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Native species seedlings in forest restoration in the Southern Amazon rapidly increase soil carbon stocks

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ABSTRACT

Forest degradation in the Amazon has led to severe environmental impacts, with active restoration, through mixed plantings of native and/or exotic tree seedlings, emerging as a key for ecosystem recovery. The study aimed to evaluate the soil organic carbon (SOC) and total nitrogen (TN) stocks of legal reserve (LR) restoration treatments in the southern Amazon after 10 years of implementation. The experiment was conducted from 2012 to 2022, followed a randomized block design with five treatments and four replicates. Treatments included three active restoration techniques using seedling planting, one passive regeneration treatment (area isolation), and a secondary forest as reference. Soil samples were collected from 60 × 80 m plots down to a depth of 1 m to determine C, N, bulk density, and SOC and TN stocks. Photosynthetically active radiation (PAR) was monitored from 2015 to 2019 using sensors equipped with automatic data loggers. Active restoration significantly increased SOC stocks compared with passive regeneration ($p < 0.05$), reaching up to 120 Mg ha^{-1} in seedling-based treatments versus ~100 Mg ha^{-1} under passive regeneration (~100 Mg ha^{-1}). Seedling-based treatments also exhibited higher annual SOC accumulation rates (1.4–2.5 Mg ha^{-1} year^{-1}). Total N (TN) was not significantly affected by the treatments, except in the surface layer, where the secondary forest showed the higher values. Principal component analysis (PCA) revealed a negative correlation between SOC and understory PAR, indicating that increased canopy development enhanced organic matter input and SOC accumulation. PCA also indicated that the inclusion of exotic species, or a higher proportion of them relative to native species, may delay increases in soil C and N. Planting native species was the most effective restoration strategy for rapidly increasing SOC stocks, highlighting its potential as a viable and sustainable approach for forest restoration.

1. Introduction

Forest degradation has generated significant environmental debt over the past decades, particularly in the southern and eastern regions of the Amazon biome, where land-use change has reduced native vegetation cover in areas legally designated for conservation, such as legal reserves (LRs) or permanent preservation areas (PPAs) (Cruz et al., 2021; Lima et al., 2022; Liévano-Latorre et al., 2025). The Brazilian Forest Code (BFC), originally established in 1965 and revised under Law 12,651/2021, assigns LRs the role of ensuring the sustainable use of natural resources on rural properties, maintaining ecological processes, and promoting biodiversity conservation, including the protection of native flora and fauna (Brasil, 1965, 2012). Ecological restoration of these areas is therefore directly linked to the provision of essential ecosystem services that sustain human well-being (Liévano-Latorre et al., 2025).

Among the strategies encouraged by the BFC are passive or natural regeneration (with and without management) and the planting of native species through direct seedling or seedling establishment, as well as the temporary use of exotic pioneer species intercropped with natives (Embrapa, 2021). Although scientific advances have expanded knowledge on methods and designs, and restoration has been increasingly

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recognized as a complementary strategy for mitigating climate change (Lima et al., 2022; Werden et al., 2024; Liévano-Latorre et al., 2025), the recovery of biodiversity and ecosystem functions remains a long-term process, as tree-based interventions often require decades for measurable ecological responses (Meli et al., 2017; Poorter et al., 2021; Brancalion et al., 2025).

Despite the slow responses, particularly in achieving the same metrics as a native forest, soil attributes show faster results, usually within the first decade (Poorter et al., 2021; Chazdon et al., 2025). In soils, the responses regarding increases in SOC and TN in forest restoration areas depend on the region (tropical vs. temperate), strategy (passive vs. active), land-use history and soil class, as well as the restoration time (Allek et al., 2023; Xu et al., 2024). Accrual in C and N are directly related to the input of organic material (OM) into the soil (Silva and Mendonça, 2007; Wiesmeier et al., 2019), which can indirectly contribute to understanding the growth of forest species that compose restoration models. Furthermore, C and N are directly related to soil health, improving the water cycle, nutrient cycling, water and nutrient absorption by plants, and the proper functioning of the micro-watersheds they comprise (Weil and Brady, 2017).

The responses regarding the accrual of C and N under the edaphoclimatic conditions of the southern Amazon would help to identify more suitable restoration models considering agricultural land-use history, contributing to the selection of the more appropriate strategies for this purpose. Based on evidence that native tree species respond to higher nutrient availability in soils (Melo, 1999; Wright, 2019; Jaquetti, 2020),

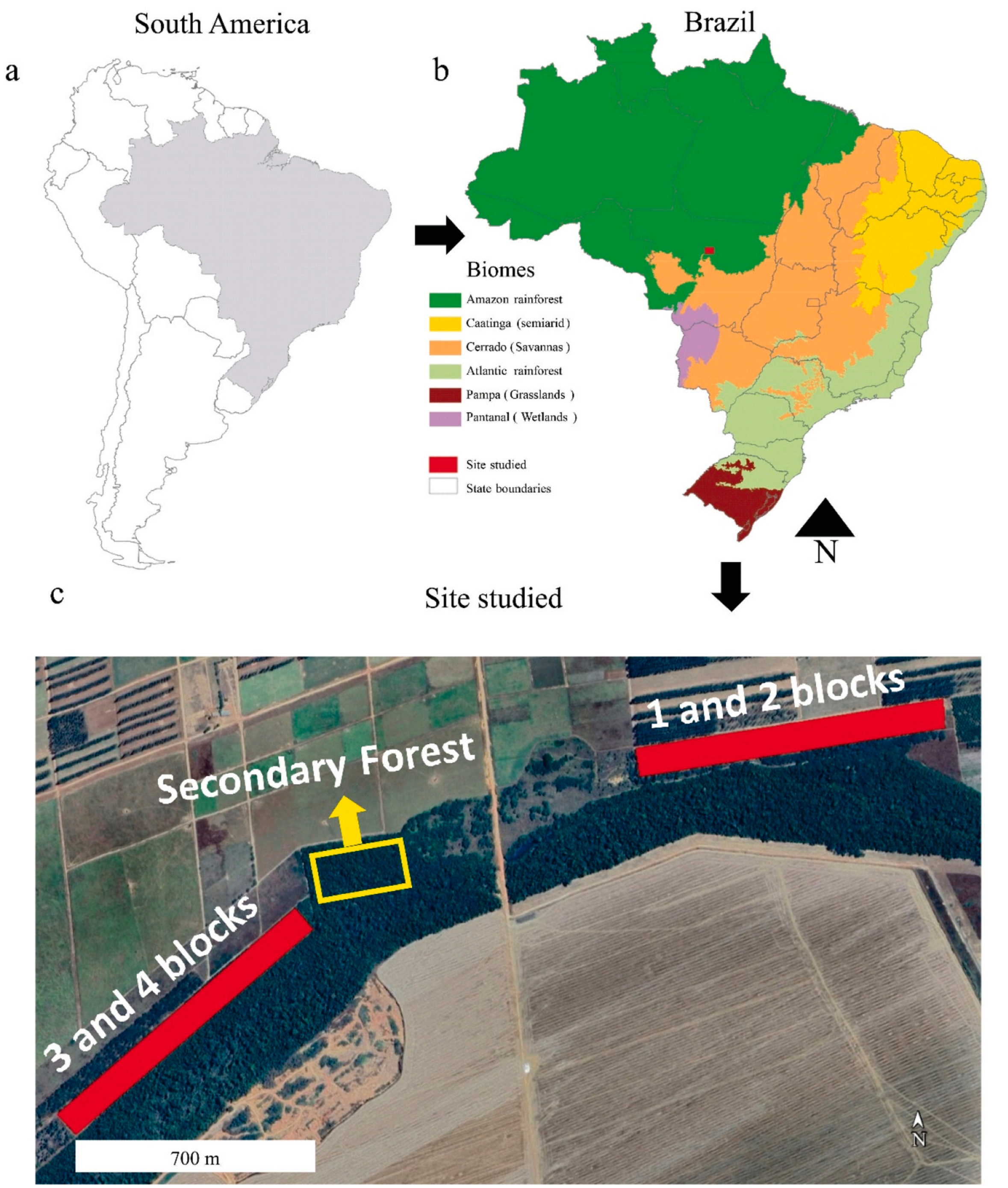

Fig. 1. Location of the study area, blocks, and secondary forest (c) in the southern Amazon biome, Brazil (b).

and considering that soil fertility tends to be enhanced in areas with a history of agricultural use, we hypothesize that forest restoration using native species seedlings in these soils promotes faster accumulation of SOC and TN than passive regeneration under the edaphoclimatic conditions of the southern Amazon. Hence, the present study aimed to evaluate soil SOC and TN stocks from LR restoration treatments in the southern Amazon. To expand the relevance of the findings and align the study with the goals of the United Nations as Decade on Ecosystem Restoration (Sewell et al., 2020), we additionally sought to understand how species composition (native vs. native+exotic) and structural development of the vegetation influence soil C and N during the first decade of restoration. To achieve this, we addressed the following specific objectives: to evaluate SOC and TN stocks down to 1 m depth across active and passive restoration treatments and a secondary forest reference; to assess how structural variables (tree density, diameter at breast height-DBH, canopy cover, and height) and understory PAR are associated with SOC and TN accumulation; and to determine whether the inclusion of exotic species affects early restoration trajectories and soil recovery.

2. Material and methods

2.1. Location

The LR restoration experiment, installed in December 2012, was conducted in the experimental field of Embrapa Agrossilvipastoril, in the municipality of Sinop/state of Mato Grosso, at a latitude of 11°51'S, a longitude of 55°35'W, and an average altitude of 384 m (Fig. 1). According to the description made by Viana et al. (2015) using the Brazilian Soil Classification System, the soil of the experimental field is classified as Plinthic Dystrophic Red Yellow Latosol (Santos et al., 2018), and according to soil taxonomy (USDA, 1999), it is Hapludox, very clayey with a flat relief.

According to the Köppen climate classification (Alvares et al., 2013), the region has a tropical monsoon climate (Am). The average annual air temperature is 25°C, with an average minimum of 18°C and an average maximum of 33°C. The average annual relative humidity is 83 %, and the average annual accumulated precipitation is 2250 mm. The average daily air temperature (°C) and precipitation (mm) from August 2013 to December 2022 is shown in Fig. S1. These data were obtained from the meteorological station located within the same experimental field (Embrapa Agrossilvipastoril, 2019).

Although officially part of the Amazon biome, the region is phytogeographically considered a transitional area (ecotone) between the Amazon and Cerrado biomes, with a predominantly forested physiognomy (Araújo et al., 2009). Prior to the installation of the experiment, the land was used for mechanized agriculture with grain cultivation. Once abandoned in 2011 when Embrapa was installed, the area was occupied by a dense layer of invasive exotic grasses that was previously controlled in preparation for the experiment. Figures from S2 to S7 illustrate the history of land use in the experimental area. While it is impossible to determine the precise year that the blocks 1 and 2 were converted for agricultural use due to the absence of noise-free satellite images from this period, the recovered images suggest that this conversion occurred between 1975 and 1984, over 40 years ago. Using Google® images, it was determined that the areas corresponding to blocks 3 and 4 were converted between 2003 and 2004, i.e., over 20 years ago.

2.2. Experimental description

The following 4 LR restoration treatments (forest restoration) were evaluated: Nat+Euca: planting of regional native seedlings intercropped with eucalyptus seedlings (*Eucalyptus urograndis*, clone H13); Nat+Rubber: planting of regional native seedlings in association with rubber tree seedlings; Passive: natural regeneration with the abandonment of the area and monitoring of regenerating species; and Native (Nat): planting of only regional native species seedlings, considered an ecological restoration *stricto sensu*.

A total, 17 native species were used (Table S1), according to the following criteria: regional occurrence, emphasizing native flora adapted to local conditions and traditional knowledge; ecological role, focusing on the contribution to ecosystem restoration, such as fauna attraction, N fixation, and successional classification (pioneers, secondary, and climax); and economic interest, also considering the potential for sustainable management of vegetation in the LR. Due to the treatment arrangements, each Nat plot had 100 more semi-deciduous or deciduous individuals than the Nat+Euca and Nat+Rubber treatment plots.

The experimental followed a randomized block design with four replicates (blocks) and each plot measured 0.48 ha (60 × 80 m). Additional details, such as the randomized distribution of treatments and plot size, can be found in S8. The spacing was 4 m between rows and 3 m between plants, except for rubber trees, where the spacing was 4 m between plants.

The area was previously treated with a non-selective, systemic post-emergence herbicide (October 2012), ensuring that all blocks and treatments started from the same starting point in the experiment. Variations and adjustments in implementation and maintenance are described below. For the treatment with passive regeneration, no action was taken to control weed since the implementation of the experiment. Only the eucalyptus and rubber trees were subjected to base fertilizer (approximately 150 g of NPK 4:14:8 per individual), with subsequent installments of topdressing fertilizer (NPK 20:0:20). Mechanized or semi-mechanized maintenance was carried out during the initial implementation phase to avoid herbicide drift, both within and between planting rows. Weed competition control was performed three to four times during each rainy season (November–April), with a higher intensity than would normally be applied, since this was an experiment. In the treatments where seedlings were planted, replanting was conducted within the two months after implementation. Regular of control leaf-cutting ants were carried out across the experimental area using sulfluramid-based ant bait. Firebreaks were also maintained by creating and maintaining pathways around and between the plots.

In addition to the treatments, the reference area, a fragment of secondary forest immediately adjacent to the experimental site (Fig. 1), was also included in the assessments, following the same scientific procedures as for the treatments. From here on it will be called just secondary forest. For this, 4 areas of the same size as the experimental plot were delimited, and all sampling procedures and determination were performed in the same manner.

2.3. PAR assessment

For the analysis of the variation in photosynthetically active radiation (PAR) related to microclimatic modifications in the forest restoration treatments and in the secondary forest, a station was installed in the center of each treatment plot in only on replicate. Measurements were conducted continuous from 2015 to 2019. PAR sensors were installed at a height of 1.9 m and coupled to automatic data acquisition systems (data logger), programed to take readings every 5 s and obtain average and total values every 15 min. To calculate the daily mean PAR values, the 15-min averages obtained by the station were used from 8 am to 4 pm for all days of the year. The daily means were then used to calculate the annual mean PAR, which provides a comprehensive overview of this variable in each year of treatment development. Such a perspective is more difficult to extract from a smaller scale data (as daily or monthly scales) due to variation imposed by multiple factors inherent to field experiments that may influence each treatment to different degrees, such as rainfall, wind, the presence of animals, among others, which do not necessarily reflect causal relationships with the treatments. Since complete meteorological station is expensive and difficult to acquire, it is important to note that such equipment was installed in only one block.

As direct assessment of the litter production for each treatment was not feasible, the input of OM via aboveground biomass of the trees in the evaluated treatments was indirectly inferred using Eq. 1, referred to as the percentage variation index of PAR transmittance (iPAR) (adapted from Dufrêne and Bréda, 1995). This index considers the relative variation of PAR transmissivity (tPAR) between the rainiest months (December, January, February, and March) and the driest months (August and September).

$$\text{Index(iPAR)} = \frac{(\text{tPARdry} - \text{tPARrainy})}{\text{tPARrainy}} \times 100 \quad (1)$$

where tPARdry is the average tPAR radiation (%) in dry months; and tPARrainy is the average tPAR radiation (%) in rainy months.

Eq. 2 (adapted from Pezzopane et al., 2024) was used to calculate the tPAR for each period:

$$\text{tPAR(dry or rainy)} \quad (\%) = \frac{\begin{array}{c}\text{PAR(Nat + Euca, Nat + Rubber,}\\ \text{Passive, Nat or Forest)}\end{array}}{\text{PAR central meteorological station}} \times 100 \quad (2)$$

PAR data from the central station were used for the calculations, obtained upon request (Embrapa Agrossilvipastoril, 2019), representing PAR without interferences, corresponding the full PAR (100 %). While tPAR was calculated for dry and rainy seasons of each year, iPAR was calculated annually, and the mean values for each treatment were then derived from five-year period of meteorological assessments. The PAR measured under the canopy is directly influenced by the foliage density, and during periods of greater defoliation (dry season), more radiation passes through the canopy and reaches the sensor, resulting in higher tPAR values. Comparing tPAR in rainy months (when trees generally have greater leaf density) with dry months (when defoliation tends to be more pronounced in many species) is a logical approach to determining iPAR. In this sense, a higher index indicates greater tree defoliation (higher light transmission) and, consequently, greater annual OM input. Conversely, a lower index indicates little seasonal variation in canopy density and lower annual OM input.

2.4. Soil collection and analysis

For soil sampling in each treatment plot, trenches were opened and manual augerings were performed down to a depth of 1.0 m. Trenches were dug in the center of each plot, and augerings were performed at 6 points evenly distributed, following the scheme shown in the S8b. From the augerings, one composite sample was collected at each depth, while multiple points within the same depth were sampled from the trenches to obtain a representative sample. In addition to the disturbed samples (which do not preserve the original field structure) collected from the augers and trenches, undisturbed samples (which preserve the original field structure) were also collected in 100 cm^3 cylinders, but only from the trenches.

Those soil samples were collected in September and October 2022 from the secondary forest and LR restoration treatment plots in the following depths: 0.0–0.1, 0.1–0.2, 0.2–0.3, 0.3–0.4, 0.4–0.6, 0.6–0.8, and 0.8–1.0 m. Disturbed samples, collected using a shovel and a knife, were air-dried and passed through 2 mm mesh sieve to obtain air-dried fine soil (ADFS), which was subsequently ground in an agate mortar. Approximately 50 mg of each sample were weighed on a high-precision balance (to four decimal places), and the elemental contents of C and N were determined by dry combustion (Nelson and Sommers, 1982). The undisturbed samples were collected from each layer in 100 cm^3 cylinder to determine soil bulk density (Ds) following Grossman and Reinsch (2002).

2.5. C and N stocks

SOC and TN stocks in the treatments and in the secondary forest were calculated following Batjes (1996). The SOC and TN stocks on an equivalent mass basis were calculated following Sisti et al. (2004) and adjusted using the Ds from the secondary forest.

2.6. CO2 equivalent

The conversion of SOC to carbon dioxide equivalent (CO_2eq) was performed following the methodology recommended by the IPCC (IPCC, 2006). According to this guideline, SOC stocks can be expressed in terms CO_2 by applying a stoichiometric conversion factor of 44/12, corresponding the molecular weight ratio between CO_2 (44) and C (12).

2.7. Statistical analysis

Mathematical models were fitted to describe the PAR curve as a function of time (annual mean data from daily averages collected between 2015 and 2019), and the coefficient of determination (R^2) was used to identify the best-fitting model for Nat+Euca, Nat+Rubber, and Nat treatments. Data on C and N content, the C:N ratio, and SOC and TN stocks of the treatments and the secondary forest were analyzed using ANOVA, and the means were compared using Tukey's test at a 5 % significance level. To assess the rate of SOC and TN accumulation in the soil, the values obtained under passive were subtracted from those from the tree-based treatments, and the same statistical analysis of the stocks described previously was applied. These values were then divided by 10, corresponding to the duration of the experiment in years, thereby yielding the annual sequestration rate in accordance with IPCC (IPCC, 2006) guideline. Principal component analysis (PCA) was performed to understand the distribution pattern of the evaluated treatments and the secondary forest, taking into account SOC, TN, PAR, iPAR, tree density, diameter at breast height-DBH, canopy cover, and height data. Further for PCA, in addition to including the layer down to 1 m depth, SOC and TN stocks were also calculated to a depth of 0.3 m, as this represents the surface layer most affected by the treatments and corresponds to the minimum soil depth considered by the IPCC (IPCC, 2006). For all statistical analyses, R-studio software (R Development Core Team, 2021) was used.

3. Results

3.1. PAR

The lowest and highest PAR from 2015 to 2019, the evaluation

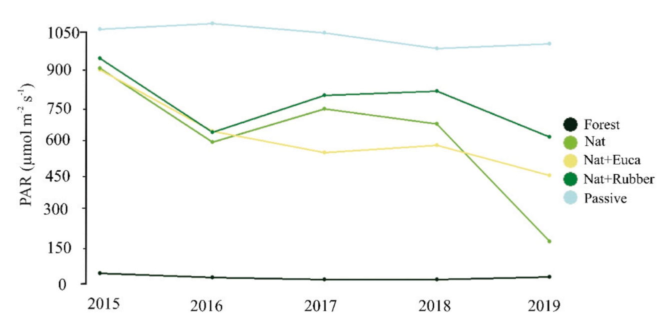

Fig. 2. PAR from sensors installed at 1.9 m above ground level in LR restoration treatments and in a secondary forest in southern Amazonia. Treatments: Forest – secondary forest; Nat - only regional native species seedlings; Nat+Euca - regional native seedlings intercropped with eucalyptus seedlings; Nat+Rubber - regional native seedlings in association with rubber tree seedlings; Passive - natural regeneration with the abandonment of the area and monitoring of regenerating species.

period for this variable, were observed in secondary forest and passive, respectively (Fig. 2). Restoration treatments involving the planting of seedlings generally presented decreasing PAR values over time (years), with a more pronounced effect in the Nat treatment. At the beginning of the measurements in active treatments, all treatments exhibited comparable values of approximately 900 μmol m^{-2} s^{-1}, with a decline to 600 μmol m^{-2} s^{-1} in 2016, one year after the initiation of the PAR measurements.

From 2016 onwards, the PAR below the canopy of Nat+Euca continued to decrease in 2017, increased slightly in 2018, and reached 450 μmol m^{-2} s^{-1} in 2019. Nat+Rubber exhibited higher PAR values in 2017 and 2018 compared to 2016, returning to similar values of 610–640 μmol m^{-2} s^{-1} in 2019. In Nat, PAR below the canopy increased in 2017 and decreased in 2018 and 2019, with values of 671 and 170 μmol m^{-2} s^{-1}, respectively. PAR values in the secondary forest remained virtually stable from 2015 to 2019, close to zero, indicating a closed canopy even after previous interventions.

Among the models fitted for Nat+Euca, Nat+Rubber, and Nat, the decreasing logistic trend provided the best R^2 values, at 85 %, 32 %, and 84 %, respectively. However, the parameters of the logistic equation were significant ($p < 0.05$) only for Nat treatment. Among all structural variables, canopy cover showed the closest relationship and best explained the PAR radiation data (Table S2).

3.2. iPAR

The iPAR values were highest in Nat, with mean values above 35 (Fig. 3), indicating greater variation in PAR transmissivity between the dry and rainy seasons compared with other treatments and the secondary forest. With an iPAR of approximately 20, the secondary forest exhibited the second-highest value, followed by Nat+Euca, whereas the lowest values were observed in Nat+Rubber and passive.

3.3. Carbon

There was effect of treatment on soil C content, except in the 0.3–0.4 m and 0.8–1.0 m layers (Fig. 4a). Across all evaluated layers, the lowest contents were observed in passive. In the surface layer (0–0.1 m), the highest values, ranging from 22 to 25 g kg^{-1} of C, were observed in secondary forest, Nat, and Nat+Rubber. In the 0.1–0.3 m layers, the highest C content was observed in Nat, with values between 14 and 17 g kg^{-1} of C, differing only from passive. With the exception of the surface (0–0.1 m) and the 0.6–0.8 m layer, the C content in the other layers of the secondary forest were similar to those observed in the treatments.

SOC stocks were generally lower under passive regeneration

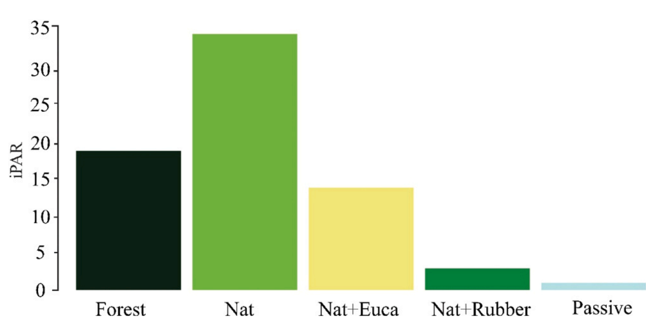

Fig. 3. Index of percentage variation in PAR transmittance (iPAR) of LR restoration treatments and secondary forest in southern Amazon. Treatments: Forest – secondary forest; Nat - only regional native species seedlings; Nat+Euca - regional native seedlings intercropped with eucalyptus seedlings; Nat+Rubber - regional native seedlings in association with rubber tree seedlings; Passive - natural regeneration with the abandonment of the area and monitoring of regenerating species.

(Fig. 4b), although they did not differ from those in the Nat+Euca treatment in the surface (0–0.1 m), 0–0.4 m, and 0–0.6 m sections of the soil profile. The highest SOC stocks were recorded in the secondary forest, Nat, and Nat+Rubber treatments. Considering the soil depth most commonly recommended by the IPCC (IPCC, 2006), total SOC accumulation down to 1.0 m was higher in the secondary forest, Nat, Nat+Euca, and Nat+Rubber, all of which differed from passive, which averaged approximately 100 Mg ha^{-1}. A similar pattern was observed down 0.3 m, where the passive regeneration showed the lowest SOC stock (around 45 Mg ha^{-1}) whereas the other treatments exceeding 50 Mg ha^{-1}. In the soil surface layer, SOC stocks were also lower in passive regeneration (below 20 Mg ha^{-1}) and higher in secondary forest and the other treatments (> 23 Mg ha^{-1}).

Regarding the passive regeneration, all tested restoration strategies resulted in a higher mean accumulated SOC stocks across all evaluated layers (Fig. 5). At the 5 % significance level, no treatment effect was detected among Nat, Nat+Euca, and Nat+Rubber. However, based on the standard error of the mean, Nat treatment stood out compared with Nat+Euca. In the 0–0.3 m layer, although Nat exhibited an SOC accumulation 13.5 Mg ha^{-1} higher than passive, this difference was approximately 8 Mg ha^{-1} in Nat+Euca. At 1 m depth, these values reached approximately 25 and 14 Mg ha^{-1}, respectively. Nat+Rubber showed intermediate SOC accumulation values of 9.3 and 17.9 Mg ha^{-1} of SOC for the 0–0.3 and 0–1.0 m layers, respectively. Considering the 0–1.0 m layer, treatments involving tree seedlings resulted in annual SOC accumulation rate that was between 1.4 and 2.5 Mg ha^{-1} $year^{-1}$ higher than those observed under passive regeneration.

3.4. Nitrogen

Soil N content decreased with depth and differed between restoration treatments and the secondary forest in the 0–0.1 m layer (Fig. 6a). In the other layers, no significant differences were observed at the 5 % probability level ($p > 0.05$). In the surface layer, secondary forest, with a value of 1.85 g kg^{-1} of N, differed only from Nat+Euca, which had 1.41 g kg^{-1} of N. The mean N contents in the downward layers (0.1–0.2, 0.2–0.3, 0.3–0.4, 0.4–0.6, 0.6–08, and 0.8–1.0 m) were 1.10, 0.86, 0.72, 0.56, 0.47, and 0.44 g kg^{-1}, respectively.

Significant differences in soil TN stocks were observed only in the surface layer ($p < 0.05$). In the other layers, no treatments effect was observed at the 5 % level (Fig. 6b). The TN stock in the 0–0.1 m layer of the secondary forest was approximately 2 Mg ha^{-1}, whereas in Nat+Euca, which showed the lowest value, it was approximately 1.5 Mg ha^{-1}. These treatments differed from each other but were similar to the other treatments. The mean cumulative TN values in the subsurface layers were 2.90, 3.74, 4.48, 5.70, 6.81, and 7.74 Mg ha^{-1}.

Unlike the SOC results, in which the use of tree seedlings led to greater increases than passive regeneration, the mean soil TN accumulation values were negative for Nat+Euca and Nat+Rubber and positive for Nat (Fig. 7). No significant treatment effects were detected ($p > 0.05$), even considering the standard error of the mean, no differences in soil TN accumulation were observed among the treatments across all evaluated layers.

3.5. C:N ratio

The C:N ratio of soil organic matter (SOM) differed between the treatments and the secondary forest, but only up to the 0.3 m layer (Fig. 8), with the highest values observed in Nat and the lowest in passive. The C:N ratio in the secondary forest did not differ from any of the restoration treatments.

Overall, the C:N ratio across all layers of the treatments and the secondary forest ranged from approximately 12–18, with a tendency to increase with depth. In the layers where a treatment effect was observed ($p < 0.05$), passive, with the lowest value, ranged from approximately 12 and 14, whereas Nat exhibited the highest values, ranging from

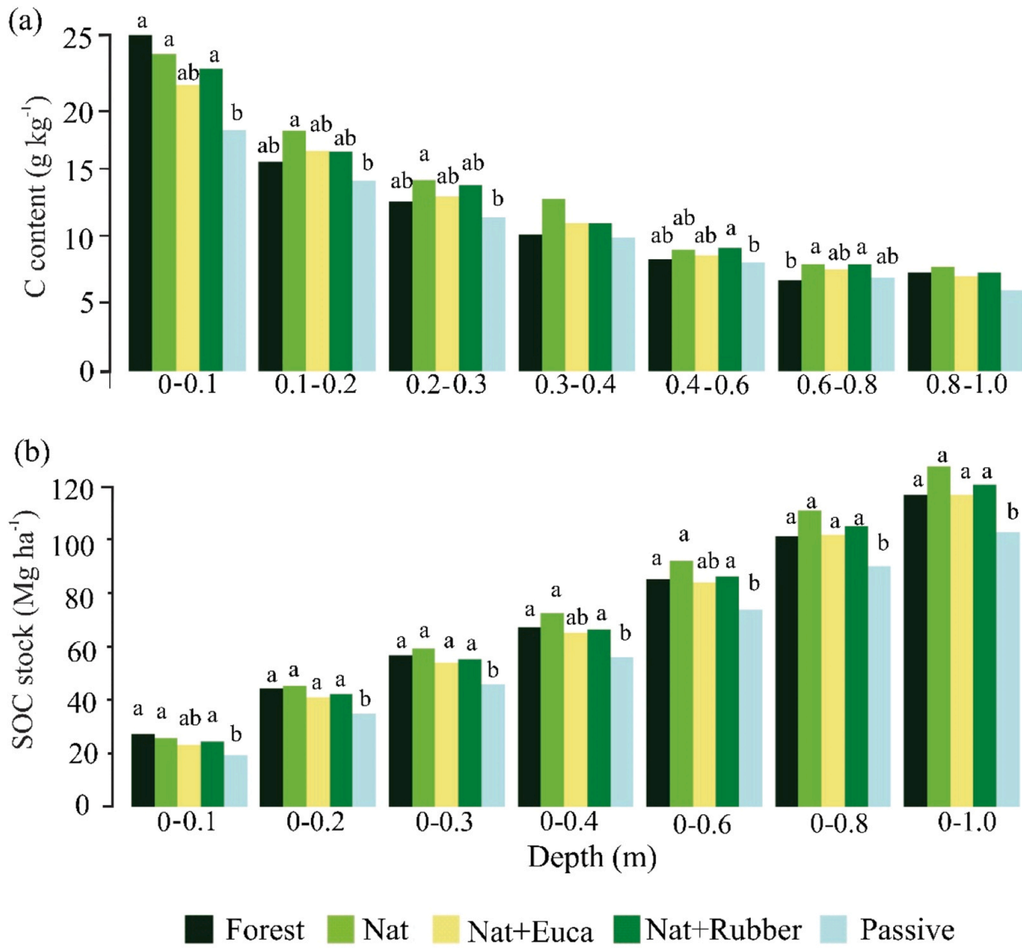

Fig. 4. Average soil C content (a; g kg^{-1}) and SOC stock (b; Mg ha^{-1}) up to 1 m depth in the secondary forest and in LR restoration treatments in southern Amazon. Values followed by the same letter within each layer do not differ from each other at the 5 % probability level. In the averages where the letters do not appear, there was no effect at the 5 % level. Treatments: Forest – secondary forest; Nat - only regional native species seedlings; Nat+Euca - regional native seedlings intercropped with eucalyptus seedlings; Nat+Rubber - regional native seedlings in association with rubber tree seedlings; Passive - natural regeneration with the abandonment of the area and monitoring of regenerating species.

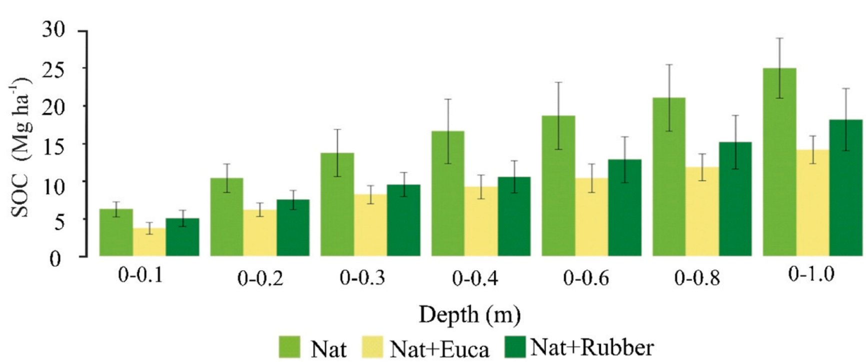

Fig. 5. Differences in mean accumulated SOC stocks (Mg ha^{-1}) up to 1 m depth between seedling planting treatments and passive regeneration in southern Amazonia. In the means where letters do not appear, there was no effect at the 5 % level. The vertical bars correspond to the standard error of the mean of each treatment. Treatments: Nat - only regional native species seedlings; Nat+Euca - regional native seedlings intercropped with eucalyptus seedlings; Nat+Rubber - regional native seedlings in association with rubber tree seedlings.

approximately 16–17 (Fig. 8).

3.6. PCA

The first two principal components (PC1 and PC2) jointly explained 78.2 % of the total variance, with 57.47 % attributed to PC1 and 20.73 % to PC2 (Fig. 9a). The restoration treatments (Nat, Nat+Euca, Nat+Rubber, and passive) and the secondary forest were well separated, indicating distinct patterns (Fig. 9a). PC1 was strongly associated with the canopy openness gradient (smaller or no canopy), as evidenced by the strong positive correlation with PAR (0.77) and strong negative correlations with SOC up to 1 m depth (SOC1, −0.81) and SOC up to

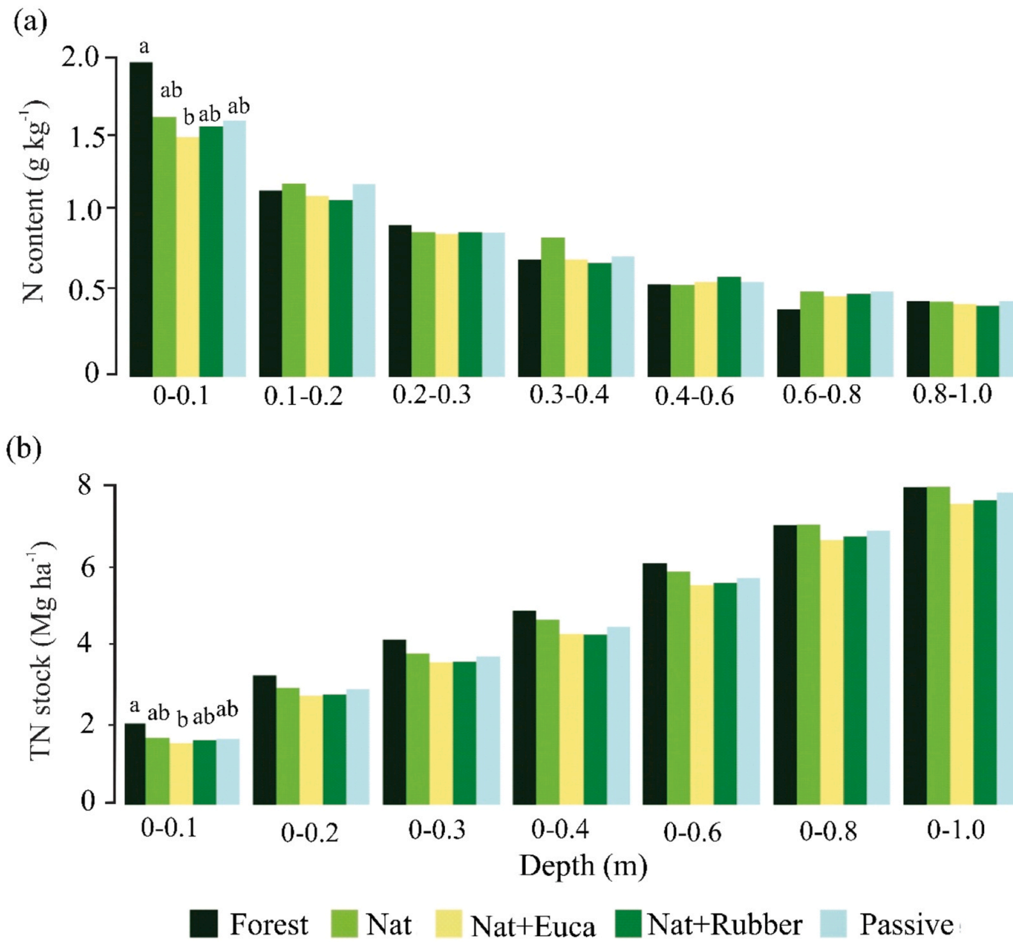

Fig. 6. Average soil N content (a; g kg^{-1}) and TN stock (b; Mg ha^{-1}) up to 1 m depth in the secondary forest and in LR restoration treatments in southern Amazonia. Values followed by the same letter within each layer do not differ from each other at the 5 % probability level. In the averages where the letters do not appear, there was no effect at the 5 % level. Treatments: Forest – secondary forest; Nat - only regional native species seedlings; Nat+Euca - regional native seedlings intercropped with eucalyptus seedlings; Nat+Rubber - regional native seedlings in association with rubber tree seedlings; Passive - natural regeneration with the abandonment of the area and monitoring of regenerating species.

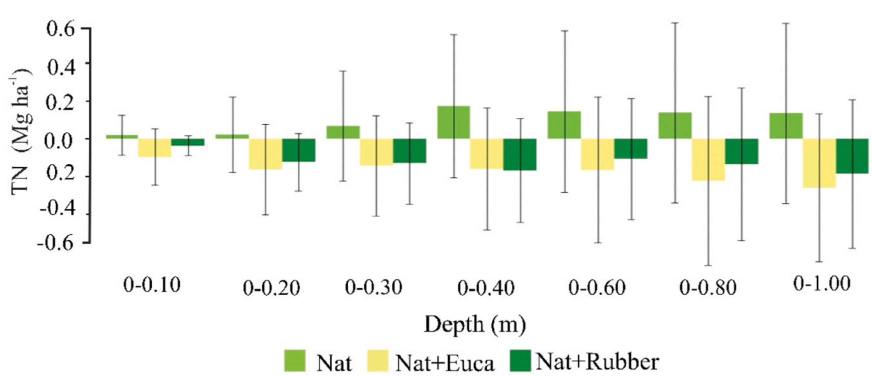

Fig. 7. Differences in mean accumulated stocks of TN (Mg ha^{-1}) in soil up to 1 m depth between LR restoration treatments and passive regeneration in southern Amazon. In the means where letters do not appear, there was no effect at the 5 % level. The vertical bars correspond to the standard error of the mean of each treatment. Treatments: Nat - only regional native species seedlings; Nat+Euca - regional native seedlings intercropped with eucalyptus seedlings; Nat+Rubber - regional native seedlings in association with rubber tree seedlings.

0.3 m depth (SOC0.3, −0.88) and the PAR transmission variation index (iPAR, −0.71) (Fig. 9b). Still showing a strong negative correlation, the structural variables stand out: density (–0.84), DBH (–0.90), canopy cover (–0.96), and height (–0.84). PC1 differentiated areas with forest restoration associated with higher SOC stocks and iPAR values, and lower PAR levels

PC2 reflected variations in soil N stocks, showing positive correlations with TN up to a 1 m depth (TN1, 0.90), up to a 0.3 m depth (TN0.3, 0.93), and a negative correlation with height (-0.41) and DBH (-0.31). Areas restored with only native trees exhibited higher C stocks and higher defoliation rates, whereas areas without the exclusive use of these species had a higher PAR and lower SOC and TN stocks. Nat+Euca

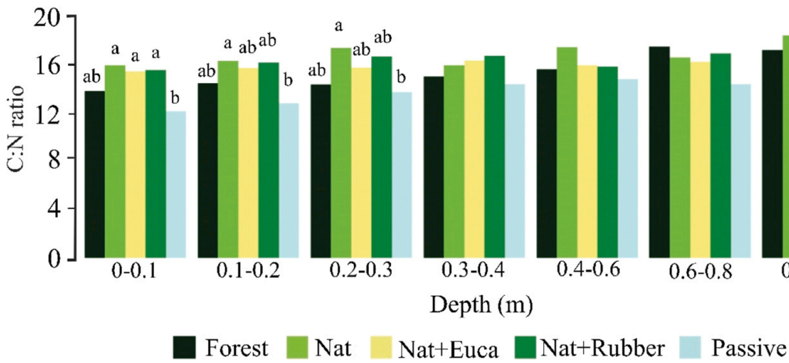

Fig. 8. C:N ratio up to 1 m soil depth of LR restoration treatments and the secondary forest in southern Amazon. Values followed by the same letter within each layer do not differ from each other at the 5 % probability level. In the means where the letters do not appear, there was no effect at the 5 % level. Treatments: Forest – secondary forest; Nat - only regional native species seedlings; Nat+Euca - regional native seedlings intercropped with eucalyptus seedlings; Nat+Rubber - regional native seedlings in association with rubber tree seedlings; Passive - natural regeneration with the abandonment of the area and monitoring of regenerating species.

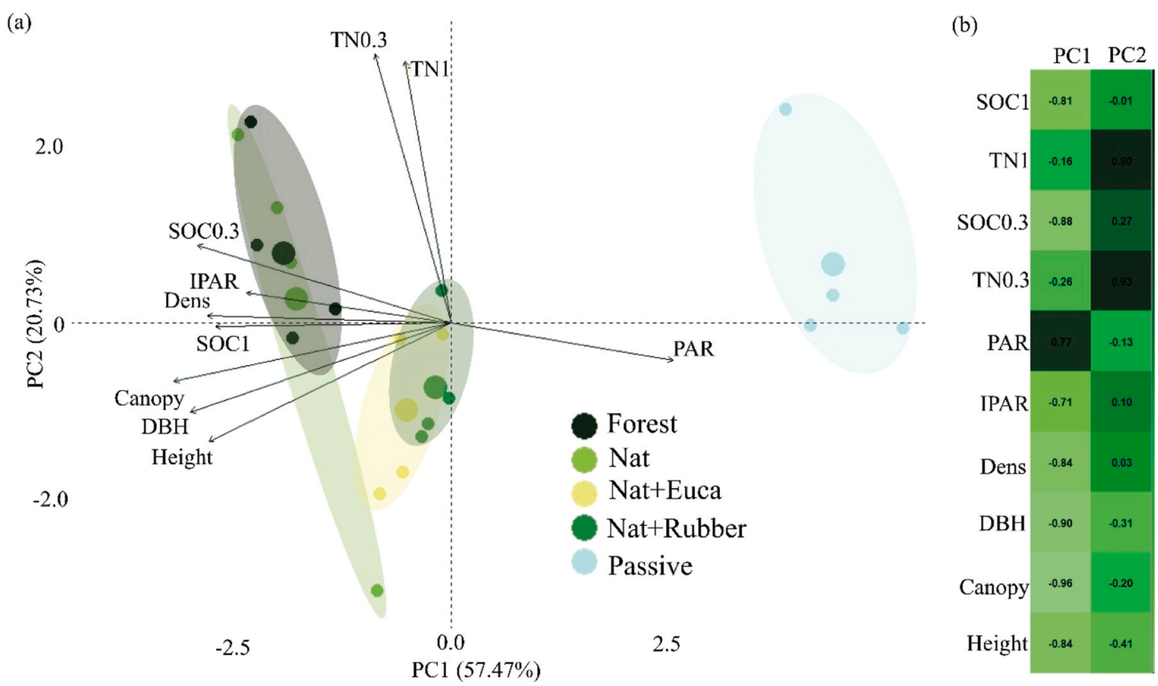

Fig. 9. Biplot for PCA of the variables in the different LR restoration treatments and secondary forest (a) and correlation of the variables with PC1 and PC2 (b). Treatments: Forest – secondary forest; Nat - only regional native species seedlings; Nat+Euca - regional native seedlings intercropped with eucalyptus seedlings; Nat+Rubber - regional native seedlings in association with rubber tree seedlings; Passive - natural regeneration with the abandonment of the area and monitoring of regenerating species. SOC1 – C stock up to 1 m depth. TN1 – N stock up to 1 m depth. SOC0.3 – C stock up to 0.3 m depth. TN0.3 – N stock up to 0.3 m depth. PAR – Photosynthetically Active Radiation. iPAR - Index of percentage variation in PAR transmittance. SOC – soil organic carbon. TN – total nitrogen. Dens - Tree density. DHB - Diameter at breast height. Canopy - Canopy cover. Height - Tree height.

and Nat+Rubber displayed intermediate and transient patterns between the extremes, suggesting that the inclusion of exotic species, or their higher proportion relative to native species, may delay increases in soil C and N in LR restoration treatments in the southern Amazon, at least within the study period. These patterns should be further evaluated over a longer time span to confirm the observed trends.

4. Discussion

4.1. C and N increments in restoration treatments

Soil C and N contents under the LR restoration treatments tested, as well as in the secondary forest in the southern Amazon decreased with depth, which is a characteristic of Oxisols (Santos et al., 2018). Soil C and N contents in all layers under the treatments were similar to those of the secondary forest, with the exception of the 0.6–0.8 m layer for C. Nevertheless, soil C and N contents under the passive regeneration were similar to the secondary forest, the exception of the first layer for C content. This can be attributed to the fact that the secondary forest is a site of secondary vegetation, which contributes to the lower contents compared to a primary forest, even after several years without disturbance (Don et al., 2011).

The results presented here corroborate those of Allek et al. (2023) and Xu et al. (2024), who reported substantial increases in SOC stocks in forest restoration areas with a recent history of agriculture use. However, they contradict the findings of Feldpausch et al. (2004), who observed that passive (natural regeneration) led to increases in SOC stocks in the central Amazon only when the area was isolated, one outcome not observed in the present study. Similarly, these results do not align with those of Meli et al. (2017), who found that forest recovery could occur only with area isolation. Possible explanations for these discrepancies may be related to the passive regeneration potential of the area and its land-use history (Prach et al., 2019). In this context, the intensity of prior land use, as shown in Figs. S2-S7, appear to have been sufficient (or even exceeded the threshold) to inhibit passive regeneration within ten years after treatment implementation (Chazdon et al., 2025). Additionally, passive regeneration would be more appropriate for smaller areas subjected to lower abiotic stress (Prach et al., 2019), under environmental conditions distinct from those observed in the present study.

To promote SOC storage, particularly in the layers recommended by the IPCC (IPCC, 2006), up to 0.3 and 1.0 m in depth, all treatments, except passive regeneration, proved effective in increasing SOC after 10 years of implementation. The contrast in SOC stocks between passive regeneration and the other treatments at both depths represents an accumulation rate exceeding 2 Mg ha^{-1} $year^{-1}$, which is noteworthy, given that agricultural systems typically accumulate at most around 1 Mg ha^{-1} $year^{-1}$, even under well-managed pastures (Tenelli et al., 2025). These findings emphasize the potential of forest restoration treatments to sequester atmospheric C in mineral soils of humid tropics regions with a history of annual cropping (Allek et al., 2023; Xu et al., 2024).

These rapid increases in SOC stocks can be attributed to enhanced soil fertility resulting from the application of soil amendments and fertilizers to crops prior to the implementation of the experiment (Table S3). This management history provided a soil environment more favorable to root growth, plant establishment, and overall development (Taiz and Zeiger, 2009). Consequently, the soil became more efficient in stabilizing, protecting, and storing added C, which is typically associated with increased plant productivity under such conditions (Laganière et al., 2010; Xu et al., 2024). Furthermore, increases in SOC stocks in regions located at latitudes lower than 20°, such as in the present study area (11°51'S), tend to occur more rapidly than in higher-latitude regions (Allek et al., 2023; Xu et al., 2024).

The vegetative growth of native species adapted to the humid tropical environments is strongly influenced by soil fertility (Melo, 1999; Wright, 2019; Jaquetti, 2020). Therefore, the increases in SOC observed in the present study may reflect the high base saturation (Ca^{2+}, Mg^{2+}, and K^{+}) and reduction or absence of Al^{3+} (toxic to plants), and the elevated P levels down to 0.6 m depth in the restoration area compared to the secondary forest (Table S3). The soil fertility observed in the present study represents an ideal condition for the growth of annual crops, which generally have grater nutrient demands (Sousa and Lobato, 2004) than native plant species (Melo, 1999).

The results presented here, showing a higher C:N ratio of SOM, particularly up to 0.3 m depth in treatments using seedlings, may indicate that the observed increases in SOC stocks are associated with a less stable SOM fraction (Cotrufo and Lavallee, 2022). This fraction represents an important source of nutrient in the cycling process but can be easily lost (oxidized) due to changes in land use or management practices (Lavallee et al., 2020). Organic materials with a higher C:N ratio, which reflect the biochemistry of more structural compounds such as lignin, cellulose, and hemicellulose, commonly found in tree species, tend to accumulate in the less stable fraction linked to the soil particulate fraction (Cotrufo et al., 2015, 2019; Crow et al., 2009). Nascimento et al. (2025) observed that in silvopastoral systems with a greater tree presence, the addition of plant material with a higher C:N ratio results in most of the SOM being associated with the less stable OM fraction in the soil. Among the species used in the treatments, eight are deciduous or sub-deciduous depending on environment conditions (Carvalho, 2003). In the treatment with only native seedlings, these species were more abundant (Table S1), likely contributing to greater OM input through leaf litter deposition during the region's seasonal dry period, as also indicated by iPAR, leading to greater C accumulation. The succession of understory species following canopy closure is a factor that should be evaluated in future studies to better understand its role in enhancing soil C inputs.

The secondary forest was more efficient in storing N in the surface layers compared to passive regeneration and treatments involving the inclusion of other native species. However, significant differences between the treatments and the secondary forest were observed only in the surface layer according to the mean test. These lower N values in the restoration areas may be associated with the continuous growth of trees, which efficiently use N mineralized from OM, a process that contributes to the OM stabilization (Silva and Mendonça, 2007; Wiesmeier et al., 2019).

4.2. Relationship of PAR with soil C and N

The increase in SOC stocks under different treatments was closely linked to the structural variables and to the PAR dynamics, the first meteorological variable affected by tree establishment (Dufrêne and Bréda, 1995; Brenner, 1996). The treatment with only native species exhibited the greatest reductions in PAR (measured at 1.9 m above ground) by the end of the evaluation period, indicating that the plant canopy closed more rapidly between 2015 and 2019, as a response to the structural variable changes (Table S2). It also exhibited the highest iPAR, suggesting that greater light penetrated the canopy during the dry season compared to the rainy season than in the other treatments over the five-years period. This pattern may be associated with increased leaf fall during the dry season and, consequently, greater input of OM, which serves as primary source for the formation of SOM and contains C and N (Silva and Mendonça, 2007; Wiesmeier et al., 2019).

Restoration treatments involving seedling planting exhibited a mathematical adjustment of PAR over time in the understory, with the highest R^2 values observed for the logistic model, mainly for Nat. This finding corroborates Terra et al. (2022), who reported similar logistic growth patterns for native species used in forest restoration in the southern Amazon. Accordingly, as species growth follows a logistic trajectory, the decline in mean PAR reaching the understory slows over time along the same logistic pattern. PAR data were negatively correlated with increases in soil C and N stocks (Fig. 9b), as higher PAR in the understory indicated less canopy development and, consequently, lower photosynthetic input. In contrast, because iPAR reflects the potential OM input, it showed a strong correlation with SOC stocks (Fig. 9), particularly down to 1 m soil depth.

Although treatments did not differ according to the mean test, considering all variables expressed in the PCA, the use of native species stood out due to the increases in SOC associated with seasonal variations in PAR and with structural variables. This strongly indicates that this treatment converts more radiation (PAR) into organic components through photosynthesis in annual plants. Furthermore, this treatment exhibited a higher iPAR, providing raw material for SOM formation (Xu et al., 2013).

At certain section of the soil profile, such as 0–0.1, 0–0.4, and 0–0.6 m, SOC stocks under Nat+Euca were similar to those under passive regeneration (Fig. 6). This is likely because eucalyptus, being a fast-growing clone, may have shaded the native species planted in the consortium. Since the planted native species are not understory, the shading caused by eucalyptus may have decreased primary production, consequently lowering the input of OM to the soil and negatively affecting SOC stocks (Xu et al., 2013).

4.3. CO_2eq sequestration

The results presented here indicate a high potential for LR restoration areas to generate C credits. On average, over 10 years, the soils under Nat+Euca, Nat+Rubber, and Nat achieved sequestration of 51, 66, and 90 Mg ha^{-1} CO_2eq up to 1.0 m depth, corresponding to annual rate of 5.1, 6.6, and 9.0 Mg ha^{-1} $year^{-1}$ CO_2eq, respectively. These values represent 30–150 % more C stored in the soil during the same period than in the most C-sequestering agricultural systems, such as well-managed pasture (Tenelli et al., 2025). Unlike agricultural systems, which may experience changes in soil management leading to C leakage (Oldfield et al., 2022), LR restoration models, as mandated by law, are more conserved, ensuring C sequestration with minimal leakage, providing greater security for C projects (Oldfield et al., 2022). Furthermore, these models also offer the opportunity to ensure C sequestration through plant biomass (Liévano-Latorre et al., 2025), given the legal requirement to maintain standing forest (Brasil, 2012).

Thus, following an economic feasibility analysis that considers the issues to be addressed, the potential incorporation of C into C credit projects could contribute to project financing, given the high cost of seedlings required to restore these areas (Chazdon and Uriarte, 2016; Chazdon et al., 2016). Furthermore, it would support the country's efforts to mitigate emissions from related sectors, such as land use and agriculture (Malfs, 2021). The use of resources from a potential C credit or payment for environmental services (Benayas et al., 2009) would enable the implementation of additional forest restoration projects (Chazdon and Uriarte, 2016; Chazdon et al., 2025).

4.4. Main results

By consolidating the main results into a single figure, showing only one active treatment (using native species), the secondary forest, and the passive regeneration (Fig. 10), the contribution of each approach to increases SOC can be clearly identified. Regarding PAR interception by the tree canopy, considering the 5-year average, the highest values were observed in the secondary forest, intercepting 98 % of the PAR. The mean PAR below the canopy (1.9 m above the ground) over the 5 years was lowest in the secondary forest, intermediate in the active treatment, and exceeded 1000 μmol m^{-2} s^{-1} in the passive regeneration, where tree interference was absent. For iPAR, greater seasonality in the canopy indicates that the active treatment, mainly using only native species, contributes a higher annual input of C to the soil. Consequently, the active treatments produced the greatest increases in SOC, with measurable effects extending throughout the deepest soil section, down to 1.0 m. In contrast, TN stocks appeared unaffected by LR restoration approaches tested in the southern Amazon.

The history of agricultural land use in the evaluated restoration areas, combined with the humid tropical conditions at low latitude (Allek et al., 2023; Xu et al., 2024), promoted greater growth of native species, particularly in the treatment with exclusive use of native forest species. This led to higher primary production and a greater input of plant material into the soil, both at the surface or subsurface layers. The decomposition process is accelerated by the high temperatures and humidity of the southern Amazon region (Alvares et al., 2013), resulting in increased incorporation of more OM (C) into the mineral soil (Oxisol) (Silva and Mendonça, 2007). Although land use may appear uniform across sites, local differences in soil properties and land-use history can hinder or prevent the same results observed in the present study, potentially leading to failures in the restoration technique. Therefore, these parameters must be carefully considered to ensure the success of degraded forest restoration.

5. Conclusion

Ecological restoration treatments using seedling planting significantly increased SOC stocks down to 1 m depth after 10 years, reaching values comparable to those in the secondary forest. Our results demonstrate that species selection adapted to the biome's edaphoclimatic conditions, combined with land-use history (which enhanced soil fertility), and the low-latitude climate, drives high annual SOC accumulation rates, providing empirical evidence for the role of the factors in tropical forest restoration. In contrast, TN stocks were largely unaffected, indicating that C and N dynamics respond differently to restoration strategies. Structural variables and the decline in understory PAR and its seasonal variation (iPAR) was strongly correlated with SOC increases, particularly in treatments containing a higher proportion of deciduous or sub-deciduous species. This finding provides new insight into mechanistic link between canopy development, litter input, and SOC sequestration in restored tropical forests. Passive regeneration was insufficient for substantial SOC accumulation within the studied timeframe, highlighting the critical role of active restoration with native species for effective soil C recovery. Overall, our study demonstrates that restoration outcomes are strongly influenced by the presence of tree

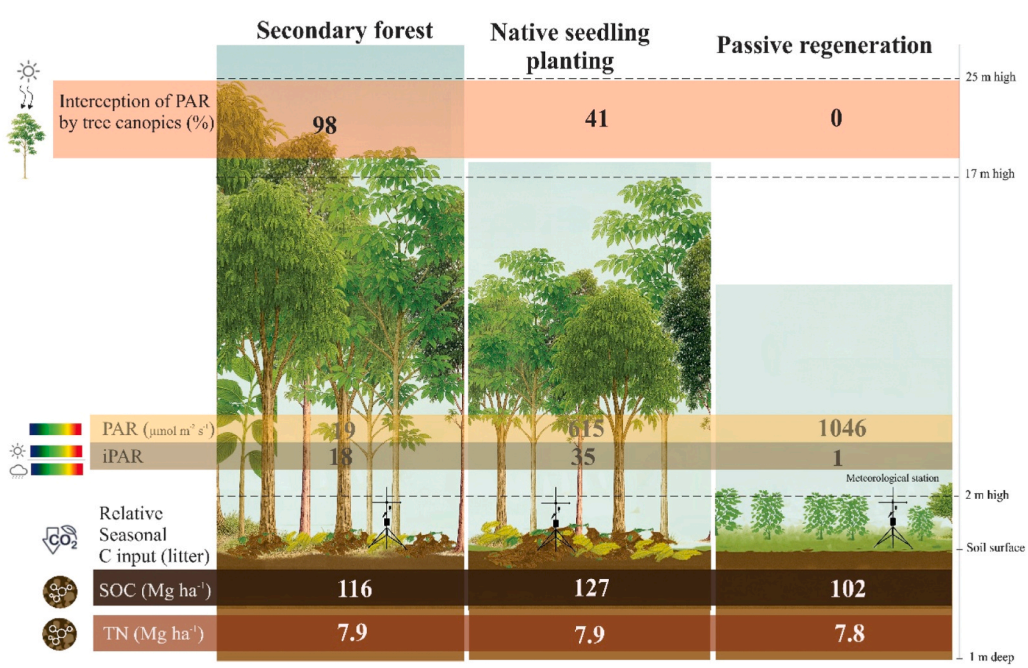

Fig. 10. Summary of the main results comparing the secondary forest, planting of native seedlings and passive regeneration for the restoration of LR at the end of the 10 years since the implementation of the treatments. Photosynthetically Active Radiation. iPAR - Index of percentage variation in PAR transmittance.

native species, local land-use history, and climatic conditions, offering practical guidance for maximizing SOC sequestration in LR restorations in the southern Amazon.

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CRediT authorship contribution statement

Alexandre Ferreira do Nascimento: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Austeclínio Lopes de Farias Neto:** Writing – review & editing, Writing – original draft, Visualization, Validation, Resources, Project administration, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Jorge Lulu:** Writing – review & editing, Writing – original draft, Visualization, Validation, Resources, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Ingo Isernhagen:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Jussane Antunes Fogaça dos Antunes:** Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Investigation, Formal analysis. **Antonio Okada:** Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Investigation, Formal analysis.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: AFN reports equipment, drugs, or supplies was provided by Sustainable Rural. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.123467.

Data availability

Data will be made available on request.

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