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RESEARCH

Disentangling the relationship of aboveground biomass, structure and tree diversity in a mixed Acacia plantation in Northern Vietnam

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Abstract

The trend of implementing a diversification strategy, which involves introducing two or more species, is becoming increasingly prevalent on a global scale, particularly in tropical forest plantations that were previously dominated by single-species compositions. Improving productivity and enhancing other ecosystem services are the main reasons for this conversion. While mixing effects in temperate forests and plantations are well supported by empirical data, such information is scarce for tropical forest plantations. We analyzed the quantitative aboveground tree biomass—structure—tree diversity relationship in a tropical mixed-forest plantation in Northern Vietnam, hypothesizing that aboveground tree biomass would be increased with greater structural and species diversity. The study site was in a mixed abandoned plantation of *Acacia mangium* and *Acacia auriculiformis* in Northern Vietnam. A one-hectare permanent plot was installed in which all trees were identified individually by species, measured (diameter and height), and georeferenced. The descriptive analysis found that the study area contains 110.66 tons/ha of biomass in the aboveground tree compartments. The structural and species diversity analysis indicated high richness and evenness. A set of models was fitted and ranked to determine the relationship between aboveground tree biomass and structural and specific diversity. The results indicate that the species diversity and evenness, described by the Shannon index, and height differentiation indexes were negatively significant for both species while basal area was only positively significant for *Acacia mangium*. According to the model sensitivity analysis, aboveground tree biomass—and therefore carbon concentration—decreases as species diversity increases.

Keywords Tropical forests · Mixed plantation · Spatial pattern · Forest structure

Introduction

Until recently, most forest plantations in the tropics only included one tree species, but using two or more tree species is becoming more frequent during the planting phase. Plantation diversification can also be achieved through natural succession by incorporating individuals from different tree species that have been sourced from adjacent patches or have sprouted and germinated in the local seed bank. Thus, it is not unusual in tropical forest plantations to observe that the main planted species (*Acacia sp., Pinus sp. Eucalyptus sp*, …) is mixed with native tree species (Pryde et al. 2015). This creates potential for complementarity in resource acquisition (Lu et al. 2018) and ecological gains (Erskine et al. 2006). This transition towards mixed-species plantations reflects a paradigm shift in forestry practices, emphasizing the multifaceted benefits of species diversity beyond traditional monoculture approaches. As mixed-species plantations become more prevalent, there arises an imperative to

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accurately estimate biomass, given its pivotal role in assessing carbon storage potential and supporting various ecosystem services. Forest plantations can compensate for carbon emissions efficiently by storing CO_2 in the tree biomass. Forest biomass estimation is essential for its many applications in a range of ecosystem services, from trade to timber use (Morgan and Moss 1985) to analysis of the global carbon cycle. Due to difficulties in collecting information on belowground biomass, most studies predict biomass based solely on aboveground data (Lu 2006).

As Vietnam embraces diversified planting approaches, the need for accurate biomass estimation becomes increasingly evident, not only to assess carbon storage potential but also to support the country's energy sustainability initiatives. Biomass energy plays a vital role in fulfilling Vietnam’s Nationally Determined Contribution commitment (Socialist Republic of Vietnam 2022), its green growth strategy (The Prime Minister of Vietnam 2020) and in working towards achieving the UN Sustainable Development Goals. Approximately 90% of domestic energy consumption in rural areas is derived from biomass such as fuelwood, agricultural residues (e.g. rice straw and husks), and charcoal (SNV Netherlands Development Organisation Vietnam 2012). In Vietnam, studies on biomass and forest carbon stocks have been receiving attention since 1988, when Vietnam became a Partner Country of the United Nations Collaborative Programme on Reducing Emissions from Deforestation and Forest Degradation in Developing Countries, known as UN-REDD. Implementing REDD + requires knowledge of local biomass and carbon stocks, and Vietnam has made substantial efforts to participate. This includes remarkable achievements such as forest stratification resulting in the identification of two ecological zones, eight ecological regions and 47 ecological sub-regions in Vietnam (Vũ et al. 2011a) and the development of tree allometric equations for estimating above-ground forest biomass in several ecoregions (Bảo et al. 2012; Nguyễn et al. 2012a, c, b; Phùng et al. 2012; Vũ et al. 2012). Many other works have focused on tree biomass estimation, and some case studies involve research on grass and shrub carbon stock in *Acacia mangium, Acacia auriculiformis, Eucalyptus urophylla, Acacia hybrid* or *Pinus kesiya* plantations (Võ 2007, 2009; Nguyễn and Võ 2008). Vietnam stands out for having achieved a net increase in forest cover in recent years (Pham et al. 2019) mainly due to the expansion of plantations (Vũ et al. 2011a).

In the past 20 years, many studies have focused on the relationship between species diversity and ecosystem functions. One of the most common topics addresses the connection between productivity and species richness (Mittelbach et al. 2001; Hooper et al. 2005; Keddy 2005; Huang et al. 1979). Interrelationships between biodiversity and the carbon cycle are believed to be an important consideration for climate change loss and damage mitigation, in addition to diminishing the alteration of natural ecosystems (Midgley et al. 2010). Many studies have reported that the relationship between tree species diversity and productivity is generally (Huang et al. 1979). This could result from the idea of complementarity in resource acquisition, which involves different tree species in a mixed stand using resources like water, nutrients, and sunlight in complementary ways. Essentially, each species has unique resource needs or uptake mechanisms, enabling them to coexist and utilize resources more efficiently than in a monoculture. A strong positive relationship between tree-species richness and net basal area growth has been determined for conifer stands in western North America (Edgar and Burk 2001), subtropical forests in Asia (Huang et al. 1979) and various mixtures in Europe (López-Marcos et al. 2021; del Río et al. 2022). Tree species richness in production forests has also resulted in positive relationships with multiple ecosystem services. (Gamfeldt et al. 2013) reported that trees in a mixed forest of five species produced up to 50% more biomass than a monoculture. The negative effect of species diversity loss on forest productivity also highlights the potential advantages of mixed species over monocultures (Liang et al. 2016). However, other studies have found neutral effects or even a negative relationship between aboveground tree biomass and species diversity (Chen and Klinka 2003; Szwagrzyk and Gazda 2007; Cavard et al. 2010; Bourdier et al. 2016).

While species richness has long been recognized as a key driver of ecosystem productivity, understanding the structural composition of forest stands provides additional insights into productivity patterns. This shift in focus underscores the multidimensional nature of species diversity—productivity relationships and highlights the need for comprehensive assessments of forest ecosystems. Stand structure can be described in terms of the stand density or vertical and horizontal tree spartial distribution patterns. Tree spatial distribution patterns and population structures result directly from complex dynamics involving species characteristics and environmental factors along with the intraspecific or interspecific interactions of individual trees over a long period. Tree spatial distribution patterns depend on the small-scale biological characteristics of the tree and large-scale environmental heterogeneity factors such as soil, pH, nutrition, water, canopy cover, and terrain (Condit et al. 1979). Research has shown that species mixing significantly enhances structural heterogeneity, potentially leading to over-yielding compared to monospecific stands, with changes in stand structure influenced by both species-specific traits and interactions, thus contributing to the observed structural complexity, and highlighting the crucial role of crown complementarity and vertical stratification in the canopy for enhancing ecosystem productivity, particularly in light-demanding species (Riofrío et al. 2017). A positive relationship (weak correlation) between aboveground tree biomass and stand structural diversity were also found in boreal forests (Wang et al. 2011).

In tropical forest sites, biomass carbon stock can also be driven by a complex mechanism involving multiple factors. There, large trees and selective species were found to act as key regulators, while factors such as structural attributes, species richness, and species diversity had a significant positive influence (Kaushal and Baishya 2021). However, the positive, negative, or null effects of mixed species on productivity depend on diversity, biomass yield and species identity. The relationship between tree biomass and diversity can also vary among the species analyzed (Lindén and Agestam 2003; Chen and Klinka 2003; Baeten et al. 2019; Bravo et al. 2021).

Research on the relationship between diversity and productivity in forest ecosystems has focused mainly on species diversity or stand structure. Although the two factors may interact, it is not always possible to isolate the effect of each factor on productivity (Ishii et al. 2004; Vilà et al. 2005; Dănescu et al. 2016; Bohn and Huth 2017; Díaz-Yáñez et al. 2017; Ercanli 2018). However, a combined analysis of species diversity and stand structure might illustrate aboveground tree biomass or carbon sequestration in tree communities better than species diversity or stand structure alone.

The main objective of this study was to analyze the relationship between aboveground tree biomass and stand diversity. To achieve that, a one-hectare permanent plot was established in a forest plantation in Northern Vietnam, in which all individual trees were identified, measured, and geo-positioned. From this data, aboveground tree biomass and tree species diversity metrics were obtained. We hypothesized that increased structural and tree species diversity levels would lead to enhanced aboveground tree biomass in the forest.

Materials and methods

Study site

The study area was located in the Hoa Lac Campus of Vietnam National University, in the Thach That Commune, located 40 km from Hanoi (latitude 21º0′35.0″N and longitude 105º30′51.2″E) (Fig. 1C). The Hoa Lac forest is a transitional area between the mountainous and midland areas in the North and the Northern plains. The climate at the study site is characterized as monsoon tropical with wet, cold winters and hot, humid summers (Fig. 1B). The stratigraphy of the study area consists of a clay-loam layer extending to a depth of 5 m below the ground surface, with heterogeneous mixed-clay layers under that. The geological profile includes Precambrian, Paleozoic, Mesozoic, and Kainozoic rocks. Soil types include red-yellow, brown–red and yellow feralite soils, red-brown basaltic soils, alluvial soils, valley soils, and gleysols (Nguyễn et al. 2009).

A one-hectare permanent plot (Hoa Lac Marteloscope) was established in 2017, following the Marteloscope design by Schuck et al. 2015 and the installation protocol of the BioEcon Project (Bravo et al. 2018), within an area of an abandoned plantation, and there was no information on its previous management regimes. It consists of a 100 m × 100 m plot divided into 16 permanent subplots or *quadrats* measuring 25 × 25 m each and is planned to be utilized for training purposes in the future, enhancing educational opportunities and facilitating hands-on learning experiences (Fig. 1A).

To set up the Hoa Lac Marteloscope, the four outer corners were established using GPS, and the corners of the 16 inner quadrats were marked. The site is nearly flat, so no slope correction was required. All standing trees with a diameter at breast height (dbh) of 5 cm or more were identified to species level, and their dbh, total height, and spatial position were recorded. Aboveground tree biomass was calculated using species-specific allometric equations; see Supplementary A for a complete list of equations (Brown et al. 1989; Nguyễn et al. 2012a; Phạm 2014; Ounban et al. 2016; Traoré et al. 2018). The estimates included biomass from the stem, branches, and leaves, while root biomass was not considered. Only living, standing trees were included, excluding deadwood and fallen trees. The total aboveground tree biomass for each quadrat and for the entire Marteloscope was obtained by summing the biomass of individual trees. The conversion of aboveground tree biomass to carbon was conducted following the guidelines outlined by the IPCC Good Practice Guidance for Land Use, Land-Use Change and Forestry (Penman et al. 2003), which stipulate that carbon content is estimated to be 50% of the above-ground biomass of each living tree.

Seven different tree species were found in the Hoa Lac Marteloscope (446 trees/ha plus 61 standing dead trees/ha), including *Acacia mangium, Acacia auriculiformis, Eucalyptus camaldulensis, Senna siamea, Litsea glutinosa, Aporosa villosa* and *Averrhoa carambola*. Of these, *Acacia mangium* and *Acacia auriculiformis* were the two most abundant species, with 300 and 108 individuals, respectively (Table 1). The standing dead tree species could not be identified due to their level of decay.

Structural and species diversity

Various tree diversity and mixture measurements were computed for each tree with R version 3.5.3, using the "vegan" and "spatstat" packages (Baddeley et al. 2015; Oksanen et al. 2019; R Core Team 2019) to estimate species richness and diversity, species intermingling and horizontal and vertical tree distribution patterns (del Río et al. 2018a, b) (Table 2).

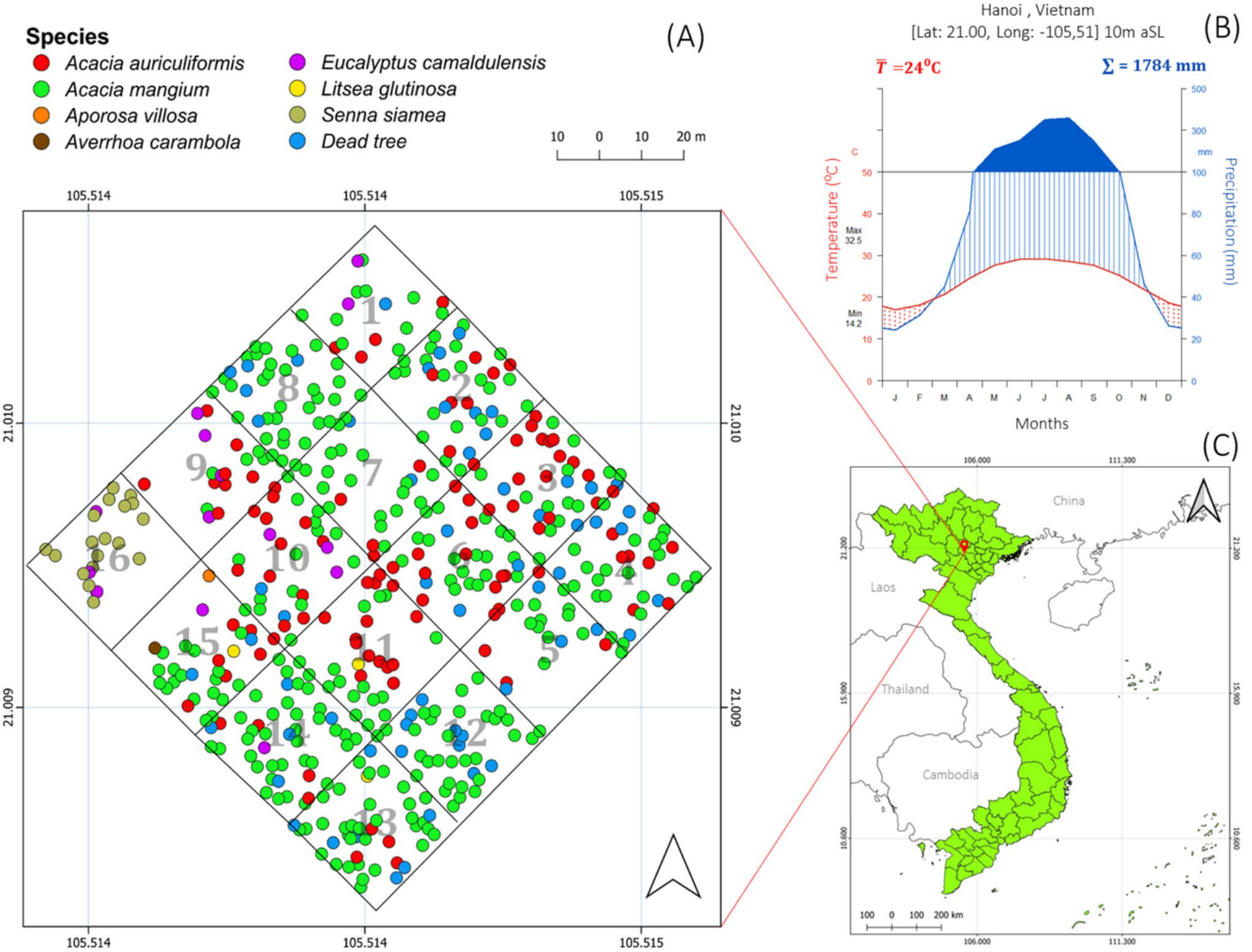


Fig. 1 Hoa Lac Marteloscope study area (**A**) location in northern Vietnam (**C**). The climate diagram (**B**) displays monthly average temperature in degrees Celsius (°C) (red line) and precipitation in millimeters (mm) (blue line), using Walter and Lieth climate diagram standards. Data for 1970–2000 was obtained from the gridded dataset of Climatic Research Unit (CRU) at the University of East Anglia (https://crudata.uea.ac.uk/cru/data/hrg/)

Table 1 General characteristics of each species in the Hoa Lac 1 ha Marteloscope

Species	n	dbh				ht				AGB	C	CO_2
		Mean	Median	Max	Min	Mean	Median	Max	Min			
Acacia mangium	300	20.61	19.74	78.62	6.05	15.06	14.90	24.00	1.70	65.71	32.86	120.45
Acacia auriculiformis	108	22.07	21.96	49.97	6.68	15.24	15.00	22.50	6.00	23.70	11.85	43.45
Eucalyptus camaldulensis	15	17.76	18.14	30.88	7.00	15.41	13.50	22.00	8.50	2.05	1.02	3.75
Senna siamea	18	38.87	39.15	75.12	15.92	12.00	11.75	16.00	7.50	13.64	6.82	25.00
Litsea glutinosa	3	11.46	11.46	15.60	7.32	8.60	6.80	12.50	6.50	0.15	0.08	0.28
Aporosa villosa	1	11.46	–	–	–	4.70	–	–	–	0.02	0.01	0.04
Averrhoa carambola	1	11.46	–	–	–	7.50	–	–	–	0.04	0.02	0.07
Dead trees	61	15.35	13.85	56.98	6.37	9.25	9.00	17.50	1.30			

n: number of individuals; dbh: diameter at breast height (cm); ht: total height (m); AGB: total aboveground tree biomass of each species (tons); C: weight of carbon of each species (tons); CO_2: weight of carbon dioxide sequestered of each species (tons)

Table 2 General characteristics of each species in the Hoa Lac 1 ha Marteloscope

Species richness & diversity	Tree distribution pattern		
	Species intermingling	Vertical spatial pattern	Horizontal spatial pattern
Simpson diversity index (1-Sm) (Simpson 1949) $\mathrm{Sm} = 1 - \frac{\sum_{i=1}^{R} \mathrm{ni}\times(\mathrm{ni}-1)}{\mathrm{N}\times(\mathrm{N}-1)}$ Shannon index (Sh) (Shannon et al. 1949) $Sh = -\sum_{p_i}^{s} p_i \times \ln\left(p_i\right)$ Berker-Parker index (D) (Berger and Parker 1970) $\mathrm{D} = \frac{\mathrm{N_{max}}}{\mathrm{N}}$ Evenness index (E) (Pielou 1975) $E = \frac{H'}{\ln S}$	Segregation index (S) (Pielou 1961) $\mathrm{S} = 1 - \frac{\mathrm{p_{ij}}}{\mathrm{E}\left(\mathrm{p_{ij}}\right)}$ Mingling index (Mi) (Füldner 1995) $M_i = \frac{1}{n}\sum_{j=1}^{n} v_j$ Spatial Diversity Status (MS) (Von Gadow and Hui 2002a, b) $\mathrm{MS_i} = \frac{\mathrm{S_i}}{\mathrm{n_{max}}} \times \mathrm{M_i}$	Vertical Species Profile (A) (Pretzsch 1995) $A = -\sum_{i=1}^{S}\sum_{i=1}^{Z} p_{ij} \times \ln\left(p_{ij}\right)$ Height Differentiation index (TH) (Gadow 1993) $\mathrm{TH_{ij}} = 1 - \frac{\mathrm{MIN(H_i, H_j)}}{\mathrm{MAX(H_i, H_j)}}$	L-function (Ripley 1977) $\hat{\mathrm{L}}(\mathrm{r}) = \sqrt{\frac{\hat{\mathrm{K}}(\mathrm{r})}{\pi}}$, for $\mathrm{r} \geq 0$ $\hat{\mathrm{K}}(\mathrm{r}) = \frac{1}{\lambda} \times \sum_{i=1}^{n}\sum_{j=1}^{n} \frac{\mathrm{P_{ij}(r)}}{\mathrm{n}-1}$, with $P_{ij}(r) = \begin{cases} 1 \text{ if } r_{ij} \leq r \\ 0 \text{ if } r_{ij} \geq r \end{cases}$ Aggregation index (R) (Clark and Evans 1954) $\mathrm{R} = \frac{\bar{\mathrm{r}}_{\mathrm{observer}}}{\mathrm{E(r)}}$, with $E(r) = 0.5 \times \sqrt{\frac{A}{N}}$ Uniform Angle Index (W) (Gadow 1993) $W_i = \frac{1}{n}\sum_{j=1}^{n} v_j$ $where v_j = \begin{cases} 1, \alpha_j < \alpha_0 \\ 0, otherwise \end{cases}$

The Simpson's Diversity index (Sm) (Simpson 1949) is a measure of dominance, emphasizing the abundance of the most common species rather than species richness. It reflects the probability of two individuals being from different species, with higher values indicating greater diversity. The Shannon's index (H') (Shannon et al. 1949) considers both abundance and evenness, where higher values suggest higher diversity and more even distribution of species. The Berger–Parker index (D) (Berger and Parker 1979) quantifies the dominance of the most abundant species, with higher values indicating greater dominance. The reciprocal of this index (1/D) is often used to highlight diversity. The Evenness index (E) (Pielou 1975) compares the actual diversity value (the Shannon–Wiener Index, H') the maximum possible diversity (H_max = ln S), indicating how evenly species are distributed in the community. Species richness and diversity indices and other stand structural metrics (basal area, number of trees per hectare) were derived from all tree species present in each quadrat to capture overall diversity and stand structure patterns.

The segregation index (S) by (Pielou 1961) is commonly used to describe the intermingling of two tree species A and B. The Segregation index (S) describes the relative mixing of two species regardless of their spatial pattern. This method is based on the nearest neighbor distances and compares the observed number of mixed pairs with the one expected under random conditions. S is considered as the ratio of the observed probability (p_{ij}) that the reference tree i and its neareast neighbor j belong to different species along with the same probability for completely random distributed or independent species attributes (Río et al. 2018a, b). The segregation index range between -1 and 1. The trend toward association is indicated by value below 0, while a trnd towards segregation is indicated by value greater than 0. The Mingling index (Mi) (Füldner 1995) describes the species pattern around the reference tree. Mingling index is expressed by the proportion of the n nearest neighbour trees of the i^{th} reference tree that do not belong to the same species. This index is generally used to derive a distribution of trees that belong to a certain structure class. (Aguirre et al. 2003). The Mingling index ranges from 0 to 1, the larger the mingling variable Mi, the more the different tree species are intermingled. A high value of mean mingling Mi represents a high intermingling of the different species, while a small value near 0 will indicates large groups of one single species and segregation. The Spatial diversity status (MS) is an improvement of the Mingling index, which considers not only the spatial mingling, but also the number of tree species. Spatial diversity status of a particular tree species is determined by the relative species richness within the stand or analyzed spatial unit i and the degree of mingling of the reference tree (Río et al. 2018a, b). The Spatial diversity status ranges from 0 to 1 ($0 \leq MS \leq 1$). A reference tree of a common species is more likely to have neighbors of the same species, which is reflected by low values of MS_i. In contrast, a rare species is likely to produce a high proportion of high MS values. Thus, MS is especially sensitive to rare species. (von Gadow and Hui 2002a, b).

The Vertical species profile (A) (Pretzsch 1995) is based on the common diversity index of Shannon (Shannon 1948). A index considers the presence of the species in different height zones in addition to the proportion of the species within a stand. The value of Vertical species profile is greater than 0 ($A > 0$) is for a single-layered pure stand. The more heterogeneous the vertical profile, the higher the A value. In order to calculate Vertical Species profile A by using R-studio, the Height were devided into 3 zones. Assume the height of the highest tree in the stand is 100%, zone I extends from 100 to 80% of maximal tree height (H_{max}), zone 2 from 80 to 50% of H_{max} and zone 3 from 50% to the forest ground which is 0% of H_{max}. A tree is considerd in the zone where the top of the tree is located. The Height Differentiation index (TH) was developed by (Gadow 1993). It measures the differences of size between the reference tree i and its neighboring trees on a continuous scale and describes spatial distribution of tree sizes. TH reveals small-scale variability in the height for the i reference tree and its n nearest neighbours $j(j = 1 \ldots n)$. The Height Differentiation index (TH) range from 0 to 1. Value of 1 indicates that the neighbour trees have high differentiation in height, while TH = 0 means the neightbour trees have an equal height.

The L-function defined by (Besag 1977) was used to define the spatial distribution of the trees. L-function was calculated by dividing the K—function (Ripley 1977) by π and by taking the square root of the quotient, which yields the L -function with both statistical and graphical advantages over the K -function. The L—function allowed tree distribution patterns to be quantified more precisely. In this study, the L—function was applied at whole stand level, quadrat level and species level (within and between interactions of species) in each quadrat. Point patterns can vary from complete random patterns ($\widehat{L}(r) = 0$) by being either aggregated ($\widehat{L}(r) > 0$) or regular ($\widehat{L}(r) < 0$) (Grigoropoulou and Butt 2010). Therefore, if $\widehat{L}(r)$ falls on the expected values (dotted diagonal lines), the trees have a random distribution; if $\widehat{L}(r)$ r falls above the expected values (dotted diagonal lines), the trees have a clumpy distribution; if $\widehat{L}(r)$ r falls below the expected values (dotted diagonal lines), the trees have a uniform distribution. The Aggregation index (R) (Clark and Evans 1954) is the ratio of the observed mean nearest neighbor distance in the pattern to that expected mean distance in a random tree distribution. The index ranges between 0 (greatest clumping, all objects occur at the same point) and 2.1491 (strictly regular hexagonal pattern), and indicates whether the trees are distributed regularly, randomly or in clumps across an area. $R > 1$ describe a tendency towards regular distribution, $R < 1$ indicates a tendency towards clustering and Value around 1 shows random distribution. The Uniform Angle Index (W) developed by (Gadow 1993) describes the degree of regularity in the spatial distribution of trees. This index is based on the classification of angles between nearest neighbours tree of the reference tree (Gadow and Hui 2002a, b). The Uniform Angle Index ranges from 0 to 1. $W < 0.5$ shows regular tree distribution pattern; $0.5 \leq W \leq 0.6$ illustrate random distribution while $W > 0.6$ can be considered as clumpled. Tree distribution pattern indices were computed using all tree species present in each quadrat to capture species mixing, spatial clustering, and vertical stratification. This approach ensures that spatial relationships among trees are accurately represented, providing a comprehensive assessment of stand structure and interspecific interactions.

Data analysis: model selection and evaluation

To investigate the relationship between stand complexity and individual tree biomass, a total of 524 models was fitted, focusing on *Acacia mangium* and *Acacia auriculiformis.* Other species were excluded from the statistical analysis due to limited sample sizes. Model selection was based on Akaike's Information Criterion (AIC), Bayesian Information Criterion (BIC), coefficient of determination (R^2), and mean square error (MSE) to evaluate model performance and ensure a balance between explanatory power and complexity (Schwarz 1978; Akaike 1998; Bravo et al. 2009; Wang et al. 2011).

AIC was prioritized as it provides a trade-off between model fit and complexity, penalizing excessive parameters that do not substantially improve predictive power. BIC applies a stronger penalty for model complexity, potentially leading to underfitting in ecological datasets where a slightly larger model may be justified. R^2, while commonly used to assess explanatory power, tends to increase as more variables are added, regardless of their relevance. MSE evaluates prediction error but does not address overfitting. Given the limitations of R^2 and MSE, and the more conservative nature of BIC, AIC was chosen as the primary criterion for model selection to identify models that optimize both interpretability and predictive capability.

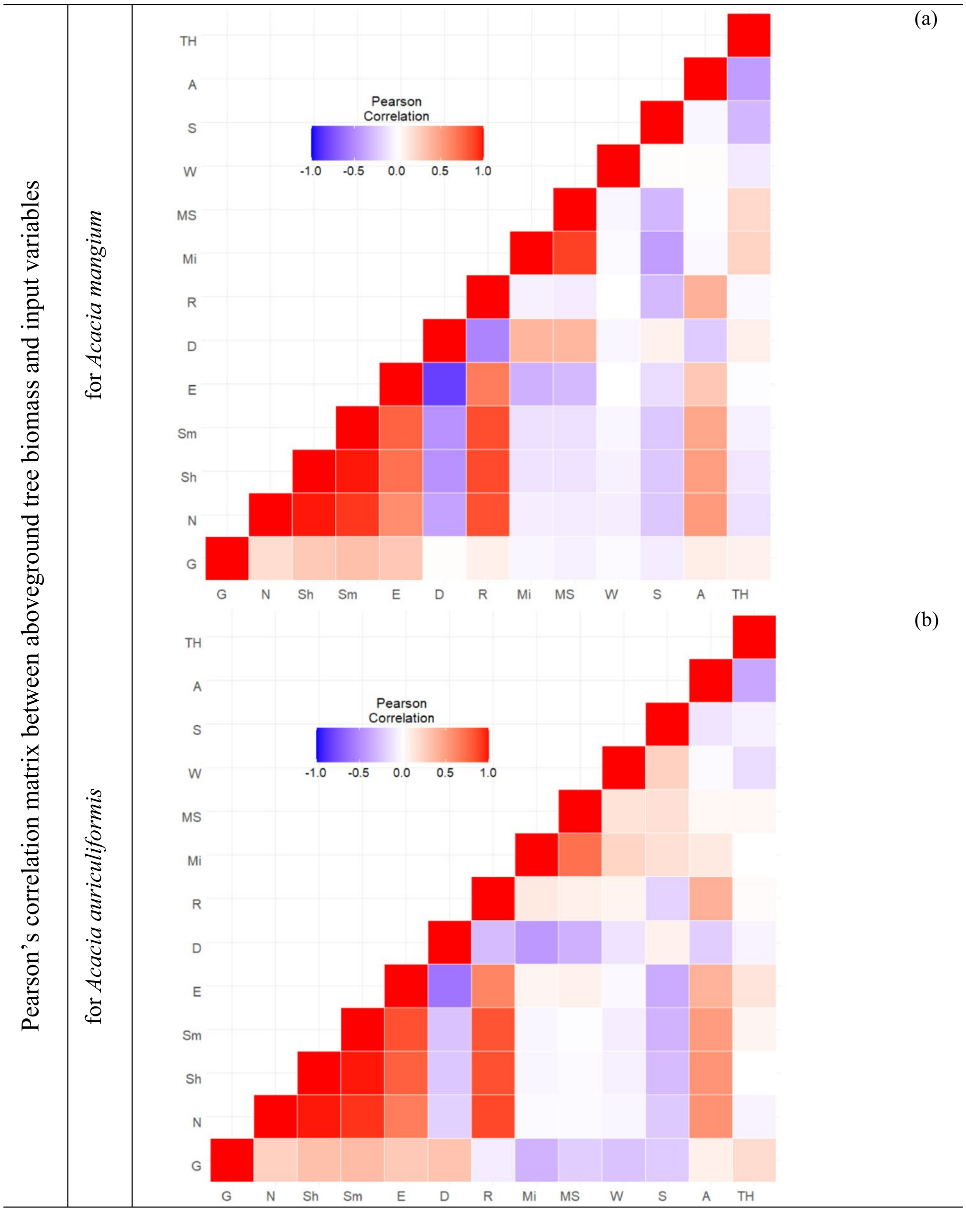
Three general model structures were tested: additive (Eq. 1), exponential (Eq. 2) and multiplicative models (Eq. 3), each capturing different aspects of the relationship between stand structure and aboveground tree biomass. The additive model assumes independent contributions of explanatory variables to biomass accumulation, making it suitable for assessing direct, linear effects of stand structure and biodiversity. The multiplicative model accounts for interactions among variables, meaning that the effect of one factor depends on the values of others. This is particularly relevant in forest ecosystems, where tree biomass is influenced by the combined effects of stand density, species diversity, and spatial arrangement. The exponential model captures nonlinear growth patterns, where biomass accumulation may increase disproportionately with structural complexity, especially in mixed-species stands where competition and resource availability create nonlinear responses.

Table 3 Descriptive statistics for the response variable and candidate explanatory variables

		Variables	Mean	Max	Min	St.Dev
Response variable		AGB	218.26	3010.28	6.92	8.84
Candidate explanatory variables at quadrat level	Stand structure metrics	G	20.628	43.233	11.057	5.916
		N	546.15	720.00	272.00	126.66
	Species diversity indices	Sh	3.36	3.71	2.55	0.29
		Sm	0.96	0.97	0.90	0.02
		E	0.96	1.00	0.90	0.02
		D	1.64	2.21	1.16	0.35
	Species Intermingling	Mi	0.48	1.00	0.00	0.33
		MS	0.19	0.60	0.00	0.15
	Horizontal tree Distribution patterns	R	1.08	1.20	0.82	0.10
		W	0.50	1.00	0.00	0.22
		S	0.22	1.00	-0.03	0.17
	Vertical tree distribution patterns	A	2.46	3.42	0.00	0.59
		TH	0.26	0.91	0.04	0.14

AGB: aboveground tree biomass of each individual tree (kg). G: basal area (m2/ha); N: number of trees per hectare; Sh: Shannon index; Sm: Simpson index; E: evenness index; D: Berger-Parker index; R: aggregation index; Mi: mingling index; MS: spatial diversity status; W: uniform angle index; S: segregation index; A: vertical species profile; TH: height differentiation index

Fig. 2 Pearson's correlation matrix between aboveground tree biomass and input variables



Explanatory variables were selected based on their ecological relevance to tree biomass dynamics and were categorized into four main groups: species richness and diversity, species intermingling, horizontal tree distribution patterns, and vertical tree distribution patterns. Additionally, stand structure metrics were considered into account for competition effects and biomass accumulation potential. A detailed summary of these variables is provided in Table 3. Quadrats that did not contain either *Acacia mangium* or *Acacia auriculiformis*, such as Quadrat 16, were excluded from aboveground tree biomass modeling to maintain consistency in biomass estimation. This exclusion ensured that biomass–structure–tree diversity models were specific to the two target species and prevented non-target species from influencing model outcomes. However, these quadrats still contributed to the computation of quadrat-level diversity metrics, which were used as explanatory variables in the models.

A correlation analysis was conducted to identify and remove highly correlated variables, ensuring that models remained statistically robust. Only variable pairs with correlation coefficients within the range $-0.5 \leq r \leq 0.5$ were retained together in the same model. Pairs exceeding this threshold were excluded to minimize redundancy and collinearity (Fig. 2). The full correlation matrix is provided in Supplementary C.

To ensure model assumptions were met, log transformation was applied to all models using Eq. 2 (exponential model) and Eq. 3 (multiplicative model), where both the dependent variable and explanatory variables were

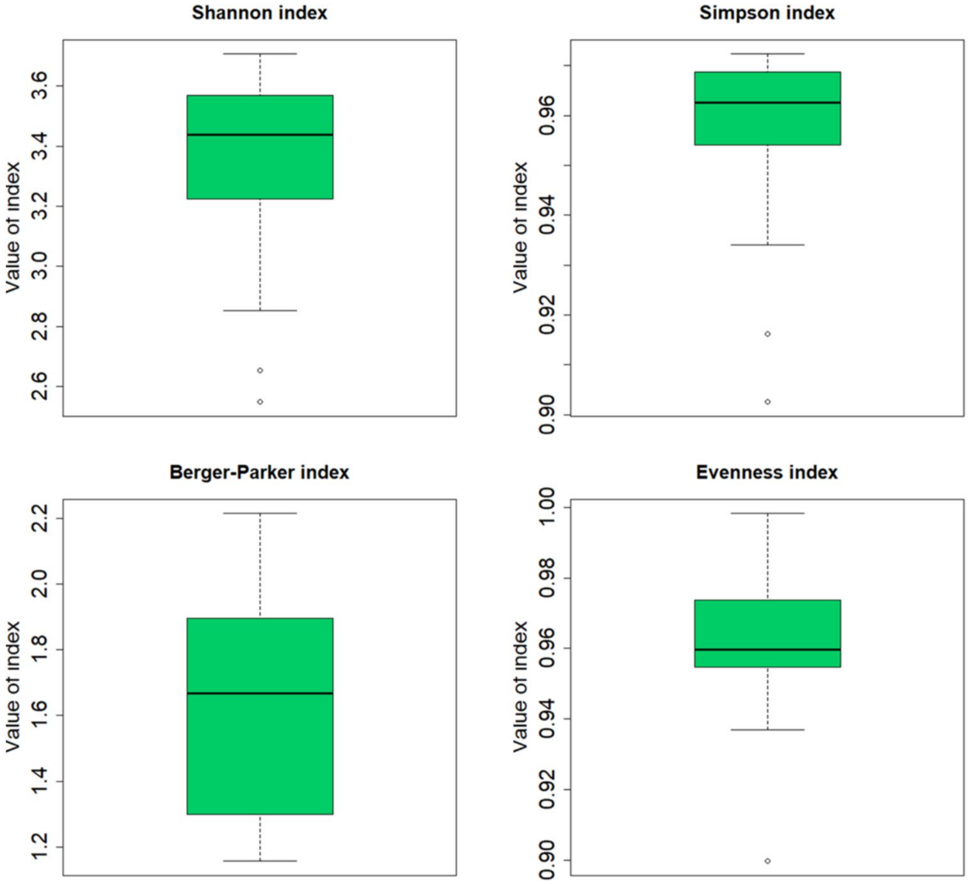


Fig. 3 Stand diversity indexes for the Marteloscope

log-transformed. This transformation was performed to improve normality by making the distribution more symmetric, stabilize variance by reducing the impact of large values, and minimize heteroscedasticity, ensuring that the variability of residuals remained constant across different levels of the explanatory variables. For the exponential model (Eq. 2), log transformation linearized the relationship between aboveground tree biomass and explanatory variables, simplifying estimation and interpretation. In the multiplicative model (Eq. 3), log transformation converted multiplicative effects into additive relationships, making coefficient interpretation more intuitive as elasticity measures. The three tested model structures were formulated as follows:

$$\mathrm{AGB} = \beta_0 + \sum_{\mathrm{i}=1}^{\mathrm{n}} \beta_{\mathrm{i}} \mathrm{X}_{\mathrm{i}} + \varepsilon \quad (1)$$

$$AGB = e^{\beta_0 + \sum_{i=1}^{n} \beta_i X_i} + \varepsilon \quad (2)$$

$$\mathrm{AGB} = \beta_0 \times \mathrm{X}_1^{\beta_1} \times \cdots \times \mathrm{X}_{\mathrm{n}}^{\beta_{\mathrm{n}}} + \varepsilon \quad (3)$$

where AGB represents aboveground tree biomass (kg), X_{i} denotes explanatory variables, β_0 is the intercept representing the expected AGB when all explanatory variables are zero, β_{i} are estimated model coefficients indicating the effect of each explanatory variable, and ε is the error term accounting for unexplained variability in the model.

After selecting the optimal model, a sensitivity analysis was conducted to assess how fluctuations in explanatory variables influenced aboveground tree biomass. This was done by keeping one independent variable at its average value and observing the behavior of the dependent variable when the remaining independent variables varied. The analysis provided crucial insights into the broader relationship between explanatory variables and tree biomass.

All statistical analyses were conducted using R version 3.5.3 (R Core Team 2019).

Results

Stand diversity

The Shannon Index, which indicates species richness and evenness, ranged from 2.55 to 3.71 with a median value of 3.43. Only 25% of the Shannon index values were below 3.22, indicating a mean abundance of more than three species (Fig. 3). Similarly, the Simpson index ranged from 0.90

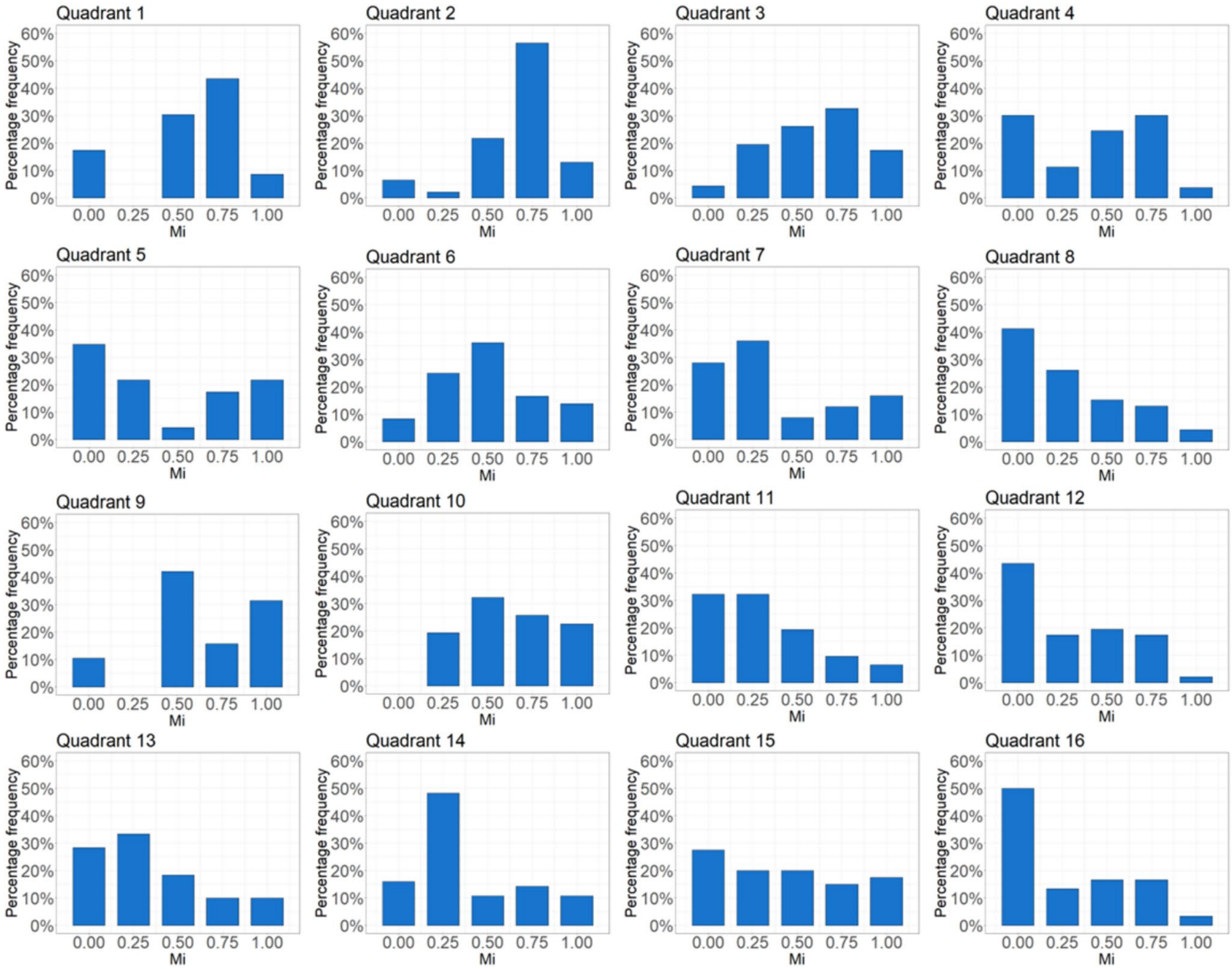


Fig. 4 Percentage frequency distribution of the mingling index (Mi) in each quadrat

to 0.97, with a median of 0.96, indicating high diversity in the plot. The evenness index results also clearly indicated high or complete evenness in the community, with values ranging between 0.90 and 1. The Berger-Parker index illustrated the importance of the most abundant species, with values ranging from 1.16 to 2.21.

Tree distribution, as depicted by the mingling index, varied considerably throughout the 16 quadrats (Fig. 4). A higher component in the 0.25 value class can be observed in quadrats 7, 13, 14, 16, indicating that only two of four nearest neighbors *j* belong to species other than the reference tree *i*. This is indicated by the greater prevalence of weak mingling, or low small-scale mixture. However, small monospecific groups were more present in quadrats 8 and 12, where a high percentage of the mingling index had a value of 0. A general mingling value distribution trend towards monospecific groups was observed in quadrats 7, 8, 11, 12, 13, 14 and 16; towards mean mingling in quadrats 4, 5, 6, 9 and 15; and towards multi-specific groups in quadrats 1, 2, 3 and 10.

The reference trees in quadrats 4, 5, 7, 8, 11, 12, 13, 14 and 16 were more likely to have neighbors of the same species (Fig. 5a), as reflected by the low MS value. Meanwhile, quadrats 1, 2, 3, 6, 9, 10 and 15 had a high MS value, indicating high diversity, and the reference trees were observed to be more likely to have neighbors of different species.

The height differentiation index (TH) had a relatively low value (Fig. 5b) despite the presence of outliers with high values in certain quadrats. Examination of the TH class based on the two most abundant species (Fig. 6) revealed that at least 40% of the TH values fell within the ranges of 0 to 0.2 and 0.2 to 0.4. This explains why only limited height differences were observed between neighboring trees.

The L-function line deviates very slightly from the expected values (red-line) (Fig. 7); when r is small, the actual values are just below the expected values. While

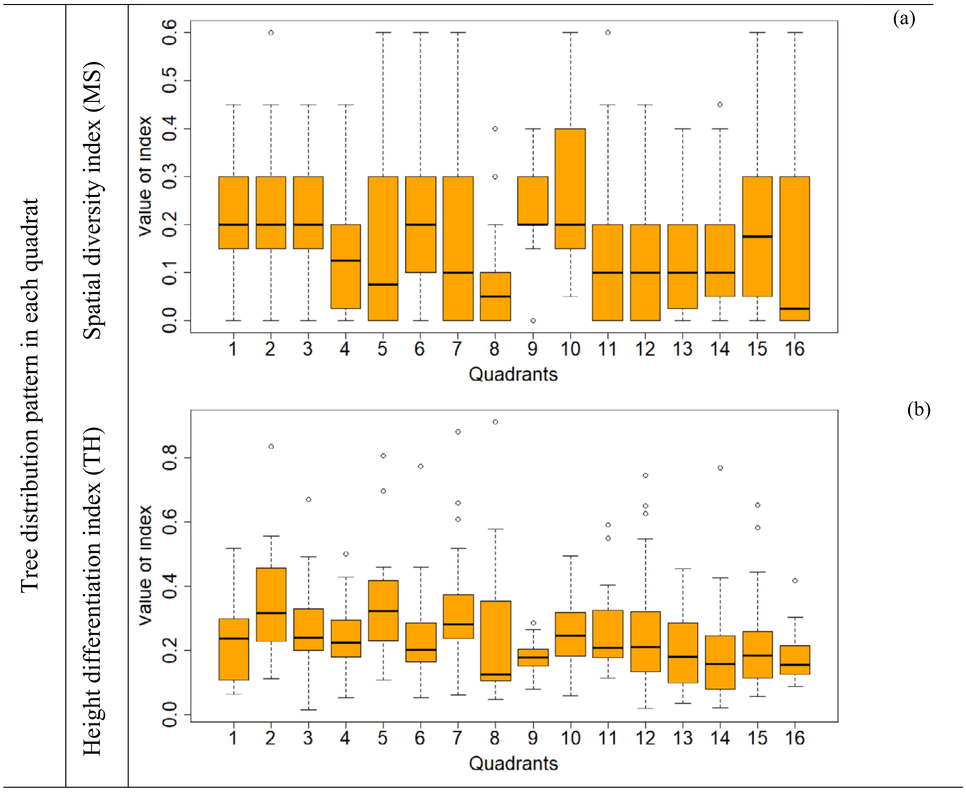


Fig. 5 Tree distribution pattern at the study site

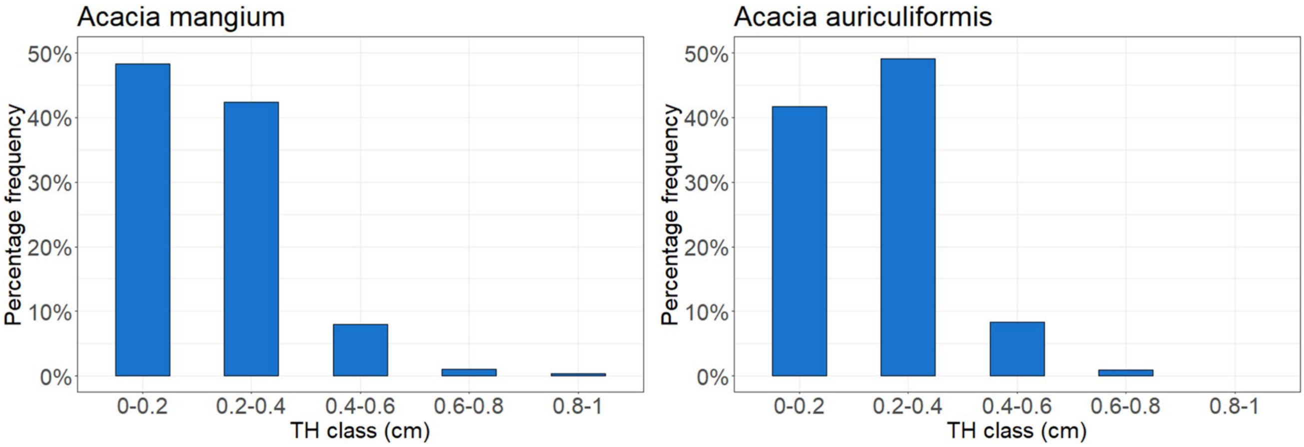


Fig. 6 TH classes of the two most abundant species

this may suggest uniform distribution, it is more accurate to interpret it as reflecting random distribution because the deviations are not significant enough to be considered uniform. For bigger r, the actual values mostly coincide with the expected values, indicating random distribution. This can be observed in almost all quadrats, but since the deviation from the expected value is slight, it would be very easy to mistakenly interpret this L-function line as random, uniform or clumpy distribution. The Clark and Evans aggregation index (R) for the entire Marteloscope are $R = 1.11$ indicated random distribution. For each quadrat, R ranged from 0.82 to 1.20, indicating that all quadrats and species in the Marteloscope displayed a tendency towards random distribution. Though the study area had once been a plantation, the results from functions and indexes depicting horizontal spatial patterns indicate that the trees in the Marteloscope followed a trend towards random (Poisson) distribution.

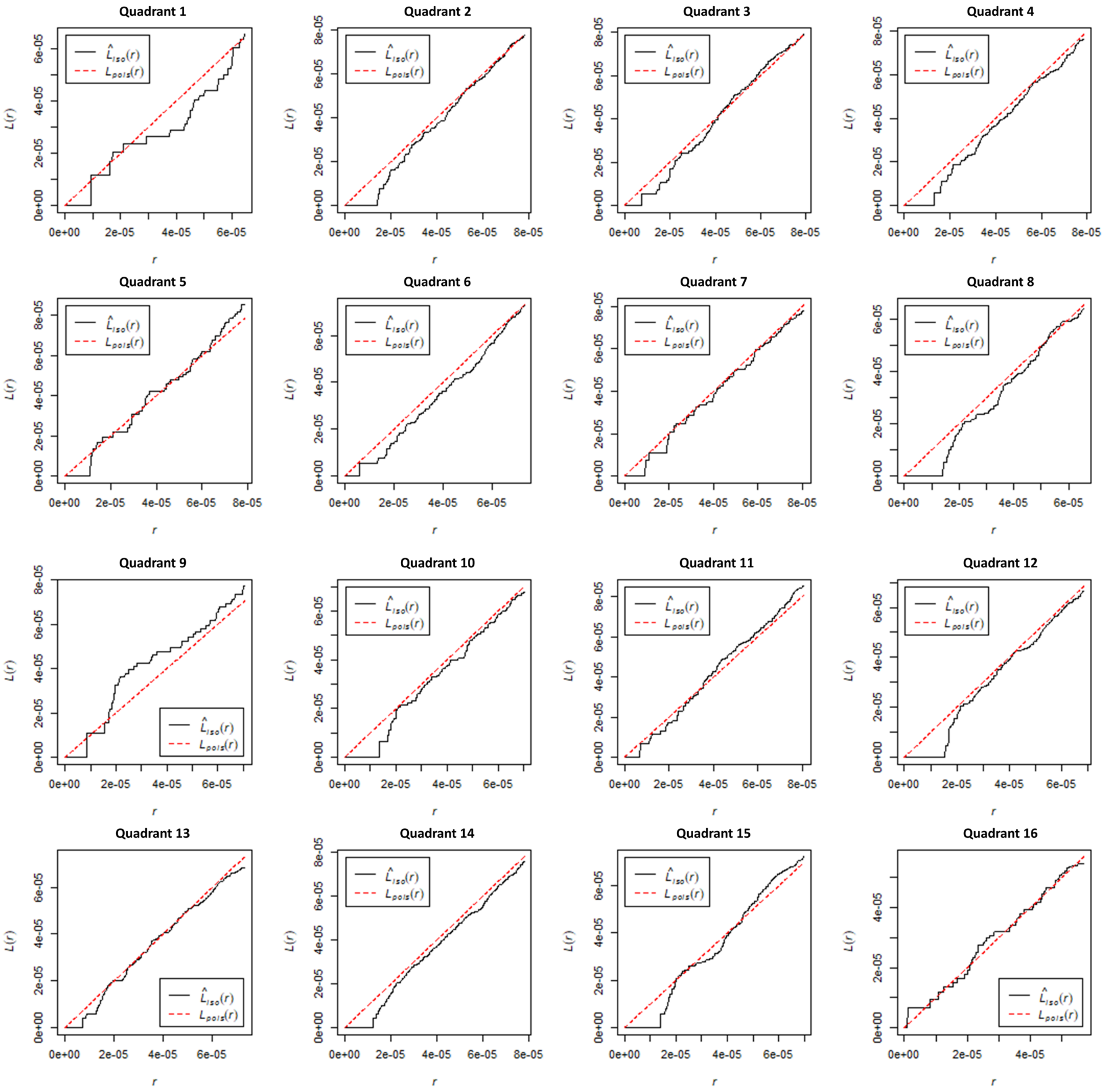


Fig. 7 L – function for all quadrats

Model selection and evaluation

Only models that met regression assumptions, such as homogeneity of variance, normality, linearity, and non-autocorrelation, with a high goodness of fit were selected (Table 4). The R^2 was low for all models, indicating a weak relationship between aboveground tree biomass and the independent variables. Despite the low goodness-of-fit, low R^2 values were acceptable in this context because the primary goal of the models is not to predict aboveground tree biomass precisely but to explain its relationships with species diversity. While the models explain only a small proportion of aboveground tree biomass variability, the statistical significance of key predictors (Supplementary D) suggests that tree species diversity and stand structure have consistent, non-random influences on aboveground tree biomass dynamics. This indicates that even though the models do not capture all sources of variation, they still provide valuable insights into how species diversity and stand structure contribute to biomass accumulation. Such findings are crucial for ecological studies and forest management, where identifying key

Table 4 The 10 best-fitted models for *Acacia mangium* and *Acacia auriculiformis*

No	Model	β_0	β_1	β_2	β_3	R^2	p-value	MSE	AIC	BIC
Acacia mangium										
1.1	$AGB = e^{\beta_0+\beta_1 G^2+\beta_2 Sh^2+\beta_3 TH^2}$	6.0575	0.0011	− 0.1115	− 1.5179	0.0974	1.14E-06	0.5747	691.1749	709.6938
1.2	$AGB = e^{\beta_0+\beta_1 G^2+\beta_2 Sh+\beta_3 TH^2}$	7.1698	0.0011	− 0.7120	− 1.5047	0.0960	1.44E−06	0.5757	691.6658	710.1847
1.3	$AGB = e^{\beta_0+\beta_1 G^2+\beta_2 Sh^{0.5}+\beta_3 TH^2}$	9.4081	0.0011	− 2.5318	− 1.4976	0.0951	1.65E−06	0.5762	691.9466	710.4655
1.4	$AGB = e^{\beta_0+\beta_1 G^2+\beta_2 Sh^2+\beta_3 \frac{1}{A}}$	6.7986	0.0010	− 0.1370	− 1.2259	0.0931	2.28E− 06	0.5775	692.6277	711.1466
1.5	$AGB = e^{\beta_0+\beta_1 G^2+\beta_2 \frac{1}{Sh}+\beta_3 TH^2}$	2.6654	0.0011	6.9634	− 1.4747	0.0922	2.63E−06	0.5781	692.9230	711.4419
1.6	$AGB = e^{\beta_0+\beta_1 G^2+\beta_2 Sh+\beta_3 \frac{1}{A}}$	8.1637	0.0010	− 0.8762	− 1.2104	0.0915	2.91E−06	0.5785	693.1402	711.6591
1.7	$AGB = e^{\beta_0+\beta_1 G^2+\beta_2 Sh^{0.5}+\beta_3 \frac{1}{A}}$	10.9158	0.0010	− 3.1168	− 1.2001	0.0906	3.38E−06	0.5791	693.4517	711.9706
1.8	$AGB = e^{\beta_0+\beta_1 G^2+\beta_2 Sh^2+\beta_3 \frac{1}{\sqrt{A}}}$	7.2766	0.0010	−0.1370	− 1.5461	0.0898	3.82E−06	0.5796	693.7098	712.2287
1.9	$AGB = e^{\beta_0+\beta_1 G^2+\beta_2 Sh+\beta_3 \frac{1}{\sqrt{A}}}$	8.6284	0.0010	− 0.8756	− 1.5201	0.0882	4.93E−06	0.5806	694.2415	712.7604
1.10	$AGB = e^{\beta_0+\beta_1 G^2+\beta_2 Sm^2+\beta_3 TH^2}$	10.8937	0.0011	− 6.6910	− 1.4250	0.0881	5.01E−06	0.5807	694.2774	712.7964
Acacia auriculiformis										
2.1	$AGB = e^{\beta_0+\beta_1 TH^2+\beta_2 Sh^2}$	6.7478	− 4.2598	− 0.1284	–	0.1742	4.32E-05	0.6891	271.2262	281.9547
2.2	$AGB = e^{\beta_0+\beta_1 TH^2+\beta_2 Sh}$	7.9406	− 4.2273	− 0.7887	–	0.1736	4.49E− 05	0.6896	271.3042	282.0327
2.3	$AGB = e^{\beta_0+\beta_1 TH^2+\beta_2 \frac{1}{Sh}}$	3.1556	− 4.1631	7.1301	–	0.1712	5.22E− 05	0.6916	271.6158	282.3444
2.4	$AGB = e^{\beta_0+\beta_1 TH^2+\beta_2 Sm^2}$	11.4450	− 4.0997	− 6.7161	–	0.1700	5.64E− 05	0.6926	271.7741	282.5026
2.5	$AGB = e^{\beta_0+\beta_1 TH^2+\beta_2 \sqrt{N}}$	7.1923	− 4.3516	− 0.0810	–	0.1698	5.70E− 05	0.6927	271.7947	282.5232
2.6	$AGB = e^{\beta_0+\beta_1 TH^2+\beta_2 Sm}$	17.2928	− 4.0937	− 12.5392	–	0.1696	5.77E− 05	0.6929	271.8211	282.5496
2.7	$AGB = e^{\beta_0+\beta_1 TH^2+\beta_2 N^2}$	5.9176	− 4.4299	0.0000	–	0.1661	7.24E−05	0.6959	272.2871	283.0157
2.8	$AGB = e^{\beta_0+\beta_1 TH^2+\beta_2 \sqrt{E}}$	27.4966	− 3.7967	− 22.7417	–	0.1587	1.15E−04	0.7020	273.2345	283.9630
2.9	$AGB = e^{\beta_0+\beta_1 TH^2+\beta_2 E}$	16.4912	− 3.7974	− 11.7468	–	0.1586	1.15E−04	0.7020	273.2418	283.9703
2.10	$AGB = e^{\beta_0+\beta_1 TH^2+\beta_2 E^2}$	10.9873	− 3.7988	− 6.2643	–	0.1585	1.16E−04	0.7021	273.2585	283.9870

AGB: aboveground tree biomass (kg); TH: height differentiation index; Sh: Shannon index; Sm: Simpson diversity index; N: number of trees per hectare; E: evenness index; G: basal area of each quadrat (m^2/ha); A: vertical species profile

drivers of biomass is often more important than achieving high predictive accuracy.

After comparing AIC, BIC, R^2 and MSE, Model (4) (Model 1.1, Table 4) for *Acacia mangium* and Model (5) (Model 2.1, Table 4) for *Acacia auriculiformis* were selected as the optimal models for explaining the relationship between tree aboveground tree biomass and species diversity. The results of the model evaluation for the selected models (4) and (5) indicate a negative relationship between aboveground tree biomass (AGB) and species diversity (Fig. 8), as represented by a given set of values for the basal area of each quadrat (G), the Shannon index (Sh) and the height differentiation index (TH).

$$AGB = e^{6.0575+0.0010\times G^2-0.1115\times Sh^2-1.5179\times TH^2} \tag{4}$$

$$AGB = e^{6.7478-4.2598\times TH^2-0.12839\times Sh^2} \tag{5}$$

Figure 8 presents the sensitivity analysis of aboveground tree biomass in response to key explanatory variables within the selected models for *Acacia mangium* (4) and *Acacia auriculiformis* (5). For *Acacia mangium*, the effects of species diversity (Sh), height differentiation (TH), and G on aboveground tree biomass are examined across four fixed levels (13, 17, 21, and 25) (Fig. 8a). The results show a negative relationship between Sh and aboveground tree biomass, meaning that as species diversity increases, biomass decreases. This effect is especially pronounced when G is high, suggesting that interspecific competition limits biomass accumulation despite the overall productivity increase associated with larger basal area. Additionally, aboveground tree biomass declines as TH increases, indicating that a more uneven canopy structure leads to competitive asymmetry, where taller trees outcompete smaller ones for resources. Aboveground tree biomass reaches its highest values in quadrats with high G, low Sh, and low TH (Fig. 9a). While G positively influences aboveground tree biomass, the quadratic term suggests that although biomass continues to rise with increasing G, the

Fig. 8 Sensitivity analysis of models (4) and (5)

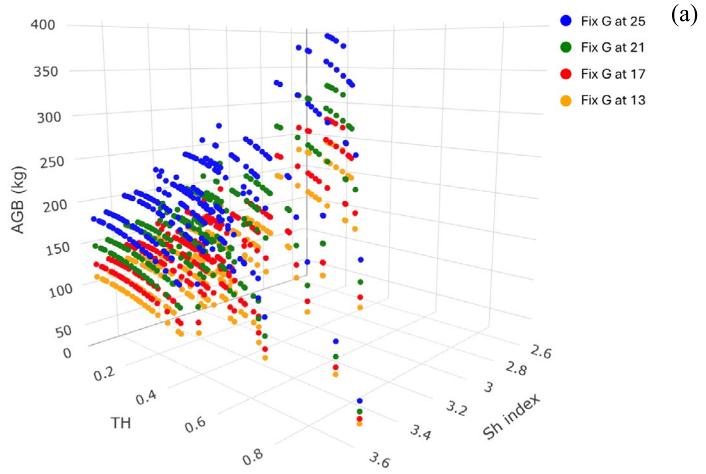
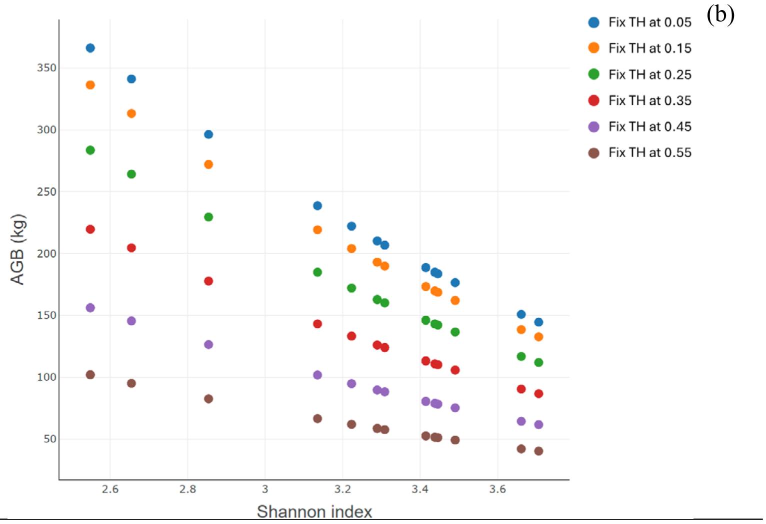
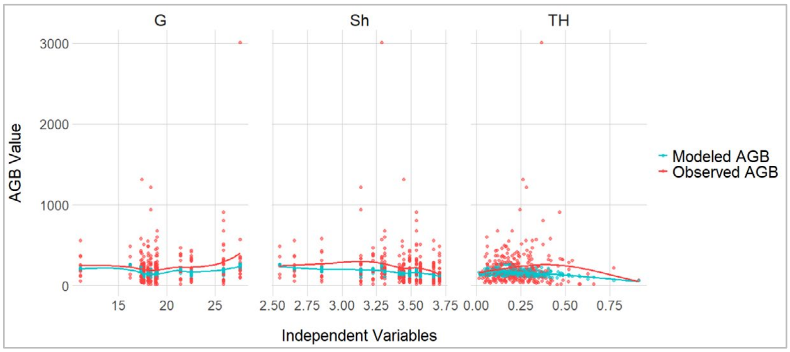
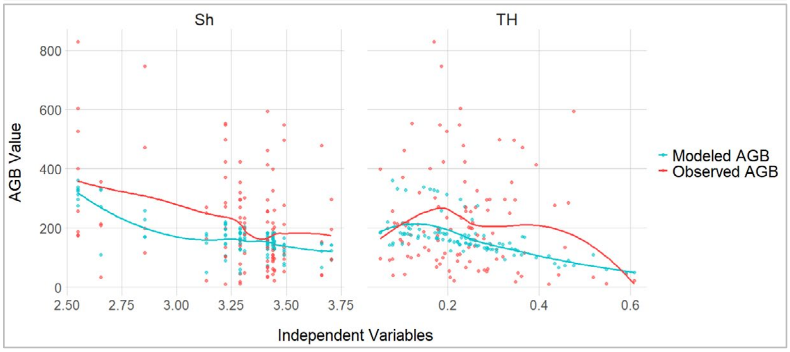
Sensitivity analysis	Model 1.1 - *Acacia mangium* (see https://plot.ly/~dtnmahbu/1/#/ for 3D version)	 (a)
	Model 2.1 - *Acacia auriculiformis* (see https://plotly.com/~dtnmahbu/43/ for online version)	 (b)

Fig. 9 Modeled AGB versus Observed AGB of models (4) and (5)

Tree distribution pattern in each quadrat	Model 1.1 - *Acacia mangium*	 (a)
	Model 2.1 - *Acacia auriculiformis*	 (b)

rate of accumulation slows at higher values, likely due to intensified competition.

Figure 8b further explores this relationship in *Acacia auriculiformis*, showing the effect of Sh on aboveground tree biomass while holding TH constant at six levels (0.05, 0.15, 0.25, 0.35, 0.45, and 0.55). The declining trend of aboveground tree biomass with increasing Sh remains consistent, confirming the negative impact of Sh on aboveground tree biomass. Moreover, the effect of TH is evident, as plots with higher TH consistently exhibit lower aboveground tree biomass. The model indicates that aboveground tree biomass is highest in stands with low TH and low Sh, while greater TH and Sh are associated with reduced aboveground tree biomass. TH has a strong negative impact on aboveground tree biomass, with aboveground tree biomass decreasing as TH increases. The quadratic term suggests that this effect becomes more severe at higher TH values, indicating that stands with a more uniform canopy structure are more productive. Observed data (Fig. 9b) confirm this pattern, as plots with high TH values indicate significantly lower aboveground tree biomass. Sh also negatively affects aboveground tree biomass, though to a lesser extent than TH. Aboveground tree biomass remains relatively high at low Sh values but declines as Sh increases. This suggests that interspecific competition reduces aboveground tree biomass, likely by limiting the growth of dominant individuals. The quadratic relationship indicates that the negative effect is most pronounced in highly diverse stands.

The sensitivity analysis highlights that both species exhibit a similar response to variations in Sh and TH, with lower aboveground tree biomass observed in more diverse and vertically stratified quadrats. While G has a positive effect on aboveground tree biomass, this does not offset the negative impact of Sh and TH. The results suggest that aboveground tree biomass is maximized in stands with low Sh and uniform TH, emphasizing the role of competition in shaping aboveground tree biomass.

Discussion

This study examines the relationships among stand structure, species diversity, and aboveground tree biomass in a mixed *Acacia* plantation in Northern Vietnam. The findings reveal that the plantation exhibits high species diversity. The Shannon index values range from 2.55 to 3.71 (median = 3.43), while the Simpson and Evenness indices indicate a near-uniform species distribution. These metrics suggest that most quadrats contain more than three species with relatively balanced abundances. Spatial analyses using the L-function and the Clark–Evans aggregation index further demonstrate that tree distribution follows a predominantly random pattern rather than a clumped or uniform structure. This spatial arrangement implies that resource competition at the local scale is primarily governed by individual interactions rather than strong spatial segregation. For *Acacia mangium*, Model (4) identifies a strong positive relationship between basal area (G) and aboveground tree biomass, aligning with the expectation that higher cumulative tree cross-sectional area contributes to greater carbon storage and biomass accumulation. However, sensitivity analysis reveals a key interaction: in quadrats with higher species diversity, the positive effect of G on aboveground tree biomass is weakened. Specifically, while higher stand density (high G) generally enhances productivity, its benefits are offset in more diverse quadrats. As the Shannon index increases, aboveground tree biomass declines, even when basal area remains high. This suggests that in functionally similar species groups, additional species may exacerbate competition rather than enhance resource-use efficiency. Similarly, height differentiation (TH), which quantifies vertical heterogeneity in the canopy, exhibits a consistent negative association with aboveground tree biomass in both *Acacia mangium* and *Acacia auriculiformis*. In stands with high TH, taller trees likely capture a disproportionate share of light and other resources, suppressing the growth of smaller individuals. Sensitivity analyses (Figs. 8) show that quadrats with lower TH values tend to have higher biomass, reinforcing the idea that a more uniform canopy structure facilitates a more equitable distribution of resources and promotes overall productivity. For *Acacia auriculiformis*, Model (5) indicates that basal area is not a significant predictor of aboveground tree biomass. Instead, the negative effects of species diversity (Shannon index) and vertical heterogeneity (TH) are even more pronounced. This suggests that, for *Acacia auriculiformis*, competitive interactions driven by high species diversity and canopy stratification play a dominant role in limiting biomass accumulation, outweighing the influence of stand density. Overall, these results highlight a key trade-off in the studied plantation: while greater basal area generally support higher biomass, its benefits are counteracted by increased species diversity and vertical heterogeneity. In stands where species share similar functional traits—such as the two *Acacia* species in this study—the expected advantages of niche complementarity are not realized. Instead, interspecific competition intensifies, leading to lower aboveground tree biomass. This balance between stand density benefits and competition costs is central to understanding the observed biomass patterns.

The negative relationship observed between species diversity (Shannon index) and aboveground tree biomass in the current study are consistent with some previous findings in the literature. For example, studies conducted by Szwagrzyk and Gazda (2007) in Central Europe and by Suo et al. (2008) in Chinese Quercus forests have reported that increased species diversity can be associated with reduced biomass accumulation. In these cases, when the species coexisting in a stand exhibit similar functional traits, the benefits of resource partitioning through niche complementarity are minimal. Instead, intense interspecific competition results in lower biomass production. In this analysis, although the evenness index was initially included in the candidate models, it showed no significant relationship with aboveground tree biomass, likely due to the relatively uniform species proportions across the study area. In contrast, the Shannon index, which accounts for both species abundance and evenness, exhibited a negative correlation with aboveground tree biomass. This suggests that higher species diversity, particularly among functionally similar species, intensifies competition rather than improving resource use efficiency.

Stand density, measured as the number of trees per hectare, is another factor that can influence diversity–productivity relationships, as well as stand biomass and basal area. When stand density is low, interactions between trees—whether competitive or complementary—are weak. Previous studies have suggested that stand density can be a stronger determinant of productivity than species richness (Paquette and Messier, 2011; Vilà et al. 2013). In this study, N (number of trees per hectare) was included as an explanatory variable in the model fitting process. Among the 20 best candidate models (Table 4), some incorporated N alongside other predictors such as the Shannon index (Sh), basal area (G), and height differentiation (TH). However, in the best-fitted models (Models 4 and 5), which provide the most accurate representation of aboveground tree biomass variation in *Acacia mangium* and *Acacia auriculiformis*, N was not retained as a significant predictor. This indicates that while stand density was considered in multiple high-ranking models, its explanatory power was insufficient for it to be included in the optimal models. Thus, compared to other structural and diversity-related variables, N did not contribute substantially to explaining variations in aboveground tree biomass. On the other hand, in this study, the Shannon index and height differentiation index (TH) were significant predictors for both *Acacia mangium* and *Acacia auriculiformis*. However, only the model for *Acacia mangium* showed a good fit for basal area (G) at the quadrat level, likely reflecting differences in species distribution patterns. This suggests *Acacia mangium* is more influenced by these indices, whereas *Acacia auriculiformis* may be less responsive due to different ecological or physiological traits. These findings underscore that the biomass–diversity relationship is multifactorial. It can be influenced by factors such as similarity in functional traits between analyzed species (both were Acacias), species complementarity (Riofrío et al. 2016; Bravo et al. 2021), site conditions (Huber et al. 2014), stand density (Condés and del Río 2015) or environmental conditions (Wang and Kimmins 2002; Manso et al. 2014) that were not fully explained by the indicators included in our analysis. This suggests that the relatively negative correlation between diversity and aboveground tree biomass in our study might be partially driven by the fact that increased species diversity in a functionally homogeneous stand does not enhance resource partitioning; rather, it intensifies competition among trees for limited resources such as light, water, and nutrients. Moreover, shifting the focus from diversity based solely on species identity to diversity based on functional traits could yield results more consistent with literature associating higher diversity with increased biomass growth and yield yield (Roscher et al. 2012; Hisano and Chen 2020). In essence, our results suggest that, in systems where species have similar ecological roles—as in the studied mixed Acacia plantation—the introduction of additional species can intensify competitive interactions, thereby reducing overall biomass accumulation. This integrated understanding, which draws on both our findings and previous literature, highlights the importance of considering multiple dimensions—including stand density, vertical heterogeneity, and functional trait diversity—when assessing the impacts of species diversity on forest productivity. While the results of the model evaluation of (Eq. 1) and (Eq. 2) for *Acacia mangium* and *Acacia auriculiformis* illustrate that species richness and diversity negatively affected tree aboveground tree biomass and carbon sequestration, (Li et al. 2018) indicated the opposite result across forest strata in their work on the relationship between species richness and aboveground biomass in a primary *Pinus kesiya* forest, which was generalized to all forest vegetation strata. Global research by (Liang et al. 2016) highlighted the negative impact of species diversity loss on forest productivity, indicating that species loss in forest ecosystems worldwide could substantially reduce forest productivity and forest carbon absorption rates, compromising the global forest carbon sink. Another interesting contrast to the results of this study is found in Day et al. (2013), who observed that the trend of species diversity to aboveground tree biomass varied at different locations within the study area. While some high-diversity plots had relatively low biomass, other low-diversity plots had high biomass because the study areas were in several forest types with different plot management approaches, altitude and climate conditions. Though the correlation was only weakly significant, the author claimed that there was evidence of a general positive relationship between species diversity and between biomass compartments. A study by Riofrío et al. (2016) on the effects of specific mixtures (*Pinus sylvestris* L. and *Pinus pinaster* Ait.) also reported that species mixing positively modified the aboveground forest yield. Positive relationships between biomass and tree species diversity were also found when examining data from managed forests dominated by relatively young secondary stands in forest plots in Catalonia, NE Spain (Vilà et al. 2005).Research results also corroborate this relationship in the north-central USA (Caspersen and

Pacala 2001) in simulations of German mixed-forests (Bohn and Huth 2017), and for the entire range of forested ecosystems across Canada (Zhang et al. 2016, 2017). This general trend of a positive species diversity—productivity relationship has been confirmed on a global scale (Liang et al. 2016) by combining data across different forest biomes (Global Forest Biodiversity permanent sample plots, https://www.gfbinitiative.org/). A key factor underlying these differences appears to be the functional traits of the species involved. In our mixed Acacia plantation, both *Acacia mangium* and *Acacia auriculiformis* exhibit relatively similar functional traits. This functional similarity likely limits the potential for resource partitioning and niche complementarity, intensifying competition rather than enhancing productivity when additional species are present. In contrast, studies reporting positive diversity–productivity relationships often involve forests where co-occurring species exhibit a broader range of functional traits, facilitating complementary resource use (Williams et al. 2017; del Río et al. 2017). Moreover, the environmental context and stand management practices differ markedly between these studies. For instance, the research by Li et al. 2018 was conducted in a primary Pinus kesiya forest, where the variability in environmental conditions and species composition may have allowed for stronger positive diversity effects. In our study, the relatively uniform species proportions and the limited range of environmental variation in the plantation likely constrained the potential benefits of increased diversity, instead highlighting the competitive suppression of biomass accumulation. Thus, while global analyses and studies in more functionally diverse forests have found that greater species diversity can promote productivity, the results of the present study underscore that in systems where species are functionally similar—such as this mixed Acacia plantation—increased diversity may intensify competition for limited resources and consequently reduce aboveground tree biomass.

From a silvicultural perspective, the results of this study indicate that silvicultural strategies should aim to maintain an optimal balance between basal area and resource competition. Thinning strategies should target an optimal stocking level that maximizes biomass accumulation while preventing excessive density that may lead to competition and resource depletion. Specifically, for *Acacia mangium*, controlling basal area through appropriate thinning may maximize biomass, whereas for *Acacia auriculiformis*, achieving a more uniform canopy with even-height distribution appears crucial for enhancing productivity. Moreover, the negative effects of species diversity on biomass accumulation suggest that, in this specific system, monocultures of *Acacia mangium* might yield higher biomass than mixed-species stands. However, promoting monocultures comes at the cost of reduced species diversity, a trade-off well recognized in forest management. While higher biomass may improve timber yield and carbon sequestration, it can compromise other ecosystem services such as resilience to pests, nutrient cycling, and overall biodiversity conservation. Therefore, management decisions must carefully balance productivity with the broader multifunctional benefits of forest ecosystems.

Although the findings of our study provide valuable insights into the dynamics of species diversity and stand structure on biomass accumulation, several limitations must be acknowledged, as these may influence the interpretation and broader applicability of the results. First, the study is based on a single plot in Northern Vietnam. This limited spatial sampling means that while the findings are robust for that particular site, they may not be representative of all mixed plantation systems. Variations in soil type, microclimate, and historical management practices across different plantation systems could lead to different patterns of biomass accumulation. Therefore, while the results are robust for the studied plot, caution should be exercised when extrapolating these findings to other regions or forest types.

In addition, the statistical models used in the analysis exhibit relatively low overall R^2 values. Although key explanatory variables—such as the Shannon index, basal area, and height differentiation index (TH)—were found to be statistically significant, a considerable portion of the variation in aboveground tree biomass remains unexplained. This unexplained variance suggests that additional factors not considered in the current analysis—such as soil nutrient availability, moisture levels, microtopography, or past management practices—may play important roles in determining biomass. The low R^2 values emphasize the inherent complexity of forest ecosystems and the need for more comprehensive models that integrate a broader range of environmental variables.

Furthermore, the indices used to measure diversity and canopy structure have inherent limitations. While the Shannon index provides a useful measure of species richness and evenness, it does not capture functional trait differences that may influence competitive dynamics. In systems where species are functionally similar, the Shannon index may not fully reflect the interspecific competition that drives biomass accumulation. Similarly, the height differentiation index (TH), although indicative of vertical heterogeneity, may oversimplify the complexity of canopy structure. Finally, the legacy effects of previous management practices—such as planting density, thinning, or selective harvesting—may have influenced the current stand structure and species composition. These historical factors could confound the relationships observed in the study and represent an additional source of uncertainty.

Future research should focus on several key areas to enhance the understanding of biomass accumulation dynamics in mixed-species plantations. Expanding the spatial scope to multiple sites will help determine whether the observed negative relationship between species diversity and aboveground tree biomass is site-specific or a general pattern, while also allowing for the isolation of local factors such as soil, climate, and management practices. Incorporating additional environmental variables like soil nutrients, moisture, and microclimate will improve model accuracy and provide a more comprehensive understanding of aboveground tree biomass dynamics. Furthermore, measuring functional traits, such as wood density and leaf area, alongside traditional diversity indices will clarify the role of species functional diversity in biomass accumulation and competitive interactions. Establishing long-term monitoring plots and applying process-based models will improve predictions of biomass accumulation over time, guiding management practices. Additionally, integrating remote sensing technologies, such as LiDAR and multispectral imaging, with ground-based measurements will enable large-scale assessments of stand structure and biomass, improving the generalizability of findings. Future studies should evaluate trade-offs between biomass production and other ecosystem services, such as carbon sequestration and biodiversity conservation, to inform balanced management strategies.

Conclusion

This study highlights a key trade-off in mixed Acacia plantations: while higher stand density promotes biomass accumulation, increased species diversity and vertical heterogeneity reduces aboveground tree biomass due to intensified competition among functionally similar species. These findings suggest that monocultures or low-diversity plantations may be more effective for maximizing productivity, though this must be balanced against ecological resilience and biodiversity considerations.

From a carbon sequestration perspective, Acacia plantations play an important role in afforestation efforts, but our results indicate that species diversity does not necessarily enhance biomass accumulation or carbon storage. Future management strategies should optimize stand density and thinning regimes to balance productivity with long-term sustainability.

Further research is needed to assess whether incorporating functionally diverse species could mitigate competition effects while maintaining ecosystem stability. Expanding studies across different plantation types and environmental conditions will be crucial for developing sustainable management guidelines that integrate productivity, carbon sequestration, and biodiversity conservation.

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Author contributions DTNM, VVM, and FB conceptualized the study and formulated the research goals. DTNM, VVM, IR, and FB contributed to the methodology development, formal analysis, validation, and visualization of the results. DTNM and VVM collected and curated the dataset. DTNM wrote the original draft of the manuscript, and all authors contributed to reviewing and editing the manuscript. FB and VVM supervised the project, coordinated research activities, and acquired funding. All authors contributed to the project analysis and approved the final submitted version.

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Data availability All data generated or analyzed during this study are available upon reasonable request to the corresponding author.

Declarations

Conflict of interest The authors declare no competing interests.

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