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Interacting and dynamic effects of species and structural diversity promote annual woody biomass production in a tropical tree diversity experiment

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ABSTRACT

Different aspects of diversity, such as species richness and structural diversity, have been shown to enhance forest ecosystem functions, including biomass production. However, whether diversity-productivity relationships change over time or with climatic conditions remains uncertain. We analyzed above-ground woody biomass increment (AWBI) derived from annual inventory data and micro-densitometry on stem disks from 'Sardinilla' in Panama, one of the oldest tropical tree diversity experiments. We investigated AWBI in five tree species growing in monospecific and species-rich neighborhoods. We hypothesized that a) species and structural diversity would increase AWBI, with these effects strengthening over time, b) species diversity effects on AWBI would be mediated by structural diversity, and c) overyielding in diverse neighborhoods would persist under drought. We observed higher AWBI in species-rich compared to monospecific neighborhoods despite slightly decreasing wood density. The strong complementarity effects in mixtures increased over time, indicating progressive strengthening of diversity effects. Species diversity strongly effected AWBI by directly enhancing productivity and indirectly, via increasing structural diversity. Structural diversity had a direct positive effect on AWBI, but this effect weakened with tree age. Overyielding in species-rich neighborhoods persisted or even increased under extremely dry conditions likely due to complementary water use among species. Our results corroborate that mixed planted forests are more productive and have a greater ability to maintain their performance under stressful conditions compared to monocultures. Forest management aiming at maximizing carbon sequestration in plantations should include fast-growing species with high wood density and promote not only tree species richness but also structural diversity.

1. Introduction

It has been shown that tree species mixtures can provide multiple ecosystem services at a higher level than monocultures (Gamfeldt et al., 2013; van der Plas et al., 2016). Importantly, mixed species forests are often reported to be more productive than monocultures (Forrester and Bauhus, 2016; Zhang et al., 2012) and thus to capture and store more carbon (Schnabel et al., 2025). Increasing the sequestration and long term storage of atmospheric carbon in forests is recognized as an important nature-based solution for climate change mitigation (Griscom et al., 2017). For that purpose, large-scale forest restoration efforts have been initiated to increase forest coverage, in particular in tropical regions, where extensive forest areas have been degraded or lost in recent decades, with detrimental effects on the global carbon cycle (Hansen et al., 2013; Poorter et al., 2016). Restoring these extensive areas that have been deforested is crucial not only for capturing C from the

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atmosphere, but also for biodiversity and communities living in and around (de)forested areas (Koch and Kaplan, 2022). Increasing tree diversity in these new planted forests has been proposed as a strategy to provide multiple ecosystem services at a higher level and to increase resilience against disturbances (Messier et al., 2021; Bauhus et al., 2010).

Positive interactions among species in mixtures, including facilitation and reduction of competition for limited resources, often outweigh competitive interactions, leading to a net positive complementarity effect of diversity on productivity (i.e. overyielding) (Bauhus et al., 2017b; Kelty, 1992). Positive diversity effects on biomass productivity in mixed forest stands have been attributed to both below- and above-ground processes that can influence their performance (see also Forrester, 2017 for a comprehensive summary of known processes). Trees can exploit the soil more efficiently for nutrients and/or water, for example, by either having differing rooting patterns (e.g. Schwendenmann et al., 2015) or by altering the characteristics and spatial configuration of roots and fine roots when in species-rich neighborhoods (Sun et al., 2017; Brassard et al., 2013; Wambsganss et al., 2021). Above-ground, higher canopy light capture and light-use efficiency as a result of inter-specific differences in shade-tolerance, crown structures, or plastic changes of crown morphology in species-rich neighborhoods can lead to canopy stratification and hence more efficient occupation of canopy space than in monocultures (Jucker et al., 2015; Forrester, 2014; Menalled et al., 1998; Guillemot et al., 2020; Kunz et al., 2019).

It is, however, uncertain whether reported benefits and processes or mechanisms that drive overyielding in species-rich neighborhoods are attributable to species diversity alone or also, at least partially, to structural diversity (i.e. size inequality) (McElhinny et al., 2005). Positive effects on productivity of comparable or even stronger magnitude than those reported for species diversity (e.g. richness) have been attributed to structural diversity (e.g. Dănescu et al., 2016; Schnabel et al., 2019; LaRue et al., 2019). Similar to species diversity, increased variation in diameters and heights of trees in a neighborhood might increase niche separation and growth partitioning among differently sized trees (Pretzsch, 2017). Increasing productivity by promoting structural diversity in forests can have significant practical implications, since size inequality can be enhanced with relative ease, using targeted silvicultural interventions (Forrester, 2019). While the effects of structural diversity on productivity may be relatively easily quantified in monocultures, in mixed species forests it is not always possible to separate the effects of structural diversity from those of tree species diversity (Jucker et al., 2015; Zhang and Chen, 2015). The effects of species diversity may be partially attributable to structural diversity and vice versa, since different tree species in mixed forests may have very different growth patterns and dimensions that can lead to aboveground and belowground stratification (Dănescu et al., 2016; Zhang and Chen, 2015; Bauhus et al., 2004). Among mixed-species forests, planted tree diversity experiments are most suitable to separate the effects of structural diversity and species diversity on tree function but also whether and to what extent the effects of species richness are mediated by structural diversity. However, most planted tree diversity experiments are still relatively young so that variation of tree sizes within neighborhoods or communities might not be sufficiently pronounced to test for these effects.

It has been suggested that the relationship between diversity and tree productivity changes in time and with environmental conditions (e.g. water availability) (Jucker et al., 2020; Cardinale et al., 2007; Forrester and Bauhus, 2016; Forrester, 2014). Because trees are typically of similar size and at relatively wide spacing at the time of planting, it can be expected that interactions among neighboring trees intensify as trees become larger and their crowns and root systems begin to influence each other. These changing interactions might increase complementarity or intensify competitive interactions, respectively. Recent studies have identified increasingly positive effects of species diversity on productivity with tree age (Jucker et al., 2020; Bongers et al., 2021; Schnabel et al., 2019; Urgoiti et al., 2022; Shovon et al., 2022). However, there is little information on the temporal dynamics of the relationship between structural diversity and productivity especially at the tree neighborhood level (Forrester, 2019). Methodologically, assessing the effects of structural diversity and their interaction with tree or stand age can be challenging, since structural diversity might correlate strongly with age (and/or size) (Forrester, 2019). These collinear relationships need to be accounted for when examining the separate and interacting effects of age and structural diversity.

Another aspect of mixed forests, which is of outmost significance in the context of climate change, is that diverse forests can be more resilient to a range of stresses and disturbances compared to monocultures, either by spreading the risk among the species or by increasing the resilience of participating species (Bauhus et al., 2017a). Climate models project more frequent and extreme drought events for different regions, including the tropics, over the next century (Boisier et al., 2015; Duffy et al., 2015). Currently, however, little is known about how tropical tree species respond to extreme droughts, especially when these are accompanied by above average temperatures. In recent studies, drought was found to be a key driver of increasing mortality rates in moist tropical forests (McDowell et al., 2018). Whether tree diversity can increase tree performance under extreme drought conditions remains inconclusive (Grossiord, 2020; Grossiord et al., 2014; Haberstroh and Werner, 2022). This is especially the case for understudied regions such as the tropics. Recent studies reported positive, but also neutral or even negative diversity effects on tree productivity under drought (Belluau et al., 2021; Fichtner et al., 2020; Sachsenmaier et al., 2024; Schnabel et al., 2024; Serrano-León et al., 2024). Positive effects or increased resistance and resilience to extreme droughts in mixtures are expected if, for instance, neighboring trees have contrasting strategies or needs in available water resources, which are progressively depleted during a drought event (Grossiord, 2020; Decarsin et al., 2024).

Uncertainties in assessing diversity-productivity relationships and difficulties in synthesizing existing results might arise – amongst other factors - from the choice of units used to assess productivity (Ammer, 2019; Sheil and Bongers, 2020). Most studies are based on radial or volume increment as measures of productivity as they are easier measured than biomass increment. However, wood density might vary with tree neighborhood conditions (Zeller et al., 2017) and could either amplify or dampen tree diversity effects reported from radial or volume increment.

Here, we used precise annually resolved measures of biomass increment derived from dendroecological, forest inventory and micro-densitometry data, to assess the drivers of biomass increment of trees growing at one of the oldest tree diversity experiments, “Sardinilla”, which was established in 2001 in Panama (Scherer-Lorenzen et al., 2004). In particular, we were interested in examining the relationship between different aspects of diversity (species and structural) and annual biomass productivity as well as in understanding the temporal development of such relationships. In case of significant relationships, we asked whether these effects are independent or whether species and structural diversity interact in influencing biomass productivity. Finally, we aimed at investigating whether diversity-productivity relationships would persist under extreme climatic conditions (extremely dry or wet conditions). We addressed these questions at the tree and neighborhood level, since this is the scale where tree-tree interactions take place (Guillemot et al., 2020; Schnabel et al., 2019; Kunz et al., 2019; Potvin and Dutilleul, 2009; Trogisch et al., 2021). We hypothesized that:

(1) annual biomass increment increases with increasing diversity (species and structural) and over time,

(2) structural diversity increases with tree species diversity, and

(3) trees in species-rich neighborhoods exhibit higher annual biomass increment compared to monospecific neighborhoods even under extreme climatic conditions.

2. Methods

2.1. Study site, sampling

We analyzed the performance of individual trees in relation to their surrounding tree neighbors in the Sardinilla tree diversity experiment established in 2001 in Panama. This experiment was specifically designed to test how tree species richness influences ecosystem functioning such as nutrient cycling and productivity (Scherer-Lorenzen et al., 2004). The climate at the site is tropical with an annual precipitation sum of 2664 mm and mean temperature of 25.4 °C on average for the period between 2001 and 2016) (see additional information regarding the climate at the study site in Figures S1- S3)) and is characterized by a pronounced dry season from January to March (Barro Colorado Island (BCI), Physical Monitoring Program of the Smithsonian Tropical Research Institute). Six native tree species were originally planted in monocultures and mixtures of different species richness levels in 2001. The tree species were selected from different functional groups comprising two fast-growing (LS: *Luehea seemanii* and CA: *Cordia alliodora*), two light-intermediate (AE: *Anacardium excelsum* and HC: *Hura crepitans*), and two slow-growing and shade-tolerant species (CO: *Cedrela odorata* and TR: *Tabebuia rosea*) (Scherer-Lorenzen et al., 2004). Species were classified into these functional groups based on their relative growth rates and on their frequency of occurrence in gaps or closed forests in nearby natural forests in Barro Colorado Island (Scherer-Lorenzen et al., 2004). A total of 24 plots (45 ×45 m, each) were established on a former pasture. Plots comprised monocultures of all six species ($N = 12$), different three-species combinations ($N = 6$) and mixtures of all six-species ($N = 6$) with an average of 233 individuals per plot (equaling 1150 trees ha^{-1}) (Potvin and Dutilleul, 2009). The distance between trees was 3 m, in line with the local reforestation practices in Panama. Richness levels were allocated randomly, following a randomized, substitutive, block design. Each of the six species was thus represented in two monocultures, in 3 three-species plots and in all six-species plots to allow for the control of sampling effects. Since *C. alliodora* suffered significant mortality shortly after planting, this species was excluded from the analyses. Between May and August 2017, we harvested 167 trees from all five species to obtain stems discs at 1.3 m stem height for dendroecological and micro-densitometry analyses. Selected trees were distributed among all tree diversity levels and tree sizes (see Guillemot et al., 2020 for a detailed description of tree sampling).

2.2. Measures of annual wood biomass production

Wood density in tree rings was determined by X-ray densitometry using an automated system (Decoux et al., 2004; Jacquin et al., 2017). Two 2.1 mm thick strips were cut from each disk in the radial plane using a twin blade saw. Following conditioning of the cut samples at a temperature of 20 °C and a relative air humidity of 65 %, X-ray CT scanning of the wood strips was performed at a resolution of one measurement each 20 microns in radial direction. This yielded high resolution density profiles that were used to identify ring boundaries and measure ring width and wood density related variables at an annual resolution, such as minimum, maximum and average density, using the software CERD (Dietrich et al., 2024; Mothe et al., 1998). Ring-width (RW) series were subsequently converted to series of basal area increment, assuming a circular cross-section of the trees. Tree-ring series that were obtained on the basis of wood density profiles were compared against visually detected tree-ring series and annually-resolved diameter increments from inventory data to ensure that each ring was assigned to the corresponding year of its formation (see also Dietrich et al., 2024 for further details).

We estimated aboveground woody biomass increment (AWBI) based on the annually-resolved basal area increment (BAI) series at 1.3 m stem height and wood density measurements (see also Vannoppen et al., 2018). Previous studies investigating diversity-productivity relationships were based solely on annual basal area (including studies that used tree-ring width) or on stem volume increment as an indicator of biomass production (e.g. Huang et al., 2018). In contrast, our AWBI estimates included precise, annually resolved measurements of wood density as we expected significant variation in average wood density among species, within species and even within individual trees which might amplify or dampen tree diversity effects detected when using basal area or volume increments alone**.**

The following equation was used to estimate AWBI for each tree j and year i:

$$AWBI_{year\_ji} = T_{year\_i} * BAI_{year\_ji} * Avg.Dens_{year\_ji} * height_{year\_ji}\ (kg) \qquad (1)$$

Where T_{year_i} is an index for taper for each species and year calculated as 1- $A_{1.3}/A_{base}$ (A_x: cross-sectional area (cm^2) at height x), BAI_{year_ji} is the BAI for each tree and year (m^2), $Avg.Den_{syear\_ji}$ is the average density for each tree and year ($kg\ m^{-3}$) and $height_{year\_ji}$ is the height (m) for each tree and year.

To assess the quality of the developed ring-width and AWBI series and to evaluate the correct identification of annual rings, we calculated the descriptive statistics EPS (expressed population signal), Rbar (mean interseries correlation) and SNR (signal to noise ratio), which are commonly used in dendroecological studies. EPS indicates how well a chronology represents a theoretical infinite population (Wigley et al., 1984). Rbar is the mean correlation between series within a chronology and indicates the common signal strength in tree-ring chronologies (Speer, 2010). Finally, SNR expresses the ratio of the desired signal in each chronology versus the amount of unwanted information and random variation (Speer, 2010). These descriptive statistics were calculated using the *dplR* package (Bunn et al., 2012) in R version 4.3.0.

2.3. Diversity indices

All the analyses were performed at the tree neighborhood level taking inter-annual changes in species and structural diversity indices into account. The neighborhood of the harvested focal trees was defined as the area within a radius of 5 m, which captured all their immediate neighbors based on the original planting positions. This translates into a maximum of 8 living neighbors in the fixed planting design of the plantation (3 ×3 m). Neighborhood diversity was quantified in terms of diversity of tree species and structural attributes. Although this experiment was not designed to test the effects of structural diversity on tree productivity, the large size inequalities after 16 years of growth offer the unique opportunity to disentangle the effects of structural diversity from those of species diversity as well as the temporal development of such relationships within this period. Tree species diversity was quantified as species richness ($Richness_s$), as Shannon-Diversity ($Shannon_s$) and evenness ($Eveness_s$), calculated as Shannon index divided by its theoretical maximum. Structural diversity was quantified based on variation in diameters and height. The metrics used included: coefficient of variation of tree diameter at breast height and of tree height (CV_d and CV_h), Gini coefficient (GC_d and GC_h, Gini, 1912), Shannon index ($Shannon_d$ and $Shannon_h$) and evenness ($evenness_d$ and $evenness_h$), all based on 1-cm diameter and 1-m height classes. Classes of 1-cm diameter and 1-m height have been used in previous studies, also in Sardinilla (Schnabel et al., 2019). In the young tree stands studied here, 1 cm difference in diameter corresponds roughly to 1 m difference in tree height, which represents about 10 % of the vertical crown profile. These small differences in diameter are therefore ecologically meaningful in terms of capturing crown layering and vertical structure. Further information on the calculated indices can be found in Schnabel et al. (2019).

2.4. Analyses of woody biomass production in diverse neighborhoods

To understand whether species interactions in species-rich tree neighborhoods translate into higher wood biomass production, we calculated relative AWBI for each year following Forrester and Pretzsch (2015) and Forrester (2017). To assess whether the benefits of diversity become more important with time, as interactions among trees increased, we analyzed temporal dynamics of net complementarity effects by calculating relative productivity as follows:

$$\text{Relative AWBI}_{\text{year\_i}}\ (\%) = (\text{AWBI}_{\text{mixed}} / \text{AWBI}_{\text{monospecific}}) * 100 \qquad (2)$$

where AWBI_{mix} is the AWBI of a tree growing in a species-rich neighborhood and $\text{AWBI}_{\text{monospecific}}$ is the median AWBI of all trees of the same species growing in monospecific neighborhoods in the same year.

We used linear mixed effects models to understand the temporal development of relative AWBI in mixed compared to monospecific neighborhoods. Initially, we fitted a linear mixed effects model to predict relative AWBI of all species in mixtures with age as fixed effect and species identity as random effect. Subsequently, following a methodology similar to the one outlined below for AWBI (see section ‘Modelling age and neighborhood effects on AWBI’, steps 1–3), we modeled relative AWBI for each species separately as a function of age to assess differences in the temporal development of relative AWBI among species.

To assess the performance of trees in species-rich neighborhoods under different climatic conditions and especially under extreme drought, we compared relative productivity of trees under extremely dry, normal and extremely wet conditions (see also section ‘Climate data and identification of extremes’ above). Differences in terms of AWBI under dry, wet or normal conditions between conspecific trees growing in monospecific and mixed neighborhoods were assessed by performing Wilcoxon rank sum tests.

2.5. Climate data and identification of extremes

Monthly resolved series of temperature, precipitation and potential evapotranspiration were acquired from the BCI, Physical Monitoring program of STRI and were used to calculate the standardized precipitation evapotranspiration index (Vicente-Serrano et al., 2010) for an accumulation period of 12 months (SPEI12). The SPEI reflects the climatic water balance and can be used to detect and monitor drought conditions over time, taking into account both precipitation and evapotranspiration. It is calculated as the difference between precipitation and potential evapotranspiration over a specified period (accumulation period). Series of SPEI12 of December summarize the hydroclimatic conditions during the whole year and have been used previously also in Sardinilla to quantify water availability and drought stress (see for instance, Hutchison et al., 2018 and Schnabel et al., 2019). Accordingly, the two most extreme dry and wet years at our study site were identified by classifying SPEI12 of December and annual precipitation sums for the time-period between 2006 and 2016 into ‘drought’ (lowest 10 %), ‘normal’ (11–90 %) and ‘wet’ (91–100 %). Based on both variables, 2015 was identified as the driest year (drought), and 2010 as the wettest year. All other years were characterized as normal (’11–90 %’). The years 2010 and 2015 are among the most extreme dry and wet years, respectively, in terms of total annual precipitation since the beginning of instrumental climate data collection in BCI (see also Figure S1) It is worth noting that 2015 was not only the driest, but also the warmest year of the observation period (see also Figure S2 and Figure S3).

2.6. Modelling age and neighborhood diversity effects on AWBI

We used linear mixed effects models to assess the temporal development of neighborhood diversity effects (species and structural) on AWBI as well as the influence of other variables related to neighborhood competition and mortality that are known to affect tree biomass increment. Linear mixed models were selected to account for the hierarchical structure in our data (repeated measures of AWBI for each tree, which were nested in subplots, nested in plots). To test whether species and/or structural diversity had a significant effect on AWBI of each species, we followed a modeling approach following the methodology proposed in Zuur et al. (2009). The effects of each index describing aspects of either species or structural diversity were tested individually, similarly to Schnabel et al. (2019) and Dănescu et al. (2016). Modelling AWBI for each species included the following steps:

1. Specifying a ‘beyond-optimal model’, including as many possible fixed effects not related to diversity. These fixed effects were related to tree age, competition (Hegyi competition index (Hegyi, 1974), BAN: the summed basal area of the neighborhood and BAL: the summed basal area of all trees larger than the target tree), dominance and neighborhood mortality (relM: relative mortality) (see S5 for further information on these indices).
2. Finding the optimal random structure (random effects, temporal autocorrelation, variance structure) using the ‘beyond-optimal model’ (see also S.5). To reduce the temporal autocorrelation and the heteroscedasticity of the residuals, we also tested different covariance structures (i.e., a first-order autoregressive function as well as different variance functions). The final decision regarding the random and covariance structures was made by assessing the autocorrelation of residuals, visual assessment of the residual plots and the AIC.
3. Choose the optimal null model structure via removing all non-significant fixed effects.
4. Testing species and structural diversity indices one by one and their interaction with age and evaluating index performance based on AIC and ANOVA.
5. Fitting a final diversity model including the highest-ranking species diversity and structural diversity index determined in step four, into one final model.

The response variable AWBI and the Hegyi competition index were log transformed to account for their non-normal distributions. To avoid collinearity, only variables that were not strongly correlated to each other were included as predictors in the models (Spearman’s rho < 0.7 and a variance inflation factor (VIF) < 3, see also Dormann et al., 2013). Linear mixed models were fitted using the *nlme* (Pinheiro et al., 2023) package in R.

We used piecewise structural equation models (SEMs) to assess possible effects of species diversity on structural diversity and test whether species diversity indirectly affects AWBI by influencing structural diversity. For each species, the SEMs consisted of a first part, in which we included the final diversity model, described above, using mixed effects models, without the interactions between the indices describing species or structural diversity and age. The second part included a hypothetical causal link which predicted structural diversity as a function of species diversity using mixed effects models that had the same random variance structure as the respective final diversity model for each species. For the latter part, the most important index describing species and structural diversity, as identified in the final diversity model, were tested, per species. The fit of each SEM was assessed by calculating the Fisher’s C statistic (a model-wide $p > 0.05$ implies that the structure of the model is supported by the data and that no potentially significant missing paths were excluded). Significant missing paths or dependencies in our dataset were identified by tests of directed separations. These were included as partial correlations to improve the global model fit (for the full structure of these models, see S.6). Structural equation models were constructed using the *piecewiseSEM* package (Lefcheck, 2016) in R.

3. Results

Mean annual RW of the five species in the Sardinilla diversity experiment—*Luehea seemanii* (LS), *Anacardium excelsum* (AE), *Hura* *crepitans* (HC), *Cedrela odorata* (CO) and *Tabebuia rosea* (TR)—ranged from 4 to 8.1 mm per year (Table 1). Mean wood density of the fast-growing LS was the highest among the five investigated species, while the lowest density was observed for the intermediate-growth-rate species HC. We observed high variation in AWBI values within each species, indicated by standard deviation values higher than the mean values (Table 1). The descriptive statistics (Rbar, EPS and SNR) calculated for the different species suggest an overall good quality of the developed annual series of AWBI and a general agreement among series within each species, except for CO, for which, Rbar was relatively low (Rbar = 0.12), and EPS (EPS = 0.78) was slightly below the commonly used threshold value of 0.85. Similar descriptive statistics, were obtained also for the species-specific chronologies developed using ring-width series (see Table S.1).

All investigated species had a greater AWBI in species-rich compared to monospecific neighborhoods (Fig. 1). These differences were statistically significant for the species LS, AE and CO. Although on average HC seemed to be nearly twice as much productive in species-rich neighborhoods (median relative AWBI = 194 %), the difference in biomass productivity between species-rich and monospecific neighborhoods was not statistically significant (Wilcoxon Rank Sum, $p > 0.05$). The highest relative productivity among all species was observed for the slow growing species CO (median relative AWBI = 284 %). The two faster growing species LS and AE grew 1.5 and 2.4 times faster in mixtures compared to monocultures, respectively and the slow growing species TR had only 1.12 times greater biomass production in mixtures compared to monocultures.

3.1. Temporal development of relative AWBI

Linear mixed models revealed an overall increase of relative AWBI in mixtures with tree age (Fig. 2). This trend was significant ($p < 0.001$) when pooling relative AWBI across species. Similarly, a significant increase in relative productivity with tree age was observed for 3 species (LS ($p < 0.001$), HC ($p < 0.001$) and CO ($p < 0.001$)) while relative AWBI of the remaining two species AE and TR appeared to be relatively stable over time and did not show any significant relationship with age ($p > 0.05$) (see also detailed results in S6).

3.2. Relative AWBI under extreme climatic conditions

To assess whether diversity effects change under extreme climatic conditions, we examined relative AWBI in species-rich neighborhoods separately in an extremely dry year, under normal conditions and in an extremely wet year. Except for HC, trees from all species growing in species-rich neighborhoods were significantly more productive than trees growing in monospecific neighborhoods in the extremely dry year and under normal conditions (Fig. 3). In contrast, only the two fast growing species (LS and AE) were significantly more productive in species-rich compared to monospecific neighborhoods in the extremely wet year. Relative AWBI in species-rich neighborhoods appeared to increase with increasing water availability for AE and TR, while no pattern could be observed for LS and HC (Fig. 3). For the slower growing species CO, relative AWBI decreased with increasing water availability. Interestingly, relative AWBI decreased in the dry year compared to the relative AWBI observed under normal conditions for the two fast growing species (LS and AE). Similar levels of relative AWBI in the extremely dry year and under normal growing conditions were observed for HC and TR, while the slow growing species CO showed higher levels of relative AWBI in the driest year compared to years with normal climatic conditions.

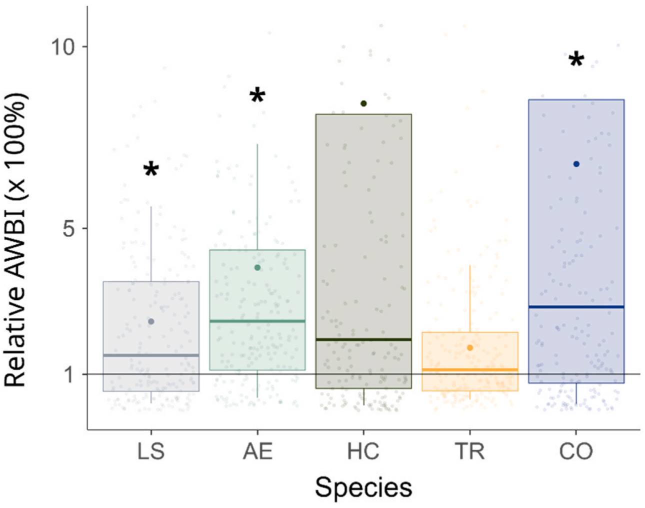

Fig. 1. Relative aboveground wood biomass increment (AWBI) per species growing in species-rich neighborhoods. Colored bold points show the mean per species, colored lines indicate the median. Bold stars indicate significant differences in terms of AWBI between conspecific trees growing in mixtures and monocultures. Species are ordered from left to right based on their growth rates in nearby natural forests. The solid horizontal black line at Relative AWBI = 1 denotes equal productivity in species-rich and monospecific neighborhoods and thus no diversity effects on productivity of subject trees.

3.3. Annual tree productivity and neighborhood species richness

Regardless of species identity, we observed an overall increased productivity, both in terms of AWBI and RW for trees growing in species-diverse neighborhoods (Fig. 4a-b). Trees growing in neighborhoods with two, three, and four tree species demonstrated similar levels of productivity, which were higher than for trees in monospecific neighborhoods, while the highest productivity was observed for neighborhoods with five tree species. Importantly, RW appeared to increase more strongly with increasing tree species richness (Fig. 4b) than AWBI (Fig. 4a). Annual mean wood density, in contrast, decreased with increasing species richness (Fig. 4c). The observed trends in these three variables (RW, AWBI and wood density) with increasing neighborhood species richness were not uniform among the five investigated species (Figure S6). The pioneer species LS showed increasing average wood

Table 1

Summary of annual ring width (RW), aboveground wood biomass increment (AWBI) and mean annual wood density (Density) per species as well as statistics and characteristics of AWBI series (Rbar, mean correlation between individual tree series; EPS, expressed population signal and SNR, signal to noise ratio). Species are ordered based on their growth rates in nearby natural forests.

					AWBI series statistics		
Species	**N. trees**	**RW (mm) Mean (sd)**	**Density (kg/m^3) Mean (sd)**	**AWBI (kg) Mean (sd)**	**Rbar**	**EPS**	**SNR**
Luehea seemanii (LS)	31	8.1 (5.3)	622 (85)	9.1 (11.7)	0.53	0.97	27.32
Anacardium excelsum (AE)	31	6.6 (3.9)	459 (54)	3.4 (5.8)	0.49	0.96	24.33
Hura crepitans (HC)	29	4.9 (4.6)	398 (67)	1.6 (3)	0.35	0.93	12.27
Tabebuia rosea (TR)	31	4 (2.3)	537 (61)	1.2 (1.6)	0.60	0.97	36.50
Cedrela odorata (CO)	32	5.5 (4.9)	447 (86)	2.1 (3.5)	0.12	0.78	3.49

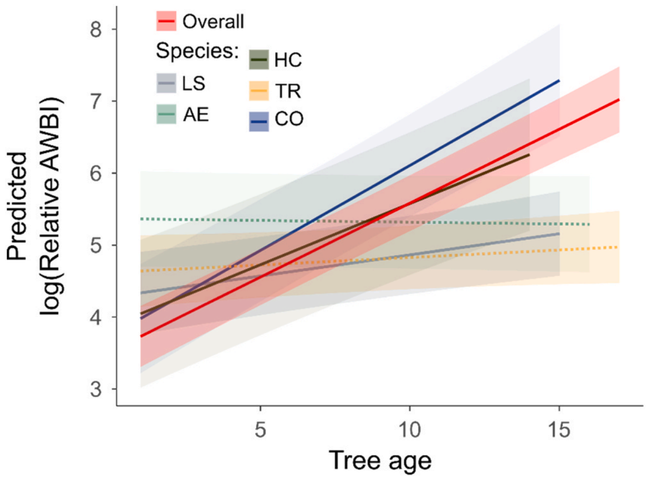

Fig. 2. Predicted relative aboveground woody biomass increment ($AWBI_{mix}$/$AWBI_{mono}$, log transformed) in species-rich neighborhoods compared to monospecific neighborhoods as a function of tree age; overall mean for all species (in red) and separately for each of the five investigated species (LS: *Luehea seemanii*; AE: *Anacardium excelsum*; HC: *Hura crepitans*; CO: *Cedrela odorata* and TR: *Tabebuia rosea*). Solid lines show significant relationships between tree age and relative AWBI, while dashed lines show insignificant relationships. Colored areas show the 95 % confidence intervals of linear mixed-effects model fits.

density with increasing species richness, while average wood density of the two shade tolerant species TR and CO appeared to decrease with increasing species richness (Figure S6). Notably, the two intermediate species showed no clear trend in wood density with increasing species richness (Figure S6).

3.4. *Drivers of AWBI*

For all species, the best models describing AWBI included plot as a random effect and a temporal autoregressive correlation structure (using the corAR1 function). All final species-specific models had substantial explanatory power with R_c values (conditional R^2 values representing the variance explained by fixed and random effects) greater than 0.63 and R_m (marginal R^2 values representing the variance explained by fixed effects) greater than 0.59 (Fig. 5a, but see also detailed results in S.5).

Indices describing neighborhood species diversity had a significant positive effect on AWBI in three out of the five species (LS, HC, CO). For AE and TR, no significant positive relationship with species diversity indices was identified (Fig. 5a). Although all investigated indices showed the same direction of effects, different species diversity indices were found to perform best for the different species. Neighborhood richness ($Richness_s$) performed best ($p < 0.05$) in predicting AWBI of the pioneer species LS, while $Shannon_s$ performed best in modelling productivity of HC ($p < 0.01$) and CO ($p < 0.01$). Mixed models revealed a significant positive interaction effect of tree age and species diversity indices on AWBI of the intermediate species HC ($p < 0.05$) and the shade tolerant CO ($p < 0.01$), pointing to increasing effects of species diversity over time for these two comparably slower growing species. Notably, the interaction between tree age and species diversity indices was not significant for the two faster growing species LS and AE ($p > 0.05$).

Indices describing neighborhood structural diversity had a strong positive effect on AWBI of the species LS ($p < 0.01$), AE ($p < 0.001$) and CO ($p < 0.05$) (Fig. 5a). Similar to the indices used to quantify species diversity, all investigated indices of structural diversity showed the same direction of effects, However, different structural diversity indices were found to perform best for the different species. When comparing models, for two out of the five species (LS and AE), the highest-ranking structural diversity index was the Shannon index of diameter classes in the tree neighborhood ($Shannon_d$), while for the other three species (HC, TR, CO) the Shannon index of height classes ($Shannon_h$) was the most important. There was a consistent significant negative interaction between tree age and structural diversity indices for all species, indicating a weakening of structural diversity effects on AWBI over time.

All five species-specific models revealed increasing biomass increment (AWBI) with tree age ($p < 0.001$) (Fig. 5a). Furthermore, the Hegyi competition index had a significant negative effect ($p < 0.001$) on AWBI of all five species. Notably, mortality of neighboring trees (relM) had a significant negative effect on AWBI of the pioneer species LS ($p < 0.001$) and the slow growing species TR ($p < 0.05$).

Four out of the five species-specific structural equation models (SEMs) fit the productivity datasets well (LS: Fishers' C = 3.16, $p = 0.21$; AE: Fishers' C = 4.65, $p = 0.10$, HC: Fishers' C = 0.215, $p = 0.89$ and

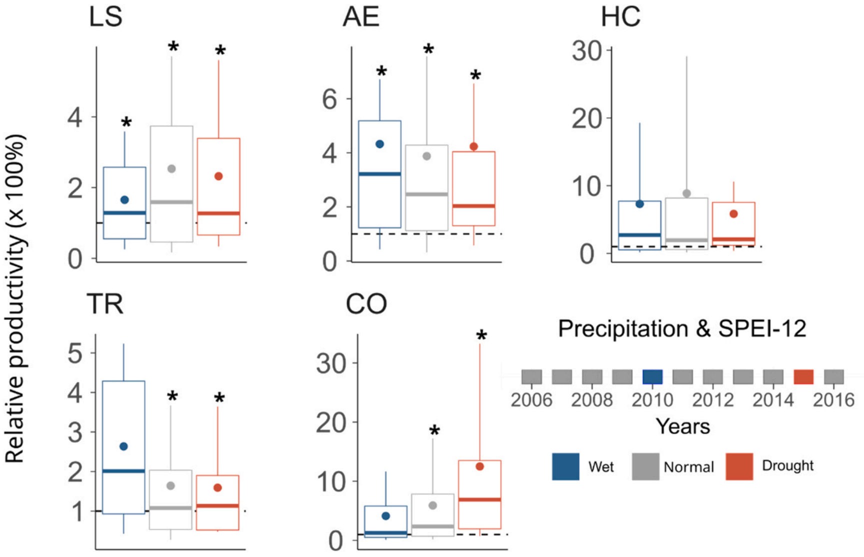

Fig. 3. Relative aboveground woody biomass increment ($AWBI_{mix}$/$AWBI_{mono}$) in species-rich compared to monospecific neighborhoods under dry, normal and wet conditions, for the five investigated species (LS: *Luehea seemanii*; AE: *Anacardium excelsum*; HC: *Hura crepitans*; CO: *Cedrela odorata* and TR: *Tabebuia rosea*). Years were characterized as dry, wet or normal (11–90 % of the cases) based on their annual precipitation sum and the SPEI12 value of December. Dotted lines mark the 100 % relative productivity, which indicate productivity of monocultures. Stars denote statistically significant differences ($p < 0.05$) between trees growing in species-rich and monospecific neighborhoods.

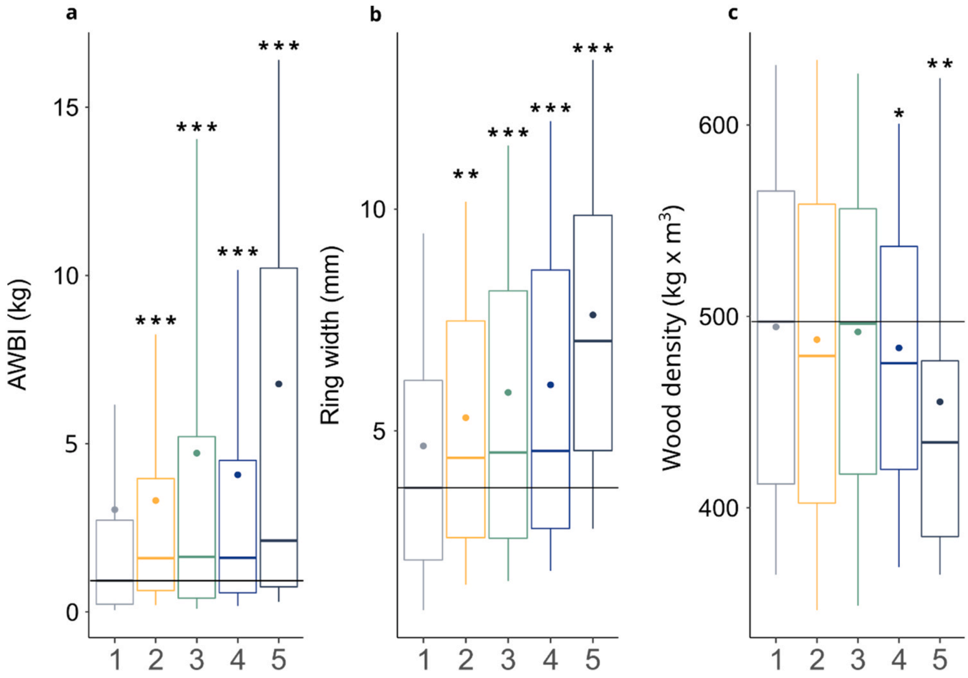

Fig. 4. Tree productivity (a) AWBI: Above ground woody biomass increment, b) and ring width and c) average tree ring density for different richness levels at the tree neighborhood level. Lines within boxplots show the median and points show the mean value. Horizontal lines denote the median value of monocultures. The stars represent statistically significant differences between monospecific and species-rich neighborhoods (*: $p < 0.05$, **: $p < 0.01$, and ***: $p < 0.001$).

TR: Fishers' C = 1.66, $p = 0.44$). For the species CO, global goodness of fit of the SEM suggested a poor fit (Fisher's C = 32.179, $p < 0.05$). Although no causal relationships can be implied for this species, we report here the results including CO but they should be considered with caution and interpreted as correlations.

SEMs confirmed the results obtained by the mixed models revealing strong direct effects of both species and structural diversity on AWBI (Fig. 5b-f), also after accounting for dependencies among predictors. More importantly, species-specific SEMs revealed additional positive indirect effects of species diversity on AWBI via increasing structural diversity for the species LS, AE and CO. In all species-specific SEMs we identified strong positive direct relationships between indices describing species diversity and those describing structural diversity. Standardized path coefficients between species and structural diversity indices ranged from 0.57 ($p < 0.001$) for LS to 1.10 ($p < 0.001$) for TR. The amount of variation in structural diversity indices which was explained by species diversity indices (Rm of structural diversity indices) was substantial and ranged between 21 %, for LS and 45 %, for AE (see also detailed results in S.6)

The magnitude of the indirect effects of species diversity on AWBI via increasing structural diversity varied among the different species. The strongest indirect effect was observed for AE (standardized coefficient = 0.16). Interestingly, for this species, we did not find a direct effect of Evenness_s on AWBI. The indirect effects of species diversity on AWBI via structural diversity were of rather low magnitude for LS (standardized coefficient = 0.06), TR (standardized coefficient = 0.04) and CO (standardized coefficient =.0.06). For TR there was almost no indirect species diversity effect on AWBI (standardized coefficient = 0.01).

4. Discussion

4.1. Species and structural diversity promote woody biomass increment

This is the first tree-ring based study that analyzed diversity-productivity relationships in mixed species experiments based on both the width as well as wood density of tree rings. We found strong positive relationships between both aspects of diversity (species and structural) and above-ground woody biomass productivity. These findings agree with those of earlier studies in the Sardinilla experiment (Potvin and Gotelli, 2008; Guillemot et al., 2020) and in particular those of Schnabel et al. (2019) who also reported strong positive effects of structural diversity on tree productivity. Evidence for positive relationships between different aspects of diversity and productivity is becoming increasingly available from observational studies and planted experiments in the tropics (e.g. Huang et al., 2018; Schnabel et al., 2019) and other forest biomes (e.g. Jucker et al., 2014). Several of the mechanisms that explain the strong overyielding in mixed neighborhoods in Sardinilla can be also attributable to the effects of structural diversity. Our results support this idea, as we found strong positive relationships between structural diversity and AWBI for three out of the five species in Sardinilla. In some cases, these relationships were similar to, or even stronger than those between species diversity and AWBI.

Several mechanisms or processes at the neighborhood level can explain the observed greater productivity in species-rich compared to monospecific neighborhoods. These are generally shaped by tree-tree interactions and relate to the availability of resources (light, water and nutrients), but also to the ability of trees to capture and use these resources (Forrester, 2017). Results from previous studies in the Sardinilla experiment suggest that several drivers, most likely acting simultaneously, can explain overyielding in mixed neighborhoods. Recently, Guillemot et al. (2020) concluded that biomass overyielding in mixtures, based on destructive biomass measurements 16 years after the establishment of the Sardinilla experiment was promoted by changes in architecture and biomass allocation within tree crowns, i.e. among branch orders, which ultimately improved canopy packing and above-ground space-use efficiency in diverse tree neighborhoods. Earlier, Sapijanskas et al. (2014) reported that not only changes in crown architectural differences among species and plastic morphological changes in response to tree-tree interactions in mixtures, but more importantly that temporal niche differences in light capture among species promoted overyielding in mixtures in the Sardinilla experiment. There is also evidence that the observed greater productivity in mixed compared to monospecific neighborhoods is partially attributable to below-ground processes including complementary use of water (Schwendenmann

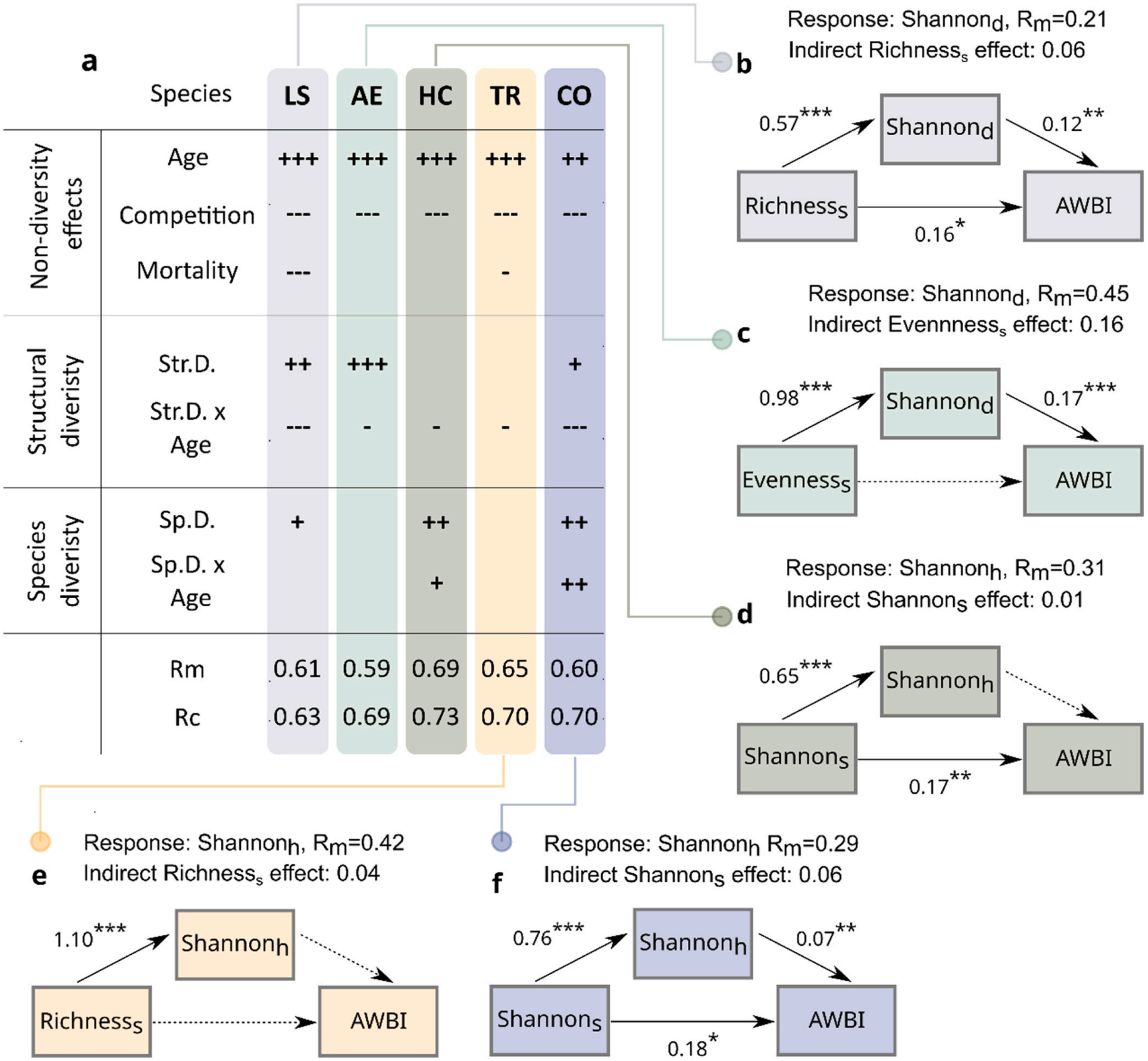

Fig. 5. Graphical summary of mixed effects modeling for each tree species, (ordered based on their growth rates in nearby natural forests from left to right: LS: *Luehea seemanii*; AE: *Anacardium excelsum*; HC: *Hura crepitans*; CO: *Cedrela odorata* and TR: *Tabebuia rosea*) including non-diversity effects (age, competition and mortality) as well as the effects of the highest-ranking indices describing structural (Str.D.) or species diversity (Sp.D.) on aboveground woody biomass increment (AWBI) (a). Plus (+) and minus (-) symbols indicate positive and negative fixed effects, respectively. The number of symbols for each fixed effect and species in panel a) represent statistical significance (±: $p < 0.05$, ±±: p < 0.01, and ± ± ± : $p < 0.001$). Results of structural equation models (SEMs) depicting the direct and indirect effects of species diversity indices on AWBI for each species are depicted in panels b)-f). Richness$_s$: species richness, Shannon$_s$: Shannon diversity index, Evenne$_s$s$_s$: evenness index, Shannon$_d$: Shannon index based on 1-cm diameter classes, Shannon$_h$: Shannon index based on 1-m heig$_h$t classes. Numbers next to the arrows in panel b)-f) represent standardized path coefficients and stars denote significance (*: $p < 0.05$, **: $p < 0.01$, and ***: $p < 0.001$). Rm marginal R^2 values representing the variance explained by fixed effects while Rc values are the conditional R^2 values representing the variance explained by both fixed and random effects.

et al., 2015), as well as complementary nutrient uptake as a result of differences in species-specific nutrient needs and sharing of resources among different species via litter production in diverse neighborhoods (Sapijanskas et al., 2013). Similarly, shortly after the establishment of the Sardinilla experiment, Zeugin et al. (2010) found increased nitrogen and phosphorus use-efficiencies in mixtures for the two fast growing and overyielding species (LS and AE).

Importantly, the strong positive relationships between diversity (species and structural) and annual biomass productivity persisted after considering average annual wood density, which decreased overall with increasing species richness. Stronger diversity effects than those reported for AWBI were obtained when comparing productivity among species richness levels using only the more commonly measured parameter RW. This clearly shows the importance of taking into account precise wood density measurements in tree rings to avoid reporting biased diversity effects (see also Ammer, 2019). Our study demonstrates that large intraspecific variation in wood density can be expected with varying species diversity in tree neighborhoods. This information should be considered when planning the establishment of forests aimed at maximizing biomass production and carbon sequestration. Previous studies reported similar reductions in wood density of some species growing in mixtures or at varying levels of competition in the neighborhood (Zeller et al., 2017). In their study, Zeller et al. (2017) suggested that wood density changes in mixed neighborhoods reflect adjustments to interspecific neighborhoods, with trees prioritizing growth and expansion rather than stability and defense when in mixtures. Similarly, climatic conditions at the time of wood formation or even the year before can influence annual wood density, with studies attributing up to 40 % of variation in wood density to climate variables (Vannoppen et al., 2018; Oliveira et al., 2021). Recent studies in the tropics highlighted the importance of accounting for precise wood density when assessing forest biomass and carbon accumulation, since wood density of tree species can vary considerably across scales but also with tree dimensions and species composition (Phillips et al., 2019; Sæbø et al. 2022; Sullivan et al., 2025). Therefore, wood density measurements combined with annually resolved dendrometric inventory data offer precise and realistic estimations of biomass productivity. In addition, wood density incorporates information regarding mechanical strength and also, importantly, hydraulic safety and efficiency of tree stems (Zanne et al., 2010; Hoeber et al., 2014; Guillemot et al., 2022). It has been shown recently that wood density relates to differentiation in stem expansion, crown architecture and light capture strategies among co-occurring species in a tropical forest, with low wood density species showing a more efficient height expansion and high density species showing an efficient horizontal crown expansion (Iida et al., 2012). These examples demonstrate that in the context of biodiversity-ecosystem functioning research, information about wood density can not only improve estimations of woody biomass productivity, but also holds great potential when examining species with complementary strategies for resource use (water) and capture (light).

4.2. *Temporal development of diversity-productivity relationships*

Overall, our results suggested that diversity effects on annual woody biomass production strengthen over time with increasing tree age as reported in previous studies from relatively old (16 – 20 years old) tree diversity experiments (Jucker et al., 2020; Schnabel et al., 2019). In forests and tree diversity experiments, interactions among neighboring trees might need longer to develop, as neighboring trees slowly occupy the available above- and belowground space before they start competing for resources. It is, however, remarkable that the temporal development of diversity effects on biomass increment in the Sardinilla experiment differed not only among the different species but also for the two different aspects of diversity examined (species and structural diversity). Here, a strengthening of the relationship between species diversity and biomass increment was observed for the two relatively slow growing species (HC and CO), whereas for the fast-growing species LS, positive species diversity effects seemed to be stable over time. These results indicate that diversity effects for slow growing, shade tolerant species might be delayed or that they might need time to fully uncover as the competitive ability of conservative species increases with time (van de Peer et al., 2018). Likewise, it may be expected that diversity-productivity relationships would become weaker at later stages of stand development for fast-growing species as the slower growing and shade tolerant species become more competitive. Contrary to our expectation, the effects of structural diversity on biomass increment decreased over time across all species. One possible explanation could be that structural diversity is rather important for the early stages of stand development and decreases with time as canopies close, and competition for light increases (see also Forrester, 2014). In addition, high structural diversity and increased canopy packing at the early stages of stand development could reduce the availability of light for understory plants and, thus, lead to reduced competition from the herbaceous layer (Zheng et al., 2022). The fact that structural diversity had a strong positive effect on productivity in three out of the five investigated species, irrespective of their shade tolerance, is an important result for forest management (e.g., of planted forests) and restoration efforts. Considering its strong effects, increasing structural diversity early on, for instance, via staggered planting, choosing tree species with contrasting growth rates or thinning to maintain sub-canopy species, could boost productivity of young forests. In our study, indices describing structural diversity correlated with age. Although, collinear predictors were not included in our models (Variance Inflation Factor, VIF<3, Dormann et al., 2013) and we accounted for correlated errors among predictors in our SEMs, the exact effect size of age and structural diversity might be affected by this collinear relationship and should be viewed with some caution. Overall, our findings support the notion that diversity-productivity relationships are to a large extent dynamic and that results at early stages of experiments, at one single point in time and from studies that do not consider annual and precise records of biomass productivity could be markedly different from those reported here. Still, our results do not cover all phases of stand development and studies that cover subsequent phases are needed to quantify the long-term effects of initial tree diversity.

4.3. *Interacting effects of species and structural diversity*

Structural equation modeling confirmed our hypothesis that the effects of species and structural diversity on AWBI are not completely independent. Here, species diversity promoted structural diversity, which, in turn had a strong positive relationship with biomass production in three out of five species in Sardinilla. Interestingly, in the case of AE the effects of species diversity were only indirect and mediated via structural diversity. Considering these results, it could be argued that with the exception of TR, all species in the Sardinilla experiment benefitted from either the direct and/or indirect effects of species diversity. It is worth noting though that TR showed the lowest growth rates (both in terms of RW and AWBI) among the investigated species, possibly indicating strong negative effects of asymmetric competition. These results also highlight the fact that both aspects of diversity, species and structural, are important for promoting biomass productivity, and additionally, that structural diversity and its' effects on productivity are strengthened in species-rich neighborhoods. Similar results have been reported in previous studies (e.g., Jucker et al., 2015; Zhang and Chen, 2015), which generally support the idea that species richness increases productivity via increasing tree size inequality (Pretzsch, 2017). In Sardinilla, the combination of species with contrasting growth rates and shade tolerance might have increased the variation of tree sizes and favored above-ground niche separation. However, given the moderate levels of explained variation when modelling structural diversity as a function of species diversity, it would be misleading to state that the effects of structural diversity can be exclusively attributed to species diversity or that the effects of species richness on tree productivity are fully mediated by structural diversity.

4.4. *Overyielding under drought and heat stress*

Our comparison of relative AWBI in mixtures under differing climatic conditions revealed that trees growing in species-rich neighborhoods were more productive than those in monospecific neighborhoods even under extremely dry conditions. In contrast, this was not the case in the extremely wet year, when only two out of five planted species showed significantly higher AWBI in mixtures. These findings are consistent with the stress gradient hypothesis, which suggests stronger diversity effects under stressful conditions. Results from existing studies on the effects of diversity on tree performance under extremely dry conditions are rather inconclusive, with evidence for positive, negative or neutral effects (Grossiord et al., 2014; Grossiord, 2020; Decarsin et al., 2024). Although we did not explicitly assess the growth resilience of individual trees to drought (e.g., by using the indices described by Lloret et al., 2011), our results are in line with the majority of existing studies that found stronger diversity effects on growth under extremely dry conditions (Grossiord, 2020). In the Sardinilla experiment, this greater productivity in mixtures compared to monocultures is most likely attributable to complementary use of water, since the studied species were found to have distinct spatial and temporal water uptake patterns (Schwendenmann et al., 2015). This complementary water-use among the different species in Sardinilla might have led to competitive reduction in species-rich neighborhoods but also facilitation due to hydraulic redistribution of water from the deep and moist to the shallow and dry soil layers (Forrester, 2017). It should be noted, however, that this greater productivity under drought conditions could be related to greater water use and increased transpiration, which could be associated with greater soil water depletion and greater mortality risk under long-term water deficit (Forrester, 2017). However, no measurements on water use and transpiration have been conducted in the drought of 2015 in Sardinilla.

5. Conclusions and management recommendations

Our results show that biomass increment in the Sardinilla experiment increased with species and structural diversity at the neighborhood level. These effects were slightly dampened by decreasing wood density in species-rich neighborhoods compared to the effects observed when only considering diameter or volume increment. This clearly demonstrates the importance of considering high resolution wood density measurements to accurately quantify diversity-productivity relationships. In addition, considering changes in wood density in relation to stand structure and composition should be considered when designing plantations for maximizing carbon sequestration and in cases when product volume is not the primary aim of management. Our results also indicate that increasing structural diversity can be highly beneficial especially during early stages of stand development following the establishment of plantations. This aspect is of high practical relevance for forest management as increasing structural diversity early on, for instance, via use of nurse crops, staggered planting or careful selection of species with varying growth rates and shade tolerance, could significantly boost productivity of young forests. Both aspects of diversity directly promoted biomass productivity in species-rich neighborhoods, but species diversity promoted biomass productivity also indirectly, through increasing structural diversity. The effects of species and structural diversity on biomass productivity were highly dynamic and changed with tree age and to a certain extent with prevailing climatic conditions. Diversity-productivity relationships take time to unfold and intensify over time especially for slow growing and shade tolerant species. This result shows that mixing tree species can be recommended particularly for plantations with long rotation cycles that allow diversity-productivity relationships to develop. Although the relationships and their dynamics reported here might differ from those expected in dense naturally regenerated forests, our results are highly valuable in the context of young tree plantations and especially restoration efforts in tropical regions. Our results also support the idea that diversity-productivity relationships are dynamic and thus need to be monitored over long periods, ideally throughout all stages of stand development. Importantly, the fact that overyielding in mixtures was maintained even under extremely dry conditions corroborates, that diverse (planted) forests are more productive than monocultures even during climatic extremes, which are expected to become more frequent in many parts of globe.

Authors contributions

JB and JS conceived and designed the study. JB and JS acquired funding for this study. CP initiated and managed the Sardinilla tree diversity experiment. CP, JG and FS collected field data. Material preparation and laboratory analyses were performed by GS with substantial input from JML. GS conducted the analyses and wrote the manuscript with substantial inputs from all co-authors.

CRediT authorship contribution statement

Jean-Michel Leban: Writing – original draft, Resources, Methodology, Conceptualization. **Florian Schnabel:** Writing – original draft, Methodology, Data curation, Conceptualization. **Georgios Skiadaresis:** Writing – original draft, Visualization, Project administration, Methodology, Formal analysis, Data curation, Conceptualization. **Jürgen Bauhus:** Writing – original draft, Supervision, Resources, Methodology, Funding acquisition, Conceptualization. **Catherine Potvin:** Writing – original draft, Resources. **Schwarz Julia Annick:** Writing – original draft, Supervision, Methodology, Funding acquisition, Conceptualization. **Joannès Guillemot:** Writing – original draft, Methodology, Conceptualization.

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Declaration of Competing Interest

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

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.122844.

Data availability

Data will be made available on request.

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