

## Article

# Scaling Plant Functional Strategies from Species to Communities in Regenerating Amazonian Forests: Insights for Restoration in Deforested Landscapes

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## Abstract

Understanding how main plant functional strategies scale from species to communities is critical for guiding restoration in tropical disturbed areas by unsustainable livestock grazing; yet, the patterns and drivers of functional trait space along successional trajectories remain poorly understood. Here, we investigated functional trait space using principal component analyses (PCAs) based on eight traits related to leaf, stem, and seed morphology across 226 tree species and 33 forest communities along a chronosequence of natural regeneration following cattle ranching abandonment in deforested landscapes of the Colombian Amazon. We identified three species-level functional axes—namely, the ‘Structural–Reproductive Allocation Axis’, the ‘Mechanical Support and Tissue Investment Axis’, and the ‘Leaf Economics Axis’—and two community-level axes: the ‘Colonization–Longevity Axis’ and the ‘Persistence–Acquisition Axis’. These axes aligned with the life-history strategies of short-lived pioneers, long-lived pioneers, and old-growth species, and reflected their relationships with key environmental drivers. Community-level functional composition reflected species-level patterns, but was also shaped by soil properties, microclimate, and tree species richness. Forest age and precipitation promoted conservative strategies, while declining soil fertility suggested a decoupling between above- and belowground recovery. Functional richness and divergence were highest in mid-successional forests dominated by long-lived pioneers. Our findings highlight the role of environmental and successional filters in shaping functional trait space and emphasize the value of functionally diverse communities. Particularly, our results indicate that long-lived pioneers (LLP) such as *Astrocaryum chambira* Burret and *Pouteria campanulata* Baehni, with traits like large height, intermediate wood density, and larger seed size, represent ideal candidates for early enrichment strategies due to their facilitation roles in succession supporting restoration efforts in regenerating Amazonian forests.

**Keywords:** functional traits; functional trait space; ecological restoration; Amazonian forests; secondary succession; community assembly



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## 1. Introduction

The Amazon plays a critical role in global biodiversity conservation and carbon storage. However, it is increasingly threatened by deforestation and ecological transformation, including the risk of critical transitions and loss of ecosystem resilience [1–3]. In many parts of the Amazon, including Brazil and Ecuador, deforestation typically follows a road-driven expansion pattern—such as fishbone configurations—where road construction facilitates subsequent agricultural conversion [4,5]. In contrast, in the Colombian Amazon—particularly in the department of Caquetá—deforestation is primarily driven by agricultural expansion and cattle ranching, but it follows a distinct spatial pattern along river corridors, which serve as the main access routes in the absence of major road infrastructure [6,7]. Additionally, human settlements contribute to the disruption of ecological connectivity between the Andes and Amazon lowlands, with less than 12% of the region retaining primary or secondary forest cover, while pastures for livestock occupy approximately 68% of the territory [8,9].

Within this context, secondary tropical forests play a central role in ecological recovery and biodiversity conservation in landscapes affected by extensive land-use change. Areas undergoing natural regeneration after cattle ranching abandonment offer a key opportunity to understand how ecological strategies reorganize along successional trajectories [10,11]. However, these trajectories are highly variable due to legacy effects (e.g., seed bank), environmental conditions (soil, climate, topography), and past land use, which complicates the identification of clear recovery patterns [12–14].

Functional traits—morphological, physiological, and reproductive attributes that influence species performance—offer a framework for evaluating ecosystem recovery [15,16]. These traits are effective descriptors of plant ecological strategies [17,18], as they reflect presence, dominance, and adaptation to different environments over time [19,20]. However, it remains unclear how land cover changes affect key components of functional diversity, such as composition, richness, evenness, and divergence [21,22].

Trait-based ecology posits that plant species are organized along coordinated functional spectra reflecting trade-offs between resource acquisition, structural investment, and reproductive effort [16,23]. These spectra span gradients such as the leaf economic spectrum (e.g., specific leaf area, leaf dry matter content, leaf thickness), structural or hydraulic spectra (e.g., wood density), and reproductive trade-offs (e.g., seed size and number), all linked to life-history strategies. Understanding how these spectra manifest in regeneration contexts is key to identifying dominant functional archetypes. This leads to our first research question: (1) Which species-level functional trait spaces do tree species occupy in secondary forests regenerating after cattle ranching abandonment?

At the community level, shifts in functional trait space may reflect not only species turnover but also environmental filtering and functional convergence or divergence throughout succession [24,25]. However, it remains uncertain whether community-level strategy spectra faithfully reflect aggregated species-level patterns or are transformed by local processes. Moreover, it has been proposed that communities with greater functional diversity exhibit higher resilience to environmental fluctuations [26–28], as the coexistence of multiple functional strategies provides a buffering effect against disturbance [29,30]. This leads to our second question: (2) Do community-level functional trait spaces resemble those observed at the species level across a successional gradient? Answering this question is key for evaluating scale dependence in functional patterns and the validity of trait-based monitoring across organizational levels.

Several frameworks have been proposed to explain how functional diversity influences ecosystem functioning. The niche complementarity hypothesis suggests that higher trait diversity enables more efficient and complementary resource use [31,32], while the mass

ratio hypothesis proposes that traits of dominant species (e.g., community-weighted means) drive ecosystem functions [33,34]. Both perspectives emphasize the importance of characterizing community-level functional patterns using metrics such as community-weighted means (CWMs) [35].

During succession, it is expected that secondary forests will shift from dominance by acquisitive species to those with more conservative strategies, which can be assessed through combinations of traits associated with the leaf economic spectrum, plant structural traits, and reproductive parameters [15,36]. These combinations also enable classification into Competitor–Stress-tolerator–Ruderal (CSR) strategies [37].

The environmental context in which forests regenerate influences both trait expression and functional assembly. Soil conditions, microclimate, topography, and land-use legacies all affect functional composition [38,39]. This brings us to our final question: (3) How do environmental variables, successional stage, and community composition interact to shape community-level functional trait space? This question aims to evaluate how abiotic gradients influence the distribution of functional traits and life-history strategies thorough chronosequence.

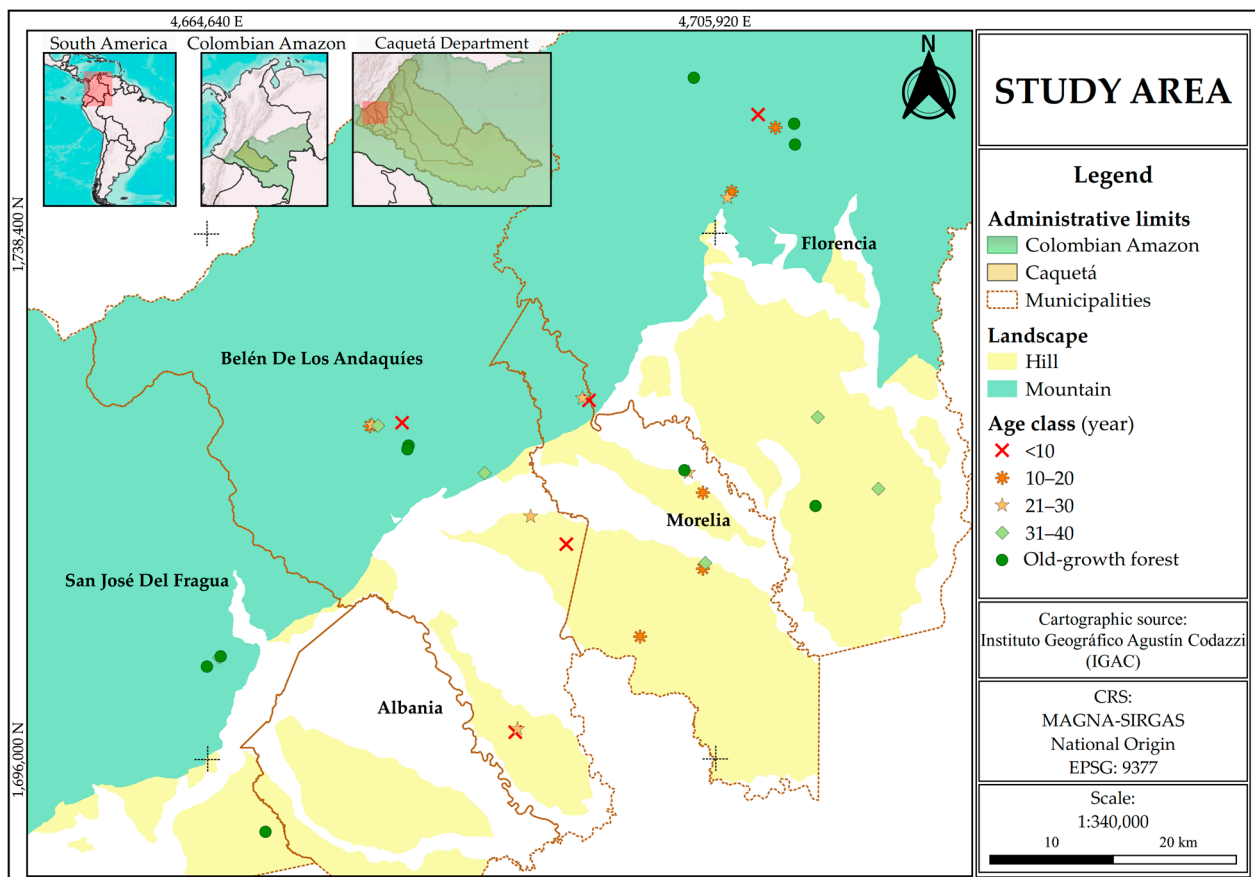
We hypothesize that species and communities organize along major functional space—such as colonization–longevity and persistence–acquisition—and that environmental filtering modulates these patterns across succession. Specifically, we expect mid-successional forests dominated by long-lived pioneers to exhibit peak functional divergence due to the coexistence of acquisitive and conservative strategies. These expectations provide a framework for interpreting the observed functional patterns and their implications for restoration.

By integrating species- and community-level trait data with environmental and successional gradients, this study provides an understanding of forest recovery dynamics in a critically deforested region of the Colombian Amazon. This functional perspective is particularly valuable for supporting ecological restoration and monitoring practices, as it facilitates the identification of trait-based indicators and syndromes associated with forest structure, function, and resilience. Ultimately, our findings offer robust evidence to inform restoration strategies in tropical landscapes affected by extensive cattle ranching, highlighting the value of functional traits as tools to assess successional trajectories and restoration outcomes.

## 2. Materials and Methods

### 2.1. Study Area and Sampling Design

The study was conducted in the department of Caquetá, located in the northwestern Colombian Amazon, encompassing the municipalities of Florencia (1°36'50" N; 75°36'46" W), Morelia (1°29'09" N; 75°43'28" W), Belén de los Andaquíes (1°24'59.1" N; 75°52'21.2" W), San José del Fragua (1°19'52" N; 75°58'28" W), and Albania (1°19'44" N; 75°52'42" W) (Figure 1). The sampling sites are in a humid-warm tropical climate with a unimodal precipitation regime, an average annual rainfall of 3376 mm, and a mean temperature of 25.04 °C. Soils in the region are predominantly Oxisols and Ultisols, characterized by low fertility and aeration, acidic conditions (pH < 6), high aluminum saturation (>60%), and clayey texture [40]. Physiographically, the landscape is mainly composed of hilly terrain (altitudes below 300 m, slopes ranging from 7% to 12%), representing the typical undulating landscape of the Amazonian plains, and mountainous terrain (altitudes above 300 m, slopes between 12.1% and 75%), forming part of the Andean–Amazon transition. Land cover is dominated by pastures used for cattle ranching, crops, remnants of secondary forests, and mature forest, as described by Rodríguez-León et al. [41,42].



**Figure 1.** Location of the 33 study plots in the northwestern Colombian Amazon. Abbreviations: <10, secondary forest regenerating for less than 10 years after livestock abandonment; 10–20, secondary forest regenerating for 10–20 years; 21–30, regenerating for 21–30 years; 31–40, regenerating for 31–40 years; OF, Old-growth forest.

A total of 33 plots measuring  $50 \times 50$  m (0.25 ha each) were independently established across two landscape types: hill (14 plots) and mountain (19 plots). Within each landscape unit, plots were classified along a chronosequence of abandoned pastures (based on time since abandonment as a proxy for secondary forest age) up to mature forest, into five successional categories, as defined by Rodríguez-Léon et al. [42]: (i) <10 years (early succession), (ii) 10–20 years (young secondary), (iii) 21–30 years (intermediate), (iv) 31–40 years (advanced secondary), and (v) mature or old-growth forest (~100 years; OF) (Supplementary Figure S1). A total of five, six, six, six, and ten plots were evaluated in the <10, 10–20, 21–30, 31–40, and OF categories, respectively. All plots were located on lands previously dedicated to extensive cattle grazing, which was the dominant land-use type before abandonment. Time since abandonment was determined through interviews with owners of local farms. After abandonment, human use in most sites has been limited to occasional collection of firewood and non-timber forest products, with no evidence of intensive logging or conversion to other land uses.

The 0.25 ha plot size was selected to balance logistical feasibility with ecological representativeness across a heterogeneous landscape. While we acknowledge that this area may be more than sufficient to capture compositional and structural variation in early successional shrub-dominated vegetation, it may indeed underrepresent large tree diversity and structural complexity in old-growth forests [43]. However, 0.25 ha plots remain a widely used standard for trait-based studies and functional ecology across successional gradients in tropical forests [44,45], offering a reasonable compromise between spatial coverage and sampling intensity. To mitigate potential underestimation of richness in older

forests, we increased the number of OF plots ( $n = 10$ ), which also served as reference sites with no recent disturbance history. Although larger plots (e.g., 1 ha) might better capture old-growth structure [46], our design prioritized replication across successional stages over exhaustive sampling within individual plots. This approach has been shown to provide robust inference on trait–environment relationships and community-level functional composition [10,47].

## 2.2. Floristic Data Collection

Within each plot, all trees with a diameter at breast height (DBH)  $\geq 10$  cm were tagged and identified. Total height (TH) and commercial height (CH) were measured using a Suunto PM-5 clinometer. Collected specimens were processed, taxonomically identified according to the Angiosperm Phylogeny Group IV classification [48], and deposited at the Colombian Amazon Herbarium (COAH) of the Instituto SINCHI in Bogotá, Colombia. For the functional trait analyses, we selected species that together accounted for at least 55% of the cumulative Importance Value Index (IVI) within each successional age class. This threshold was chosen to focus on the most ecologically dominant and functionally relevant species while minimizing the influence of rare species with negligible impact on community structure. This approach aligns with previous trait-based studies that have adopted similar criteria to ensure analytical robustness and ecological representativeness [49,50]. Species-level IVI values were averaged across plots belonging to the same forest age class, treating plots as independent replicates nested within each age class. From a total of 541 fully identified species, those with a minimum of 10 replicate individuals were prioritized, resulting in a final subset of 226 species (Supplementary Table S1).

## 2.3. Trait Sampling and Life-History Strategies

Vegetative and reproductive functional traits were assessed in five individuals per species, totalling 1130 individuals across 226 species in 33 plots. Sampling prioritized a single individual per species per plot (0.25 ha) within each successional category, as recommended for species-rich plant communities [51]. Vegetative traits corresponding to foliar and wood traits were measured following the standardized protocols of Pérez-Harguindeguy et al. [52], such as leaf area (LA,  $\text{mm}^2$ ), leaf thickness (LTh, mm), leaf dry matter content (LDMC,  $\text{mg dry mass g}^{-1}$ ), specific leaf area (SLA,  $\text{mm}^2 \text{mg}^{-1}$ ), tree height (H, m), and wood density (WD,  $\text{g cm}^{-3}$ ). Reproductive traits corresponding to seed mass (SM, mg) and seed size (SS,  $\text{mm}^3$ ) were obtained from the red Global Ecosystems Monitoring (GEM) [53], ForestPlots.net [54], the Botanical Information and Ecology Network (BIEN) [55], the Plant Trait Database (TRY) [56,57], the Global Inventory of Floras and Features (GIFT) [58], and previous studies [35,59–61].

Life-history strategies represent coherent sets of functional traits that describe how species grow, survive, and reproduce in their environment over time [16,62]. In this study, we compared three functional life-history types, defined by differences in longevity, growth rate, and successional position, following research by Steege et al. [25,62] and Finegan [63]: short-lived pioneers (SLP), which establish in the early stages of succession; long-lived pioneers (LLP), which arrive later and persist over extended periods; and old-growth species (OGS), typical of stable, undisturbed environments, where they persist long term and compete efficiently for ecosystem resources. Pioneers are defined by combining low wood density and low seed mass (wood density  $< 0.7 \text{ g cm}^{-3}$ ), where SLP have a seed mass of  $< 0.1 \text{ g}$  and LLP have a seed mass of  $\geq 0.1 \text{ g}$ , and OGS have a wood density of  $> 0.7 \text{ g cm}^{-3}$ . This classification was implemented as a mutually exclusive categorical variable, with species assigned a binary code (0/1) for each life-history category. Subsequently, frequency

analyses were performed to determine the proportion of each life-history type within each plot.

#### 2.4. Environmental Parameters

Sixteen environmental parameters were assessed in each plot, following methodologies comparable to those reported in previous studies [41,64]: (i) Four variables related to aboveground conditions: slope (%) measured with a laser hypsometer (Forestry Pro II, Nikon Corporation, Tokyo, Japan); elevation (m a.s.l.) obtained with a GPS-enabled digital altimeter (GPSMAP 64CSX, Garmin Ltd., Olathe (operations), KS, USA); ambient temperature (°C) and precipitation (mm year<sup>-1</sup>), both extracted from the WorldClim dataset [65]. (ii) Twelve soil physicochemical properties: penetration resistance (MPa) measured in situ using a 3 m hand penetrometer (Eijkelkamp Soil & Water, Giesbeek, Gelderland, The Netherlands); texture (sand, clay, and silt) (%) determined via direct analysis/Bouyoucos method [66]; bulk density (g cm<sup>-3</sup>) using an Eijkelkamp hand auger; soil moisture (%) via saturation paste/gravitational method (USDA S.L.) [66]; pH measured by saturation paste/conductometric method (USDA S.L.) [66]; cation exchange capacity (CEC) (meq 100 g<sup>-1</sup>) via NaOH 1 M titration [66]; electrical conductivity (EC) (dS m<sup>-1</sup>) using saturation paste/conductometric method (USDA S.L.) [66]; exchangeable acidity (EA) (mg kg<sup>-1</sup>) via 1N KCl volumetric method (NTC 5263) [67]; soil organic carbon (SOC) (%) determined using the potassium dichromate colorimetric method (NTC 5403, Walkley–Black) [67]; and total nitrogen (N) content via the Kjeldahl method [66]. Five measurements per plot were taken to assess slope and soil physico-chemical properties.

#### 2.5. Data Analysis

To explore functional trait spaces at different ecological levels, three principal component analyses (PCAs) were performed as follows: (i) species-level (across all species); (ii) lineage-level (focusing on dominant families); and (iii) community-level. The PCA restricted to the five most dominant families (81 species) was purely descriptive and was not used for statistical inference, but served to illustrate potential functional clustering linked to phylogenetic lineages. The main levels of analysis remain the species and community levels, as consistently stated throughout this study. The functional trait spaces were constructed using the princomp and funspace functions from the stats v. 4.3.3 [68] and funspace v. 0.2.2 [69,70] packages, respectively, in R language version 4.3.3 [71]. PCAs were used to identify the fundamental functional axes [16,25,70]. For the community-level PCA, species abundances were used as weights to calculate community-weighted means (CWMs). These calculations were performed using the dbFD function from the FD v. 1.0-12.3 R package [72]. Prior to PCAs, trait data were log<sub>10</sub>-transformed and scaled to a mean of 0 and a standard deviation of 1. Horn's parallel analysis [73] was used to determine the optimal dimensionality of each PCA [74]. This analysis was carried out with the paran function from the R package paran v. 1.5.3 [73]. Life-history characteristics and environmental factors were subsequently incorporated into the functional trait space as supplementary variables using the envfit function from the R package vegan v. 2.6-10 [75].

Linear mixed-effects models (LMMs) were fitted to assess the effect of chronosequence on functional composition (i.e., PC1 and PC2 scores, and traits of the community-level) using the lme function from the nlme v. 3.1-164 R package [76], implemented through the InfoStat v.2020 interface [77]. Landscape (hill and mountain) was included as a random effect (1 | Landscape). Normality and homoscedasticity were evaluated through exploratory analysis of the models residuals. Variables were transformed using log(score – min(score) + 1) to improve normality. To account for heteroscedasticity across forest age classes, a

variance function (varIdent) [76] was applied. Post hoc comparisons of means across chronosequence were conducted using Fisher's LSD test ( $\alpha = 0.05$ ).

To assess whether trait association patterns were consistent between the species-level and community-level PCAs, we compared the loadings (arrows) of the same set of eight traits in both ordinations. Euclidean distances were computed among traits based on their PCA loadings in each space, resulting in two  $8 \times 8$  distance matrices (traits  $\times$  traits). A Mantel test was then performed using the mantel function from the vegan R package.

To explore the potential drivers of functional axes (i.e., PC1 and PC2), we evaluated the influence of forest age, tree species richness, and environmental factors (i.e., soil properties and aboveground conditions). First, a Mantel test was applied to assess the correlation between trait-based functional distances and environmental dissimilarity matrices, using the mantel\_test function from the LinkET v. 0.0.7.4 R package [78]. Second, LMMs were fitted using the lmer function from the lme4 v. 1.1-35.2 [79] and lmerTest v. 3.1-3 [80] R packages to evaluate how these potential drivers influenced the functional axes. Landscape was again included as a random effect. To evaluate multicollinearity among predictors, variance inflation factor (VIF) analysis was conducted using the vif function from the car v. 3.1-2 R package [81]. After removing collinear variables, the resulting full models for PC1 and PC2 were used in a model averaging procedure to identify the best combination of predictors explaining variation in functional axes. Model selection was based on all possible combinations of the predictors using the dredge, subset, and model.avg functions in the MuMIn v. 1.48.4 R package [82], following a maximum likelihood approach and ranked according to the Akaike Information Criterion ( $\Delta AIC \leq 2$ ) [38,74]. Finally, structural equation models (SEMs) were used to examine the direct and indirect effects of these potential drivers on the community-level functional axes (PC1 and PC2). The best SEMs were selected based on the chi-square test ( $\chi^2$ ), degrees of freedom (df), Comparative Fit Index (CFI), Tucker–Lewis Index (TLI), Root Mean Square Error of Approximation (RMSEA), and Standardized Root Mean Square Residual (SRMR). SEMs were performed using the sem and semPaths functions from the lavaan v. 0.6-19 [83] and semPlot v. 1.1.6 [84] R packages, respectively. All statistical analyses in R were conducted using the RStudio v.2025.05.0 interface [85].

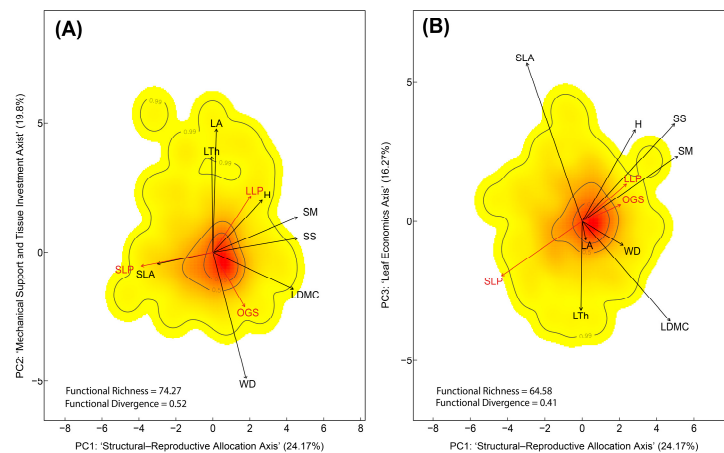
### 3. Results

#### 3.1. Plant Functional Trait Space at Species Level

To address the first research question—regarding the species-level functional trait space in secondary forests regenerating after cattle ranching abandonment—we conducted two PCAs, each preceded by Horn's parallel analysis to determine the number of components to retain: one based on all 226 species (Figure 2; Supplementary Figures S2 and S3) and another on a subset of 81 species from the five most representative families (i.e., Fabaceae, Melastomataceae, Burseraceae, Lauraceae, and Moraceae) (Supplementary Figures S4–S7).

In both cases, Horn's parallel analysis retained the first three principal components (PCs) (Supplementary Figures S2 and S4). Life-history strategies (SLP, LLP, OGS) were included as supplementary variables in the PCAs to aid interpretation of the functional gradients. In the first PCA (Figure 2), PC1 explained 24.17% of the total variance (Supplementary Table S2) and was interpreted as the Structural–Reproductive Allocation Axis, as it reflects coordinated variation in plant height (H), seed mass (SM), and seed size (SS)—traits associated with structural development and reproductive investment (Table 1). This axis was primarily associated with SLP (72 species) (Supplementary Table S3). Species such as *Albizia pedicellaris* (DC.) L.Rico, *Croton lechleri* Müll. Arg., and *Miconia aurea* (D. Don) Naudin—representatives of SLP—were positioned at the lower end of PC1, characterized by high SLA and low values of H, SS, and SM, reflecting acquisitive resource-use strategies.

In contrast, LLP and OGS, including *Astrocaryum chambira* Burret, *Pouteria campanulata* Baehni, and *Licania heteromorpha* Benth., were located at the upper end of PC1, exhibiting high values of H, SM, and SS, and low SLA, indicating a strategy focused on long-term persistence and reproductive investment.



**Figure 2.** Functional trait space of 226 tree species in regenerating Amazonian forests following livestock abandonment. **(A)** Trait space defined by the PC1–PC2 plane. PC1 (eigenvalue = 1.64) represents the Structural–Reproductive Allocation Axis (H, SS, SM). PC2 (eigenvalue = 1.40) captures the Mechanical Support and Tissue Investment Axis (WD, LA, LTh). PC1 was strongly associated with SLP species (negatively), whereas PC2 was linked to LLP and OGS (positively and negatively, respectively). **(B)** Trait space defined by the PC1–PC3 plane. PC3 (eigenvalue = 1.20), represents the Leaf Economics Axis (SLA, LDMC), and was mainly associated with SLP species (negatively). Colors indicate the probability density of functional trait combinations in multivariate space (red = high probability; yellow = low), while contour lines represent the 0.99, 0.50, and 0.25 quantiles of that distribution. Functional Richness (FRic) and Functional Divergence (FDiv) indices are shown, representing the volume of trait space occupied and the dispersion of species within that space, respectively. Life-history strategies are depicted in brown: Old-Growth Species (OGS), Long-Lived Pioneers (LLP), and Short-Lived Pioneers (SLP). Trait vectors are shown in black: Wood Density (WD), Tree Height (H), Leaf Area (LA), Specific Leaf Area (SLA), Leaf Dry Matter Content (LDMC), Leaf Thickness (LTh), Seed Mass (SM), and Seed Size (SS).

**Table 1.** Percentage of variance explained by each trait within each functional trait axis, based on the full-species PC1–PC2 and PC1–PC3 trait spaces.

| Trait | Trait Variation PC1–PC2 = 43.97% |       |                |         | Trait Variation PC1–PC3 = 40.44% |       |                |         | Axis  |
|-------|----------------------------------|-------|----------------|---------|----------------------------------|-------|----------------|---------|-------|
|       | PC1                              | PC2   | R <sup>2</sup> | p-Value | PC1                              | PC3   | R <sup>2</sup> | p-Value |       |
| WD    | 0.091                            | 0.551 | 0.641          | 0.001   | 0.091                            | 0.009 | 0.100          | 0.001   | MSTIA |
| LA    | 0.001                            | 0.538 | 0.539          | 0.001   | 0.001                            | 0.008 | 0.009          | 0.368   | MSTIA |
| SM    | 0.500                            | 0.037 | 0.536          | 0.001   | 0.500                            | 0.071 | 0.570          | 0.001   | SRAA  |
| SS    | 0.496                            | 0.006 | 0.501          | 0.001   | 0.496                            | 0.167 | 0.662          | 0.001   | SRAA  |
| LDMC  | 0.454                            | 0.040 | 0.494          | 0.001   | 0.454                            | 0.176 | 0.630          | 0.001   | LEA   |
| LTh   | 0.000                            | 0.325 | 0.325          | 0.001   | 0.000                            | 0.183 | 0.183          | 0.001   | MSTIA |
| H     | 0.179                            | 0.084 | 0.263          | 0.001   | 0.179                            | 0.162 | 0.341          | 0.001   | SRAA  |
| SLA   | 0.213                            | 0.004 | 0.217          | 0.001   | 0.213                            | 0.526 | 0.739          | 0.001   | LEA   |

Wood Density (WD), Tree Height (H), Leaf Area (LA), Specific Leaf Area (SLA), Leaf Dry Matter Content (LDMC), Leaf Thickness (LTh), Seed Mass (SM), and Seed Size (SS). PC1: Structural–Reproductive Allocation Axis (SRAA), PC2: Mechanical Support and Tissue Investment Axis (MSTIA), PC3: Leaf Economics Axis (LEA). R<sup>2</sup> values indicate the proportion of variance explained by each trait within the functional space, and *p* denotes the level of statistical significance.

PC2 accounted for 19.8% of the variance and was labeled the Mechanical Support and Tissue Investment Axis, defined by wood density (WD), leaf thickness (LTh), and

leaf area (LA). These traits reflect structural toughness and tissue construction costs, and were predominantly associated with LLP (109 species) and OGS (45 species). Species such as *Endlicheria robusta* (A.C.Sm.) Kosterm., *Perebea mollis* (Poepp. & Endl.) Huber, and *Pseudolmedia macrophylla* Trécul—representatives of LLP—as well as *Talisia cerasina* (Benth.) Radlk, *Calliandra surinamensis* Benth., and *Licania harlingii* Prance, typical of OGS, were positioned at the lower end of PC2, characterized by high WD and low values of LA and LTh. PC3 captured 16.27% of the variance and was interpreted as the Leaf Economics Axis, corresponding to the globally recognized Leaf Economic Spectrum (LES). This axis distinguishes acquisitive species with high specific leaf area (SLA) from conservative species with high leaf dry matter content (LDMC), reflecting trade-offs between rapid resource acquisition and structural durability.

Functional richness (FRich) and functional divergence (FDiv) were higher in the PC1–PC2 trait space (FRich = 74.27%, FDiv = 0.52) (Figure 2A) than in the PC1–PC3 space (FRich = 64.58%, FDiv = 0.41) (Figure 2B). FRich and FDiv were also calculated for each life history within the global trait space (Supplementary Figure S3). Thus, LLP and SLP exhibited higher FRic and FDiv values in both trait spaces compared to OGS. This pattern indicated that pioneer species exhibited more varied and divergent functional strategies than those typical of OGS.

In the second PCA (Supplementary Figure S5), the relative contribution of traits to the first three PCs shifted compared to the full-species PCA. PC1 (eigenvalue = 1.61) explained 26.33% of the total variance (Supplementary Table S4) and was primarily defined by SM and SS, representing the Structural–Reproductive Allocation Axis (Supplementary Table S5), consistent with the full-species PCA. This axis contrasted SLP with LLP and OGS (Supplementary Table S6). In this case, PC2 (eigenvalue = 1.42) accounted for 21.56% of the variance and grouped traits related to the Leaf Economic Axis, with acquisitive species showing higher SLA and lower LDMC, WD, and LTh values. Finally, PC3 (eigenvalue = 1.22) explained 16.27% of the variance and captured traits associated with the Mechanical Support and Tissue Investment Axis, particularly in OGS, which exhibited higher values of WD and LDMC.

FRich was greater in the trait space defined by PC1 and PC2, with a value of 63.35, compared to 55.20 in the PC1–PC3 space. Conversely, FDiv was slightly lower in the PC1–PC2 space (0.51) than in PC1–PC3 (0.58). These results suggest that greater functional richness—but somewhat lower trait dispersion—is expressed along the PC1–PC2 axes, primarily reflecting the wide range of strategies associated with LLP. Conversely, the higher FDiv observed in the PC1–PC3 plane may reflect the greater structural trait differentiation typical of OGS (Supplementary Figure S6).

When examining the functional space for each family in the PC1–PC2 plane, the families with the highest functional richness and divergence (FRich; FDiv) were as follows: Melastomataceae (36.63; 0.48), Fabaceae (32.97; 0.43), Moraceae (32.77; 0.43), Lauraceae (25.39; 0.38), and Burseraceae (25.60; 0.50). Traits most strongly associated with PC1 in this plane were SM and SS. In contrast, in the PC1–PC3 plane, the families with the highest functional contributions were Fabaceae (36.43; 0.47), Moraceae (34.17; 0.44), Burseraceae (29.47; 0.57), Melastomataceae (22.20; 0.43), and Lauraceae (22.02; 0.37). In this space, the traits most strongly associated with PC1 were LA and LTh, and with PC3 were SLA and LDMC (Supplementary Figure S7). While informative, these family-level PCAs were not used to define the main functional axes, which are based on the global species-level PCA and form the foundation for all subsequent interpretations.

### 3.2. Plant Functional Trait Space at Community-Level

In response to question two—whether community-level functional trait space resemble those observed at the species level—we first identified the functional trait axes at the community level observed in secondary forests regenerating after livestock abandonment. Then, we compared the similarity between the two functional spaces by correlating their pairwise distance matrices.

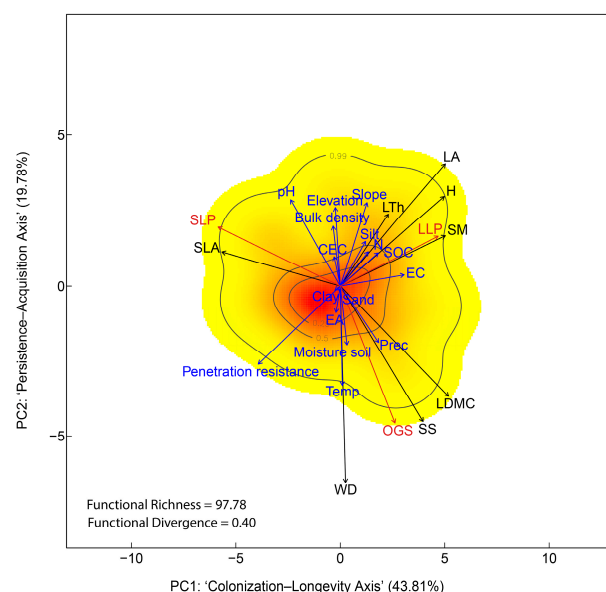
To identify community-level functional trait space, a third PCA was performed on the CWMs values of eight traits from 33 plant communities distributed along the chronosequence. Additionally, 16 environmental variables and three life-history strategies were included as supplementary variables (Figure 3 and Table 2). In this case, Horn's parallel analysis retained only the first two principal components (Supplementary Figure S8). PC1 (eigenvalue = 2.69; 43.81% of the variance) represented the Colonization–Longevity Axis (Supplementary Table S7), contrasting SLP with LLP (Supplementary Table S8). Communities dominated by SLP (negative PC1 axis), with species such as *A. pedicellaris*, *Henriettea fascicularis* (Sw.) M. Gómez and *Jacaranda copaia* (Aubl.) D. Don, were identified in secondary forests less than 10 years old and were characterized with highly acquisitive traits (e.g., high SLA, rapid colonization). In contrast, LLP-dominated communities (positive PC1 axis), with species such as *A. chambira*, *Astrocaryum cuatrecasianum* Dugand, and *P. campanulata*, were identified in secondary forests ranging from 10 to 40 years old and were associated with structurally persistent traits, such as greater height and heavier seeds (Table 2). Thus, SLP communities reflect acquisitive colonization strategies, whereas LLP assemblages are defined by competitive and persistent trait investment. PC2 (eigenvalue = 1.10; 19.78% of the variance) represented the Persistence–Acquisition Axis, separating OGS from both pioneer types (SLP and LLP). OGS, with species such as *Compsoeura capitellata* (Poepp. ex A. DC.) Warb., *T. cerasina*, *C. surinamensis*, *L. harlingii*, *Hymenaea oblongifolia* Huber, *Dialium guianense* (Aubl.) Sandwith, and *Cedrela odorata* L., identified in mature forests, were associated with traits linked to structural persistence and conservative resource use (e.g., high WD, SS and LDMC), consistent with their dominance in stable, late-successional forest environments.

Regarding the environmental variables projected into global functional space, stronger associations were found with PC1 for penetration resistance, SOC, and N. In contrast, ambient temperature, pH, bulk density, and EA were primarily associated with PC2 (Supplementary Table S8).

When exploring the successional categories projected into the global trait space defined by the PCA (Supplementary Figure S9), the greatest FRich was observed in OF (FRich = 71.33) and in secondary forests aged 10–20 years (FRich = 68.41), while the lowest FRich was found in the youngest forests (<10 years; FRich = 58.5). This trend paralleled tree species richness patterns, which mean values generally decreased from OF to early-successional forests: 22.40 species (OF), 20.17 (31–40 years), 12.67 (10–20 years), 9.67 (21–30 years), and 10.1 species (<10 years). These observations suggest that, despite selective logging interventions, old-growth fragments retain a structurally and functionally richer composition compared to early-successional forests. In this context, significant changes were observed in PC1 and PC2 scores along the chronosequence (Figure 4 and Supplementary Table S9).

Early-stage secondary forests (<10 and 10–20 years), with pioneer colonizing species, exhibited higher SLA values associated with negative scores on the PC1 axis (i.e., the colonization–longevity axis). Conversely, forests dominated by long-lived pioneer species (>20 years) and old-growth species showed higher values for traits such as H, LA, LTh, and SM, and were associated with positive scores of PC1 (Figures 4A and S10; Supplementary Table S10). Meanwhile, traits such as WD, LDMC, and SS, associated

with the negative end of PC2 (i.e., the persistence–acquisition axis), were more prevalent in OF which are dominated by persistent species. In contrast, acquisitive traits linked to the positive end of PC2 were characteristic of pioneer species in secondary forests (Figures 4B and S10; Supplementary Table S10).

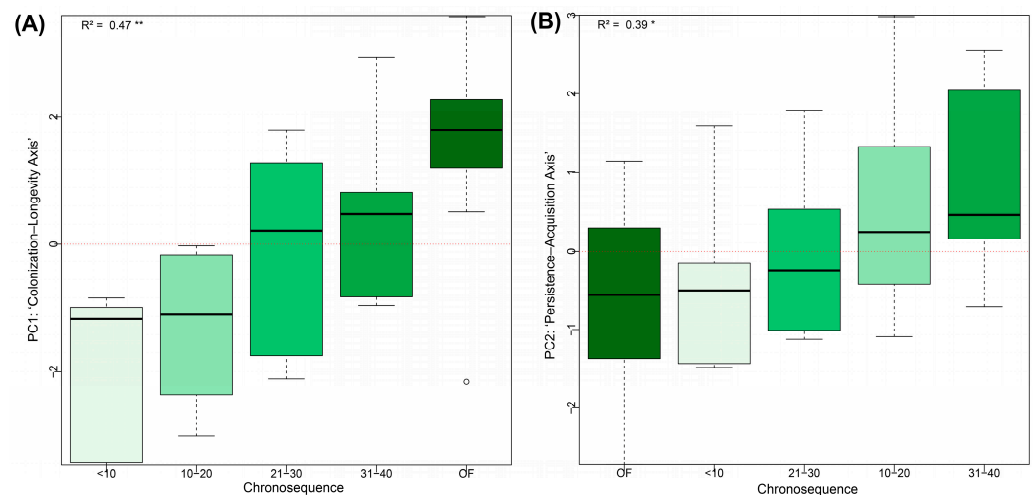


**Figure 3.** Trait space based on the community-weighted means of eight traits from 33 tree communities in regenerating Amazonian forests following livestock abandonment. Trait space defined by PC1 and PC2 (eigenvalues = 2.69 and 1.10, respectively). PC1 represents the Colonization–Longevity Axis, contrasting SLP species—with fast-acquisition traits such as high SLA—with LLP species characterized by taller stature and larger, heavier seeds. PC2 reflects the Persistence–Acquisition Axis, separating OGS from both pioneer types based on conservative structural traits such as WD and LDMC. Colors indicate the probability density of functional trait combinations in multivariate space (red = high probability; yellow = low), while contour lines represent the 0.99, 0.50, and 0.25 quantiles of that distribution. Functional Richness (FRic) and Functional Divergence (FDiv) indices are shown. Life-history strategies are depicted in brown: Old-Growth Species (OGS), Long-Lived Pioneers (LLP), and Short-Lived Pioneers (SLP). Environmental factors displayed in blue: elevation, ambient temperature (Temp), precipitation (Prec), penetration resistance, texture (sand, clay, and silt), bulk density, soil moisture, pH, cation exchange capacity (CEC), electrical conductivity (EC), exchangeable acidity (EA), soil organic carbon (SOC), total nitrogen (N). Trait vectors are shown in black: Wood Density (WD), Tree Height (H), Leaf Area (LA), Specific Leaf Area (SLA), Leaf Dry Matter Content (LDMC), Leaf Thickness (LTh), Seed Mass (SM), and Seed Size (SS).

**Table 2.** Percentage of variance explained by the community-weighted mean (CWM) of each trait within each functional trait axis, based on community-level PC1–PC2 trait space.

| Trait | PC1   | PC2   | R <sup>2</sup> | p-Value | Axis |
|-------|-------|-------|----------------|---------|------|
| WD    | 0.003 | 0.816 | 0.819          | 0.001   | PAA  |
| LA    | 0.615 | 0.179 | 0.794          | 0.001   | CLA  |
| LDMC  | 0.191 | 0.578 | 0.769          | 0.001   | PAA  |
| SS    | 0.067 | 0.621 | 0.688          | 0.001   | PAA  |
| H     | 0.551 | 0.087 | 0.639          | 0.001   | CLA  |
| SLA   | 0.625 | 0.011 | 0.636          | 0.001   | CLA  |
| SM    | 0.509 | 0.025 | 0.534          | 0.001   | CLA  |
| LTh   | 0.141 | 0.067 | 0.208          | 0.027   | CLA  |

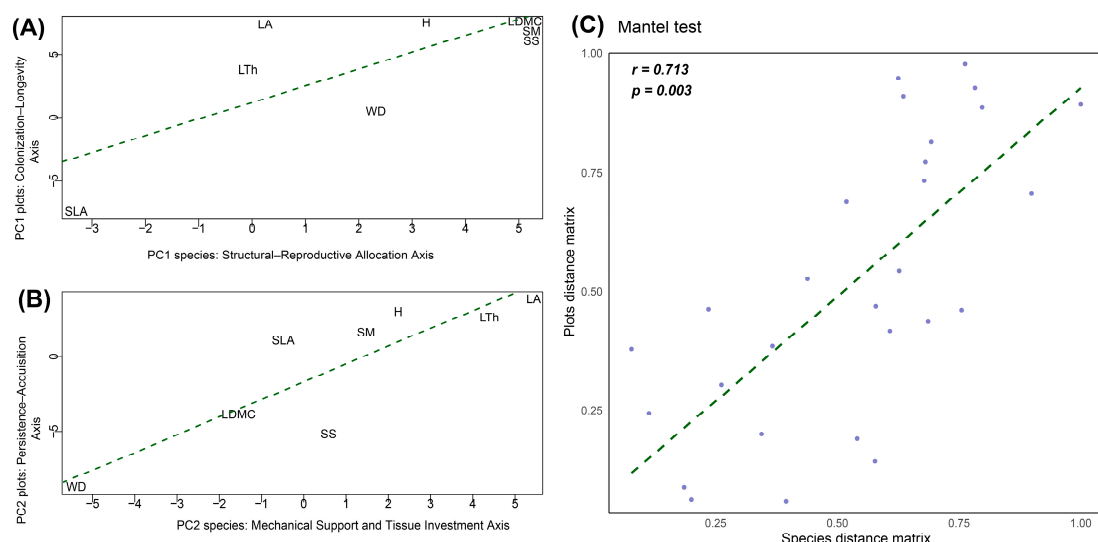
Wood Density (WD), Tree Height (H), Leaf Area (LA), Specific Leaf Area (SLA), Leaf Dry Matter Content (LDMC), Leaf Thickness (LTh), Seed Mass (SM), and Seed Size (SS). PC1: Colonization–Longevity Axis (CLA), PC2: Persistence–Acquisition Axis (PAA). R<sup>2</sup> values indicate the proportion of variance explained by the CWM of each trait within the functional space, and *p* denotes the level of statistical significance.



**Figure 4.** Changes in functional axes scores (PC1 and PC2) along a natural regeneration chronosequence following livestock abandonment. (A) Plot-level PC1 scores representing the Colonization–Longevity Axis. (B) Plot-level PC2 scores representing the Persistence–Acquisition Axis.  $^{**} p < 0.01$ ;  $^* p < 0.05$ .

### 3.3. Correspondence Between Plant Functional Trait Space at Species and Community Levels

To evaluate the similarity of trait association patterns between the species-level and community-level PCAs (question two), a Mantel test was conducted (Figure 5). PC1 scores for species and plots were significantly similar ( $R^2 = 0.51$ ,  $p = 0.028$ ) (Figure 5A), and very similar for PC2 scores ( $R^2 = 0.73$ ,  $p = 0.004$ ) (Figure 5B). The Mantel correlation coefficient revealed a significant association between trait distance matrices at the species level and the community-weighted means (CWM) at the plot level ( $r = 0.713$ ,  $p = 0.003$ ) (Figure 5C). This pattern of correspondence was mainly explained by similar PC1 and PC2 scores across species and community-level trait spaces. These results suggest that functional axes derived from species-level traits are consistently reflected at the community level supporting the validity of trait-based monitoring across organizational scales.

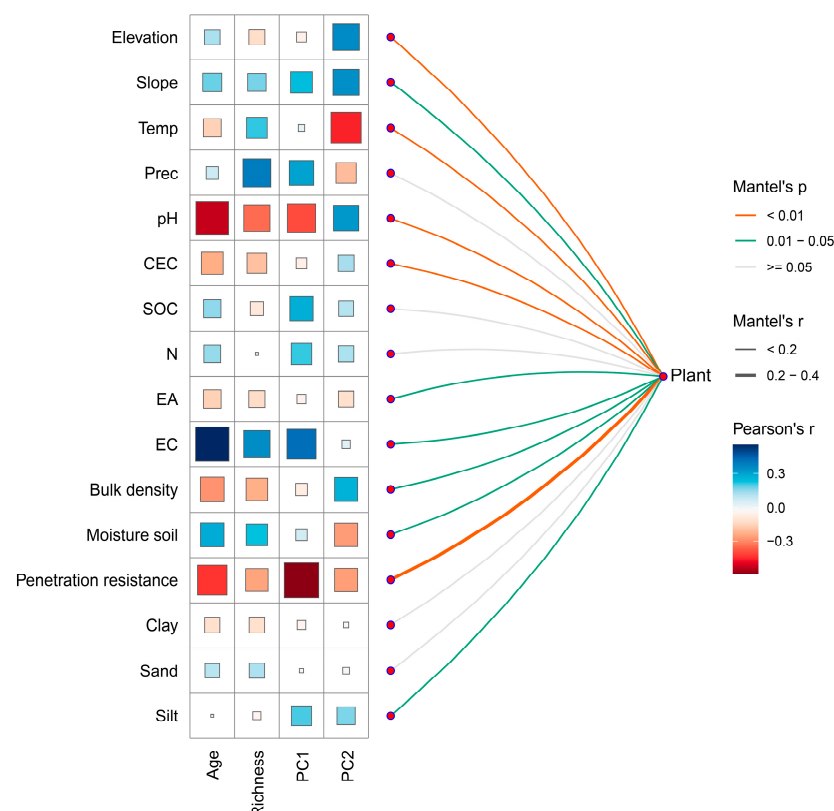


**Figure 5.** Correspondence between species-level and community-level functional trait spaces. (A) Comparison between species-level PC1 scores and plot-level PC1 scores ( $R^2 = 0.51$ ,  $p < 0.05$ ). (B) Comparison between species-level PC2 scores and plot-level PC2 scores ( $R^2 = 0.73$ ,  $p < 0.01$ ). (C) Mantel test between distance matrices of species-level and plot-level functional trait spaces ( $r = 0.71$ ,  $p < 0.01$ ). Wood Density (WD), Tree Height (H), Leaf Area (LA), Specific Leaf Area (SLA), Leaf Dry Matter Content (LDMC), Leaf Thickness (LTh), Seed Mass (SM), and Seed Size (SS).

### 3.4. Relationships Between Environmental Factors, Forest Age, Richness, and Functional Trait Space

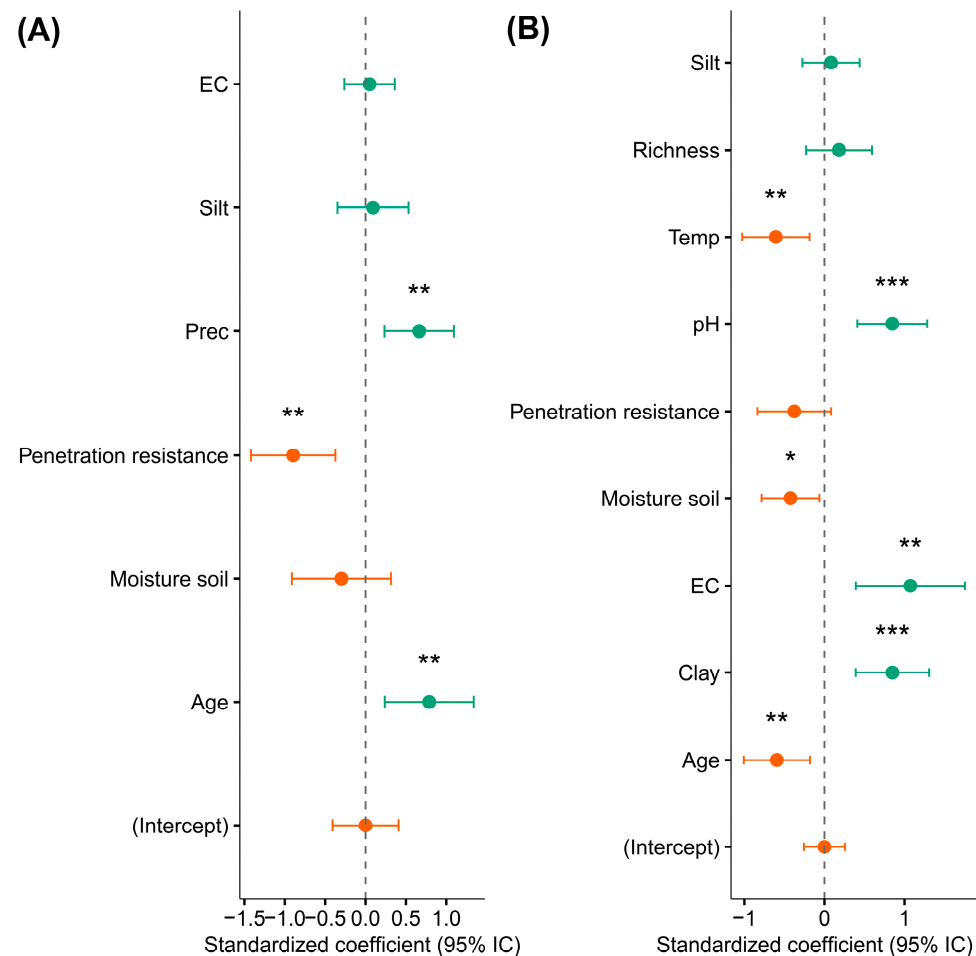
To address question three—regarding the relationships between environmental factors, successional stage, and community functional trait space—we analyzed the degree of association, dependency relationships, and the structured direct and indirect effects among variables.

The Mantel test revealed significant correlations ( $p < 0.05$ ) between community composition (based on Bray–Curtis dissimilarity) and 11 environmental variables (Figure 6; Supplementary Table S11). The strongest correlations to Mantel's  $r$  were found for penetration resistance ( $r = 0.23$ ), pH ( $r = 0.19$ ), ambient temperature ( $r = 0.17$ ), CEC ( $r = 0.15$ ), and elevation ( $r = 0.14$ ) (all,  $p < 0.01$ ). These variables also showed stronger Pearson correlations with the community-level functional trait axes (PC1 and PC2). EC and elevation were positively and significantly correlated with PC1 ( $r = 0.42$ ,  $p < 0.05$ ) and PC2 ( $r = 0.36$ ,  $p < 0.05$ ), respectively. In contrast, penetration resistance and pH were negatively and significantly correlated with PC1 ( $r = -0.59$ ,  $p < 0.001$  and  $r = -0.40$ ,  $p < 0.05$ , respectively), while ambient temperature was negatively correlated with PC2 ( $r = -0.45$ ,  $p < 0.01$ ). Strong correlations were also observed between precipitation, CEC, and pH with tree species richness, and between EC, pH, and penetration resistance with forest age. These results suggest that both abiotic conditions and community-level properties—including forest age, tree species richness, and functional axes (PC1 and PC2)—are linked to variations in species composition across sites.



**Figure 6.** Mantel tests between community composition (based on species abundances) and 16 environmental factors, and Pearson correlations between community-level functional trait axes (PC1: Colonization–Longevity Axis; PC2: Persistence–Acquisition Axis), forest age (Age), and tree species richness (Richness) with environmental variables. Edge thickness represents the strength of the Mantel correlation ( $r$ ), while color indicates the level of statistical significance. For Pearson correlations, both the size and color of the squares indicate the strength and direction of the bivariate association, respectively. Environmental factor acronyms are defined in Figure 3.

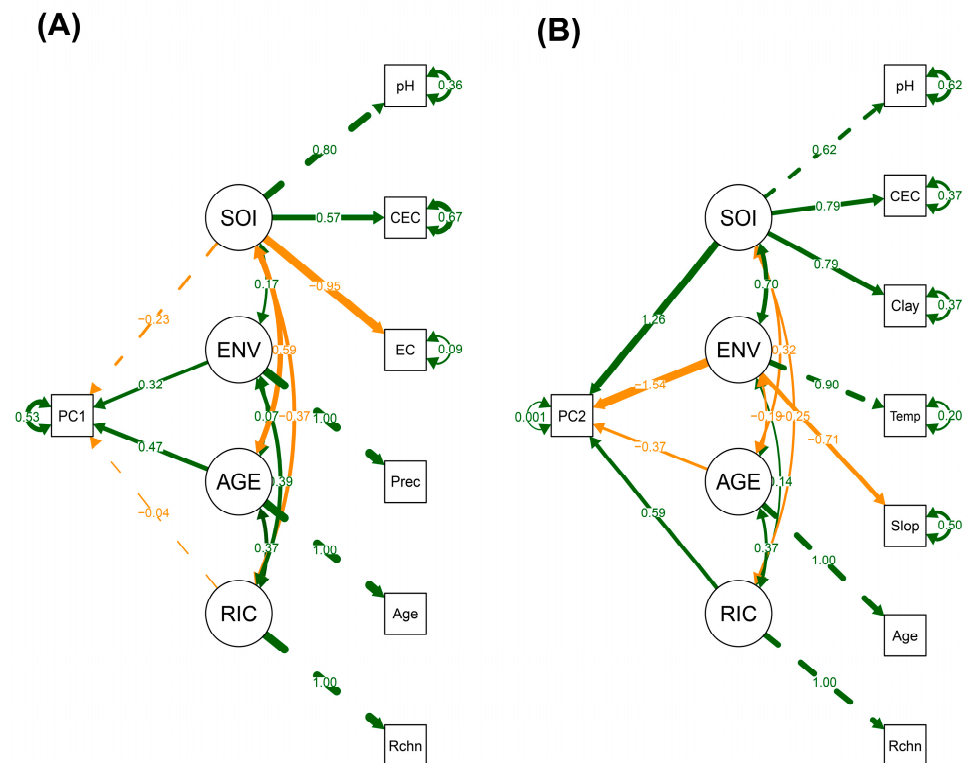
We used LMMs to evaluate the dependency of community-level functional trait axes (PC1 and PC2) on environmental variables, forest age, and tree species richness. The results showed a significant positive effect of forest age and precipitation on PC1, whereas penetration resistance had a significant negative effect (Figure 7A; Supplementary Table S12). In contrast, PC2 was positively and significantly influenced by pH, EC, and clay content, and negatively influenced by forest age, ambient temperature, and soil moisture (Figure 7B; Supplementary Table S13). Our results indicated that EC, silt, and soil moisture did not significantly affect PC1, while variables such as silt, tree species richness, and penetration resistance had no significant impact on PC2.



**Figure 7.** Model-averaged parameters for different predictors of community-level functional axes scores (PC1 and PC2) ( $n = 33$  plots). **(A)** PC1: Colonization–Longevity Axis. **(B)** PC2: Persistence–Acquisition Axis. Green dots represent positive coefficients, while orange dots indicate negative coefficients. Asterisks above each dot denote statistically significant coefficients (\*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ ). Dots without asterisks indicate non-significant coefficients ( $p > 0.05$ ). Vertical dashed lines represent the mean threshold location, and horizontal error bars show 95% confidence intervals. Environmental factor acronyms as defined in Figure 3.

Finally, we implemented two separate SEMs to examine how environmental factors and structural and compositional attributes of the community influenced the two main axes of functional trait space (i.e., PC1 and PC2) (Figure 8; Supplementary Tables S14 and S15). Each model included four latent variables: soil properties (SOI), aboveground conditions (ENV), forest age (AGE), and tree species richness (RIC). Both models showed good fit to the data (PC1 model:  $\chi^2 = 4.99$ ,  $df = 8$ ,  $p = 0.76$ ; CFI = 1.00; TLI = 1.10; RMSEA = 0.00;

SRMR = 0.05; PC2 model:  $\chi^2 = 21.68$ ,  $df = 13$ ,  $p = 0.06$ ; CFI = 0.91; TLI = 0.80; RMSEA = 0.14; SRMR = 0.11).



**Figure 8.** Structural equation models (SEMs) illustrating the relationships between functional trait axes (PC1, PC2), forest age, tree species richness, and environmental factors. (A) PC1: Colonization–Longevity Axis as a function of soil properties (SOI: pH, CEC, EC), aboveground conditions (ENV: Prec), forest age (AGE: Age), and species richness (RIC: Rchn). (B) PC2: Persistence–Acquisition Axis as a function of SOI (pH, CEC, clay), ENV (temp and slope), AGE, and RIC. Arrow thickness and color indicate the strength and direction of the relationship, respectively—green for positive and orange for negative associations. Solid arrows indicate statistically significant paths ( $p < 0.05$ ), while dashed arrows represent either fixed loadings (set to 1.0) or non-significant paths ( $p > 0.05$ ). Environmental factor acronyms are defined in Figure 3.

In the PC1 model (Figure 8A; Supplementary Table S14), functional strategies were positively influenced by AGE ( $\beta = 0.47$ ,  $p = 0.00$ ) and ENV ( $\beta = 0.32$ ,  $p = 0.04$ ). Notably, ENV was defined exclusively by precipitation, indicating the importance of rainfall in shaping the functional variation captured by PC1. In addition, SOI was negatively and significantly associated with AGE (covariance =  $-0.59$ ,  $p = 0.01$ ), whereas RIC-mediated positive covariation with both AGE (covariance =  $0.37$ ,  $p = 0.04$ ) and ENV (covariance =  $0.39$ ,  $p = 0.04$ ). These results indicate that soil variables such as pH, CEC, and EC declined with forest age, while tree species richness increased throughout succession and with higher precipitation levels.

In the PC2 model (Figure 8B; Supplementary Table S15), functional strategies were significantly impacted by all latent predictors as follows: positively by SOI ( $\beta = 1.26$ ,  $p = 0.04$ ) and RIC ( $\beta = 0.59$ ,  $p = 0.04$ ), and negatively by ENV ( $\beta = -1.54$ ,  $p = 0.01$ ) and AGE ( $\beta = -0.37$ ,  $p = 0.04$ ). The positive effect of SOI on PC2 underscores the key role of soil properties—such as pH, CEC and clay content—in shaping the functional strategies represented along this axis. In contrast, the negative effect of ENV on PC2 emphasizes the joint influence of temperature and slope, with the direction of their contributions reflected in the composition of the ENV latent variable (i.e., positive loading for temperature and negative loading for slope). Among the covariances, only the relationships between AGE

and RIC (covariance = 0.37,  $p = 0.01$ ), and between SOI and ENV (covariance = 0.70,  $p = 0.02$ ), were statistically significant.

## 4. Discussion

### 4.1. Species-Level Functional Trait Space Reflect Life-History Trade-Offs

The organization of functional trait space at the species level revealed three orthogonal axes that capture key ecological trade-offs in plant strategies: the Structural–Reproductive Allocation Axis (SRAA), the Mechanical Support and Tissue Investment Axis (MSTIA); and the Leaf Economics Axis (LEA). These axes are consistent with theoretical expectations of multidimensional trait organization in tropical forests [16,23,25], listed as follows: (i) the SRAA shaped by investment in size and dispersal capacity; (ii) the MSTIA reflected here in woodiness and toughness traits (i.e., stem mechanical or economic spectrum); and (iii) the LEA related to resource acquisition and conservation. Their separation confirms that trait variation in tropical trees is structured along independent yet ecologically coherent gradients.

The SRAA, defined by plant height, seed mass, and seed size, captures the classical trade-off between colonization potential and structural persistence. It differentiates SLP species characterized by rapid growth and small seeds, from LLP and OGS which invest more in stature and reproductive output. This axis reflects how reproductive allocation covaries with competitive dominance and longevity—an ecological pattern well documented in tropical secondary succession [10,62,63].

The MSTIA, shaped by traits such as wood density, leaf thickness, and leaf area, reflects investment in anatomical robustness and mechanical resistance. These traits contribute to stress tolerance and tissue durability, and their prominence among LLP and OGS highlights the increasing relevance of conservative structural strategies in resource-limited or competitive environments [15,21,86].

The LEA describes variation in resource-use strategies, contrasting acquisitive species—marked by high SLA, fast photosynthesis, and short leaf lifespan—with conservative species that exhibit high LDMC, slow growth, and long tissue turnover. Its strong expression among SLP species aligns with global trait coordination patterns related to light capture, nutrient cycling, and rapid regeneration [15,16,18].

From a life-history perspective, the clustering of species into distinct regions of trait space according to their classification as SLP, LLP, or OGS reinforces the ecological validity of this framework. SLP species occupy the acquisitive end of both the SRAA and LEA, while LLP and OGS express higher wood density and seed investment—traits associated with persistence and later successional dominance. This supports the idea that life-history categories reflect multidimensional trait syndromes shaped by ecological filtering [17,21,87].

The high values of FRich and FDiv observed in the SRAA  $\times$  MSTIA space (PC1–PC2) suggest that these forests harbor a broad spectrum of trait combinations. This dispersion implies strong potential for niche differentiation, which may enhance species coexistence and functional resilience through trait complementarity [22,26]. Interestingly, this functional heterogeneity was highest among LLP species, suggesting that mid-successional assemblages play a central role in maintaining trait diversity and facilitating regeneration.

The consistent emergence of the SRAA across both the complete species set and subsets of dominant families underscores the generality of these patterns across taxonomic groups. Some families, such as Fabaceae and Melastomataceae, exhibited particularly broad functional occupation, consistent with their ecological versatility and structural dominance in Neotropical forests [10,12].

From a restoration perspective, identifying these functional strategies has direct implications. First, it supports selecting species not only by taxonomic identity but also by their

ecological roles and positions in trait space. Second, it highlights that early-successional assemblages dominated by SLP species may be insufficient to meet long-term restoration goals related to biomass recovery, carbon storage, or structural resilience. Therefore, restoration planning in deforested Amazonian landscapes should integrate functionally diverse species pools, ensuring the inclusion of LLP and OGS strategies to promote successional transitions and enhance ecosystem resilience.

We acknowledge that PCA generates orthogonal axes that maximize trait variance, which may not fully represent distinct ecological processes. Therefore, while the identified functional spectra provide useful summaries of trait covariation, they should be interpreted as statistical approximations of biological strategy gradients rather than definitive axes of ecological function.

#### 4.2. Community-Level Functional Trait Space Mirrors Species-Level Patterns

At the community level, trait space followed clear successional trajectories, structured primarily along two functional axes: the Colonization–Longevity Axis (CLA) and the Persistence–Acquisition Axis (PAA). These axes captured changes in the dominance of life-history strategies (SLP, LLP, OGS) and were shaped by both species' traits and environmental filters.

The CLA (PC1) differentiated communities dominated by SLP species—with acquisitive traits such as high SLA and small seeds—from those dominated by LLP, characterized by increased investment in height, wood density, and seed mass. This shift reflects the replacement of fast-growing, opportunistic species by structurally persistent types as succession progresses, in line with findings across Neotropical forests [10,12,63].

Functional convergence along this axis was most evident in forests dominated by LLP. In these communities, high values of FRich and FDiv suggest the co-occurrence of multiple strategies—particularly those combining structural investment with moderate acquisitive capacity. This trait complementarity may contribute to both forest persistence and resilience under variable environmental conditions.

The PAA (PC2) further separated OGS from pioneer types, based on traits such as wood density, LDMC, and seed size. These traits were more frequent in plots with stable environmental conditions, lower temperature, and higher clay content—typical of later successional stages. This pattern underscores the role of edaphic conditions in promoting the establishment of species with conservative, persistence-oriented strategies [16,21].

Importantly, both axes showed strong associations with life-history strategies: SLP communities occupied the acquisitive end of both axes, while OGS and LLP communities were increasingly dominant in later stages. FRich and FDiv peaked in mid- to late-successional plots, suggesting higher trait dispersion and niche complementarity in more structurally complex forests. This supports the hypothesis that functional diversity increases with successional age, potentially enhancing ecosystem resilience and multifunctionality [26,30,88].

Our results also indicate that community-level trait space mirror the aggregation of species-level strategies but are further shaped by local environmental conditions. The strong correlation between forest age and the abundance of conservative traits suggests that successional time acts as a primary ecological filter, but that soil properties and microclimate modulate the rate and direction of functional recovery [21,89].

From a restoration perspective, these findings reinforce the value of monitoring community-weighted means of key traits (e.g., SLA, WD, seed size) to assess functional recovery over time. They also highlight the importance of promoting functionally diverse assemblages that include LLP and OGS to accelerate the convergence toward mature forest structure and function.

The strong correspondence observed between species- and community-level functional space confirms that patterns of trait variation scale coherently from individuals to entire assemblages. The significant Mantel correlation between species trait distances and community-weighted means indicates that community-level functional composition largely reflects the aggregated expression of species-level strategies, shaped by life-history attributes and filtered by succession.

This alignment was particularly evident along the two principal functional axes. The SRAA (PC1) at both levels revealed similar gradients from acquisitive SLP species to long-lived species with greater investment in reproduction and structural dominance (LLP, OGS). Similarly, the MSTIA (PC2) captured increasing investment in tissue density and leaf construction across both organizational levels. The close correspondence between PC1 and PC2 scores at both scales demonstrates that trait-based signals are maintained through community assembly, supporting the use of community-weighted trait means as proxies for functional structure [21,25,90].

These findings reinforce the concept that species-level strategies are not decoupled from community-level dynamics but instead shape and constrain the trajectory of forest regeneration. They also validate the ecological relevance of the life-history classification (SLP–LLP–OGS), which consistently explains trait aggregation patterns across scales. Such consistency suggests that the main drivers of trait expression—successional time, environmental conditions, and ecological trade-offs—operate similarly at both levels [16,17].

From a methodological perspective, this cross-scale congruence provides a robust foundation for monitoring and restoration. Trait-based indicators measured at the species level can inform the expected functional composition of communities, and vice versa. This is particularly relevant in highly diverse systems where full community-level trait sampling is logistically challenging. Relying on species-level trait data can provide reliable inferences about the functional state of regenerating forests.

Overall, these results support the integration of hierarchical trait-based approaches in tropical forest ecology, where species traits inform community function, and community-weighted strategies reflect the cumulative outcome of ecological filtering and successional processes.

#### *4.3. Community Functional Trait Space Driven by Environmental Factors, Forest Age, and Species Richness*

The functional trait space in regenerating communities is shaped by complex interactions among successional stage, environmental filters, and species richness. Our results show that forest age exerts a dominant influence on functional trait space, particularly along the CLA (PC1), where older plots are increasingly dominated by species with greater structural and reproductive investment (LLP and OGS). This trajectory is facilitated by declining soil compaction (i.e., penetration resistance), suggesting that the physical recovery of soils enhances the transition from acquisitive to conservative trait strategies.

The PAA (PC2), by contrast, was more strongly influenced by soil chemistry, texture, and microclimatic conditions. Traits associated with structural persistence (e.g., high WD, LDMC, SS) were more frequent in plots with higher clay content, lower pH, and lower temperatures, reflecting the importance of edaphic stability in supporting conservative strategies [16,21].

Consistent with the well-established understanding that Amazonian soils are inherently nutrient-poor, our SEM results revealed a negative covariance between forest age and soil fertility (SOI)—particularly variables such as pH and CEC. This pattern suggests that, even as vegetation structure recovers during succession, soil chemical properties may remain low or even decline, likely due to nutrient depletion, leaching, and legacy effects of prior land use. Such a decoupling between vegetation recovery and soil chemical

improvement is therefore not unexpected in this context, but it reinforces the importance of considering active soil management (e.g., organic amendments, erosion control) to enhance restoration outcomes in degraded Amazonian landscapes.

Tree species richness also played a mediating role. SEMs showed that richness increased with forest age and precipitation, and positively influenced PC2, suggesting that more diverse communities support a broader array of structurally persistent strategies. This supports the insurance hypothesis, where biodiversity buffers against environmental variability and promotes long-term functional stability [26,91].

Moreover, environmental variables had both direct and indirect effects on functional composition. For instance, precipitation enhanced PC1 scores, while temperature and slope negatively influenced PC2. Soil variables influenced both axes, either directly or via interactions with forest age and species richness. These patterns underscore the need to view community assembly as the outcome of interacting abiotic and biotic processes, rather than unidirectional succession.

From a restoration perspective, these findings call for context-aware interventions. Functional recovery depends not only on successional time but also on the specific combination of soil quality, climatic constraints, and species pool composition. Monitoring and improving belowground conditions should be considered essential components of long-term restoration strategies, especially in chronically degraded or compacted sites.

From a restoration planning perspective, our results support the intentional design of functionally diverse species pools that reflect target ecosystem functions and are temporally aligned with successional dynamics. This includes not only early colonizers (e.g., *A. pedicellaris*, *H. fascicularis*, *J. copaia*), but also long-lived pioneers (e.g., *A. chambira*, *A. cuatrecasasianum*, *P. campanulata*) and old-growth species (e.g., *C. capitellata*, *T. cerasina*, *C. surinamensis*, *L. harlingii*, *H. oblongifolia*, *D. guianense*, *Cedrela odorata*) that contribute to carbon storage, canopy complexity, and ecological and disturbance resilience.

While the inclusion of slow-growing, shade-tolerant species in early restoration stages has been widely debated due to their poor establishment in open, high-light environments [92,93], our results offer a refined strategy: targeting mid-successional forests as transitional platforms for enrichment planting. These forests harbor higher functional richness and structural complexity, creating microclimatic and ecological conditions more suitable for the successful integration of late-successional species. This approach is consistent with trait-based and successional frameworks that advocate for a temporal layering of species introduction [49,94].

By strategically enriching functionally diverse species at appropriate stages of forest regeneration, practitioners can enhance ecosystem function and resilience while avoiding the high mortality rates commonly observed when introducing late-successional species too early. This trait-informed approach can serve as a practical guide for designing adaptive restoration interventions that align with successional filters and improve long-term outcomes in regenerating Amazonian landscapes.

## 5. Conclusions

This study provides a multiscale functional analysis of regenerating Amazonian forests, demonstrating that plant communities assemble along consistent trait-based spaces that reflect ecological trade-offs, life-history strategies, and environmental filtering. At the species level, three dominant functional axes—Structural–Reproductive Allocation Axis, Mechanical Support and Tissue Investment Axis, and the Leaf Economics Axis—capture key dimensions of plant ecological strategies in tropical systems. These functional trait axes aligned closely with life-history types (SLP, LLP, OGS), confirming their relevance for interpreting successional processes and guiding ecological restoration.

At the community level, trait composition followed predictable trajectories along the successional gradient, mirroring species-level patterns. Early-stage assemblages were dominated by acquisitive, short-lived pioneer species, while older plots were increasingly composed of long-lived pioneers and old-growth species exhibiting structurally conservative traits—consistent with the Colonization–Longevity Axis and the Persistence–Acquisition Axis. Functional richness and divergence peaked in mid- to late-successional stages, highlighting the critical role of intermediate forests dominated by long-lived pioneers as functional bridges that support both biodiversity accumulation and structural transition toward mature forest conditions.

The observed congruence between species- and community-level trait spaces supports the use of community-weighted means as indicators of functional assembly and ecosystem recovery. These metrics retain ecological signal across scales and offer a practical tool for monitoring restoration outcomes, especially in data-limited contexts.

Crucially, our findings reveal that functional recovery is not determined by forest age alone, but results from the interplay of successional processes, tree species richness, and environmental filtering. Soil compaction, nutrient availability, texture, and climatic factors (e.g., precipitation, temperature, slope) significantly influenced trait expression across the landscape.

These insights emphasize the importance of matching species' functional traits to site-specific environmental conditions, particularly in relation to soil physical and chemical properties and local microclimate. Restoration outcomes can be enhanced by selecting species adapted to the constraints and opportunities of each site, rather than relying on generalized successional expectations. This trait–environment matching is especially relevant in degraded Amazonian landscapes, where edaphic legacies can hinder functional convergence. Such trait–environment matching represents a critical principle in designing context-aware restoration strategies in degraded Amazonian landscapes.

**Supplementary Materials:** The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/d17080570/s1>. Figure S1: Successional categories of the 33 study plots in the northwestern Colombian Amazon; Figure S2: Horn's parallel analysis based on a simulated dataset with 5000 permutations using mean eight functional trait values of 226 tree species in regenerating Amazonian forests; Figure S3: Functional trait space of three life-history strategies projected onto the global trait space defined by a PCA based on all 226 tree species in regenerating Amazonian forests; Figure S4: Horn's parallel analysis based on a simulated dataset with 5000 permutations using mean eight functional trait values of 81 tree species from the five most representative families in regenerating Amazonian forests; Figure S5: Functional trait space of 81 tree species from the five most representative families in regenerating Amazonian forests following livestock abandonment; Figure S6: Functional trait space of three life-history strategies projected onto the global trait space defined by a PCA based on 81 tree species from the five most representative families in regenerating Amazonian forests; Figure S7: Functional trait space of the five most representative families projected onto the global trait space defined by a PCA based on 81 tree species in regenerating Amazonian forests; Figure S8: Horn's parallel analysis based on a simulated dataset with 5000 permutations using the community-weighted means of eight traits from 33 tree communities in regenerating Amazonian forests following livestock abandonment; Figure S9: Functional trait space of five successional categories projected onto the global trait space defined by a PCA based on the community-weighted means of eight traits from 33 tree communities in regenerating Amazonian forests; Figure S10: Changes in functional traits along a natural regeneration chronosequence following livestock abandonment. Table S1: Importance Value Index (IVI) and its components for tree species across successional age classes; Table S2: Summary of the principal component analysis (PCA) applied to eight functional traits of 226 tree species in regenerating Amazonian forests following livestock abandonment; Table S3: Loadings and ex-

plained variance of three life-history strategies for 226 species in the functional space defined by the first three principal components of the PCA; Table S4: Summary of the principal component analysis (PCA) applied to eight functional traits of 81 tree species belonging to the five most representative families in regenerating Amazonian forests following livestock abandonment; Table S5: Percentage of variance explained by each trait within each functional trait space, based on the PC1–PC2 and PC1–PC3 trait spaces constructed from a subset of 81 tree species belonging to the five most representative families; Table S6: Loadings and explained variance of three life-history strategies for 81 species belonging to the five most representative families in the functional space defined by the first three principal components of the PCA; Table S7: Summary of the principal component analysis (PCA) applied to the community-weighted mean (CWM) of eight traits of 33 plots in regenerating Amazonian forests following livestock abandonment; Table S8: Loadings and explained variance of 16 environmental factors and three life-history strategies for 33 tree communities in the functional space defined by the first two principal components of the PCA; Table S9: Adjusted means and standard errors of PC1 and PC2 scores across different successional categories, derived from linear mixed-effects model analysis; Table S10: Adjusted means and standard errors of the community-weighted means (CWM) of eight traits across different successional categories, derived from linear mixed-effects model analysis; Table S11: Pearson correlation coefficients among environmental variables, forest age, tree species richness, and functional space scores (PC1 and PC2); Table S12: Summary of the estimated coefficients from the selected averaged model for PC1: Colonization-longevity Axis (CLA). \*\*\*  $p < 0.01$ ; \*\*  $p < 0.01$ ; \*  $p < 0.05$ ; Table S13: Summary of the estimated coefficients from the selected averaged model for PC2: Persistence-acquisition Axis (PAA).: \*\*\*  $p < 0.001$ ; \*\*  $p < 0.01$ ; \*  $p < 0.05$ ; Table S14: Details of structural equation model in PC1; Table S15: Details of structural equation model in PC2.

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