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2 **HIGH TREE DIVERSITY ENHANCES LIGHT INTERCEPTION IN TROPICAL**  
3 **FORESTS**

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53 **Running title:** Diversity enhances light interception

54

55 **Article type:** Research article

57 1. Understanding the processes that underlie the effects of tree diversity on primary  
58 production is of foremost importance to enhance climate change mitigation by tropical  
59 forests. Here, we investigated the effects of tree diversity on light interception over space  
60 and time in two tropical tree experiments, located in Panama – *Sardinilla* site  
61 (monocultures to 18-species mixtures), and in Brazil – *Anhembi* site (20- to 114-species  
62 mixtures).

63 2. We assessed intercepted photosynthetic active radiation (iPAR) over horizontal  
64 grids and vertical transects (up to 5 meters high in *Sardinilla* and up to 4 meters high in  
65 *Anhembi*), in plots containing different richness levels and combinations of species.

66 3. Light interception increased from monocultures to 5-species mixtures in *Sardinilla*  
67 and from 20- to 114-species mixtures in *Anhembi* (during the dry season). At the *Sardinilla*  
68 site, 5-species mixtures showed iPAR comparable to the best performing monocultures,  
69 despite substantial differences observed amongst monocultures. Diversity-iPAR  
70 relationships changed seasonally and were more pronounced during the dry season. Tree  
71 richness promoted a less variable temporal and spatial (i.e. both horizontal and vertical)  
72 distribution of light interception.

73 *Synthesis:* High tree diversity (i.e., over a hundred species in mixture) maximizes the amount  
74 of light intercepted by the canopy in restored tropical forests through more even capture in  
75 space and time. Diversity-light interception relationships should be critically considered for  
76 designing cost-efficient large-scale tropical forest restoration programs.

77

78 Keywords: BEF Theory; Biodiversity and Ecosystem Functioning Theory;  
79 Complementarity; Ecological processes; Ecosystem services; Light partitioning;  
80 Restoration Ecology.

81

83 1. Compreender os mecanismos que fundamentam os efeitos da diversidade arbórea  
84 sobre a produção primária é fundamental para maximizar o papel de florestas tropicais na  
85 mitigação de mudanças climáticas. Neste trabalho, investigamos os efeitos do número de  
86 espécies sobre a interceptação de luz pelo dossel de florestas tropicais, em dois  
87 experimentos de diversidade arbórea, localizados no Panamá – área *Sardinilla* (contendo  
88 monoculturas a misturas de 18 espécies) e no Brasil – área *Anhembi* (com misturas de 20 a  
89 114 espécies).

90 2. Avaliamos a radiação fotossinteticamente ativa interceptada (iPAR) ao longo do  
91 espaço horizontal e de transectos verticais (de até 5 m de altura em *Sardinilla* e de até 4 m  
92 de altura em *Anhembi*) nas parcelas contando com diferentes níveis de riqueza e  
93 combinações de espécies.

94 3. A interceptação de luz aumentou de monoculturas a misturas de cinco espécies em  
95 *Sardinilla* e entre misturas de 20 a 114 espécies em *Anhembi* (na estação seca). Em *Sardinilla*,  
96 a mistura de cinco espécies mostrou iPAR equivalente às das monoculturas mais eficientes  
97 em interceptar luz, apesar da grande diferença nos resultados apresentados pelas  
98 monoculturas aqui estudadas. A relação entre diversidade e iPAR variou entre estações,  
99 mais pronunciada na estação seca. Riqueza arbórea promoveu interceptação de luz de  
100 forma mais homogênea temporal e espacialmente (tanto horizontal quanto verticalmente).

101 *Síntese.* A alta diversidade arbórea (mesmo superior a 100 espécies em misturas) é capaz de  
102 maximizar a quantidade de luz interceptada pelo dossel de florestas tropicais em  
103 restauração, por meio de uma captura de luz mais homogênea no espaço e no tempo. A  
104 relação entre biodiversidade e interceptação de luz deve ser levada em conta para um  
105 planejamento custo-eficiente de programas de restauração florestal em larga escala.

106

107 Palavras-chave: Complementaridade; Ecologia de restauração; Processos ecológicos;

108 Serviços ecossistêmicos; Partição de luz; Teoria BEF; Teoria de Biodiversidade e

109 Funcionamento de Ecossistemas.

110

## 111 Introduction

112 Biodiversity and ecosystem functioning (BEF) theory predicts that increased  
113 species diversity can enhance resource capture at community level and foster ecosystem  
114 functioning (Loreau *et al.*, 2001). Experiments corroborating this theory have been  
115 historically carried out on grasslands (Balvanera *et al.*, 2006), and extended in the last 15  
116 years to forests (Potvin & Gotelli, 2008; Gamfeldt *et al.*, 2013; Guerrero-Ramírez *et al.*,  
117 2017; Ratcliffe *et al.*, 2017), mainly in temperate biomes. Moreover, forest BEF studies are  
118 commonly based on a limited number of tree species (usually less than a dozen) that does  
119 not compare to the high diversity of tropical biomes (Paquette *et al.*, 2018), nor to the  
120 species richness usually found in tropical restoration plantings (Brancalion *et al.*, 2018).  
121 Consequently, the role of high tree species richness in the functioning of hyperdiverse  
122 tropical forests, among the most species- and biomass-rich ecosystems on Earth (Barlow *et*  
123 *al.*, 2018), remains poorly understood (Clarke *et al.*, 2017). This knowledge gap is  
124 particularly important because tropical forest re-growth has been promoted worldwide as a  
125 central solution to mitigate climate change (Brancalion *et al.*, 2019b; Lewis *et al.*, 2019; Pugh  
126 *et al.*, 2019), as well to provide multiple ecosystem services that underpin human wellbeing  
127 (Chazdon & Brancalion, 2019). Understanding the effects of tree diversity on forest growth  
128 is key for maximizing carbon sequestration in forest restoration (Potvin *et al.*, 2011; Hulvey  
129 *et al.*, 2013; Sapijanskas *et al.*, 2014).

130 Current evidence suggests a positive but saturating relationship between species  
131 richness and ecological processes (Cardinale *et al.*, 2011; Clarke *et al.*, 2017; Guerrero-  
132 Ramírez *et al.*, 2017). In a meta-analysis considering various types of ecosystems, from  
133 aquatic to terrestrial, Cardinale *et al.* (2011) found that maximum biomass achieved by  
134 primary producers (plants and algae), in mixtures containing increasing numbers of species,  
135 was on average 2.38 times higher than the average biomass of monocultures, and that half

136 of this yield would be reached with 1.35 species. Levels of diversity required to saturate  
137 ecosystem functions is, however, still an unresolved issue (Cardinale *et al.*, 2012), especially  
138 when considering large spatial scales (Srivastava & Vellend, 2005; Cardinale *et al.*, 2011),  
139 varying species compositions (Srivastava & Vellend, 2005), multiple ecosystem functions  
140 (Meyer *et al.*, 2018) and services (Isbell *et al.*, 2011), and long-term resilience (Brockerhoff *et*  
141 *al.*, 2017).

142 Forest structural complexity has been shown to be an important determinant of  
143 forest productivity (Hardiman *et al.*, 2011; Gough *et al.*, 2019), and may partly explain  
144 overyielding (i.e., increased productivity of mixtures compared to monocultures; (Dănescu  
145 *et al.*, 2016; Schnabel *et al.*, 2019). This suggests that light-related interactions are key drivers  
146 of BEF relationships in tree-species mixtures (Morin *et al.*, 2011; Forrester & Bauhus, 2016;  
147 Guillemot *et al.*, 2020). Recent studies showed that diverse forests are more efficient in  
148 filling canopy space with leaves, which likely results in enhanced light interception  
149 (Pretzsch, 2014; Sapijanskas *et al.*, 2014; Jucker *et al.*, 2015; Williams *et al.*, 2017). However,  
150 the effects of tree species richness on forest light interception have seldom been directly  
151 quantified across time and space (Binkley *et al.*, 1992; Forrester *et al.*, 2012, 2018, 2019; le  
152 Maire *et al.*, 2013; Forrester & Albrecht, 2014; Sapijanskas *et al.*, 2014; Sercu *et al.*, 2017).  
153 This lack of empirical evidence of diversity effect on light interception is particularly acute  
154 in tropical forests, which typically display very high tree diversity and complex multi-layered  
155 canopy structure (Laurans *et al.*, 2014; Trogisch *et al.*, 2017). Studying the effects of tree  
156 diversity on light interception is therefore key to understand the functioning of diverse  
157 forests and how biodiversity loss can affect vital ecological processes, such as carbon  
158 sequestration. Moreover, light interception is linked to a number of key objectives of forest  
159 restoration, such as the control of invasive grass (Rodrigues *et al.*, 2009; Brancalion *et al.*,  
160 2019a). Understanding how tree diversity affects patterns of light absorption in tropical  
161 forests is then of great importance for designing cost-effective large-scale restoration

162 programs, which are expected to expand in the current United Nations decade on  
163 ecosystem restoration (2021-2030).

164 Here, we explored patterns of light interception through time and space across  
165 tree diversity gradients in two tropical forests. Specifically, we quantified: 1) total amount  
166 of intercepted light; 2) the horizontal variation of intercepted light 3) the vertical variation  
167 of intercepted light in the canopy; 4) the temporal variation in canopy light interception  
168 (between and within years); 5) the differences in light interception between mixtures of  
169 species and their constituent monocultures (for this purpose, to support our conclusions,  
170 we also compared crown volumes of trees in monocultures and mixtures). We carried out  
171 our investigation based on two experiments: a 15-year-old BEF experiment established in  
172 Sardinilla, Panama (Scherer-Lorenzen *et al.*, 2005), which presented its species in  
173 monocultures and mixtures (up to 18 species), and a nine-year-old tree diversity experiment  
174 established in Anhembi, Brazil with unprecedented high tree species richness (up to 114  
175 species), which allowed linking BEF theory to tropical forest restoration.

176

## 177 **Material and Methods**

### 178 **Study sites**

179 We included in this study two sites that contained experiments based on different  
180 methodological approaches to test the influence of tree diversity on light interception by  
181 tropical forests. The *Sardinilla* site, in Panama, consists of an experiment especially designed  
182 for BEF studies. It contains, in two distinct plantations, five species in monocultures and in  
183 different combinations of up to 18 species (Scherer-Lorenzen *et al.*, 2005). Its maximum  
184 richness level of plots was based on the diversity of natural, old-growth forests nearby the  
185 experimental areas (TreeDivNet, 2017). The *Anhembi* site, in Brazil, holds an experiment

186 designed to assess effects of very high tree diversity levels on tropical forest functioning. It  
187 does not include species in monocultures, but its design allows for testing the effects of an  
188 unprecedented tree diversity level on ecosystem processes and functions, using similar tree  
189 species diversity as found in high-diversity restoration projects (at least 80 species, for  
190 Brazilian Atlantic Forest; Brancalion *et al.*, 2018).

191 The *Sardinilla* experiment was established in Panama, under an Am (equatorial  
192 monsoon) climate (Köppen-Geiger; Kottek *et al.* 2006; see supporting information,  
193 Methods S1 for detailed information on this site). It consists of two native tree plantations  
194 started at different times. In both of them, spacing between seedlings was 3 x 3 m. The  
195 hereafter called “main plantation”, established in 2001 (plantation was 15 years old at onset  
196 of field surveys), presented six species – fast-growing: *Luehea seemannii* Triana & Planch  
197 (Malvaceae) and *Cordia alliodora* (Ruiz & Pav.) Oken (Boraginaceae); intermediate:  
198 *Anacardium excelsum* (Bertero ex Kunth) Skeels (Anacardiaceae) and *Hura crepitans* L.  
199 (Euphorbiaceae); slow-growing: *Cedrela odorata* L. (Meliaceae) and *Tabebuia rosea* (Bertol.)  
200 Bertero ex A.DC. (Bignoniaceae) – in 24 experimental plots of approximately similar  
201 dimensions (45 x 45 m, 45 x 48 m or 48 x 48 m), containing monocultures (12 plots: two  
202 replicates for each species) and combinations of three (six plots containing different  
203 combinations of a fast-growing, a slow-growing and an intermediate species) and of six  
204 species (six replicates of the same mixture), in a Latin-square design (Potvin & Dutilleul  
205 2009). All six species shed leaves during the dry season – *C. odorata* being deciduous and the  
206 other five, semi-deciduous. One of the species (*C. alliodora*) was not considered here  
207 because almost all individuals died after plantation establishment (Kunert *et al.*, 2012). Our  
208 effective plots were thus: two replicates of five distinct monocultures, three combinations  
209 of two species, three combinations of three species, and six replicates of a five-species  
210 combination (Supporting information, Figure S1). The hereafter called “high diversity  
211 plantation” (HD) was established in 2003 (plantation was 13 years old at onset of field

212 surveys), in 24 18 x 18 m plots organized in eight blocks, each one containing one plot of  
213 each richness level: 6, 9 and 18 species. Smaller species pools were subsets of larger ones,  
214 all of them within a 28-species pool (supporting information, Table S1). The eight blocks  
215 contained four different species combinations (hereafter called groups), thus there were  
216 two replicates of each group (Ruiz-Jaen & Potvin 2011).

217         The *Anhembi* experiment was established in southeastern Brazil, under Cfa (humid  
218 subtropical, oceanic, hot summer) climate (Köppen; Alvares *et al.* 2013). This region was  
219 once covered by seasonal semi-deciduous forest (Morellato & Haddad, 2000), where 30-  
220 50% of species shed leaves (Gandolfi *et al.*, 2009). This forest type is part of one of the  
221 most threatened biogeographical regions of the Atlantic Forest (Ribeiro *et al.*, 2009), a  
222 leading global hotspot for both biodiversity conservation (Laurance, 2009) and tropical  
223 forest restoration (Brancalion *et al.*, 2019b). The experiment was established in 2006  
224 (plantation was nine years old at onset of field sampling) using different tree richness levels:  
225 20, 58 and 114 native tree species (see supporting information, Table S2), in a completely  
226 randomized design with four replicates (A-D) of each (see supporting information, Figures  
227 S1 and S2 and Methods S2). The smaller species pools were subsets of the larger ones. The  
228 spatial distribution of species was randomly determined for the first replicate and then  
229 repeated in the others of the same treatment. Seedlings were planted in 45 x 48 m plots (3 x  
230 1.5 m spacing - 480 individuals per plot). We were able to find information on leaf  
231 phenology for 94% of the 114 species. Among them, within the 20-species treatment,  
232 18.0% of all living individuals in 2016 were evergreen and 58.7% were deciduous (the other  
233 23.3% varied between evergreen and deciduous). Within the 58-species treatment, 15.3%  
234 of them were evergreen and 52.4% were deciduous. Within the 114-species treatment,  
235 19.8% of them were evergreen and 45.4% were deciduous (Lorenzi, 1992, 1998, 2009;  
236 Lorenzi *et al.*, 2003). Nevertheless, it is important to stress that, as we did not assess leaf  
237 phenology in our field surveys, this information was entirely taken from the literature.

238 Among deciduous species, duration and percentage of leaf loss may vary. Even for the  
239 same species, leaf phenology traits may vary from site to site, according to climatic and  
240 edaphic conditions. Thus, this information would be more accurate if it were specific to the  
241 study area.

### 242 **Light interception assessment**

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

262 At the *Sardinilla* site, a leveled Skye (Powis, UK) SKR 110 sensor was used to

263 measure R:FR in periods with ca. 100% diffuse incoming light. This sensor contains a  
264 cosine-corrected light-collecting tip, in order to receive radiation from a 180° hemisphere.  
265 We measured R:FR at 49 sample points per plot, obtained by 6 x 6 m grids that  
266 encompassed the entire plots (leaving out only one or two rows of trees, depending on the  
267 size of the plot, as borders) in the main plantation (hereafter “*Sardinilla*-main: horizontal  
268 R:FR”, Dataset S1, available in the Dryad Digital Repository, DOI  
269 10.5061/dryad.5mkkwh75q) and 17 points per plot (obtained by 3 x 3 m grid in the central  
270 part of the plot and additional points near the border of the plot) at the HD plantation  
271 (hereafter “*Sardinilla*-HD: horizontal R:FR”, Dataset S2, DOI 10.5061/dryad.5mkkwh75q;  
272 see supporting information, Figure S3, for experimental design at both plantations, and  
273 Figure S4 for data collection illustration). Each sample point determined by these grids was  
274 equidistant to the four nearest neighbor trees planted, so that those trees would likely  
275 equally influence light interception at each sample point. Measurements were always taken  
276 1.7 m above ground and from 9:50 AM to 2:15 PM, during the rainy season (July and  
277 August, 2016). The conversion of R:FR into iPAR can be obtained through  $\ln [iPAR/(1-$   
278  $iPAR)] = 6.76 - 6.85 * R:FR$  (see supporting information, Methods S3 and (hereafter  
279 “*Sardinilla* iPAR-R:FR regression”, Dataset S3, DOI 10.5061/dryad.5mkkwh75q).

280 At the *Anhembi* site, we used two leveled Decagon AccuPAR LP-80 ceptometers  
281 (Pullman WA, USA), calibrated with each other, to measure PAR inside and outside (in an  
282 open field next to the plantation, without any obstruction of sunlight) the tree plantations  
283 and calculate iPAR (see supporting information’s Methods S4). Within plots, we measured  
284 iPAR one meter above ground, at 98 points per plot, regularly determined by a 3 x 6 m  
285 grid, which encompassed the entire plots (leaving out only two tree rows as borders), and  
286 equidistant to the four nearest planted trees (supporting information, Figure S5).  
287 Measurements were taken at the peak of the dry season (August 2015), when iPAR was  
288 expected to be at its lowest level due to canopy deciduousness (hereafter “*Anhembi*: dry

289 season horizontal iPAR”, Dataset S4, DOI 10.5061/dryad.5mkkwh75q), and at the end of  
290 the wet season (March and early April 2016), when it was expected to be at its highest  
291 levels (hereafter “*Anbemi*: wet season horizontal iPAR”, Dataset S5, DOI  
292 10.5061/dryad.5mkkwh75q). All iPAR measurements (for all sections of this work) took  
293 place between 10:00 AM and 2:20 PM, under either completely overcast or completely  
294 sunny (but always stable) weather conditions. As each ceptometer had a probe measuring  
295 80 cm and containing 80 sensors, we always positioned the equipment at the center of the  
296 sample points and headed it to the same direction as the other ceptometer outside the  
297 forest (approximately NNE, see supporting information, Figure S4).

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

### 303 **iPAR variation**

#### 304 *Horizontal iPAR variation*

305 We used the four datasets obtained in the previous section (“*Sardinilla*-main:  
306 horizontal R:FR”, “*Sardinilla*-HD: horizontal R:FR”, “*Anbemi*: dry season horizontal  
307 iPAR” and “*Anbemi*: wet season horizontal iPAR”, Datasets S1, S2, S4 and S5, DOI  
308 10.5061/dryad.5mkkwh75q) to assess how iPAR varied in horizontal space, both at the  
309 *Sardinilla* (main and HD plantations) and at the *Anbemi* (dry and wet seasons) sites.

#### 310 *Vertical light variation*

311 At the *Sardinilla* site, we established six vertical transects in each plot of the main  
312 plantation, and four vertical transects in each plot of the HD plantation, regularly located  
313 within the plots and equidistant to the four nearest neighbor trees planted (supporting  
314 information, Figure S6). Using a ladder, we conducted R:FR measurements over the  
315 vertical transects, every meter, from the heights of 1 to 5 m, during the rainy season (July  
316 and August 2016), at the main (hereafter “*Sardinilla*-main: vertical R:FR”, Dataset S6, DOI  
317 10.5061/dryad.5mkkwh75q) and HD (hereafter “*Sardinilla*-HD: vertical R:FR”, Dataset S7,  
318 DOI 10.5061/dryad.5mkkwh75q) plantations, always from 9:30 AM to 2:40 PM and under  
319 overcast sky.

320 At the *Anhembi* site, we established 12 systematically-distributed vertical transects,  
321 equidistant to the four nearest neighbor trees planted, in each plot of the *Anhembi* site  
322 (supporting information, Fig. S7 and S8). Also using a ladder, we measured iPAR every  
323 meter over the vertical transects, from 0 to 4 m, during the dry season (August 2015;  
324 hereafter “*Anhembi*: dry season vertical iPAR”, Dataset S8, DOI  
325 10.5061/dryad.5mkkwh75q). The measurements were repeated during the wet season  
326 (February 2016, hereafter “*Anhembi*: wet season vertical iPAR”, Dataset S9, DOI  
327 10.5061/dryad.5mkkwh75q), always from 10:00 AM to 2:00 PM.

328 Measurements were carried out at different heights over the vertical transects at  
329 each study site because 1) the understory in many plots of the *Sardinilla* site had a large  
330 amount of invasive weeds, which made it very difficult to take measurements on the  
331 ground level and 2) it was possible to reach higher heights (up to 5 m) using the F:FR  
332 sensor, compared to the ceptometer. As a reference, mean heights (and standard errors) of  
333 living trees were 13.60 ( $\pm$  0.08) m at the main plantation and 16.10 ( $\pm$  0.20) m at the HD  
334 plantation of the *Sardinilla* experiment and 8.20 ( $\pm$  0.06) m at the *Anhembi* experiment (all  
335 data were taken from the botanical inventories carried out in 2016).

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### *Light temporal variation*

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At the *Anbemi* site, we measured iPAR one meter above ground at 12 points per plot (the same as the vertical transects in *Anbemi*, 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 “*Anbemi*: seasonal iPAR”, Dataset S10, DOI 10.5061/dryad.5mkkwh75q). We also took monthly iPAR measurements for one year, from April 2017 to March 2018, at the same 12 points per plot mentioned above, one meter above ground (hereafter “*Anbemi*: monthly iPAR”, Dataset S11, DOI 10.5061/dryad.5mkkwh75q). We intended to assess how iPAR varied between years, seasons, and months within a year.

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### **Crown volume assessment**

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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 center, to minimize influences from neighbor 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, Fig. 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, DOI 10.5061/dryad.5mkkwh75q). We

360 calculated crown volume as a cylinder (Sapijanskas *et al.*, 2014) (crown volume = (crown  
361 radius)<sup>2</sup> \*  $\pi$  \* crown depth). We acknowledge that, by assuming a simple cylinder form for  
362 all species, we overlooked potential variations in crown shapes among species and likely  
363 overestimated their volumes. Nevertheless, more realistic models of crown shape require  
364 data that were not available in this study. Our purpose here was not to provide an accurate  
365 measurement of crown volumes, but to compare them at the species level, in monoculture  
366 versus mixture. Therefore, analyses were not biased by the choice of assuming a cylinder  
367 shape for crowns.

## 368 **Data analyses**

### 369 *Light interception*

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

374 At the *Sardinilla* site (both main and HD plantations), to analyze if mean R:FR  
375 within plots varied between different levels of richness, we used the “*Sardinilla*-main:  
376 horizontal R:FR” and the “*Sardinilla*-HD: horizontal R:FR” datasets (Datasets S1 and S2,  
377 DOI 10.5061/dryad.5mkkwh75q) and fitted multivariate covariance generalized linear  
378 models (McGLM) (Bonat & Jørgensen, 2016; Bonat, 2018), separately for the main and  
379 HD plantations. These models are useful in this case, because they allow for the  
380 simultaneous modeling of the mean and dispersion, with covariates. It is possible to  
381 separate the variation induced by the mean-variance relationship from the extra-variability  
382 that may be accounted for with regressors. Because the data from the *Sardinilla* site are  
383 continuous and not bounded, a normal model with identity link function was a reasonable

384 assumption, coupled with a constant mean-variance assumption. We included the effects of  
385 richness, percentage of survival and coordinates of each sample point determined by the  
386 horizontal grids (orthogonal coordinates x and y, in meters, relative to the top-left corner  
387 of the plot), as well as the interaction between coordinates x and y, in the linear predictors  
388 for both the mean and dispersion parameters. It was important to include the percentage of  
389 survival within each plot as a covariate, since there was high mortality in some plots and  
390 the density of individuals is a factor that can influence light interception. By using this  
391 covariate, our intention was not to penalize, in our analyses, plots that had experienced  
392 high mortality, especially the ones that contained *Cordia alliodora*, which were expected to  
393 present lower light interception due to the missing individuals (please check supporting  
394 information's Figure S10: it is possible to note that, at the main plantation, survival was  
395 lower in 2-species mixtures, where 1/3 of planted individuals were *C. alliodora*, and in 5-  
396 species mixtures, where 1/5 of planted individuals were from this species). It was also  
397 important to include in our models the coordinates x and y of sample points, as spatial  
398 covariates, since light interception is a variable likely influenced by neighborhood, thus  
399 F:RF (and also iPAR) measurements cannot be considered spatially independent.

400         At the *Anbemi* site, we also fitted McGLMs to analyze if iPAR means (both for  
401 dry and wet seasons, using the datasets “*Anbemi*: dry season horizontal iPAR” and  
402 “*Anbemi*: wet season horizontal iPAR” – Datasets S4 and S5, DOI  
403 10.5061/dryad.5mkkwh75q), varied with richness (20-, 58- and 114-species mixtures).  
404 However, since iPAR is bounded between 0 and 1, we used a logit link for the mean linear  
405 predictor, and assumed a mean-variance relationship analogous to the one for the binomial  
406 model, since we are modeling continuous proportions. Hence, by making these first and  
407 second moment assumptions, the non-gaussianity of the data was accounted for by the  
408 mean-variance relationship, whereas the extra-variability was modeled via an extra  
409 dispersion parameter, which depended on the covariate effects we wanted to study.

410 Treatment replicate (four replicates), coordinates within the plot (orthogonal distances x  
411 and y from the top-left corner of the plot, in meters) and percentage of survival were  
412 included in the linear predictors for the mean and dispersion parameters. As done for the  
413 *Sardinilla* experiment, we used percentage of survival as a covariate, since high richness  
414 levels presented higher mortality at the *Anbembí* experiment (supporting information,  
415 Figure S10). High mortality was observed at high richness levels after plantation  
416 establishment, at the *Anbembí* site, as the initial study design included an unprecedented  
417 level of tree diversity (114 species), and not all species available for plantation were  
418 adequately adapted to the area's conditions.

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

#### 421 *Horizontal light variation*

422 At both *Sardinilla* and *Anbembí* sites, we used the same models described in the  
423 previous section to analyze means and dispersion of light (F:FR or iPAR, in different  
424 datasets: “*Sardinilla*-main: horizontal R:FR”, “*Sardinilla*-HD: horizontal R:FR”, “*Anbembí*:  
425 dry season horizontal iPAR” and “*Anbembí*: wet season horizontal iPAR” – Datasets S1, S2,  
426 S4 and S5, DOI 10.5061/dryad.5mkkwh75q). F:FR or iPAR dispersion parameters, in  
427 McGLMs, are a proxy of spatial heterogeneity in light distribution (a higher dispersion  
428 parameter corresponds to higher heterogeneity in R:FR or iPAR), thus representing  
429 horizontal light variation in this work.

#### 430 *Vertical light variation*

431 For the *Sardinilla* site, to analyze light variation across vertical space (vertical  
432 transects measured), we also used McGLMs to determine whether means and dispersion of

433 R:FR varied between richness levels and heights. For the main plantation (“*Sardinilla*-main:  
434 vertical R:FR”, Dataset S6, DOI 10.5061/dryad.5mkkwh75q), the predictors of both the  
435 mean and dispersion were richness level (1, 2, 3 and 5 species), percentage of survival,  
436 vertical transect identity (each vertical transect measured was identified, as spatial  
437 covariate), height of R:FR measurement (1 to 5 m) and interaction between richness and  
438 height of R:FR measurement (to assess if R:FR presented distinct behaviors over the  
439 vertical space, at different richness levels). For the HD plantation (“*Sardinilla*-HD: vertical  
440 R:FR”, Dataset S7, DOI 10.5061/dryad.5mkkwh75q), effects accounted for were richness  
441 level (6, 9 and 18 species), percentage of survival, vertical transect identity, height of R:FR  
442 measurement (1 to 5 m) and interaction between richness and height of R:FR  
443 measurement.

444 For the vertical iPAR variation at the *Anhembí* site (in both dry and wet seasons,  
445 *Anhembí*: dry season vertical iPAR” and “*Anhembí*: wet season vertical iPAR”, Datasets S8  
446 and S9, DOI 10.5061/dryad.5mkkwh75q), we fitted McGLMs including as effects richness  
447 level (20, 58, and 114 species), replicate (four replicates of each treatment), height of iPAR  
448 measurement, interaction between richness level and height of iPAR measurement, vertical  
449 transect identity and percentage of survival in both the linear predictors for the mean and  
450 dispersion parameters.

#### 451 *Temporal variation in light interception*

452 For iPAR in different seasons and years (“*Anhembí*: seasonal iPAR”, Dataset S10,  
453 DOI 10.5061/dryad.5mkkwh75q), we fitted mixed beta regression models, including the  
454 effects of season, species richness and their interaction as fixed effects and year and  
455 replicate within year as random effects. For monthly iPAR over one year (“*Anhembí*:  
456 monthly iPAR”, Dataset S11, DOI 10.5061/dryad.5mkkwh75q), we also fitted mixed beta  
457 regression models, including different quadratic predictors over time per species richness

458 level and the effects of replicate within year as random. In both cases, we assessed the  
459 significance of the fixed effects using likelihood-ratio (LR) tests for nested models.

#### 460 *Species in monocultures x mixtures*

461 We carried out an analysis of variance to compare mean R:FR within plots of  
462 *Sardinilla's* main plantation (“*Sardinilla-main*: horizontal R:FR”, Dataset S1, DOI  
463 10.5061/dryad.5mkkwh75q) between different species compositions (12 levels: 5  
464 monocultures, 3 combinations of two species, 3 combinations of three species and 1  
465 combination of five species). Since the data was continuous and not bounded, a normal  
466 model was a reasonable assumption. We used percentage of survival within each plot as a  
467 covariate. We used Tukey test at a 95% confidence level for multiple comparisons, with  
468 Bonferroni correction for the global confidence level. We established specific contrasts to  
469 compare mean R:FR i) Between monocultures; ii) Between each monoculture and their  
470 combinations of two or three species; iii) Amongst two or three species mixtures; iv)  
471 Between five species mixture and each of the other treatments.

472 We also compared crown volume between the five main species in monocultures  
473 and 5-species mixtures (“*Sardinilla-main*: crown”, Dataset S12, DOI  
474 10.5061/dryad.5mkkwh75q) using a two-way ANOVA, with log-transformed crown  
475 volume as dependent variable and tree species and plot richness level (one or five species)  
476 as independent variables. All analyses were carried out in the R environment (R Core Team  
477 2018).

478

480 **Results**481 **Light interception**

482 Tree species richness enhanced iPAR at both sites. At the *Sardinilla* site's main  
483 plantation, mean iPAR increased significantly with species richness ( $\chi^2=310.34$ , d.f.=3,  
484  $P<0.0001$ ; Figure 1A, supporting information's Table S3). Five-species mixtures presented  
485 higher light interception than 2- or 3-species mixture plots ( $P<0.05$ ), which did not differ  
486 from each other, and all mixtures significantly intercepted more light than monocultures  
487 ( $P<0.0001$ ). At the HD plantation, light interception was not influenced by richness levels  
488 ( $\chi^2=1.54$ , d.f.=2,  $P=0.46$ ).

489 At the *Anhembi* site, increasing levels of richness enhanced iPAR in both seasons  
490 ( $\chi^2=108.07$ , d.f.=2,  $P<0.0001$  for the dry and  $\chi^2=57.91$ , d.f.=2,  $P<0.0001$  for the wet  
491 season; Figure 1B). In the dry season all treatments showed significantly different iPAR  
492 ( $P<0.05$ ) (see supporting information, Figure S11). In the wet season, iPAR also increased  
493 with tree richness ( $\chi^2=57.91$ , d.f.=2,  $P<0.0001$ ), but 58 and 114 species did not differ from  
494 each other ( $P>0.05$ ).

495 See supporting information (Table S4) for estimates and associated standard  
496 errors of the parameters estimated using the McGLMs for R:FR or iPAR.

497 **Horizontal light variation**

498 Horizontal light variation (assessed by the dispersion parameter of the McGLMs  
499 fit for "*Sardinilla*-main: horizontal R:FR" and "*Sardinilla*-HD: horizontal R:FR", Datasets S1  
500 and S2, DOI 10.5061/dryad.5mkkwh75q) decreased (thus evenness in iPAR distribution  
501 increased) from monocultures to mixtures at the *Sardinilla site*'s main plantation ( $\chi^2=258.41$ ,

502 d.f.=3,  $P<0.0001$ ) and from 6-species to richer mixtures in the HD plantation ( $\chi^2=8.08$ ,  
503 d.f.=2,  $P<0.05$ ; Figure 2). In the main plantation, horizontal dispersion was significantly  
504 higher for monocultures, intermediate for 3-species and lower for 2- and 5-species  
505 mixtures ( $P<0.05$ ). That means that light interception was more evenly distributed over the  
506 horizontal space in mixtures when compared to monocultures. In the HD plantation,  
507 horizontal light dispersion was lower for 9 and 18 species than for 6 species ( $P<0.050$ ).  
508 Thus, in the HD plantation, higher diversity was also associated with more even  
509 distribution of light interception over the horizontal space.

510         At the *Anhembi* site, horizontal variance in iPAR decreased with richness, differing  
511 between all richness levels during the dry season, and all but the 58- to 114- species  
512 mixtures in the rainy season (Figures 2, S12 and S13), following the same pattern of mean  
513 PAR interception. Since we assumed a quadratic mean-variance relationship (typical for  
514 proportion data), with maximum variance obtained at a proportion of 50%, the further  
515 data are from 50%, the lower their variance (McCullagh & Nelder, 1989). Therefore, stands  
516 with higher richness accounted for lower iPAR horizontal variance (more even light  
517 interception over the horizontal space at higher diversity). Moreover, we also modeled the  
518 dispersion parameter, which represents an extra source of variation, independent from the  
519 mean (Bonat & Jørgensen, 2016). At the *Anhembi* site, during the dry season, the dispersion  
520 parameter did not vary according to richness level ( $\chi^2=0.9364$ , d.f.=2,  $P=0.63$ ), but during  
521 the wet season it did so, with lower dispersion values (thus higher evenness of light  
522 interception) for 58 species, when compared to 20 species ( $\chi^2=6.7155$ , d.f.=2,  $P=0.03$ ).

### 523         **Vertical light variation**

524         At both *Sardinilla* and *Anhembi* sites, higher richness levels were able to intercept  
525 higher amounts of PAR over different layers of the canopy, thus being more efficient in  
526 filling space with vegetation. At the *Sardinilla* site's main plantation, iPAR at different

527 heights increased with richness, significantly differing from monocultures to mixtures  
528 ( $\chi^2=77.2180$ , d.f.=3,  $P<0.0001$ ) but, between mixtures, increasing only from three to five  
529 species (Figure 3). Effects of interaction between richness and height were not significant  
530 ( $\chi^2=4.1200$ , d.f.=3,  $P=0.25$ ), which means that mixtures maintained higher iPAR in all  
531 layers of the canopy, compared to monocultures. Dispersion effects (dispersion parameter  
532 of the McGLM fit for the “*Sardinilla*-main: vertical R:FR”, Dataset S6, DOI  
533 10.5061/dryad.5mkkwh75q) over the vertical transects also decreased from monocultures  
534 to mixtures ( $\chi^2=68.1179$ , d.f.=3,  $P<0.0001$ ), indicating that all mixtures could intercept  
535 light more evenly, in different layers of vegetation, than monocultures, at the main  
536 plantation. In the HD plantation, iPAR over vertical transects was not influenced by  
537 richness ( $\chi^2=5.5849$ , d.f.=2,  $P=0.0613$ ) or by its interaction with height ( $\chi^2=3.6841$ , d.f.=2,  
538  $P=0.1585$ ), and its dispersion (dispersion parameter of the McGLM fit for the “*Sardinilla*-  
539 HD: vertical R:FR”, Dataset S7, DOI 10.5061/dryad.5mkkwh75q) did not vary among  
540 richness levels either ( $\chi^2=1.4887$ , d.f.=2,  $P=0.4750$ ).

541 At the *Anbembi* site, in the dry season, iPAR over the vertical transects  
542 significantly increased with richness ( $\chi^2=97.2058$ , d.f.=2,  $P<0.0001$ ), differing between  
543 every richness level at a 95% confidence level (Figure 3). There was no interaction between  
544 the number of species and height of measurements ( $\chi^2=4.0268$ , d.f.=2,  $P=0.1335$ ).  
545 Increasing richness showed decreasing dispersion of iPAR (dispersion parameter of the  
546 McGLM fit for the *Anbembi*: dry season vertical iPAR”, Dataset S8, DOI  
547 10.5061/dryad.5mkkwh75q;  $\chi^2=12.3733$ , d.f.=2,  $P=0.0021$ ), which means that higher  
548 diversity levels could intercept light more evenly in different layers of vegetation over the  
549 canopy, during the dry season.

550 During the wet season, in *Anbembi*, iPAR over the vertical transects was higher in  
551 plots containing 58 and 114 species ( $\chi^2=39.6361$ , d.f.=2,  $P<0.0001$ ) and did not respond to  
552 interaction between height and richness level ( $\chi^2=1.5535$ , d.f.=2,  $P=0.4599$ ) (Figure 3).

553 Dispersion effects did not significantly differ according to richness level (dispersion  
554 parameter of the McGLM fit for the *Anbembí*: wet season vertical iPAR”, Dataset S9, DOI  
555 10.5061/dryad.5mkkwh75q;  $\chi^2=2.5248$ , d.f.=2, P=0.2830).

### 556 **Temporal variation in light interception**

557 There was a significant interaction effect of season and richness level on iPAR at  
558 the *Anbembí* site, i.e., plots containing different numbers of species displayed different  
559 iPAR seasonal dynamics (LR=17.2, d.f.=2, P<0.001). The interaction was mostly driven by  
560 the difference between wet and dry seasons for 20- and 58-species but not for 114-species  
561 mixtures. In general, 114-species mixtures had larger iPAR than 20-species mixtures, on  
562 average (Figure 4).

563 Analyzing iPAR monthly over one year, there was a significant interaction effect  
564 between time and richness level (LR=12.9574, d.f.=2, P=0.0154), and a quadratic behavior  
565 over time (minimum point of the curve in September; LR=11.9910, d.f.=1, P=0.0005),  
566 meaning that richer plots had more even distributions of light interception over the year. In  
567 general, 114- and 58- had larger iPAR than 20-species mixtures, on average, and at the  
568 beginning of the study, 114-species presented larger iPAR than 58-species treatment  
569 (Figure 4).

### 570 **Species in monocultures and mixtures**

571 Analyzing different compositions within each richness level, at the *Sardinilla*'s  
572 main plantation, some monocultures differed between each other regarding light  
573 interception, as well as two species mixtures. This indicates that some species intercept  
574 more PAR than the others. Most mixtures maintained light interception at least equivalent  
575 to their best monocultures, except for *T. rosea* + *H. crepitans*. The 5-species mixtures tended

576 to have the highest iPAR values, compared to monocultures and to other mixtures (Figure  
577 5).

578 Crowns presented higher volume in five-species mixtures than in monocultures  
579 ( $F_{1,110}=19.9248$ ,  $P<0.0001$ , supporting information's Fig. S14)

580

## 581 Discussion

582 In this study, light interception - a key ecological process related to primary  
583 production and forest dynamics (Canham *et al.*, 1990; Binkley *et al.*, 2013; Sapijanskas *et al.*,  
584 2014) - was influenced by tropical tree diversity, both at low (one to five species) and very  
585 high (58 to 114 species) levels. We therefore report substantial effects of biodiversity on  
586 light interception in tropical forests undergoing restoration. Theory proposes that  
587 ecosystem functions saturate as species diversity increases (Cardinale *et al.*, 2012), which is  
588 commonly reported to take place at low richness levels (Lamb 2018). In grasslands, for  
589 instance, less than a dozen species were responsible for maintaining some specific  
590 ecosystem processes (Hector & Bagchi 2007). These species, however, are mixed with  
591 others in a community assemblage, in which they can play different roles. Therefore,  
592 experimental design and species choice can influence results of experiments (Srivastava &  
593 Vellend, 2005). Nevertheless, in our work, even a richness level as high as 58 tree species  
594 was still not able to saturate light interception, in the dry season, which is an unprecedented  
595 result for a BEF experiment.

596 The comparison between our study sites illustrates how different locations and  
597 designs can affect the outcomes of ecological processes (Hooper *et al.*, 2005; Hector &  
598 Bagchi, 2007; Jucker *et al.*, 2015). Our results (iPAR at *Sardinilla* not increasing beyond six  
599 species, but not presenting a saturation point even for more than a hundred species at  
600 *Anbembí*, during the dry season) highlight that one must be careful when concluding about

601 levels of species saturation in BEF. Distinct sets of species may present different functional  
602 traits and thus taxonomic diversity does not necessarily reflect functional diversity  
603 (Bruehlheide *et al.*, 2014). However, we must point out that measurements at the *Sardinilla*  
604 site took place during the rainy season, when the differences between diversity treatments  
605 were the lowest at the *Anhembi* site.

#### 606 *Tree diversity effects on the horizontal variation in light interception*

607 We report that increased light interception at higher richness levels is related to  
608 less horizontal variation of iPAR. The duration and intensity of deciduousness (Gandolfi *et*  
609 *al.*, 2009), crown shapes and arrangements (Pretzsch, 2014; Sapijanskas *et al.*, 2014; Jucker *et*  
610 *al.*, 2015), growth speed (Poorter & Arets, 2003), maximum achievable height, and leaf  
611 traits (Ruiz-Jaen & Potvin, 2011) differ among species and crucially determine mixture  
612 outputs. In addition, these traits can show plasticity in mixtures, promoting complementary  
613 use of light (Ruiz-Jaen & Potvin, 2011; Forrester & Albrecht, 2014; Sapijanskas *et al.*, 2014;  
614 Forrester *et al.*, 2018). Trees of distinct species may intersperse their crowns and better  
615 occupy empty spaces throughout the canopy (Pretzsch, 2014), thus enhance light capture  
616 (Sapijanskas *et al.*, 2014). In both experiments, we showed that higher levels of species  
617 richness were associated with more spatially even distribution of light interception. This is  
618 likely a consequence of a better occupation of the canopy by tree branches and leaves  
619 (Guillemot *et al.*, 2020), a process linked to competitive reduction (Forrester & Bausch,  
620 2016). In fact, at the *Sardinilla* site, previous studies have shown that biomass allocation to  
621 branches was higher in mixtures than in monocultures (Potvin & Dutilleul, 2009;  
622 Guillemot *et al.*, 2020).

#### 623 *Tree diversity effects on the vertical variation in light interception*

624 Higher tree richness also allowed the canopy to intercept light more evenly

625 throughout the vertical canopy profile. When different species are combined, the diversity  
626 of forms of occupying the canopy at different heights is enhanced, thus resulting in a  
627 denser packing (Sapijanskas *et al.*, 2014; Jucker *et al.*, 2015). Moreover, as the crowns grow  
628 and touch branches from other trees, they tend to change direction of growth (Pretzsch,  
629 2014) and fill spaces with leaves. According to Sapijanskas *et al.* (2014), however, up-to-  
630 date studies fail to show whether multiple canopy layers promoting differential light  
631 interception over the space is really a cause of higher light interception or not. At the  
632 *Anhembi* site and *Sardinilla's* main plantation, high diversity plots intercepted more light  
633 than low diversity plots across all measured heights. Moreover, vertical dispersion of  
634 intercepted light was, in general, lower at higher richness levels. This is evidence that high  
635 diversity allowed trees to better distribute their crowns, and thus light interception, over the  
636 vertical space.

#### 637 *Tree diversity effects on the temporal variation in light interception*

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

650 phenology patterns (Sapijanskas *et al.*, 2014).

651 *Towards a mechanistic understanding of light interception in diverse forests*

652 Plant species diversity can influence ecosystem functioning via two distinct  
653 pathways: by selection effects, where a single species is responsible for playing a major role  
654 in a specific ecosystem function; or by complementarity effects, where interactions between  
655 species are responsible for higher ecosystem functioning, comparing to what would be  
656 expected from single species performances (Loreau & Hector, 2001). In this work, it was  
657 not possible to separate selection and complementarity effects on light interception, since  
658 we cannot single out the amount of light intercepted by each species of the mixtures and  
659 there is no easily measured weighting coefficient to represent species-specific contributions  
660 to light interception (Grossiord *et al.*, 2013). However, we evidenced that species in  
661 mixtures developed larger crown volumes than in monocultures, probably a consequence  
662 of competitive reduction (Forrester & Bauhus, 2016). This crown plasticity was shown to  
663 be linked to shifts in biomass allocation and branching pattern (Guillemot *et al.*, 2020),  
664 which suggests that complementarity effects occur in mixtures, at least to some extent (as  
665 suggested by Sapijanskas *et al.*, 2014). In addition to species richness, composition  
666 influenced ecosystem processes (Naeem, 2016), since different monocultures and different  
667 species mixtures of the same richness levels performed differently in intercepting light at  
668 the *Sardinilla* site. At this site, average iPAR across species richness levels (see Figure 1 A)  
669 agreed well with BEF theory, which states that mean light interception increases with  
670 richness, while the dispersion between different compositions of the same richness level  
671 decreases (Wright *et al.*, 2009). The five-species mixtures showed PAR interception  
672 comparable to the best monocultures, as shown by other BEF works (Wright *et al.*, 2009).  
673 This may lead to ask whether high diversity is necessary to maintain ecosystem functions,  
674 as some monocultures are good performers. Nevertheless, the advantage of holding more

675 species is their ability to keep multifunctionality (Hector & Bagchi, 2007; Wright *et al.*,  
676 2009; Cardinale *et al.*, 2012) and functional redundancy (Hooper *et al.*, 2005). Ecosystems  
677 containing higher diversity will likely present better overall functioning than less diverse  
678 ones (Aerts & Honnay, 2011). In fact, in this study, the five-species mixture was in no case  
679 outperformed by any of the monocultures, even though it contained, in the same plot,  
680 species that had contrasting abilities in intercepting light.

### 681 *Conclusions: implications for tropical forest restoration*

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

696

697

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717 **Data availability statement:** Raw data used for analyses and results displayed and  
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721

722 **Authors' contribution**

723 MMD, PHSB and CP designed the research. CP and JLS designed tree plantations  
724 (*Sardinilla* and *Anbemi* respectively). MMD and CIFZ collected data. RAM and WHB  
725 carried out data analyses. MMD, PHSB, RAM, CIFZ and JG interpreted data. MMD wrote  
726 a first draft of the manuscript and PHSB, JG, RAM and CP contributed substantially to the  
727 final version.

728

729

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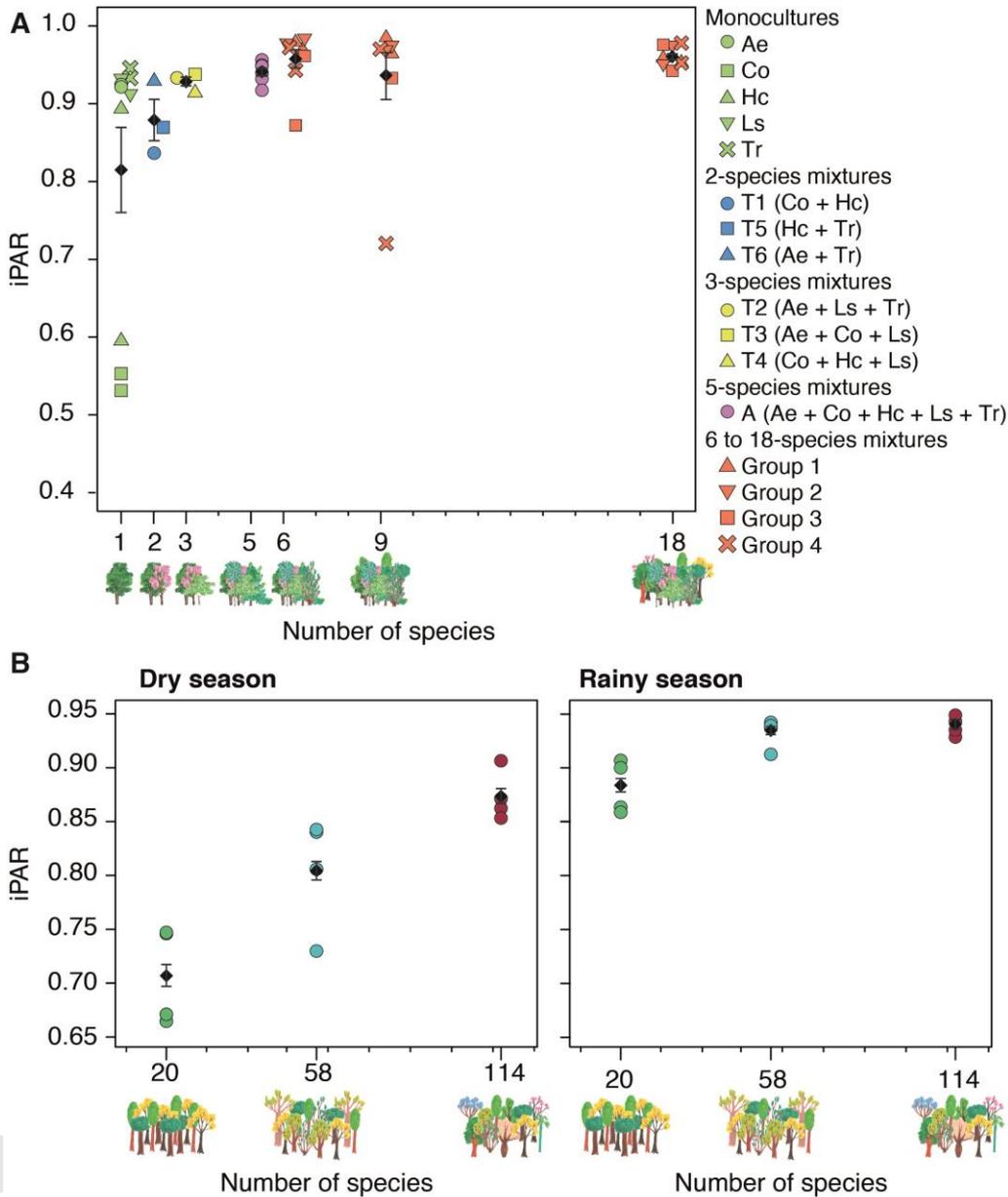
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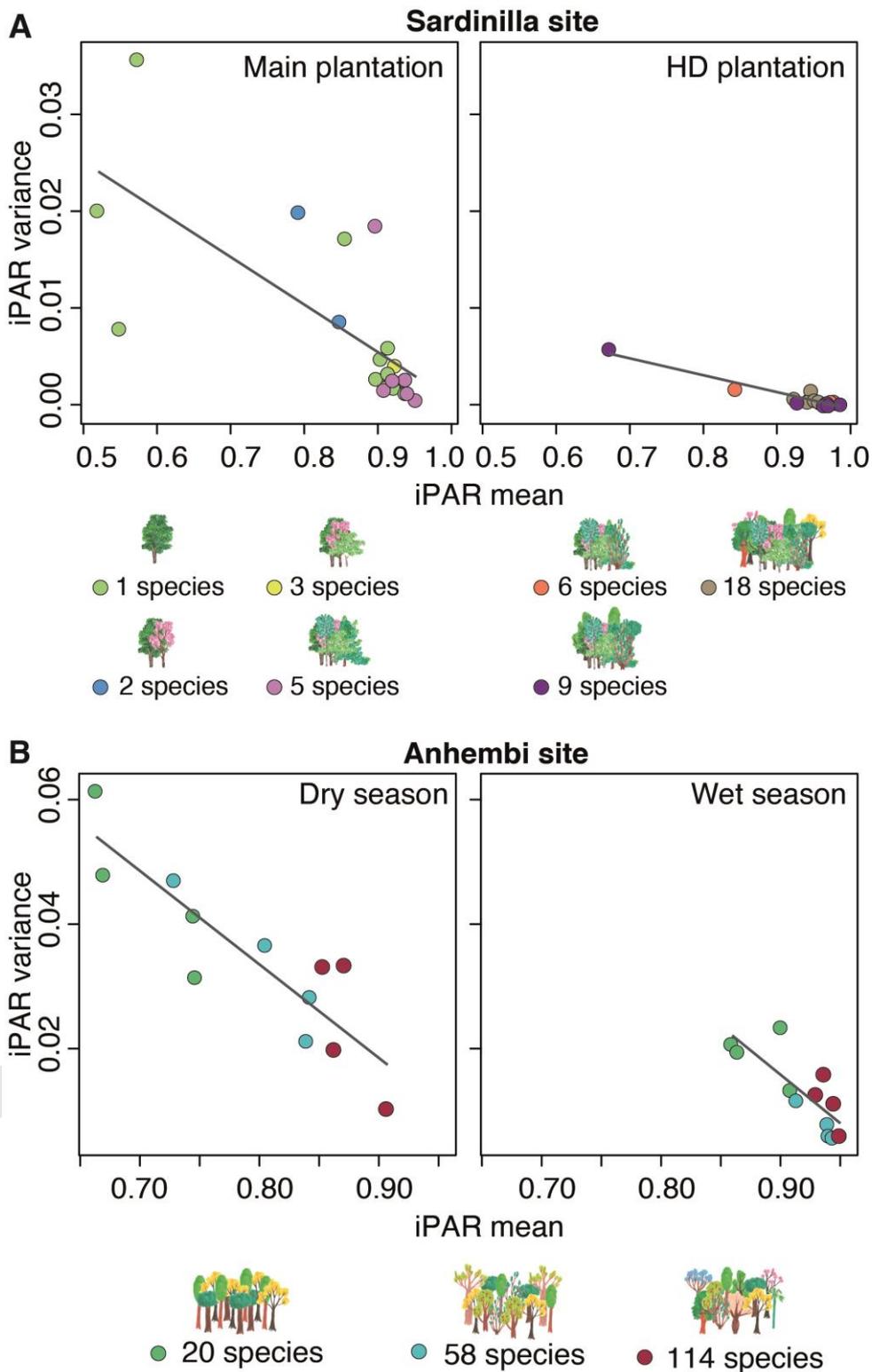
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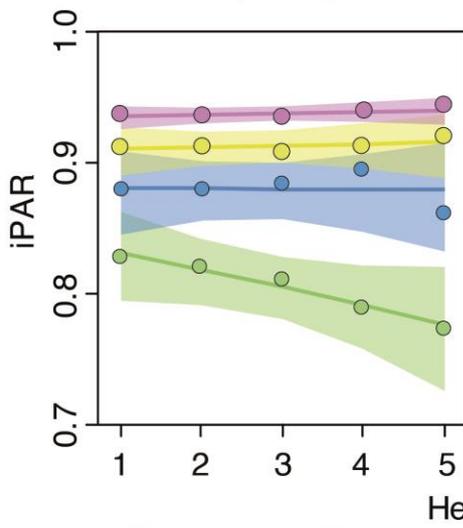
951 **Figure 1.** Mean iPAR for different treatments at the *Sardinilla* and *Anhembi* sites. A)  
 952 Mean iPAR (black points) and standard error (bars) at each richness level, measured during  
 953 the rainy season (July and August, 2016), at the *Sardinilla* site (Sardinilla, Panama). The  
 954 monocultures, 2-, 3- and 5-species combinations are part of the main plantation  
 955 (established in 2001), thus they are two years older than the 6-, 9- and 18-species mixtures,  
 956 which are part of the high diversity plantation (established in 2003). Colored marks  
 957 represent all plots measured. Different shapes of marks represent distinct compositions  
 958 within each richness level. Tree species in monocultures are: Ae = *Anacardium excelsum*, Co  
 959 = *Cedrela odorata*, Hc = *Hura crepitans*, Ls = *Luehea seemannii*, Tr = *Tabebuia rosea*. B) Mean  
 960 iPAR (black points) and standard errors (bars) measured for different species richness  
 961 levels at the *Anhembi* experiment (Brazil, established in 2006), in dry ( $\chi^2=108.07$ , d.f.=2,  
 962  $P<0.0001$ , measurements in August, 2015) and rainy ( $\chi^2=57.91$ , d.f.=2,  $P<0.0001$ ,  
 963 measurements in March and April, 2016) seasons. Colored points represent every plot  
 964 measured within each richness level.



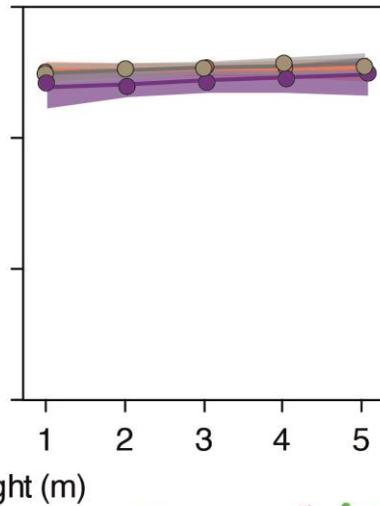
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967 **Figure 2.** Relationship between iPAR means and variance for different richness levels  
 968 (points in distinct colors) over horizontal measurements grids, at *Sardinilla* (A - Sardinilla,  
 969 Panama) and *Anhembi* sites (B - Anhembi, Brazil). Please check supporting information,  
 970 Figures S12 and S13, to visualize how light interception was distributed horizontally over  
 971 the plots.

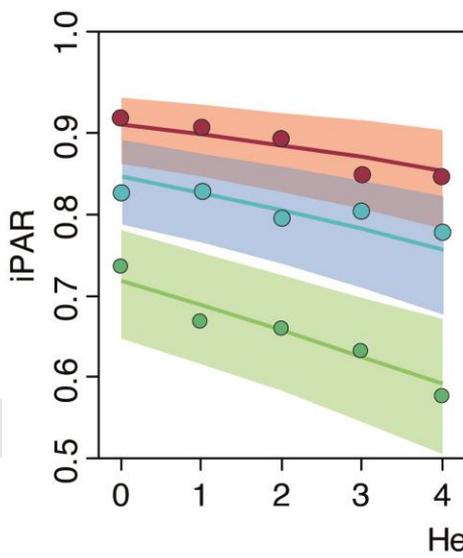
### A. Sardinilla (main)



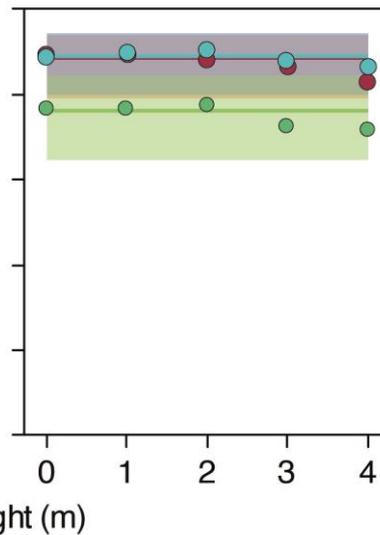
### B. Sardinilla (HD)



### C. Anhembi (dry season)



### D. Anhembi (wet season)



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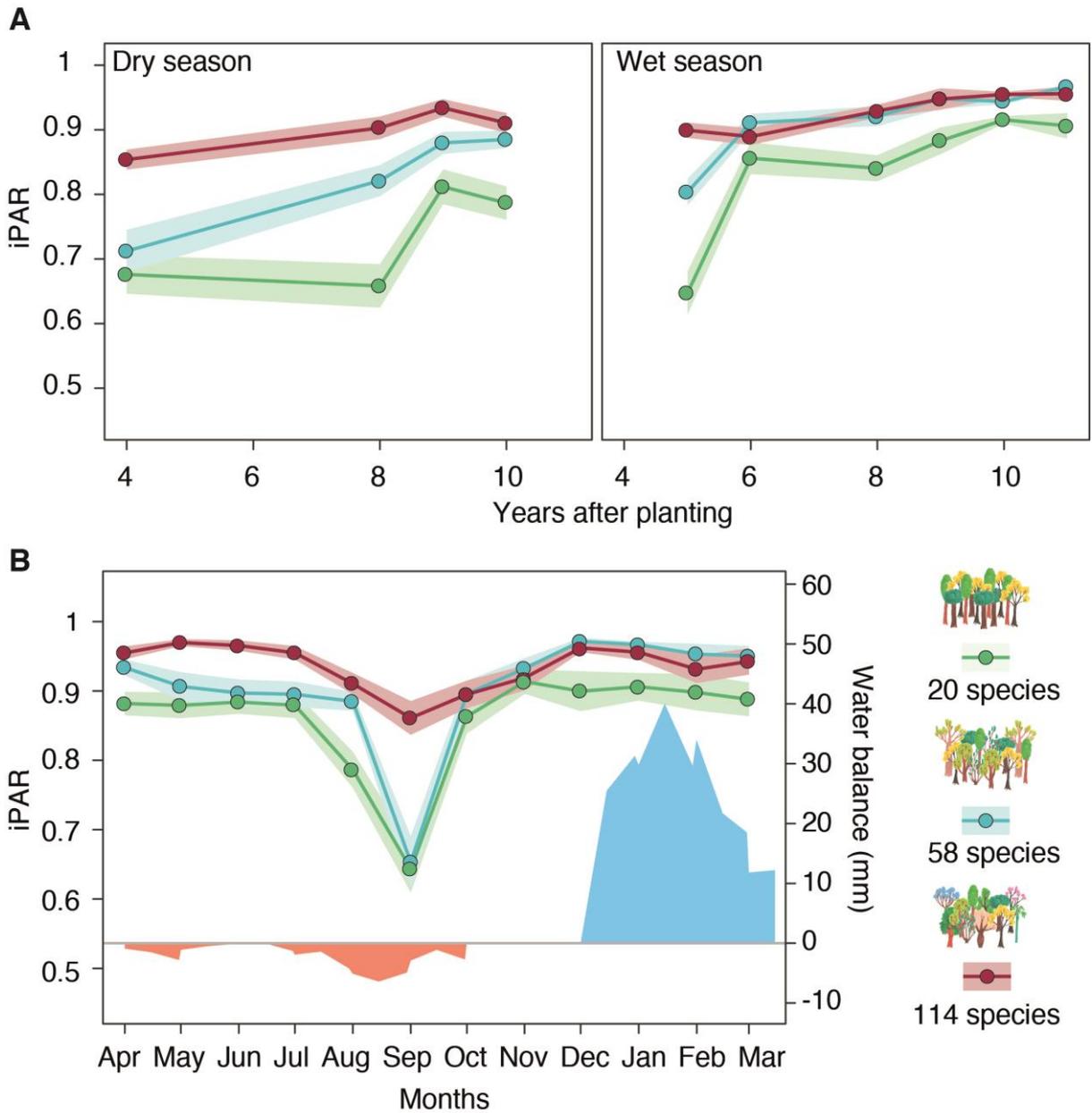
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**Figure 3.** Mean intercepted photosynthetically active radiation (iPAR, points in different colors) and 95% confidence intervals (shaded areas) measured for different species richness levels (indicated in legends), at different heights within the 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.



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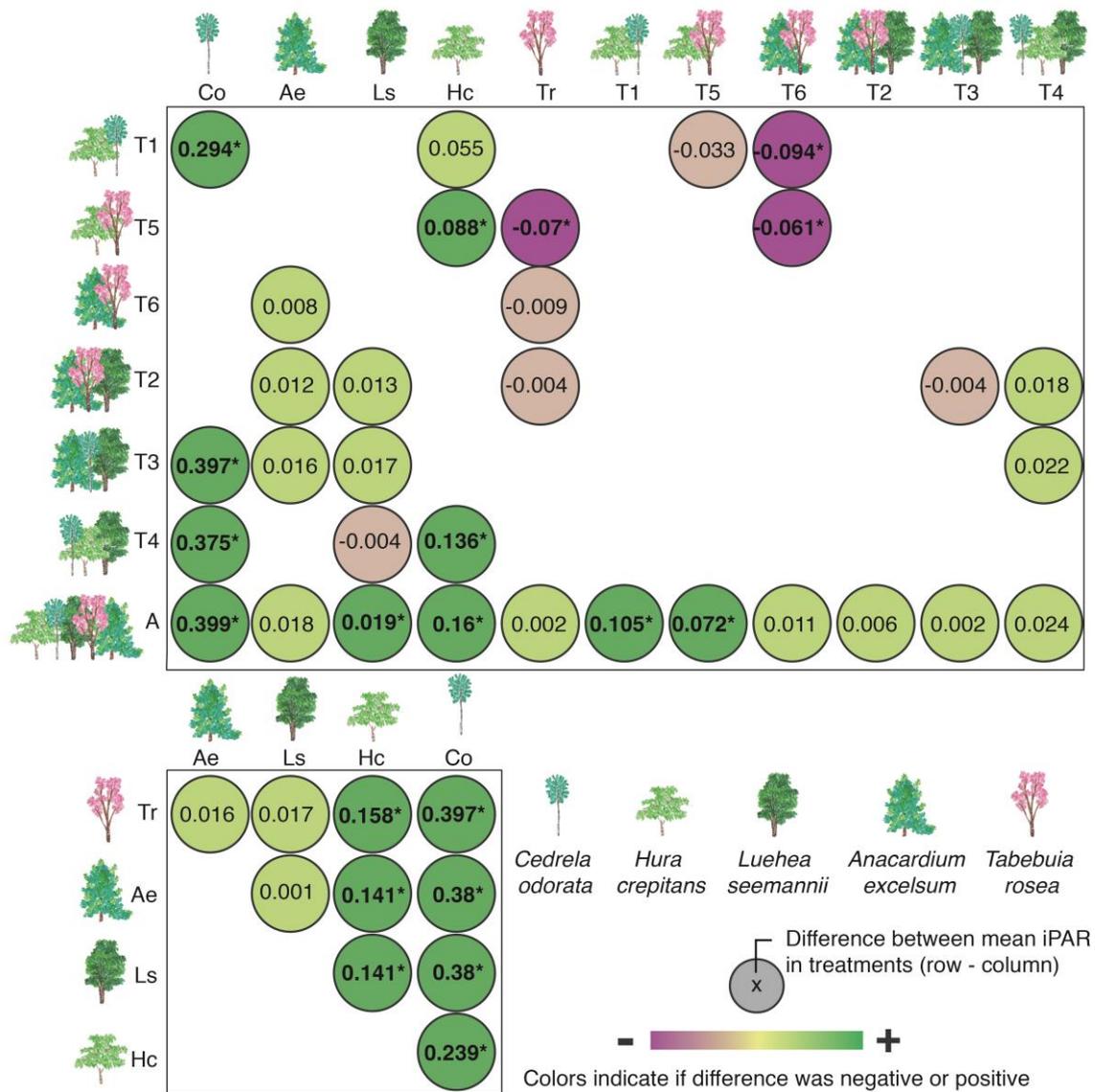
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**Figure 4.** iPAR in different years (2011 to 2017) in wet and dry seasons (A) and monthly variation of iPAR and water balance over one year, from April 2017 to March 2018 (B) at the *Anhembi* experiment (Anhembi, Brazil, planted in 2006). Water balance 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.



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**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 = *Hura crepitans*, Ls = *Luehea seemannii*, 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 colored in green, while negative differences are colored in purple. Intensity of color 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.