

High tree diversity enhances light interception in tropical forests

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Abstract

1. Understanding the processes that underlie the effects of tree diversity on primary production is of foremost importance to enhance climate change mitigation by tropical forests. Here, we investigated the effects of tree diversity on light interception over space and time in two tropical tree experiments, located in Panama—*Sardinilla* site (monocultures to 18-species mixtures), and in Brazil—*Anhembi* site (20- to 114-species mixtures).
2. We assessed intercepted photosynthetically active radiation (iPAR) over horizontal grids and vertical transects (up to 5 m high in *Sardinilla* and up to 4 m high in *Anhembi*), in plots containing different richness levels and combinations of species.
3. Light interception increased from monocultures to 5-species mixtures in *Sardinilla* and from 20- to 114-species mixtures in *Anhembi* (during the dry season). At the *Sardinilla* site, five-species mixtures showed iPAR comparable to the best performing monocultures, despite substantial differences observed among monocultures. Diversity-iPAR relationships changed seasonally and were more pronounced during the dry season. Tree richness promoted a less variable temporal and spatial (i.e. both horizontal and vertical) distribution of light interception.
4. *Synthesis*. High tree diversity (i.e. over a hundred species in mixture) maximizes the amount of light intercepted by the canopy in restored tropical forests through more even capture in space and time. Diversity-light interception relationships should be critically considered for designing cost-efficient large-scale tropical forest restoration programs.

KEYWORDS

BEF theory, biodiversity and ecosystem functioning theory, complementarity, ecological processes, ecosystem services, light partitioning, restoration ecology

1 | INTRODUCTION

Biodiversity and ecosystem functioning (BEF) theory predicts that increased species diversity can enhance resource capture at community level and foster ecosystem functioning (Loreau et al., 2001). Experiments corroborating this theory have been historically carried out on grasslands (Balvanera et al., 2006), and extended in the last two decades to forests (Gamfeldt et al., 2013; Guerrero-Ramírez et al., 2017; Potvin & Gotelli, 2008; Ratcliffe et al., 2017), mainly in temperate biomes. Moreover, forest BEF studies are commonly based on a limited number of tree species (usually less than a dozen) that does not compare to the high diversity of tropical biomes (Paquette et al., 2018), nor to the species richness usually found in tropical restoration plantings (Brancalion et al., 2018). Consequently, the role of high tree species richness in the functioning of hyper-diverse tropical forests, among the most species- and biomass-rich ecosystems on Earth (Barlow et al., 2018), remains poorly understood (Clarke et al., 2017). This knowledge gap is particularly important because tropical forest re-growth has been promoted world-wide as a central solution to mitigate climate change (Brancalion, Niamir, et al., 2019; Lewis et al., 2019; Pugh et al., 2019), as well to provide multiple ecosystem services that underpin human wellbeing (Chazdon & Brancalion, 2019). Understanding the effects of tree diversity on forest growth is key for maximizing carbon sequestration in forest restoration (Hulvey et al., 2013; Potvin et al., 2011; Sapjanskas et al., 2014).

Current evidence suggests a positive but saturating relationship between species richness and ecological processes (Cardinale et al., 2011; Clarke et al., 2017; Guerrero-Ramírez et al., 2017). In a meta-analysis considering various types of ecosystems, from aquatic to terrestrial, Cardinale et al. (2011) found that maximum biomass achieved by primary producers (plants and algae), in mixtures containing increasing numbers of species, was on average 2.38 times higher than the average biomass of monocultures, and that half of this yield would be reached with 1.35 species. Levels of diversity required to saturate ecosystem functions are, however, still an unresolved issue (Cardinale et al., 2012), especially when considering large spatial scales (Cardinale et al., 2011; Srivastava & Vellend, 2005), varying species compositions (Srivastava & Vellend, 2005), multiple ecosystem functions (Meyer et al., 2018) and services (Isbell et al., 2011) and long-term resilience (Brockerhoff et al., 2017).

Forest structural complexity has been shown to be an important determinant of forest productivity (Gough et al., 2019; Hardiman et al., 2011), and may partly explain overyielding (i.e. increased productivity of mixtures compared to monocultures; Dănescu et al., 2016; Schnabel et al., 2019). This suggests that light-related interactions are key drivers of BEF relationships in tree species mixtures (Forrester & Bauhus, 2016; Guillemot et al., 2020; Morin et al., 2011). Recent studies showed that diverse forests are more efficient in filling canopy space with leaves, which likely results in enhanced light interception (Jucker et al., 2015; Pretzsch, 2014; Sapjanskas et al., 2014; Williams et al., 2017). However, the effects of tree species richness on forest light interception have seldom

been directly quantified across time and space (Binkley et al., 1992; Forrester & Albrecht, 2014; Forrester et al., 2012, 2018, 2019; le Maire et al., 2013; Sapjanskas et al., 2014; Sercu et al., 2017). This lack of empirical evidence of diversity effect on light interception is particularly acute in tropical forests, which typically display very high tree diversity and complex multi-layered canopy structure (Laurans et al., 2014; Trogisch et al., 2017). Studying the effects of tree diversity on light interception is therefore key to understand the functioning of diverse forests and how biodiversity loss can affect vital ecological processes, such as carbon sequestration. Moreover, light interception is linked to a number of key objectives of forest restoration, such as the control of invasive grass (Brancalion, Campoe, et al., 2019; Rodrigues et al., 2009). Understanding how tree diversity affects patterns of light absorption in tropical forests is then of great importance for designing cost-effective large-scale restoration programs, which are expected to expand in the current United Nations decade on ecosystem restoration (2021–2030).

Here, we explored patterns of light interception through time and space across tree diversity gradients in two tropical forests. Specifically, we quantified: (a) total amount of intercepted light; (b) the horizontal variation of intercepted light; (c) the vertical variation of intercepted light in the canopy; (d) the temporal variation in canopy light interception (between and within years); and (e) the differences in light interception between mixtures of species and their constituent monocultures (for this purpose, to support our conclusions, we also compared crown volumes of trees in monocultures and mixtures). We carried out our investigation based on two experiments: a 15-year-old BEF experiment established in Sardinilla, Panama (Scherer-Lorenzen et al., 2005), which presented its species in monocultures and mixtures (up to 18 species), and a 9-year-old tree diversity experiment established in Anhembi, Brazil with unprecedented high tree species richness (up to 114 species), which allowed linking BEF theory to tropical forest restoration.

2 | MATERIALS AND METHODS

2.1 | Study sites

We included in this study two sites that contained experiments based on different methodological approaches to test the influence of tree diversity on light interception by tropical forests. The *Sardinilla* site, in Panama, consists of an experiment especially designed for BEF studies. It contains, in two distinct plantations, five species in monocultures and in different combinations of up to 18 species (Scherer-Lorenzen et al., 2005). Its maximum richness level of plots was based on the diversity of natural, old-growth forests nearby the experimental areas (TreeDivNet, 2017). The *Anhembi* site, in Brazil, holds an experiment designed to assess effects of very high tree diversity levels on tropical forest functioning. It does not include species in monocultures, but its design allows for testing the effects of an unprecedented tree diversity level on ecosystem processes and functions, using similar tree species diversity as found in

high-diversity restoration projects (at least 80 species, for Brazilian Atlantic Forest; Brancalion et al., 2018).

The *Sardinilla* experiment was established in Panama, under an Am (equatorial monsoon) climate (Köppen-Geiger; Kottek et al., 2006; see Supporting Information, Methods S1 for detailed information on this site). It consists of two native tree plantations started at different times. In both of them, spacing between seedlings was 3×3 m. The hereafter called 'main plantation', established in 2001 (plantation was 15 years old at onset of field surveys), presented six species—fast growing: *Luehea seemanii* Triana & Planch (Malvaceae) and *Cordia alliodora* (Ruiz & Pav.) Oken (Boraginaceae); intermediate: *Anacardium excelsum* (Bertero ex Kunth) Skeels (Anacardiaceae) and *Hura crepitans* L. (Euphorbiaceae); slow-growing: *Cedrela odorata* L. (Meliaceae) and *Tabebuia rosea* (Bertol.) Bertero ex A.DC. (Bignoniaceae)—in 24 experimental plots of approximately similar dimensions (45×45 m, 45×48 m or 48×48 m), containing monocultures (12 plots: two replicates for each species) and combinations of three (six plots containing different combinations of a fast-growing, a slow-growing and an intermediate species) and of six species (six replicates of the same mixture), in a Latin-square design (Potvin & Dutilleul, 2009). All six species shed leaves during the dry season—*C. odorata* being deciduous and the other five, semi-deciduous. One of the species (*C. alliodora*) was not considered here because almost all individuals died after plantation establishment (Kunert et al., 2012). Our effective plots were thus: two replicates of five distinct monocultures, three combinations of two species, three combinations of three species and six replicates of a five-species combination (Supporting Information, Figure S1). The hereafter called 'high-diversity plantation' (HD) was established in 2003 (plantation was 13 years old at onset of field surveys), in 24 18×18 m plots organized in eight blocks, each one containing one plot of each richness level: 6, 9 and 18 species. Smaller species pools were subsets of larger ones, all of them within a 28-species pool (Supporting Information, Table S1). The eight blocks contained four different species combinations (hereafter called groups), thus there were two replicates of each group (Ruiz-Jaen & Potvin, 2011).

The *Anhembi* experiment was established in southeastern Brazil, under Cfa (humid subtropical, oceanic, hot summer) climate (Köppen; Alvares et al., 2013). This region was once covered by seasonal semi-deciduous forest (Morellato & Haddad, 2000), where 30%–50% of species shed leaves (Gandolfi et al., 2009). This forest type is part of one of the most threatened biogeographical regions of the Atlantic Forest (Ribeiro et al., 2009), a leading global hotspot for both biodiversity conservation (Laurance, 2009) and tropical forest restoration (Brancalion, Niamir, et al., 2019). The experiment was established in 2006 (plantation was 9 years old at onset of field sampling) using different tree richness levels: 20, 58 and 114 native tree species (see Supporting Information, Table S2), in a completely randomized design with four replicates (A–D) of each (see Supporting Information, Figures S1 and S2 and Methods S2). The smaller species pools were subsets of the larger ones. The spatial distribution of species was randomly determined for the first replicate and then repeated in the others of the same treatment. Seedlings were planted

in 45×48 m plots (3×1.5 m spacing—480 individuals per plot). We were able to find information on leaf phenology for 94% of the 114 species. Among them, within the 20-species treatment, 18.0% of all living individuals in 2016 were evergreen and 58.7% were deciduous (the other 23.3% varied between evergreen and deciduous). Within the 58-species treatment, 15.3% of them were evergreen and 52.4% were deciduous. Within the 114-species treatment, 19.8% of them were evergreen and 45.4% were deciduous (Lorenzi, 1992, 1998, 2009; Lorenzi et al., 2003). Nevertheless, it is important to stress that, as we did not assess leaf phenology in our field surveys, this information was entirely taken from the literature. Among deciduous species, duration and percentage of leaf loss may vary. Even for the same species, leaf phenology traits may vary from site to site, according to climatic and edaphic conditions. Thus, this information would be more accurate if it was specific to the study area.

2.2 | Light interception assessment

Light interception was characterized using intercepted photosynthetically active radiation (iPAR, Nouvellon et al., 2000) at the *Anhembi* site. At this site, we measured iPAR, as a proxy for absorbed PAR (aPAR). While aPAR is the fraction of the PAR that actually enters a leaf and can potentially be used for photosynthesis, iPAR is simply the difference between total PAR that reaches a canopy and the amount of this radiation that passes through it (Nouvellon et al., 2000). It considers neither the amount of light that reached the canopy and was not absorbed—but reflected by leaves and non-green parts of the canopy (Weiss et al., 2004)—nor the light reflected by the soil which could be absorbed by the abaxial surface of leaves. Due to practical difficulties in directly measuring aPAR at the tree plantation level, it is commonly predicted from iPAR. Nevertheless, the relationship between them is variable, especially between early and late stages of vegetation (Nouvellon et al., 2000). As all the plots compared in our experiments were closed-canopy forests of the same age, iPAR and aPAR were expected to vary congruently. On the other hand, due to specific climate conditions of each site, which required different equipment to take measurements more efficiently and accurately, at the *Sardinilla* site, light interception was characterized using the ratio of red:far-red light spectra (R:FR), instead of iPAR. Under diffuse light, R:FR measurements are a good proxy for iPAR (Capers & Chazdon, 2004). Data from this site were converted from R:FR into iPAR for illustration, in figures and in part of the tables. However, all analyses were carried out using raw data (R:FR).

At the *Sardinilla* site, a levelled Skye (Powis, UK) SKR 110 sensor was used to measure R:FR in periods with c. 100% diffuse incoming light. This sensor contains a cosine-corrected light-collecting tip, in order to receive radiation from a 180° hemisphere. We measured R:FR at 49 sample points per plot, obtained by 6×6 m grids that encompassed the entire plots (leaving out only one or two rows of trees, depending on the size of the plot, as borders) in the main plantation (hereafter '*Sardinilla*-main: horizontal R:FR', Dataset S1, available in the Dryad Digital Repository, Duarte et al., 2021) and

17 points per plot (obtained by 3 × 3 m grid in the central part of the plot and additional points near the border of the plot) at the HD plantation (hereafter 'Sardinilla-HD: horizontal R:FR', Dataset S2, Duarte et al., 2021; see Supporting Information, Figure S3, for experimental design at both plantations, and Figure S4 for data collection illustration). Each sample point determined by these grids was equidistant to the four nearest neighbour trees planted, so that those trees would likely equally influence light interception at each sample point. Measurements were always taken 1.7 m above-ground and from 9:50 a.m. to 2:15 p.m., during the rainy season (July and August, 2016). The conversion of R:FR into iPAR can be obtained through $\ln [iPAR/(1-iPAR)] = 6.76 - 6.85 * R:FR$ (see Supporting Information, Methods S3 and hereafter 'Sardinilla iPAR-R:FR regression', Dataset S3, Duarte et al., 2021).

At the *Anhembi* site, we used two levelled Decagon AccuPAR LP-80 ceptometers (Pullman WA, USA), calibrated with each other, to measure PAR inside and outside (in an open field next to the plantation, without any obstruction of sunlight) the tree plantations and calculate iPAR (see Supporting Information's Methods S4). Within plots, we measured iPAR 1 m above-ground, at 98 points per plot, regularly determined by a 3 × 6 m grid, which encompassed the entire plots (leaving out only two tree rows as borders), and equidistant to the four nearest planted trees (Supporting Information, Figure S5). Measurements were taken at the peak of the dry season (August 2015), when iPAR was expected to be at its lowest level due to canopy deciduousness (hereafter '*Anhembi*: dry season horizontal iPAR', Dataset S4, Duarte et al., 2021), and at the end of the wet season (March and early April 2016), when it was expected to be at its highest levels (hereafter '*Anhembi*: wet season horizontal iPAR', Dataset S5, Duarte et al., 2021). All iPAR measurements (for all sections of this work) took place between 10:00 a.m. and 2:20 p.m., under either completely overcast or completely sunny (but always stable) weather conditions. As each ceptometer had a probe measuring 80 cm and containing 80 sensors, we always positioned the equipment at the centre of the sample points and headed it to the same direction as the other ceptometer outside the forest (approximately NNE, see Supporting Information, Figure S5).

Light measurements within grids were more easily taken at different heights, when using different instruments, that is, 1.7 m above-ground using the R:FR sensor (at *Sardinilla*) and 1 m above-ground using the ceptometer (at *Anhembi*), which allowed us to optimize collection time. This was important since we wanted to characterize light interception at specific times of the year, thus measurements should all be done during a short time frame.

2.3 | iPAR variation

2.3.1 | Horizontal iPAR variation

We used the four datasets obtained in the previous section ('*Sardinilla*-main: horizontal R:FR', '*Sardinilla*-HD: horizontal R:FR', '*Anhembi*: dry season horizontal iPAR' and '*Anhembi*: wet season

horizontal iPAR', Datasets S1, S2, S4 and S5, Duarte et al., 2021) to assess how iPAR varied in horizontal space, both at the *Sardinilla* (main and HD plantations) and at the *Anhembi* (dry and wet seasons) sites.

2.3.2 | Vertical light variation

At the *Sardinilla* site, we established six vertical transects in each plot of the main plantation, and four vertical transects in each plot of the HD plantation, regularly located within the plots and equidistant to the four nearest neighbour trees planted (Supporting Information, Figure S6). Using a ladder, we conducted R:FR measurements over the vertical transects, every metre, from the heights of 1 to 5 m, during the rainy season (July and August 2016), at the main (hereafter '*Sardinilla*-main: vertical R:FR', Dataset S6, Duarte et al., 2021) and HD (hereafter '*Sardinilla*-HD: vertical R:FR', Dataset S7, Duarte et al., 2021) plantations, always from 9:30 a.m. to 2:40 p.m. and under overcast sky.

At the *Anhembi* site, we established 12 systematically distributed vertical transects, equidistant to the four nearest neighbour trees planted, in each plot of the *Anhembi* site (Supporting Information, Figures S7 and S8). Also using a ladder, we measured iPAR every metre over the vertical transects, from 0 to 4 m, during the dry season (August 2015; hereafter '*Anhembi*: dry season vertical iPAR', Dataset S8, Duarte et al., 2021). The measurements were repeated during the wet season (February 2016, hereafter '*Anhembi*: wet season vertical iPAR', Dataset S9, Duarte et al., 2021), always from 10:00 a.m. to 2:00 p.m.

Measurements were carried out at different heights over the vertical transects at each study site because (a) the understorey in many plots of the *Sardinilla* site had a large amount of invasive weeds, which made it very difficult to take measurements on the ground level and (b) it was possible to reach higher heights (up to 5 m) using the F:FR sensor, compared to the ceptometer. As a reference, mean heights (and standard errors) of living trees were 13.60 (±0.08) m at the main plantation and 16.10 (±0.20) m at the HD plantation of the *Sardinilla* experiment and 8.20 (±0.06) m at the *Anhembi* experiment (all data were taken from the botanical inventories carried out in 2016).

2.3.3 | Light temporal variation

At the *Anhembi* site, we measured iPAR 1 m above-ground at 12 points per plot (the same as the vertical transects in *Anhembi*, described in the previous section) in different seasons (wet and dry) from 2011 to 2017. iPAR measurements during the dry season took place in July 2011, August 2015, June 2016 and August 2017, whereas measurements in wet season were in January 2012, January 2013, February 2015, February 2016, February 2017 and January 2018 (hereafter '*Anhembi*: seasonal iPAR', Dataset S10, Duarte et al., 2021). We also took monthly iPAR measurements for

one year, from April 2017 to March 2018, at the same 12 points per plot mentioned above, 1 m above-ground (hereafter 'Anhembi: monthly iPAR', Dataset S11, Duarte et al., 2021). We intended to assess how iPAR varied between years, seasons and months within a year.

2.4 | Crown volume assessment

At the *Sardinilla* site, in July 2016, we measured crown volume of each of the main plantation's species, both in monocultures and in the five-species mixtures to account for growth differences of the same species in distinct combinations. We chose five individuals per monoculture and two individuals per species in each five-species mixture, the ones closest to the plot centre, to minimize influences from neighbour plots. Using a Haglöf (Långsele, Sweden) distance measurer (DME), we measured the projection of the crown in four different diameters: the largest diameter, its perpendicular diameter and the two diagonals, using a compass (see Supporting Information, Figure S9). We calculated the crown radius from the mean of those four diameters divided by two. We used a Haglöf vertex (Långsele, Sweden) to determine crown depth (difference between crown and tree heights; hereafter 'Sardinilla-main: crown', Dataset S12, Duarte et al., 2021). We calculated crown volume as a cylinder (Sapijanskas et al., 2014) (crown volume = (crown radius)² × π × crown depth). We acknowledge that, by assuming a simple cylinder form for all species, we overlooked potential variations in crown shapes among species and likely overestimated their volumes. Nevertheless, more realistic models of crown shape require data that were not available in this study. Our purpose here was not to provide an accurate measurement of crown volumes, but to compare them at the species level, in monoculture versus mixture. Therefore, analyses were not biased by the choice of assuming a cylinder shape for crowns.

2.5 | Data analyses

2.5.1 | Light interception

We analysed whether levels of richness enhanced light interception, for both the *Sardinilla* and the *Anhembi* experiments. For these analyses, R:FR data were kept in their original units, but were converted to iPAR for results and graphical representation, to allow for more intuitive comprehension and easy comparison among sites.

At the *Sardinilla* site (both main and HD plantations), to analyse if mean R:FR within plots varied between different levels of richness, we used the 'Sardinilla-main: horizontal R:FR' and the 'Sardinilla-HD: horizontal R:FR' datasets (Datasets S1 and S2, Duarte et al., 2021) and fitted multivariate covariance generalized linear models (McGLM; Bonat, 2018; Bonat & Jørgensen, 2016), separately for the main and HD plantations. These models are useful in this case, because they allow for the simultaneous modelling of the mean and

dispersion, with covariates. It is possible to separate the variation induced by the mean–variance relationship from the extra-variability that may be accounted for with regressors. Because the data from the *Sardinilla* site are continuous and not bounded, a normal model with identity link function was a reasonable assumption, coupled with a constant mean–variance assumption. We included the effects of richness, percentage of survival and coordinates of each sample point determined by the horizontal grids (orthogonal coordinates *x* and *y*, in metres, relative to the top-left corner of the plot), as well as the interaction between coordinates *x* and *y*, in the linear predictors for both the mean and dispersion parameters. It was important to include the percentage of survival within each plot as a covariate, since there was high mortality in some plots and the density of individuals is a factor that can influence light interception. By using this covariate, our intention was not to penalize, in our analyses, plots that had experienced high mortality, especially the ones that contained *Cordia alliodora*, which were expected to present lower light interception due to the missing individuals (please check Supporting Information's Figure S10: it is possible to note that, at the main plantation, survival was lower in two-species mixtures, where 1/3 of planted individuals were *C. alliodora*, and in five-species mixtures, where 1/5 of planted individuals were from this species). It was also important to include in our models the coordinates *x* and *y* of sample points, as spatial covariates, since light interception is a variable likely influenced by neighbourhood, thus F:RF (and also iPAR) measurements cannot be considered spatially independent.

At the *Anhembi* site, we also fitted McGLMs to analyse if iPAR means (both for dry and wet seasons, using the datasets 'Anhembi: dry season horizontal iPAR' and 'Anhembi: wet season horizontal iPAR'—Datasets S4 and S5, Duarte et al., 2021), varied with richness (20-, 58- and 114-species mixtures). However, since iPAR is bounded between 0 and 1, we used a logit link for the mean linear predictor, and assumed a mean–variance relationship analogous to the one for the binomial model, since we are modelling continuous proportions. Hence, by making these first and second moment assumptions, the non-gaussianity of the data was accounted for by the mean–variance relationship, whereas the extra-variability was modelled via an extra dispersion parameter, which depended on the covariate effects we wanted to study. Treatment replicate (four replicates), coordinates within the plot (orthogonal distances *x* and *y* from the top-left corner of the plot, in metres) and percentage of survival were included in the linear predictors for the mean and dispersion parameters. As done for the *Sardinilla* experiment, we used percentage of survival as a covariate, since high richness levels presented higher mortality at the *Anhembi* experiment (Supporting Information, Figure S10). High mortality was observed at high richness levels after plantation establishment, at the *Anhembi* site, as the initial study design included an unprecedented level of tree diversity (114 species), and not all species available for plantation were adequately adapted to the area's conditions.

We used Wald tests to assess the significance of effects in the fitted McGLMs and obtain the 95% confidence intervals for the true parameters.

2.5.2 | Horizontal light variation

At both *Sardinilla* and *Anhembi* sites, we used the same models described in the previous section to analyse means and dispersion of light (F:FR or iPAR, in different datasets: '*Sardinilla*-main: horizontal R:FR', '*Sardinilla*-HD: horizontal R:FR', '*Anhembi*: dry season horizontal iPAR' and '*Anhembi*: wet season horizontal iPAR'—Datasets S1, S2, S4 and S5, Duarte et al., 2021). F:FR or iPAR dispersion parameters, in McGLMs, are a proxy of spatial heterogeneity in light distribution (a higher dispersion parameter corresponds to higher heterogeneity in R:FR or iPAR), thus representing horizontal light variation in this work.

2.5.3 | Vertical light variation

For the *Sardinilla* site, to analyse light variation across vertical space (vertical transects measured), we also used McGLMs to determine whether means and dispersion of R:FR varied between richness levels and heights. For the main plantation ('*Sardinilla*-main: vertical R:FR', Dataset S6, Duarte et al., 2021), the predictors of both the mean and dispersion were richness level (one, two, three and five species), percentage of survival, vertical transect identity (each vertical transect measured was identified, as spatial covariate), height of R:FR measurement (1 to 5 m) and interaction between richness and height of R:FR measurement (to assess if R:FR presented distinct behaviours over the vertical space, at different richness levels). For the HD plantation ('*Sardinilla*-HD: vertical R:FR', Dataset S7, Duarte et al., 2021), effects accounted for were richness level (6, 9 and 18 species), percentage of survival, vertical transect identity, height of R:FR measurement (1 to 5 m) and interaction between richness and height of R:FR measurement.

For the vertical iPAR variation at the *Anhembi* site (in both dry and wet seasons, '*Anhembi*: dry season vertical iPAR' and '*Anhembi*: wet season vertical iPAR', Datasets S8 and S9, Duarte et al., 2021), we fitted McGLMs including as effects richness level (20, 58, and 114 species), replicate (four replicates of each treatment), height of iPAR measurement, interaction between richness level and height of iPAR measurement, vertical transect identity and percentage of survival in both the linear predictors for the mean and dispersion parameters.

2.5.4 | Temporal variation in light interception

For iPAR in different seasons and years ('*Anhembi*: seasonal iPAR', Dataset S10, Duarte et al., 2021), we fitted mixed beta regression models, including the effects of season, species richness and their interaction as fixed effects and year and replicate within year as random effects. For monthly iPAR over 1 year ('*Anhembi*: monthly iPAR', Dataset S11, Duarte et al., 2021), we also fitted mixed beta regression models, including different quadratic predictors over time per species richness level and the effects of replicate within year as

random. In both cases, we assessed the significance of the fixed effects using likelihood-ratio (LR) tests for nested models.

2.5.5 | Species in monocultures × mixtures

We carried out an analysis of variance to compare mean R:FR within plots of *Sardinilla*'s main plantation ('*Sardinilla*-main: horizontal R:FR', Dataset S1, Duarte et al., 2021) between different species compositions (12 levels: five monocultures, three combinations of two species, three combinations of three species and one combination of five species). Since the data were continuous and not bounded, a normal model was a reasonable assumption. We used percentage of survival within each plot as a covariate. We used Tukey's test at a 95% confidence level for multiple comparisons, with Bonferroni correction for the global confidence level. We established specific contrasts to compare mean R:FR (a) Between monocultures; (b) Between each monoculture and their combinations of two or three species; (c) Among two or three species mixtures; (d) Between five-species mixture and each of the other treatments.

We also compared crown volume between the five main species in monocultures and five-species mixtures ('*Sardinilla*-main: crown', Dataset S12, Duarte et al., 2021) using a two-way ANOVA, with log-transformed crown volume as dependent variable and tree species and plot richness level (one or five species) as independent variables. All analyses were carried out in the R environment (R Core Team, 2018).

3 | RESULTS

3.1 | Light interception

Tree species richness enhanced iPAR at both sites. At the *Sardinilla* site's main plantation, mean iPAR increased significantly with species richness ($\chi^2 = 310.34$, $df = 3$, $p < 0.0001$; Figure 1a, Supporting Information's Table S3). Five-species mixtures presented higher light interception than two- or three-species mixture plots ($p < 0.05$), which did not differ from each other, and all mixtures significantly intercepted more light than monocultures ($p < 0.0001$). At the HD plantation, light interception was not influenced by richness levels ($\chi^2 = 1.54$, $df = 2$, $p = 0.46$).

At the *Anhembi* site, increasing levels of richness enhanced iPAR in both seasons ($\chi^2 = 108.07$, $df = 2$, $p < 0.0001$ for the dry and $\chi^2 = 57.91$, $df = 2$, $p < 0.0001$ for the wet season; Figure 1b). In the dry season all treatments showed significantly different iPAR ($p < 0.05$) (see Supporting Information, Figure S11). In the wet season, iPAR also increased with tree richness ($\chi^2 = 57.91$, $df = 2$, $p < 0.0001$), but 58 and 114 species did not differ from each other ($p > 0.05$).

See Supporting Information (Table S4) for estimates and associated standard errors of the parameters estimated using the McGLMs for R:FR or iPAR.

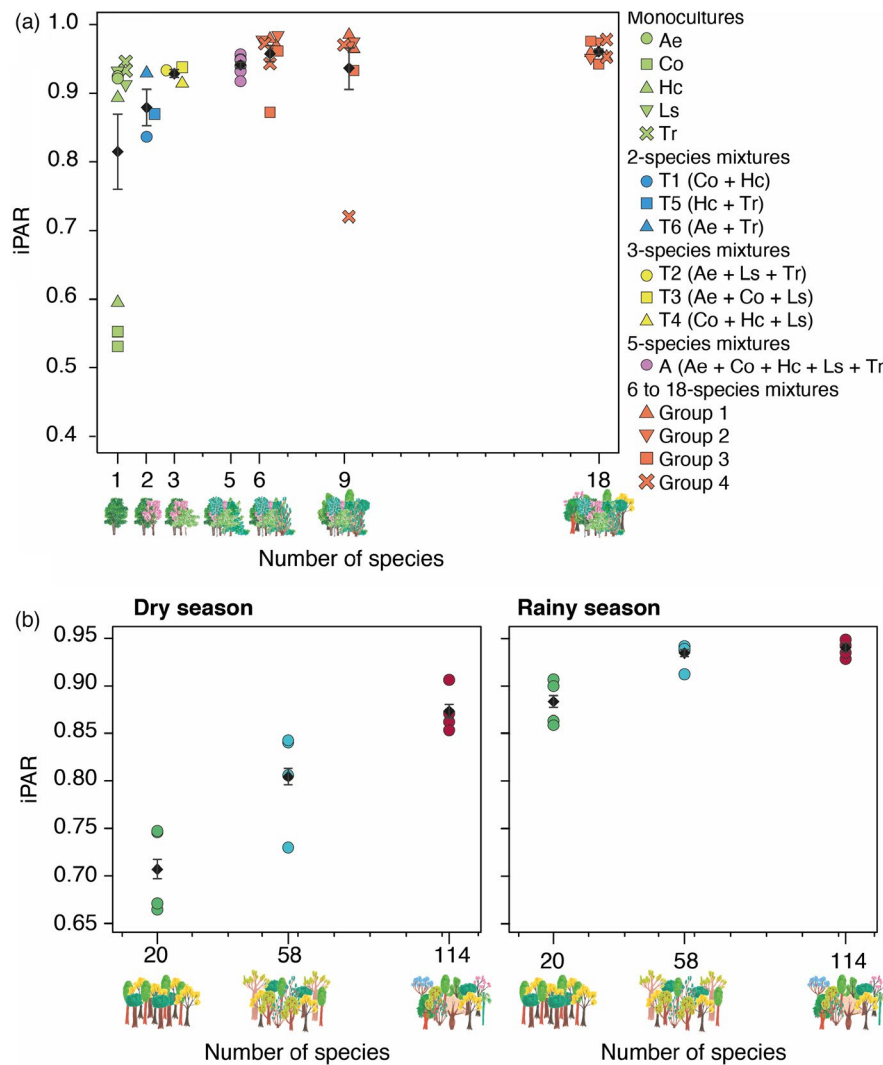


FIGURE 1 Mean iPAR for different treatments at the *Sardinilla* and *Anhembi* sites. (a) Mean iPAR (black points) and standard error (bars) at each richness level, measured during the rainy season (July and August, 2016), at the *Sardinilla* site (Sardinilla, Panama). The monocultures, 2-, 3- and 5-species combinations are part of the main plantation (established in 2001), thus they are 2 years older than the 6-, 9- and 18-species mixtures, which are part of the high-diversity plantation (established in 2003). Coloured marks represent all plots measured. Different shapes of marks represent distinct compositions within each richness level. Tree species in monocultures are: Ae = *Anacardium excelsum*, Co = *Cedrela odorata*, Hc = *Huracrepitans*, Ls = *Luehseemannii*, Tr = *Tabebuia rosea*. (b) Mean iPAR (black points) and standard errors (bars) measured for different species richness levels at the *Anhembi* experiment (Brazil, established in 2006), in dry ($\chi^2 = 108.07$, $df = 2$, $p < 0.0001$, measurements in August, 2015) and rainy ($\chi^2 = 57.91$, $df = 2$, $p < 0.0001$, measurements in March and April, 2016) seasons. Coloured points represent every plot measured within each richness level

3.2 | Horizontal light variation

Horizontal light variation (assessed by the dispersion parameter of the McGLMs fit for '*Sardinilla*-main: horizontal R:FR' and '*Sardinilla*-HD: horizontal R:FR', Datasets S1 and S2, Duarte et al., 2021) decreased (thus evenness in iPAR distribution increased) from monocultures to mixtures at the *Sardinilla* site's main plantation ($\chi^2 = 258.41$, $df = 3$, $p < 0.0001$) and from six species to richer mixtures in the HD plantation ($\chi^2 = 8.08$, $df = 2$, $p < 0.05$; Figure 2). In the main plantation, horizontal dispersion was significantly higher for monocultures, intermediate for three species and lower for two- and five-species mixtures ($p < 0.05$). That means that light interception was more evenly

distributed over the horizontal space in mixtures when compared to monocultures. In the HD plantation, horizontal light dispersion was lower for 9 and 18 species than for 6 species ($p < 0.05$). Thus, in the HD plantation, higher diversity was also associated with more even distribution of light interception over the horizontal space.

At the *Anhembi* site, horizontal variance in iPAR decreased with richness, differing between all richness levels during the dry season, and all but the 58- to 114-species mixtures in the rainy season (Figure 2; Figures S12 and S13), following the same pattern of mean PAR interception. Since we assumed a quadratic mean-variance relationship (typical for proportion data), with maximum variance obtained at a proportion of 50%, the further data are from 50%, the

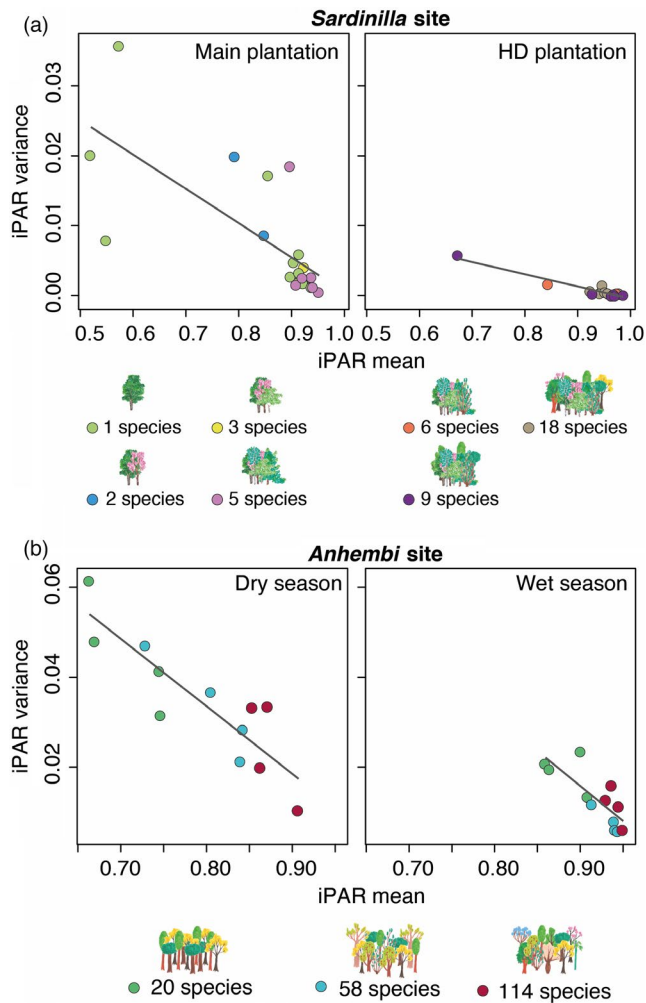


FIGURE 2 Relationship between iPAR means and variance for different richness levels (points in distinct colours) over horizontal measurements grids, at *Sardinilla* (a—*Sardinilla*, Panama) and *Anhembi* sites (b—*Anhembi*, Brazil). Please check Supporting Information, Figures S12 and S13, to visualize how light interception was distributed horizontally over the plots at the *Anhembi* site

lower their variance (McCullagh & Nelder, 1989). Therefore, stands with higher richness accounted for lower iPAR horizontal variance (more even light interception over the horizontal space at higher diversity). Moreover, we also modelled the dispersion parameter, which represents an extra source of variation, independent from the mean (Bonat & Jørgensen, 2016). At the *Anhembi* site, during the dry season, the dispersion parameter did not vary according to richness level ($\chi^2 = 0.9364$, $df = 2$, $p = 0.63$), but during the wet season it did so, with lower dispersion values (thus higher evenness of light interception) for 58 species, when compared to 20 species ($\chi^2 = 6.7155$, $df = 2$, $p = 0.03$).

3.3 | Vertical light variation

At both *Sardinilla* and *Anhembi* sites, higher richness levels were able to intercept higher amounts of PAR over different layers of the

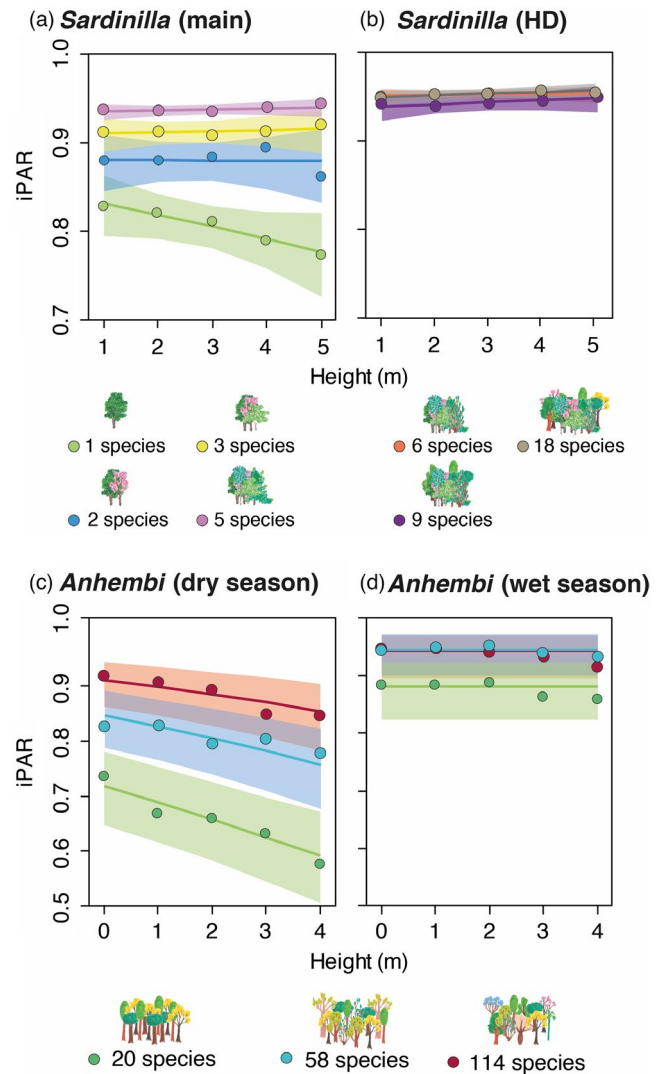


FIGURE 3 Mean intercepted photosynthetically active radiation (iPAR, points in different colours) and 95% confidence intervals (shaded areas) measured for different species richness levels (indicated in legends) at different heights within the canopy, at *Sardinilla* site's main (a) and high-diversity (b) plantations (*Sardinilla*, Panama) and at *Anhembi* site (*Anhembi*, Brazil) during the dry (c) and wet (d) seasons

canopy, thus being more efficient in filling space with vegetation. At the *Sardinilla* site's main plantation, iPAR at different heights increased with richness, significantly differing from monocultures to mixtures ($\chi^2 = 77.2180$, $df = 3$, $p < 0.0001$) but, between mixtures, increasing only from three to five species (Figure 3). Effects of interaction between richness and height were not significant ($\chi^2 = 4.1200$, $df = 3$, $p = 0.25$), which means that mixtures maintained higher iPAR in all layers of the canopy, compared to monocultures. Dispersion effects (dispersion parameter of the McGLM fit for the '*Sardinilla*-main: vertical R:FR', Dataset S6, Duarte et al., 2021) over the vertical transects also decreased from monocultures to mixtures ($\chi^2 = 68.1179$, $df = 3$, $p < 0.0001$), indicating that all mixtures could intercept light more evenly, in different

layers of vegetation, than monocultures, at the main plantation. In the HD plantation, iPAR over vertical transects was not influenced by richness ($\chi^2 = 5.5849$, $df = 2$, $p = 0.0613$) or by its interaction with height ($\chi^2 = 3.6841$, $df = 2$, $p = 0.1585$), and its dispersion (dispersion parameter of the McGLM fit for the 'Sardinilla-HD: vertical R:FR', Dataset S7, Duarte et al., 2021) did not vary among richness levels either ($\chi^2 = 1.4887$, $df = 2$, $p = 0.4750$).

At the *Anhembi* site, in the dry season, iPAR over the vertical transects significantly increased with richness ($\chi^2 = 97.2058$, $df = 2$, $p < 0.0001$), differing between every richness level at a 95% confidence level (Figure 3). There was no interaction between the number of species and height of measurements ($\chi^2 = 4.0268$, $df = 2$, $p = 0.1335$). Increasing richness showed decreasing dispersion of iPAR (dispersion parameter of the McGLM fit for the 'Anhembi: dry season vertical iPAR', Dataset S8, Duarte et al., 2021; $\chi^2 = 12.3733$, $df = 2$, $p = 0.0021$), which means that higher diversity levels could intercept light more evenly in different layers of vegetation over the canopy, during the dry season.

During the wet season, in *Anhembi*, iPAR over the vertical transects was higher in plots containing 58 and 114 species ($\chi^2 = 39.6361$, $df = 2$, $p < 0.0001$) and did not respond to interaction between height and richness level ($\chi^2 = 1.5535$, $df = 2$, $p = 0.4599$; Figure 3). Dispersion effects did not significantly differ according to richness level (dispersion parameter of the McGLM fit for the 'Anhembi: wet season vertical iPAR', Dataset S9, Duarte et al., 2021; $\chi^2 = 2.5248$, $df = 2$, $p = 0.2830$).

3.4 | Temporal variation in light interception

There was a significant interaction effect of season and richness level on iPAR measured in different years and seasons at the *Anhembi* site ('Anhembi: seasonal iPAR', Dataset S10, Duarte et al., 2021), that is, plots containing different numbers of species displayed different iPAR seasonal dynamics (LR = 17.2, $df = 2$, $p < 0.001$). The interaction was mostly driven by the difference between wet and dry seasons for 20- and 58-species but not for 114-species mixtures. In general, 114-species mixtures had larger iPAR than 20-species mixtures, on average (Figure 4).

Analysing iPAR monthly over 1 year ('Anhembi: monthly iPAR', Dataset S11, Duarte et al., 2021), there was a significant interaction effect between time and richness level (LR = 12.9574, $df = 2$, $p = 0.0154$), and a quadratic behaviour over time (minimum point of the curve in September; LR = 11.9910, $df = 1$, $p = 0.0005$), meaning that richer plots had more even distributions of light interception over the year. In general, 114- and 58-species had larger iPAR than 20-species mixtures, on average, and at the beginning of the study, 114-species presented larger iPAR than 58-species treatment (Figure 4).

3.5 | Species in monocultures and mixtures

Analysing different compositions within each richness level, at the *Sardinilla's* main plantation, some monocultures differed between

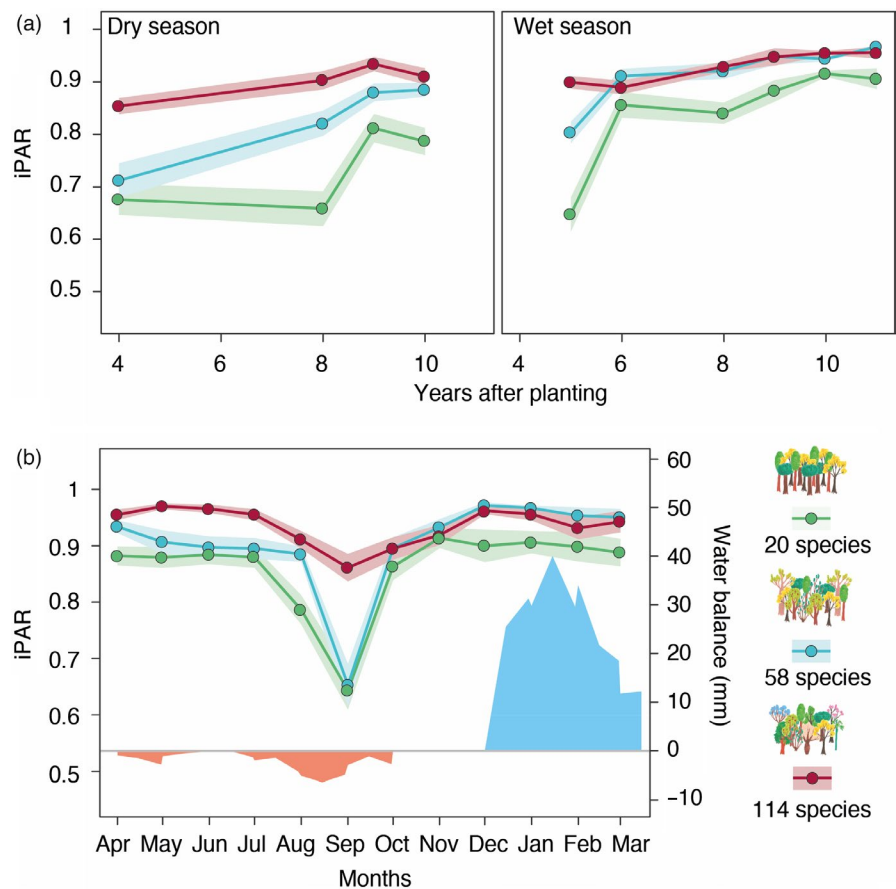


FIGURE 4 iPAR in different years (2011 to 2018) in wet and dry seasons (a) and monthly variation of iPAR and water balance over 1 year, from April 2017 to March 2018 (b) at the *Anhembi* experiment (*Anhembi*, Brazil, planted in 2006). Water balance data were taken from the 'Luiz de Queiroz' Campus (Piracicaba, SP, Brazil) Climate Dataset, Department of Biosystems Engineering, 'Luiz de Queiroz' College of Agriculture, University of São Paulo

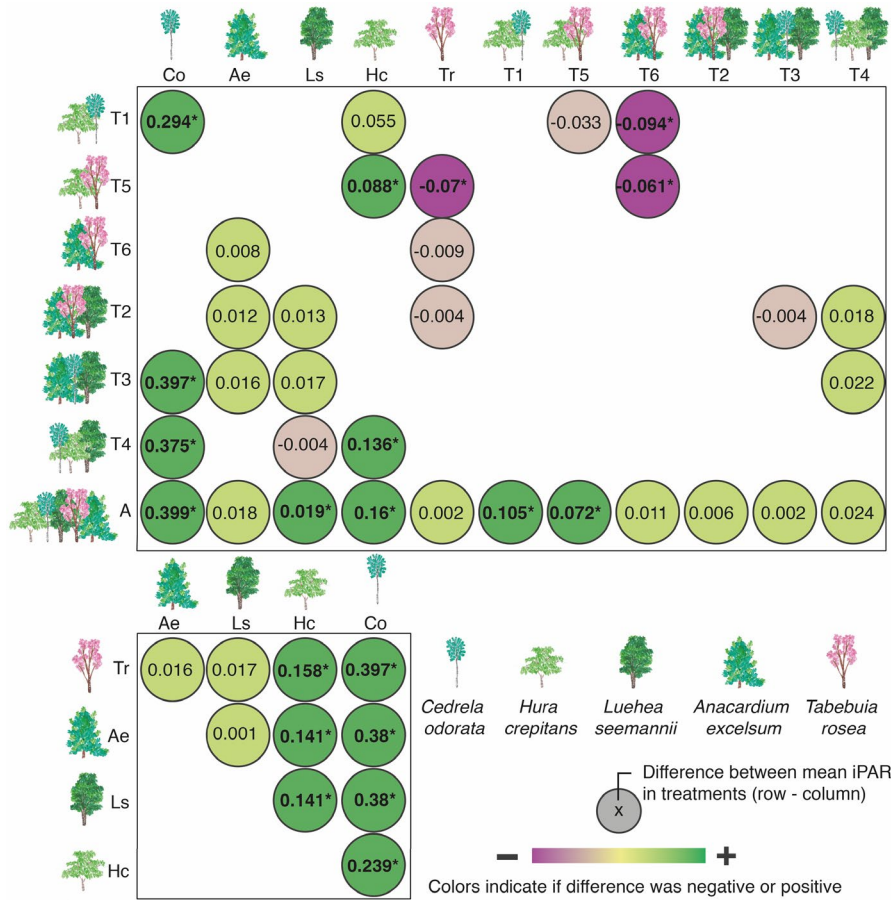


FIGURE 5 Comparisons of contrasts between different treatments' mean iPAR at the Sardinilla site's main plantation (Sardinilla, Panama, established in 2001), measured in 2016. Numbers within the cells represent the difference between mean iPAR from the treatment in the row and from the treatment in the column. Treatments: (1) monocultures: Ae = *Anacardium excelsum*, Co = *Cedrela odorata*, Hc = *Huracrepitans*, Ls = *Lueheaseemannii*, Tr = *Tabebuia rosea*; (2) two species combinations: T1 (Co + Hc), T5 (Hc + Tr), T6 (Ae + Tr); (3) three species combinations: T2 (Ae + Ls + Tr), T3 (Ae + Co + Ls), T4 (Co + Hc + Ls) and (4) five-species combination: A. Positive differences (between treatment in row and treatment in column) are coloured in green, while negative differences are coloured in purple. Intensity of colour is related to magnitude of difference between means. Significant contrasts at 95% confidence level are in bold and contain an asterisk. Differences are only shown when a species is present in both treatments. Analyses were performed using R:FR data and values were converted to iPAR only for better visualization. Here, the high-diversity (HD) plantation was not considered, since we wanted to compare mixtures to their constituent monocultures, and HD plantation counted on a larger species pool than the five species from the main plantation

each other regarding light interception, as well as two-species mixtures. This indicates that some species intercept more PAR than the others. Most mixtures maintained light interception at least equivalent to their best monocultures, except for *T. rosea* + *H. crepitans* (T5). The five-species mixtures tended to have the highest iPAR values, compared to monocultures and to other mixtures (Figure 5).

Crowns presented higher volume in five-species mixtures than in monocultures ($F_{1,110} = 19.9248, p < 0.0001$, Supporting Information's Figure S14).

4 | DISCUSSION

In this study, light interception—a key ecological process related to primary production and to forest dynamics (Binkley et al., 2013;

Canham et al., 1990; Sapijanskas et al., 2014)—was influenced by tropical tree diversity, both at low (one to five species) and very high (58 to 114 species) levels. We therefore report substantial effects of biodiversity on light interception in tropical forests undergoing restoration. Theory proposes that ecosystem functions saturate as species diversity increases (Cardinale et al., 2012), which is commonly reported to take place at low richness levels (Lamb, 2018). In grasslands, for instance, less than a dozen species were responsible for maintaining some specific ecosystem processes (Hector & Bagchi, 2007). These species, however, are mixed with others in a community assemblage, in which they can play different roles. Therefore, experimental design and species choice can influence results of experiments (Srivastava & Vellend, 2005). Nevertheless, in our work, even a richness level as high as 58 tree species was still not able to saturate light interception, in the dry season, which is an unprecedented result for a BEF experiment.

The comparison between our study sites illustrates how different locations and designs can affect the outcomes of ecological processes (Hector & Bagchi, 2007; Hooper et al., 2005; Jucker et al., 2015). Our results (iPAR at *Sardinilla* not increasing beyond six species, but not presenting a saturation point even for more than a hundred species at *Anhembi*, during the dry season) highlight that one must be careful when concluding about levels of species saturation in BEF. Distinct sets of species may present different functional traits and thus taxonomic diversity does not necessarily reflect functional diversity (Bruehlheide et al., 2014). However, we must point out that measurements at the *Sardinilla* site took place during the rainy season, when the differences between diversity treatments were the lowest at the *Anhembi* site.

4.1 | Tree diversity effects on the horizontal variation in light interception

We report that increased light interception at higher richness levels is related to less horizontal variation of iPAR. The duration and intensity of deciduousness (Gandolfi et al., 2009), crown shapes and arrangements (Jucker et al., 2015; Pretzsch, 2014; Sapjanskas et al., 2014), growth speed (Poorter & Arets, 2003), maximum achievable height, and leaf traits (Ruiz-Jaen & Potvin, 2011) differ among species and crucially determine mixture outputs. In addition, these traits can show plasticity in mixtures, promoting complementary use of light (Forrester & Albrecht, 2014; Forrester et al., 2018; Ruiz-Jaen & Potvin, 2011; Sapjanskas et al., 2014). Trees of distinct species may intersperse their crowns and better occupy empty spaces throughout the canopy (Pretzsch, 2014), thus enhance light capture (Sapjanskas et al., 2014). In both experiments, we showed that higher levels of species richness were associated with more spatially even distribution of light interception. This is likely a consequence of a better occupation of the canopy by tree branches and leaves (Guillemot et al., 2020), a process linked to competitive reduction (Forrester & Bausch, 2016). In fact, at the *Sardinilla* site, previous studies have shown that biomass allocation to branches was higher in mixtures than in monocultures (Guillemot et al., 2020; Potvin & Dutilleul, 2009).

4.2 | Tree diversity effects on the vertical variation in light interception

Higher tree richness also allowed the canopy to intercept light more evenly throughout the vertical canopy profile. When different species are combined, the diversity of forms of occupying the canopy at different heights is enhanced, thus resulting in a denser packing (Jucker et al., 2015; Sapjanskas et al., 2014). Moreover, as the crowns grow and touch branches from other trees, they tend to change direction of growth (Pretzsch, 2014) and fill spaces with leaves. According to Sapjanskas et al. (2014), however, up-to-date studies fail to show whether multiple canopy layers promoting

differential light interception over the space are really a cause of higher light interception or not. At the *Anhembi* site and *Sardinilla*'s main plantation, high-diversity plots intercepted more light than low-diversity plots across all measured heights. Moreover, vertical dispersion of intercepted light was, in general, lower at higher richness levels. This is evidence that high diversity allowed trees to better distribute their crowns, and thus light interception, over the vertical space.

4.3 | Tree diversity effects on the temporal variation in light interception

Higher species richness promoted a more even distribution of light interception over time. At *Anhembi*, the most diverse plots maintained more consistent levels of light interception over the time than plots containing lower richness, both between years, and between months within a single year. Species' contributions to ecosystem functions may present seasonal patterns (Wright et al., 2009). Phenological differences among species, such as non-coincident deciduous periods, for instance, may enhance light interception at plot level (Forrester & Bausch, 2016; Sapjanskas et al., 2014). When an ecosystem contains various species, it can buffer fluctuations in individual species' functions over the time, which is called the portfolio effect (Srivastava & Vellend, 2005). Besides the portfolio effect, facilitation processes may also occur. Studies show that individuals can receive more light and grow more intensely when they contain deciduous neighbours (Pretzsch, 2014). Thus, a stand can enhance its resource use when it bears species presenting distinct leaf phenology patterns (Sapjanskas et al., 2014).

4.4 | Towards a mechanistic understanding of light interception in diverse forests

Plant species diversity can influence ecosystem functioning via two distinct pathways: by selection effects, where a single species is responsible for playing a major role in a specific ecosystem function; or by complementarity effects, where interactions between species are responsible for higher ecosystem functioning, comparing to what would be expected from single species performances (Loreau & Hector, 2001). In this work, it was not possible to separate selection and complementarity effects on light interception, since we cannot single out the amount of light intercepted by each species of the mixtures and there is no easily measured weighting coefficient to represent species-specific contributions to light interception (Grossiord et al., 2013). However, we evidenced that species in mixtures developed larger crown volumes than in monocultures, probably a consequence of competitive reduction (Forrester & Bausch, 2016). This crown plasticity was shown to be linked to shifts in biomass allocation and branching pattern (Guillemot et al., 2020), which suggests that complementarity

effects occur in mixtures, at least to some extent (as suggested by Sapijanskas et al., 2014). In addition to species richness, composition influenced ecosystem processes (Naeem, 2016), since different monocultures and different species mixtures of the same richness levels performed differently in intercepting light at the *Sardinilla* site. At this site, average iPAR across species richness levels (see Figure 1a) agreed well with BEF theory, which states that mean light interception increases with richness, while the dispersion between different compositions of the same richness level decreases (Wright et al., 2009). The five-species mixtures showed PAR interception comparable to the best monocultures, as shown by other BEF works (Wright et al., 2009). This may lead to ask whether high diversity is necessary to maintain ecosystem functions, as some monocultures are good performers. Nevertheless, the advantage of holding more species is their ability to keep multifunctionality (Cardinale et al., 2012; Hector & Bagchi, 2007; Wright et al., 2009) and functional redundancy (Hooper et al., 2005). Ecosystems containing higher diversity will likely present better overall functioning than less diverse ones (Aerts & Honnay, 2011). In fact, in this study, the five-species mixture was in no case outperformed by any of the monocultures, even though it contained, in the same plot, species that had contrasting abilities in intercepting light.

4.5 | Conclusions: Implications for tropical forest restoration

We conclude that, when diversity increases, light interception increases as well, even at very high diversity levels. Diversity enhances light distribution over space (horizontally and vertically) and time, which increases light interception overall (Forrester & Bauhus, 2016). We gathered evidence that mixtures have advantages over monocultures regarding canopy occupation and light interception, and that species composition plays important role in this process (Naeem, 2016). Our findings may lead to various practical consequences. High diversity, by intercepting more light, can help control invasion by exotic grass species, a major concern for many large-scale tropical forest restoration projects, due to the additional costs associated with herbicide application and weeding (Rodrigues et al., 2009), which can jeopardize their overall financial viability and success (Brancalion et al., 2012). It also promotes canopy photosynthesis, which can result in biomass overyielding (Guillemot et al., 2020; Sapijanskas et al., 2014), and enhanced carbon sequestration. High tree richness levels should be critically considered for designing tropical forest restoration approaches to foster carbon sequestration in a changing climate.

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AUTHORS' CONTRIBUTIONS

M.M.D., P.H.S.B. and C.P. designed the research; C.P. and J.L.S. designed tree plantations (*Sardinilla* and *Anhembi* respectively); M.M.D. and C.I.F.Z. collected data; R.d.A.M. and W.H.B. carried out data analyses; M.M.D., P.H.S.B., R.d.A.M., C.I.F.Z. and J.G. discussed data; M.M.D. wrote a first draft of the manuscript and P.H.S.B., J.G., R.d.A.M. and C.P. contributed substantially to the final version.

DATA AVAILABILITY STATEMENT

Raw data used for analyses and results displayed and discussed in this manuscript were included in the Dryad Digital Repository <https://doi.org/10.5061/dryad.5mkkwh75q> (Duarte et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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