Exploring plant functional traits and their relationship to biomass dynamics in secondary forests in Eastern Amazonia

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Abstract

Functional traits and trees ecological strategies can effectively indicate the progress of forest recovery during succession. The objective of this study is to investigate variations in leaf and wood traits, CSR ecological strategies - which classify plants into three ecological strategies: competitors (C%), tolerant to stresses (S%), and ruderals (R%) - and trade-offs in resource acquisition strategies in secondary forests of different recovery ages, comparing them to old-growth forests. We also examined the relationships between traits, aboveground biomass dynamics, and edaphic variables in the Bragantina region, Eastern Amazon. Our evaluation focused on leaf area (LA), specific leaf area (SLA), leaf dry matter content (LDMC), and wood density (WD). Secondary forests exhibited higher LDMC and WD compared to old-growth forests, with low trait variation among secondary forests regardless of recovery age. Stress tolerance strategy (S%) was dominant in secondary forests, whereas old-growth forests showed a balanced proportion of S% and C% strategies. Coordination was identified among WD, S%, and LDMC. Significant relationships were found between functional traits and soil variables in secondary forests. Our results highlight that the slow functional recovery of secondary forests in the Bragantina region may be influenced by the intense land use prior to natural regeneration and the highly fragmented landscape.

Keywords: Aboveground biomass, CSR strategies, leaf traits, trait coordination, wood density

1. Introduction

Tropical forests, such as the Amazon rainforest, have been significantly impacted by deforestation, mainly due to land conversion for agriculture and other uses (Burgess & Barbier, 1997). Thus, recovering forests or secondary forests, which are regenerating after clear-cutting, are rapidly expanding and may serve as important biodiversity reservoirs (Chazdon et al., 2010; Rozendaal et al., 2019; Elias et al., 2022; Poorter et al., 2021a). Secondary forests undergo important changes in structure and floristic composition across successional stages (Chazdon et al., 2010; Poorter et al., 2021b). However, the successional pathways in these forests are complex and varied (Arroyo-Rodrigues et al., 2017), with biodiversity and carbon recovery depending on factors such as forest legacies (e.g. soil seed bank); environmental conditions (e.g. landscape, soil, and climate variables); and the previous land use, making recovery difficult to predict (Poorter et al., 2016; Rozendaal et al., 2019; Elias et al., 2022). Understanding how these forests recover functional traits, ecological strategies, and biomass dynamics is essential for predicting their role in maintaining ecosystem services and carbon storage (Poorter et al., 2021b). Despite this, little is known about functional recovery of secondary forests. Therefore, analyzing functional traits can improve our understanding of successional processes and biomass recovery in these forests compared to old-growth forests.

Functional traits can be suitable descriptors of plants' ecological strategies (Violle et al., 2007; Reich, 2014), reflecting species occurrence and adaptation in different environments over time (Maracahipes et al., 2018; Maynard et al., 2022). The acquisitive-conservative trade-off model, represented by the leaf and wood economics spectra, predicts a continuum of plant strategies in response to resource availability and environmental pressures (Wright et al., 2004; Chave et al. 2009; Reich, 2014). For instance, traits like high specific leaf area (SLA) and low leaf dry matter (LDMC) and wood density (WD) are associated with acquisitive strategies that optimize rapid resource acquisition, while conservative traits reflect strategies that favoring long-term survival under resource scarcity (Wright et al., 2004; Chave et al., 2009). Based on these models, it is expected that secondary forests in early successional stages will be dominated by species with acquisitive traits (e.g., high SLA, low LDMC, low WD), transitioning to conservative traits (e.g., low SLA, high LDMC, high WD) as succession progresses.

Additionally, integrating leaf traits, such as leaf area, SLA and LDMC, allows species' classification into CSR strategies (Grime, 2001; Pierce et al., 2017) categorizing species as competitors (C%), stress-tolerant (S%), or ruderal (R%). This classification enables a deeper understanding of plant ecological strategies, as it integrates leaf traits related to leaf size and acquisitive-conservative economics (Pierce et al., 2017). Therefore, the tool proposed by Pierce et al. (2017) provides the percentage of each ecological strategy that integrates the variation in leaf traits and reflects how species adapt to environmental conditions over time. In the context of secondary forest succession, CSR theory can predict shifts in species strategies, with ruderal and competitive traits dominating early successional stages and stress-tolerant traits becoming more prominent as forests mature. Thus, CSR theory aids in understanding ecological strategies and how species respond to environmental changes (Pierce et al., 2017).

Constraints related to species characteristics, such as physiological limits, environmental tolerances, and resource availability, can influence resource allocation patterns and lead to ecological trade-offs that affect species spatial distribution and composition (Cosme et al., 2017) and ecosystem services provision (Pan et al., 2013). Factors such as soil characteristics, degradation, climate, and community dynamics can influence plant resource allocation (Lohbeck et al., 2015; Poorter et al., 2021a).

Moreover, functional traits have the potential to act as explanatory factors for aboveground biomass, suggesting a direct link to biomass accumulation over time (Becknell et al., 2014). Thus, during succession, the natural replacement of light-dependent species with shade-tolerant ones is influenced by habitat variations and reflected in functional traits (Chazdon et al., 2014). However, significant uncertainties remain regarding functional variation throughout forest succession in the Amazon. Understanding these dynamics is crucial for addressing factors that limit effective restoration, particularly in highly degraded areas like the Bragantina region, characterized by low forest cover, high fragmentation, and intensive land use, where diversity and carbon stock recovery are extremely slow (Vieira et al., 2012; Almeida et al., 2010; Elias et al., 2020).

This study aims to investigate the functional trajectory in a chronosequence (i.e. set of sites in the same region differing in the time since they were formed) (Walker et al., 2010) of secondary forests in the Bragantina region, Eastern Amazon. To this end, we analyzed the leaf and wood functional traits recovery in secondary forests of different ages and their relationships with edaphic characteristics and aboveground biomass dynamics (gain and loss rates). Specifically, we asked:

(i) How do functional traits and CSR strategies vary along the chronosequence of secondary forests? We expect that younger secondary forests will exhibit more acquisitive traits (higher LA and SLA; lower LDMC and WD), with higher C% and R% strategies and that these strategies will transition to a higher S% and conservative trait (lower LA, lower SLA, higher LDMC and WD) over time.

(ii) Is there a relationship in resource allocation between leaf and wood traits along the chronosequence? We expect to observe trade-offs in resource allocation between foliar and wood traits, mainly with SLA and WD, given that these traits follow opposite directions in characterizing plant strategies. In contrast, we expect coordination in LDMC and WD, since this relationship may characterize a more conservative strategy. We also expect a positive relationship between S% and wood density, reinforcing the coordination in resource allocation.

(iii) Are aboveground biomass dynamics rates and soil characteristics associated with leaf and wood traits recovery? We expect that soil variables (mainly P and N) influence leaf and wood functional traits in secondary forests.

2. Material and methods

2.1 Study area

This study was carried out along a chronosequence of secondary forests in the municipality of Bragança, northeast of the State of Pará, Eastern Amazon (Figure 1). Secondary forests cover 28.8% of the landscape, accounting for 67.5% of the total forest cover (Elias et al., 2020). All plots are situated in small fragments of *terra-firme* forests (~30-60 ha), which were abandoned after successive agricultural cycles,mainly for cassava, maize, and rice). However, given the long duration of some plots' establishment or regeneration, the exact historical land use of each area could not be determined. The municipality of Bragança, one of the oldest in the state, has suffered intense degradation over the years, resulting in the loss of approximately 90.2% of its native forests and mangrove areas (Elias et al., 2020). Based on interviews conducted with local people, we sampled old-growth forest plots (our baseline for recovery) that retain structural characteristics and were never submitted to clear-cut. Nevertheless, it is possible selective logging and edge effects have already altered our old-growth plots. The secondary forests in this region are located on nutrient-depleted soils due to inadequate soil management, successive land-use cycles, and low forest cover in the landscape (Almeida et al., 2010).

The climate in the region is Am according to the Köppen classification, with annual precipitation ranging from 2000-3000 mm, relative humidity ranging between 80 and 91%, and mean annual temperature between 25.2 ºC and 26. 7 ºC (Alvares et al., 2013). Overall, soil texture is mostly composed by medium to high levels of clay content in all plots, with low Nitrogen (N) and Phosphorus (P) availability and higher levels of Potassium (K) with a decreasing tendency across the successional gradient (Figure S1, Table S1).

2.2 Age of secondary forests

The chronosequence was represented by five secondary forest plots aged 11, 15, 27, 53, and 63 years. The age of the secondary forests was defined by the Sustainable Amazon Network (RAS; ras-network.org) team through interviews with the landowners during the installation of the permanent plots and were confirmed using high-resolution Landsat temporal images (details in Elias et al., 2020). We did not have the complete historical land use data for these areas, but for most of them, the previous land use was shifting agriculture and pastures.

2.3 Tree censuses

The long-term studies in secondary forests in the Bragantina region began in 1999, in 0.25 ha plots. Floristic monitoring is carried out by RAS, in which 16 secondary forests and three old-growth forests are studied over time (Elias et al., 2020). For this study, we used the 2019 census to select the species and to calculate the aboveground biomass rates. All trees with a diameter at breast height (DBH; 1.3 m) ≥ 10 cm were measured. Plant identification was conducted in the field, and botanical samples were collected, if necessary, for comparison with the Embrapa Amazônia Oriental collection. Three census data are available at ForestPlots.net (Lopez-Gonzalez et al., 2011).

2.4 Species selection and aboveground biomass estimates

We selected all tree species that accounted for about 70% to 80% of each plot's aboveground biomass (AGB) for the functional traits analysis. First, we calculated AGB using the allometric equation: $AGB = 0.637 \times (\rho D^2 H)^{0.976}$, where ρ represents tree wood density ($g\ cm^3$) extracted from the Global Wood Density Database (Chave et al., 2009); D represents stem dbh (cm) and H is the total height (m) estimated by region-level height-diameter models (Sullivan et al., 2018). The AGB estimate was performed using the 'BIOMASS' package (Réjou-Méchain et al., 2017) in the R software (R Core Team, 2022). We selected approximately 3395 individuals from 50 species (Table SM2). Specifically, we selected fifteen species in the 11-year-old forest, seven in the 15-year-old forest, nine in the 27-year-old forest, eleven in the 53-year-old forest, ten in the 63-year-old forest, fifteen species in one old-growth forest, and nine species in another old-growth forest.

2.5 Functional traits sampling

Sampling was carried out at the end of the rainy season, in June 2022. Three to five individuals were collected for each species per plot. From each individual, we selected ten expanded and sun-exposed leaves and two branch sections (~5cm). A set of traits related to leaf size (leaf area) and economics spectrum (specific leaf area and leaf dry matter content), and wood density were measured, based on a standardized protocol (Pérez-Harguindeguy, 2016). Below is the measurements description.

a) Leaf area (LA): we estimated the leaf area (mm^2) by scanning the adaxial face of ten leaves of each individual and after analyzing the total area using the BiocManager package in the R software (Morgan, 2022).

b) Specific leaf area (SLA): we calculated the specific leaf area (SLA) (m^{-2} g^{-1}) through the ratio between the leaf area and the dry mass of ten leaves of each individual. To obtain the dry mass, the leaves were dried in an oven at 65° C for 72 hours and weighed on a digital scale with a precision of 0.001g.

c) Leaf dry matter content (LDMC): To analyze the LDMC (mg g^{-1}), we used the same leaves to calculate the SLA and LA. LDMC is the leaf dry mass divided by its fresh mass saturated with water. The fresh mass saturated with water was measured on a precision scale after the leaves were hydrated in a container wrapped in a dark bag to prevent transpiration.

d) Wood density (WD): to measure the wood density (g cm^3), we used segments of the same branches that were used to measure leaf traits. We calculated the wood density as the ratio between the dry mass and the displaced volume of each segment through the Archimedes principle (in which each segment is immersed in a recipient with water placed on a scale and the measured mass increment, in g, corresponds to the volume of water displaced, and therefore to the volume of the branch, in cm^3). The dry mass of the branch fragments was determined after drying in an oven at 65°C for 72 hours.

We used the Pérez-Harguindeguy et al. 2016 protocol for measuring all traits. Each trait's association and ecological function are described below (Table 1).

2.6 CSR strategies calculation

We calculated the percentage of each strategy — S%, R%, and C% — using the global vascular plant CSR calculator in Excel format, the 'StrateFy' tool proposed by Pierce et al. (2017), which is available in the paper's supplementary material. This method encompasses plant size variation and conservative versus acquisitive economics (Pierce et al., 2017), using three leaf traits: LA, LDMC, and SLA. Details of the calculations can be found in Pierce et al. (2017).

2.7 Estimating aboveground biomass losses and gains

From the values of individuals' aboveground biomass between the years 2017 and 2019, we calculated the loss rates (mortality) (Korning and Balslev, 1994; Oliveira-Filho et al., 2007) and the gain rates (growth) (Salami et al., 2017) of aboveground biomass (AGB). The loss rates in AGB were defined as follows: the loss of biomass (P) is calculated as 1 minus the ratio of the final biomass (which includes the initial biomass of the trees, the biomass of dead trees, and the biomass lost) to the initial biomass, raised to the power of 1 divided by the time interval between inventories, multiplied by 100. Specifically, we have: $P = \{1 - [(\text{initial AGB} - \text{dead tree AGB} + \text{lost AGB}) / \text{initial AGB}]^{(1/t)}\} \times 100$, where initial AGB is the biomass at the beginning of the period, dead tree AGB is the biomass of dead trees, lost AGB is the biomass lost, and t is the time interval between inventories.

The gain rates in AGB were calculated as follows: the gain of biomass (G) is calculated as 1 minus the ratio of 1 to the ratio of the biomass of recruited trees plus the biomass gained to the final biomass, raised to the power of 1 divided by the time interval between inventories, multiplied by 100. Thus, we have: G = {1 - [1 - (recruited tree AGB + gained AGB) / final AGB]^(1/t)} × 100, where recruited tree AGB is the biomass of newly established trees, gained AGB is the biomass gained by the trees over time, and final AGB is the biomass at the end of the period.

2.8 Edaphic variables

Soil properties were evaluated in each plot by collecting five random samples at depths of 0-10 cm, 10-20 cm, and 20-30 cm. For each depth, we created a composite sample from three random subsamples taken throughout the plot. We estimated the phosphorus (P) and potassium (K) contents using the Mehlich-I method; total nitrogen (N) using the Kjeldahl method; and granulometry (sand, clay, and silt) by the Bouyoucos method. All analyses were carried out at the Laboratório de Solos of Embrapa Amazônia Oriental, following the guidelines of the Embrapa soil analysis (Teixeira et al., 2017).

2.9 Statistical analyses

To assess differences in functional traits along the chronosequence and evaluate recovery relative to old-growth forests (question 1), we conducted a PERMANOVA with a post hoc pairwise permutation test using 'RVAideMemoire' package (Herve M., 2023). Means and confidence intervals were calculated using the ‘dplyr’ package (Wickham, H. et al., 2023). To facilitate the visualization of differences between forest types and identify patterns and relationships between leaf and wood traits, we performed a Principal Component Analysis (PCA) using the ‘prcomp’ function from the base R package 'stats' (R Core Team, 2022). We calculated the percentage of C%, S%, and R% strategies using the “StrateFy” tool and we evaluated differences among strategies among forests using a

PERMANOVA. We also used a Principal Component Analysis associated with PERMANOVA to evaluate and compare the functional traits composition along the chronosequence.

To evaluate the trade-offs between WD and leaf traits (LA, SLA, and LDMC), and the percentage of CSR strategies in the secondary forests (question 2), we used Generalized Linear Models with lognormal exponential distribution performed in the 'stats' package (R Core Team, 2022). We also fitted lognormal models to evaluate the influence of soil variables (N, P, K, clay content) and aboveground biomass losses and gains on functional traits (question 3). All data matrices were log-transformed (log+1), and we removed the outliers using Cook's distance performed in the 'stats' package. The assumptions were checked by graph analyses. All the analyses and graphs were carried out in R 4.4.0 (R Core Team, 2022).

3. Results

3.1 Variation in functional traits and CSR strategies

Except for LA, all traits showed significant differences among forests along the chronosequence (Figure 2). Contrary to our expectations, SLA showed higher mean values in late-successional (53 and 63 years old) and old-growth forests ($F=4.04$; $p<0.01$) contrasting with other areas (Figure 2b; Table S2). LDMC was higher in the 63-year-old forest, which diverged from the 11-year-old and the old-growth ones with the lowest mean values (Figure 2c). WD was higher in the 53-year-old forest compared to early successional ones ($F=4.14$; $p<0.01$) but did not follow an expected pattern entirely as our old-growth forests presented the lowest WD (Figure 2d). WD mean values ranged from 0.57 ± 0.07 to 0.80 ± 0.05 representing intermediate/denser woods even in the youngest secondary forest.

The first and second axes of PCA explained 34.9% and 28.6% of the functional data variation, respectively (Figure 3, Table S1). The first axis was negatively correlated to LA and WD, while axis 2 was negatively correlated with LDMC and SLA. We did not observe a tendency to group formation among forests, which was confirmed by the PERMANOVA (F=1.63; p=0.11 value. Figure 2).

In the secondary forests, we observed notable variations in the proportion of S% (S/CS) and C% (CS) strategies across different forest ages (Figure 4). However, these differences do not necessarily indicate 'biotic homogenization' across the areas. The proportion of C% and S% strategies differed among the forests (Figure S2). For instance, the 53-year-old forest and one of the old-growth forests showed a higher proportion of C% strategies compared to the 27-year-old forest (F= 3.50; p>0.01). Additionally, the proportion of the S% strategy was higher for the 63-year-old forest compared to the lower values observed in old-growth forests (F=2.72; p=0.02). These variations in plant strategies may reflect underlying ecological drivers such as forest age, resource availability, or site-specific conditions influencing the balance between acquisitive and conservative strategies.

3.2 Relationships between wood density, leaf traits, and CSR strategies

WD showed a positive relation with LDMC and S% strategy in our secondary forest plots (Table 2). We did not observe a significant association between WD vs the other traits (LA, SLA), and WD and ecological strategies (C% and R%).

3.3 Modeling the functional traits among secondary forests with aboveground biomass dynamics rates and edaphic variables

We observed a negative association between LA and biomass losses, as well as between SLA and clay content. LDMC showed a positive association with P and a negative association with N. WD exhibited a positive association with K (Table 3). Differences between forests regarding these associations are detailed in the supplementary material (Figure S1), which illustrates how these variables vary among different forest types.

4. Discussion

We demonstrated that forest functional recovery in the Bragantina region in the Eastern Amazon does not follow the expected trend observed in moist tropical forests. Our findings indicate the following: 1) a prevalence of S% strategy and low variation in leaf and wood functional traits along the chronosequence of secondary forests, regardless of their recovery ages and even when compared to old-growth forests for some traits; 2) coordination in resource allocation between leaf and WD, with species varying along a continuum from more fast/acquisitive to more slow/conservative strategy. This relationship was also underscored by the correlation between stress tolerance and WD, highlighting the need for greater investments in carbon for survival in these areas; 3) trait variation was more strongly influenced by soil fertility than aboveground biomass dynamics in the secondary forests. Therefore, we observed a functional convergence between the secondary forest gradient and with primary forests.

4.1 Variation in functional traits and CSR strategies along the successional gradient

Our results reveal divergent patterns of variation in economic leaf and wood traits from those expected in wet successional forests. Generally, these forests range from acquisitive strategies with faster return rates favoring growth and reproduction (i.e. high

SLA and low LDMC and WD) in early-successional forests to conservative strategies predominating in late-successional forests (Poorter et al. 2016; Jakovac et al. 2016). However, we observed opposite patterns with higher SLA in old-growth and late-successional forests. Intermediate and high WD prevailed throughout successional trajectories and old-growth forests had the lowest WD. Interestingly, our results resemble trajectories found in dry secondary forests, where early successional forests tend to invest in more conservative traits such as high WD that confers higher drought resistance to survive in seasonal environments and late-successional forests show a decrease in WD over time, while wet forests generally show an increase in WD (Poorter et al., 2019). Both wet and dry forests tend to converge to similar values of WD in late-successional forests (Poorter et al., 2019). In the Bragantina region, multiple land uses have altered the nutritional availability (Figure S1) and microclimatic conditions, which can act as strong environmental filters, limiting natural regeneration. Species with conservative/slow traits are more likely to survive under harsh conditions (Lohbeck et al. 2013; Oliveira et al. 2021), explaining the prevalence of conservative traits in early-successional stages.

The conservative traits are reflected in the predominance of S% and C% strategies in our plots, highlighting that environmental conditions in the Bragantina region are hostile to the recovery of functional traits. The stress tolerance strategy tends to be expressive in degraded and poor-nutrient environments enabling plants to survive in adverse conditions (Pierce et al. 2017; Ricotta et al. 2023). In these conditions plants show a *trade-off*, investing resources to protect tissues from stress damage at the expense of rapid growth to outcompete with neighbors (Pierce et al. 2017). The Bragantina region, characterized by extensive deforestation and limited forest remnants, exhibits a notably slow recovery of both carbon stocks and plant diversity (Almeida et al., 2010; Elias et al. 2020), which also influences plant resource allocation patterns and their strategies. We observed a higher proportion of the stress tolerance strategy compared to competition in most of the secondary forests (11, 15, 27, and 63 years), which contrasts with the old-growth forests where the proportions of stress tolerance and competition strategies are similar (Figure S2). Over time, there are changes in environmental conditions, where in old-growth forests the microclimate is likely wetter, and species may outcompete each other for light (Wen et al. 2023). However, the late-successional forest (63 years) shows similar strategies and functional traits to early successional forests rather than to old-growth forests, suggesting a delay in functional recovery during the time in this region.

4.2 Resource allocation in secondary forests

The positive relationship between LDMC, S%, and WD reveals the coordination of these traits during forest recovery. This coordination is indicative of the range of variation in the plants' strategies, varying from more acquisitive species with a fast strategy to conservative ones, investing in long-lived and resistant tissues to increase resistance against water and nutrient limitations (Chave et al. 2009; Reich 2014).

This coordination is indicative of the range of variation in the plants' strategies, varying from more acquisitive species with a fast resource acquisition strategy to conservative ones, investing in long-lived and resistant tissues to increase resistance against water and nutrient limitations (Chave et al. 2009; Reich 2014). Strong integration of traits from different plant tissues to predict productivity – fast/acquisitive versus persistence – slow/conservative, are considered advantageous at the whole-plant scale (Reich 2014). In this direction, an important trade-off between mortality and growth is well documented for tropical forests, with fast-growing species tending to have higher mortality (Poorter et al. 2008, Oliveira et al. 2021).

The relationship between WD and S% also reinforces the coordination in resource allocation. This integration in leaf traits related to both size and economic continuum determining the higher S% and WD underscores the harsh and degraded environment in the studied areas, selecting species with durable and resistant leaf and wood tissues (intermediate to high wood densities). This corroborates that investments in mechanical resistance and long-lived tissues have higher survival rates (Martinez-Cabrera et al. 2009; Poorter et al. 2008), delaying the species turnover. We also observed some independent variation among leaf and wood economic spectra, such as the absence of relationship between SLA and WD, as well as between leaf area and WD, as shown for other tropical forests (Baraloto et al. 2010). .

4.3 Relationships between functional traits, soil variables, and aboveground biomass loss rate

Our findings highlight soil variables as important drivers in functional responses along successional trajectories. The negative association between SLA and clay content implies a coordinated response between soil water retention and carbon allocation to leaves tissue construction. Generally, a higher clay proportion in soil is associated with greater water and nutrient retention capacity, which can directly influence plant development (Cai et al. 2021; Gerdol et al. 2018) and favor species with more acquisitive traits, as expected by the leaf global economic spectrum (Wright et al. 2004). However, we found the opposite pattern. This may be related to the depauperate soils observed in these secondary forests due to the long history of agricultural land use in the region.

LDMC during the recovery process was influenced by the two most limiting nutrients for plants in tropical ecosystems (N and P) (Sullivan et al., 2019). However, the positive relationship with P is contrary to what is expected from the global leaf economic spectrum (Wright et al., 2004). A decrease in LDMC is expected as soil fertility increases. Thus, our results suggest that other factors such as light, humidity, and symbiotic associations may also influence leaf allocation patterns. Another important factor to consider is pH, as it primarily affects soil P availability. Phosphorus decreases with reduced pH because more phosphate is adsorbed by or precipitated with Fe3+, Al3+, and Mn2+ ions released during soil acidification (Vitousek et al. 2010). Among the study sites, the area with a 63-years of recovery showed higher soil P concentration and lower pH (Figure S1), and this community exhibited a higher average LDMC. Therefore, some of the P may not be available to plant species uptake, explaining the positive relationship observed during the secondary forest recovery in Bragantina region.

Moreover, we observed a positive relationship with K and WD. K availability can facilitate tissue construction and growth processes in plants (Sardan and Peñuelas, 2021), where soils with more K content the trees may invest in denser wood, regulated via biochemical signaling feedback in cambium activity, enhancing mechanical resistance and durability (Fromm, 2010). Along the successional gradients, there is a general low variability in K content (Figure S1), with high concentrations in young forests, where we observed high WD. In contrast, old-growth forests have lower K content and lower WD. Thus, this higher concentration of K in juvenile forests enables plant communities to invest in carbon allocation to wood construction as a strategy to deal with the adverse conditions in the Bragantina region.

Lastly, successional trajectories patterns in the Bragantina region reveal weak relationships between biomass dynamics rates and functional traits. The only negative association was between leaf area and aboveground biomass loss rates, suggesting that species with larger leaves have lower mortality, contrary to our expectations based on faster return rates costs for tree communities' survival (Reich 2014; Salguero-Gómez

2017; Oliveira et al. 2021). This relationship indicates that greater investments in leaf area possibilities higher light interception, potentially enhancing biomass construction (Poorter et al. 2009), mainly in early-successional forests (Selaya et al. 2007), as observed in our study plots (11, 15, and 27 years old) with lower biomass loss rates (Figure S1 - f). Higher biomass loss rates in the 53- and 63-year-old plots (Figure S1 - f), combined with low soil fertility, highlight the slow functional recovery of secondary forests in the Bragantina region. This suggests that, despite 63 years of land abandonment, edaphic factors continue to limit the recovery process, emphasizing the role of intense prior land use and the fragmented landscape.

Higher biomass loss rates in 53- and 63-years old plots (Figure S1 - f), associated with low soil fertility in these areas emphasize that edaphic factors limit functional recovery in the Bragantina region even after 63 years of land abandonment.

5. Conclusion

Functional recovery in the Bragantina region is limited by adverse edaphic conditions and a slow recovery of carbon stocks, even after 50 years of land abandonment. Our findings reveal the dynamic and continuous nature of succession processes, which are influenced by leaf traits (LDMC) and wood traits (WD), in a region characterized by intensive and long-term land use within a highly fragmented landscape. We did not observe a clear pattern of change in leaf and wood traits following the successional process. However, species appear to be coordinated in their investments to cope with the environment along the fast-slow continuum, with plants showing higher leaf dry matter content (LDMC) and S% also exhibiting higher WD. The relationships between soil and leaf functional traits did not follow the expected patterns of the global leaf economic spectrum, which may be explained by the harsh soil fertility conditions in these forests, the intense land use prior to natural regeneration, and the highly fragmented landscape limiting colonization. Thus, our results highlight the complexity of forest succession processes in the Eastern Amazon, emphasizing the need to consider edaphic characteristics for enabling functionally diverse regeneration of secondary forests.

CRediT authorship contribution statement

Grazielle S. Teodoro: Writing – review & editing, Project administration, Methodology, Supervision, Funding acquisition. **Fernando Elias:** Writing – review & editing, Project administration, Formal analysis, Methodology. **Luane Botelho:** Writing – review & editing, Investigation, Formal analysis, Methodology. **Beatriz V. Barbosa:** Data curation, Formal analysis, Writing – review & editing. **Karoline C. Silva:** Data curation, Writing – review & editing**. Vanessa N. Rodrigues:** Data curation, Writing – review & editing. **Jucelino S. Coutinho:** Data curation. **Euciney E. S. Barbosa:** Data curation. **Joice Ferreira:** Review, Resources, Funding acquisition. **Jos Barlow:** Review, Resources, Funding acquisition.

Declarations of Competing Interest

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