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Effectiveness of spatially patterned methods to restore semideciduous tropical forest

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Abstract

1. Spatially patterned restoration methods, such as applied nucleation and planting in strips, are promising approaches for scaling up projects to meet ambitious restoration commitments in an ecologically and economically sound manner. However, to date, these planting approaches have mostly been compared in small experimental plots, and the comparative costs have not been quantified.

2. We compared five restoration treatments—nuclei and strip planting each covering 25% and 50% of the plot area and full planting—in replicated 1-ha plots in seasonal semideciduous forest in southeastern Brazil. We report on field measurements of planted tree survival, tree recruitment, woody above-ground biomass and grass cover 7 years after planting, as well as LiDAR-derived measures of canopy height, canopy cover and leaf area index after 5 and 7 years. Finally, we report detailed cost estimates and effectiveness for each treatment.

3. After 7 years, above-ground biomass, canopy height, canopy cover and leaf area index were greatest in the full planting treatment, intermediate in both 50% nuclei and strips treatments and lowest in the two 25% planting treatments. Grass cover was greater in planted areas of nuclei than strips. Woody recruitment was dominated by ruderal species and did not show strong treatment trends.

4. Planting a quarter or half of the area cost ~50%–60% and ~70%–80%, respectively, of the price of planting the entire area. For the most part, planting 100% was similarly cost-effective per unit of biomass accumulation and canopy cover as spatially patterned restoration methods after 7 years.

5. *Synthesis and applications*: Our study shows that choosing the most effective restoration strategy at scale depends equally if not more on economic and logistical than ecological constraints. If rapid carbon sequestration is a primary project goal, then full planting for forest restoration is the most cost-effective strategy

over the first few years unless natural regeneration is fast in the system. In regions with flat land, where mechanical restoration methods are feasible, planting strips is logistically easier to implement than nuclei.

1 | INTRODUCTION

Given the many ambitious international commitments to restore forests and other ecosystems globally (e.g. Bonn Challenge, UN Decade on Ecosystem Restoration), there is a critical need for restoration methods that are ecologically sound, cost-effective and scalable to hundreds or thousands of hectares (Brancalion & Holl, 2025; Langhammer et al., 2024). One potential strategy is spatially patterned restoration methods, namely seeding or planting a portion of a restoration site, often in clusters or strips (Corbin & Holl, 2012; Shaw et al., 2020); ideally tree cover spreads into the unplanted area over time by planted species growing vegetatively, attracting faunal dispersers of unplanted species, improving local site conditions to enhance the establishment of newly colonizing species and serving as seed sources once plants become reproductive. This approach depends on sufficient sources of seeds and seed-dispersing fauna in the surrounding landscape. These methods have the advantage of creating heterogeneous habitat conditions (Holl et al., 2013) and mimicking natural regeneration processes which are typically patchy (Corbin & Holl, 2012; Yarranton & Morrison, 1974). Moreover, spatially patterned planting methods require fewer seeds and seedlings than full planting, which is a major advantage given limited funding and the highly constrained seed and seedling supply chain for restoration globally (Fargione et al., 2021; National Academy of Sciences, 2023; Valette et al., 2020). In principle, spatially patterned methods also have lower implementation costs, but this premise has yet to be rigorously tested.

Although some studies show that planting in clusters can be an effective strategy for catalysing forest recovery over the first decade or two (Corbin et al., 2016; Holl et al., 2020; Procknow et al., 2023), most prior studies have limited value to inform large-scale restoration efforts (Holl et al., 2024). The vast majority of these studies have been conducted in small plots (e.g. <10m^2), have only monitored results for the first years post-planting and have not surveyed the spread of planted areas over time (e.g. La Mantia et al., 2019; Pilon et al., 2018; Rojas-Botero et al., 2020). Moreover, few studies have compared multiple spatially patterned methods directly to the more common forest restoration approach of planting trees in rows throughout the site (Holl et al., 2024). Past studies have also generally focused on ecological outcomes without considering the social feasibility, logistical challenges and costs of implementation and maintenance of these approaches. Zahawi et al. (2014) highlight

a key potential social challenge of spatially patterned restoration, namely that landholders often prefer systematic tree planting, as they see it as a more productive use of the land with a less 'messy' appearance. Moreover, Ramírez-Soto et al. (2018) note that implementing spatially patterned methods requires additional training of restoration crews who are more accustomed to standard tree planting designs.

We conducted a large-scale experiment in seasonal semideciduous forest in southeastern Brazil to compare two spatially patterned planting designs and investigate what proportion of a restoration site needs to be actively planted to accelerate forest recovery. We tested the methods in 1-ha replicate plots and used standard site preparation, planting and maintenance methods for restoring Brazilian Atlantic forest (Rodrigues et al., 2009) to increase the applicability of our methods to the large-scale restoration projects being undertaken in the region. We hypothesized that spatially patterned methods would be less effective in reducing grass cover and increasing canopy cover and above-ground biomass (AGB) than full planting as a consequence of the reduced number of trees planted per plot. However, the greater individual growth of trees resulting from the reduced shading by nuclei and strip plantings, combined with the lower implementation costs, could make strip and nuclei planting more affordable than standard planting.

We compared planting relatively high proportions (25% and 50%) of the entire restoration site as we anticipated a relatively large percentage of the area would need to be planted given that (1) competition with invasive grasses is high, (2) tree growth rates would be moderate given the low-nutrient soils and extended dry season and (3) natural regeneration would be low due to reduced native forest cover in the region (César et al., 2018). Determining the necessary proportion of area to plant is particularly salient in this study system because of the high costs for the standard full planting approach are prohibitively expensive for most rural producers (around US\$5500ha^{-1}). Reducing restoration costs is critical for compliance with the Native Vegetation Protection Law (Law 12651/2012), which requires landowners to restore Areas of Permanent Protection (e.g. around water springs, along riparian buffers, on steep slopes) and Legal Reserves (20%–80% of the farm area, depending of the region) in previously deforested areas (Brancalion et al., 2016). As this law allows landowners up to 20years to restore the areas needed for compliance, a slower but cheaper restoration approach is permissible. Moreover, less costly restoration methods for carbon accumulation are critical for unlocking additional

investments in the voluntary carbon market, which is growing quickly and is now regulated in Brazil (Law 15042/2024).

We also compared the efficacy of planting a mix of native trees in clusters (i.e. applied nucleation, Corbin & Holl, 2012) versus strips. We anticipated that planting in strips would be more effective than square clusters in this semideciduous forest ecosystem because strips would: (1) be less impacted by competition with invasive grasses and (2) be less costly to implement given the mechanization of restoration operations typically used in the region.

2 | MATERIALS AND METHODS

2.1 | Site description

This study was established in 2017 at the Itatinga Experimental Station of Forest Sciences of the University of São Paulo, located in the municipality of Itatinga, São Paulo state, Brazil (23°02′56″ S, 48°38′59″ W). The study area is located at a mean elevation of 850 m with an average annual temperature of 19.7°C, ranging from 9.1°C in July to 28.0°C in January. It is classified as a Cwa humid subtropical region according to Köppen climate classification with a mean annual rainfall of 1388 mm per year with most precipitation occurring from October to March (Xavier et al., 2022). The soil is sandy (86% sand, 2% silt, 12% clay content), acidic (pH 4.8) and nutrient-poor (sum of bases = 0.23 cmol(+) kg^{-1}). The site was a monoculture eucalyptus plantation devoid of native vegetation for nearly a century. A few months prior to the start of the experiment, eucalypts were harvested, and coarse woody residues were removed from the area. The site is adjacent to a 70-year-old abandoned eucalyptus plantation with abundant native species, including mature trees that are potential sources of seeds dispersing to the experimental site. The closest substantial remnant forest (50 ha) is ~3 km away.

2.2 | Experiment setup

We tested five restoration treatments (Figure 1): nuclei planting covering 25% and 50% of the 1-ha plots (hereafter nuclei 25% and nuclei 50%), strip planting covering 25% and 50% of the plot area
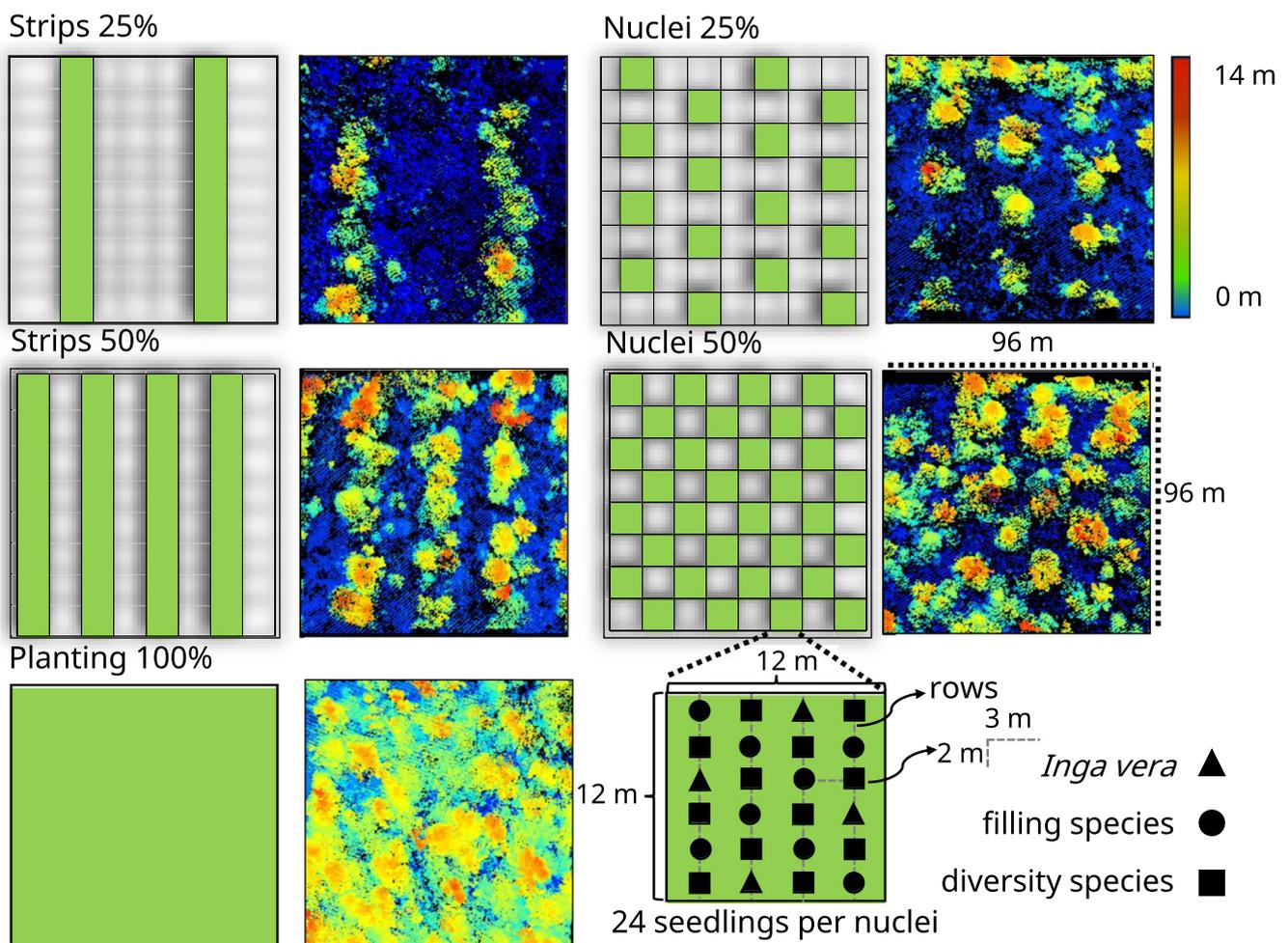

FIGURE 1 Experimental design. For the left panels, the green areas indicate where seedlings were planted, and the white areas were unplanted. For the right panels, colour variation indicates the canopy height 7 years after planting in example plots, based on remotely sensed LiDAR.

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(strips 25% and strips 50%) and planting throughout the entire plot area (planting 100%). Each treatment was replicated once in each of five blocks located along a terrain and proximity-to-forest gradient; blocks ranged from locations at the bottom of the catchment with greater soil moisture and closer to an abandoned eucalyptus plantation with abundant natural regeneration and seed sources to those at the top of the catchment with contrasting conditions. Tree nuclei (12×12 m) were planted in April–May 2017 with 24 nursery-grown, ~20 cm height seedlings at 3×2 m spacing; the 25% and 50% nuclei treatments had 16 and 32 nuclei, respectively. Tree strips were 12×96 m and had 129 seedlings; 25% strips and 50% strips planting plots had two and four strips, respectively (Figure 1). We planted a total of 42 native tree species: 17 animal-dispersed and 24 abiotic-dispersed. Consistent with the methodology of Rodrigues et al. (2009), which aims to balance fast-growing trees to shade out grasses with a greater diversity of species for conservation and attraction of seed dispersers, the trees were grouped into two planting groups: 'filling' species (fast-growing and wide-canopy species) and 'diversity' species (Table S1). We established nuclei with three distinct species compositions, which included the 41 species; the species *Inga vera* was planted in higher density at the nuclei edges (Figure 1; Figure S1), due to its rapid lateral canopy expansion and concomitant shade. The strips and planting 100% were established by aligning the same three nuclei in a row, so the species composition and distribution were similar across treatments. We employed a randomized block design, with five replicates and 1-ha plots, totalling 25 ha of experimental area.

Prior to planting, lime was distributed across the entire experimental area (2 t ha^{-1}) to increase pH and Ca availability following the standard approach for both restoration and commercial forestry in the region. Soil was prepared to a 70-cm depth with a subsoiler. Seedlings, grown in 56-cm^3 plastic tubes with organic substrate, were planted with a pottiputki planter, fertilized with 120 g N:P:K 6:30:6 per seedling (base fertilization) and irrigated once after planting (5 L per seedling); 150 days after planting, seedlings received 150 g of N:P:K 18:06:24 as top-dressing fertilization. In the planted areas, non-native grasses, mostly *Urochloa decumbens*, were controlled with glyphosate spraying (4 L ha^{-1}) twice yearly until the fifth year; no weed control was performed in the unplanted areas. Leaf cutter ants (mostly *Atta* spp., but also *Acromyrmex* spp.) were controlled with insecticide baits (sulfluramid) across all of the plots for the entire study, yet some ant nests and moderate levels of herbivory remained.

We did not need a scientific permit for this study, as it was conducted on land of a research station that was part of a voluntary restoration project financed by the Environmental Secretary of the State of São Paulo; moreover, all sampling was non-destructive.

2.3 | Cost estimates

We hired a restoration company to implement and maintain the experiment. After the completion of each intervention, we quantified the inputs and costs for each treatment for the following activities: controlling leaf cutter ants, spraying herbicide, preparing soil (subsoiling and base fertilization), distributing lime, planting and replanting seedlings, and fertilizing post-planting. We recorded the quantity of inputs (e.g. seedlings, top-dressing fertilizer, lime and insecticide baits) used per treatment. Subsoiling costs were proportionally higher in nucleation as compared to strips and full planting treatments, as it was operationally unfeasible to remove and insert the subsoiler into the soil when the tractor was passing through the unplanted areas of nucleation treatments; hence, the soil was prepared in the entire plot area in nuclei 50% and in half of the area in nuclei 25%. The cost of using herbicide to reduce grass competition was much greater in nuclei and strips treatments since grass cover was not reduced by tree canopy shade in the unplanted areas. Moreover, maintenance was more challenging given the irregular planting design in the nucleation treatment, so field staff needed more time to find the nuclei and then the seedlings hidden by grass. Since soil preparation and spraying herbicide did not scale to the number of seedlings planted, we quantified the cost of the 100% planting treatment and multiplied it by the proportion of time spent on each of the spatially patterned planting methods (e.g. for the nuclei 25%, staff spent 65% of the time required to prepare the soil in relation to the planting 100%).

2.4 | Field sampling

In each nuclei and strips plot, we randomly located four sampling subplots of 12×12 m in planted areas and four in unplanted areas, totalling eight sampling subplots per plot. We sampled a total of four subplots in the planting 100% plots, which did not have unplanted areas.

In years 5 (2022) and 7 (2024), we measured the height and diameter of all *planted trees* and of *larger recruits* (individuals with ≥5-cm diameter) in all subplots. We also counted *smaller recruits* (<5-cm diameter and ≥50-cm height) in the subplots. A few large shrub species were included as 'recruiting trees'. Tree height was measured using an electronic hypsometer (Haglöf Sweden brand, Vertex 5) and tree diameter at 30 cm above ground; we measured the diameter at this height (rather than the standard 1.3 m) to allow the use of species-specific allometric equations for biomass estimation based on this method, which was developed from a 6-year-old restoration planting in the same region (Ferez et al., 2015). We further classified recruits as 'pioneer' or 'nonpioneer', with pioneer species defined as trees that typically colonize pastures and open areas (Table S1).

We compared AGB between treatments for the planted and unplanted areas separately. We estimated the plot-level AGB per hectare for each experimental design by scaling the values to the percentage of planted and unplanted areas. To measure cover of non-native grasses, which often inhibit tree recruitment, we ran two diagonal 17-m line transects across each 12×12 m subplot and quantified the percentage of the line that intercepted grass cover.

2.5 | LiDAR

LiDAR data were collected in two UAV flights conducted in March 2022 (year 5) and 2024 (year 7). We collected LiDAR data using the VLP-16 sensor (Velodyne Lidar, Inc.), which emits and receives 600,000 laser pulses per second at a 905-nm wavelength. The sensor's range is up to 100 m and the vertical field of view is $30° \pm 15°$. The sensor is attached to a data acquisition unit, which is combined with an Applanix APX-15 inertial measurement unit and mounted on a DJI M600 Pro drone using a DJI Ronin 3-axis gimbal for stabilization.

We post-processed the data to improve positional accuracy of the LiDAR points using the methodology described in detail in Ferreira et al. (2024). The final planimetric and altimetric accuracy of the LiDAR points was ± 3 cm and ± 5 cm, respectively. We used the *lidR* R package (Roussel et al., 2020) to combine the *.las* files from each flight into a single file, which resulted in a final LiDAR point cloud with an average density of 1000 points per m^2.

We calculated the canopy height model (CHM), canopy cover and leaf area index (LAI) from LiDAR to quantify the vertical and horizontal vegetation structure of the treatments. To minimize edge effects, a 3-m buffer was removed at the edge of each plot, corresponding to one planting line and removing approximately 12% of the plot area.

We computed the CHM by first normalizing the point cloud's height using cloth simulation filtering (Zhang et al., 2016), which separates ground from non-ground points to ensure that the normalized point cloud accurately reflects the height of each point relative to the ground surface. We then generated the CHM through a rasterization process using a 1×1-m square grid. The CHM was computed by assigning the maximum LiDAR return value to each grid cell to capture the top canopy height.

We computed the percentage of the plot with canopy cover >5 m using the ForestGAP R package (Silva et al., 2019). The ForestGAP package quantifies the canopy cover by calculating the proportion of LiDAR points above a certain height threshold (>5 m in our case) compared to the total points within each plot.

We estimated the LAI, defined as the area of leaves per unit ground surface area (m^2/m^2). LAI retrieval from LiDAR data is based on calculating the penetration or transmittance ratio of laser pulses, followed by applying the Beer–Lambert Law to convert transmittance into LAI (Nilson, 1971). We estimated LAI from the LiDAR point cloud using the *leafR* R package and the approach proposed by Almeida et al. (2019). The point cloud was divided into 1-m^3 canopy volume units (voxels), and the leaf area density (LAD) was estimated using the first returns within each voxel. LAI was then calculated by summing the vertical profiles (voxel columns) of LAD. The result was a raster in which each 1×1 m cell contained the corresponding LAI value. For statistical analyses, we used means of the 1×1 m cell values of the CHM and LAI rasters for each plot.

2.6 | Statistical analysis

All analyses were performed using R version 4.4 (R Core Team, 2024). We used a generalized linear mixed model approach to fit the variable of interest with treatment as a fixed factor and block as a random factor. For models that only compared treatment and year effects we considered plot as the replicate. For those that also compared planted versus unplanted areas, we used subplots as replicates to compare the different regions within the plots. For each variable of interest, we analysed the best fit family of distributions also suited to zero-inflated and overdispersed data (Table S2), and we analysed model assumptions by their residuals with the R package DHARMa (Hartig, 2024). Then, we performed pairwise comparisons using Tukey contrasts to infer statistical differences between treatments (p-level = 0.05) using the emmeans R package (Lenth, 2025).

For variables for which we present data from years 5 and 7, we initially included year as a fixed factor and tested its interaction with treatment. Given that the year×treatment interaction was significant in nearly all cases, we ran separate models for each year. We also compared the change in values per year between years 5 and 7. We then used the emmeans package to estimate marginal means and perform Tukey's pairwise comparisons between each treatment group.

We also compared abundance and species richness of smaller recruits excluding two hyper-abundant (80.2% of smaller recruits), ruderal Asteraceae species (*Baccharis dracunculifolia* and *Vernonia polyanthes*). We compared species richness across treatments using rarefaction and extrapolation curves (Hill $q = 0$) with the iNEXT package (Hsieh et al., 2016). For each treatment in planted and unplanted areas, we calculated individual-based species accumulation curves up to 450 individuals, which allows standardized comparisons of observed and estimated species richness while accounting for differences in sample sizes (Hsieh et al., 2016).

Finally, we calculated the cost-effectiveness of each treatment relative to biomass accumulation and canopy cover. We divided the treatment-level total cost (i.e. implementation and maintenance) per hectare by the plot-level AGB and canopy cover for years 5 and 7. We used the same approaches for model fitting and selection and post hoc comparisons as for previously described response variables.

3 | RESULTS

3.1 | Field data

Per cent survival of planted trees after 7 years was lowest in nuclei 25% planting (39.2%), intermediate in strips 25% (46.9%) and highest in the other three treatments (nuclei 50% = 48.2%, strips 50% = 50%, planting 100% = 52.3%, Table S2). The odds of survival in the nuclei 25% treatment were 42% lower than the planting 100% treatment (estimate $\pm$ SE = 0.54 $\pm$ 0.13, $p < 0.001$, Table S3).

As expected, grass cover was significantly greater in unplanted than in planted regions in year 7 and was similarly high across treatments in unplanted areas (Figure 2; Tables S2 and S3). In the planted areas, the planting 100% and strips 50% treatments had the lowest levels of grass cover; grass cover was intermediate in the unplanted areas of strips 25% and highest in the nuclei 25% and 50% treatments.

Smaller woody recruits (0.5 m ≤ height ≤ 2 m, 92.3% pioneers) were more abundant in planted than unplanted areas and were most abundant in the planted areas of nuclei and strips 50% (Figure 3a; Tables S2 and S3). However, these differences were driven by two widespread, wind-dispersed pioneer species—*Baccharis dracunculifolia* and *Vernonanthura polyanthes*—that comprised 48.9% and 31.3% of small recruits, respectively, and smaller recruit abundance did not differ by treatment or planted versus unplanted areas when those species were removed from the analysis (Tables S2 and S3). The 95% confidence intervals for species richness of smaller recruits overlapped for all the treatments (Figure S2). Larger woody recruits (height >2 m) were comprised of 42.1% pioneers and 57.9% non-pioneers that mostly had resprouted from stems established before the start of the experiment, and abundance did not differ significantly across treatments in planted or unplanted areas (Figure 3b; Table S2); *Leptolobium elegans*, *Senna rugosa* and *Baccharis dracunculifolia* were common larger recruits. Only 8% and 11% of the total number of re-generating individuals (22% and 18% of species) inside and outside of planted areas, respectively, were of planted tree species.

Total AGB (planted and unplanted trees) did not differ significantly across the nuclei and strips treatments in year 5 but was greater in nuclei 50% than 25% planting treatments by year 7 (Figure 4). AGB was much greater in the 100% planting treatment in both years, given that >95% of the woody AGB was comprised of planted trees. AGB in the unplanted areas did not differ across treatments (Figure 4; Tables S2 and S3). The difference in AGB between
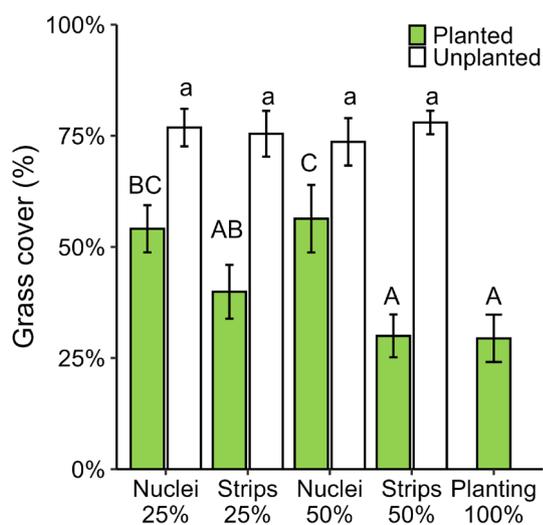

FIGURE 3 Density (mean ± SE individuals ha⁻¹) of smaller (a) and larger (b) tree recruits in planted and unplanted areas in year 7. Treatments with the same capital (planted) or lowercase letter (unplanted) do not differ significantly (p > 0.05) in total recruit abundance in that year using a Tukey's mean comparison procedure. Crosshatched areas indicate the number of smaller recruit individuals comprised by *Baccharis dracunculifolia* and *Vernonia polyanthes*.

FIGURE 2 Per cent grass cover (mean ± SE) across treatments in planted and unplanted areas in year 7. Treatments with the same capital letter (planted) and lowercase letter (unplanted) do not differ significantly (*p* > 0.05) using a Tukey's mean comparison procedure.
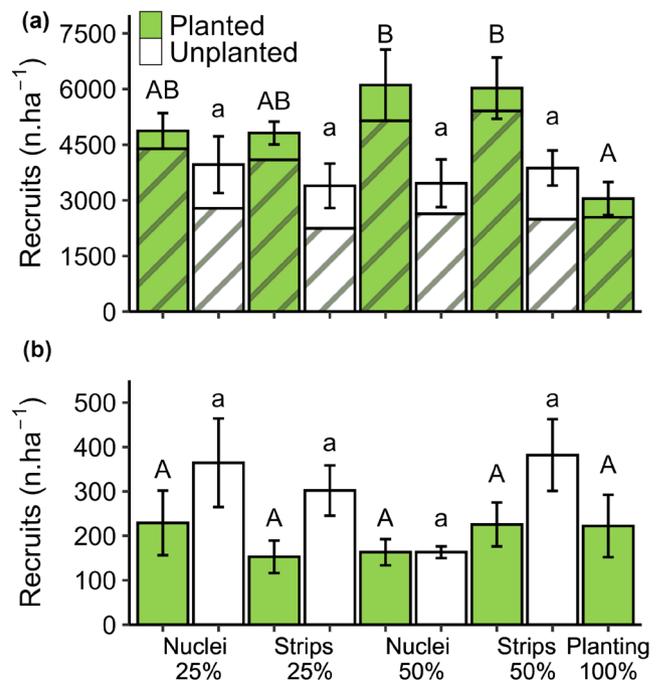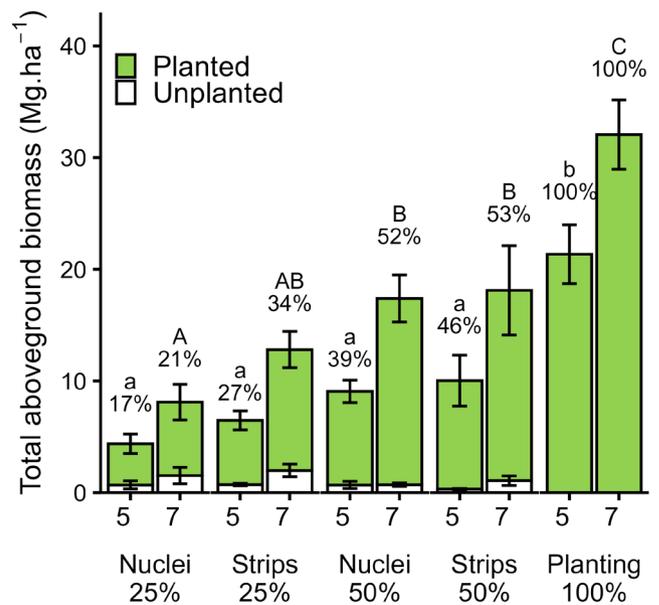

FIGURE 4 Woody above-ground biomass (mean ± SE) in planted and unplanted areas, across treatments and years. Treatments sharing the same uppercase letters (5 years) or lowercase letters (7 years) do not differ significantly (Tukey's HSD, *p* > 0.05). Numbers above the bars indicate the percentage of the planting 100% value achieved by that treatment in the same year.

100% planting and the other treatments diminished over time, but by year 7 planting 100% treatment still had approximately twice the biomass as the nuclei and strips 50% treatments and about 3–4 times more biomass than the 25% treatments.

3.2 | LiDAR

The canopy height model, canopy cover and leaf area index (LAI) were significantly greater in the planting 100% treatment compared to the other treatments in both years 5 and 7 ($p < 0.001$, Figure 5; Tables S2 and S3). Canopy height was significantly greater in 50% than 25% plantings by year 7, and patterns were similar for canopy cover and LAI, though those differences were not all significant given the high within-treatment variance. The annual increase in CHM, canopy cover and LAI between the two sampling periods did not differ significantly (Tables S2 and S3).

3.3 | Cost

Implementation and maintenance costs were highest in the full planting treatment, as expected, but total costs did not scale linearly with the area planted; planting a quarter or half of the area cost ~50%–60% and ~70%–80%, respectively, of the cost of planting 100% (Table 1). The cost of strip planting was slightly less than nuclei planting.

Contrary to our hypothesis, planting 100% was similarly cost-effective per unit of AGB and canopy cover as all spatially patterned treatments, except for nuclei 25% planting, which was less cost-effective than full planting for AGB (both years, Figure 6a) and canopy cover (year 5 only, Figure 6b).

4 | DISCUSSION

Despite the recent interest in spatially patterned restoration strategies (Cole et al., 2024; Holl et al., 2024; Shaw et al., 2020), these approaches have rarely been tested at a scale relevant for restoration implementation. We tested five different planting strategies in replicated 1-ha plots, so we were able to use the standard mechanized methods employed in projects of hundreds of hectares in the region and compare associated costs of multiple approaches. This is the first well-replicated test of spatially patterned restoration in tropical semideciduous forest which experiences seasonal drought stress, so many tree species lose their leaves during the dry season, tree mortality is greater, and trees grow more slowly. Hence, more time is required to develop a canopy that shades out light-demanding pasture grasses than in wet tropical forest where most prior spatially patterned restoration research has been done. Finally, we planted a larger number (42) of tree species than in most prior studies (e.g. Holl et al., 2020; Ramírez-Soto et al., 2018; Zahawi & Augspurger, 2006).
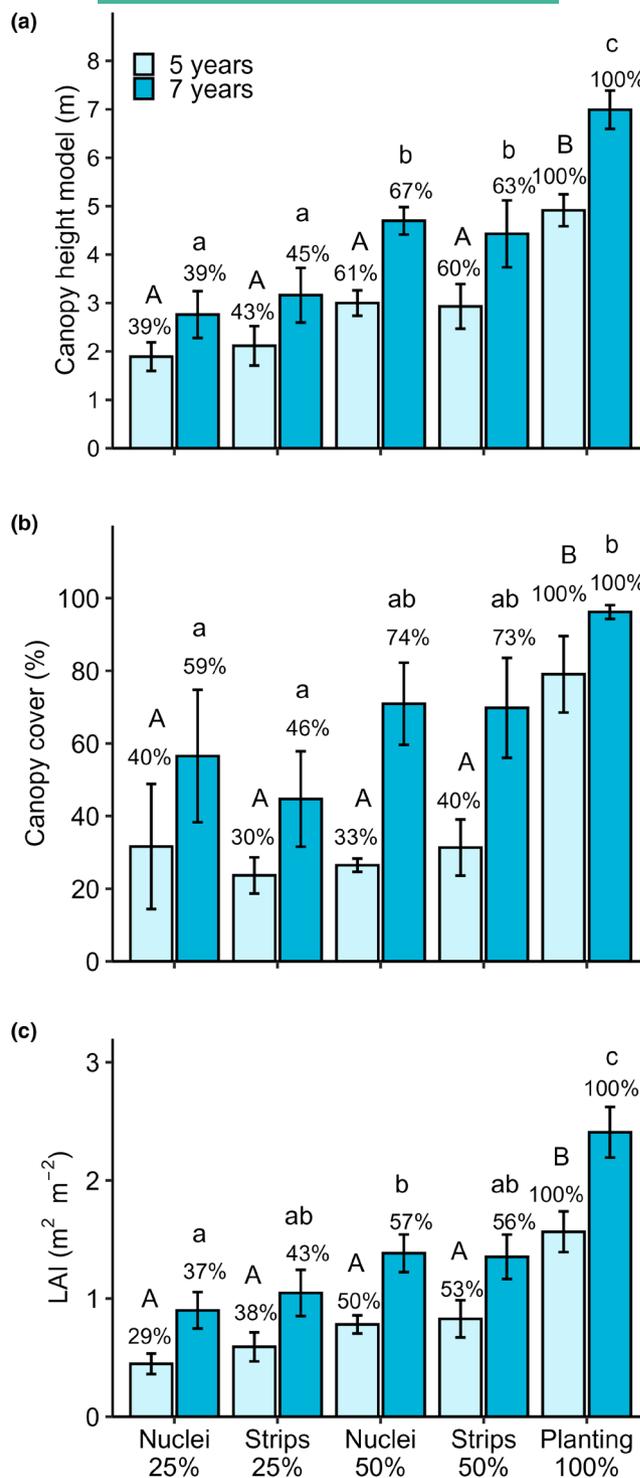

FIGURE 5 Canopy height model (a), canopy cover (b) and leaf area index (LAI) (c) across the treatments. Error bars indicate ±1 SE. Treatments sharing the same uppercase letters (5 years) or lowercase letters (7 years) do not differ significantly (Tukey's HSD, $p > 0.05$). Numbers above the bars indicate the percentage of the planting 100% value achieved by that treatment in the same year.

Our study shows that full planting results in greater AGB, canopy height, canopy cover and LAI 7 years following restoration, similar to a prior applied nucleation study in tropical wet forest (Holl &

TABLE 1 Overall implementation and maintenance costs per hectare associated with each of the planting treatments.

Activities	Nuclei 25%	Strips 25%	Nuclei 50%	Strips 50%	Planting 100%
Leaf cutter ant control	$296	$296	$296	$296	$296
Herbicide spraying	$581	$430	$620	$536	$559
Subsoiling and base fertilization	$77	$39	$154	$77	$154
Tree planting	$27	$27	$55	$55	$109
Tree replanting	$10	$10	$19	$19	$39
Irrigation	$39	$26	$78	$52	$103
Top-dressing fertilization	$28	$13	$38	$25	$50
Lime distribution	$45	$45	$45	$45	$45
Labor and machinery subtotal	**$1103**	**$885**	**$1304**	**$1105**	**$1355**
Tree seedlings	$166	$166	$331	$331	$662
Fertilizer	$75	$75	$149	$149	$299
Lime	$79	$79	$79	$79	$79
Insecticide baits	$121	$121	$121	$121	$121
Herbicide	$13	$13	$26	$26	$52
Inputs subtotal	**$453**	**$453**	**$706**	**$706**	**$1213**
Total cost per hectare	**$1556**	**$1338**	**$2010**	**$1811**	**$2568**

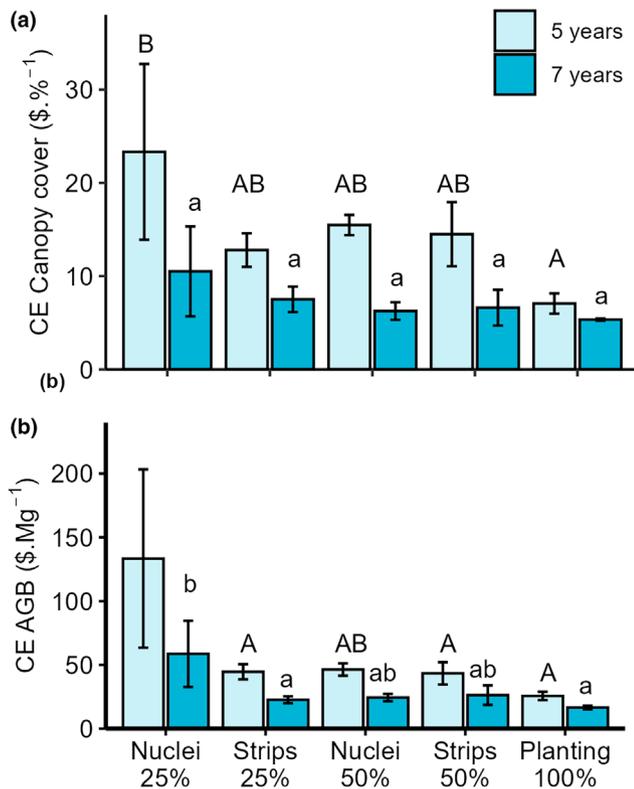*Note*: Values are rounded to the nearest US$.

FIGURE 6 Cost-effectiveness (CE, mean ± SE) of restoration treatments 5 and 7 years after implementation, expressed as US dollars per unit of (a) canopy cover (%$^{-1}$) and (b) above-ground biomass (AGB; Mg^{-1}). Treatments sharing the same uppercase letters (5 years) or lowercase letters (7 years) do not differ significantly (Tukey's HSD, $p > 0.05$).

Zahawi, 2014). In year 7, values for AGB mostly scaled with the area planted, whereas canopy cover and LAI in the spatially patterned treatments were greater than the area planted (e.g. canopy cover was 59% and LAI was 37% of full planting in the 25% nuclei treatment), showing that nuclei and strips are spreading over time.

Despite this likely future AGB convergence, a major and growing source of funding for reforestation projects is the voluntary carbon market (Brancalion et al., 2024; Busch et al., 2024) and these funders want to sequester carbon as quickly as possible. From this perspective, planting 100% was slightly more cost-effective by year 5, though the difference with all the spatially planted treatments except 25% nuclei was small and had diminished by year 7. This suggests that spatially patterned methods can be cost-effective and may be a favoured strategy in the case of an insufficient seedling supply, which commonly limits large-scale restoration projects in Brazil (Brancalion et al., 2018) and elsewhere (Fargione et al., 2021; Valette et al., 2020). Spatially patterned methods can also be cost-effective in areas where implementation costs are higher, like in steep lands where mechanization of planting is not feasible.

Past studies comparing costs of spatially patterned versus full planting restoration methods have reported contrasting results. Holl et al. (2020) asserted that restoration costs scaled to the area planted, whereas Ramírez-Soto et al. (2018) reported that applied nucleation was more expensive than full planting due to the more complex planting design. We did a detailed cost analysis of site preparation, planting and maintenance and found that spatially patterned methods were cheaper than full planting. However, the difference in costs was proportionally less than the difference in area planted, because some restoration interventions are implemented

at the site level, and maintenance is more complicated with a spatially patterned design. Interestingly, in our study system, planting in strips was slightly less costly than nuclei, due to the mechanized site preparation and planting. That result would likely differ in more rugged terrain where planting is done manually. Our and other studies (Holl et al., 2020; Ramírez-Soto et al., 2018) concur that implementing the applied nucleation approach is somewhat more logistically challenging than the more standard method of planting rows of trees throughout part or all of the site.

The ecological outcomes of planting in nuclei versus strips were mostly similar. One difference was that grass cover within the strips was slightly, albeit not significantly, lower in the planted areas of strips than nuclei. This likely reflects the greater amount of canopy edge in the nuclei plantings, which favours light-demanding forage grasses. Likewise, planted trees survived less in the 25% nuclei than the other treatments, which probably resulted from the greater grass cover (Florido et al., 2022) and possibly due to more stressful microclimatic conditions at nuclei edges (Ewers & Banks-Leite, 2013). Interestingly, the slight differences in grass cover did not affect the density of the recruits, which was similar in the two planting designs, suggesting that both approaches show similar promise for facilitating vegetation recovery, at least for early successional species.

Abundance and species richness of recruits showed minimal differences across treatments and planted versus unplanted areas when the two hyper-abundant, wind-dispersed ruderal species were removed from the analyses. This result contrasts with other studies showing that greater planted tree canopy increases the abundance and richness of recruits (Li et al., 2018; Mendes et al., 2021; Schubert et al., 2025). The species recruiting were primarily pioneer species, many of which are considered pasture weeds in the region, that grow quickly in open areas. Prior research in the region has shown that few species recruit in the understory of restoration plantations in the first few years after planting, but once forest structure develops and conditions are appropriate for the regeneration of mid- to late-successional species, recruitment increases rapidly (Brancalion et al., 2019). So, we anticipate that species richness and abundance of non-pioneer recruits will increase substantially in the planted areas in coming years but that will depend on the presence of seed-dispersing fauna, the arrival of seeds from neighbouring areas, and the suppression of invasive grasses by shading. The high abundance of *Baccharis dracunculifolia* and *Vernonia polyanthes* (both Asteraceae) in planted areas of nuclei and strips treatments reflects the fact that (1) fruiting individuals were widespread in the landscape; (2) they were able to establish in the understory of the planted areas of nuclei and strips where competition was reduced due to grass control for multiple years; and (3) they are shade intolerant, so did not establish so well in the planting 100% treatment where light levels were low throughout the understory.

An important management question is what proportion of the land area needs to be planted to accelerate forest recovery. A study in wet forest Holl et al. (2017) found that planting ~25% of the area in tree nuclei resulted in similar levels and composition of woody recruitment as planting the entire area, though biomass and canopy cover were lower in the first decade of recovery in the applied nucleation compared to the full planting treatment (Holl & Zahawi, 2014). Indeed, most desired conditions in the current study (e.g. higher biomass, lower grass cover) recovered more quickly in 50% compared to 25% planting, particularly for the nuclei planting pattern. An earlier study in moist forest in Costa Rica (Fink et al., 2009; Zahawi et al., 2013) showed that a minimum nuclei size of ~$100\,m^2$ is necessary to attract seed-dispersing birds and shade out dense forage grasses to effectively catalyse recovery.

5 | CONCLUSIONS

Whereas most restoration studies focus on the rate of recovery of plant, animals or other ecological variables, which restoration strategy is most effective at scale depends equally if not more so on economic and logistical constraints (Busch et al., 2024; Ramírez-Soto et al., 2018; Toro et al., 2024). In regions with flat land, where using mechanical methods of restoration is feasible, strip planting is much easier to implement logistically than nuclei. Importantly, strip planting also offers the opportunity to plant a valuable timber tree in the unplanted areas which can help to offset planting costs and reduce herbicide costs (Brancalion et al., 2020). If rapid carbon sequestration is a primary project goal, then full planting for forest restoration is the most cost-effective strategy unless conditions for natural regeneration and tree growth are favourable in the system. However, spatially patterned planting has other advantages such as requiring less planting stock and enhancing habitat heterogeneity (Holl et al., 2013). Finally, this and many other studies (e.g. Banin et al., 2023; Giles et al., 2024; Holl et al., 2020) have found highly variable recovery even within replicate plots, so if possible, it is wise to allow the system to regenerate for a couple of years, then determine how much planting is needed in a given area and focus planting in areas that regenerate more slowly.

AUTHOR CONTRIBUTIONS

Karen D. Holl and Pedro H. S. Brancalion conceived the ideas and designed the methodology; Pedro H. S. Brancalion oversaw the collection and compilation of the field data and cost estimates; Rildo M. Moreira and Flavia G. Flórido led field activities related to experiment implementation and maintenance and calculated the cost data; Gabriel Parreiras led forest inventories; Matheus Pinheiro Ferreira and Danilo R. Almeida oversaw the collection and compilation of the LiDAR data; Juliano van Melis analysed the data and created most of the figures; Karen D. Holl led the writing of the manuscript; Pedro H. S. Brancalion, Juliano van Melis and Matheus Pinheiro Ferreira contributed critically to the drafts, and all authors gave final approval for publication.

CONFLICT OF INTEREST STATEMENT

Pedro H. S. Brancalion is a partner at re.green, a forest restoration company.

DATA AVAILABILITY STATEMENT

Data and code for analysis are archived at https://doi.org/10.5281/zenodo.17289451 (Brancalion et al., 2025).

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REFERENCES

Almeida, D. R. A., Stark, S. C., Shao, G., Schietti, J., Nelson, B. W., Silva, C. A., Gorgens, E. B., Valbuena, R., Papa, D. D. A., & Brancalion, P. H. S. (2019). Optimizing the remote detection of tropical rainforest structure with airborne lidar: Leaf area profile sensitivity to pulse density and spatial sampling. *Remote Sensing*, 11, 92. https://doi.org/10.3390/rs11010092

Banin, L. F., Raine, E. H., Rowland, L. M., Chazdon, R. L., Smith, S. W., Rahman, N. E. B., Butler, A., Philipson, C., Applegate, G. G., Axelsson, E. P., Budiharta, S., Chua, S. C., Cutler, M. E. J., Elliott, S., Gemita, E., Godoong, E., Graham, L. L. B., Hayward, R. M., Hector, A., … Burslem, D. F. R. P. (2023). The road to recovery: A synthe-sis of outcomes from ecosystem restoration in tropical and sub-tropical Asian forests. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, 378, 20210090. https://doi.org/10.1098/rstb.2021.0090

Brancalion, P. H. S., Amazonas, N. T., Chazdon, R. L., van Melis, J., Rodrigues, R. R., Silva, C. C., Sorrini, T. B., & Holl, K. D. (2020). Exotic eucalypts: From demonized trees to allies of tropical forest restoration? *Journal of Applied Ecology*, 57, 55–66. https://doi.org/10.1111/1365-2664.13513

Brancalion, P. H. S., Balmford, A., Wheeler, C. E., Rodrigues, R. R., Strassburg, B. B. N., & Swinfield, T. (2024). A call to develop carbon credits for second-growth forests. *Nature Ecology & Evolution*, 8, 179–180. https://doi.org/10.1038/s41559-023-02288-2

Brancalion, P. H. S., Bello, C., Chazdon, R. L., Galetti, M., Jordano, P., Lima, R. A. F., Medina, A., Pizo, M. A., & Reid, J. L. (2018). Maximizing biodiversity conservation and carbon stocking in restored tropical forests. *Conservation Letters*, 11, e12454. https://doi.org/10.1111/conl.12454

Brancalion, P. H. S., Campoe, O., Mendes, J. C. T., Noel, C., Moreira, G. G., van Melis, J., Stape, J. L., & Guillemot, J. (2019). Intensive silvi-culture enhances biomass accumulation and tree diversity recovery in tropical forest restoration. *Ecological Applications*, 29, e01847. https://doi.org/10.1002/eap.1847

Brancalion, P. H. S., Garcia, L. C., Loyola, R., Rodrigues, R. R., Pillar, V. D., & Lewinsohn, T. M. (2016). A critical analysis of the Native Vegetation Protection Law of Brazil (2012): Updates and ongoing initiatives. *Natureza & Conservação*, 14(Suppl. 1), 1–15. https://doi.org/10.1016/j.ncon.2016.03.003

Brancalion, P. H. S., & Holl, K. D. (2025). Upscaling ecological resto-ration by integrating with agriculture. *Frontiers in Ecology and the Environment*, 23, e2802. https://doi.org/10.1002/fee.2802

Brancalion, P. H. S., van Melis, J., Ferreira, M. P., Almeida, D. R., Florido, F. G., Parreiras, G., Moreira, R. M., & Holl, K. D. (2025). Data avail-able from: Effectiveness of spatially patterned methods to restore semideciduous tropical forest. *Zenodo*. https://doi.org/10.5281/zenodo.17289451

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. *Nature Climate Change*, 14, 996–1002. https://doi.org/10.1038/s41558-024-02068-1

César, R. G., Moreno, V. S., Coletta, G. D., Chazdon, R. L., Ferraz, S. F. B., de Almeida, D. R. A., & Brancalion, P. H. S. (2018). Early ecological outcomes of natural regeneration and tree plantations for restor-ing agricultural landscapes. *Ecological Applications*, 28, 373–384. https://doi.org/10.1002/eap.1653

Cole, R. J., Werden, L. K., Arroyo, F. C., Quirós, K. M., Cedeño, G. Q., & Crowther, T. W. (2024). Forest restoration in practice across Latin America. *Biological Conservation*, 294, 110608. https://doi.org/10.1016/j.biocon.2024.110608

Corbin, J. D., & Holl, K. D. (2012). Applied nucleation as a forest res-toration strategy. *Forest Ecology and Management*, 265, 37–46. https://doi.org/10.1016/j.foreco.2011.10.013

Corbin, J. D., Robinson, G. R., Hafkemeyer, L. M., & Handel, S. N. (2016). A long-term evaluation of applied nucleation as a strategy to facili-tate forest restoration. *Ecological Applications*, 26, 104–114. https://doi.org/10.1890/15-0075

Ewers, R. M., & Banks-Leite, C. (2013). Fragmentation impairs the micro-climate buffering effect of tropical forests. *PLoS One*, 8, e58093. https://doi.org/10.1371/journal.pone.0058093

Fargione, J., Haase, D. L., Burney, O. T., Kildisheva, O. A., Edge, G., Cook-Patton, S. C., Chapman, T., Rempel, A., Hurteau, M. D., Davis, K. T., Dobrowski, S., Enebak, S., De La Torre, R., Bhuta, A. A. R., Cubbage, F., Kittler, B., Zhang, D., & Guldin, R. W. (2021). Challenges to the reforestation pipeline in the United States. *Frontiers in Forests and Global Change*, 4, 629198. https://doi.org/10.3389/ffgc.2021.629198

Ferez, A. P. C., Campoe, O. C., Mendes, J. C. T., & Stape, J. L. (2015). Silvicultural opportunities for increasing carbon stock in resto-ration of Atlantic forests in Brazil. *Forest Ecology and Management*, 350, 40–45. https://doi.org/10.1016/j.foreco.2015.04.015

Ferreira, M. P., Martins, G. B., de Almeida, T. M. H., da Silva Ribeiro, R., da Veiga Júnior, V. F., da Silva Rocha Paz, I., de Siqueira, M. F., & Kurtz, B. C. (2024). Estimating aboveground biomass of tropical urban for-ests with UAV-borne hyperspectral and LiDAR data. *Urban Forestry & Urban Greening*, 96, 128362. https://doi.org/10.1016/j.ufug.2024.128362

Fink, R. D., Lindell, C. A., Morrison, E. B., Zahawi, R. A., & Holl, K. D. (2009). Patch size and tree species influence the number and du-ration of bird visits in forest restoration plots in southern Costa Rica. *Restoration Ecology*, 17, 479–486. https://doi.org/10.1111/j.1526-100X.2008.00383.x

Florido, F. G., Regitano, J. B., Andrade, P. A. M., Andreote, F. D., & Brancalion, P. H. S. (2022). A comprehensive experimental assessment of gly-phosate ecological impacts in riparian forest restoration. *Ecological Applications*, 32, e02472. https://doi.org/10.1002/eap.2472

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., … Jakovac, C. (2024). Simple ecological indi-cators benchmark regeneration success of Amazonian forests. *Communications Earth & Environment*, 5, 780. https://doi.org/10.1038/s43247-024-01949-9

Hartig, F. (2024). *DHARMa: Residual diagnostics for hierarchical (multi-level/mixed) regression models*. R package version 0.4.7. https://doi.org/10.32614/CRAN.package.DHARMa

Holl, K. D., Reid, J. L., Chaves-Fallas, J. M., Oviedo-Brenes, F., & Zahawi, R. A. (2017). Local tropical forest restoration strategies affect tree recruitment more strongly than does landscape forest cover. *Journal of Applied Ecology*, 54, 1091–1099. https://doi.org/10.1111/1365-2664.12814

Holl, K. D., Reid, J. L., Cole, R. J., Oviedo-Brenes, F., Rosales, J. A., & Zahawi, R. A. (2020). Applied nucleation facilitates tropical forest recovery: Lessons learned from a 15-year study. *Journal of Applied Ecology*, 57, 2316–2328. https://doi.org/10.1111/1365-2664.13684

Holl, K. D., Reid, J. L., Zahawi, R. A., de Siqueira, L. P., & Brancalion, P. H. S. (2024). A call for practical spatially patterned forest restoration methods. *Restoration Ecology*, 32, e14266. https://doi.org/10.1111/rec.14266

Holl, K. D., Stout, V. M., Reid, J. L., & Zahawi, R. A. (2013). Testing heterogeneity-diversity relationships in tropical forest restoration. *Oecologia*, 173, 569–578. https://doi.org/10.1007/s00442-013-2632-9

Holl, K. D., & Zahawi, R. A. (2014). Factors explaining variability in woody above-ground biomass accumulation in restored tropical forest. *Forest Ecology and Management*, 319, 36–43. https://doi.org/10.1016/j.foreco.2014.01.024

Hsieh, T. C., Ma, K. H., & Chao, A. (2016). iNEXT: An R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods in Ecology and Evolution*, 7, 1451–1456. https://doi.org/10.1111/2041-210X.12613

La Mantia, T., Rühl, J., Massa, B., Pipitone, S., Lo Verde, G., & Bueno, R. S. (2019). Vertebrate-mediated seed rain and artificial perches contribute to overcome seed dispersal limitation in a Mediterranean old field. *Restoration Ecology*, 27, 1393–1400. https://doi.org/10.1111/rec.13009

Langhammer, P. F., Bull, J. W., Bicknell, J. E., Oakley, J. L., Brown, M. H., Bruford, M. W., Butchart, S. H. M., Carr, J. A., Church, D., Cooney, R., Cutajar, S., Foden, W., Foster, M. N., Gascon, C., Geldmann, J., Genovesi, P., Hoffmann, M., Howard-McCombe, J., Lewis, T., … Brooks, T. M. (2024). The positive impact of conservation action. *Science*, 384, 453–458. https://doi.org/10.1126/science.adj6598

Lenth, R. V. (2025). *emmeans: Estimated marginal means, aka least-squares means*. R package version 1.11.0. https://doi.org/10.32614/CRAN.package.emmeans

Li, L., Cadotte, M. W., Martínez-Garza, C., Peña-Domene, M., & Du, G. (2018). Planting accelerates restoration of tropical forest but assembly mechanisms appear insensitive to initial composition. *Journal of Applied Ecology*, 55, 986–996. https://doi.org/10.1111/1365-2664.12976

Mendes, L. M., César, R. G., Uezu, A., Beltrame, T. P., Rodriguez, L. C. E., Gomes, H. B., & Cullen, L. (2021). Large canopy and animal-dispersed species facilitate natural regeneration in tropical forest restoration. *Restoration Ecology*, 29, e13406. https://doi.org/10.1111/rec.13406

National Academy of Sciences. (2023). *An assessment of native seed needs and the capacity for their supply: Final report*. The National Academies Press. https://doi.org/10.17226/26618

Nilson, T. (1971). A theoretical analysis of the frequency of gaps in plant stands. *Agricultural Meteorology*, 8, 25–38. https://doi.org/10.1016/0002-1571(71)90092-6

Pilon, N. A. L., Buisson, E., & Durigan, G. (2018). Restoring Brazilian savanna ground layer vegetation by topsoil and hay transfer. *Restoration Ecology*, 26, 73–81. https://doi.org/10.1111/rec.12534

Procknow, D., Rovedder, A. P. M., Piaia, B. B., Camargo, B., de Moraes Stefanello, M., da Silva, M. P. K. L., da Silva, P. S., Croda, J. P., & Dreyer, J. B. B. (2023). Monitoring ecological restoration of riparian forest: Is the applied nucleation effective ten years after implementation in the Pampa? *Forest Ecology and Management*, 538, 120955. https://doi.org/10.1016/j.foreco.2023.120955

R Core Team. (2024). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. http://www.R-project.org/

Ramírez-Soto, A., Lucio-Palacio, C. R., Rodríguez-Mesa, R., Sheseña-Hernández, I., Farhat, F. N., Villa-Bonilla, B., Landa Libreros, L., Gutiérrez Sosa, G., Trujillo Santos, O., Gómez Sánchez, I., & Ruelas Inzunza, E. (2018). Restoration of tropical montane cloud forests: A six-prong strategy. *Restoration Ecology*, 26, 206–211. https://doi.org/10.1111/rec.12660

Rodrigues, R. R., Lima, R. A. F., Gandolfi, S., & Nave, A. G. (2009). On the restoration of high diversity forests: 30 Years of experience in the Brazilian Atlantic Forest. *Biological Conservation*, 142, 1242–1251. https://doi.org/10.1016/j.biocon.2008.12.008

Rojas-Botero, S., Solorza-Bejarano, J., Kollmann, J., & Teixeira, L. H. (2020). Nucleation increases understory species and functional diversity in early tropical forest restoration. *Ecological Engineering*, 158, 106031. https://doi.org/10.1016/j.ecoleng.2020.106031

Roussel, J.-R., Auty, D., Coops, N. C., Tompalski, P., Goodbody, T. R. H., Meador, A. S., Bourdon, J.-F., de Boissieu, F., & Achim, A. (2020). lidR: An R package for analysis of Airborne Laser Scanning (ALS) data. *Remote Sensing of Environment*, 251, 112061. https://doi.org/10.1016/j.rse.2020.112061

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. *Ecological Applications*, 35, e3053. https://doi.org/10.1002/eap.3053

Shaw, J. A., Roche, L. M., & Gornish, E. S. (2020). The use of spatially-patterned methods for vegetation restoration and management across systems. *Restoration Ecology*, 28, 766–775. https://doi.org/10.1111/rec.13198

Silva, C. A., Valbuena, R., Pinagé, E. R., Mohan, M., de Almeida, D. R. A., North Broadbent, E., Jaafar, W. S. W. M., de Almeida Papa, D., Cardil, A., & Klauberg, C. (2019). ForestGapR: An r package for forest gap analysis from canopy height models. *Methods in Ecology and Evolution*, 10, 1347–1356. https://doi.org/10.1111/2041-210X.13211

Toro, L., Torres-Romero, F., Salinas, S. M., Avella-Munoz, A., Galatowish, S., Secchi, S., & Powers, J. S. (2024). Cost-effectiveness of management strategies in a nucleation experiment in a tropical dry forest. *Restoration Ecology*, 32, e14094. https://doi.org/10.1111/rec.14094

Valette, M., Vinceti, B., Gregorio, N., Bailey, A., Thomas, E., & Jalonen, R. (2020). Beyond fixes that fail: Identifying sustainable improvements to tree seed supply and farmer participation in forest and landscape restoration. *Ecology and Society*, 25, art30. https://doi.org/10.5751/ES-12032-250430

Xavier, A. C., Scanlon, B. R., King, C. W., & Alves, A. I. (2022). New improved Brazilian daily weather gridded data (1961–2020). *International Journal of Climatology*, 42, 8390–8404. https://doi.org/10.1002/joc.7731

Yarranton, G. A., & Morrison, R. G. (1974). Spatial dynamics of a primary succession: Nucleation. *Journal of Ecology*, 62, 417–428. https://doi.org/10.2307/2258988

Zahawi, R. A., & Augspurger, C. K. (2006). Tropical forest restoration: Tree islands as recruitment foci in degraded lands of Honduras. *Ecological Applications*, 16, 464–478. https://doi.org/10.1890/1051-0761

Zahawi, R. A., Holl, K. D., Cole, R. J., & Reid, J. L. (2013). Testing applied nucleation as a strategy to facilitate tropical forest recovery. *Journal of Applied Ecology*, 50, 88–96. https://doi.org/10.1111/1365-2664.12014

Zahawi, R. A., Reid, J. L., & Holl, K. D. (2014). Hidden costs of passive restoration. *Restoration Ecology*, 22, 284–287. https://doi.org/10.1111/rec.12098

Zhang, W., Qi, J., Wan, P., Wang, H., Xie, D., Wang, X., & Yan, G. (2016). An easy-to-use airborne LiDAR data filtering method based on cloth simulation. *Remote Sensing*, 8, 501. https://doi.org/10.3390/rs8060501

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. List of planted and naturally recruiting tree species.

Table S2. Summary of restoration metrics across treatments and areas at different times after planting.

Table S3. GLMMs results for multiple response variables showing model specifications, fit statistics, and parameter estimates (±SE), *Z*-values, and *p*-values.

Figure S1. Planting designs.

Figure S2. Sample based species rarefaction curve of smaller recruits (excluding *Baccharis dracunculifolia* and *Vernonia polyanthes*) by treatment and in planted and unplanted areas of nuclei and strip plantings.