network (BIEN), Global Biodiversity Information Facility (GBIF), and SpeciesLink. The herbarium data covered an extended period between 1900 and 2022, providing a historical perspective on species occurrence records at sampling points before significant land use conversion, typically through forest suppression.

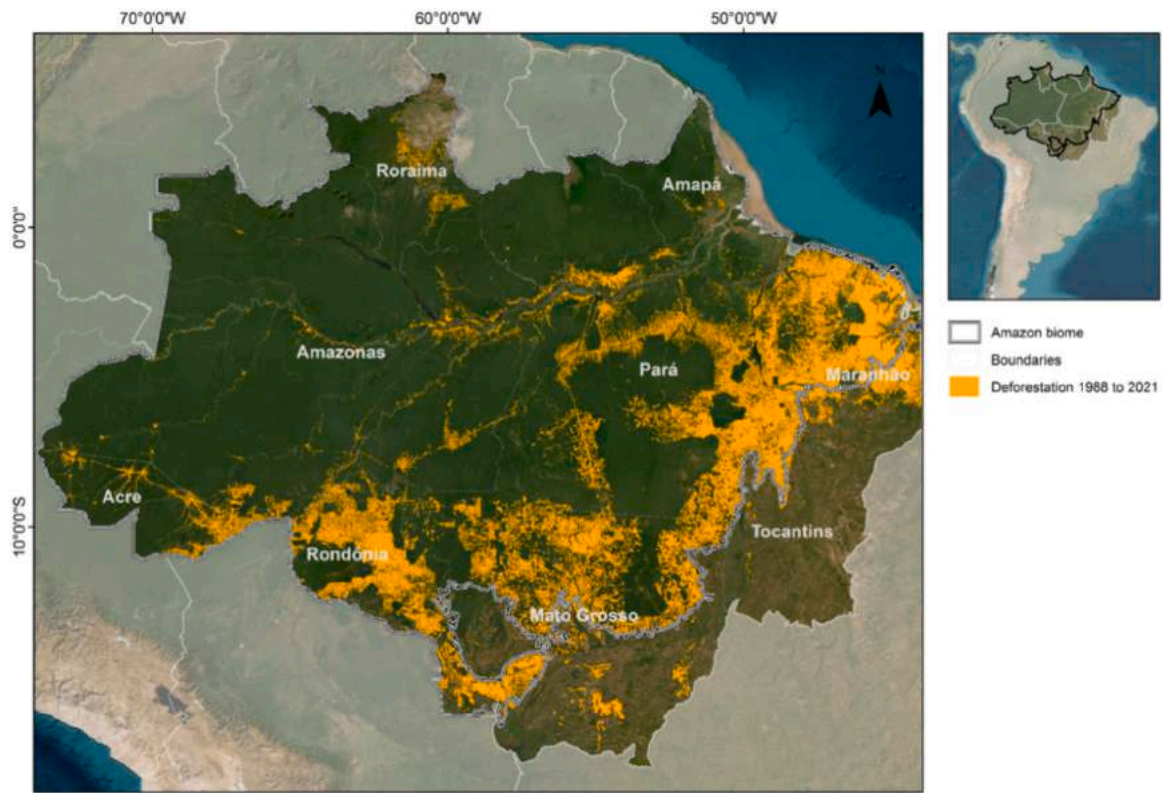


Fig. 1. Amazon biome within Brazilian territory, predominantly covered by tropical forest (in green) and cumulative deforestation between 1988 and 2021 (in yellow) based on the historical records produced by PRODES (2022).

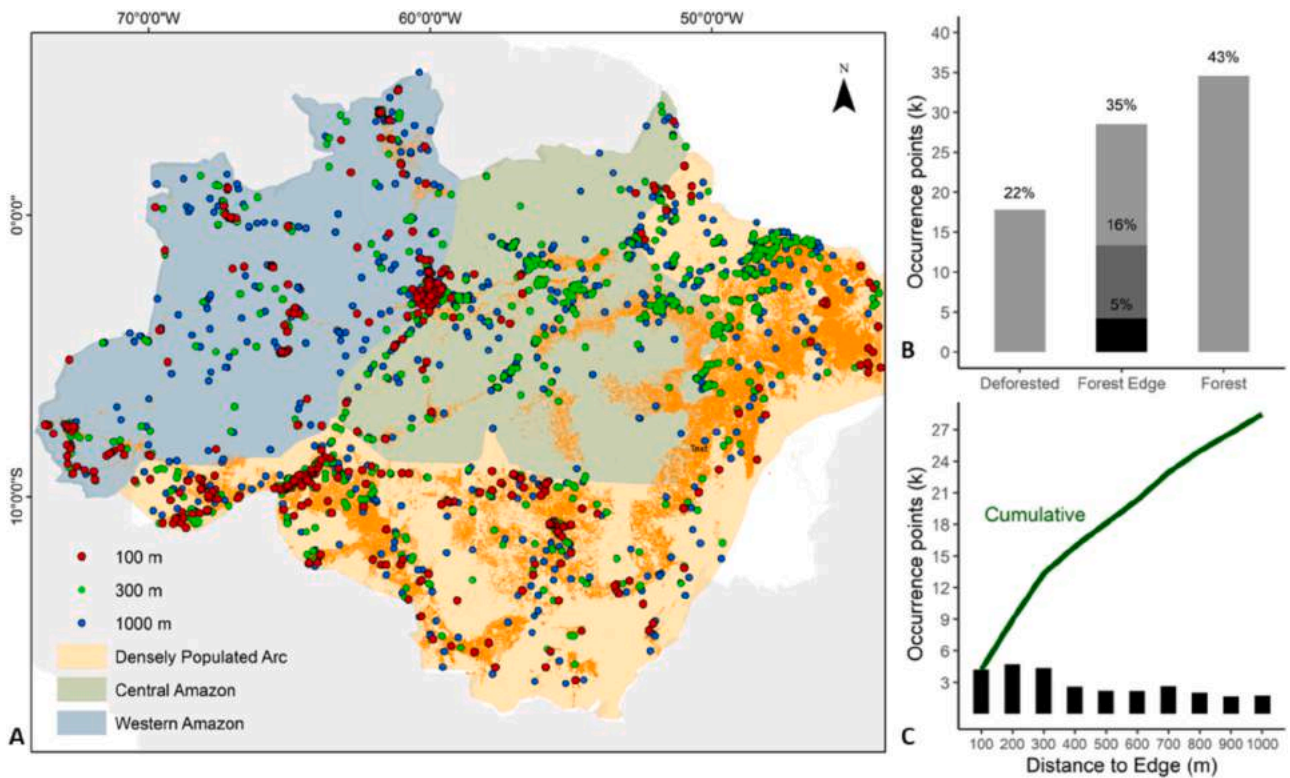


Fig. 2. Tree species occurrence in the Brazilian Amazon. A. Distribution map of occurrence records of hyperdominant tree species on 100 m, 300 m and 1 000 m from the edge and territory subdivision proposed by Becker et al. (2004). B. Proportion of occurrence records (in thousands) in deforested areas, forest edge areas, and continuous forest. The dark gray portion represents the proportion of occurrence points up to 300 m from the edge, and the black portion represents occurrences up to 100 m from the forest edge. C. Occurrence points (in thousands) at each distance from the edge and the increasing accumulation in distance categories (green line).

2.3. Data preparation and statistical analysis

To estimate how much of the species' original known range has been lost, we overlaid the tree species occurrence points with information derived from the PRODES cumulative deforestation maps for the period of 1988–2021, freely available at (<http://terrabrasilis.dpi.inpe.br/downloads/>). The proportion of each species' occurrence within areas classified as deforested at the regional scale was then estimated.

To assess how much of the selected species' occurrences are located at forest edges, we defined distances from PRODES cumulative deforestation perimeters toward the forest core. Distances of 100 m, incremented by 100 m up to 1 km, were then created from the perimeter of each detected forest fragment across the biome, creating an area considered to be progressively affected by forest edge effects. We considered areas most affected within the first 100–300 m from the edge and areas susceptible to progressive deforestation and subsequent edge effects from 300 to 1 000 m (Laurance et al. 2018). This procedure allowed us to determine the proportion of occurrences present in forested areas but exposed to edge effects.

To assess changes in forest dynamics under edge effects on a local scale at the community level, we selected and compared data from species with more than five individuals, performing 93 tree species. The trees were located in 36 of 1 ha permanent plots (100 × 100 m) in forest fragments within 100 m of the forest edge, and data from 29 of 1 ha permanent plots in continuous forests located beyond 100 m from the forest edge, covering approximately 30 years of census data; 14,083 trees were analyzed, 8115 located in forest fragments and 5967 in continuous forest, representing 21.5% of the total trees monitored in the BDFFP.

We calculated the community mortality rate for each time interval using the formula: $[\log(N1) - \log(N2)] / [T2 - T1]$, where N1 is the number of individuals in the first census, N2 is the number of individuals in the last census excluding recruits, that is, individuals who were included in the census for reaching the minimum DBH (10 cm) in that year, T1 is the year of the first census, and T2 is the year of the last census (Laurance et al. 2009). The equation used to calculate the recruitment rate was $[\log(N2) - \log(N1)] / [T2 - T1]$, and by averaging the estimated mortality and recruitment rates, we calculated the turnover rate. Because the plots differed in the interval between censuses, a correction factor was applied to both mortality and recruitment rates, as well as the turnover rate, to minimize bias caused by differences in time intervals: $\lambda_{corr} = \lambda \cdot t \cdot 0.08$, where λ is the rate and t is the interval between censuses in years (Lewis et al. 2004). Annual relative growth was calculated using the equation $[\log(DAP2) - \log(DAP1)] / [T2 - T1]$, where DAP1 represents diameter at breast height (cm) in the first census and DAP2 in the last. The non-parametric Mann-Whitney test (Wilcoxon rank sum test) was used to compare rates between continuous and fragmented forests for each time interval.

Considering the species-level analysis of RGR, we selected species with at least five individuals in all time intervals in each area (30 spp.). Marginal and conditional R-squared values (proportion of variance explained by fixed effects - R^2_m , and random and fixed effects - R^2_c) were calculated following Nakagawa and Schielzeth (2013). The year of establishment of forest fragments and the frequency of demographic censuses were different among plots. Considering the timing differences, the timeline was divided into six periods ranging from 5 to 30 years, considering each plot's start year of the forest fragmentation process.

We applied a logarithmic transformation to the community and species-level rates to ensure a normal distribution of the residuals. All analyses were performed in the R programming environment.

To assess the difference in dynamics between edge and continuous forests over time, we fitted mixed-effects linear models using the *lmer* function from the *lme4* package. For RGR, we fitted the model: $RGR_{[i]} = \beta_0 + \beta_1 year_{[i]} + \beta_2 location_{[i]} + \beta_3 year * location_{[i]} + Residuals_{[i]}$, where i = individual relative growth rate, year refers to the time interval and location refers to fragmented and continuous forest categories. At the

community level, plot ID was used as a random factor to control for the co-occurrence of individuals on the same plot, while at the species level, species ID was used as a random factor to control for species identity. For the analysis of mortality and turnover rates, we fitted the same interaction model, but i = the mortality or turnover rates at the plot level ($n = 65$).

3. Results

3.1. Exposure to deforestation and edge effect - regional scale

Of the 80 thousand hyperdominant species occurrence points in the Brazilian Amazon recorded from the permanent plots and herbaria data set, 43% of the occurrence points were in unbroken forest, 35% were located within 1000 m of a forest edge, and 22% were located in areas already deforested between 1988 and 2021. Specifically related to the forest edges, there was a concentration of points in the first 300 m from the edges; 15% were located within the first 100 m, and about half of the records (46%) were within the first 300 m of the edge (Fig. 2B). The records decreased between 400 and 700 m from the edge (Fig. 2C).

The highest concentration of hyperdominant tree occurrences was recorded in the Central Amazon (45.5%), followed by the Densely Populated Arc region (33.5%), while the lowest concentration was recorded in the Western Amazon (21%). The distribution pattern changes when only points in deforested areas are considered, with a higher concentration in the Arc (48%), followed by the Central Amazon (36%), and again a lower concentration in the Western Amazon (16%). At the forest edge, points are mainly located in the Central Amazon (38%) and the Arc (38%). This pattern continues for points 300 m from the forest edge. For points within the forest, there is a predominant concentration in the Central Amazon (58.5%), followed by a balanced distribution between the Arc (21%) and the Western Amazon (20.5%) (Fig. 2A).

For about 4% of the species, most occurrences overlap with deforested areas. Another 30% of species occur predominantly at forest edges, and 80% showed a higher concentration of records within the first 300 m of the edge (Table 1). Among the species with the majority of records in already deforested areas or at the edge, predominantly within the first 300 m, three main patterns of occurrence were observed based on the registers: species restricted to one region of the Brazilian Amazon, generally with little information on their distribution; species with few records in the Brazilian Amazon, but widespread in the rest of South America; and species with widely distributed records throughout the biome (see Table 1). Additionally, we included in Table 1 two crucial parameters in determining the potential accumulation of carbon, the maximum diameter at breast height (DBH) and wood density. A total of 60% of the listed species reached a high DBH (>60 cm; Lutz et al. 2018) and 56% a high wood density (>0,69 g/cm³; Fearnside, 1997) (see Table 1). Such characteristics indicate that those tree species are essential to building up the forest's vertical structure, composing the canopy and the emergent tree strata. Meanwhile, based on the wood density, they exhibit a slow-growing pattern. It is notable, but not surprisingly, that 40% of the species belong to the Fabaceae family. This highly diverse family may vary in the growth pattern and wood density but are essential components of the structure and, in most cases, in the function in the forest, especially in its role of N fixer through the mycorrhizal association (Costa et al. 2021; Myster et al. 2023).

3.2. Edge effect on tree mortality and carbon accumulation - local scale

Considering the forest dynamics among the hyperdominant species occurring in the BDFFP, in a comparative scenario between fragmented forest areas (FF) and continuous forest areas (CF), we found that for the selected tree community (93 spp.), the average mortality rate was more than twice as high in FF compared to CF (FF = 1.79% ± 0.24% yr⁻¹ vs. CF = 0.75% ± 0.18% yr⁻¹, $W = 188$, $p < 0.05$) during the first five years

Table 1

Proportional distribution pattern of tree species occurrence in deforested areas from 1988 to 2021, forests located 300 and 1000 m from the edge, and continuous forests: Part A. Tree species occur more frequently in deforested areas, and Part B. Tree species occur more frequently in edge areas. Occurrence is predominant at the edge, mainly in the first 300 m. The maximum diameter at breast height (DBH) data was obtained from the Global Wood Density Database, referred to as [Chave et al. \(2005\)](#) and [Zanne and Amy \(2009\)](#).

A. Predominance in deforested area														
Occurrence pattern	Species	Family	Max DBH (cm)	Wood density (g/cm ³)	Deforested (%)	Forest Edge	Forest (%)							
						Distance range (m)	%							
South America wide distribution	<i>Anadenanthera colubrina</i>	Fabaceae	57.8	0.8375	54.1	300	5.4	16.2						
						1000	29.7							
Biome wide distribution	<i>Dipteryx micrantha</i>	Fabaceae	124.7	0.8710	42.3	300	11.5	25						
						1000	32.7							
						300	18.5	25.8						
Biome wide distribution	<i>Hymenaea courbaril</i>	Fabaceae	89.9	0.7815	38.6	1000	35.6							
						300	16.5	30						
						1000	33.3							
Restricted to Brazilian Amazon	<i>Vouacapoua americana</i>	Fabaceae	70.6	0.7936	40.4	300	24.3	27.5						
						1000	32.1							
						300	15.2	29.9						
South America wide distribution	<i>Lecythis idatimon</i>	Lecythidaceae	38.7	0.7985	39.9	1000	30.2							
						300	20.7	25.9						
						300	50.8							
South America wide distribution	<i>Parkia pendula</i>	Fabaceae	108.5	0.5212	23.4	300	22	29.4						
						1000	48.2							
						300	21.3	24.2						
						1000	46.6							
						300	22.8	31.2						
						1000	43.8							
						300	20.5	31.5						
						1000	42.8							
						300	20.8	27.4						
						1000	39							
300	22.3	36.6												
Biome wide distribution	<i>Sloanea guianensis</i>	Elaeocarpaceae	87.2	0.8212	18.9	1000	44.5							
						300	22.3	36.6						
						1000	44.5							
						300	20.6	26.2						
						1000	47.1							
						300	19.8	31.9						
						1000	40.7							
						300	19.6	33.7						
						1000	40.4							
						300	16.1	37.6						
Biome wide distribution	<i>Pseudolmedia macrophylla</i>	Moraceae	34.1	0.6602	26.7	1000	39.5							
						300	19.8	35.8						
						1000	39.5							
						300	16.3	28.7						
						1000	38.2							
						300	22.6	19						
						1000	45.3							
						300	22.6	32.3						
						1000	45.2							
						300	25.5	39.2						
Restricted to Brazilian Amazon	<i>Tachigali paraensis</i>	Fabaceae	96.3	0.6880	35.8	1000	43.1							
						300	17.1	27.7						
						1000	41.5							
						300	18.2	38.6						
						1000	39.14							
						300	20.2	29.8						
						1000	36.2							
						Biome wide distribution	<i>Chrysophyllum lucentifolium</i>	Sapotaceae	113	0.7870	27.5	300	19.8	31.9
												1000	40.7	
												300	19.6	33.7
1000	40.4													
300	16.1	37.6												
Biome wide distribution	<i>Licania canescens</i>	Chrysobalanaceae	40.3	0.8800	25.9	1000	39.5							
						300	19.8	35.8						
						1000	39.5							
						300	16.3	28.7						
						1000	38.2							
Biome wide distribution	<i>Astronium lecointei</i>	Anacardiaceae	57.9	0.7903	22.8	300	22.6	19						
						1000	45.3							
						300	22.6	32.3						
						1000	45.2							
						300	25.5	39.2						
Biome wide distribution	<i>Sterculia pruriens</i>	Malvaceae	58.6	0.4862	24.7	1000	43.1							
						300	17.1	27.7						
						1000	41.5							
						300	18.2	38.6						
						1000	39.14							
Biome wide distribution	<i>Bertholletia excelsa</i>	Lecythidaceae	169.6	0.6240	33.1	300	20.2	29.8						
						1000	36.2							
						300	45.3							
						1000	45.2							
						300	25.5	39.2						
Restricted to Brazilian Amazon	<i>Protium altissimum</i>	Burseraceae	55.5	0.7078	30.8	1000	41.5							
						300	17.1	27.7						
						1000	41.5							
						300	18.2	38.6						
						1000	39.14							
Biome wide distribution	<i>Aspidosperma carapanauba</i>	Apocynaceae	89.8	0.7504	19.1	300	20.2	29.8						
						1000	36.2							
						300	45.3							
						1000	45.2							
						300	25.5	39.2						
Biome wide distribution	<i>Pouteria oppositifolia</i>	Sapotaceae	93	0.6500	34	1000	39.14							
						300	20.2	29.8						
						1000	36.2							
						300	45.3							
						1000	45.2							

after the area isolation, maintaining this pattern in FF up to 15 years after fragmentation ($W = 771$, $p < 0.05$). After this period, there was a decrease in the mortality rate in FF, while simultaneously, there was an increase in CF (Fig. 3A). Following the mortality pattern, the turnover rate was higher in the early years of FF and decreased over time, while there was an increase in CF (Fig. 3B).

During the first 15 years after fragment isolation, RGR was higher in

FF than in CF ($W5 = 3268243$; $W10 = 6871246$; $W15 = 9473088$, $p < 0.05$). In addition, the decline in RGR was more significant in FF, converging after 30 years to annual rate values similar to CF, indicating a reduction in the intensity of the consequences of the fragmentation process over time (Fig. 3C). In the RGR species analyses (30 spp.), 18 species showed an interaction between time and location influencing the variation in growth rate ($p < 0.05$). There was a predominant trend of

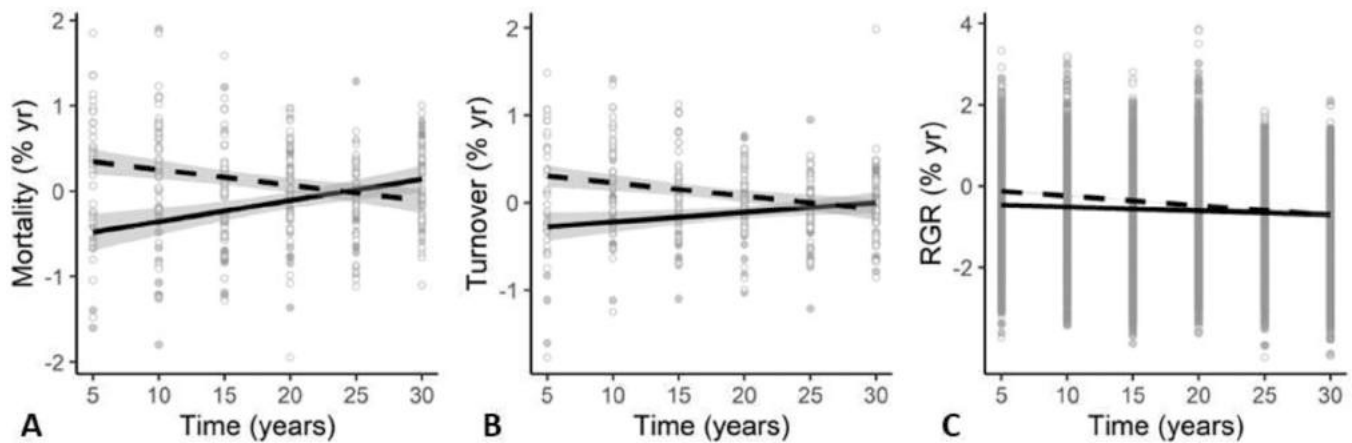


Fig. 3. Community dynamics of hyperdominant tree species (93 spp.) over 30 years in fragmented forest areas (FF, dashed line) and adjacent continuous forest areas (CF, solid line) from BDFFP, Central Amazon. A. Mortality rate (% yr⁻¹); B. Turnover rate (% yr⁻¹) and C. Relative Growth Rate (RGR, % yr⁻¹). All values are in logarithmic scale.

convergence in RGR, except for *Swartzia reticulata*, which exhibited higher growth in CF than in FF after 30 years (Fig. 4 and see Supplementary Material, Table A2).

4. Discussion

We found that about 20% of the occurrence records have already been lost due to deforestation. These points were prevalent in the Densely Populated Arc deforested areas, which can be attributed to the ongoing deforestation in the region. As suggested by Becker (2004), this area is characterized by consolidated settlements in a historical process of occupation, where deforestation was considered an improvement that added value to the land (Gomez et al. 2015; Aguiar et al. 2007). The presented data is consistent with a recently published study that demonstrates a one-third reduction in the recorded occurrence area of tree species due to deforestation, mainly in the Arc region. (Stropp et al. 2020).

One of the critical global consequences of deforestation is the release of stored C into the atmosphere, resulting from the loss of forest biomass and necromass (Loarie et al. 2009; Galford et al. 2011). Areas previously covered by forest and converted to pasture, agricultural land, or burned lose their accumulated C stocks significantly above ground (Berenguer et al. 2014; Nunes et al. 2022; Mapbiomas, 2023), compromising the functional capacity of the forest to act as a sink (Gatti et al. 2022). Thus, we highlight the contribution of the 20% occurrence records of the most C-storing tree species to the conversion of forests, once sinks, into net C sources due to land use conversion (Gatti et al. 2021).

In addition to C emissions from deforestation, which remains the primary source of C loss, it is imperative to consider emissions associated with forest degradation in general and forested areas under the effect of edges (Pearson et al. 2017). Edge effects alone can account for up to half of the carbon loss from deforestation in the Amazon (Silva Junior et al. 2020). As a result, approximately one-third of hyperdominant tree occurrences within 1 km of the edge are vulnerable to C loss due to the adverse effects of forest fragmentation. Even more alarming, approximately half of these populations may already be experiencing these effects within 300 m of the forest edge, where the effects are significantly more pronounced (Laurance, 1997, 1998a). However, it is essential to recognize that this pattern could be biased by collection strategies and the establishment of forest inventory plots, which are often located in easily accessible areas near roads and rivers and, thus, close to forest edges (Oliveira et al. 2016). Therefore, it is imperative to conduct more comprehensive analyses to investigate such bias and its implications for studies related to edge-induced forest degradation.

Another critical consideration is that forests close to the edges are

also vulnerable to deforestation. Given the ongoing deforestation trends, these populations are at imminent risk of decline, in line with projections that deforestation will advance up to 40% of the forest by 2050 if we continue with current trends in agricultural expansion (Soares-Filho et al. 2006).

Fabaceae was the most common family among species in deforested areas or edges, probably because of its diversity and mainly due to its abundance amongst the hyperdominant species (ter Steege et al., 2013). Several Fabaceae species are recognized as reaching one of the largest basal areas within the Amazonian trees, representing most of the large trees in the Amazonian rainforest. Thus, they are among the most influential families responsible for building the structural component of the forest (Costa et al. 2021; Myster et al. 2023).

Primarily due to continued high mortality rates, especially within the first 15 years after the generation of forest edges through the fragmentation process, we can infer a loss of C in FF. The increased mortality and turnover have resulted from the new microclimatic conditions established at the edge, high temperatures, and strong winds leading to canopy desiccation and physical damage (Camargo and Kapos, 1995; Laurance et al. 1998a, 2000, 2004; Ferreira and Laurance, 1997). Besides the fact that dead trees will slowly release C through the decomposition of the necromass, they will no longer sequester or accumulate carbon, reducing the overall sink potential of the forest. There is also C loss through branch breakage, one of the primary forms of biomass loss in areas under the edge effect, which poses a risk of damage to smaller nearby trees, also reducing their C contribution to the overall C pool in the forest (Esquivel-Muelbert et al. 2020; Nunes et al. 2023).

Although turnover is more pronounced in FF, studies show that recruitment consists primarily of smaller pioneer tree species, shrubs, and lianas (Laurance et al., 1997; Mesquita et al. 2001). This process potentially leads to C accumulation below pre-fragmentation levels (Silva Junior et al. 2020), implying a reduction of C storage in FF and a continuous loss of C accumulation potential over time (Ferreira and Laurance, 1997; Laurance et al. 1997). Therefore, there is an acceleration of the C cycle in FF, characterized by a shorter residence time of C in the biomass along the successional gradient compared to large trees in continuous areas (Nascimento and Laurance, 2004; Reis et al., 2022).

In addition, FF individuals exhibited higher RGR immediately after edge establishment, which decreased steadily over 15 years until it equaled the relative growth observed in CF. The initial higher growth in FF could be attributed to increased light availability due to higher tree mortality and, consequently, the changes in the forest structure close to the edges in the early years following forest fragmentation (Oliver et al. 1996). However, this pattern did not hold for the studied species, which generally are slow-growing under natural conditions. Thus, while edge

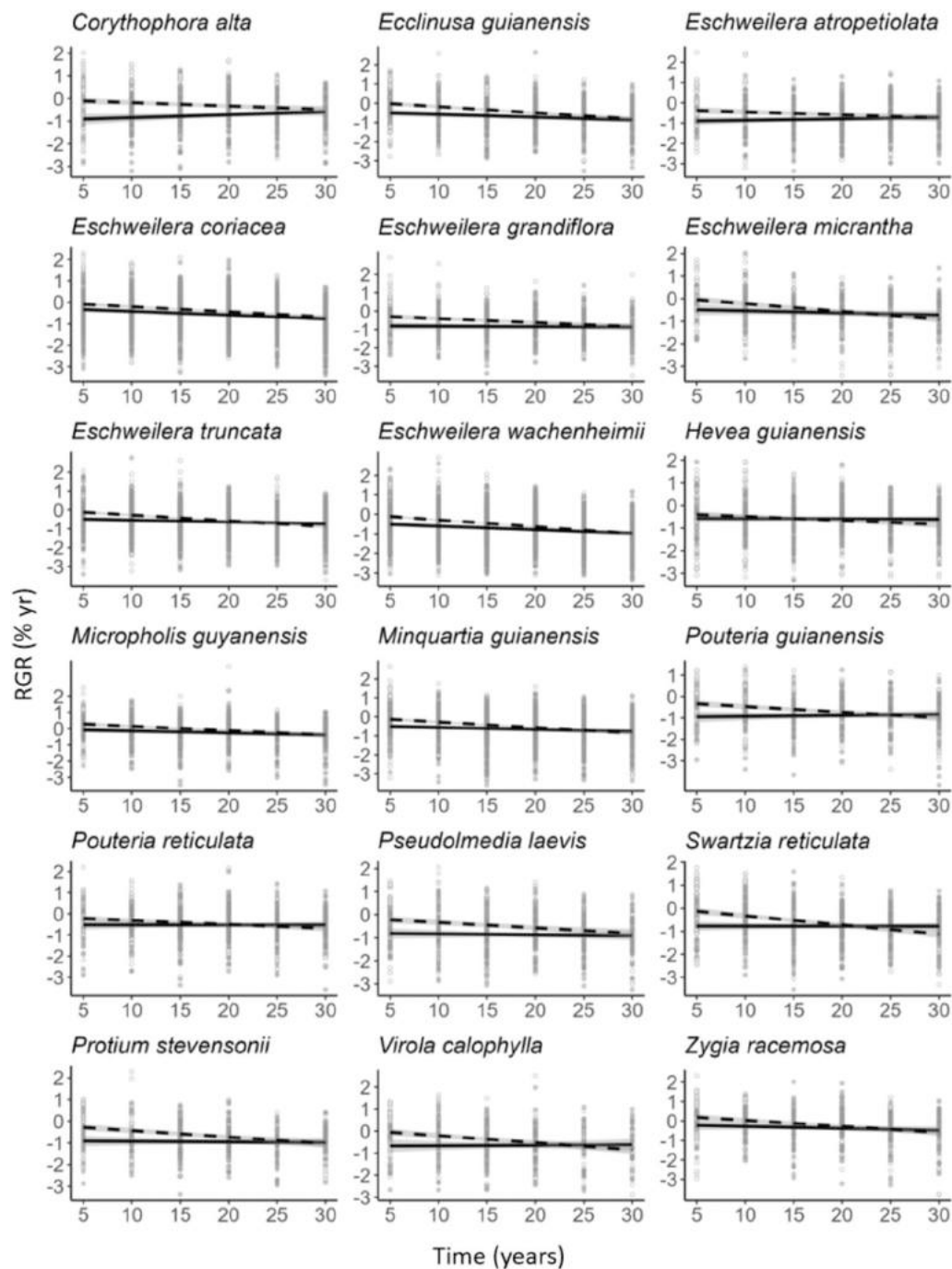


Fig. 4. Relative Growth Rate ($\% \text{ yr}^{-1}$) of hyperdominant tree species (30 spp.) over 30 years in fragments (FF, dashed lines) and continuous forests (CF, solid lines) from BDFFP, Central Amazon.

formation may favor initial growth, the slow-growing pattern returns as the forest structure starts to be rebuilt. And, then, it did not translate into a consistent contribution to C stock over time.

Although more pronounced in FF, the overall reduction in tree growth over 30 years, as well as the increased mortality observed in FC, may be related to the higher frequency of extreme climatic events lately, as evidenced by the decrease in tree growth during El Niño years (Aleixo et al. 2019; Stahle et al. 2020).

The contribution to the regional-scale results provided an overview of species vulnerability. In contrast, the local-scale results provided insight into how species dynamics have changed over time, signaling significant regional dynamics in the Amazon basin. A similar pattern could occur in at least 15% of the areas located within the first 100 m of

the forest edge.

4.1. Conservation relevance and management of protected areas

Population parameters analysis, such as relative growth or mortality, allowed us to infer the dynamics of tree populations in fragmented areas within the biome. Details on the local scale pattern registered by some of the studied species caught our attention; for example, *Miquartia guianensis* and *Eschweilera truncata* were affected by forest fragmentation and, at the regional scale, were predominantly recorded close to edge areas. Also, *Lecythis idatimon* and *Vouacoupa americana* showed a worrying conservation status, with a former higher concentration of records in already deforested areas and a restricted distribution in

Brazil, mainly in the Northern regions of the Amazon. *V. americana* was already listed as "Critically Endangered" in the International Union for Conservation of Nature's (IUCN) Red List of Threatened Species (IUCN, 2022). We also highlighted species such as *Protium altissimum*, *Pouteria oppositifolia*, and *Tachigali paraensis*, whose records were not only restricted to forest edges but also had the second-highest concentration of occurrence in deforested areas.

Such situations highlighted the need for conservation politics, such as deforestation control and preventing vegetation suppression in new areas. The complex interplay of urbanization, territorial policies, and land use dynamics driven by integration into national economic cycles may define the destiny of the tree species in Central Amazon (Becker, 2004; Fearnside, 2001; Aguiar et al. 2002, 2007). Conversely, the Western Amazonian region lacks comprehensive data due to information gaps caused by local inaccessibility and significant distances from major research centers, making material gathering expensive and challenging (Aguiar et al. 2007; Carvalho et al. 2023). These regions host vital Conservation Units (UCs) and Indigenous Territories (TIs), crucial areas for forest protection. However, even such protected areas are vulnerable to degradation due to the expansion of deforestation, the legal or illegal exploitation of natural resources, the settlement along rivers, and the invasion of TIs and UCs (Oliveira Souza, 2020; Schielein and Börner, 2018; Silva et al. 2021). For species that predominantly occur in contiguous areas, 40% of forest points were located on UCs or TIs, highlighting these areas' critical role in environmental conservation. Such fact emphasizes the need to allocate more areas for conservation, to combat deforestation, and consequently reduce C emissions (Walker et al. 2009, 2020; Blackman and Veit, 2018; Sousa et al. 2023; Londono et al. 2016; Soares-Filho et al. 2023).

On top of all these points, we should also consider managing and recuperating degraded areas and passively or actively promoting regeneration into secondary forests, which is crucial for C accumulation and maintaining biodiversity and ecosystem functions (Lewis et al. 2019). However, studies highlighted that over 70 years may be required for forests to restore C stocks to pre-disturbance levels, showing a slow and gradual process that should be aligned with policies to combat deforestation in new areas, with strategies that are sensitive to local specificities (Poorter et al. 2016; Lennox et al. 2018).

Although this study provides valuable insights into tree species dynamics, in-depth investigations are essential for a comprehensive understanding of these patterns in the Amazon. Therefore, we recommend using C measurement methods in future studies at the community level and involving fragmented areas, such as LiDAR, which has shown robust results by capturing mortality-related changes and recurrent tree breakage in edge areas (Nunes et al. 2023). In addition, robust models that include specific environmental variables of edge areas and tree age are needed to better understand the effect of forest fragmentation on tree growth patterns. Furthermore, it is crucial to consider the age of forest edges in future studies, as naturally regenerating vegetation tends to mitigate the influence of edges over the years.

5. Conclusion

Hyperdominant tree species exposed to forest edges exhibited double mortality rates in the Central Amazon during the 15 years following forest fragmentation. This pattern was accompanied by initial growth that was not sustained over time. This scenario suggests a significant carbon loss in these areas, mainly due to unbalanced tree mortality.

We also found that deforestation led to a 22% reduction in the available knowledge about these species, resulting in the release of carbon into the atmosphere and consequent negative impacts due to tree removal. In addition, there has been a considerable decrease in the scientific information on these species. Furthermore, it is plausible to assume that the populations of several hyperdominant species residing along the edges throughout the Amazon may exhibit similar responses to edge-induced degradation, leading to reduced biomass that generally is

not considered in any evaluation. Thus, this phenomenon underscores the importance of these trends in Amazonian carbon estimates and balance. It highlights the need for conservation and management strategies that consider the responses of high-carbon stock trees to the environment.

Ethics approval

Ethics approval was not required for this study according to local legislation

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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.

Data Availability

Data will be made available on request.

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Consent to participate

Not applicable

Consent for publication

Not applicable

Code availability

Study is available from the corresponding author on reasonable request.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.foreco.2024.121926](https://doi.org/10.1016/j.foreco.2024.121926).

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