Species diversity reduces risk in tropical forest restoration: a portfolio effect across heterogeneous sites

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Abstract

Assisted restoration is essential for recovering degraded tropical forests. Biodiversity-stability theory predicts that functionally diverse communities should produce more reliable, predictable outcomes than monocultures, but broad-scale field experiments in tropical restoration are scarce. We established 120 plots spanning five planting treatments (two monocultures – of a fast-growing nitrogen-fixer or a fleshy-fruit species – and 2-, 6-, and 12-species mixes), with species selected at each richness level to maximize functional trait diversity, across four sites in southwestern Costa Rica. After three years we measured height, canopy cover, carbon stocks, survival, and structural heterogeneity. *Inga edulis* monocultures (the same nitrogen-fixer at all four sites) achieved the highest mean carbon stocks (5.4 Mg C ha^{-1}) and fastest height growth (3.7 m vs 1.7-2.2 m in mixtures) but survived less and far less predictably across sites (78%, 56-100%, versus 90%, 83-95% in mixtures). Which species survived consistently therefore mattered more than which grew fastest. Each site's mixtures comprised different locally adapted species yet converged on consistent outcomes, so predictability appeared to be a property of diverse mixtures generally, not of any single shared species. Diverse mixtures were three- to four-fold less variable in survival across sites and developed up to 140% more within-plot structural heterogeneity than monocultures, suggesting a dual benefit of more structurally complex habitat within plots and more predictable establishment across them. Because functional diversity saturated at roughly six species, six-species mixes captured most of this benefit, with only marginal gains at twelve. Our results provide evidence for a biodiversity portfolio effect (*i.e.,* biodiversity insurance) in assisted tropical restoration, whereby functionally diverse plantings trade peak productivity for predictability, buffering against the unpredictable, low-survival outcomes that drive replanting costs, at little added expense.

Introduction

Tropical forests harbor more than half of terrestrial vertebrate species (Pillay et al., 2022) and are critical for carbon sequestration, yet more than half of the world's original tropical forest has been lost (Barlow et al., 2016; Lewis et al., 2015; Malhi et al., 2014). As a result, natural climate solutions have emerged as a key pathway alongside fossil fuel reduction to address the climate crisis (Griscom et al., 2017, 2019; Seddon et al., 2021), and restoring degraded land to forests is scaling rapidly under commitments such as the Bonn Challenge and the UN Decade on Ecosystem Restoration (Holl, 2017). Restoration practices span a continuum from natural regeneration to assisted restoration involving direct tree planting, with the latter often required in degraded landscapes where natural recovery is slow (Chazdon et al., 2024; Crouzeilles et al., 2020; Stanturf, 2021). Assisted restoration is the most resource-intensive approach necessary in the most degraded ecosystems, where species selection is a key determinant of its outcomes (Butterfield, 1996; Fremout et al., 2021; Werden et al., 2018). However, many reforestation programs prioritize fast-growing species for rapid carbon sequestration, often resulting in low-diversity plantations that may underperform across variable site conditions (Holl et al., 2022). As climate change intensifies the unpredictability of restoration outcomes across landscapes, understanding whether species diversity can buffer outcomes against site-level variation has become an urgent question for both restoration science and policy, with implications for how carbon crediting programs may assess permanence risk.

A long history of evidence from biodiversity-ecosystem functioning research suggests that species diversity can enhance mean ecosystem productivity, and can also stabilize it across space and time (Hector et al., 2010; Isbell et al., 2015; Loreau & De Mazancourt, 2013; Tilman, 1999). The biodiversity insurance hypothesis predicts that diverse communities buffer ecosystem functioning against environmental variability because different species respond differently, providing functional redundancy when individual species underperform (Van De Peer et al., 2016; Yachi & Loreau, 1999). In this sense the planting of diverse mixtures of species provides the benefits of a financial portfolio. That is, by spreading investment across many species, each with a different response to local conditions, it is possible to lower the risk that the whole planting underperforms, in exchange for somewhat lower average early returns than the single best-performing species. Yet, until now, the existence of a trade-off between stability and peak performance remains untested under field conditions within a tropical restoration setting.

Beyond stabilizing average outcomes, species diversity in planted forests is expected to increase structural heterogeneity – the variation in tree size, canopy architecture, and biomass within and among plots (Holl et al., 2013; Huang et al., 2018). Structural heterogeneity enhances light capture, niche partitioning, and microhabitat diversity, and is increasingly recognized as a key indicator of overall performance (Baruffol et al., 2013; Coverdale & Davies, 2023; Perles-Garcia et al., 2021). Broad-scale studies have generally revealed a positive effect of diversity on productivity across global forests (Liang et al., 2016; Zhang et al., 2012), and experimental tree diversity networks have demonstrated complementarity and insurance effects in planted systems (Verheyen et al., 2016). Functional diversity offers a practical framework for designing species mixes that maximize niche complementarity and resource use efficiency (Cadotte et al., 2011; Díaz et al., 2007; Laughlin, 2014; Ostertag et al., 2015; Petchey & Gaston, 2002). However, until now, most experimental evidence for diversity-stability relationships in tree plantations comes from temperate and boreal systems. Whether diversity acts as insurance for outcomes in tropical restoration, where environmental heterogeneity is high and the stakes for global carbon and biodiversity are greatest, remains an open question (for temperate sites *see* Van De Peer et al., 2016).

Here, we present three-year outcomes from a tropical wet forest restoration experiment spanning four degraded sites across a steep environmental gradient (450-1,160 m elevation, 3,800-6,140 mm rainfall) in southwestern Costa Rica. We planted 120 plots in five treatments ranging from monocultures to 12-species mixes (plus 24 unplanted controls), with species selected to maximize functional trait space at each richness level. We selected species at each richness level to maximize functional trait diversity from the locally available nursery pool, so the richness gradient is, by design, a functional-diversity gradient. This lets us test whether more functionally diverse plantings produce greater structural complexity and more predictable outcomes across variable sites. We therefore read richness effects as functional-diversity effects, noting the design does not isolate the two. We assessed three specific questions: (1) Do fast-growing monocultures outperform diverse mixes, and does the answer depend on site? (2) Through what pathways does planted diversity (functional diversity, manipulated via species richness) shape within-plot structural heterogeneity? (3) Does this diversity reduce cross-site variability in multivariate outcomes? We predicted that diverse treatments would show lower mean productivity than the best-performing monoculture at this early stage but greater consistency across sites – consistent with a portfolio effect of planting functionally diverse species across a strong environmental gradient.

Methods

Study sites

We conducted the study at four sites, each covering 3-4 hectares, in collaboration with four restoration-focused organizations: Loma Linda Field Station (LLFS), Finca Cantaros Environmental Association (FCEA), Finca Aguas Buenas (FAB) and Tropical Field Station La Gamba – University of Vienna (GAM). These organizations had the facilities to collect seeds and grow seedlings of a wide variety of tree species native to the local area. All sites were degraded lands located in tropical forest zones in southern Costa Rica, captured a range of local conditions, and were widely separated (>8km), allowing us to generalize across a broader region. The sites in this study are located at the boundary between the Tropical Wet Forest and Premontane Wet/Rain Forest zones (Holdridge et al., 1971), range in elevation from 450 to 1,160 meters, and receive an average annual rainfall of 3,800-6,140 mm, with a drier season from December to March that is weak at the wettest site (La Gamba, ~6,140 mm yr^{-1}). The mean annual temperature ranged from 21-28°C. All sites were used for cattle grazing and mixed agriculture for >22 years (Table S1). At the start of the study, the sites were primarily dominated by opportunistic non-native forage grasses including *Axonopus scoparius*, *Pennisetum purpureum*, *Melinis minutiflora*, and *Urochloa brizantha*, along with the fern *Pteridium arachnoideum*. Each site featured diverse, rugged terrain, with slopes ranging from 5 to 32 degrees. The soils, of volcanic origin, were mildly acidic and low in phosphorus.

Species selection

To include the broadest range of tree functional diversity in our experimental design, we compiled a list of native tree species for which seedlings could be produced in sufficient quantities at each site (82 species at LLFS, 56 at FCEA, 49 at FAB and 59 at GAM). We standardized taxonomic names using the *Treemendous* package (Specker et al., 2024). We then extracted available data from the TRY Plant Trait Database (Kattge et al., 2020) for 18 tree traits, including leaf (area, specific leaf area, density, thickness, nitrogen, phosphorus, potassium), seed mass, bark thickness, wood density, architectural traits (maximum crown height and diameter, maximum height, diameter), physiological traits (stem conduit diameter, stomatal conductance, Vcmax), and maximum root depth (see Table S2 for full trait list and units). For species with missing trait data, we imputed missing trait values using the models generated in Maynard et al. (2022), which integrate phylogenetic and environmental information.

After compiling the functional trait data, we visualized all candidate species in trait space using principal components analysis (PCA). We coded categorical trait values to highlight species by nitrogen-fixing status (non-fixer, nitrogen-fixer) and dispersal syndrome (animal-dispersed, animal-dispersed with carbohydrate-rich fleshy fruit, other; Fig. S1). This approach aligns with calls to make functional trait–based species selection more accessible to restoration practitioners (Gornish et al. 2023), as tools such as the freely available Restoring Ecosystem Services Tool (REST) allow users to upload a .csv file of species and trait data, then perform and visualize a PCA for species selection (Rayome et al., 2019). From each PCA biplot, we selected two core species based on predetermined traits: a fast-growing nitrogen-fixer and a species that produces carbohydrate-rich, fleshy fruit (Table S3). We then selected additional native candidate species to maximize trait diversity by filling as much trait space as possible within each quadrant of the biplot, adding approximately one species per quadrant to construct the 6SP treatments, then an additional six distributed across quadrants to build the 12SP treatments, ensuring nursery seedling availability of each selected species. Because sites were located across a diverse landscape, the selected species reflected local availability and conditions. As a result, species composition (except for the *Inga edulis* monoculture; M1) varied across sites, although functionally analogous species were included in the same proportions across all sites (Table S3). This design created a gradient in which planted species richness covaries with functional trait space occupancy, allowing us to test whether greater diversity stabilized restoration outcomes across heterogeneous sites.

Experimental design

We set up the sites over a three-year period: one in 2021 (LLFS), two in 2022 (FCEA and FAB) and the last in 2023 (GAM) (Fig. 1a). Each site consisted of six blocks, to account for differences in microtopography, each of which contained six different tree planting treatment plots (n = 6 plots × 6 treatments × 4 sites = 144 plots total) (Fig. 1b). Of these, 120 plots comprised the five planted treatments analyzed here, and 24 were unplanted controls (not analyzed here). The treatments included: (1) a fast-growing nitrogen-fixing monoculture (always *Inga edulis*; M1); (2) a monoculture of a carbohydrate-rich fruit producer (M2), using a locally selected species at each site: *Ficus insipida* (FAB), *Saurauia montana* (FCEA), *Citharexylum cooperi* (GAM), and *Calophyllum brasiliense* (LLFS); (3) a 50/50% mix of these two core species (*i.e.,* 50% M1 species + 50% M2 species = 2SP treatment); (4) a mix of the two core species plus four additional species (6-species mix); (5) a mix of the same six species plus six more species (12-species mix); and, for design completeness, a sixth

unplanted control (natural regeneration) that we describe but did not analyze (Table 1). The unplanted control plots will be used in follow-up studies examining seed rain, seedling recruitment, and natural regeneration dynamics across the treatments. These treatments contrast restoration strategies practitioners typically use in assisted tropical forest restoration: a fast-growing nitrogen-fixer monoculture (M1, a regional default), a fleshy-fruit monoculture intended to attract seed dispersers (M2), and a 2 → 6 → 12-species richness ladder in which each level maximized functional trait diversity from the local nursery pool. All species were planted in equal amounts within each treatment plot.

Table 1. Details of each of the six treatments (control not analyzed). Each block has six 15 × 15m plots with one of each of the following treatments.

Treatment	Treatment code	Number of species planted
Control (*i.e.,* natural regeneration; not included in analysis)	C	0
Monoculture of a fast-growing nitrogen-fixer	M1	1
Monoculture of species that produces carbohydrate-rich fruit	M2	1
Nitrogen-fixer + fruit producer	2SP	2
Nitrogen-fixer + fruit producer + 4 additional species with diverse traits	6SP	6
Nitrogen-fixer + fruit producer + 4 species used above + 6 additional species with diverse traits	12SP	12

In 2021 at LLFS, 2022 at FAB and FCEA and 2023 at GAM, we established 36 plots per site, 30 of which were planted with 48 trees each (5,760 seedlings total) spaced 2.5 m apart in a grid pattern (Fig. 1c). Plots measured 15 × 15m, were spaced a minimum of 10 m apart from each other, and at least 10 m away from any other existing trees or forest edges. We distributed seedlings in the mixed-species treatments evenly across each plot following two possible designs for the 2-species mix, and four possible planting designs for the 6- and 12- species mixes. We randomly assigned these designs to each plot to minimize planting location biases and ensure a fair comparison of species interactions.

Site preparation, tree planting and maintenance followed standard forestry practices in the region (Holl et al., 2011). We prepared the sites by clearing naturally established vegetation to ground level with machetes or string trimmers immediately prior to planting. Seedlings were planted into uniform holes (35 cm deep × 30 cm diameter) with 30 g of NPK

(10-30-10) fertilizer and 5 g of granular nematicide (Mocap®) mixed into the soil in the root zone. For the first year post-planting, all other vegetation within all plots (including unplanted controls) was cleared at 4-month intervals to promote seedling establishment / ensure similar initial conditions for recovery of native vegetation. During the second year, clearing was restricted to a 1-m radius around individual seedlings until they overtopped the surrounding vegetation, after which maintenance ceased. Inter-plot spaces were not cleared. Seedlings that died in the first and second year were replaced.

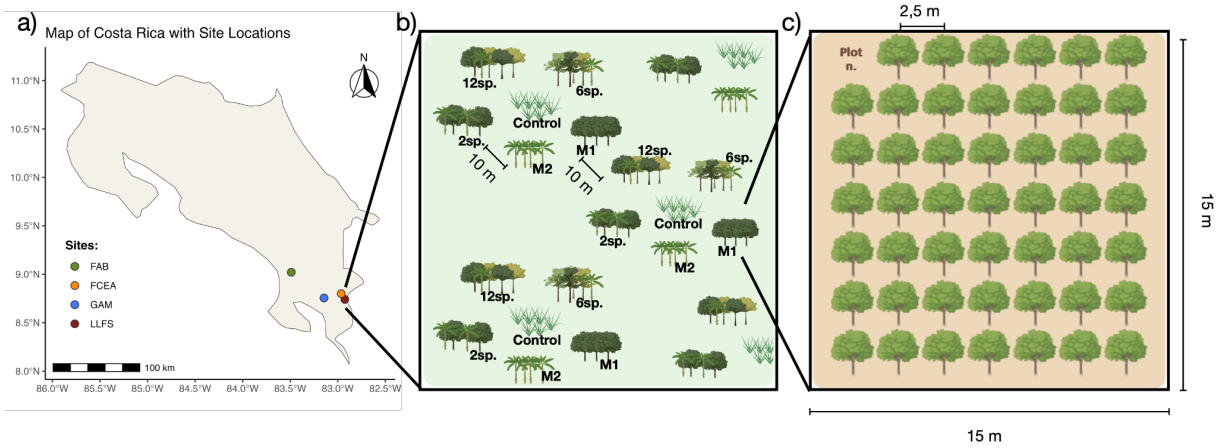

Figure 1. Experimental design in southwestern Costa Rica. (a) Geographic location of the four experimental sites. (b) At each site, six blocks each containing six randomly assigned treatment plots, spaced ≥ 10 m apart and ≥ 10 m from forest edges. (c) Each plot is 15 × 15 m with 48 trees spaced 2.5 m apart; control plots are unplanted.

Data collection

We measured planted seedling survival annually, including all replanted seedlings starting in 2022 at LLFS, 2023 at FCEA and FAB and 2024 at GAM. In February-March 2024, 2025, and 2026 (3 years after planting each site), we measured height (base of trunk to apical meristem) and DBH (Diameter at Breast Height; 1.3 m) for all seedlings with a DBH ≥ 1 cm to quantify planted seedling performance. To simplify data collection, we measured height and DBH of a random half of monoculture seedlings (24 of 48 per plot) from 2024 onward, after preliminary measurements showed highly homogeneous growth in these plots. From 2024 to 2026, we measured percent canopy cover using a spherical densiometer at 6 locations within each plot.

Statistical analysis

Our statistical approach addressed our three questions at two levels of analysis. First, we tested treatment effects on seven plot-level vegetation recovery metrics (height, canopy cover, carbon, survival, and three Gini heterogeneity indices) using linear mixed-effects models and used structural equation models to identify the pathways through which richness shaped structural heterogeneity. Second, we assessed whether species richness stabilized multivariate outcomes across sites using principal components analysis and multivariate dispersion. All analyses were conducted in R v4.5.0 (R Development Core Team, 2025).

Plot-level calculations:

We calculated plot-level productivity (carbon stocks, total basal area), vegetation recovery (mean height, canopy cover, survival), and structural heterogeneity (Gini coefficients of height, canopy cover, and carbon) for all plots after three years of growth. We estimated mean plot-level height and canopy cover as the arithmetic mean of all individuals in each plot (48 individuals x plot, height) or all transects measured in each plot (6 transects x plot, percent canopy cover). Then, we calculated plot-level survival as the proportion of the 48 planted tree positions per plot with a living individual at year 3; positions where the original seedling died during years 1-2 and was successfully replanted are counted as alive, consistent with our annual survival census above, which included all replanted seedlings. Sensitivity analyses excluding replanted individuals from the multivariate dispersion analysis are reported in Table S4.

We estimated aboveground biomass (AGB) using the Chave et al. (2014) pantropical allometric model implemented in the BIOMASS package (Réjou-Méchain et al., 2017). We assigned each species a best-estimate wood density compiled across the BIOMASS package, the BIEN database (Maitner et al., 2018), the Global Wood Density Database (Chave et al., 2009), the Tervuren Xylarium Wood Density Database (Verbiest et al., 2026), and the CIRAD wood-density database (Vieilledent et al., 2017) using species-level values where available and genus-level means for the 11 of 35 species lacking species-level data (17% of biomass-measured individuals). We estimated carbon as AGB × 0.47 and scaled to Mg C ha^{-1}. We calculated total plot-level basal area by summing the basal areas of all seedlings with a DBH ≥ 1 cm within each plot at year 3 and calculated individual basal area and height of *Inga edulis* per treatment at all sites to monitor monoculture species performance across treatments.

We also calculated plot-level heterogeneity of tree height, canopy cover, and carbon stocks across all planted seedlings for all assisted restoration plots (6 plots per 5 treatments per site) at the end of year 3 using the Gini coefficient:

$$\text{Gini coefficient} = [\ \Sigma_{i=1}^{n} (2i - n - 1)\ x_i\ ] / (\ n\ \Sigma_{i=1}^{n} x_i\ )$$

where x_i are the values for the i-th individual (tree height, canopy cover, or carbon stocks) sorted in ascending order and n is the number of individuals per plot: 48 individuals for tree height and carbon Gini, and 6 densiometer transect points for canopy cover Gini.

Comparing between treatments:

We used linear mixed-effects models (*lme4* and *lmerTest*) to test how planting treatments influenced plot-level outcomes. All plot-level models included treatment (5 levels: M1, M2, 2SP, 6SP, 12SP), site (4 levels: FAB, FCEA, GAM, LLFS), and their interaction as fixed effects, with block nested within site as a random intercept: response ~ Treatment × Site + (1|Site:Block). We examined model assumptions using simulated residuals (*DHARMa*). Where diagnostics indicated non-normality, we log-transformed responses (carbon, total basal area, *Inga edulis* basal area). We modeled survival as a binomial GLMM on plot-level alive/dead counts using *glmmTMB*. The survival binomial GLMM showed no significant overdispersion (DHARMa test, $p = 0.12$), so we retained a binomial rather than a beta-binomial. We tested the significance of fixed effects using Type-III ANOVAs with Satterthwaite denominator degrees of freedom and computed partial eta-squared ($\eta^2 p$) as an effect size. When ANOVAs were significant, we performed pairwise treatment comparisons using estimated marginal means (*emmeans*) with Tukey-adjusted p-values, and compact letter displays indicated significant differences at $\alpha = 0.05$.

To assess whether species diversity stabilized multivariate restoration outcomes across sites, we scaled the seven plot-level metrics (mean height, carbon, canopy cover, survival, height Gini, canopy Gini, carbon Gini) to unit variance and performed principal components analysis (PCA). We quantified how consistently each treatment performed across plots and sites by measuring multivariate dispersion – the spread of plots around their treatment means in seven-dimensional outcome space (betadisper; *vegan*). We first tested whether monocultures and polycultures differed in multivariate dispersion using betadisper with a permutation test (all five treatments included).

We then tested whether dispersion decreased monotonically along the designed richness gradient (M1, 2SP, 6SP, 12SP). The richness gradient followed the designed planting sequence; M2 tested a different species identity at richness = 1 across sites, so we

did not include it as part of this gradient (though we report M2-inclusive sensitivity below). As our primary test of monotonic decrease, we computed the Spearman correlation between richness and distance to centroid and assessed significance using a permutation test (9,999 permutations) with standardized effect size (SES), as permutation tests do not rely on distributional assumptions that linear models on multivariate distances may violate. We assessed robustness via leave-one-site-out sensitivity, exclusion of replanted individuals, and a temporal trajectory across years 1–3. We also re-ran the Spearman test with M2 included (coded as richness = 1 alongside M1) to confirm the dispersion–richness trend was not an artifact of M2 exclusion. Because the permutation test treats plots as exchangeable, we also fit a linear mixed-effects model on betadisper distances with richness as a fixed effect and site and block as random intercepts, so that the richness effect is estimated while accounting for the four-site structure. To check that the richness–dispersion relationship was not an artifact of metrics scaling with their mean, we re-estimated it under log- and rank-transformations and on a bounded-only subset (survival plus the three Gini indices) and examined each metric's among-site CV and mean-variance coupling. We also computed Rao's Q and functional dispersion (FDis) per treatment (*FD* package, using Gower trait distances) to test whether functional diversity saturated along the richness gradient.

Finally, we used structural equation models (*piecewiseSEM*) to test the hypothesized pathway from planted species richness through carbon accumulation and canopy cover to structural heterogeneity, with site as a random effect. Again, we excluded M2 from the structural equation models because it shared richness = 1 with M1 but differed in species identity across sites; as a reparameterization check, a supplementary structural equation model recoded the gradient as *I. edulis* proportion (collinear with richness) and included all treatments.

Results

We present results pooled across all four sites. Site-specific results, model diagnostics, and robustness analyses are in the supplement (Figs. S2-S12, Tables S4-S8).

Plot-level ecosystem outcomes:

Planted species richness strongly influenced plot-level ecosystem outcomes after three years (Table 2; Fig. 2). Mean tree height differed significantly among treatments ($F_{4,79}$ = 46.34, $p < 0.001$, $\eta^2p = 0.70$), with *I. edulis* monocultures (M1) reaching 3.70 ± 1.06 m compared to 1.66-2.20 m in mixed-species treatments and 1.29 m in M2. Canopy cover

followed a similar pattern ($F_{4,79} = 29.35$, $p < 0.001$, $\eta^2p = 0.60$), with M1 averaging 71% versus 23-42% in mixed treatments and 11% in M2. Estimated carbon stocks were highest in M1 (5.44 ± 4.06 Mg C ha^{-1}) and lowest in M2 (0.09 Mg C ha^{-1}), with 2SP-12SP treatments intermediate at 1.76-2.60 Mg C ha^{-1} ($F_{4,75.5} = 44.84$, $p < 0.001$, $\eta^2p = 0.70$). The Treatment × Site interaction was significant for carbon ($p = 0.045$), reflecting M1's variable performance across sites (*see* Figs. S3-S6).

Survival differed among treatments (Wald $\chi^2 = 72.3$, df = 4, $p < 0.001$) with a strong Treatment × Site interaction (Wald $\chi^2 = 165.9$, df = 12, $p < 0.001$). Mixed-species treatments averaged 90% survival (83–95% across sites) and performed similarly across the three richness levels (each ~90–91%), while both monocultures were lower and more variable: M1 averaged 78% but ranged from 56% at FCEA and LLFS to 99-100% at FAB and GAM, and M2 averaged 78% but with high among-plot variability (SD = 26%).

Structural heterogeneity:

Within-plot structural heterogeneity, measured with the Gini coefficient, increased with planted species richness for all three metrics (Fig. 3). Height heterogeneity showed the strongest treatment effect ($F_{4,79.2} = 135.82$, $p < 0.001$, $\eta^2p = 0.87$), increasing 140% – from 0.16 in M1 to 0.39 in 12-species plots – with a significant Treatment × Site interaction ($F_{12,79.2} = 5.23$, $p < 0.001$). Canopy cover heterogeneity followed a similar gradient ($F_{4,77.9} = 24.57$, $p < 0.001$, $\eta^2p = 0.56$), though M2 was an outlier with the highest values (0.49) due to patchy seedling mortality. Carbon stock heterogeneity likewise increased with richness ($F_{4,76.1} = 37.73$, $p < 0.001$, $\eta^2p = 0.67$), from 0.28 in M2 and 0.43 in M1 to 0.62 in 12-species plots, reflecting the combined effects of species mixes on wood density and growth rates.

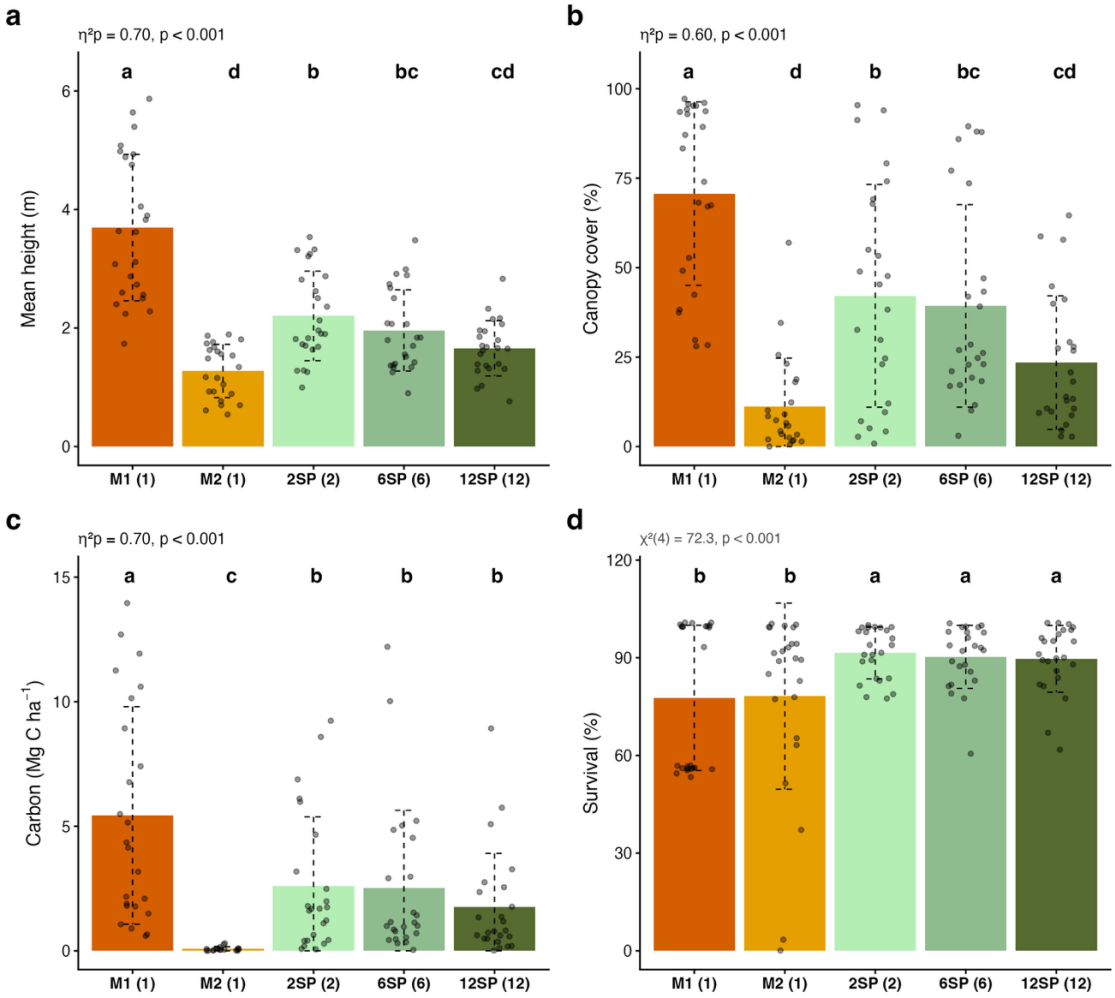

Figure 2. Ecosystem outcomes across planting treatments pooled across four sites after three years. (a) Mean tree height, (b) canopy cover, (c) carbon stocks, and (d) survival. Bars are treatment means ± standard errors. Letters denote significant pairwise differences (Tukey HSD for panels a-c; Sidak-adjusted for panel d; $p < 0.05$); η^2p from linear mixed models with block nested within site as a random effect. M1 = *Inga edulis* monoculture, M2 = fleshy-fruit monoculture, 2SP/6SP/12SP = 2-, 6-, and 12-species mixes.

Table 2. Results of linear mixed-effects models for seven plot-level ecosystem outcomes, with treatment, site, and their interaction as fixed effects and block nested within site as a random intercept. F-values, numerator (df_1) and denominator (df_2) degrees of freedom, p-values, and partial eta-squared (η^2p) shown for each fixed effect. Denominator degrees of freedom estimated via Satterthwaite approximation. Survival modeled as a binomial GLMM. Survival rows report Wald χ^2 (df shown), not F.

Metric	Term	F	df_1	df_2	p-value	η^2p
Mean height (m)	Treatment	46.34	4	79.0	< 0.001	0.70
	Site	12.28	3	19.7	< 0.001	0.65
	Treatment × Site	1.13	12	79.0	0.346	0.15
Canopy cover (%)	Treatment	29.35	4	79.0	< 0.001	0.60
	Site	7.62	3	19.8	0.001	0.54
	Treatment × Site	1.51	12	79.0	0.139	0.19
Carbon (Mg C ha^{-1})	Treatment	44.84	4	75.5	< 0.001	0.70
	Site	5.55	3	20.4	0.006	0.45
	Treatment × Site	1.92	12	75.3	0.045	0.23
Height Gini	Treatment	135.82	4	79.2	< 0.001	0.87
	Site	8.03	3	19.9	0.001	0.55
	Treatment × Site	5.23	12	79.2	< 0.001	0.44
Canopy Gini	Treatment	24.57	4	77.9	< 0.001	0.56
	Site	10.23	3	19.3	< 0.001	0.61
	Treatment × Site	1.86	12	77.8	0.052	0.22
Carbon Gini	Treatment	37.73	4	76.1	< 0.001	0.67
	Site	1.81	3	20.7	0.176	0.21
	Treatment × Site	1.35	12	75.9	0.209	0.18
Survival (%)	Treatment	72.33	4	-	< 0.001	-
	Site	45.82	3	-	< 0.001	-
	Treatment × Site	165.9	12	-	< 0.001	-

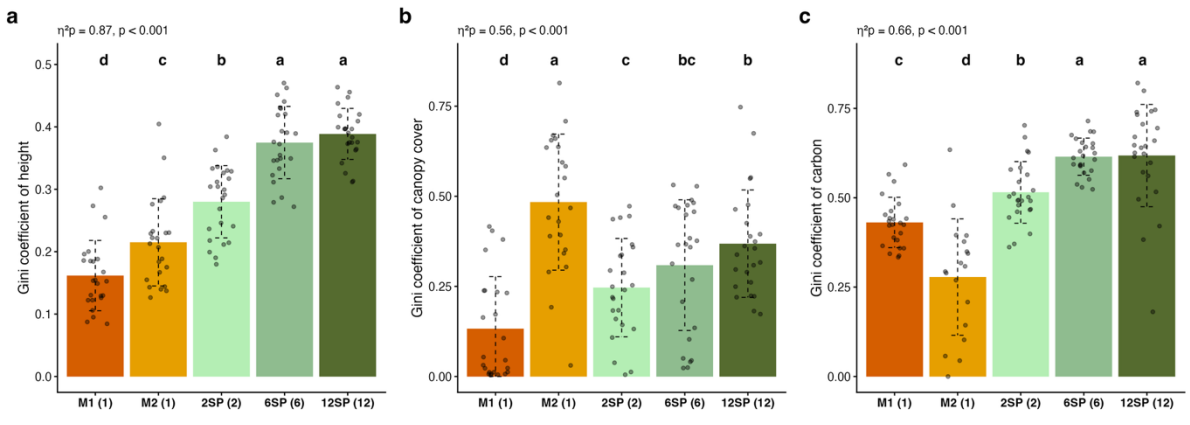

Figure 3. Within-plot structural heterogeneity (Gini coefficient) for (a) tree height, (b) canopy cover, and (c) carbon stocks after three years. Higher values indicate greater within-plot inequality. Bars are treatment means ± standard errors. Letters denote significant pairwise differences (Tukey HSD, $p < 0.05$); η^2p from linear mixed models with block nested within site as a random effect.

Multivariate synthesis and diversity-stability:

A principal components analysis of the seven plot-level metrics (Fig. 4b) showed clear separation of treatments in multivariate space. PC1 (51.5%) separated monocultures from mixed treatments along a gradient from higher productivity (height, carbon, canopy cover) to greater canopy heterogeneity. PC2 (23.4%) captured a gradient from structural uniformity (monocultures) to height and carbon heterogeneity, with survival loading in the same direction as the Gini indices. Notably, the 95% confidence ellipses for M1 were visibly larger than those for diverse treatments, a pattern quantified by the betadisper analysis below, indicating greater multivariate variability across sites. Monocultures were significantly more dispersed than mixed-species treatments in multivariate outcome space (permutest $F = 28.69$, $p = 0.001$; all five treatments included). This difference was concentrated in the fast-growing *I. edulis* monoculture (M1), which was significantly more dispersed than every other treatment, including the fleshy-fruit monoculture (all pairwise $p \leq 0.004$; Table S4C); no other pair differed ($p \geq 0.37$).

Along the designed richness gradient (M1, 2SP, 6SP, 12SP), outcomes became more consistent across sites as planted richness increased (all seven-metric dispersion: Spearman $\rho = -0.41$, permutation $p < 0.001$, Table S4A, Fig. 4b; mixed-effects model accounting for site: $\beta = -0.061$, $p < 0.001$, Table S4B). This did not appear to be an artifact of the productivity metrics' high values: the trend was as strong when restricted to only the bounded survival and structural-heterogeneity metrics, which could not be inflated by high means ($\rho = -0.41$, $p < 0.001$; Table S5). This pattern was strongest when examining only survival, the one outcome immune to mean-variance scaling, and most variable across monocultures (survival-only $\rho = -0.52$, $p < 0.001$). This composite dispersion trend was partly an artifact of scale. It weakened when the metrics were rank-transformed, because the productivity metrics' among-site variability tracked their means rather than falling with richness. The cross-site predictability benefit therefore rested primarily on the bounded survival and structural outcomes (Table S5). Six-species plots captured most of this benefit, with only marginal further gains at twelve. This saturation was confirmed by the trait data, as functional diversity (Rao's Q) rose from monocultures through two- and six-species mixes (~0.035 and 0.070, respectively), but only ~4% further to twelve species (Table S6, Fig. S12), with the six additional species adding little functional diversity across all sites.

This result was robust to the removal of any single site (leave-one-site-out: $\rho = -0.48$, $p < 0.001$ without FAB; $\rho = -0.33$, $p = 0.004$ without FCEA; $\rho = -0.35$, $p = 0.003$ without GAM; $\rho = -0.30$, $p = 0.010$ without LLFS; Table S4D), to exclusion of replanted individuals

(ρ = -0.37, p = 0.0002; 8.1% of trees; Table S4E), and to log-transformed richness (p < 0.001). Including M2 in the richness gradient confirmed the pattern (ρ = -0.31, p = 0.001). The trend direction was consistent across measurement years, strengthening from year 2 (ρ = -0.20, p = 0.088) to year 3 (ρ = -0.38, p = 0.001) in the three-site temporal subset (Table S4F). Partitioning this dispersion into among- and within-site components showed that planted richness reduced variability at both scales (Table S4G). The probability that a stand fell below 70% survival declined from 23% in monocultures to 2.5% in 12-species mixtures (odds ratio 0.80 per added species, p = 0.02; Table S7).

The normalized radar plot (Fig. 4a) illustrates treatment profiles across all seven metrics, with M1 dominating productivity-related axes but scoring lowest on heterogeneity. Although M1 held the highest mean carbon, it accumulated the most at its two lowest-survival sites (8.28 Mg C ha^{-1} at LLFS, 4.74 at FCEA, both ~56% survival), decoupling carbon from establishment success. At the individual scale, *I. edulis* basal area averaged 28% higher in 12-species plots than in monoculture, overyielding at three of four sites (Fig. S10).

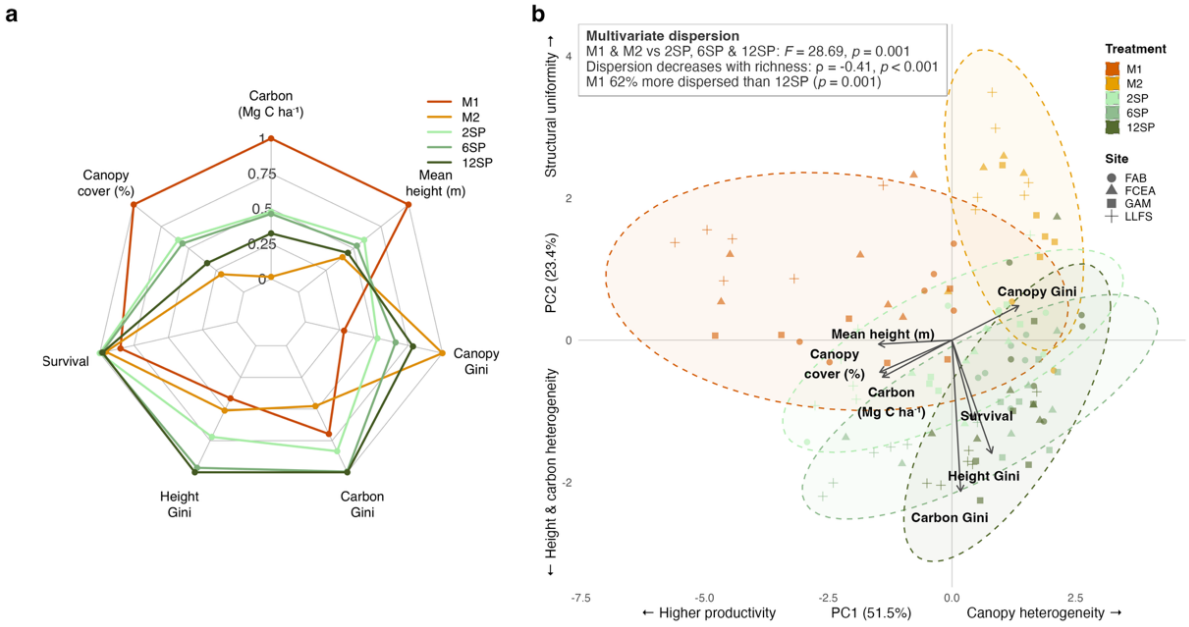

Figure 4. Multivariate synthesis of treatment outcomes. (a) Radar plot of seven plot-level metrics averaged by treatment, normalized to each metric's maximum (1.0 = highest-performing treatment). (b) Principal components analysis of the same metrics with 95% confidence ellipses; PC1 (51.5%) separates monocultures from diverse treatments along productivity and survival, PC2 (23.4%) captures structural heterogeneity. Cross-site consistency increased with planted richness (seven-metric dispersion ρ = -0.41, p < 0.001), most robustly in the bounded survival and structural outcomes (survival-only ρ = -0.52; Table S5). M2 (fleshy-fruit monoculture) is shown but excluded from the dispersion–richness correlation as a different species identity at richness = 1 rather than a point on the designed gradient (M2-inclusive ρ = -0.31, p = 0.001).

Structural equation model:

The piecewise structural equation model (excluding M2; Fisher's C = 8.55, df = 6, p = 0.20) revealed that planted species richness was associated with structural heterogeneity through two pathways (Fig. 5). Richness showed a strong positive association with height heterogeneity (β = 0.83, p < 0.001) and a negative effect on carbon accumulation (β = -0.35, p < 0.001). Carbon in turn had a strong positive effect on canopy cover (β = 0.68, p < 0.001), while canopy cover strongly reduced canopy heterogeneity (β = -0.81, p < 0.001). The direct effect of richness on canopy cover was negative (β = -0.29, p < 0.05), and the path from height heterogeneity to canopy cover was non-significant (β = 0.03, ns). Marginal R^2 values (fixed effects only) were 0.68 (height Gini), 0.11 (carbon), 0.67 (canopy cover), and 0.75 (canopy Gini); conditional R^2 values (including site random effect) were 0.72, 0.40, 0.68, and 0.76 respectively. A supplementary structural equation model using *I. edulis* proportion as the predictor (all treatments included) recovered the same pathways (Fig. S11, Table S8). Individual-level performance of *Inga edulis* across treatments is reported in Fig. S10.

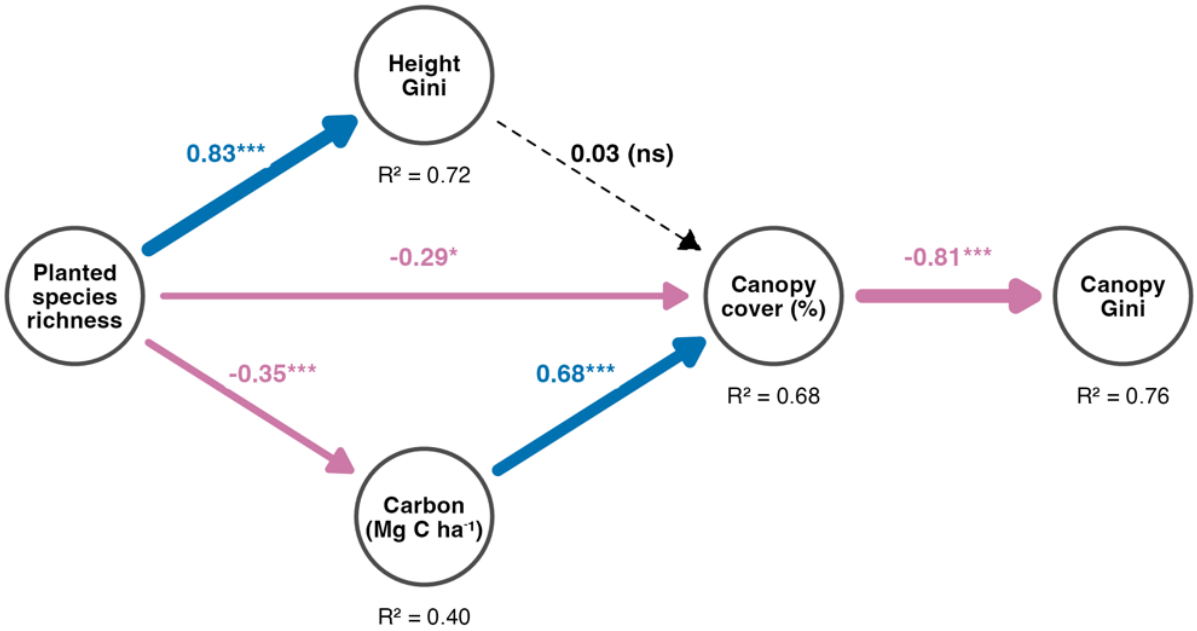

Figure 5. Piecewise structural equation model of pathways from planted species richness (log-transformed) to ecosystem outcomes (M2 excluded; Fisher's C = 8.55, p = 0.20). Arrow widths proportional to standardized path coefficients (β); blue arrows indicate positive effects, pink arrows negative effects. Solid arrows significant (p < 0.05), dashed arrows non-significant. The non-significant direct path from richness to canopy Gini (β = 0.08, p = 0.19) is omitted for clarity (Table S8). R^2 values are conditional (including site random effect).

Discussion

We found a dual benefit of increased planted species richness in assisted tropical forest restoration. (1) Within plots, structural heterogeneity rose sharply (height Gini: 0.16 in monocultures to 0.39 in 12-species plots; a 140% increase and the strongest treatment effect of any metric). (2) Across sites, multivariate outcome variability fell, most clearly in survival, which varied three- to four-fold more across sites in monocultures than in diverse mixtures. This combination of effects means more complex forests can provide more predictable outcomes across landscapes, with direct implications for how we design restoration plantings to maximize success. Notably, our diverse treatments used different locally adapted species at each site yet showed similarly low multivariate dispersion (M2-inclusive $\rho = -0.31$, $p = 0.001$), so the stabilization appeared to reflect functional diversity rather than any single shared species composition. This mean-variance trade-off mirrors classic portfolio theory (e.g., Schindler et al., 2015) and provides early multi-site experimental evidence for portfolio-like cross-site buffering with increasing species diversity in tropical forest restoration (Yachi & Loreau, 1999).

The biodiversity insurance hypothesis predicts that diverse communities buffer ecosystem functioning against environmental variation through response diversity, the differential responses of species to local conditions (Elmqvist et al., 2003; Yachi & Loreau, 1999). Our results appeared consistent with this prediction. This buffering may represent the assisted restoration corollary of the insurance effect that functional diversity confers on forest functioning under fluctuating conditions (Chen et al., 2025). This insurance effect was clearest for survival and structural outcomes, and is the spatial counterpart of the temporal stability of productivity that tree diversity confers at the long-running Sardinilla experiment (Schnabel et al., 2019), and is consistent with the positive effects of tree diversity on tropical restoration documented in Sabah (Veryard et al., 2023). With only four sites we could not cleanly separate a pure among-site (spatial) insurance effect from greater within-site consistency, and co-occurring species shared local conditions that would limit independent responses; variance partitioning (Table S4G) indicated that diversity reduced variability at both scales, so we interpreted the result as portfolio-like buffering rather than spatial insurance in the strict sense. Prior work has shown tree diversity stabilizing individual outcomes, most notably reduced variability in sapling survival under drought across 34 TreeDivNet experiments (Blondeel et al., 2024), but primarily in temperate systems. Our study builds on this evidence by evaluating the recovery of multiple ecosystem metrics

simultaneously, and assessing predictability across heterogeneous sites rather than through time (Depauw et al., 2024; Liu et al., 2026).

Species richness also appeared to increase within-plot structural heterogeneity, and the structural equation model linked richness to heterogeneity through two pathways: a direct positive effect on height diversity ($\beta = 0.83$), and an indirect negative pathway through carbon accumulation and canopy cover (richness to carbon $\beta = -0.35$, carbon to canopy cover $\beta = 0.68$, canopy cover to canopy heterogeneity $\beta = -0.81$). These pathways appeared to trade off. Fast-growing *Inga edulis* monocultures closed the canopy quickly but with a structurally uniform overstory typical of species-poor tropical plantations (Menalled et al., 1998), and their high carbon was concentrated in a thinned cohort of larger survivors. Diverse treatments instead developed more heterogeneous, multi-layered canopies with gaps, which as these forests mature may create a wider range of light environments and facilitate recruitment of shade-tolerant species (Bullock et al., 2022; Coverdale & Davies, 2023; Holl et al., 2013). Whether this structural advantage translates into greater natural recruitment remained a key question for continued monitoring.

The site-dependent performance of *I. edulis* appeared to make the risk-management case concrete. In monocultures it reached 99-100% survival at FAB and GAM but just 56% at FCEA and LLFS, likely driven by density-dependent competition in pure stands. Embedded in diverse mixes, its individual basal area matched or exceeded monoculture values – averaging 28% higher in 12-species plots and overyielding at three of four sites – consistent with reduced intraspecific competition and the complementarity effects reported in other biodiversity-ecosystem functioning experiments (Huang et al., 2018; Schnabel et al., 2019). More broadly, which species established reliably appeared to matter more than which maximized mean performance: *I. edulis* monocultures had the highest carbon at all four sites but the lowest, most variable survival (78%, 56-100%), whereas mixed treatments maintained more consistently high survival (90%, 83-95%). Although the monoculture accumulated more carbon at this early stage, mixed plantings tend to overtake monocultures in carbon over time (Schnabel et al., 2025; Warner et al., 2023). Six-species mixes captured most of the stabilizing benefit (31% dispersion reduction from monocultures, only 7% more at 12 species), suggesting that roughly six functionally complementary species may suffice where sourcing many is logistically difficult.

The cost of this insurance appeared modest. Assisted tree planting in Latin America costs ~US$3,000/ha through establishment (Brancalion et al., 2019; Cole et al., 2024), and because trees planted per hectare are fixed regardless of species count, diversifying adds only

569 the logistical cost of sourcing multiple natives, not a financial one. For that low marginal
570 cost, mixtures established more reliably (~90% vs 78% survival) and varied less across sites
571 (ρ = -0.41), lowering the risk of the most expensive outcome: replanting after low survival.
572 This ecological portfolio effect may have an economic parallel in the same country: across
573 two northern Costa Rican sites, mixed-species plantations outperformed monocultures by up
574 to US$3,135/ha in timber net present value (and US$3,500–16,800/ha once carbon credits
575 were included), with the advantage greatest when evaluated from the planting decision a
576 practitioner faces before outcomes are known (Pinnschmidt et al., 2023). This benefit was
577 one of establishment reliability rather than carbon: I. edulis had both the highest mean carbon
578 (5.4 Mg C ha^{-1}) and the lowest carbon CV (~80% vs 107-124% for mixes), so judged on
579 carbon accumulation alone the monoculture remained the stronger early choice. Whether
580 diversity also lowers the longer-term carbon risk that buffer pools are designed to cover –
581 reversal under drought, pests, or disturbance, against which standards such as Verra and Gold
582 Standard withhold credits (Anderegg et al., 2020, 2025) – is plausible but needs further
583 investigation. Diverse stands also spread carbon across more stems and species, whereas the
584 monoculture concentrated it in a few large individuals, so we framed any buffer-deduction
585 benefit as a hypothesis our results motivate but cannot yet confirm. This portfolio argument
586 may add a practical risk-management dimension to existing ecological rationales for diverse
587 plantings (Biggs et al., 2020; Paterno et al., 2024).
588 A deeper question is whether practitioners could predict in advance which
589 monoculture would perform reliably, and our experiment suggested they could not. *I. edulis*
590 was chosen for its strong regional track record yet established poorly at two sites, and the
591 fleshy-fruit monocultures (M2) established poorly everywhere (0.09 Mg C ha^{-1}).
592 Diversification appeared to hedge against this unpredictability whether the mechanism was
593 statistical averaging, complementarity, or dilution of a volatile species (a SEM recoded with
594 *I. edulis* proportion recovered the same pathways; Fig. S11). The result's reach is nonetheless
595 bounded. Richness covaried with functional diversity by design, species were selected to
596 maximize trait space at each level, as practitioners would, so we could not separate the two,
597 and the stabilization was most plausibly a functional-diversity effect that functionally
598 redundant mixes would be expected to lack. Additionally, the analysis spanned only four sites
599 with contrasting land-use histories and only the first three years of establishment, the window
600 when most mortality occurs in tropical tree plantings (Charles et al., 2018; Werden et al.,
601 2018), so the effect should be tested across larger networks as tropical tree diversity
602 experiments mature. Reliable early establishment may nonetheless be a precondition for the

diversity-productivity gains that tend to strengthen with stand age (e.g., Bongers et al., 2021; Liu et al., 2026), so the buffering we observed could compound rather than decline over time.

These results may have direct implications for restoration under climate change. If diversity buffers outcomes across our current spatial environmental gradient (450-1,160 m elevation, 3,800-6,140 mm rainfall), it may also buffer against the temporal shifts climate change will impose on individual sites, a hypothesis that would warrant longer-term monitoring, as plantings established today face changing temperature, precipitation, and novel pest and pathogen pressures (Malhi et al., 2014). Our evidence is consistent across four sites tracked simultaneously, but extending it to temporal buffering of climate change at a single site remains untested, a question that only longer-term monitoring can examine. Because carbon crediting and ecosystem-service programs depend on predictable, long-term outcomes (Anderegg et al., 2020), a monoculture that establishes unreliably across sites would undermine that predictability, making robustness to environmental variability a financial as well as an ecological question.

To meet global restoration commitments, the question of which species to plant has become increasingly consequential. Our results show that monocultures of fast-growing species can maximize carbon at individual sites, but they can also underperform at others. In contrast, diverse plantings deliver more consistent and predictable outcomes, particularly across the heterogeneous landscapes where restoration is most needed. Given the considerable financial risks undertaken by forest restoration practitioners across the globe, our results highlight that species diversity can provide a vital level of insurance, assembling a portfolio that trades peak performance for reliability. Across variable conditions, designing diverse, trait-complementary species mixes that perform reliably is not just ecologically sound but essential for meeting landscape-level recovery goals.

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CRediT author contributions

Conceptualization: RJC, LKW. *Methodology:* RJC, DM, LKW, TWC. *Formal analysis:* RQ, LKW. *Investigation:* RJC, GQC, LKW, DR, JT, AW. *Data curation:* RQ, RJC, LKW. *Writing - original draft:* RQ, LKW, RJC. *Writing - review and editing:* all authors. *Visualization:* RQ, LKW. *Supervision:* RJC, LKW. *Funding acquisition:* RJC, LKW, TWC.

Conflict of interest

LKW is a pro-bono scientific advisor to Plant-for-the-Planet Foundation and Green Again Madagascar, non-profit organizations implementing tropical restoration. RJC is the founder of the non-profit Tropical Landscape and Climate Program, where LKW is a pro-bono board member. TWC is the founder of the non-profit Restor Eco AG and serves on the Foundation board in a pro bono capacity.

Data and code availability statement

All data and code required to reproduce the analysis are openly available in FxnDiv-restoration-portfolio at https://zenodo.org/records/20942837.

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Supplementary material for:

Species diversity reduces risk in tropical forest restoration: a portfolio effect across heterogeneous sites

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Figures

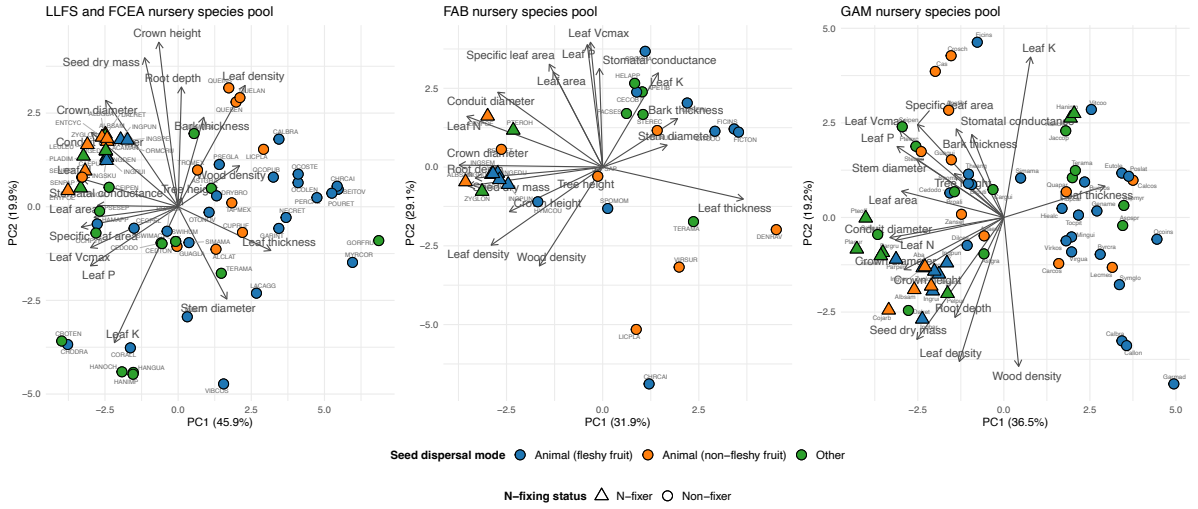

Figure S1. Principal components analysis of functional trait space for the nursery species pool at each site. Species codes are the first three letters of the genus and the first three letters of the specific epithet (*e.g.,* INGEDU = *Inga edulis*; see Table S3 for full names). Each point represents a candidate species, colored by seed dispersal mode and shaped by nitrogen-fixing status. Loading arrows show the contribution of 18 imputed functional traits (Table S2) to the first two principal components. LLFS and FCEA, FAB, and GAM. Species were selected at each richness level to maximize trait space occupancy (Table S3)

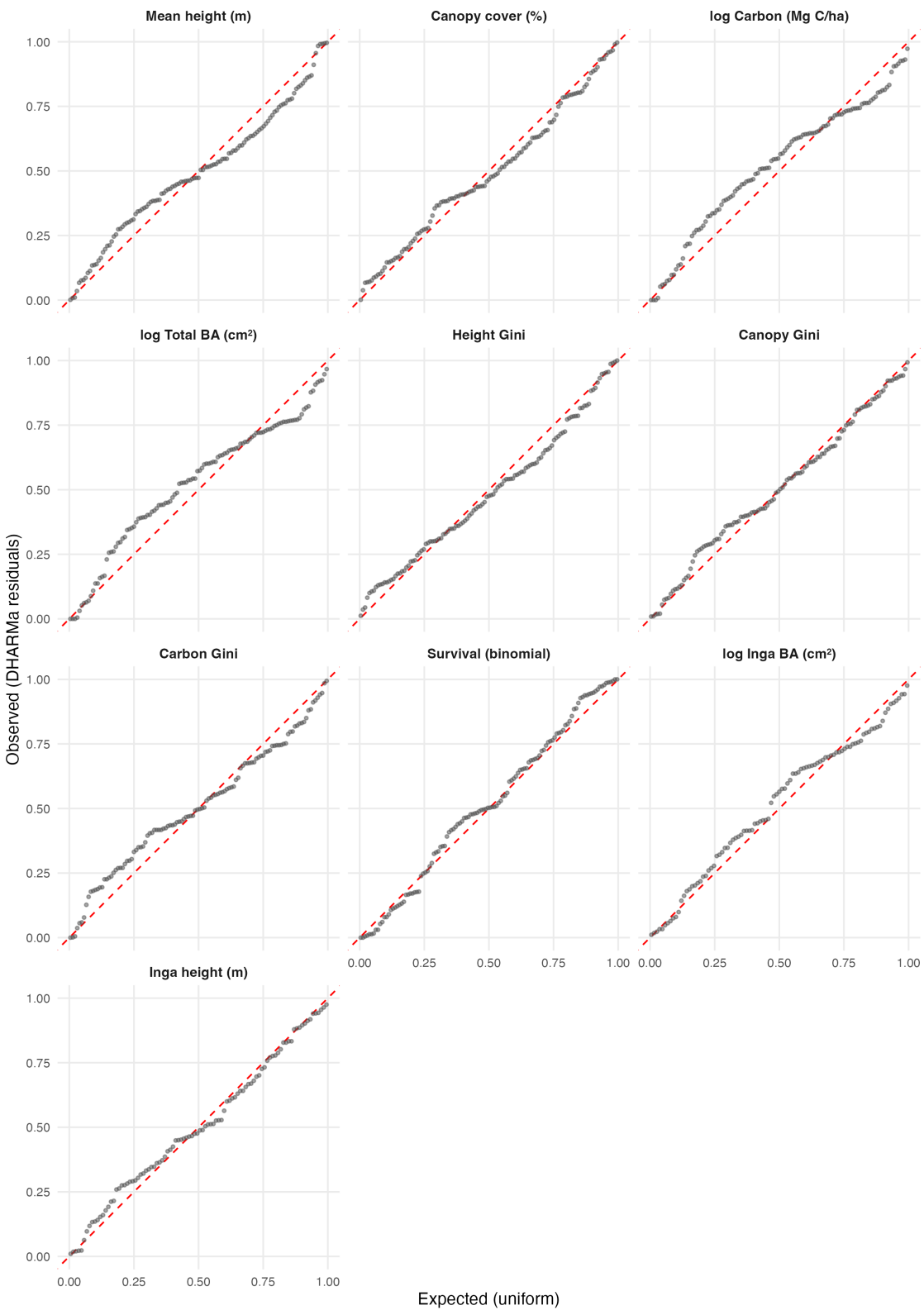

Figure S2. Quantile-quantile plots of DHARMa simulated residuals for all mixed-effects models. Each panel shows one response variable; the dashed red line indicates the expected uniform distribution. Carbon, total basal area, and *Inga* basal area were log-transformed; survival was modeled as a binomial GLMM (glmmTMB).

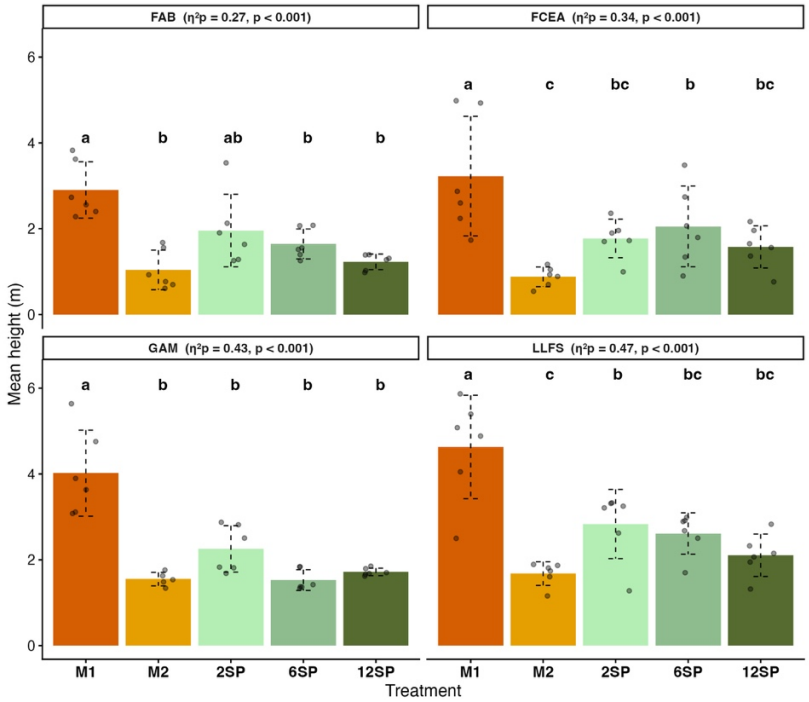

Figure S3. Mean tree height (m) by treatment at each site after three years. Bars show treatment means; error bars show standard deviations; points are individual plots (N = 6 per treatment per site). Letters denote significant pairwise differences (Tukey HSD, $p < 0.05$). Partial eta-squared (η^2p) and p-values for the treatment effect are shown for each site.

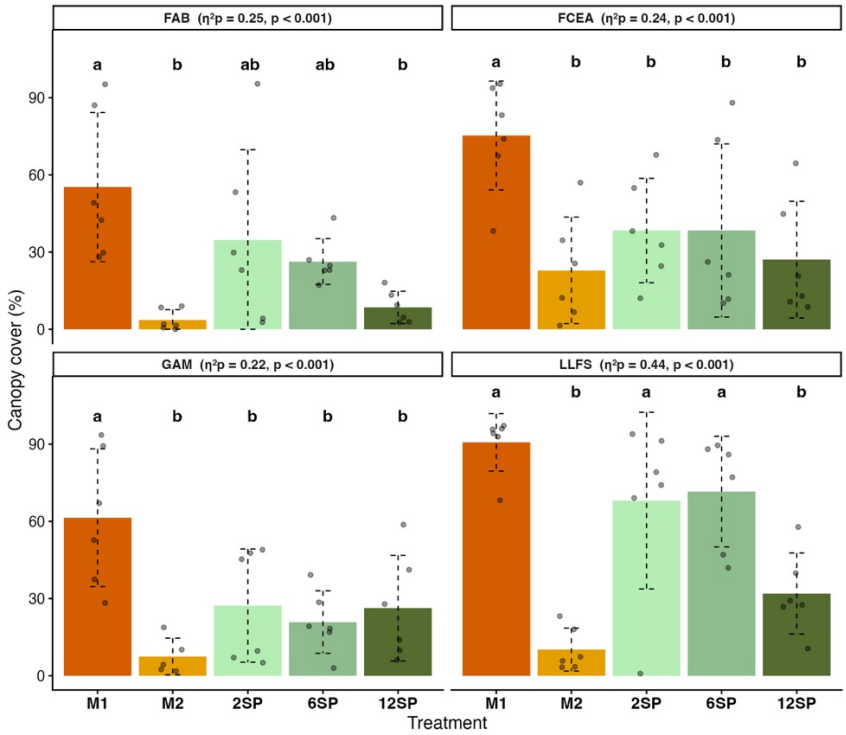

Figure S4. Canopy cover (%) by treatment at each site after three years. Statistics reported as in Figure S3.

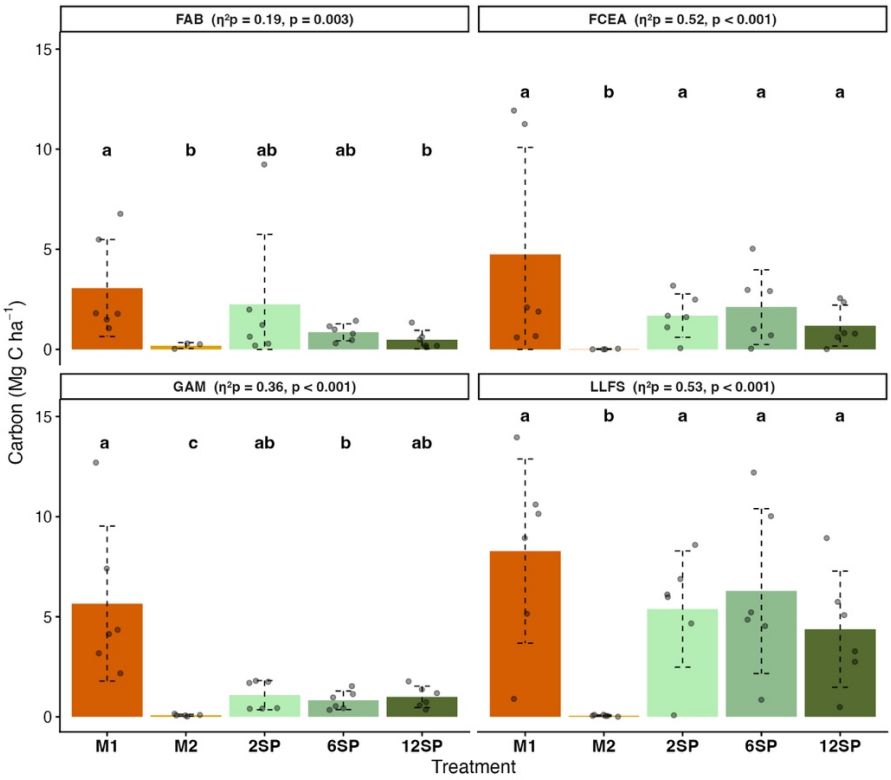

Figure S5. Carbon stocks (Mg C ha^{-1}) by treatment at each site after three years. Statistics reported as in Figure S3.

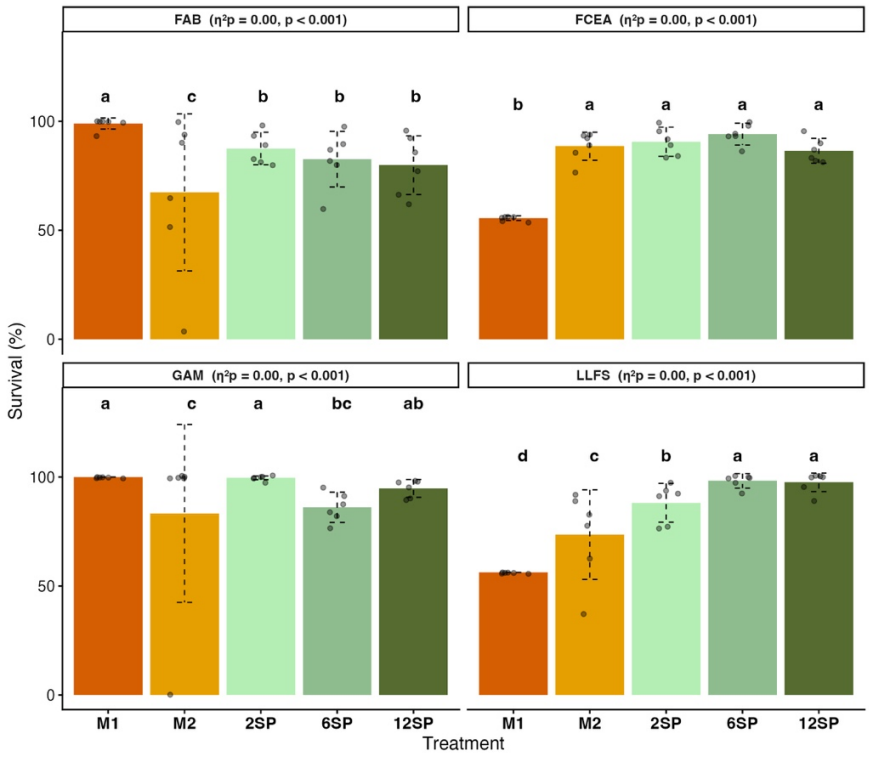

Figure S6. Survival (%) by treatment at each site after three years. Statistics reported as in Figure S3. Survival was modeled as a binomial GLMM; pairwise letters are Sidak-adjusted, not Tukey.

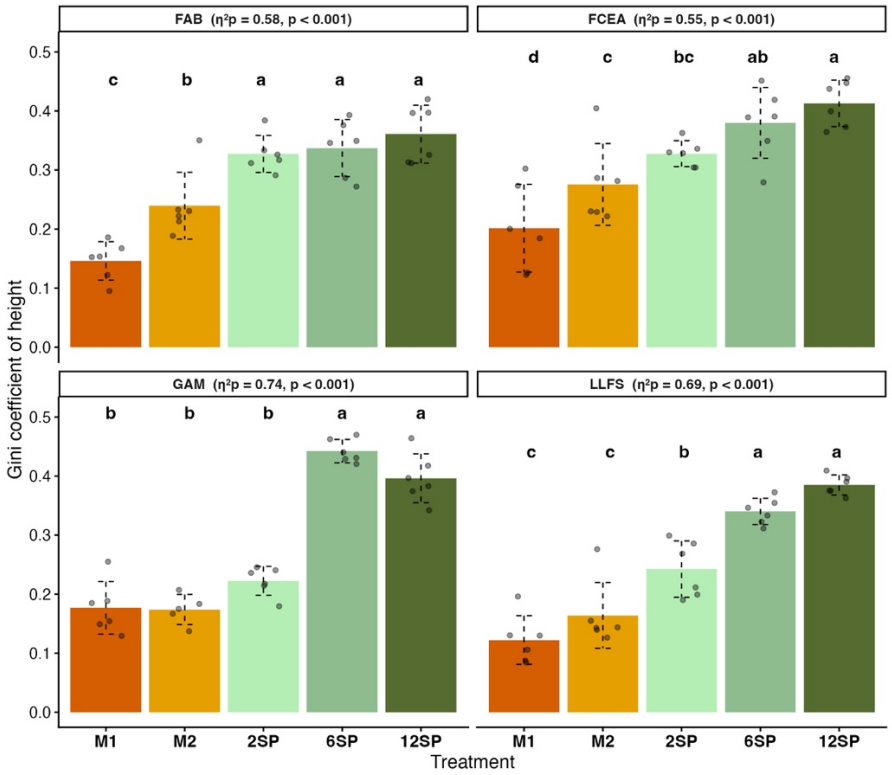

Figure S7. Within-plot height heterogeneity (Gini coefficient) by treatment at each site after three years. Statistics reported as in Figure S3.

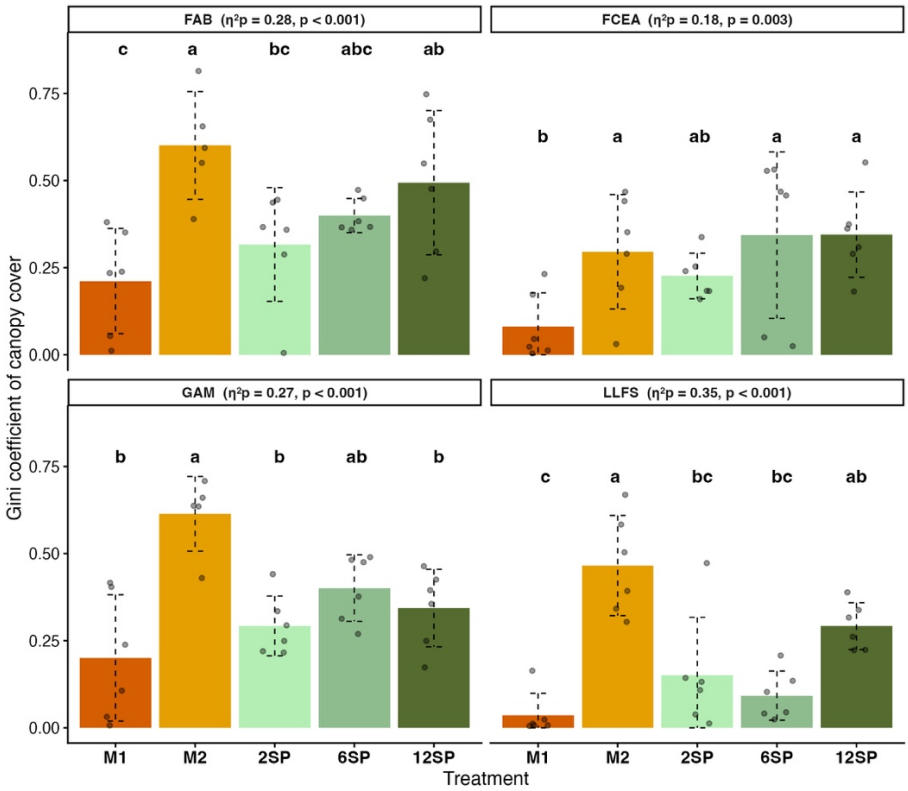

Figure S8. Within-plot canopy cover heterogeneity (Gini coefficient) by treatment at each site after three years. Statistics reported as in Figure S3.

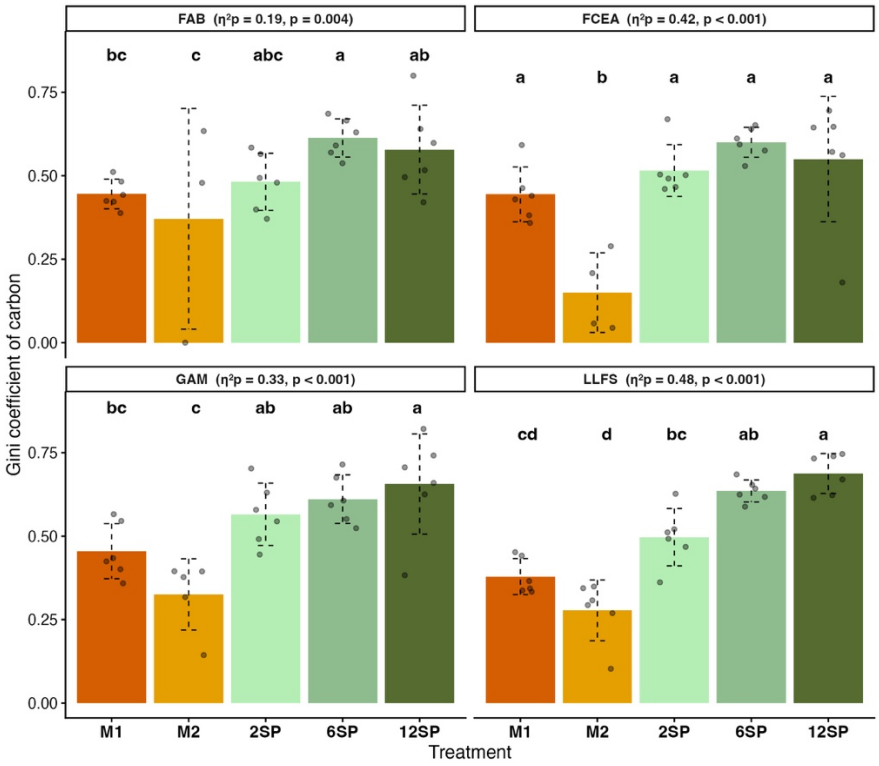

Figure S9. Within-plot carbon heterogeneity (Gini coefficient) by treatment at each site after three years. Statistics reported as in Figure S3.

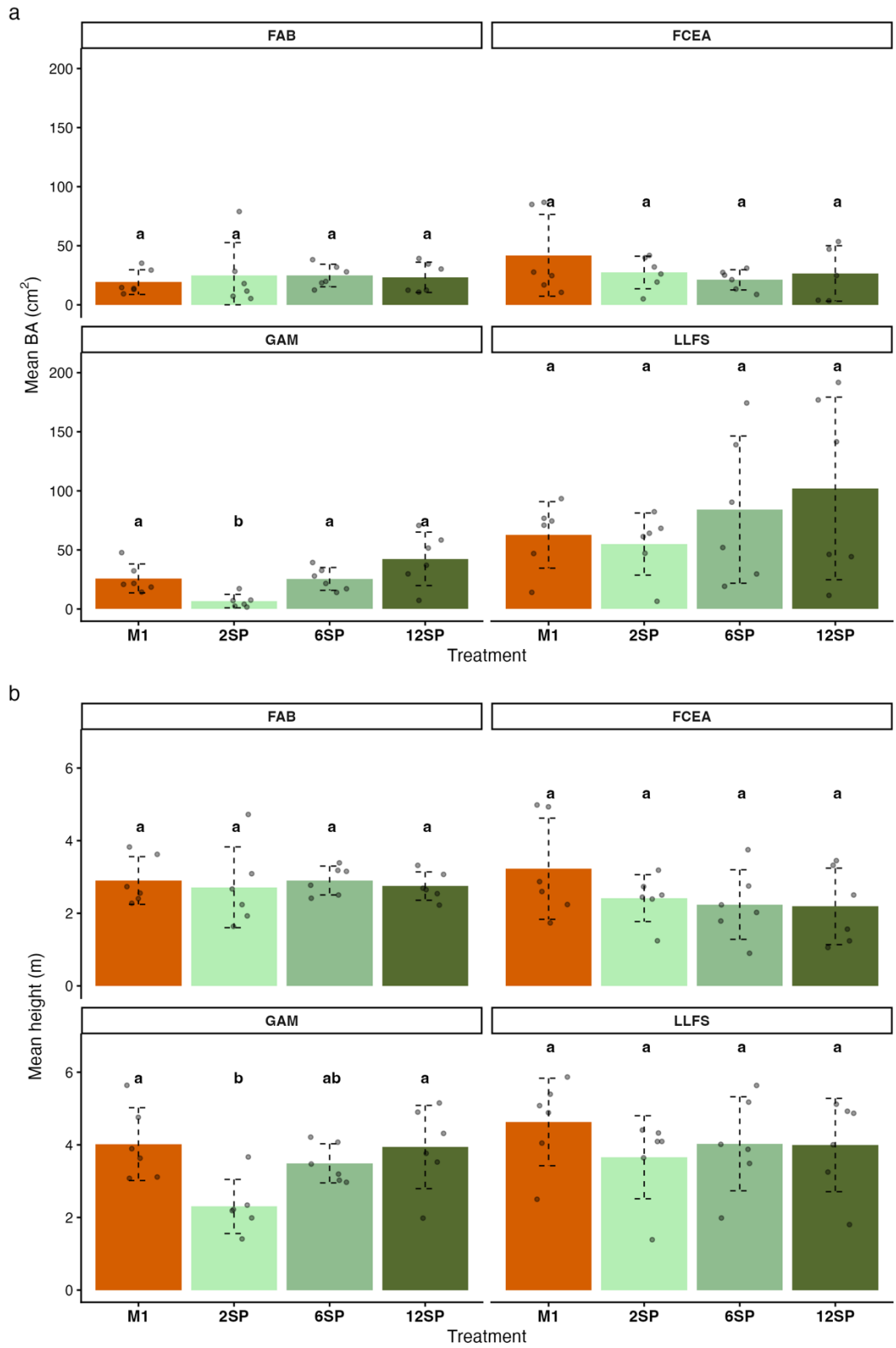

Figure S10. Individual-level performance of *Inga edulis* across treatments at each site. (a) Mean individual basal area (cm²) and (b) mean individual height (m) in M1 (monoculture) versus mixed-species treatments (2SP, 6SP, 12SP). M2 is excluded because it does not contain *Inga*.

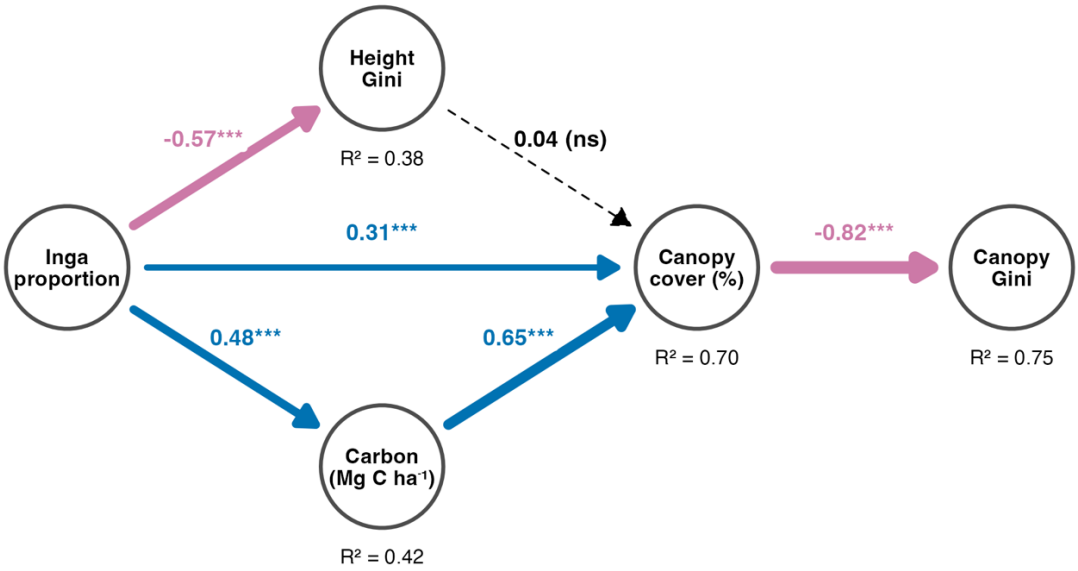

Figure S11. Piecewise structural equation model of Figure 5 recoded with *Inga edulis* proportion in place of log-transformed species richness (all five treatments included). Because *I. edulis* proportion is collinear with planted richness by design, this is not an independent test but confirms that the structural pathways are not an artifact of the richness coding. Arrow colors and widths as in Figure 5; R^2 values are conditional (including the site-level random effect).

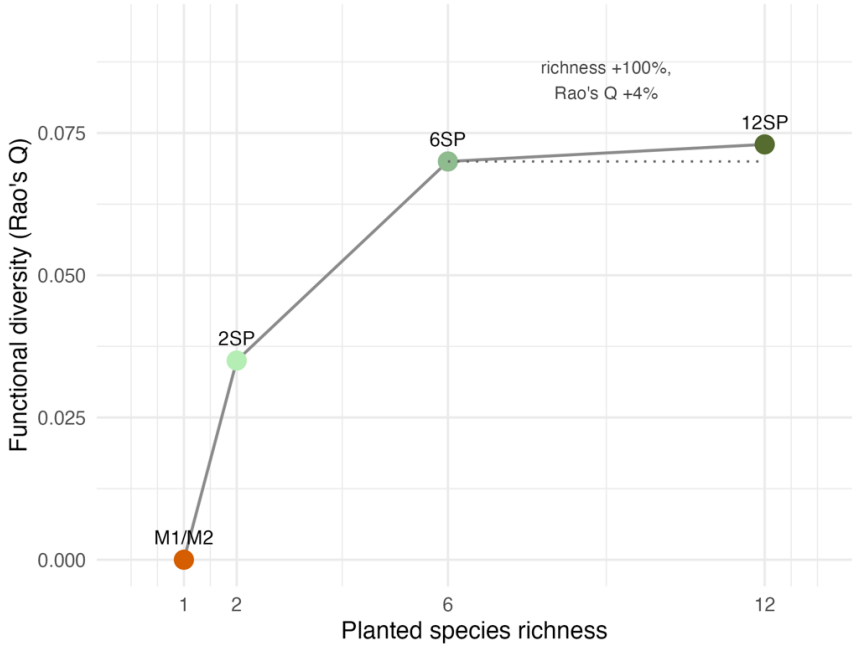

Figure S12. Functional diversity saturates along the planted-richness gradient. Functional diversity (Rao's Q) per treatment, averaged across the four sites, rises from monocultures (0) through two- and six-species mixes (~0.035, 0.070, respectively) then levels off. Doubling richness from six to twelve species increases Rao's Q by ~4% on average across sites (to 0.073), so the additional species appear largely functionally redundant. (The dispersion scale-robustness and survival-variability results are presented in Tables S5 and S7)

Tables

Table S1. Details on the restoration sites in southwestern Costa Rica.

Site	Site Code	Coordinates	Elevation	Mean Annual Rainfall	Mean Annual Temperature	Land Use History
Finca Aguas Buenas	FAB	N: 9°1'16", W:83°29'22"	930 m	4100 mm	22 °C	Cattle Grazing
Finca Cantaros Environmental Association	FCEA	N: 8°47'58", W:82°57'51"	1100 m	4000 mm	21 °C	Cattle Grazing
Loma Linda Field Station	LLFS	N: 8°44'31", W:82°55'33"	1160 m	3800 mm	21°C	Cattle Grazing, Mixed Agriculture
La Gamba Tropical Station	GAM	N: 8°45'17.8 W: 83°08'41.2	450 m	6,140 mm	28 °C	Cattle Grazing

Table S2. List of functional traits and units used to design tree species mixes for the treatments

Functional trait	Units
Bark thickness	mm
Crown diameter, maximum	m
Crown height, maximum	m
Leaf area	cm^2
Leaf density	$g\ cm^{-3}$
Leaf K per mass	$mg\ g^{-1}$
Leaf N per mass	$mg\ g^{-1}$
Leaf P per mass	$mg\ g^{-1}$
Leaf thickness	mm
Leaf V_{cmax}	$\mu mol\ g^{-1}\ s^{-1}$
Root depth, maximum	m
Seed dry mass	mg
Specific leaf area	$mm^2\ mg^{-1}$
Stem conduit diameter	µm
Stem diameter	m
Stomatal conductance	$mmol\ m^{-2}\ s^{-1}$
Tree height, maximum	m
Wood density	$g_{dry}\ cm_{wet}^{-3}$

Table S3. Species used in the experiment and their allocation across sites and treatments (species denoted with * were planted in 6-species mix only at LLFS)

Species	Common Name	Site	Treatment Codes
Aspidosperma myristicifolium	Guatambu	GAM	6SP, 12SP
Astronium graveolens	Ron Ron	GAM	12SP
Calophyllum brasiliense	Santa Maria	LLFS	M2, 2SP, 6SP, 12SP
Cedrela tonduzii	Cedro dulce	FCEA	12SP
Chrysophyllum cainito	Caimito	FAB	12SP
Citharexylum cooperi	Dama	GAM	M2, 2SP, 6SP, 12SP
Cojoba arborea	Lorito	GAM	12SP
Cordia alliodora	Laurel	FCEA, LLFS	12SP
Croton draco	Targua	FCEA, LLFS	6SP, 12SP
Croton schiedeanus	Colpachi	GAM	6SP, 12SP
Cupania rufescens	Guavillo	FCEA	12SP
Dendropanax ravenii	Fosforillo	FAB	12SP
Erythrina poeppigiana	Poro	FAB, FCEA, LLFS	12SP
Ficus insipida	Higueron	FAB	M2, 2SP, 6SP, 12SP
Ficus maxima	Higueron	GAM	12SP
Garcinia madruno	Madrono	GAM	6SP, 12SP
Handroanthus impetiginosus	Roble de sabana	GAM	12SP
Handroanthus ochraceus	Corteza amarilla	LLFS	12SP
Heliocarpus appendiculatus	Burio	FAB, FCEA	6SP, 12SP
Inga edulis	Guaba	FAB, FCEA, LLFS, GAM	M1, 2SP, 6SP, 12SP
Lacistema aggregatum	Copalchi	LLFS	6SP, 12SP
Moquilea platypus	Sonzapote	FAB	6SP, 12SP
Ocotea puberula	Aguacatillo	FCEA, LLFS	12SP
Persea caerulea	Aguacatillo	LLFS	12SP
Platymiscium curuense	Cristobal	GAM	6SP, 12SP
Quercus insignis	Roble	FCEA, LLFS	6SP, 12SP
Saurauia montana	Moquillo	FCEA	M2, 2SP, 6SP, 12SP
Simarouba amara	Aceituno	LLFS	12SP
Spondias mombin	Jobo	FAB	6SP, 12SP
Sterculia recordiana	Pie de danta	FAB	12SP
Terminalia amazonia	Amarillon	FAB	6SP, 12SP
Theobroma simiarum	Cacao de mono	GAM	12SP
Viburnum costaricanum	Cura	FCEA	6SP, 12SP
Vitex cooperi	Cuajada	FAB	12SP
Zygia longifolia	Zota caballo	FAB, FCEA, LLFS, GAM	6SP*, 12SP

Table S4. Robustness and sensitivity analyses for the richness–dispersion relationship (seven plot-level metrics scaled to unit variance). (A) Permutation test (n = 9,999) with standardized effect size (SES). (B) Linear mixed-effects model on betadisper distances along the designed richness gradient (richness fixed, Site/Block random; Satterthwaite df; N = 96, M2 excluded). (C) Pairwise betadisper comparisons between all treatment pairs. (D) Leave-one-site-out sensitivity, testing whether the correlation depends on any single site. (E) Replanting sensitivity, excluding replanted individuals (8.1% of trees) and comparing Height Gini ANOVA and betadisper trend with and without replants. (F) Temporal dispersion trajectory (years 2-3) at the three sites with complete temporal data (FAB, FCEA, LLFS), using height and height Gini only. (G) Among- versus within-site variance partitioning of the seven scaled outcomes along the designed richness gradient (M1, 2SP, 6SP, 12SP; M2 excluded). This mean-based variance partition is complementary to the Fig. 4 betadisper dispersion (which uses the spatial-median centroid).

A. Permutation test (9,999 permutations)

Test	Value
Spearman rho	-0.4139
Permutation-p (one-tailed)	< 0.001
SES	-4.03

B. Linear mixed-effects model on betadisper distances

Term	β	SE	df	t	p-value
(Intercept)	2.204	0.205	4.62	10.75	< 0.001
Richness	-0.061	0.017	71	-3.53	< 0.001

C. Pairwise betadisper

Pair	Distance 1	Distance 2	Difference	P-value
M1-M2	2.513	1.724	0.788	0.003
M1-2SP	2.513	1.738	0.775	0.001
M1-6SP	2.513	1.735	0.778	0.004
M1-12SP	2.513	1.551	0.962	0.001
M2-2SP	1.724	1.738	-0.014	0.958
M2-6SP	1.724	1.735	-0.01	0.975
M2-12SP	1.724	1.551	0.173	0.498
2SP-6SP	1.738	1.735	0.003	0.985
2SP-12SP	1.738	1.551	0.187	0.400
6SP-12SP	1.735	1.551	0.184	0.468

D. Leave-one-site-out sensitivity

Dropped	N plots	rho	p-value
None (full)	96	-0.414	< 0.001
FAB	72	-0.478	< 0.001
FCEA	72	-0.332	0.004
GAM	72	-0.35	0.003
LLFS	72	-0.3	0.010

E. Replanting sensitivity

Analysis	Dataset	N trees	N replants excluded	F / rho	p-value	η^2p / M1 dispersion	12SP dispersion
Height Gini	With replants	5760	0	200.7	< 0.001	0.909	NA
Height Gini	Without replants	5291	469	199	< 0.001	0.909	NA
Betadisper	With replants	5760	0	-0.414	< 0.001	2.51	1.55
Betadisper	Without replants	5291	469	-0.373	< 0.001	2.59	1.68

F. Temporal dispersion trajectory (years 2-3)

Year	N plots	rho	p-value	M1	2SP dispersion	6SP dispersion	12SP dispersion
2	72	-0.203	0.0878	1.227	0.731	0.698	0.83
3	72	-0.38	0.001	1.14	0.743	0.726	0.565

G. Among- versus within-site partition of multivariate dispersion

Treatment	n plots	Total SS	Among-site SS	Within-site SS	Among-site %	Within-site %
M1	24	162.6	81.1	81.6	50	50
2SP	24	87.4	26.9	60.5	31	69
6SP	24	92.1	44.1	47.9	48	52
12SP	24	84.4	24.3	60.1	29	71

Table S5. Robustness of the cross-site multivariate-dispersion result to standardization, and underlying mean-variance structure. (A) Spearman ρ between planted richness and dispersion under alternative standardizations/subsets; (B) per-metric mean–variance coupling (Taylor slope of variance on mean across the 16 site×treatment cells); (C) per-metric distance-to-centroid for monoculture vs 12-species; (D) among-site CV by treatment; (E) mixed model of among-site CV on richness.

A. Spearman ρ across standardizations

Standardization / metric subset	ρ (richness vs dispersion)	p	mean-variance immune
Baseline z-score (as published)	−0.41	<0.001	no
Log of productivity metrics	−0.28	0.005	partial
Rank-transform all metrics	−0.06	0.280	yes
Bounded metrics only (survival + 3 Gini)	−0.41	<0.001	yes
Survival only	−0.52	<0.001	yes

B. Mean–variance coupling (Taylor slope ≈2 = constant CV)

Metric	type	Spearman(mean, SD)	Taylor slope
Mean height	unbounded	0.81	2.92
Carbon	unbounded	0.94	1.99
Canopy cover	unbounded	0.36	0.88
Height Gini	bounded	−0.23	−0.56
Canopy Gini	bounded	0.19	0.43
Carbon Gini	bounded	−0.01	0.36
Survival	bounded	−0.60	1.19

C. Per-metric dispersion, M1 vs 12-species (ratio >1 = monoculture more variable)

Metric	type	M1	12SP	ratio M1/12SP
Mean height	unbounded	0.95	0.32	2.97
Carbon	unbounded	1.08	0.4	2.72
Canopy cover	unbounded	0.71	0.47	1.51
Height Gini	bounded	0.40	0.29	1.36
Canopy Gini	bounded	0.61	0.59	1.04
Carbon Gini	bounded	0.34	0.64	0.53
Survival	bounded	1.46	0.52	2.82

D. Among-site CV by treatment (%)

Treatment	height	carbon	canopy	ht Gini	canopy Gini	carbon Gini	survival
M1	33	80	36	35	109	16	29
2SP	34	107	74	21	55	17	9
6SP	35	124	72	16	59	9	11
12SP	28	122	80	11	40	23	11

E. Among-site CV ~ richness (LMM, metric random effect)

Metric set	β	p
All 7 metrics	0.002	0.8
Unbounded (productivity)	0.021	0.11
Bounded (survival + structure)	−0.012	0.076

Table S6. Functional diversity saturates along the richness gradient. Presence-based design FD per treatment (mean across four sites; per-site and complete-case values).

Treatment	species richness	Rao's Q (mean ± SD)	FDis
M1/M2	1	0	0
2SP	2	0.035 ± 0.017	0.183
6SP	6	0.070 ± 0.011	0.256
12SP	12	0.073 ± 0.005	0.262

Table S7. Survival reliability and below-threshold risk by treatment. (A) Mean survival, among-site standard deviation and coefficient of variation (CV), and worst-site survival for each treatment. (B) Modeled probability that a plot falls below the 70% and 80% survival thresholds, with the odds ratio per added planted species (binomial GLMM).

(A) Survival across sites

Treatment	mean survival	among-site SD	among-site CV	worst site
M1	0.78	0.25	0.32	0.56
2SP	0.92	0.06	0.06	0.88
6SP	0.9	0.07	0.08	0.83
12SP	0.9	0.08	0.09	0.8

(B) Probability a stand falls below a survival threshold

Threshold	OR per species (95% CI)	p	P(<threshold) - monoculture	P(<threshold) - 12SP
survival < 70%	0.80 (0.66-0.97)	0.023	0.23	0.025
survival < 80%	0.86 (0.75-0.99)	0.033	0.31	0.076

Table S8. Standardized path coefficients (β) from piecewise structural equation models. Main model uses log-transformed species richness as the predictor (M2 excluded; Fisher's C = 8.55, p = 0.20). The *Inga* proportion model is a robustness check using the proportion of *Inga edulis* per plot (collinear with richness; all treatments included); its coefficients mirror the main model with reversed sign. Site included as a random effect in both models. SE = standard error of the standardized estimate.

Response	Predictor	β	SE	p-value	Model
Height Gini	Log richness	0.83	0.05	< 0.001	Main
Carbon	Log richness	-0.35	0.08	< 0.001	Main
Canopy cover	Log richness	-0.29	0.11	0.007	Main
Canopy cover	Height Gini	0.03	0.11	0.796	Main
Canopy cover	Carbon	0.68	0.07	< 0.001	Main
Canopy Gini	Log richness	0.08	0.06	0.193	Main
Canopy Gini	Canopy cover	-0.81	0.06	< 0.001	Main
Height Gini	*Inga* proportion	-0.57	0.08	< 0.001	*Inga* proportion
Carbon	*Inga* proportion	0.48	0.07	< 0.001	*Inga* proportion
Canopy cover	*Inga* proportion	0.31	0.07	< 0.001	*Inga* proportion
Canopy cover	Height Gini	0.04	0.06	0.508	*Inga* proportion
Canopy cover	Carbon	0.65	0.06	< 0.001	*Inga* proportion
Canopy Gini	*Inga* proportion	-0.07	0.06	0.27	*Inga* proportion
Canopy Gini	Canopy cover	-0.82	0.06	< 0.001	*Inga* proportion