Journal of Environmental Management 414 (2026) 130508

Contents lists available at ScienceDirect

Journal of Environmental Management

journal homepage: www.elsevier.com/locate/jenvman

Research article

Carbon stocks in riparian forests in the Amazonia-Cerrado transition over 15 years: Effects of restoration methods and edaphoclimatic factors

Silvia Barbosa Rodrigues [a,g,*], Marina Guimarães Freitas [b], Lorrayne Aparecida Gonçalves [c], Tamilis Rocha [d], Lara Aranha da Costa [e], Eduardo Malta Campos-Filho [e], Icaro Abreu Sousa [a], Raphael Matias [f], Pedro Pereira Santos [g], Daniel Luis Mascia Vieira [g]

[a] University of Brasília, Institute of Biological Sciences, Graduate Program in Ecology, Brasília, DF, 70910-900, Brazil
[b] Rio de Janeiro Botanical Garden Research Institute, National School of Tropical Botany, Professional Graduate Program in Biodiversity in Conservation Units, Rio de Janeiro, RJ, 22460-036, Brazil
[c] Federal Rural University of Amazonia, Graduate Program in Forest Science, Belém, PA, 66077-830, Brazil
[d] Brazilian Institute of Environment and Renewable Natural Resources, Brasília, DF, 70818-900, Brazil
[e] Instituto Socioambiental, São Paulo, SP, 01046-912, Brazil
[f] Federal University of Jataí, Institute of Biosciences, Jataí, GO, 75801-615, Brazil
[g] Embrapa Recursos Genéticos e Biotecnologia, Brasília, DF, 70770-917, Brazil

ARTICLE INFO

Keywords:
Aboveground biomass
Chronosequence
Direct seeding
Evergreen seasonal forest
Plant community trajectory
Restoration costs
Soil organic carbon

ABSTRACT

Ecological restoration is critical to counteract land degradation and mitigate climate change. Tropical forest restoration offers major carbon sequestration potential due to rapid biomass accumulation and high storage capacity. However, the long-term carbon sequestration efficacy of different methods remains poorly understood in large-scale restoration projects. We investigated the recovery of aboveground biomass (AGB) and soil organic carbon (SOC) over a 15-year chronosequence in the Amazonia-Cerrado transition, comparing direct seeding techniques (broadcast, holes and rows) against seedling planting and natural regeneration. Using linear mixed-effects models, we assessed how restoration age and edaphoclimatic variables influenced these carbon pools. Our results show that AGB accumulation was primarily driven by the restoration age and soil fertility, with row-seeding significantly outperforming other seeding techniques and seedling plantations. This success was linked to the mechanical precision of row-seeding, which favored longer-lived pioneer species with specific seed traits. In contrast, SOC stocks remained stable across the chronosequence and were controlled by edaphoclimatic factors rather than restoration methods, underscoring the decoupling of aboveground biomass accumulation from belowground carbon dynamics. We conclude that direct seeding is a highly cost-effective method for carbon-focused restoration, but the specific technique and soil fertility significantly influenced the outcome. To maximize sequestration at scale, future efforts should prioritize soil amelioration, seeding precision, and species selection.

1. Introduction

Urgent measures are needed to mitigate climate change and unprecedented global biodiversity loss (Barnosky et al., 2011; Bustamante et al., 2023). Ecological restoration is a key strategy for reversing land degradation, conserving biodiversity, and mitigating climate change (Bustamante et al., 2023; Heinrich et al., 2021, 2023; Poorter et al., 2016). Tropical forest restoration has a major potential for global carbon sequestration due to rapid biomass accumulation during early succession stages and the high carbon storage capacity of mature forests (Bernal et al., 2018). This potential is amplified by the vast extent of degraded tropical lands available for restoration (Houghton et al., 2015; Mo et al., 2023). Furthermore, these ecosystems encompass key areas for biodiversity conservation, making restoration in tropical regions essential to address the extensive loss of natural habitats (Strassburg et al., 2020).

* Corresponding author. University of Brasília, Institute of Biological Sciences, Graduate Program in Ecology, Brasília, DF, 70910-900, Brazil.
E-mail address: silviarodrigues.eco@gmail.com (S.B. Rodrigues).

https://doi.org/10.1016/j.jenvman.2026.130508
Received 30 October 2025; Received in revised form 20 February 2026; Accepted 15 July 2026
Available online 19 July 2026

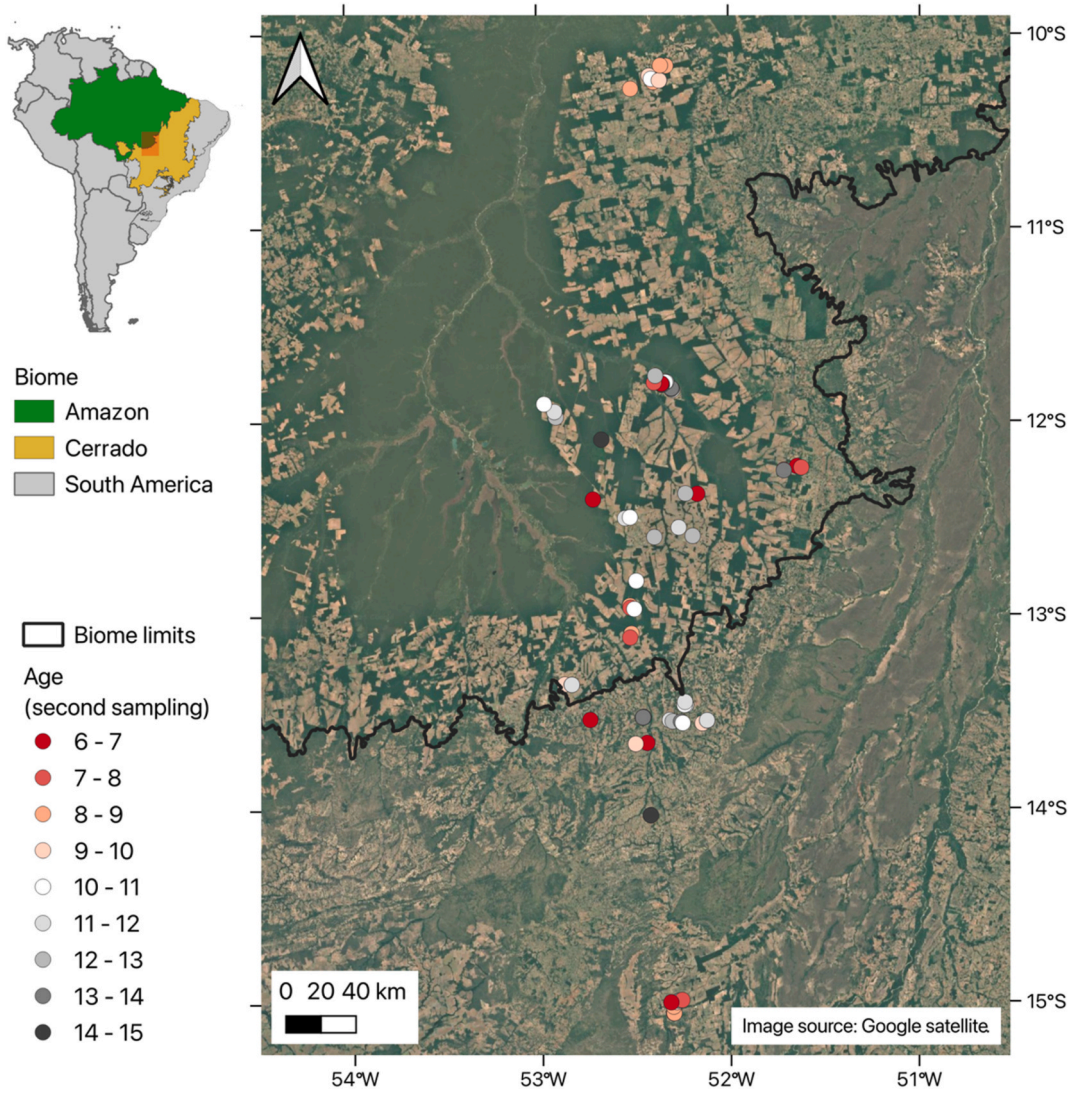

Fig. 1. Location of the 75 riparian forest restoration sites in the Amazonia–Cerrado transition, Mato Grosso, Brazil. Dot's colors represent the age of restoration sites at the second sampling event (in 2022), Base layer: Google Satellite imagery.

Carbon accumulation in restored tropical forests is highly variable and context-dependent, shaped by edaphoclimatic factors and land-use legacies (Giles et al., 2024; Heinrich et al., 2021; Jakovac et al., 2021, 2024; Poorter et al., 2016). Aboveground biomass recovery varies 11-fold across the Neotropics following 20 years of succession (Poorter et al., 2016). This discrepancy highlights a strong link between water availability and carbon sequestration, with higher accumulation rates found in humid forests. This variability is also evident regionally within the Amazon basin, where western secondary forests (<20 years) sequester carbon at rates more than 1.5 times faster than those in the east (Heinrich et al., 2021). Radiation and soil chemical composition emerge as key drivers of this regional divergence (Heinrich et al., 2021). Beyond environmental constraints, land-use history also negatively affects recovery rates; intensive or prolonged prior land-use slows the biomass accumulation by limiting species colonization, establishment, and performance (Jakovac et al., 2021).

The restoration method also strongly influences ecosystem recovery trajectories, shaping vegetation structure and species composition beyond the second decade of recovery (Schubert et al., 2025). The effectiveness of tropical forest restoration methods also varies depending across contexts (Brancalion et al., 2025; Holl and Aide, 2011). For instance, natural regeneration is effective only when local and landscape resilience are present (Giles et al., 2024; Holl and Aide, 2011). Forest growth rates differ significantly, not only between different restoration methods, but also within the same method (Brancalion et al., 2025). In the context of restoration focused on carbon sequestration, quantifying rates and identifying their determinants is critical. Particularly for active restoration projects, identifying cost-effective methods (quantified in USD tCO_2^{-1}) is a priority (Austin et al., 2020; Busch et al., 2024).

Although the aboveground biomass accumulation in the Amazon secondary forests is well studied, few studies have investigated actively restored forests (Elias et al., 2025; Gardon et al., 2020). Among active restoration methods, seedling planting is most widely implemented in the Amazon, while direct seeding is gaining increasing acceptance (da Cruz et al., 2021; Gardon et al., 2020; Guerra et al., 2020). Emerging evidence indicates that direct seeding can be a cost-effective method (Raupp et al., 2020), but its long-term viability remains under investigation. Direct seeding is applicable at a large scale (Antoniazzi et al., 2021; Campos-Filho et al., 2013; Freitas et al., 2019a) and adaptable to diverse socio-environmental contexts. It serves a wide range of factors, including technical experts and smallholder farmers (Campos-Filho et al., 2013; Urzedo et al., 2016), and fosters socioeconomic development by stimulating high demand for native seeds (Urzedo et al., 2016, 2020, 2022).

Direct seeding establishes a high initial density of recruits and undergoes rapid changes in species composition throughout the restoration

process (Freitas et al., 2019a; Rodrigues et al., 2019). Low-resilience areas restored through direct seeding attained carbon accumulation rates in the first decade equivalent to those of naturally regenerating high resilience sites (Freitas et al., 2019a). While this highlights the potential of direct seeding to catalyze forest recovery under suboptimal conditions, substantial variability in aboveground biomass accumulation was observed across sites (Freitas et al., 2019a), likely influenced by edaphoclimatic factors, community composition, and unmeasured local constraints. This underscores the need for site-specific strategies and further investigation of the ecological filters that shape restoration outcomes under direct seeding approaches.

The specific seed delivery technique is a primary determinant of restoration costs (Vieira et al., 2020), and may further influence early vegetation dynamics and long-term carbon outcomes. While operational choices are typically dictated by terrain and equipment availability (Shaw et al., 2020), different seeding techniques offer distinct trade-offs. Broadcast-seeding is recommended for flat terrain with easy mechanization; allowing flexibility in both machinery and labour input, though it generally requires a larger quantity of seeds (Shaw et al., 2020; Vieira et al., 2020). In contrast, row-seeding is suitable where specific machinery is available, while hole-seeding is recommended for steep, stump-laden, or seasonally wet areas (Campos-Filho et al., 2013; Vieira et al., 2020). Both row- and hole-seeding offer greater control over sowing depth and enable reduced seed input, yet they may favor colonization by unwanted species while simultaneously facilitating maintenance practices like weed control (Campos-Filho et al., 2013; Vieira et al., 2020).

The objective of this study was to assess the potential of direct seeding for tropical forest restoration, with a focus on carbon accumulation. We analyzed aboveground biomass (AGB) and soil organic carbon (SOC) stocks across a 15-year chronosequence of forests restored via direct seeding (three techniques), natural regeneration, and seedling plantations under varying edaphoclimatic conditions. We also evaluated the cost-effectiveness of the three direct seeding techniques (USD tCO_2^{-1}). Specifically, we addressed the following questions: (i) Do edaphoclimatic conditions determine AGB and SOC stocks over time? (ii) Does direct seeding provide similar carbon stocks compared to natural regeneration and seedling plantation? and (iii) What is the cost-effectiveness of the different direct seeding techniques applied?

2. Materials and methods

2.1. Study area

We studied 75 riparian forest sites distributed along a 500 km latitudinal gradient in Mato Grosso, central Brazil (Fig. 1). The study area is located within the Amazonia-Cerrado transition zone, comprising 48 sites in the Amazon biome and 27 in the Cerrado. Annual precipitation ranges from 1382 mm in the south to 2000 mm in the north (Abatzoglou et al., 2018), with 70% of rainfall concentrated between December and March, followed by a four-month dry season (Ivanauskas et al., 2008). The terrain is flat with prevalence of Red-Yellow Latosol (Ivanauskas et al., 2008). All sites were originally evergreen seasonal riparian forests (IBGE, 2012) before being cleared for agricultural use.

Located within the "arc of deforestation", the region has experienced extensive agricultural expansion since the 1960s. Deforestation and change in the land-use have been driven by the region's flat terrain and deep soils, which are highly suitable for commodity agriculture (Morton et al., 2006). Until 2021, the region was among of the most deforested landscapes of the Amazon (MapBiomas, 2021), remaining only 18% of forest cover on average (Freitas et al., 2019a). Historically cleared for land use, the riparian forests of the region are legally protected and mandated for restoration under the Brazilian Native Vegetation Protection Law (Brasil, 2012), creating significant demand for ecological restoration. Prior to restoration, all sites shared a similar land-use history, having been converted to extensive cattle pasture. In a few cases, sites were briefly used for commodity agriculture. Since 2006, the Instituto Socioambiental (ISA) has partnered with local landowners to restore these riparian forests (Campos-Filho et al., 2013), where our study sites are located.

2.2. Restoration methods

We evaluated riparian forest sites restored between 2006 and 2015. Each site was restored using one of the three distinct methods: natural regeneration (n = 5), seedling planting (n = 4), or one of the three direct seeding techniques: broadcast (n = 45), hole-seeding (n = 11), or row-seeding (n = 10). Direct seeding consisted of sowing 20-40 seeds m^{-2} of 40-60 native tree species representing different successional phases. Green manure species, such as *Crotalaria spectabilis* Roth, *Canavalia ensiformis* (L.) DC and *Cajanus cajan* (L.) Millsp., were also included to provide initial ground cover and improve soil conditions. While the specific species composition and seed densities for each individual site were not recorded, the general list of seeded species is provided in Table S1. Species composition varied slightly between sites and years based on seed production and availability, richness remained consistent across the chronosequence (Rodrigues et al., 2019). In broadcast-seeding sites, seeds were spread over plowed soil using a spreader; in row-seeding, seeds were sown in 50 cm-spaced rows using grain drills; and in hole-seeding, seeds were manually placed in 1 × 1 m spaced holes. Direct seeding techniques are described in detail in Campos-Filho et al. (2013), Freitas et al. (2019a), and Vieira et al. (2020).

In seedling planting sites, nursery seedlings were planted at a 3 × 2 m spacing. The planted species were selected based on functional composition, with half of the individuals consisting of fast-growing species to promote rapid canopy closure, while the remaining half comprised non-pioneer species to support long-term diversity (Campos-Filho et al., 2013). Because these sites were established as part of a large-scale, community-driven restoration program rather than a controlled scientific experiment, a standardized species list for the seedling plantings method was not maintained. In natural regeneration sites, forest recovery was allowed to occur in areas with high regeneration expression by installing fences for cattle exclusion (Freitas et al., 2019a).

2.3. Forest inventories

We conducted vegetation sampling at 75 restoration sites in 2017 and resampled the same sites in 2022, both in the latter part of the rainy season. At the first inventory, site ages ranged from 1 to 10 years, reaching 6 to 15 years by the second inventory. The sampled restored riparian forests were approximately 30 m wide, as required by Brazilian law for small rivers (Brasil, 2012), with individual site sizes ranging from 0.5 to 50.0 ha.

In each site, we established one permanent 50 × 10 m (500 m^2) plot to measure height (H) and diameter at breast height (DBH, measured at 1.30 m above the ground) of all trees with DBH ≥10 cm. Within a nested 50 × 2 m subplot, we measured the H and DBH of all saplings (H ≥ 1.30 m; DBH <10 cm). Subplots were established along the centerline of the main plot. Plots were established in 2017 parallel to the nearby watercourse and centered within the 30 m wide restoration area. All sampled trees were tagged and numbered in 2017, and recruits meeting the size criteria were also tagged in 2022. Tree species were identified in the field or through herbarium specimens at Embrapa Genetic Resources and Biotechnology (CEN).

We estimated AGB for trees and saplings with DBH ≥5 cm, following standard size criteria for tropical forests (Chave et al., 2014; Giles et al., 2024; Poorter et al., 2016). For each individual tree, AGB was calculated using the allometric equation from Chave et al. (2014):

$$AGB = 0.0673 \times \left(WD \times H \times D^2\right)^{0.976}$$

where *AGB* is the aboveground biomass (kg), *WD* is the wood density (g·cm^{-3}), *H* is the tree height (m), and D is the diameter at breast height (cm).

This equation was selected because it incorporates wood density and was developed using an extensive database that includes secondary tropical forests (Chave et al., 2014). Species-specific wood densities were obtained from Neotropical databases (Chave et al., 2009; Zanne et al., 2009).

To obtain the total AGB at the plot level, we first summed the individual AGB of all trees within the main plot (500 m^2) and all saplings within the nested subplot (100 m^2). We normalized the values to a per-hectare basis (kg ha^{-1}) by applying the respective expansion factors for each plot size. These values were then combined and converted to Mg ha^{-1} to represent the total AGB for each site.

2.4. Soil sampling

Soil samples were collected to a 0 – 20 cm depth from all plots in 2017 (three points composite sample per plot) and 2022 (a single composite sample per plot). The initial use of multiple composite samples per plot in 2017 was intended to account for potential high heterogeneity in the early stages of restoration. By 2022, a single representative composite sample was collected per plot. This shift in sampling intensity is supported by the relative stability of soil physical properties in these Latosols (Ferreira Júnior et al., 2021; Santos et al., 2025). In both years, samples were analyzed at the same laboratory for soil organic matter, content of carbon, nutrients (P, K, Ca, Mg, Fe and Al), pH, base saturation, and texture. In 2022, undisturbed soil samples (volume: 100 cm^3) were also collected to determine bulk density (g cm^{-3}). Samples were dried at 100°C for >48 h and weighed. Because bulk density was not measured in 2017, the 2022 values were used for both campaigns, a common practice given that soil structure is assumed to be relatively stable over the monitoring interval. For each plot and campaign, SOC (Mg C ha^{-1}) was calculated as:

$$SOC = \frac{C \times bd \times sd}{10}$$

where *C* is the organic carbon concentration (%), *bd* is the bulk density (g cm^{-3}) and *sd* is the soil depth (20 cm).

2.5. Climate data

To establish a direct link between forest AGB and SOC with climatic conditions, we sourced multiple climatic variables from the *TerraClimate* dataset (Abatzoglou et al., 2018). For the specific period since establishment of each restoration site, we extracted: (i) accumulated annual precipitation (AP); (ii) the annual climatic water deficit (CWD), an indicator of drought stress calculated as the difference between potential and actual evapotranspiration; and (iii) the Palmer Drought Severity Index (PDSI), a metric that reflects the severity of drought conditions. All three variables were obtained in the Google Earth Engine platform (Gorelick et al., 2017), extracting *TerraClimate* data (~4 km resolution) at each plot centroid.

The analysis was custom-made for each site, covering the period from its specific year of planting (ranging from 2006 to 2015) to the year of sampling (2017 or 2022). To better align with regional growing seasons, we defined an 'agricultural year' as the 12-month period from October to September. Using the agricultural year, we first computed annual values for AP and CWD (cumulative sum) and PDSI (average). These annual values were then averaged across the site's age.

2.6. Statistical analysis and modeling

2.6.1. Biomass and soil carbon modeling

To investigate the AGB and SOC trajectories across the 15-year chronosequence, we fitted separate linear mixed-effects models (LMMs), starting with global models followed by a model selection procedure. We combined the chronosequence approach with repeated measures from permanent plots to construct a continuous growth trajectory. Models were performed using the *lmer* function from the 'lme4' package (Bates et al., 2003), with plot ID included as random factor to account for the dependency between the 2017 and 2022 sampling events at each location. To meet the assumptions of normality and homoscedasticity, AGB was square-root transformed and SOC was log-transformed prior to model fitting. The AGB model was based on 70 sites with non-zero biomass, while the SOC model included all 75 sites.

For each response variable, we constructed a global model that included age, restoration methods (three direct seeding techniques, natural regeneration and seedling planting), soil properties and climate variables as fixed factors. We also included two-way interactions between age and all other fixed factors in the global model. To mitigate multicollinearity in global models, we excluded highly correlated variables ($r > 0.80$) from soil and climatic datasets (Table 1). Final climatic predictors included AP, CWD, and PDSI. Final soil predictors included cation exchange capacity (CEC), base saturation, P, K, organic matter, and clay, chosen as key factors for fertility and nutrient availability (Poorter et al., 2016; Townsend et al., 2008). Organic matter was excluded from the SOC model to avoid circularity.

Model selection was based on global models using the *dredge* function from the 'MuMIn' package (Bartoń, 2010), which evaluates all possible combinations of predictor variables from the global model. Models were ranked based on their corrected Akaike Information Criterion (AICc) and Akaike weight. Models with AICc < 2 were considered the most plausible and the top-ranked model was selected for

Table 1
Independent edaphoclimatic variables and time since interventions of the 75 riparian forest restoration sites in the Amazonia–Cerrado transition, Mato Grosso, Brazil. Values represent the mean and range (minimum – maximum) of variables measured across both 2017 and 2022 sampling campaigns.

	Direct seeding			Seedling planting (n = 4)	Natural regeneration (n = 5)
	Broadcast (n = 45)	Holes (n = 11)	Rows (n = 10)		
Age (years)	7 (2 – 14)	10 (2 – 15)	9 (5 – 13)	10 (7 – 14)	10 (4 – 14)
Base saturation (%)	21.4 (4.1 – 63)	17.1 (5.1 – 61.6)	30.1 (6 – 58.3)	17.4 (6.5 – 28.2)	19 (6.2 – 44.3)
Cation exchange capacity (cmolc dm^{-3})	5.4 (2.7 – 13.7)	5.4 (2.9 – 9.9)	5.9 (3.1 – 8.6)	5.7 (4.8 – 6.4)	6.5 (3.9 – 11.5)
Clay (%)	32 (13 – 63)	37 (19 – 55)	41 (21 – 64)	39 (28 – 50)	42 (26 – 57)
Magnesium (Mg cmolc dm^{-3})	0.4 (0.1 - 2)	0.3 (0.1 – 2.3)	0.6 (0.1- 1.8)	0.4 (0.1 – 0.7)	0.4 (0.1 – 0.7)
Potassium (K cmolc dm^{-3})	0.1 (0.02 – 0.28)	0.1 (0.02 – 0.23)	0.1 (0.02 – 0.51)	0.1 (0.02 – 0.22)	0.1 (0.04 – 0.22)
Organic matter (%)	2.2 (1.1 – 6.3)	2.1 (1 – 3.7)	2.5 (1.3 – 6.1)	2.5 (1.9 - 3)	2.8 (1.9 – 5.4)
Annual climatic water deficit (mm y^{-1})	397 (279 – 491)	394 (264 – 480)	382 (272 – 468)	414 (388 – 441)	404 (321 – 464)
Cumulative rainfall (mm y^{-1})	1628 (1383 – 2000)	1610 (1439 – 1801)	1627 (1476 – 1789)	1564 (1509 – 1627)	1650 (1508 – 1922)
PDSI	−0.17 (−0.74 to −0.01)	−0.14 (−0.61 – 0.02)	−0.14 (−0.65 – 0.02)	−0.08 (−0.15 – 0)	−0.10 (−0.23 – 0)

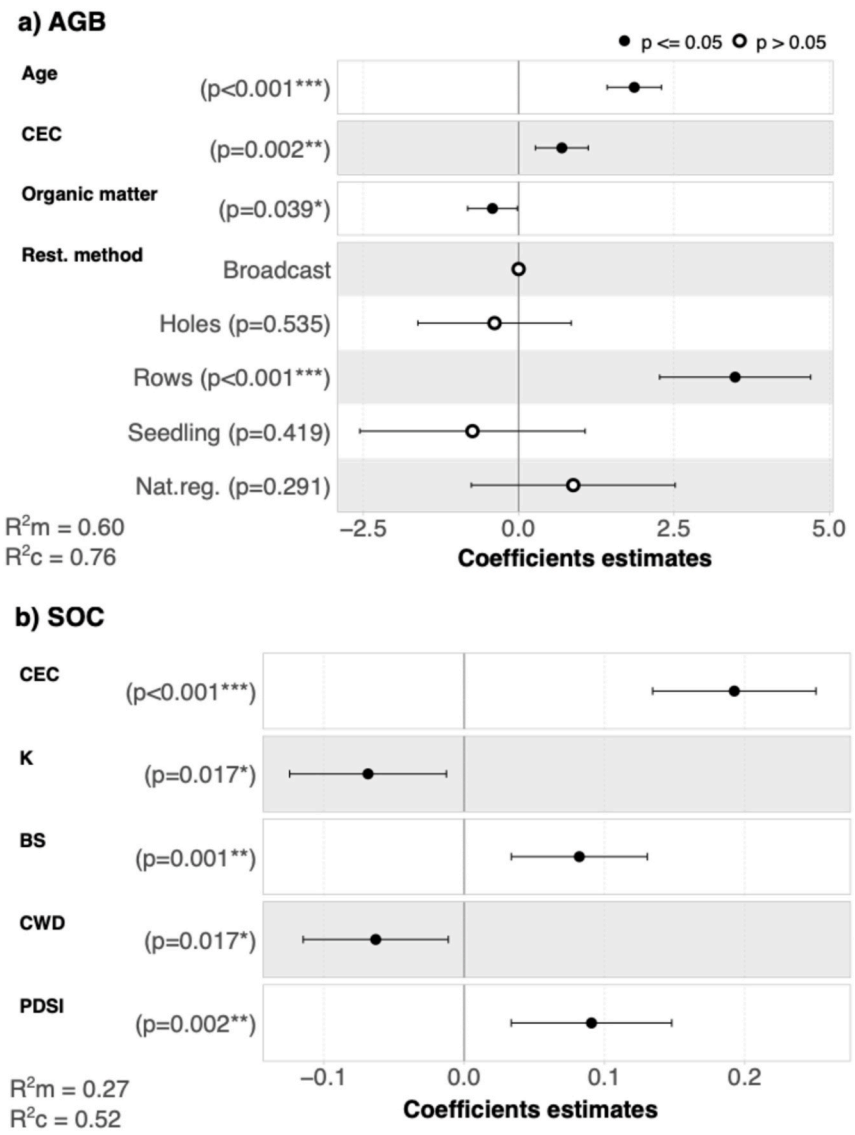

Fig. 2. Standardized coefficient estimates of the fixed effects from the best linear mixed-effects model for (a) aboveground biomass in 70 riparian forest restoration sites (AGB) and (b) soil organic carbon (SOC) in 75 riparian forest restoration sites in the Amazonia–Cerrado transition, Mato Grosso, Brazil. CEC: cation exchange capacity. K: Potassium; BS: base saturation; CWD: climatic water deficit; PDSI: Palmer Drought Severity Index.

interpretation. We retained in the model only the significant effects ($p < 0.05$). No critical autocorrelation was detected among explanatory variables (VIF <4). Model fitness was evaluated through the adjusted R^2 (conditional and marginal) which represents the amount of variance explained by the models. Marginal R^2 (R^2_m) represents the model's goodness-of-fit considering only the fixed factors, while conditional R^2 (R^2_c) reflects the goodness-of-fit considering both the fixed and random factors included in the model. Adjusted R^2 was calculated using the *r.squaredGLMM* function from the 'MuMin' package (Bartoń, 2010). Lastly, to evaluate differences between restoration methods, we performed post-hoc pairwise comparisons using estimated marginal means via the 'emmeans' package (Lenth and Piaskowski, 2017).

2.6.2. Tree size distribution and species composition

To evaluate the influence of different direct seeding techniques on forest structure and composition, we analyzed tree size distribution and species composition across sites older than 10 years. We compared tree size distribution among the three direct seeding techniques using a nonparametric two-way permutational ANOVA with the *aovp* function from the 'lmPerm' package (Wheeler and Torchiano, 2010), as density of individuals violated assumptions of normality and homogeneity of variance (assessed with Shapiro-Wilk and Levene's test). The model tested for the effects of DS technique, DBH class, and their interaction effects. Following a significant interaction, we ran pairwise permutation t-tests, with p-values adjusted by the Holm method, using the *pairwise.perm.t.test* function from the 'RVAideMemoire' package (Herve, 2011), to identify differences between techniques within each DBH class. For species composition, we analyzed compositional differences based on individuals contributing to biomass (*i.e.*, DBH >5 cm), specifically focusing on the species that accounted for 80% of basal area at each site.

2.6.3. Cost-effectiveness analysis

To compare the economic efficiency of the three direct seeding techniques, we calculated the cost-effectiveness as the total investment cost per ton of CO_2 sequestered at the 15-year mark. First, we projected the mean AGB for each technique at 15 years using a parametric bootstrap (1000 simulations) using the *bootMER* function from the 'lme4' package (Bates et al., 2003) based on our best AGB model. We then estimated total biomass (above-plus belowground) by applying a root-to-shoot ratio of 0.20 (Mokany et al., 2006) to the projected AGB.

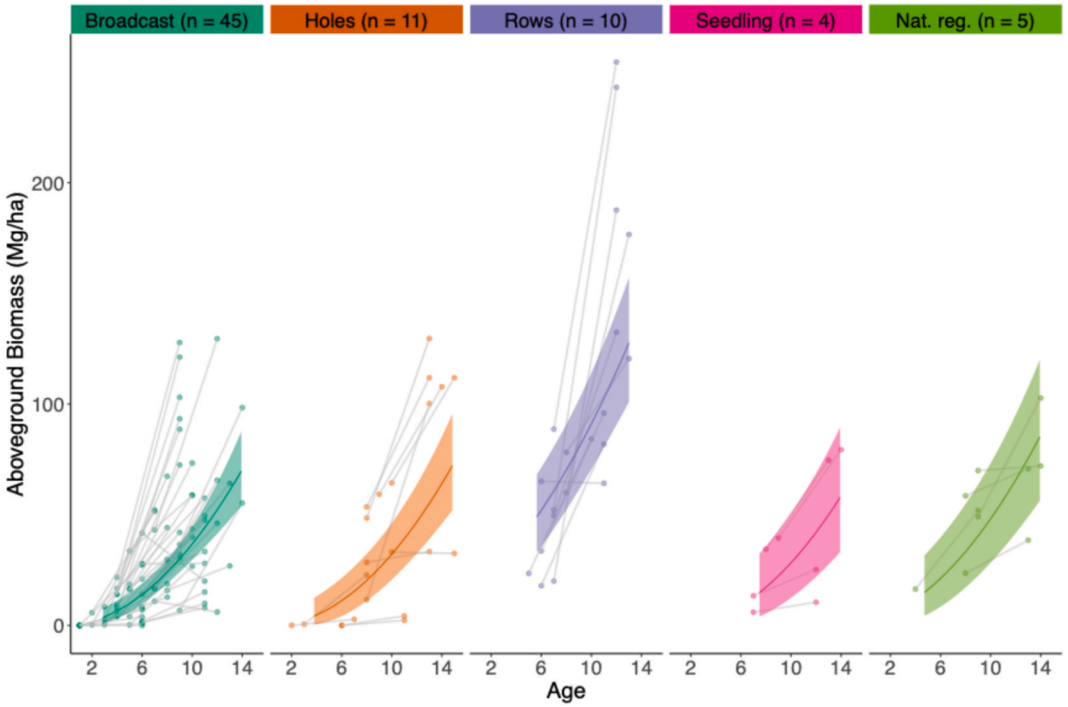

Fig. 3. Aboveground biomass in a chronosequence in 70 riparian forest sites restored through direct seeding (broadcast, holes, rows), seedlings planting, and natural regeneration in the Amazonia–Cerrado transition, Mato Grosso, Brazil. Grey lines connect the sample plot between the first and second sampling events (2017 and 2022). Shaded area represents the 95% confidence interval, and the line in the center of the shaded area shows the predicted relationship. The grey lines represent the individual trajectories of each permanent plot sampled in 2017 and 2022.

This total biomass was converted to CO_2 equivalent (tCO_2) by assuming a carbon content of 45.6% and applying the molecular weight ratio of 44/12 (Martin et al., 2018). Finally, the total costs (US$ ha^{-1}) were divided by the projected CO_2 stocks to determine the cost effectiveness (US$ tCO_2^{-1}). We estimated the total costs which involved soil preparation, seed acquisition, seeding, and 2-year management (Table S2). Costs were converted from Brazilian Reais (BRL) to US Dollars (USD) at an exchange rate of 5.457 BRL/USD (rates as of July 7th, 2025). Broadcast and row-seeding were defined as mechanized techniques for soil preparation and seeding, with a spreader and grain drill implements, respectively (Campos-Filho et al., 2013). For hole-seeding, these activities were assumed to be entirely manual, with no soil preparation necessary. To estimate costs for row-seeding, we adapted the broadcast-seeding parameters to account for a slower machinery speed, a subsequent increase in fuel consumption, and the removal of the post-planting leveling step. To determine whether cost-effectiveness differed significantly among techniques, we performed a Kruskal-Wallis test, a non-parametric alternative to ANOVA, using the *kruskal.test* function from 'stats' package (R Core Team, 2025), followed by Dunn's test to perform post-hoc pairwise comparisons using the *dunn.test* function from 'dunn.test' package (Dinno, 2024).

All analyses were carried out using R version 4.5.0 (R Core Team, 2025).

3. Results

3.1. Aboveground biomass drivers

The best model for AGB included restoration age, restoration method, CEC, and soil organic matter (Fig. 2a). Restoration age had the strongest positive effect ($F_{1,140} = 79.35$, $p < 0.0001$), followed by CEC ($F_{1,139} = 6.86$, $p = 0.0098$) and method ($F_{4,68} = 9.09$, $p < 0.0001$), while organic matter showed the smallest and negative effect ($F_{1,131} = 4.33$, $p = 0.0393$; Fig. 2a).

Row-seeding showed higher AGB stock than broadcasting, hole-seeding and seedling planting (all $p < 0.0012$), while it was not significantly different from natural regeneration ($p = 0.0572$; Fig. 3). At 15 years, row-seeding exhibited a mean AGB of 155.2 Mg ha^{-1} (95% confidence interval (CI): 120.8 - 189.7 Mg ha^{-1}) while broadcast- and hole-seeding showed values of 80.6 Mg ha^{-1} (CI: 60.2 - 101.0 Mg ha^{-1}) and 73.8 Mg ha^{-1} (CI: 51.6 - 95.9 Mg ha^{-1}), respectively. Natural regeneration reached 97.1 Mg ha^{-1} (CI: 62.0 - 132.2 Mg ha^{-1}), while seedling planting accumulated 67.8 Mg ha^{-1} (CI: 36.5 - 99.1 Mg ha^{-1}).

3.2. Soil organic carbon drivers

Soil organic carbon stock was not significantly influenced by the site age or the restoration method; instead, its variation was driven by edaphoclimatic variables. Stocks ranged from 11.4 to 73.5 Mg ha^{-1}, with an overall mean of 27.8 Mg ha^{-1}. Soil organic carbon was positively associated with CEC ($F_{1,142} = 42.76$, $p < 0.0001$) and base saturation ($F_{1,122} = 11.21$, $p = 0.0011$), but negatively associated with potassium ($F_{1,126} = 5.87$, $p = 0.0168$) (Fig. 2b). Climatic conditions were also significant predictors: PDSI had a positive effect ($F_{1,129} = 9.84$, $p = 0.0021$); while CWD had a negative effect ($F_{1,101} = 5.80$, $p = 0.0178$) (Fig. 2b).

3.3. Drivers of variation among direct seeding techniques

Given that row-seeding yielded higher AGB than broadcast or hole-seeding, we examined structural and compositional attributes in sites older than 10 years to identify the drivers of this divergence. Overall, tree density did not differ across direct seeding techniques ($F_{2,188} = 0.00$, $p = 1.0$). However, the interaction effect was significant ($F_{15,188} = 1.77$, $p < 0.0001$), indicating that the diameter classes distribution varied by technique. Broadcast-seeding had a significantly higher density of saplings (DBH <5 cm) than hole-seeding (Fig. 4). Row-seeding showed a significantly higher density of trees with DBH between 20.0 and 29.9 cm and was the only technique to include individuals with DBH larger than 45 cm (Fig. 4).

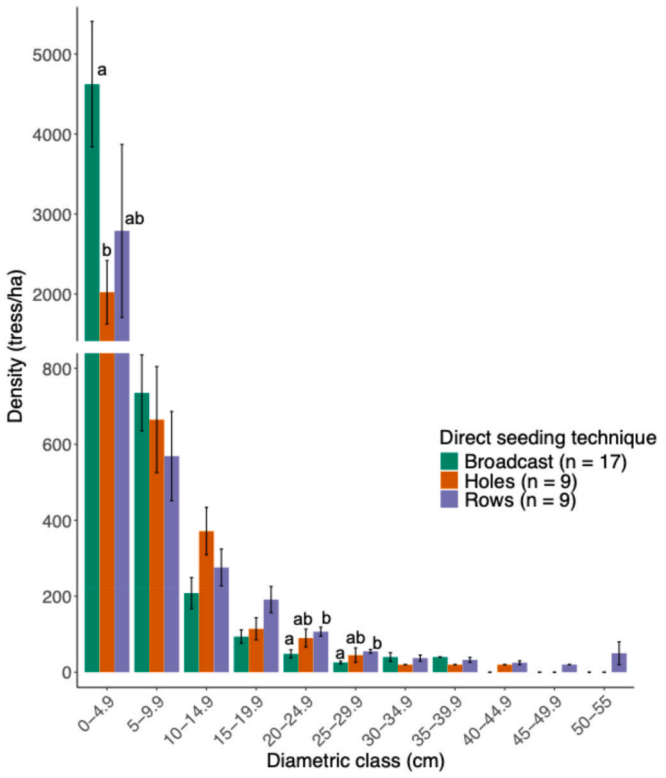

Fig. 4. Diameter at breast height (DBH) class distribution of tree species in 35 restored riparian forests aged 11 to 15 years in the Amazonia–Cerrado transition, Mato Grosso, Brazil. Bars represent mean ± standard error, and letters indicate significant differences (pairwise permutation *t*-tests, $p < 0.05$) among techniques within the same diameter class. When a given direct seeding technique was absent within a DBH class or showed no variation (SE = 0), it was excluded from the comparison for that class.

Six species were common to the three direct seeding techniques: *Tachigali vulgaris*, *Mabea fistulifera*, *Hymenaea courbaril*, *Enterolobium timbouva*, *Anadenanthera peregrina* var. *falcata*, *Simarouba amara* (Fig. 5). However, the relative contribution of species to total basal area differed among direct seeding techniques; *T. vulgaris* had the largest proportion in broadcast-seeding (22%), *E. timbouva* in row-seeding (22%) and *Caryocar brasiliense* in hole-seeding sites (26%; Fig. 5).

3.4. Cost-effectiveness of direct seeding techniques

The implementation costs were higher for hole-seeding (US$ 3246 ha^{-1}), followed by broadcast-seeding (US$ 2451 ha^{-1}), and row-seeding (US$ 2442 ha^{-1}), with seed acquisition representing the primary expense across all techniques (Table S2). Based on our 15-year projections, row-seeding accumulated significantly more carbon (21.3 tCO_2 ha^{-1} yr^{-1};CI: 16.9-25.9 tCO_2 ha^{-1} yr^{-1}) than broadcast (11 tCO_2 ha^{-1} yr^{-1};CI: 8.5-13.7 tCO_2 ha^{-1} yr^{-1}) and hole-seeding (10.2 tCO_2 ha^{-1} yr^{-1};CI: 7.5-13.3 tCO_2 ha^{-1} yr^{-1}). Consequently, row seeding emerged as the most cost-effective technique, requiring an average investment of US$ 7.91 tCO_2^{-1} sequestered over 15 years (Fig. 6). In contrast, broadcast and hole-seeding were significantly less cost-effective, with estimated mean costs of US$ 15.3 and US$ 22.1 tCO_2^{-1}, respectively (Fig. 6).

4. Discussion

Direct seeding proved effective for restoring carbon stock in tropical riparian forests, with AGB accumulation trajectories driven by the specific seeding technique and soil fertility. Although direct seeding techniques generally establish a high density of individuals (Freitas et al., 2019a), the specific technique significantly influenced long-term outcomes across the 15-year chronosequence. Notably, row-seeding outperformed other seeding techniques and seedling planting, due to the density of large, long-lived trees. In contrast, SOC dynamics appear to be primarily regulated by edaphoclimatic factors rather than successional changes. Consistent with literature, our results suggest that tropical forest soil carbon remains stable across succession, influenced more by soil chemistry and substantial climatic gradients than by aboveground biomass accretion (Berenguer et al., 2014; Brancalion et al., 2021; Marín-Spiotta and Sharma, 2013a). Similarly, studies in secondary tropical forests have found that soil carbon increases with nutrient availability rather than successional age (Jones et al., 2019).

Among the variables tested, CEC was the only factor that positively influenced both AGB and SOC, highlighting its role as a key indicator of site-level productivity. The positive effect of CEC on AGB recovery aligns with findings from other neotropical secondary forests (Poorter et al., 2016), while the influence of base saturation on SOC is consistent with results from other restored forest sites (Brancalion et al., 2021). However, climate was a factor in the decoupling between AGB and SOC. The negative relationship with CWD and the positive relationship with PDSI consistently indicate that SOC stocks are higher in moister sites. This aligns with global patterns showing that soil carbon content in tropical forests decreases as environments become drier, with the highest stocks found in moist and wet regions (Brown and Lugo, 1982; Marín-Spiotta and Sharma, 2013b). The lack of climate influence on AGB is surprising given the 1400 to 2000 mm precipitation gradient across our sites. However, this variation may be insufficient to serve as a primary constraint compared to the continental-scale gradients (e.g., 500–4000 mm) analyzed by Poorter et al. (2016), in which intermediate rainfall sites were grouped. In our study area, the influence of regional climate is likely overshadowed by more dominant local factors, such as soil fertility and the specific restoration method employed.

Our results indicate that direct seeding techniques influence the long-term structure and the species composition of the forest for up to 15 years, with subsequent effects on AGB. Although the overall density of individuals did not differ between techniques, row-seeding sites yielded higher tree density in some larger diameter classes (>20 cm), whereas broadcast-seeding predominantly yielded small saplings. While high densities of small individuals contribute little to AGB, this structure is typical of direct seeding and resembles natural regeneration, in which stem density may plateau for the first two decades of succession (Freitas et al., 2019a; Mesquita et al., 2015).

Beyond looking at structural differences, the identity of the large trees (i.e., species with great basal area) may lead to a more detailed information about the influence of the seeding technique on AGB. The distinct species importance found in direct seeding sites underscores the role of seeding techniques in filtering species based on their seed characteristics. *Tachigali vulgaris* became the dominant pioneer in broadcasting-seeding sites, contributing the most to basal area in this treatment. This species possesses ellipsoid seeds with small energy reserve (Ferreira, 2024), making it highly sensitive to burial depth; thus, it thrives in broadcast-seeding sites where seeds remain near the soil surface. Another characteristic of *T. vulgaris* is that it is a species known to perish after 10–20 years (Felfili et al., 1999). The life history of this species probably explains the observed decrease in AGB at broadcast sites after a decade, as this transitory carbon stock is being replaced by species with higher longevity (Körner, 2017). In contrast, *Enterolobium timbouva* dominated row-seeding sites older than 10 years. Its seeds are oval-shaped and possess significant energy reserves, allowing them to emerge from deeper soil layers, where burial provides essential protection against seed predators and desiccation. The substantial contribution to basal area of *E. timbouva*, a long-lived pioneer species (20 to 100 years), in row-seeding sites suggests that the mechanical precision of grain drill provides an optimal burial depth for species with these functional traits (Carvalho, 2008; Ferreira, 2024). Lastly, at hole-seeding sites, the species with the greatest basal area was *Caryocar*

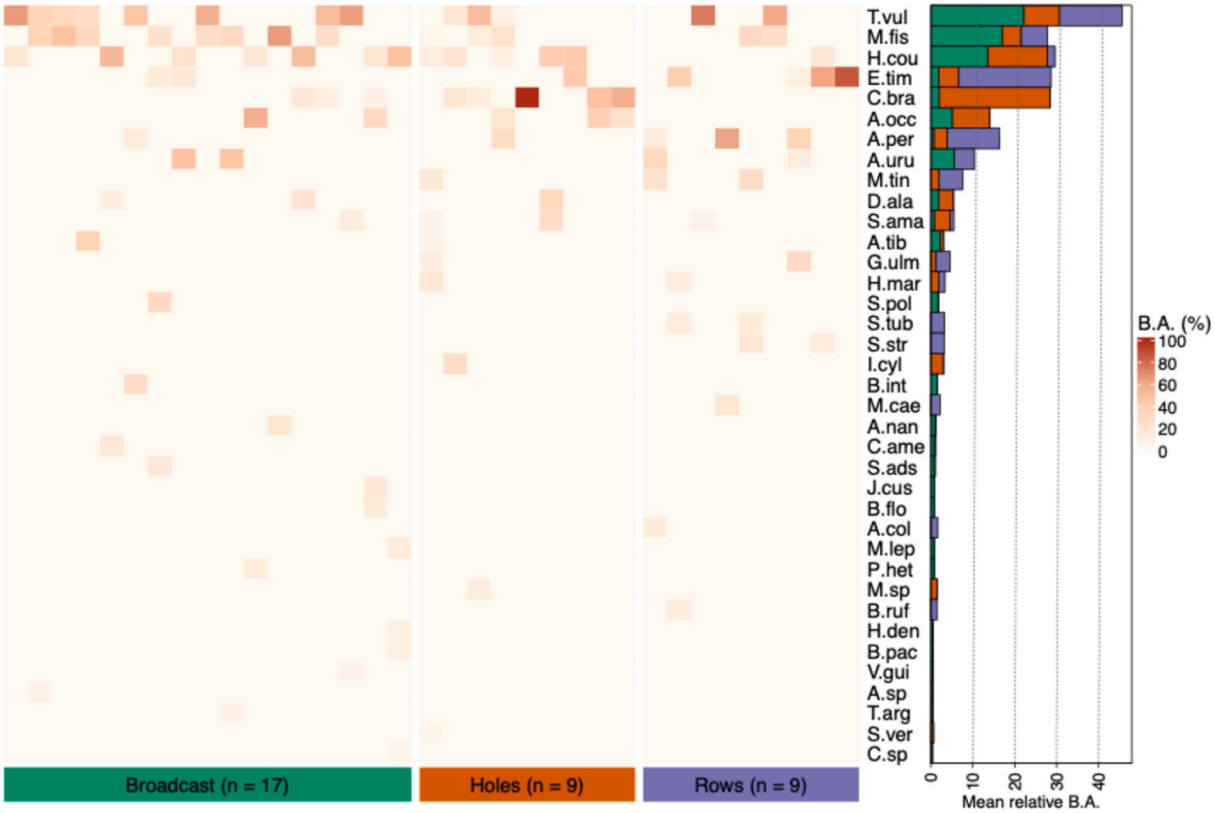

Fig. 5. Heatmap of mean relative basal area of species accounting for 80% of total basal area in 35 restored riparian forests aged 11 to 15 years in the Amazonia–Cerrado transition, Mato Grosso, Brazil. Individuals considered for basal area present diameter at breast height ≥ 5 cm.

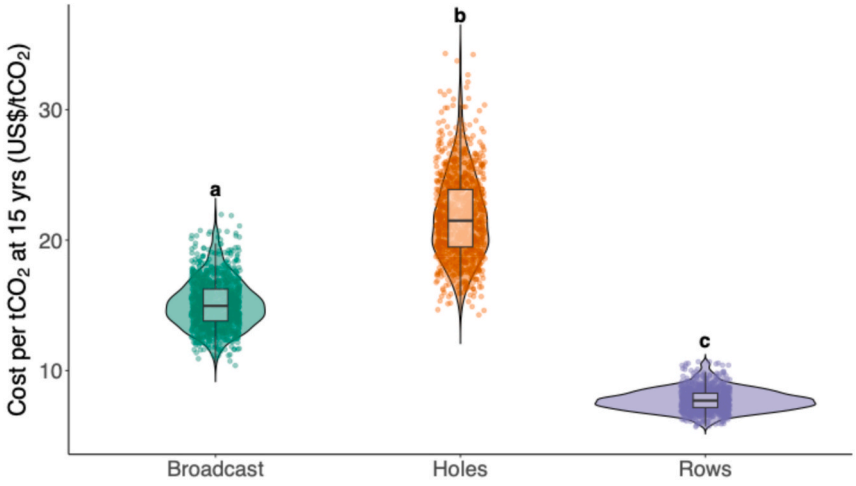

Fig. 6. The cost-per-ton of carbon dioxide in above and belowground biomass over 15 years in three different direct seeding techniques: broadcast, holes and rows. Costs were converted from Brazilian Reais (BRL) to US Dollars (USD) using an exchange rate of 5.457 BRL/USD (rates as of July 7th, 2025). Dots represent 1000 bootstrap simulations based on aboveground biomass model. Belowground biomass correspond to the root-to-shoot ratio of 0.20, standard value for tropical moist forest (Mokany et al., 2006). Different letters indicate statistically significant differences ($p < 0.05$) between direct seeding techniques.

brasiliense, a light-demanding climax species with large seeds highly sensitive to desiccation (Ferreira, 2024). The absence of *C. brasiliense* in row-seeding sites is due to its large seed size, which could not be sown with a grain drill, and the low presence of this species in broadcast-seeding may be attributed to burial depth. In fact, seed burial depth is more precise in row- and hole-seeding, than broadcasting followed by levelling disc harrow (Campos-Filho et al., 2013). This indicates that seeding in row and hole favors the establishment of species sensitive to desiccation over the soil or that cannot emerge from greater depths (Ferreira and Vieira, 2024).

Direct seeding was shown to be a cost-effective method for carbon sequestration, driven by its capacity to achieve substantial AGB accumulation and its low implementation costs. Our estimated costs for direct seeding fall within the range reported by other Brazilian studies (955-3199 USD per hectare, values adjusted for Brazilian inflation using IGP-DI) (Brancalion et al., 2019a; Raupp et al., 2020). Direct seeding and seedling planting are both considered intensive approaches that cost much more than passive restoration and assisted natural regeneration

(Brancalion et al., 2021). However, seedling planting involves significantly higher costs, 2.3 to 4.8 times those of direct seeding, primarily due to expenses associated with seedling production, transport and planting (Raupp et al. 2020). Consequently, the cost-effectiveness values we found for direct seeding techniques are substantially better than the 29.04 USD tCO_2^{-1} reported for mixed-species tree plantings (Brancalion et al., 2021). This difference reinforces the viability of direct seeding as a strategy for large-scale restoration projects.

Although international commitments for carbon dioxide removal have existed for decades, scientific research on AGB recovery in restored forests only accelerated significantly in the 2010s (Gardon et al., 2020). A review by Gardon et al. (2020) highlights that few studies have reported results from large-scale direct seeding restoration projects. The sites analyzed here are part of the most extensive direct seeding initiative in Brazil; however, they were not implemented as controlled scientific experiments. Their primary objective was to satisfy legal environmental liabilities by establishing self-sustaining vegetation, rather than to maximize carbon sequestration *per se* (Campos-Filho et al., 2013; Freitas et al., 2019a). Given that CEC was an important driver of aboveground biomass in our model, this result suggests that carbon-centered restoration outcomes could be significantly enhanced through targeted soil amendments, such as liming and fertilization (Nunes et al., 2020). Indeed, intensive silvicultural practices have been shown to increase carbon sequestration rates in restoration plantations by alleviating nutrient limitations and weed competition (Brancalion et al., 2019b). Furthermore, optimizing the seeding technique alongside strategic species selection may further reduce growth variability and ensure sustained long-term carbon gains.

Our study is subject to certain limitations inherent to large-scale, real-world restoration projects. First, the historical land use of broadcast-seeding sites was predominantly cattle pasture, whereas row-seeding sites were primarily located near or previously used as croplands. While past management may have influenced soil fertility at some sites, no significant differences in soil CEC were observed among direct seeding techniques. Additionally, the absence of site-specific records for species composition and exact seeding densities limited our ability to assess the performance of individual species across direct seeding techniques. This context helps explain the high variability in biomass observed, a pattern common in restored and secondary forests (Borges et al., 2023; Freitas et al., 2019a; Poorter et al., 2016), with significant consequences for the predictability of carbon accumulation rates.

5. Conclusion

Our study demonstrates that direct seeding is a robust and effective strategy for carbon sequestration in tropical riparian forests of the Amazonia-Cerrado transition, achieving biomass accumulation rates equivalent to traditional restoration methods over 15-year period. However, the success of aboveground biomass recovery is not uniform; it is significantly influenced by the chosen seeding technique and local soil fertility. Row-seeding emerged as the most effective technique, providing both the highest annual biomass increment and the greatest cost-effectiveness.

Our study reveals a distinct decoupling between above- and belowground carbon pools. While AGB accumulation was governed by restoration age, technique, and soil fertility, SOC stocks remained stable across the chronosequence, driven primarily by edaphoclimatic factors rather than successional stage or management intervention. This implies that while managers can actively enhance aboveground carbon sequestration by selecting specific seeding techniques, belowground carbon storage is largely constrained by inherent site-specific environmental conditions. The influence of the seeding technique on species dominance highlights its role as a functional filter, shaping future forest structure and composition. For direct seeding to realize its full potential as a large-scale carbon removal strategy, continued technological development and broader access to specialized machinery, such as grain drills adapted for diverse native seeds, are essential. Enhancing the precision of these techniques will reduce variability in outcomes and secure the long-term success of carbon-focused restoration in fragmented landscapes.

Funding sources

The study was supported by the Instituto Socioambiental, Agroicone and Embrapa Genetic Resources. Silvia B. Rodrigues and Marina G. Freitas received M.Sc. fellowship from CNPq and CAPES. Silvia B. Rodrigues has a PhD fellowship from CNPq (140074/2023-6), and Daniel L. M. Vieira has a research productivity fellowship from CNPq (314120/2023-8).

CRediT authorship contribution statement

Silvia Barbosa Rodrigues: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing – original draft, Writing – review & editing. **Marina Guimarães Freitas:** Investigation, Writing – review & editing. **Lorrayne Aparecida Gonçalves:** Data curation, Investigation, Writing – review & editing. **Tamilis Rocha:** Formal analysis, Investigation, Methodology, Writing – review & editing. **Lara Aranha da Costa:** Investigation, Writing – review & editing. **Eduardo Malta Campos-Filho:** Conceptualization, Writing – review & editing. **Icaro Abreu Sousa:** Formal analysis, Methodology, Writing – review & editing. **Raphael Matias:** Formal analysis, Methodology, Writing – review & editing. **Pedro Pereira Santos:** Formal analysis, Methodology, Writing – review & editing. **Daniel Luis Mascia Vieira:** Conceptualization, Writing – review & editing.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Silvia Barbosa Rodrigues reports financial support was provided by Instituto Socioambiental. Silvia Barbosa Rodrigues reports financial support was provided by Agroicone. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank Cleber Marcelino for fieldwork assistance.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2026.130508.

Data availability

Data will be made available on request.

References

Abatzoglou, J.T., Dobrowski, S.Z., Parks, S.A., Hegewisch, K.C., 2018. TerraClimate, a high-resolution global dataset of monthly climate and climatic water balance from 1958–2015. Sci. Data 5, 170191. https://doi.org/10.1038/sdata.2017.191.

Antoniazzi, L., Campos-Filho, E.M., Vieira, D.L.M., 2021. Seed-Based Restoration: How Experiences in Brazil are Increasing in both Scale and co-benefits. Seed.

Austin, K.G., Baker, J.S., Sohngen, B.L., Wade, C.M., Daigneault, A., Ohrel, S.B., Ragnauth, S., Bean, A., 2020. The economic costs of planting, preserving, and managing the world's forests to mitigate climate change. Nat. Commun. 11. https://doi.org/10.1038/s41467-020-19578-z.

Barnosky, A.D., Matzke, N., Tomiya, S., Wogan, G.O.U., Swartz, B., Quental, T.B., Marshall, C., McGuire, J.L., Lindsey, E.L., Maguire, K.C., Mersey, B., Ferrer, E.A., 2011. Has the Earth's sixth mass extinction already arrived? Nature 471, 51–57. https://doi.org/10.1038/nature09678.

Bartoń, K., 2010. Mumin: Multi-Model Inference. https://doi.org/10.32614/CRAN.package.MuMIn.
Bates, D., Maechler, M., Bolker, B., Walker, S., 2003. lme4: Linear Mixed-Effects Models Using "Eigen" and S4. https://doi.org/10.32614/CRAN.package.lme4.
Berenguer, E., Ferreira, J., Gardner, T.A., Aragão, L.E.O.C., De Camargo, P.B., Cerri, C.E., Durigan, M., Oliveira, R.C.D., Vieira, I.C.G., Barlow, J., 2014. A large-scale field assessment of carbon stocks in human-modified tropical forests. Glob. Change Biol. 20, 3713–3726. https://doi.org/10.1111/gcb.12627.
Bernal, B., Murray, L.T., Pearson, T.R.H., 2018. Global carbon dioxide removal rates from forest landscape restoration activities. Carbon Bal. Manag. 13, 22. https://doi.org/10.1186/s13021-018-0110-8.
Borges, S.L., Cardoso Ferreira, M., Machado Teles Walter, B., Dos Santos, A.C., Osni Scariot, A., Belloni Schmidt, I., 2023. Secondary succession in swamp gallery forests along 65 fallow years after shifting cultivation. For. Ecol. Manag. 529, 120671. https://doi.org/10.1016/j.foreco.2022.120671.
Brancalion, P.H.S., Campoe, O., Mendes, J.C.T., Noel, C., Moreira, G.G., Van Melis, J., Stape, J.L., Guillemot, J., 2019b. Intensive silviculture enhances biomass accumulation and tree diversity recovery in tropical forest restoration. Ecol. Appl. 29, e01847. https://doi.org/10.1002/eap.1847.
Brancalion, P.H.S., Guillemot, J., César, R.G., Andrade, H.S., Mendes, A., Sorrini, T.B., Piccolo, M.D.C., Peluci, M.C., Moreno, V.D.S., Colletta, G., Chazdon, R.L., 2021. The cost of restoring carbon stocks in Brazil's Atlantic Forest. Land Degrad. Dev. 32, 830–841. https://doi.org/10.1002/ldr.3764.
Brancalion, P.H.S., Hua, F., Joyce, F.H., Antonelli, A., Holl, K.D., 2025. Moving biodiversity from an afterthought to a key outcome of forest restoration. Nat. Rev. Biodivers. 1, 248–261. https://doi.org/10.1038/s44358-025-00032-1.
Brancalion, P.H.S., Meli, P., Tymus, J.R.C., Lenti, F.E.B., Benini, R.M., Silva, A.P.M., Isernhagen, I., Holl, K.D., 2019a. What makes ecosystem restoration expensive? A systematic cost assessment of projects in Brazil. Biol. Conserv. 240, 108274. https://doi.org/10.1016/j.biocon.2019.108274.
Brasil, 2012. Lei Nº 12.651, De 25 De Maio De 2012. Brasília.
Brown, S., Lugo, A.E., 1982. The storage and production of organic matter in tropical forests and their role in the global carbon cycle. Biotropica 14, 161. https://doi.org/10.2307/2388024.
Busch, J., Bukoski, J.J., Cook-Patton, S.C., Griscom, B., Kaczan, D., Potts, M.D., Yi, Y., Vincent, J.R., 2024. Cost-effectiveness of natural forest regeneration and plantations for climate mitigation. Nat. Clim. Change 14, 996–1002. https://doi.org/10.1038/s41558-024-02068-1.
Bustamante, M., Roy, J., Ospina, D., Achakulwisut, P., Aggarwal, A., Bastos, A., Broadgate, W., Canadell, J.G., Carr, E.R., Chen, D., Cleugh, H.A., Ebi, K.L., Edwards, C., Farbotko, C., Fernández-Martínez, M., Frölicher, T.L., Fuss, S., Geden, O., Gruber, N., Harrington, L.J., Hauck, J., Hausfather, Z., Hebden, S., Hebinck, A., Huq, S., Huss, M., Jamero, M.L.P., Juhola, S., Kumarasinghe, N., Lwasa, S., Mallick, B., Martin, M., McGreevy, S., Mirazo, P., Mukherji, A., Muttitt, G., Nemet, G.F., Obura, D., Okereke, C., Oliver, T., Orlove, B., Ouedraogo, N.S., Patra, P. K., Pelling, M., Pereira, L.M., Persson, Å., Pongratz, J., Prakash, A., Rammig, A., Raymond, C., Redman, A., Reveco, C., Rockström, J., Rodrigues, R., Rounce, D.R., Schipper, E.L.F., Schlosser, P., Selomane, O., Semieniuk, G., Shin, Y.-J., Siddiqui, T. A., Singh, V., Sioen, G.B., Sokona, Y., Stammer, D., Steinert, N.J., Suk, S., Sutton, R., Thalheimer, L., Thompson, V., Trencher, G., Van Der Geest, K., Werners, S.E., Wübbelmann, T., Wunderling, N., Yin, J., Zickfeld, K., Zscheischler, J., 2023. Ten new insights in climate science 2023. Glob. Sustain. 7, e19. https://doi.org/10.1017/sus.2023.25.
Campos-Filho, E.M., Da Costa, J.N.M.N., De Sousa, O.L., Junqueira, R.G.P., 2013. Mechanized direct-seeding of native forests in Xingu, central Brazil. J. Sustain. For. 32, 702–727. https://doi.org/10.1080/10549811.2013.817341.
Carvalho, P.E.R., 2008. Espécies Arbóreas Brasileiras.
Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G., Zanne, A.E., 2009. Towards a worldwide wood economics spectrum. Ecol. Lett. 12, 351–366. https://doi.org/10.1111/j.1461-0248.2009.01285.x.
Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M.S., Delitti, W.B.C., Duque, A., Eid, T., Fearnside, P.M., Goodman, R.C., Henry, M., Martínez-Yrízar, A., Mugasha, W.A., Muller-Landau, H.C., Mencuccini, M., Nelson, B.W., Ngomanda, A., Nogueira, E.M., Ortiz-Malavassi, E., Pélissier, R., Ploton, P., Ryan, C.M., Saldarriaga, J.G., Vieilledent, G., 2014. Improved allometric models to estimate the aboveground biomass of tropical trees. Glob. Change Biol. 20, 3177–3190. https://doi.org/10.1111/gcb.12629.
da Cruz, D.C., Benayas, J.M.R., Ferreira, G.C., Santos, S.R., Schwartz, G., 2021. An overview of forest loss and restoration in the Brazilian Amazon. N. For. 52, 1–16. https://doi.org/10.1007/s11056-020-09777-3.
Dinno, A., 2024. Dunn.Test: Dunn's Test of Multiple Comparisons Using Rank Sums. https://doi.org/10.32614/CRAN.package.dunn.test.
Elias, F., Teodoro, G.S., Aragão, J.S., Guilherme, F.A.G., 2025. Forest restoration in Southern Amazonia by direct seeding: linking functional traits and carbon accumulation. Trees (Berl.) 39, 82. https://doi.org/10.1007/s00468-025-02659-1.
Felfili, J.M., Hilgbert, L.F., Franco, A.C., Sousa-Silva, J.C., Resende, A.V., Nogueira, M.V. P., 1999. *Comportamento de pl?ntulas de Sclerolobium paniculatum Vog. var. rubiginosum (Tul.) Benth. sob diferentes n?veis de sombreamento, em viveiro*. Rev. Bras. Bot. 22. https://doi.org/10.1590/S0100-84041999000500011.
Ferreira, M.C., 2024. Ecologia De Sementes E Plântulas Aplicada À Restauração Por Semeadura Direta No Brasil. Phd Thesis. Universidade de Brasília, Brasília.
Ferreira, M.C., Vieira, D.L.M., 2024. Making the most of native seeds: management techniques interact with seed and seedling traits for enhancing direct seeding success. For. Ecol. Manag. 574, 122353. https://doi.org/10.1016/j.foreco.2024.122353.
Ferreira Júnior, O.J., Santos, A.C.D., Naves Júnior, C.H., Mendes, F.C., Ramalho, T.A.D. Q., Sousa, W.L.D., Teixeira, M.M., Aguiar, G.R., Flor, M.V.C., 2021. Spatial distribution of soil chemical properties in the cerrado of Tocantins. Reveng 29, 335–346. https://doi.org/10.13083/reveng.v29i1.11908.
Freitas, M.G., Rodrigues, S.B., Campos-Filho, E.M., do Carmo, G.H.P., da Veiga, J.M., Junqueira, R.G.P., Vieira, D.L.M., 2019. Evaluating the success of direct seeding for tropical forest restoration over ten years. For. Ecol. Manag. 438, 224–232. https://doi.org/10.1016/j.foreco.2019.02.024.
Gardon, F.R., Santos, R.F. dos, Rodrigues, R.R., 2020. Brazil's forest restoration, biomass and carbon stocks: a critical review of the knowledge gaps. For. Ecol. Manag. 462, 117972. https://doi.org/10.1016/j.foreco.2020.117972.
Giles, A.L., Schietti, J., Rosenfield, M.F., Mesquita, R.C., Vieira, D.L.M., Vieira, I.C.G., Poorter, L., Brancalion, P.H.S., Peña-Claros, M., Siqueira, J., Oliveira Junior, L., Do Espírito-Santo, M.M., Sarmento, P.S.D.M., Ferreira, J.N., Berenguer, E., Barlow, J., Elias, F., Cassol, H.L.G., Silva, R.C., Ribeiro, S.C., Medeiros, N., Junqueira, A.B., Massoca, P., Ferreira, M.J., Gastauer, M., Ferreira, L.V., De Almeida, D.R.A., Aragão, L.E.O.C., Jakovac, C.C., 2024. Simple ecological indicators benchmark regeneration success of Amazonian forests. Commun. Earth Environ. 5, 780. https://doi.org/10.1038/s43247-024-01949-9.
Gorelick, N., Hancher, M., Dixon, M., Ilyushchenko, S., Thau, D., Moore, R., 2017. Google Earth Engine: Planetary-scale geospatial analysis for everyone. Rem. Sens. Environ. 202, 18–27. https://doi.org/10.1016/j.rse.2017.06.031.
Guerra, A., Reis, L.K., Borges, F.L.G., Ojeda, P.T.A., Pineda, D.A.M., Miranda, C.O., Maidana, D.P.F. de L., Santos, T.M.R. dos, Shibuya, P.S., Marques, M.C.M., Laurance, S.G.W., Garcia, L.C., 2020. Ecological restoration in Brazilian biomes: identifying advances and gaps. For. Ecol. Manag. 458, 117802. https://doi.org/10.1016/j.foreco.2019.117802.
Heinrich, V.H.A., Dalagnol, R., Cassol, H.L.G., Rosan, T.M., de Almeida, C.T., Silva Junior, C.H.L., Campanharo, W.A., House, J.I., Sitch, S., Hales, T.C., Adami, M., Anderson, L.O., Aragão, L.E.O.C., 2021. Large carbon sink potential of secondary forests in the Brazilian Amazon to mitigate climate change. Nat. Commun. 12, 1785. https://doi.org/10.1038/s41467-021-22050-1.
Heinrich, V.H.A., Vancutsem, C., Dalagnol, R., Rosan, T.M., Fawcett, D., Silva-Junior, C. H.L., Cassol, H.L.G., Achard, F., Jucker, T., Silva, C.A., House, J., Sitch, S., Hales, T. C., Aragão, L.E.O.C., 2023. The carbon sink of secondary and degraded humid tropical forests. Nature 615, 436–442. https://doi.org/10.1038/s41586-022-05679-w.
Herve, M., 2011. Rvaidememoire: Testing and Plotting Procedures for Biostatistics. https://doi.org/10.32614/CRAN.package.RVAideMemoire.
Holl, K.D., Aide, T.M., 2011. When and where to actively restore ecosystems? For. Ecol. Manag. 261, 1558–1563. https://doi.org/10.1016/j.foreco.2010.07.004.
Houghton, R.A., Byers, B., Nassikas, A.A., 2015. A role for tropical forests in stabilizing atmospheric CO2. Nat. Clim. Change 5, 1022–1023. https://doi.org/10.1038/nclimate2869.
IBGE, 2012. Manual técnico da vegetação brasileira: sistema fitogeográfico, inventário das formações florestais e campestres, técnicas e manejo de coleções botânicas, procedimentos para mapeamentos. Manuais Técnicos em Geociências 1.
Ivanauskas, N.M., Monteiro, R., Rodrigues, R.R., 2008. Classificação fitogeográfica das florestas do Alto Rio Xingu. Acta Amaz 38, 387–402. https://doi.org/10.1590/S0044-59672008000300003.
Jakovac, C., Korys, K.A., Rodrigues, A.F., Ronix, A., Tubenchlak, F., Monteiro, L.M., Lemgruber, L., Santos, H.S., Mendes, M., Junqueira, A.B., Crouzeilles, R., Maioli, V., Latawiec, A.E., 2024. Meta-analysis of carbon stocks and biodiversity outcomes across Brazilian restored biomes. Sci. Total Environ. 906, 167558. https://doi.org/10.1016/j.scitotenv.2023.167558.
Jakovac, C.C., Junqueira, A.B., Crouzeilles, R., Peña-Claros, M., Mesquita, R.C.G., Bongers, F., 2021. The role of land-use history in driving successional pathways and its implications for the restoration of tropical forests. Biol. Rev. 96, 1114–1134. https://doi.org/10.1111/brv.12694.
Jones, I.L., DeWalt, S.J., Lopez, O.R., Bunnefeld, L., Pattison, Z., Dent, D.H., 2019. Above- and belowground carbon stocks are decoupled in secondary tropical forests and are positively related to forest age and soil nutrients respectively. Sci. Total Environ. 697, 133987. https://doi.org/10.1016/j.scitotenv.2019.133987.
Körner, C., 2017. A matter of tree longevity. Science 355, 130–131. https://doi.org/10.1126/science.aal2449.
Lenth, R.V., Piaskowski, J., 2017. Emmeans: Estimated Marginal Means, Aka Least-Squares Means. https://doi.org/10.32614/CRAN.package.emmeans.
MapBiomas, 2021. Relatório Anual De Desmatamento 2021. São Paulo, Brasil.
Marín-Spiotta, E., Sharma, S., 2013a. Carbon storage in successional and plantation forest soils: a tropical analysis. Global Ecol. Biogeogr. 22, 105–117. https://doi.org/10.1111/j.1466-8238.2012.00788.x.
Marín-Spiotta, E., Sharma, S., 2013b. Carbon storage in successional and plantation forest soils: a tropical analysis. Global Ecol. Biogeogr. 22, 105–117. https://doi.org/10.1111/j.1466-8238.2012.00788.x.
Martin, A.R., Doraisami, M., Thomas, S.C., 2018. Global patterns in wood carbon concentration across the world's trees and forests. Nat. Geosci. 11, 915–920. https://doi.org/10.1038/s41561-018-0246-x.
Mesquita, R.D.C.G., Massoca, P.E.D.S., Jakovac, C.C., Bentos, T.V., Williamson, G.B., 2015. Amazon rain Forest succession: stochasticity or land-use legacy? Bioscience 65, 849–861. https://doi.org/10.1093/biosci/biv108.
Mo, L., Zohner, C.M., Reich, P.B., Liang, J., De Miguel, S., Nabuurs, G.-J., Renner, S.S., Van Den Hoogen, J., Araza, A., Herold, M., Mirzagholi, L., Ma, H., Averill, C., Phillips, O.L., Gamarra, J.G.P., Hordijk, I., Routh, D., Abegg, M., Adou Yao, Y.C., Alberti, G., Almeyda Zambrano, A.M., Alvarado, B.V., Alvarez-Dávila, E., Alvarez-Loayza, P., Alves, L.F., Amaral, I., Ammer, C., Antón-Fernández, C., Araujo-Murakami, A., Arroyo, L., Avitabile, V., Aymard, G.A., Baker, T.R., Bałazy, R.,

Banki, O., Barroso, J.G., Bastian, M.L., Bastin, J.-F., Birigazzi, L., Birnbaum, P., Bitariho, R., Boeckx, P., Bongers, F., Bouriaud, O., Brancalion, P.H.S., Brandl, S., Brearley, F.Q., Brienen, R., Broadbent, E.N., Bruelheide, H., Bussotti, F., Cazzolla Gatti, R., César, R.G., Cesljar, G., Chazdon, R.L., Chen, H.Y.H., Chisholm, C., Cho, H., Cienciala, E., Clark, C., Clark, D., Colletta, G.D., Coomes, D.A., Cornejo Valverde, F., Corral-Rivas, J.J., Crim, P.M., Cumming, J.R., Dayanandan, S., De Gasper, A.L., Decuyper, M., Derroire, G., DeVries, B., Djordjevic, I., Dolezal, J., Dourdain, A., Engone Obiang, N.L., Enquist, B.J., Eyre, T.J., Fandohan, A.B., Fayle, T.M., Feldpausch, T.R., Ferreira, L.V., Finér, L., Fischer, M., Fletcher, C., Frizzera, L., Gianelle, D., Glick, H.B., Harris, D.J., Hector, A., Hemp, A., Hengeveld, G., Hérault, B., Herbohn, J.L., Hillers, A., Honorio Coronado, E.N., Hui, C., Ibanez, T., Imai, N., Jagodziński, A.M., Jaroszewicz, B., Johannsen, V.K., Joly, C.A., Jucker, T., Jung, I., Karminov, V., Kartawinata, K., Kearsley, E., Kenfack, D., Kennard, D.K., Kepfer-Rojas, S., Keppel, G., Khan, M.L., Killeen, T.J., Kim, H.S., Kitayama, K., Köhl, M., Korjus, H., Kraxner, F., Kucher, D., Laarmann, D., Lang, M., Lu, H., Lukina, N.V., Maitner, B.S., Malhi, Y., Marcon, E., Marimon, B.S., Marimon-Junior, B.H., Marshall, A.R., Martin, E.H., Meave, J.A., Melo-Cruz, O., Mendoza, C., Mendoza-Polo, I., Miscicki, S., Merow, C., Monteagudo Mendoza, A., Moreno, V.S., Mukul, S.A., Mundhenk, P., Nava-Miranda, M.G., Neill, D., Neldner, V.J., Nevenic, R. V., Ngugi, M.R., Niklaus, P.A., Oleksyn, J., Ontikov, P., Ortiz-Malavasi, E., Pan, Y., Paquette, A., Parada-Gutierrez, A., Parfenova, E.I., Park, M., Parren, M., Parthasarathy, N., Peri, P.L., Pfautsch, S., Picard, N., Piedade, M.T.F., Piotto, D., Pitman, N.C.A., Poulsen, A.D., Poulsen, J.R., Pretzsch, H., Ramirez Arevalo, F., Restrepo-Correa, Z., Rodeghiero, M., Rolim, S.G., Roopsind, A., Rovero, F., Rutishauser, E., Saikia, P., Salas-Eljatib, C., Saner, P., Schall, P., Schelhaas, M.-J., Schepaschenko, D., Scherer-Lorenzen, M., Schmid, B., Schöngart, J., Searle, E.B., Seben, V., Serra-Diaz, J.M., Sheil, D., Shvidenko, A.Z., Silva-Espejo, J.E., Silveira, M., Singh, J., Sist, P., Slik, F., Sonké, B., Souza, A.F., Stereńczak, K.J., Svenning, J.-C., Svoboda, M., Swanepoel, B., Targhetta, N., Tchebakova, N., Ter Steege, H., Thomas, R., Tikhonova, E., Umunay, P.M., Usoltsev, V.A., Valencia, R., Valladares, F., Van Der Plas, F., Van Do, T., Van Nuland, M.E., Vasquez, R.M., Verbeeck, H., Viana, H., Vibrans, A.C., Vieira, S., Von Gadow, K., Wang, H.-F., Watson, J.V., Werner, G.D.A., Wiser, S.K., Wittmann, F., Woell, H., Wortel, V., Zagt, R., Zawiła-Niedźwiecki, T., Zhang, C., Zhao, X., Zhou, M., Zhu, Z.-X., Zo-Bi, I. C., Gann, G.D., Crowther, T.W., 2023. Integrated global assessment of the natural forest carbon potential. Nature 624, 92–101. https://doi.org/10.1038/s41586-023-06723-z.

Mokany, K., Raison, R.J., Prokushkin, A.S., 2006. Critical analysis of root : shoot ratios in terrestrial biomes. Glob. Change Biol. 12, 84–96. https://doi.org/10.1111/j.1365-2486.2005.001043.x.

Morton, D.C., DeFries, R.S., Shimabukuro, Y.E., Anderson, L.O., Arai, E., Del Bon Espirito-Santo, F., Freitas, R., Morisette, J., 2006. Cropland expansion changes deforestation dynamics in the southern Brazilian Amazon. Proc. Natl. Acad. Sci. USA. 103, 14637–14641. https://doi.org/10.1073/pnas.0606377103.

Nunes, S., Gastauer, M., Cavalcante, R.B.L., Ramos, S.J., Caldeira, C.F., Silva, D., Rodrigues, R.R., Salomão, R., Oliveira, M., Souza-Filho, P.W.M., Siqueira, J.O., 2020. Challenges and opportunities for large-scale reforestation in the Eastern Amazon using native species. For. Ecol. Manag. 466, 118120. https://doi.org/10.1016/j.foreco.2020.118120.

Poorter, L., Bongers, F., Aide, T.M., Almeyda Zambrano, A.M., Balvanera, P., Becknell, J. M., Boukili, V., Brancalion, P.H.S., Broadbent, E.N., Chazdon, R.L., Craven, D., De Almeida-Cortez, J.S., Cabral, G.A.L., De Jong, B.H.J., Denslow, J.S., Dent, D.H., DeWalt, S.J., Dupuy, J.M., Durán, S.M., Espírito-Santo, M.M., Fandino, M.C., César, R.G., Hall, J.S., Hernandez-Stefanoni, J.L., Jakovac, C.C., Junqueira, A.B., Kennard, D., Letcher, S.G., Licona, J.-C., Lohbeck, M., Marín-Spiotta, E., Martínez-Ramos, M., Massoca, P., Meave, J.A., Mesquita, R., Mora, F., Muñoz, R., Muscarella, R., Nunes, Y.R.F., Ochoa-Gaona, S., De Oliveira, A.A., Orihuela-Belmonte, E., Peña-Claros, M., Pérez-García, E.A., Piotto, D., Powers, J.S., Rodríguez-Velázquez, J., Romero-Pérez, I.E., Ruíz, J., Saldarriaga, J.G., Sanchez-Azofeifa, A., Schwartz, N.B., Steininger, M.K., Swenson, N.G., Toledo, M., Uriarte, M., Van Breugel, M., Van Der Wal, H., Veloso, M.D.M., Vester, H.F.M., Vicentini, A., Vieira, I. C.G., Bentos, T.V., Williamson, G.B., Rozendaal, D.M.A., 2016. Biomass resilience of neotropical secondary forests. Nature 530, 211–214. https://doi.org/10.1038/nature16512.

R Core Team, 2025. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Raupp, P.P., Ferreira, M.C., Alves, M., Campos-Filho, E.M., Sartorelli, P.A.R., Consolaro, H.N., Vieira, D.L.M., 2020. Direct seeding reduces the costs of tree planting for forest and savanna restoration. Ecol. Eng. 148, 105788. https://doi.org/10.1016/j.ecoleng.2020.105788.

Rodrigues, S.B., Freitas, M.G., Campos-Filho, E.M., Do Carmo, G.H.P., Da Veiga, J.M., Junqueira, R.G.P., Vieira, D.L.M., 2019. Direct seeded and colonizing species guarantee successful early restoration of South Amazon forests. For. Ecol. Manag. 451, 117559. https://doi.org/10.1016/j.foreco.2019.117559.

Santos, H.G. dos, Jacomine, P.K.T., Anjos, L.H.C. dos, Oliveira, V.A. de, Lumbreras, J.F., Coelho, M.R., Almeida, J.A. de, Araújo Filho, J.C. de, Lima, H.N., Marques, F.A., Oliveira, J.B. de, Cunha, T.J.F., 2025. Sistema Brasileiro De Classificação De Solos, sixth ed. Embrapa, Brasília, DF https://www.embrapa.br/busca-de-publicacoes/-/publicacao/1176834/sistema-brasileiro-de-classificacao-de-solos.

Schubert, S.C., Zahawi, R.A., Oviedo-Brenes, F., Rosales, J.A., Holl, K.D., 2025. Active restoration increases tree species richness and recruitment of large-seeded taxa after 16–18 years. Ecol. Appl. 35, e3053. https://doi.org/10.1002/eap.3053.

Shaw, N., Barak, R.S., Campbell, R.E., Kirmer, A., Pedrini, S., Dixon, K., Frischie, S., 2020. Seed use in the field: delivering seeds for restoration success. Restor. Ecol. 28. https://doi.org/10.1111/rec.13210.

Strassburg, B.B.N., Iribarrem, A., Beyer, H.L., Cordeiro, C.L., Crouzeilles, R., Jakovac, C. C., Braga Junqueira, A., Lacerda, E., Latawiec, A.E., Balmford, A., Brooks, T.M., Butchart, S.H.M., Chazdon, R.L., Erb, K.-H., Brancalion, P., Buchanan, G., Cooper, D., Díaz, S., Donald, P.F., Kapos, V., Leclère, D., Miles, L., Obersteiner, M., Plutzar, C., De, M., Scaramuzza, C.A., Scarano, F.R., Visconti, P., 2020. Global priority areas for ecosystem restoration. Nature 586, 724–729. https://doi.org/10.1038/s41586-020-2784-9.

Townsend, A., Asner, G., Cleveland, C., 2008. The biogeochemical heterogeneity of tropical forests. Trends Ecol. Evol. 23, 424–431. https://doi.org/10.1016/j.tree.2008.04.009.

Urzedo, D., Pedrini, S., Vieira, D.L.M., Sampaio, A.B., Souza, B.D.F., Campos-Filho, E.M., Piña-Rodrigues, F.C.M., Schmidt, I.B., Junqueira, R.G.P., Dixon, K., 2022. Indigenous and local communities can boost seed supply in the UN decade on ecosystem restoration. Ambio 51, 557–568. https://doi.org/10.1007/s13280-021-01593-z.

Urzedo, D.I., Neilson, J., Fisher, R., Junqueira, R.G.P., 2020. A global production network for ecosystem services: the emergent governance of landscape restoration in the Brazilian Amazon. Glob. Environ. Change 61. https://doi.org/10.1016/j.gloenvcha.2020.102059.

Urzedo, D.I., Vidal, E., Sills, E.O., Pina-Rodrigues, F.C.M., Junqueira, R.G.P., 2016. Tropical forest seeds in the household economy: effects of market participation among three sociocultural groups in the Upper Xingu region of the Brazilian Amazon. Environ. Conserv. 43, 13–23. https://doi.org/10.1017/s0376892915000247.

Vieira, D.L.M., Malta, E., Ferreira, M., Miranda, E., Rocha, G.B., Alves, M., Sampaio, A.B., Antoniazzi, L., 2020. GUIA de SEMEADURA DIRETA para restauração de florestas e cerrados. Agroicone Ltda. São Paulo, SP.

Wheeler, B., Torchiano, M., 2010. Lmperm: Permutation Tests for Linear Models. https://doi.org/10.32614/CRAN.package.lmPerm.

Zanne, A.E., Lopez-Gonzalez, G., Coomes, D.A., Ilic, J., Jansen, S., Lewis, S.L., Miller, R. B., Swenson, N.G., Wiemann, M.C., Chave, J., 2009. Data from: towards a worldwide wood economics spectrum. https://doi.org/10.5061/DRYAD.234.