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**Disentangling the relationship of aboveground biomass, structure and tree diversity
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Abstract

A diversification strategy of introducing two or more species is becoming increasingly prevalent in forest plantations 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 biomass - structure - tree diversity relationship in a tropical mixed-forest plantation

in Northern Vietnam to gain insight into ecosystem service provision trade-offs. The study site was located in an abandoned *Acacia mangium* and *Acacia auriculiformis* (established in 2012) plantation 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 high evenness compared to other forest plantations in the study area. A set of models was fitted and ranked to determine the relationship between aboveground biomass and structural and specific diversity. The results indicate that the Shannon index and height differentiation index were significant for both species while basal area was only significant for the *Acacia mangium* model. According to the model sensitivity analysis, aboveground biomass – and therefore carbon concentration – decrease as species diversity increases.

Key words: Tropical forests, model selection, spatial pattern, forest structure, trade-offs

Declaration

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1. Introduction

Until recently, most forest plantations only included one tree species but it is becoming more frequent to use two or more tree species during the planting phase. Plantation diversification can

also be achieved 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). Forest plantations can compensate carbon emissions efficiently by storing CO₂ in the tree biomass. Forest biomass estimation is important 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).

Vietnam is one of the few global south countries with a low level of energy consumption. Biomass energy plays a very important 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. Implementation of 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) along with 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), largely 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, 2018). 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 positive (Huang et al, 2018). 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, 2018) and various mixtures in Europe (Lopez-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 biodiversity loss on forest productivity also highlights the potential advantages of mixed species over monocultures (Liang et al. 2016a). However, other studies have found neutral effects

or even a negative relationship between aboveground tree biomass (AGB) and species diversity (Chen and Klinka 2003; Szwagrzyk and Gazda 2007; Cavard et al. 2010; Bourdier et al. 2016).

Despite the many studies on the productivity – species diversity relationship, there is still a research gap concerning the relationship between forest stand structural diversity and productivity. Stand structure can be described in terms of the stand density or vertical and horizontal tree distribution patterns. Research has found augmented structural aspects in mixed species stands, leading to higher productivity compared to monocultures (Riofrío et al. 2017), as well as a positive relationship (weak correlation) between AGB and stand structural diversity in boreal forests (Wang et al. 2011).

In Central Himalayan 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 depends on diversity, biomass yield and species identity. The relationship between tree biomass and diversity can also vary among the species analyzed. (Chen and Klinka 2003; Lindén and Agestam 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; Vila et al. 2005; Dănescu et al. 2016; Bohn and Huth 2017a; Díaz-Yáñez et al. 2017; Ercanli 2018). However, a combined analysis of species diversity and stand structure might illustrate

aboveground 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 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, forest biomass and biodiversity metrics were obtained. We hypothesized that increased levels of structural and species diversity would lead to enhanced aboveground biomass in tropical forest plantations, then tested the hypothesis at the Acacia plantation in northern Vietnam.

2. Materials and Methods

2.1 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 21°0'35.0"N and longitude 105°30'51.2"E) (Fig. 1). 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. 1). The stratigraphy of the study area consists of a clay-loam layer extending to a depth of 5 meters 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 was established within the 563 ha forest patch on the campus, using a Marteloscope design (Schuck et al. 2015). The Hoa Lac Marteloscope was established in

2018, following the installation protocol of the BioEcon Project (Bravo et al. 2018). It consists of a 100m x 100m plot divided into 16 permanent subplots or *quadrats* measuring 25 × 25 m each (Fig. 1).

To set up the Hoa Lac Marteloscope, the four outer corners were established with GPS and the corners of the 16 inner quadrats were marked. The Marteloscope is on a nearly flat area so no slope correction was needed. Species identity, diameter at breast height, total height, and the position of every tree with a diameter at breast height (dbh) of 5 cm or more was recorded. Tree Biomass (total and per compartment: stem, branches, and leaves) was calculated from previously developed allometric biomass equations; see Appendix 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). Tree component biomass values were computed for each individual tree and summed up to generate a summary of tree biomass for each quadrat and for the Marteloscope as a whole.

[FIGURE 1, insert around here]

2.2 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. 2018) (Appendix B).

- Species richness and diversity

- Simpson’s diversity index (S_m) (Simpson, E 1949): indicates the probability of any two individuals randomly selected from a large population belonging to different species.

- Shannon diversity index (Sh) (Shannon et al. 1949): reflects how abundance is distributed among the constituent species of the community.
- Berger-Parker index (D) (Berger and Parker 1970): focuses on quantifying the abundance of each species in the stand.
- Evenness index (E) (Pielou 1975): compares the actual diversity value (Shannon's index) to the maximum possible diversity value, when all species are equally common.
- Species intermingling
 - Segregation index (S) (Pielou 1961): describes the relative mixing of two species regardless of their spatial pattern. This method is based on nearest-neighbor distances and compares the observed number of mixed pairs with the number expected under random conditions.
 - Mingling index (Mi) (Füldner 1995): describes the species pattern around the reference tree.
 - Spatial diversity status (MS) (Pielou 1977): is an improved mingling index that considers both spatial mingling and the number of tree species.

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. 2000).

Spatial diversity will be examined through the analysis of vertical and horizontal spatial patterns.

- Vertical spatial pattern

- Vertical species profile (A) (Pretzsch 1995): based on the Shannon index (Shannon et al. 1949), it considers the presence of a species in different height zones along with the proportion of a species within a stand.
- Height differentiation index (TH) (Gadow 1993): measures size differences between a reference tree and neighboring trees on a continuous scale to describe the spatial distribution of tree sizes.

- Horizontal spatial pattern

- L-function (Besag 1977): defines the spatial distribution of the trees.
- Aggregation index (R) (Clark and Evans 1954): the ratio of the observed mean nearest neighbor distance in the pattern to the expected mean distance in a random tree distribution.
- Uniform angle index (W) (Gadow 1993): describes the degree of regularity in the spatial distribution of individual trees.

2.4 Data analysis: Model selection and sensitivity analysis

A set of linear models were fitted to gain insight into the relationship between stand complexity and individual tree biomass by independently defining a set of models for *Acacia mangium* and *Acacia auriculiformis* (Appendix C). Other species were not considered in the statistical analysis process due to their small sample sizes. The response variable was tree aboveground biomass, and the candidate explanatory variables were the basal area of each quadrat,

the number of trees per hectare for each quadrat and the different indexes for species richness and diversity, species intermingling and vertical and horizontal patterns (Table 1).

[TABLE 1, insert around here]

A correlation analysis was conducted to check the correlation between the explanatory variables. Only the pairs of variables with a correlation coefficient of $-0.5 \leq r \leq 0.5$ were included together in the fitted models, to avoid collinearity. The three general model structures tested are presented below (eq.1 to 3), in which β_i represents the estimated parameters and X_i represents different explanatory variables. Models were log transformed when needed to ensure a linear structure (See Appendix C for the complete structure of tested models).

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

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

$$AGB = \beta_0 \times X_1^{\beta_1} \times \dots \times X_n^{\beta_n} + \varepsilon \quad (3)$$

Optimal model selection was based on Akaike's information criterion (AIC), Bayesian information criterion (BIC), coefficient of determination (R^2) and mean square error (MSE) (Akaike 1973; Schwarz 1978; Bravo et al. 2009; Wang et al. 2011). All statistical analyses were conducted with R version 3.5.3 (R Core Team 2019). After selecting the best model, we conducted a sensitivity analysis to quantify the variability between model outputs and inputs. Specifically, we assessed the sensitivity of tree aboveground biomass to fluctuations in parameters and the data used to build the model. 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 predictor variables and tree biomass.

223 **3. Results**

224 **3.1 Site description**

225 Seven different tree species were found in the Hoa Lac Marteloscope (446 trees/ha plus 61
226 standing dead trees/ha) including *Acacia mangium*, *Acacia auriculiformis*, *Eucalyptus*
227 *camaldulensis*, *Senna siamea*, *Litsea glutinosa*, *Aporosa villosa* and *Averrhoa carambola*. Of
228 these, *Acacia mangium* and *Acacia auriculiformis* were the two most abundant species, with 300
229 and 108 individuals respectively (Table 2). The standing dead tree species could not be identified
230 due to their level of decay.

231 **[TABLE 2, insert around here]**

232 **3.2 Stand diversity**

233 The Shannon Index, Simpson diversity index, evenness index, and Berger-Parker index were
234 calculated for each quadrat, as presented in Fig. 2. The Shannon Index, which indicates species
235 richness and evenness, ranged from 2.55 to 3.71 with a median value of 3.43. Only 25% of the
236 Shannon index values were below 3.22, indicating a mean abundance of more than 3 species.
237 Similarly, the Simpson index ranged from 0.90 to 0.97, with a median of 0.96, indicating high
238 diversity in the study area. As mentioned earlier, the Shannon index also reflects species evenness:
239 as species richness and evenness increase, diversity – as quantified by the Shannon index – also
240 increases. The evenness index result also clearly indicated high or complete evenness in the
241 community, with values ranging between 0.90 and 1. The Berger-Parker index illustrated the
242 importance of the most abundant species, with values ranging from 1.156 to 2.21.

243 **[FIGURE 2, insert around here]**

244 Tree distribution, as depicted by the mingling index, varied considerably throughout the 16
245 quadrats (Fig. 3). A higher component in the 0.25-value class can be observed in quadrats 2, 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 greater prevalence of weak mingling; or low small-scale mixture. However, small monospecific groups were more present in quadrats 8 and 12, which on the mingling index had 0-value. We observed a general mingling value distribution trend towards monospecific groups in quadrats 2, 7, 8, 11, 12, 13, 14 and 16; towards mean mingling in quadrats 1, 4, 6, 10 and 15; and towards multi-specific groups in quadrats 3, 5 and 9.

[FIGURE 3, insert around here]

The spatial diversity index (MSi) measures tree species richness along with an important spatial characteristic of each quadrat. The reference trees in quadrats 7, 11, 13, 14 and 16 were more likely to have neighbors of the same species (Fig. 4a), as reflected in the low MSi value. Meanwhile, quadrats 3, 6, 9 and 10 had a high MSi 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. 4b), despite the presence of outliers with high values in certain quadrats. Examination of the TH class based on the two most abundant species (Fig. 5) revealed that more than 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.

[FIGURE 4, insert around here]

The L-function line deviates very slightly from the expected values (red-line) (Fig. 6); when r is small, the actual values are just below the expected values. While 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 small, it would be very easy to mistakenly interpret this L-function line as random, uniform or clumpy distribution. Therefore, an extra test from the Clark and Evans aggregation index (R) was needed. For the entire Marteloscope, $R = 1.110826$ indicated random distribution. For each quadrat, R ranged from 0.8248 to 1.199, 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.

[FIGURE 5, insert around here]

[FIGURE 6, insert around here]

3.3 Model selection

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 3). The R^2 was low for all models, indicating a weak relationship between AGB and the predictor variables. Despite the low goodness-of-fit, low R^2 values were acceptable because the fitted models were not intended to predict fit but to explain the relationship between aboveground biomass and species diversity. After comparing AIC, BIC, R^2 and MSE, Model (1.1) for *Acacia mangium* and Model (2.1) for *Acacia auriculiformis* were selected as the optimal models for explaining the relationship between tree AGB and species diversity.

[TABLE 3, insert around here]

The results of the sensitivity analysis for the selected models (1.1) and (2.1) indicate a negative relationship between AGB and species diversity, as represented by a given set of values

for the basal area of each quadrat (G) and the height differentiation index (TH). The stand-level relationship between yield and density is based on the empirical law (Assmann et al. 1970) that yield increases with increasing density until it reaches a plateau and remains stable, then decreases with increasing density. The diversification of forest plantations, at the time of planting and through seedlings incorporated from nearby forests, allows for greater functional complexity in the soil. This facilitates more efficient carbon storage and nutrient supply to the trees (Meier and Bowman 2008; Lehmann et al. 2020). However, beyond a certain diversity level a reduction in yield can be observed because carbon sequestration was derived from tree AGB. So species diversity will have a similar negative effect on carbon storage in *Acacia mangium* and *Acacia auriculiformis*. Goodness of fit for the basal area of each quadrat only occurred in the selected model for *Acacia mangium*, which was probably due to species distribution. In the study plot, higher levels of species diversity predicted lower levels of biomass. Accordingly, increased differences in tree height among individual trees in the stand also coincided with lower biomass levels (Fig. 7).

[FIGURE 7, insert around here]

4. Discussion

The species diversity-productivity model developed in this study holds substantial value in the context of contemporary efforts to refine tools and models for quantitative silviculture, particularly in mixed stands. The information provided here can lead to quantitative improvements in forest productivity and the potential for assessing the efficiency of ecosystem functions and services. The study directly addresses current concerns about the scarcity of information for mixed plantations and the surge of interest to understand and refine the dynamics of these forest systems.

While the results of the sensitivity analysis of the models fitted for *Acacia mangium* and *Acacia auriculiformis* show that species richness and diversity negatively affected tree AGB 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. (2016b) highlighted the negative impact of biodiversity 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 AGB 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 located in several types of forest 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 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, 2015 and 2017). This general trend of a positive biodiversity-productivity relationship has been confirmed on a global scale (Liang et al. 2016a) by combining

data across different forest biomes (Global Forest Biodiversity permanent sample plots, <https://www.gfbinitiative.org/>). This positive correlation between species diversity and productivity might result from a niche interpretation in which a greater species diversity means resources are used more effectively due to their complementary in space and time (del Río et al. 2017; Williams et al. 2017).

However, it is not unusual to find a lack of positive correlation between species diversity and biomass. Our study indicates a negative relationship between aboveground biomass and carbon concentration in an unmanaged mixed-forest plantation. Authors working in diverse terrestrial ecosystems have reported analogous outcomes. Szwagrzyk and Gazda (Szwagrzyk and Gazda 2007) found a similar relationship trend in natural stands in Central Europe, as did Suo et al. (2008) for two types of *Quercus* forest in China. Although the evenness index was included in the candidate model, no relationship with AGB was found due to the roughly similar species proportions in our study area. The Shannon index, which accounts for both abundance and evenness of the species, presented negative correlations with tree AGB. Zhang et al. (2012) found that species evenness together with species richness was able to explain forest productivity. Stand density – the total number of trees per hectare – can also significantly impact diversity-productivity relationships, along with stand biomass and basal area. When stand density is very low, interactions between trees – whether competitive or complementary – will be weak. Some studies have shown that stand density can be a stronger determinant of productivity than species richness (Paquette and Messier 2011; Vilà et al. 2013). In contrast, the Shannon index and height differentiation index were significant for both species in our study but only the selected model for *Acacia mangium* showed goodness of fit for the basal area of each quadrat. This was probably due to the distribution of each species. However, the biomass-diversity relationship can be affected by

various 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. Shifting the approach from diversity in species identity to diversity in functional traits could lead to results more consistent with the literature that associates higher diversity with higher biomass growth and yield (Roscher et al. 2012; Hisano and Chen 2020).

Carbon sequestration in forests is acknowledged as having a relevant role in reducing the effect of global climate change. However, carbon sequestration is usually not the only objective in forest management. Vihervaara et al. (2012) made the noteworthy observation that local stakeholders have not sufficiently prioritized assessment of a plantation's effects on biodiversity and ecosystem degradation, particularly in relation to carbon cycles, despite their profound regional and global impacts and implications. Forest managers must also consider other ecosystem services from different perspectives – carbon storage, biodiversity conservation, local climate regulation, timber production, cultural, and aesthetic value – in their search for adequate management regimes (Bellassen and Luyssaert 2014; Ruiz-Peinado et al. 2017). Some studies affirm that unmanaged forests may store more carbon than managed forests, depending on forest stand conditions, structure, species composition, age, etc. (Krug et al. 2012; Pukkala 2017; Ruiz-Peinado et al. 2017). Moreover, forests commonly face challenges to concurrently generate multiple positive ecosystem services, which involve trade-offs and competing functions. Maximizing one ecosystem service may lead to notable declines in other services (Bennett et al. 2009). Therefore, understanding multiple forest attributes is crucial for identifying the impacts of forest management on different forest ecosystem services. Our research outcomes suggest that

promoting *Acacia* monocultures rather than mixed stands would increase tree biomass but reduce species diversity. Such changes in stand species composition can lead to a huge trade-off between productivity and biodiversity.

Our result (negative relation between diversity and yield), along with prior research findings to the contrary (Jactel et al. 2018), opens up new questions about forest diversity in relation to carbon sequestration and biomass yield and how to identify optimal diversity levels for both (Jacob et al. 2010; Bohn and Huth 2017c). Further research is needed on diversity-density-yield relationships to understand their dynamics and interaction patterns in tropical forest plantations. Disentangling cause and effect is integral to the challenge of maintaining species diversity while also favoring productive stands.

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Table 1: Descriptive statistics for the response variable and candidate explanatory variables

Variables	Mean	Max	Min	St.Dev
AGB	218.26	3010.28	6.92	258.84
G	20.628	43.233	11.057	5.916
N	546.15	720.00	272.00	126.66
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
R	1.08	1.20	0.82	0.10
Mi	0.48	1.00	0.00	0.33
MS	0.19	0.60	0.00	0.15
W	0.50	1.00	0.00	0.22
S	0.22	1.00	-0.03	0.17
A	2.46	3.42	0.00	0.59
TH	0.26	0.91	0.04	0.14

Response variables: AGB: tree aboveground biomass (kg); G: basal area of each quadrat (m²/ha)
Candidate explanatory variables: 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.

Table 2: 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			
<i>Acacia mangium</i>	300	20.61	19.74	78.62	6.05	15.06	14.90	24.00	1.70	65.71	32.86	120.45
<i>Acacia auriculiformis</i>	108	22.07	21.96	49.97	6.68	15.24	15.00	22.50	6.00	23.70	11.85	43.45
<i>Eucalyptus camaldulensis</i>	15	17.76	18.14	30.88	7.00	15.41	13.50	22.00	8.50	2.05	1.02	3.75
<i>Senna siamea</i>	18	38.87	39.15	75.12	15.92	12.00	11.75	16.00	7.50	13.64	6.82	25.00
<i>Litsea glutinosa</i>	3	11.46	11.46	15.60	7.32	8.60	6.80	12.50	6.50	0.15	0.08	0.28
<i>Aporosa villosa</i>	1	11.46	-	-	-	4.70	-	-	-	0.02	0.01	0.04
<i>Averrhoa carambola</i>	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 biomass of each species (tons); C: weight of carbon of each species (tons); CO₂: weight of carbon dioxide sequestered of each species (tons)

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Table 3: The 10 best-fitted models for *Acacia mangium* and *Acacia auriculiformis*

No.	Model	β_0	β_1	β_2	β_3	p-value	R^2	MSE	AIC	BIC
<i>Acacia mangium</i>										
1.1	$AGB = e^{\beta_0 + \beta_1 G^2 + \beta_2 Sh^2 + \beta_3 TH^2}$	6.0982	0.0011	-0.1135	-1.5549	0.0965	<0.0001	0.5754	691.7097	710.0246
1.2	$AGB = e^{\beta_0 + \beta_1 G^2 + \beta_2 Sh + \beta_3 TH^2}$	7.2306	0.0011	-0.7249	-1.5399	0.0950	<0.0001	0.5763	692.2072	710.5220
1.3	$AGB = e^{\beta_0 + \beta_1 G^2 + \beta_2 Sh^{0.5} + \beta_3 TH^2}$	9.5096	0.0011	-2.5781	-1.5319	0.0941	<0.0001	0.5769	692.4921	710.8070
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	<0.0001	0.5775	692.8318	711.1466
1.5	$AGB = e^{\beta_0 + \beta_1 G^2 + \beta_2 Sh + \beta_3 \frac{1}{A}}$	8.1637	0.0010	-0.8762	-1.2104	0.0915	<0.0001	0.5785	693.3443	711.6591
1.6	$AGB = e^{\beta_0 + \beta_1 G^2 + \beta_2 \frac{1}{Sh} + \beta_3 TH^2}$	2.6432	0.0011	7.0914	-1.5056	0.0911	<0.0001	0.5788	693.4847	711.7995
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	<0.0001	0.5791	693.6558	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	<0.0001	0.5796	693.9139	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	<0.0001	0.5806	694.4456	712.7604
1.10	$AGB = e^{\beta_0 + \beta_1 G^2 + \beta_2 Sh^{0.5} + \beta_3 \frac{1}{\sqrt{A}}}$	11.3680	0.0010	-3.1122	-1.5035	0.0872	<0.0001	0.5812	694.7653	713.0802
<i>Acacia auriculiformis</i>										
2.1	$AGB = e^{\beta_0 + \beta_1 TH^2 + \beta_2 Sh^2}$	6.7131	-4.1277	-0.1248	-	0.1697	0.0001	0.6928	272.1988	282.5390
2.2	$AGB = e^{\beta_0 + \beta_1 TH^2 + \beta_2 Sh}$	7.8752	-4.0985	-0.7675	-	0.1693	0.0001	0.6932	272.2584	282.5985
2.3	$AGB = e^{\beta_0 + \beta_1 TH^2 + \beta_2 \frac{1}{Sh}}$	3.2154	-4.0410	6.9505	-	0.1672	0.0001	0.6949	272.5302	282.8704
2.4	$AGB = e^{\beta_0 + \beta_1 TH^2 + \beta_2 \sqrt{N}}$	7.1477	-4.2258	-0.3151	-	0.1658	0.0001	0.6961	272.7099	283.0501
2.5	$AGB = e^{\beta_0 + \beta_1 TH^2 + \beta_2 Sm^2}$	11.277	-3.9718	-6.5268	-	0.1656	0.0001	0.6962	272.7349	283.0751
2.6	$AGB = e^{\beta_0 + \beta_1 TH^2 + \beta_2 Sm}$	16.9614	-3.9665	-12.1873	-	0.1653	0.0001	0.6965	272.7778	283.1180
2.7	$AGB = e^{\beta_0 + \beta_1 TH^2 + \beta_2 N^2}$	5.9042	-4.2948	-0.0005	-	0.1616	0.0001	0.6996	273.2468	283.5870
2.8	$AGB = e^{\beta_0 + \beta_1 TH^2 + \beta_2 \sqrt{E}}$	26.7711	-3.6725	-21.9943	-	0.1541	0.0002	0.7058	274.2061	284.5463
2.9	$AGB = e^{\beta_0 + \beta_1 TH^2 + \beta_2 E}$	16.1278	-3.6734	-11.3612	-	0.1541	0.0002	0.7058	274.2122	284.5524
2.10	$AGB = e^{\beta_0 + \beta_1 TH^2 + \beta_2 E^2}$	10.8051	-3.6752	-6.0591	-	0.1540	0.0002	0.7059	274.2263	284.5665

AGB: tree aboveground 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 (m²/ha); A: vertical species profile

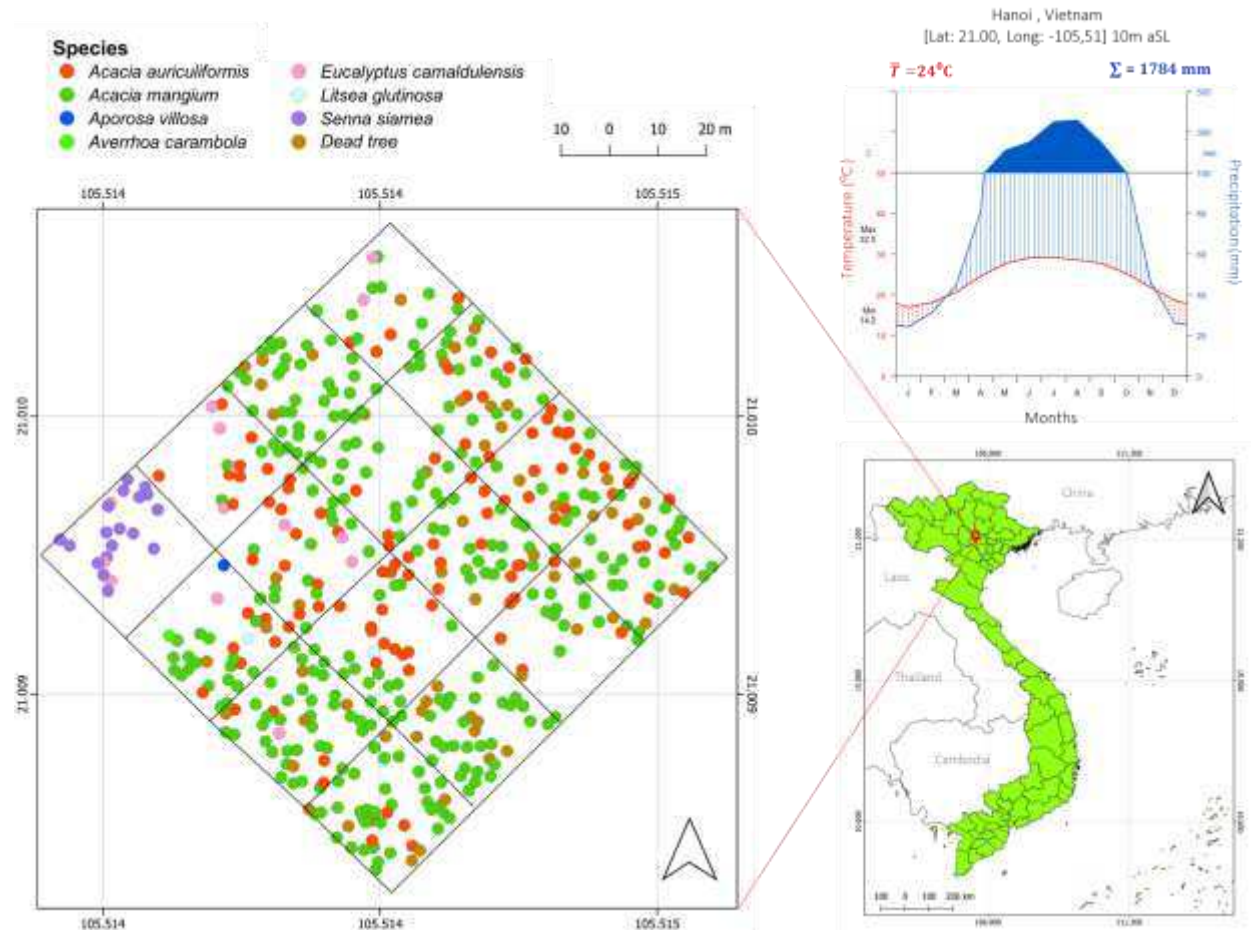
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670 **Fig. 1:** Hoa Lac Marteloscope study area location in northern Vietnam (21°0'35.0" N and 105°30'51.2"E). The climate
671 diagram displays monthly average temperature in degrees Celsius (°C) (red line) and precipitation in millimeters (mm)
672 (blue line), using Walter and Lieth climate diagram standards. Data for 1970-2000 was obtained from the gridded
673 dataset of Climatic Research Unit (CRU) at the University of East Anglia (<https://crudata.uea.ac.uk/cru/data/hrg/>).
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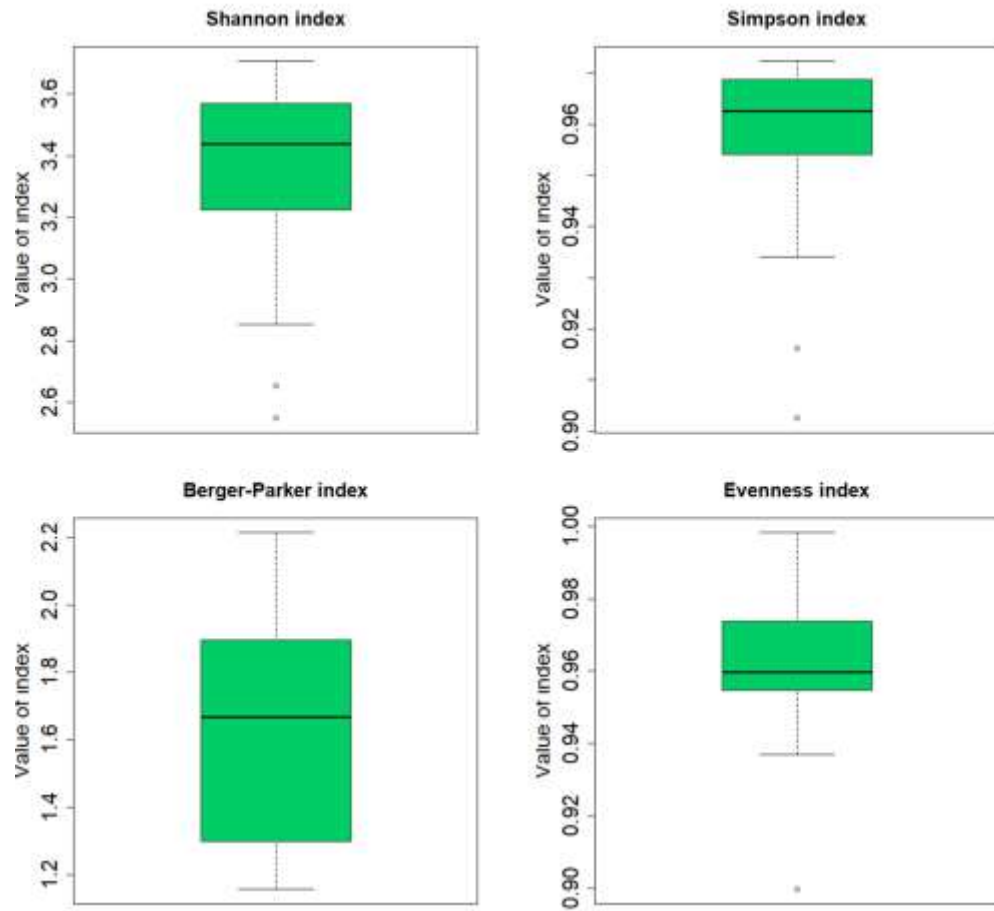


Fig. 2 Stand diversity indices for the Marteloscope

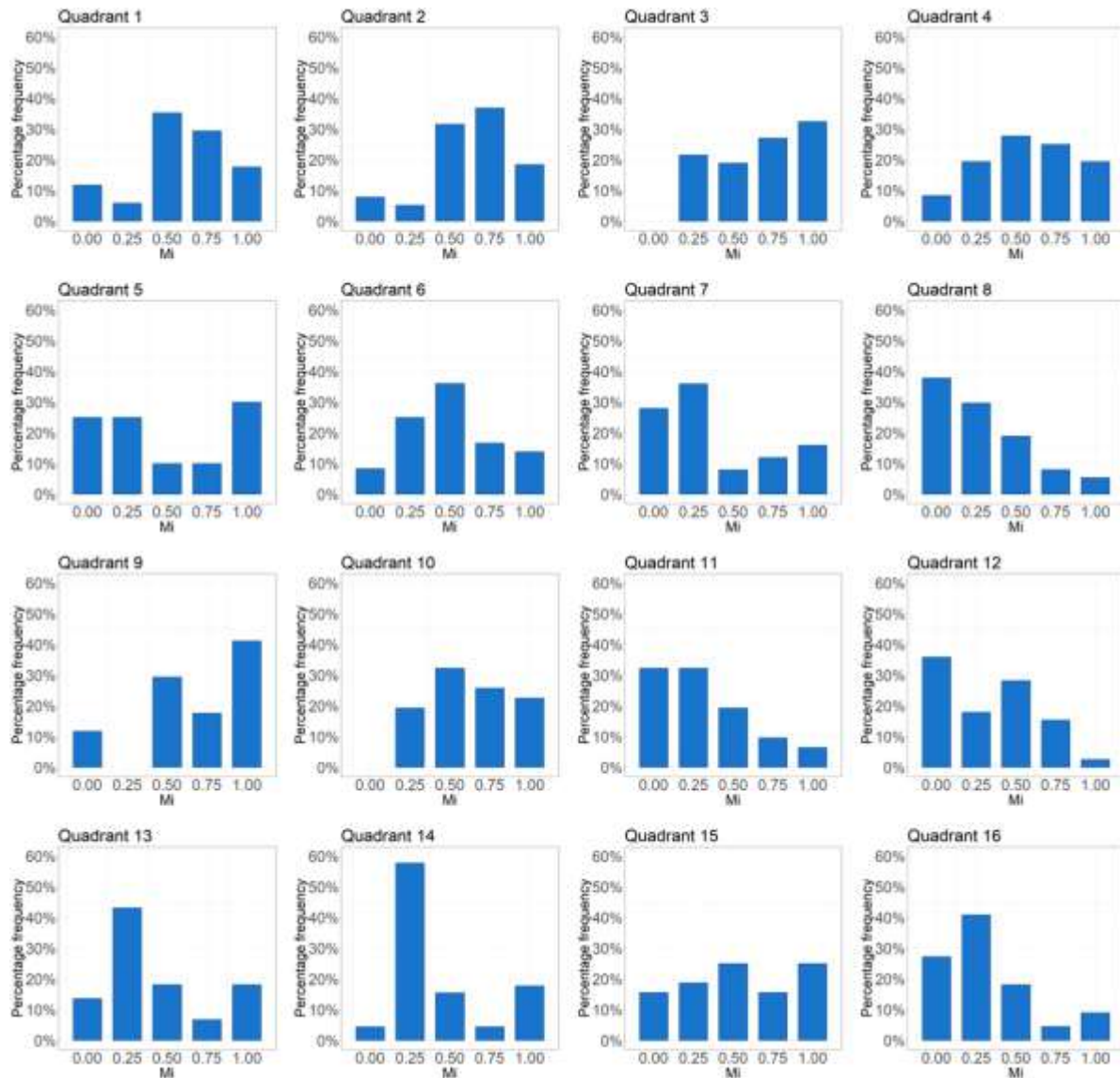


Fig. 3 Percentage frequency distribution of the mingling index (Mi) in each quadrat

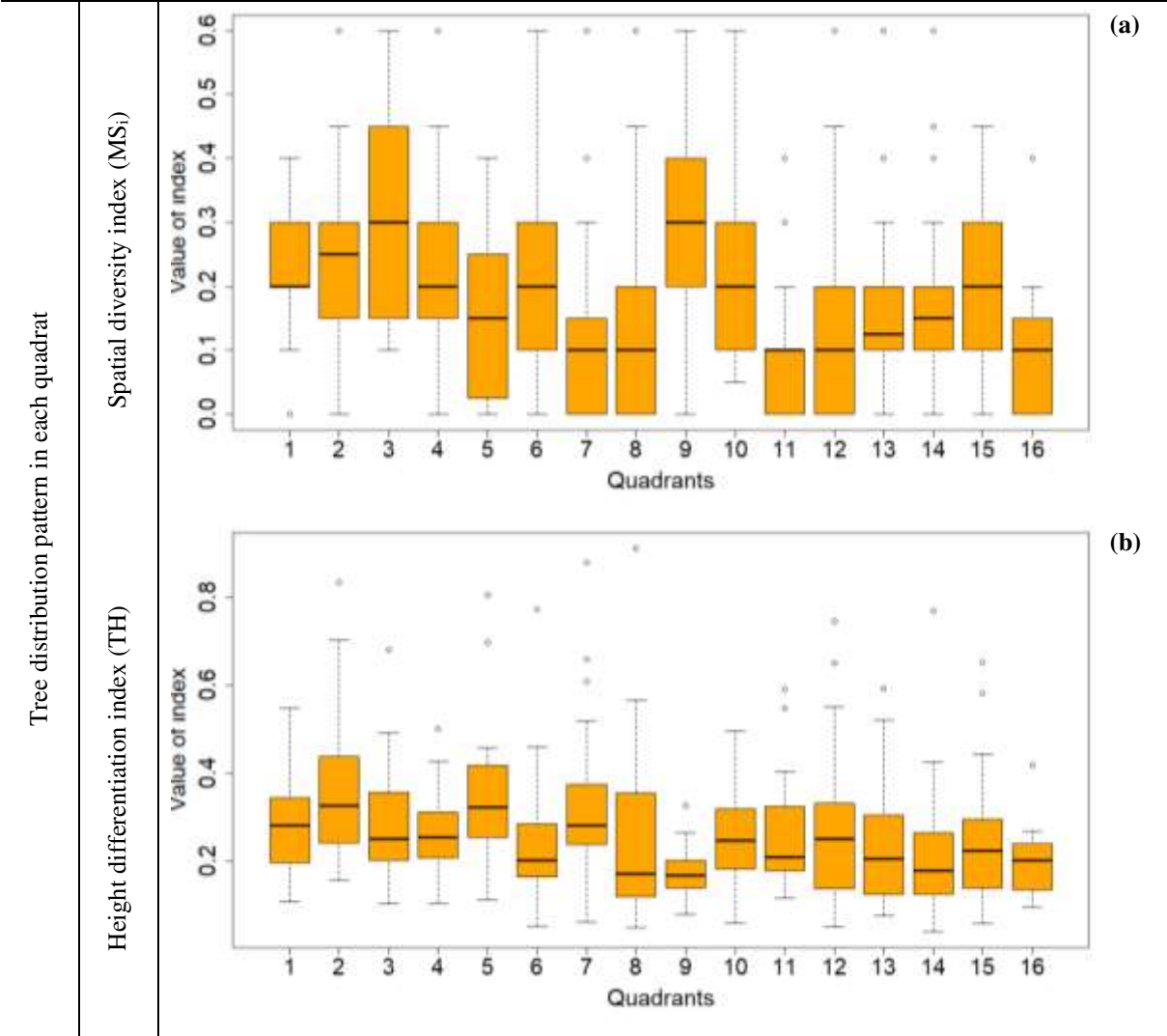


Fig. 4: Tree distribution pattern at the study site

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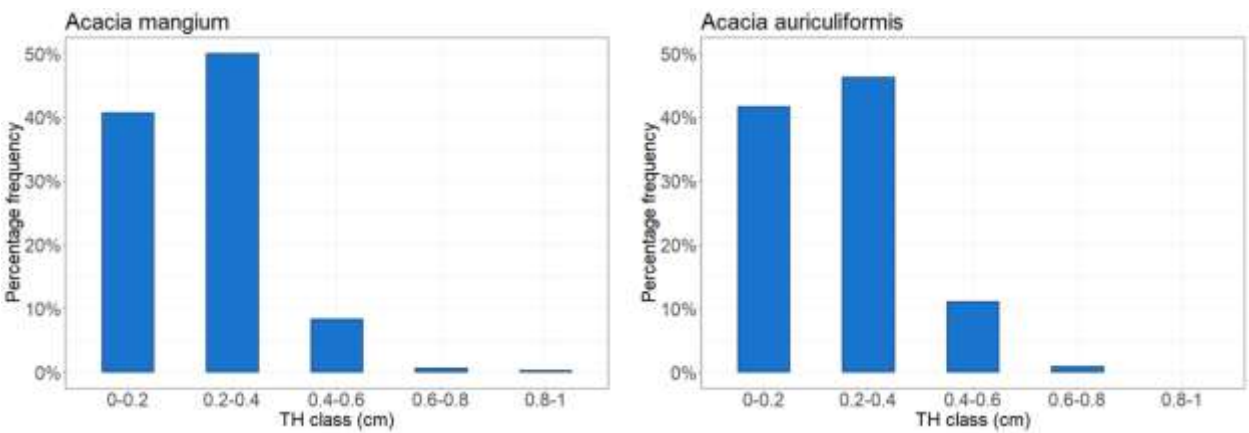


Fig. 5: TH classes of the two most abundant species

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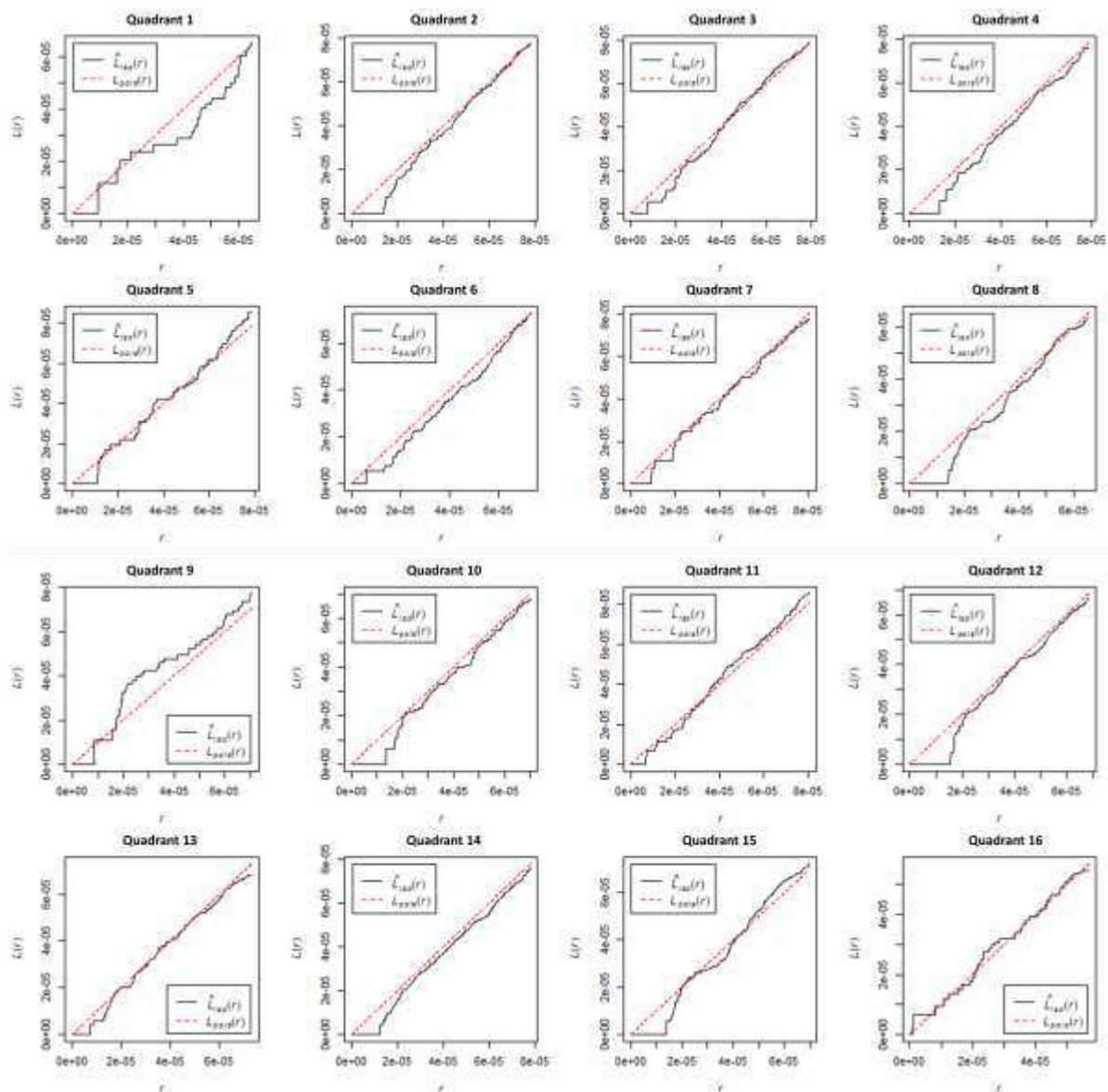


Fig. 6: L – function for all quadrats

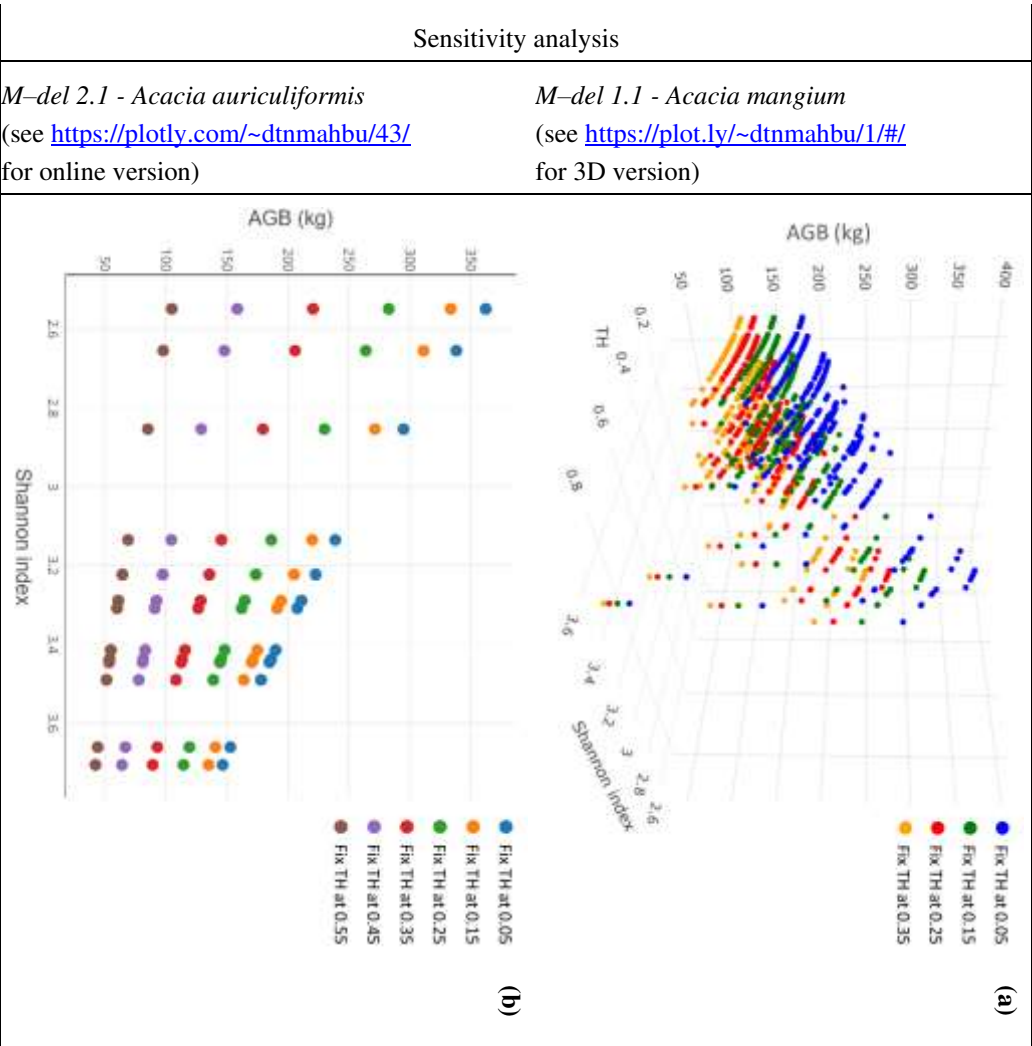


Fig. 7. Sensitivity analysis of model (1.1) and (2.1)

Supplementary Files

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- [VietnamBiomassSupplementaries.docx](#)