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Effects of species and tree size diversity on above-ground biomass in diverse heterogeneous tropical evergreen forests, Quangbinh Province, north central Vietnam

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Abstract The relationships between species diversity and size structure complexity on above ground biomass (AGB) have theoretical and practical applications for biodiversity conservation and sustainable forest management. The relationships become more complex in the high-species diversity of tropical forests and heterogeneous environmental conditions. To disentangle the complicated relationships, structural equation models were applied to examine the relative effects of species and tree size diversity on above ground biomass under different topographical conditions of two tropical evergreen forest stands. Our results showed that: (i) species diversity contributes greater to AGB in the forest stand under homogeneous topography. (ii) Structural diversity positively affected AGB in the heterogeneous topographical stand. (iii) Slope revealed a negative effect on species diversity but positive effects on structural diversity and AGB in both studied plots. We concluded that maintaining high-stand structural diversity enhances above ground biomass and local topographical conditions constrain the relationship between species and size diversity in the study area.

Keywords: species diversity, structural diversity, above ground biomass, local topography.

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Introduction

Tropical forests are terrestrial hotspots of the Earth, bearing 96% of the world's tree species and 25% of global carbon storage (Beer et al. 2010, Poorter et al. 2015), a substantial portion of this carbon amount is stored in above ground biomass (AGB) of woody trees. While it is well documented about distribution of AGB across forest ecosystems (Chisholm et al. 2013, Fotis et al. 2018), ecological mechanisms regulating AGB in each forest ecosystem are still poor understood. Both biotic and abiotic factors can distincly impact to AGB of a forest stand such as stand structure (Ali et al. 2016), species diversity (Dănescu et al. 2016, Ali et al. 2017), microclimate and soil (Murphy et al. 2015, Ali et al. 2019), topography (de Castilho et al. 2006, Jucker et al. 2018), spatial scale (Rodrigues et al. 2020). The disentangling relative importance of these forest attributes and environmental drivers on forest above ground biomass has challenged ecologists (Shen et al. 2016, Sullivan et al. 2017, Kothandaraman et al. 2020), especially under climate change and biodiversity loss by anthropogenic activities (Thompson et al. 2009, Pyles et al. 2018, Imbert et al. 2021).

Species richness may enhance forest productivity in general or above ground biomass via the niche complementarity effect, where different species' niches allow them to access more available resources, enhancing total biomass (Tilman et al. 2001, Niklaus et al. 2017). Those species may facilitate the general performance of the community through individual species' performance due to efficient habitat utilization (Loreau et al. 2001). In addition, species diversity may also increase the total productivity of the community via selection effects such as interspecific competition, in which highly productive species contribute to the community by chance (Loreau & Hector 2001, Poorter et al. 2015, Li et al. 2018). The relationship between species diversity and above ground biomass can be explained as higher species diversity leading to faster biomass accumulation in forest communities (Chisholm et al. 2013).

Structural attributes of a forest community make the community structure complex and multi-layered, especially in tropical rain forests, via tree diameter, height, tree density and leaf area index variations. Structural diversity may largely vary depending on species identity within and between tree communities due to forest disturbance and environmental conditions; therefore it may impact on community biomass and ecosystem processes differently. The complicated forest structure may also facilitate niche occupancy for efficient resource use of light, nutrients and water, thus promoting growth related resources and biomass production (Ali et al. 2016, Forrester et al. 2016, Brun et al. 2019, Tan et al. 2021). Previous studies have found various effects, such as direct, independent impacts, of species diversity and stand structure on above ground biomass (Dănescu et al. 2016, Li et al. 2018, Yuan et al. 2018, Ali et al. 2019).

However, the direct and indirect impacts of species diversity and stand structural diversity under different environmental conditions have not been documented. Abiotic factors (e.g., topography, climate and soil nutrients) are related to the variation of above ground biomass because it is well-known that climate and soil properties vary along an elevational gradient (Liang et al. 2016, Poorter et al. 2017). Topographic factors, such as elevation, slope and aspect, directly influence forest structure and diversity and indirectly on above ground biomass (Jucker et al. 2018). Local topographic differences can alter microclimate and soil properties, thus impacting species distribution, abundance and structural attributes of forest tree species (Jucker et al. 2018, Rodrigues et al. 2020).

In this study, we aim to examine the relative influence of species diversity and structural diversity on above ground biomass under heterogeneous topographical conditions of tropical evergreen forests in north-central Vietnam. Structural equation models were constructed to analyze combined and separate data of two 2-ha plots. We asked: (i) how do species diversity and structural diversity regulate above ground biomass of the two plots? (ii) How are these relationships affected by topographical variables? We hypothesize that higher diverse and complex stand structures drive higher above ground biomass along local-scale slope variation.

Materials and Methods

Study area and field measurements

The study area is located in a tropical evergreen forest belonging to Quangbinh province in North Central Vietnam (Figure 1). This region is characterized as a tropical monsoon with an average annual temperature of 23.5°C and an average annual precipitation of about 3000 mm. The rainy season lasts from September to February, while the dry season is from March to August.

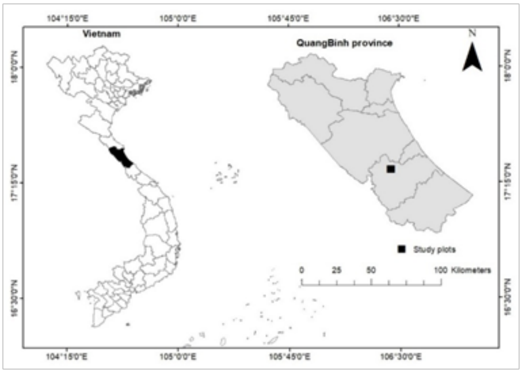

Figure 1 Locations of study region and the two studied plots.

The two 2-ha (100 x 200 m) study plots, P1 (17°20'11" N, 106°26'30" E) and P2 (17°20'15" N, 106°26'24" E) were designed and subdivided into two grid systems of 200 (10 m x 10 m) subplots for measuring tree properties and topographic data (shown in table 1). All tree individuals with a diameter at breast height (dbh) ≥ 2.5 cm were tagged, identified, geo-referenced and recorded their biophysical characteristics (i.e., species, dbh by using tape to the nearest 0.1 cm and height by using Blume-Leiss hypsometer to the nearest 0.5 m). Relative tree positions (x, y) and the topographical variables such as elevation, slope and aspect were recorded in each subplot using Garmin 60s GPS (Global Positioning System), laser distance meter (Leica Disto D2) and Suunto compass KB-14/360R. The elevation was calculated using the average values of each subplot's four corners. The slope was calculated from the mean angular deviation from the horizontal of four triangular planes by joining the three corners of the subplots. The two plots were adjacent, identically owned dominant tree species such as *Ormosia balansae*, *Garuga pierrei*, *Bursera tonkinensis*, *Tarrietia javanica*, *Paviesia annamensis*, and *Litsea glutinosa*, however their topographical conditions were distincly different (Table 1).

Data analysis

Species and structural diversity

For each subplot, we calculated species diversity indices containing:

Species richness (Rs):

$$\mathrm{Rs} = \mathrm{Ns} \quad (1)$$

Shannon index (Hs):

$$\mathrm{Hs} = -\sum_{i=1}^{Ns} \mathrm{n}_i \; x \ln(\mathrm{n}_i) \quad (2)$$

Evenness index (Es):

$$\mathrm{Es} = \mathrm{Hs}/\ln(\mathrm{Ns}) \quad (3)$$

Strutural diversity indices including:

Shannon index (Hd):

$$\mathrm{Hd} = -\sum_{j=1}^{Nd} \mathrm{n}_j \; x \ln(\mathrm{n}_j) \quad (4)$$

Evenness index (Ed):

$$\mathrm{Ed} = \mathrm{Hd}/\ln(\mathrm{Nd}) \quad (5)$$

Coefficient of variation (CvD):

$$\mathrm{CvD} = \frac{sd_{DBH}}{mean_{DBH}} \text{ for tree DBH} \quad (6)$$

where, ni- the individual number of the ith species; Ns- the total number of species in a subplot; nj- the individual number of the jth diameter class; Nd – the total number of the diameter class.

Above Ground Biomass

The Above Ground Biomass (AGB) of individual trees was calculated based on allometric equation of Chave et al. (2014)

suggested by Hai et al. (2020) for such forest type in central Vietnam region:

AGB = 0.0673 x (ρ x DBH^2 x H)$^{0.976}$ where DBH – tree diameter at breast height (cm), H – tree height (m) and ρ - species' wood density (g/cm^3).

The wood-specific density is obtained for the observed species/genera from various resources (Zanne et al. 2009, Van Con et al. 2013, Huy et al. 2016). In cases wood density for a species was unavailable, mean wood-specific density of its genus was used.

Structural equation model

To evaluate the complicated relationship between diversity and above-ground biomass in the study forest plots, we applied a structural equation model (SEM). The biotic and abiotic data of the two plots were analyzed separately to examine the effects of topographical factors and then combined to study the general effect of topography in the overall SEM.

The direct effects of species diversity and structural diversity and indirect effects of species diversity through structural diversity on AGB were examined, as shown in Figure 2. The effect of the latent topographical factors, including elevation, slope and aspect, was also quantified. Total basal area of subplots was included in the model due to commonly positive relationship with species diversity, structural diversity, and AGB (Slik et al. 2010, Ali et al. 2016). The path coefficients between variables were fitted by the maximum likelihood chi-square (χ^2) and standardized root means square residual – SRMR. The Comparative fit index – CFI and Root Mean Square Error of Approximation - RMSEA were used to evaluate a fitting model. CFI > 0.95, RMSEA < 0.08 and SRMR < 0.05 suggest a good fit.

All calculations were performed in R version 4.2.0. The diversity indices were calculated by using the package 'vegan' (Oksanen et al.

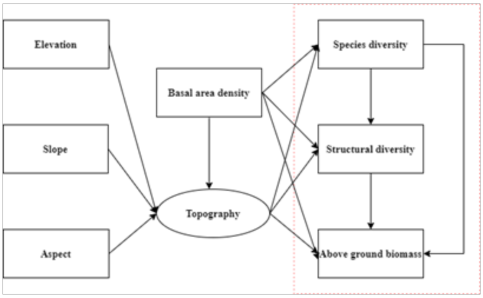

Figure 2 The theoretical framework of the structural equation model.

Table 1 Characteristics of most abundant species in P1 and P2.

No.	Tree species	P1			P2			Shade tolerance
		N	DBH (cm)	IVI (%)	N	DBH (cm)	IVI (%)	
1	*Garuga pierrei*	282	10.08 ± 10.89	8.98	232	11.30 ± 13.26	7.72	Tolerant
2	*Tarrietia javanica*	383	5.62 ± 6.39	7.28	330	4.52 ± 3.58	5.14	Intolerant
3	*Ormosia balansae*	138	17.05 ± 12.97	7.26	187	14.75 ± 10.81	6.60	Intolerant
4	*Bursera tonkinensis*	384	6.15 ± 4.16	6.72	253	6.67 ± 4.12	4.41	Medium
5	*Paviesia annamensis*	240	9.18 ± 7.64	6.02	239	6.94 ± 4.86	4.32	Intolerant
6	*Litsea glutinosa*	229	8.06 ± 6.21	4.96	264	8.26 ± 6.70	5.49	Intolerant
7	*Castanopsis indica*	168	10.21 ± 8.27	4.65	-	-		Intolerant
8	*Polyalthia nemoralis*	303	5.02 ± 1.77	4.58	244	5.53 ± 1.88	3.78	Intolerant
9	*Syzygium wightianum*	179	9.36 ± 7.04	4.40	81	11.56 ± 8.17	1.54	Intolerant
10	*Erythrophfloeum fordii*	63	18.52 ± 15.35	3.96	-	-	-	Medium
11	*Mallotus kurzii*	265	4.01 ± 0.98	3.76	114	3.71 ± 0.73	1.63	Intolerant
12	*Amoora dasyclada*	148	7.99 ± 6.73	3.28	96	8.89 ± 6.93	2.08	Medium
13	*Cinnamomun bejolghota*	100	10.71 ± 9.25	3.00	267	13.01 ± 10.59	8.51	Intolerant
14	*Gironniera Subaequalis*	92	9.71 ± 6.65	2.27	137	11.19 ± 9.28	3.73	Medium
15	*Endosperrmun sinensis*	54	11.77 ± 13.18	2.14	83	21.67 ± 13.33	4.63	Intolerant
16	*Garcinia oblongifolia*	121	6.23 ± 4.08	2.11	67	6.22 ± 3.48	1.11	Tolerant
17	*Canarium album*	-	-	-	155	11.03 ± 6.04	3.68	Intolerant
18	*Koilodepas hainanense*	104	5.83 ± 2.61	1.68	80	8.41 ± 4.52	1.54	Tolerant
19	*Cassine glauca*	74	8.41 ± 5.51	1.59	89	8.69 ± 7.66	1.97	Tolerant
20	*Litsea vang*	71	6.54 ± 3.30	1.27	76	8.72 ± 4.67	1.5	Intolerant
21	*Symplocos laurina*	55	9.31 ± 5.61	1.25	145	11.81 ± 6.86	3.71	Intolerant
22	*Engelhardtia roxburghiana*	-	-		63	28.78 ± 11.91	4.84	Tolerant

Note: N - number of individuals, IVI - Important Value Index, (relative abundance + relative basal area)/2, expressed as percentage proportion. DBH -diameter at breast height (mean ± standard deviation)

2015). The SEM was analyzed by using the package 'Lavaan' (Rosseel 2012).

Results

Diversity and AGB in the two study plots

Both plots shared 47 same species, with the most abundant species as *Ormosia balansae* (Fabaceae), *Garuga pierrei*, *Bursera tonkinensis* (Burseraceae), *Tarrietia javanica* (Malvaceae), *Paviesia annamensis* (Sapindaceae), and *Litsea glutinosa* (Lauraceae). In total, 3732 trees belonging to 61 species in P1 and 3698 trees belonging to 52 species in P2 were recorded, respectively (Table 1).

Table 2 Characteristics of diversity indices and topographical variables in the study plots.

Prop	P1			P2		
	Range	Mean	SD	Range	Mean	SD
Rs	5-18	11.39	2.39	5-19	11.48	2.68
Ds	0.51-0.92	0.87	0.05	0.69-0.93	0.88	0.03
Hs	0.18-2.73	2.22	0.36	0.19-2.86	2.29	0.29
Es	0.51-0.97	0.85	0.07	0.55-1.00	0.88	0.06
Dd	0.16-0.80	0.63	0.09	0.17-0.83	0.65	0.14
Hd	0.36-1.77	1.26	0.21	0.36-1.92	1.30	0.33
Ed	0.38-0.99	0.72	0.10	0.46-1.84	0.83	0.22
CvD	0.14-1.87	0.91	0.26	0.41-1.64	0.89	0.24
EL (m)	119-148	133.9	6.49	137.5-184.5	160.67	11.12
SL (°)	5-40	20.22	6.63	5-45	26.61	7.55
AS (°)	0-180	87.51	55.60	0-180	91.07	48.08
BA (m^2)	0.01-1.14	0.24	0.16	0.02-0.89	0.32	0.18
AGB (kg)	5.3-1124.2	155.92	14.09	9.1-850.4	215.24	154.94

Note: Prop: properties; El: elevation; SL: slope; AS: aspect; BA: basal area.

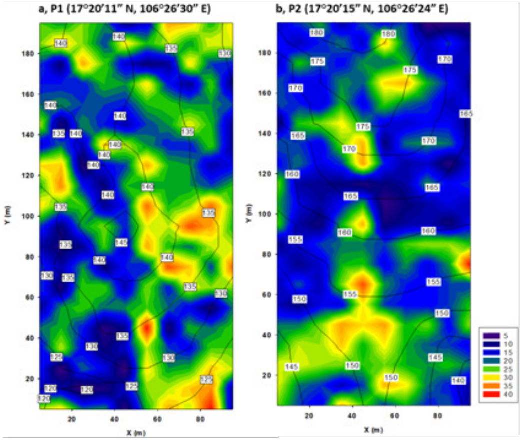

Figure 3 Elevation contour and tree density in the two 2-ha plots P1 (a) and P2 (b). Colors indicate tree density of subplots.

The species and structural diversity indices and topography are shown in Table 2. The two studied plots are geographically close (Figure 2); therefore, species compositions are quite similar. However, topographical conditions in P2 were more heterogeneous than that in P1, represented by variations of elevation and slope (Table 2, Figure 3).

Relationship between Diversity and AGB

The overall SEM of the two combined study plots showed the general pattern of the diversity-AGB relationship under the effect of topographical factors and evaluated by standardized path coefficients r. The overall model was evaluated as a good fit with CFI = 0.969 > 0.95, RMSEA = 0.040 <0.08 and SRMR = 0.035 < 0.05 (Figure 4). The direct effects of species diversity (r = 0.395, p-value = 0.046) and structural diversity (r = 0.264, p-value = 0.025) were positive on AGB. The indirect effect of species diversity on AGB through structural diversity was negative, with r = -0.463 and p-value = 0.017. In addition, the effect of the latent topographical factors represented by the slope (r = 0.56, p-value=0.00) and aspect

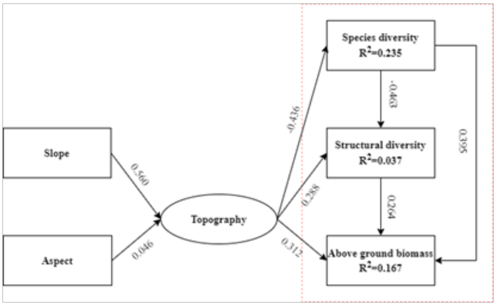

Figure 4 The overall structural equation model (SEM) for the two study plots (CFI = 0.969, RMSEA = 0.040, SRMR = 0.035). Line arrow indicates the direction of a variable's influence and represent significant effects with standardized path coefficients r. R-squared value serves as indicator of the proportion of variance.

(r = 0.046, p-value=0.00), which decrease species diversity with r = -0.436 and positive effect on structural diversity (r = 0.288, p-value=0.00) and AGB (r = 0.312, p-value = 0.013). While slope was found to have a stronger effect than aspect, elevation was found to have no significant effect on AGB.

In P1, the relationship model was good fitted with CFI = 1.00 > 0.95, RMSEA = 0.000 <0.08 and SRMR = 0.029 < 0.05 (Figure 5). The species diversity was positively affected (r = 0.273, p-value = 0.031), and structural diversity showed no impact on AGB (p-value = 0.099).

The species diversity indirectly affected AGB through structural diversity with r = -0.233 and p-value = 0.001. The latent topographical factor represented by the slope (r = 0.175, p-value = 0.037) showed a negative effect on species diversity with r = -0.163 and p-value = 0.006 and a positive effect on structural diversity (r = 0.112, p-value = 0.006) and AGB (r = 0.215, p-value = 0.003). Aspect and elevation showed no significant effect on the relationship model, indicating the homogeneous topography in this study plot (p-value = 0.394).

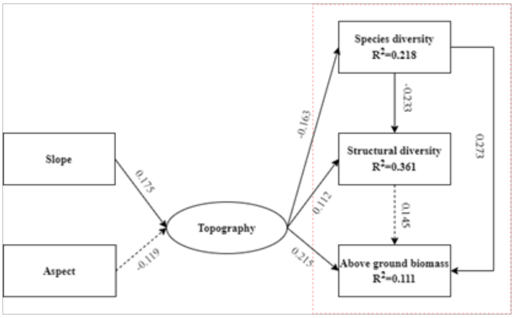

Figure 5 The structural equation model of Plot P1 (CFI = 1.000, RMSEA = 0.000, SRMR = 0.029). Line continuous arrow indicates significant path and line dashed arrow indicates non-significant path with standardized path coefficients r. R-squared value serves as indicator of the proportion of variance.

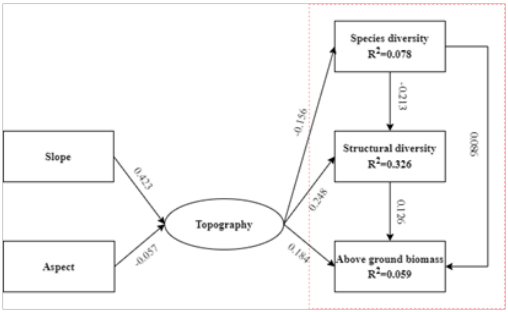

Figure 6 The structural equation model of Plot P2 (CFI = 0.988, RMSEA = 0.020, SRMR = 0.032). Line continuous arrow indicates the direction of a variable's influence and represents significant effect with standardized path coefficients r. R-squared value serves as indicator of the proportion of variance.

In P2, the relationship model was evaluated as a good fit with CFI = 0.988 > 0.95, RMSEA = 0.020 <0.08 and SRMR = 0.032 < 0.05 (Figure 6). The direct effects on AGB were found positively by species diversity (r = 0.086, p-value = 0.01) and structural diversity (r = 0.126, p-value = 0.035). The indirect effect of species diversity on AGB was negative, with r = -0.213 and p-value = 0.00. The latent topographical factors presented by the slope (r = 0.423) and aspect (r = -0.057) negatively affected species diversity with r = -0.156 and positively on structural diversity (r = 0.248, p-value=0.00) and AGB (r = 0.184, p-value = 0.01). Again, elevation showed no significant effect on the relationship model of the study plot P2.

In general, the SEMs showed that the direct effects of species diversity on AGB were positive in the two study plots; however, the indirect effects through structural diversity were negative in the two plots (Table 3, figure 4-5). The direct effects of structural diversity were only significant in P2 (Table 3). Species diversity showed stronger effects on AGB than structural diversity, indicating a greater contribution to AGB in both study plots (Table 3). Species diversity in P1 contributed more than in P2, while only structural diversity significantly affected AGB in P2.

Discussion

In this study, the combined SEM showed a general pattern of the two study plots. The results showed positive direct effects on AGB in both species and size structure, but negative indirect effects were found in species diversity. Moreover, topographical factors positively affected structural diversity and AGB but negatively on species diversity. These effects may be caused by close geographical positions and similar dominant species (Table 3), but different environmental conditions and forest structures of our forest stands.

Table 3 Effects of species diversity and structural diversity on AGB in SEMs.

Diversity	Path coefficients to AGB	P1	P2
Species diversity	Direct	0.273*	0.086**
	Indirect through structural diversity	-0.233***	-0.213***
	Total effect	0.04	-0.127
Structural diversity	Direct/Total effect	0.145	0.126*

Note: Significance levels: * $p < 0.05$, **$p < 0.01$, ***$p < 0.001$

Specifically, the separate results of the SEMs suggested that (i) species diversity contributes greater to AGB in the homogeneous topography site P1; (ii) Structural diversity reveals a positive effect with AGB in heterogeneous condition site P2; (iii) Slope shows a negative effect to species diversity but positive effects to structural diversity and AGB in both studied plots.

Our SEMs showed different effects of species diversity compared to structural diversity on AGB in the two studied plots. Under the more homogeneous environment of P1, the direct effects of species diversity were stronger than that of structural diversity, and these results are consistent with the findings of previous studies (e.g., Liang et al. 2016, Tan et al. 2021, Wang et al. 2023). Besides that, structural diversity showed a higher correlation with AGB than species diversity in the heterogeneous environment of P2, according to previous studies (Poorter et al. 2015, Ali et al. 2019). Moreover, our results also showed indirect effects of species diversity on AGB through structural diversity were negative in both studied plots, which means environmental conditions constrained only direct effects.

In our study, species diversity was constrained by the local environment and may own more information supporting the niche complementary hypothesis (Noulèkoun et al. 2024). The complementary effect comprises effects of niche differentiation and facilitation; however, it is hard to distinguish them in practice (Loreau & Hector 2001). The niche complementary hypothesis assumes that a high number of species and a variety of functional traits facilitate ecosystem functioning for efficient resource utilization, thus enhancing overall productivity (Loreau & Hector 2001, Poorter et al. 2015).

Effects of structural diversity on AGB in our SEMs showed positive effects and significance in more heterogeneous site conditions suggesting that local environmental conditions did not constrain structural diversity. Due to high variations in tree sizes, structural diversity often reflects degrees of canopy complexity, especially in tropical rain forests, as a potential driver of AGB through light absorption at forest stand level (Pretzsch 2014). Therefore, niche complementary enhances light capture through multi-layer canopies and the use efficiency of available natural resources (Ali et al. 2019). However, we did not find a positive link between species diversity and structural diversity in order to increase AGB as findings by previous studies (Poorter et al. 2015, Ali et al. 2019).

Topographical factors affect tropical forest structure and composition via constraining local nutrient and hydraulic conditions (Jucker et al. 2018). In our study, topography negatively affected species diversity but not structural diversity in terms of AGB contribution. That may be caused by strong competition for nutrients and available water that favor species on ridges and steep slopes (Paoli et al. 2008, Heineman et al. 2011), leading to lower numbers of species richness and individual abundance, therefore getting lower AGB and reducing AGB (Weiskopf et al. 2024).

In conclusion, our research highlights the significant role of species diversity, structural diversity, and environmental conditions in diverse tropical rainforests. We found that AGB is directly influenced by both species richness and structural diversity. These findings underscore the critical implications for biodiversity conservation and sustainable forest management practices aimed at preserving high forest functioning. To further elucidate the intricate relationship between diversity and productivity within tropical rainforests under environmental heterogeneity, we recommend conducting additional studies encompassing larger spatial and temporal scales. These efforts will enable a more comprehensive understanding of how various factors interact to shape the dynamics of tropical ecosystems, thereby informing more effective conservation strategies and management approaches for these invaluable environments.

Authors' contributions

Nguyen Hong Hai, Pham Van Dien, Bui The Doi, Nguyen Thanh Tuan, Trinh Hien Mai, and Nguyen Van Quy conceived and designed the experiment and collected the data; Nguyen Hong Hai and Nguyen Van Quy analysed the data; Nguyen Hong Hai wrote the draft manuscript. The authors read and approved the final manuscript.

Conflict of interest

The author declares no conflict of interest.

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