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Effects of tree diversity and stand structure on above-ground carbon storage in evergreen broad-leaved and deciduous forests in Southeast Vietnam

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Abstract

Understanding the relationship between tree species diversity and above-ground carbon (AGC) storage in tropical forests is essential for a sustainable flow of ecosystem goods and services. Although tropical forests of Vietnam are of particular interest due to their high biodiversity and carbon density, few studies have evaluated the relative importance of species composition, tree species diversity and forest structure on AGC storage by forest vegetation type. In this study, we tested for the influence of taxonomic diversity, forest structure and species composition on AGC storage in evergreen broad-leaved and deciduous forests of Southeast Vietnam. Data was collected within 137 rectangular plots (25 m × 20 m), randomly selected across a deciduous forest (DF) and four evergreen broad-leaved forest (EB) categories, with different standing volumes levels: very poor (EBG), poor (EBP), medium (EBM) and rich (EBR). In total, we identified 3687 individuals from 110 tree species belonging to 46 families in 6.85 hectares of sampled area. AGC storage significantly differed among forest categories, ranging from 14.81 Mg ha⁻¹ in EBG to 146.74 Mg ha⁻¹ in EBR. There was higher AGC in the medium diameter class (20–40 cm), except for EBR where there was higher AGC within individuals of 40–60 cm in diameter. Taxonomic diversity was weakly correlated with AGC while stand structure (stem density and maximum diameter) were strongly correlated. Our results suggest that maintaining the abundance distributions of remnant tree species, particularly that of large trees, is one important method to enhance AGC storage in the tropical ecosystems of southern Vietnam.

Keywords: Biodiversity assessment; Ecosystem functioning; Taxonomic diversity; Natural forests; Stand structure.

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Introduction

Tropical forests store the greatest volumes of biomass and carbon and hold the greatest biodiversity of all forest biomes (Poorter et al., 2015; Murdjoko et al., 2021). They are the main source of household income in many rural settings in tropical Vietnam and are estimated to cover approximately 14415 thousand hectares of the country's land surface, of which 71% are natural forests (Khuc et al., 2021) with high biodiversity (>11,300 vascular plants) (Van & Cochard, 2017) and carbon density (255 Mg ha⁻¹) (Hai et al., 2015; Van et al., 2020). These tropical forests, however, have experienced intense human pressure since the Vietnamese war, which made them one of the most deforested and least protected ecosystems in Vietnam (Nguyen & Baker, 2016; Cochard et al., 2018). A clear example of this is the aerial herbicides that were applied by the United States Army to defoliate large areas of primary forests in southern Vietnam (Van & Cochard, 2017). After disturbance, most of these second-growth forests have been regenerating gradually, but illegal logging has hindered their natural recovery (Van & Cochard, 2017).

In an attempt to prevent degradation of remnant natural forests, large reforestation programs and forestland privatization have been set up since 1990's (Van & Cochard, 2017). The country is also introducing new initiatives such as the UN-REDD+ Programme, which aims to reduce global carbon emissions from deforestation and forest degradation (Cochard et al., 2018), the latter is based on reliable data on tree above-ground biomass stocks, biodiversity assessments and on evidence-based understanding of ecosystem functioning (Sullivan et al., 2017; Cochard et al., 2018). Thus, accurate estimates of tree above-ground carbon (AGC) are needed for monitoring the stocks of carbon at different forest vegetation types (e.g., evergreen, deciduous and mixed forests) in the natural forests of southern Vietnam.

Information on AGC storage by forest vegetation type is important for the implementation of UN-REDD+ scheme, but unfortunately, this data is only available for the evergreen broad-leaved, deciduous and mixed forests of central highlands and northern Vietnam (Hai et al., 2015; Van et al., 2017; Cochard et al., 2018). Similarly, the relationship between forest attributes (e.g., forest structure, tree species diversity and functional traits) and AGC storage is less well studied (Con et al., 2013). Previous works in this ecoregion have only developed sets of allometric equations to improve estimations of tree above-ground biomass (AGB) (Huy et al., 2016a; 2016b) and remote sensing technology to estimate AGC storage (Luong et al., 2015; Avitabile et al., 2016; Nguyen & Kappas, 2020).

The relationship between AGC and tree diversity has been one of the central topics in forest ecology (Gillman & Wright, 2006; Cavanaugh et al., 2014). Gardner et al. (2012) suggested that a positive relationship would indicate mutual support, while a negative relationship would indicate difficult trade-offs between them. Biodiversity has been shown to often promote stability, primary productivity and enhance carbon storage in different biomes (Cavanaugh et al., 2014; Chisholm et al., 2013; Poorter et al., 2015; Amara et al., 2019). Similarly, many studies investigating the tree diversity-carbon stock relationship in tropical forests have reported a positive relationship (Gillman & Wright, 2006; Cavanaugh, et al., 2014; Poorter et al., 2015). Although, Kelling & Philips (2007) reported that high productive stands presented low species diversity and dominance of smaller, lighter-wooded trees, resulting in a negative diversity biomass relationship. While no relationship between tree species diversity has been reported in various ecosystems in Indonesia and Zimbabwe (Zimudzi & Chapano, 2016; Filqisthi & Kaswanto, 2017). Other studies have found a hump-shaped relationship in which species richness peaks at intermediate productivity and declines towards extreme high or low productivity (Bhattarai et al., 2004; Shirima et al., 2015). Carbon storage in forest ecosystems is also affected by other factors, such as geographical location, climatic condition, successional stage and species composition (Hai et al., 2015). Thus, more information is required, particularly on how biodiversity affects carbon stocks in different forest types to better understand the forest's role in mitigating climate change.

Species composition is also a key factor strongly influencing AGC storage. It is more important than species richness in the Central Highlands of Vietnam (Cochard et al., 2018). For instance, Cochard et al. (2018) found that the total AGB of a tropical forest in central Vietnam was largely determined by the biomass of only four species out of 172 recorded within the stand. Thus, identifying the key tree species is therefore crucial to better understand which are the most productive in terms of biomass for the tropical forests of Southeast Vietnam. This study seeks to (i) analyze the relative importance of taxonomic diversity and forest structure on AGC storage in evergreen broad-leaved and deciduous forests from southern Vietnam, (ii) test the variability of these forest attributes across deciduous forests (DF) and evergreen broad-leaved forests (EB), and (iii) evaluate the relative contribution of species composition to standing AGC storage.

Material and methods

Study area

This study was carried out in the natural forest of Binhphuoc province, Southeast Vietnam. The study area is mostly surrounded by primary forests and has an equatorial monsoon climate with two distinct seasons: rainy (May to October) and dry (November to April). Total mean annual precipitation is about 1804 mm with a mean annual temperature of 25°C (Van et al., 2020; Vu et al., 2021). The forest is characterized by Acrisols and Ferralsols soils (Lung et al., 2011) that occur at an altitude ranging from 18 to 942 m. Three different vegetation types are found in this study area, including evergreen broad-leaved, deciduous and mixed forests (Lung et al., 2011). The evergreen broad-leaved forest is dominated by the species *Syzygium cumini* (L.) Skeels. (Myrtaceae), *Litsea cambodiana* Lecomte (Eurylaimidae), *Irvingia malayana* Oliv. ex A.W.Benn (Irvingiaceae), *Millettia ichthyochtona* Drake (Fabaceae), *Vitex ajugiflora* Dop (Verbenaceae), *Catunaregam tomentosa* (Blume ex DC.) Tirveng (Rubiaceae), *Terminalia franchetii* Gagnep (Combretaceae) and *Grewia nervosa* (Lour.) Panigrahi (Malvaceae). While the most dominant species found in the deciduous forest are *Dipterocarpus tuberculatus* Roxb. (Dipterocarpaceae), *Dipterocarpus obtusifolius* Teijsm. ex Miq. (Dipterocarpaceae) and *Shorea roxburghii* G. Don (Dipterocarpaceae) (Supplementary Table S1).

Study design and field measurements

As a result of high human disturbance, particularly due to selective logging and shifting cultivation, remaining evergreen broad-leaved forests were classified into five categories by the Forest Inventory and Planning Institute of Vietnam, based on different standing volume (V , $\text{m}^3 \text{ha}^{-1}$) levels: very poor ($V \leq 10 \text{ m}^3 \text{ha}^{-1}$), poor ($10 < V \leq 100 \text{ m}^3 \text{ha}^{-1}$), medium ($100 < V \leq 200 \text{ m}^3 \text{ha}^{-1}$), rich ($200 < V \leq 300 \text{ m}^3 \text{ha}^{-1}$) and very rich ($V > 300 \text{ m}^3 \text{ha}^{-1}$) (Hai et al., 2015). Because, the very rich forest is not present in this study area, the forest cover was therefore classified into a deciduous forest (DF) and four evergreen broad-leaved forest categories, which include: very poor (EBG), poor (EBP), medium (EBM) and rich forest (EBR).

The sample plots were established using the stratified random sampling method and the stratification of plots was performed based on forest types. Sample plots were placed randomly in each forest stratum. Plots were located at least 500 m from each other within one particular forest type. In total, 137 plots ($20 \text{ m} \times 25 \text{ m}$ each) with stratified random sampling strategy were established within the study area: 19 in EBR, 30 in EBM, 47 in EBP, 24 in EBG and 17 in

DF (see Figure 1). Stand variables were determined using a hand-held GPS (Map76cx) to record the geographical location and canopy height of each forest plot. Within each plot, total tree height (H , in m) and diameter at breast height (DBH , in cm) were measured for all trees ≥ 5 cm in diameter. For each tree, two perpendicular diameters (outside-bark 1.3 m above ground level) were measured to the nearest 0.1 cm and were then averaged to obtain DBH . The total tree height (H) is the height of a tree from its stump to its tiptop (Van Laar and Akca, 2007) and was measured using a Haglof Vertex Hypsometer. Trees on the border of the plot were included if $>50\%$ of their basal area fell within the plot but were otherwise excluded. Tree species were collected and later identified in the field with the help of the regional flora data set (Ho, 2003; Ban et al., 2007). When individuals could not be identified in the field, plant specimens were taken for further identification to the Forest Inventory and Planning Institute of Ho Chi Minh City, Vietnam. The scientific names of the species were identified according to World Flora Online (2022).

Estimating tree above-ground carbon storage

The above-ground biomass (AGB, Mg ha^{-1}) of individual trees was estimated using the allometric equation of Huy et al. (2016a), which was specifically developed for evergreen broad-leaved forests of Southeast Vietnam and that incorporates wood density, diameter and height:

$$AGB = 0.647261 \times (\rho \times D^2 \times H)^{0.931} \quad (1)$$

where D is tree diameter (cm), ρ is stem wood density (g cm^{-3}) and H is total tree height (m) of standing trees. Wood-specific density values were taken from the global wood density database (Zanne et al., 2009). For species that lacked a direct measurement of it, genus-level averages were used as a substitute (Rodríguez-Hernández et al., 2021). When wood density values were not available at the genus level, we used the mean overall stand wood density in which the tree was located (Dayamba et al., 2016; Rodríguez-Hernández et al., 2021). Biomass values of each stem were then summed to obtain total above-ground carbon (AGC, Mg ha^{-1}) at plot level, where 47% of the biomass is assumed to be carbon (McGroddy et al., 2004; IPCC, 2006).

Data analysis

For each study plot, we calculated four structural attributes and three metrics of taxonomic diversity

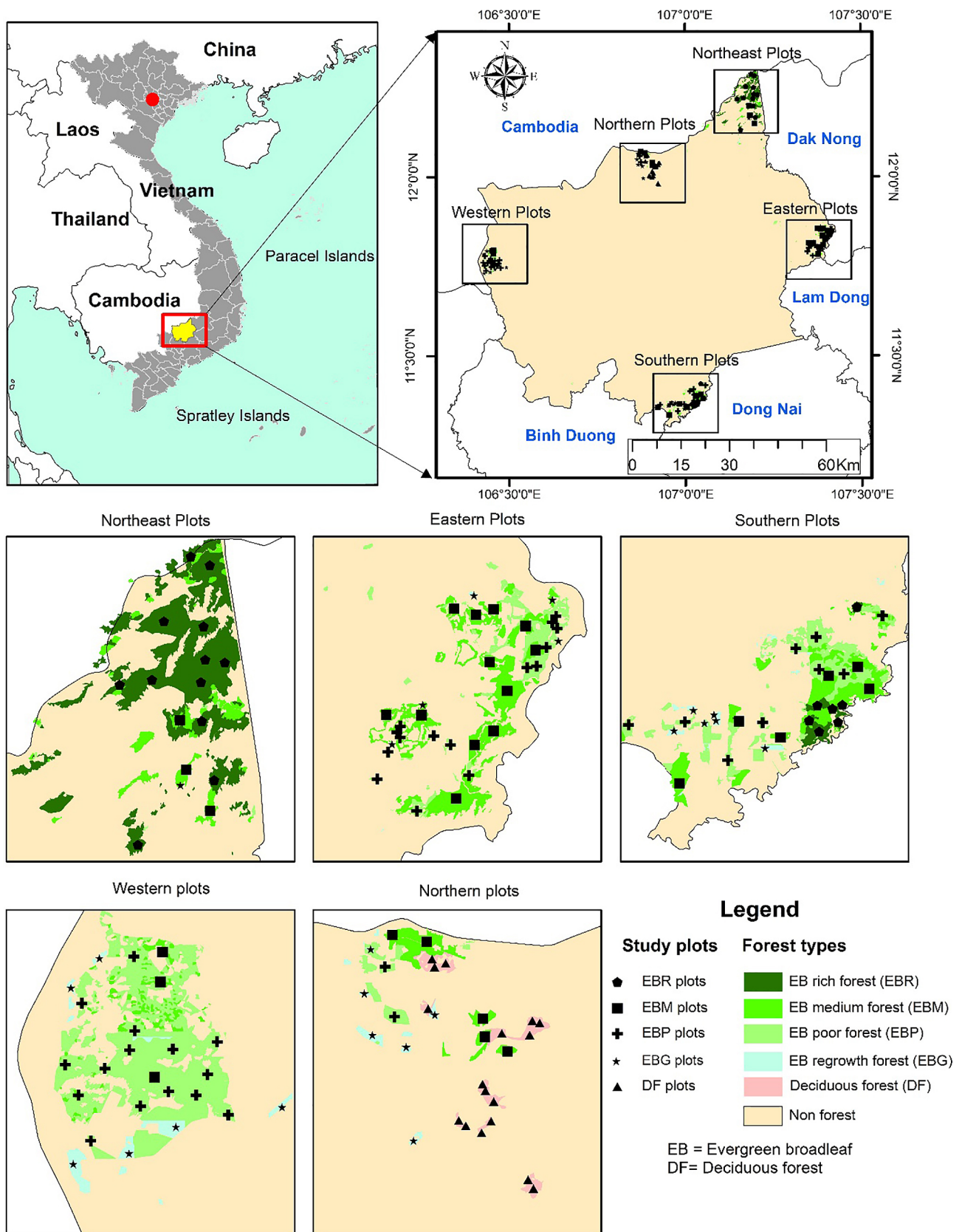


Fig. 1. Geographic location of the study area in Southeast Vietnam. The panels show the characteristic vegetation types of each study plot

for all stems ≥ 5 cm in *DBH*. For structural attributes, we determined coefficient of variation in *DBH* ($CvDBH$), maximum diameter ($MaxDBH$, in cm), basal area (BA , in $m^2 ha^{-1}$) and stem density (SD , number of stems found at each sampled plot). Stem basal area (BA , in m^2) and trunk volume (V_i , in m^3) were calculated using the following equation (Hinh, 2012; Hai et al. 2015):

$$BA = \frac{\pi \times DBH^2}{200^2} \quad (2)$$

$$V_i = BA \times H \times f \quad (3)$$

DBH is the diameter at breast height (cm), *H* is the total tree height (m), and *f* is the form factor parameter of trees ($f = 0.4826$).

Total standing volume (*V*) was calculated as the sum of all trunk volumes present within the sampled quadrats with trees ≥ 5 cm in the diameter (converted to $m^3 ha^{-1}$). Taxonomic diversity was measured using three parameters: species richness (*S*), the sum of all tree species, Shannon diversity (H') index (Shannon, 1948) as a measure of diversity which takes into account phylogenetic relations among individuals and Pielou's evenness (J') index (Pielou, 1969) which describes species evenness within the study plots. We also determined the dominant species for each forest type through the importance value index (IVI), using the following formulas (Curtis & McIntosh, 1951).

$$IVI = (RF_i + Rd_i + RBA_i) \quad (4)$$

RF_i (relative frequency of species *i*) was calculated as:

$$RF_i = 100 \times F_i / TF \quad (5)$$

F_i is the number of plots (frequency) in which species *i* is present, and *TF* is the sum of all frequencies for all species.

Rd_i (relative density of species *i*) was calculated as:

$$Rd_i = 100 \times n_i / N \quad (6)$$

n_i is the total number of individuals of species *i*, and *N* is the total number of individuals of all the species

RBA_i (relative basal area of species *i*) was calculated as:

$$RBA_i = 100 \times BA_i / TBA \quad (7)$$

BA_i is the total basal area of species *i*, and *TBA* is the total basal area of all species.

Shannon diversity (Shannon, 1948):

$$H' = -\sum_{i=1}^s p_i \ln p_i \quad (8)$$

Pielou's evenness (Pielou, 1969): $J' = H' / H'_{max}$ (9)

To determine the distribution of AGC, forest structure and taxonomic diversity among different diameter classes, we grouped all individual trees present in each study plot into five different *DBH*-classes: (5–20, 20.1–40, 40.1–60, 60.1–80 and > 80 cm). Due to lack of normality and homogeneity of variance among the variables, Kruskal–Wallis tests were performed to look for significant differences between taxonomic diversity (*S*, H' and J'), structural attributes (CV_{DBH} , MAX_{DBH} , *BA* and *SD*) and AGC storage for each forest type. Post hoc pairwise multiple comparisons were performed using Wilcoxon rank-sum test. All significant differences reported here refer to $p < 0.05$.

We used stand attributes ($CvDBH$, $MaxDBH$, *BA* and *SD*), taxonomic diversity (*S*, H' and J') and forest types as predictors of AGC. Firstly, collinearity among predictor variables was tested and only noncollinear variables (with Pearson correlation coefficient < 0.6) were selected for regression analysis (Yuan et al, 2018; Måren & Sharma, 2021). We selected 4 predictor variables: *H*, J' , $MaxDBH$ and *SD* (see the correlations among candidate predictors in Table S2 in the Electronic supplementary material). In addition, prior to the following analyses, AGC was log-10 transformed and all explanatory variables were standardized to obtain a mean of 0 and a standard deviation of 1, which aimed to improve the interpretability of regression coefficients (Schielzeth, 2010). Secondly, we analyzed the linear relationship between AGC and each of preselected non-collinear predictor variables (*H*, J' , $MaxDBH$, *SD* and forest type). After that, linear mixed effect models (LME) were applied to model AGC as a function of the selected predictor variables. A full model was then run with plot level AGC used as the response. Taxonomic diversity (J' and H); forest structure (*SD* and $MaxDBH$) and forest type (DF, EBG, EBP, EBM and EBR) were used as predictor variables. Forest types were treated as factors and included as fixed effect variables. Five sites (see in Fig. 1) were used as random variables. From the full model, nonsignificant variables were dropped, and model performance was evaluated using AICc (Corrected Akaike Information Criteria). The best model was selected by considering the lowest AICc (Burnham & Anderson, 2002) (Table S3 in the Electronic supplementary material). The model with the lowest AIC values were performed using the *dredge* function of "MuMIn" R-package. However, due to the presence of spatial autocorrelation (SAC) in the biomass data (Moran's $I = 0.312$, $p < 0.0001$), we fitted all models with an additional term describing the within-group

correlation structure using the ‘corExp’ function in *nlme* (Pinheiro et al., 2022). Finally, we applied the piecewise structural equation model (pSEM) to test the direct and indirect influence of forest type on forest structure, taxonomic diversity and AGC. According to the best multiple linear mixed model that we found in Table 4, we selected Pielou’s evenness, stem density, forest type and *MaxDBH* to model the SEM. We then assessed the best fit model (pSEM) to the data using AIC, Fisher’s C statistic and associated *P*-value (i.e. $P > 0.05$ indicates that the model is accepted). The linear mixed effect model was used in order to consider the random effect of sites and to remove the SAC in the model using R-package piecewiseSEM (Lefcheck, 2016). All statistical analyses were performed using R software program version 3.3.0 (R Core Team, 2017).

Results

Variation of diversity, forest structure and AGC across the five forest types

In total, we sampled 3867 individuals belonging to 110 tree species, 46 Families and 18 Orders (see Appendix A). Notably, across the five forest types studied, we found 18 rare and threatened species which are reported on the International Union for Conservation of Nature (IUCN) Red List, ranging from Near Threatened to Endangered. The communities with

the highest number of rare and threatened species were EBR (12 species), EBM (13 species) and EBP (11 species), respectively (see Table 1).

Among the dominant tree species in the evergreen broad-leaved forest, *S. cumini* (Myrtaceae) showed the highest relative abundance (>100%) in terms of IVI. While *D. tuberculatus* (121.41%) and *D. obtusifolius* (118.31%) were also common in the deciduous forest. The same species accounted for the highest amount of AGC storage, as *S. cumini* contributed to the largest amount of AGC in EBR, EBM, EBP and EBG with 18.17, 9.02, 4.19 and 7 Mg ha⁻¹, respectively. *D. tuberculatus* contributed to the largest AGC in DF with 9.39 Mg ha⁻¹, followed by *D. obtusifolius* with 7.84 Mg ha⁻¹ (Table 2).

BA ranged from 7.81 m² ha⁻¹ in EBG to 42.24 m² ha⁻¹ in EBR, while tree stem density ranged from 278 trees ha⁻¹ in EBG to 760 trees ha⁻¹ in EBM. Overall, EBR had significantly higher AGC, BA and *MaxDBH* than the other forest types. The highest AGC content was found in EBR forests, followed by EBM, DF, EBP and EBG with 146.74, 62.82, 48.7, 34.52 and 14.81 Mg ha⁻¹, respectively. Regarding species richness, DF and EBG had the lowest values in comparison with the other forest categories (EBR, EBM and EBP), and both also had lower Shannon diversity values (*H'*). No significant differences in Pielou’s evenness were observed among four categories of evergreen broad-leaved forests (Figure 2).

In all forest types, there was higher species richness and stem density in the lowest DBH-class (5–20 cm) and the number of stems decreased continuously

Table 1. Rare and threatened species reported in the IUCN red list that we found in the five forest vegetation types studied in Southeast Vietnam

Species	IUCN	Evergreen broad-leaved forest				Deciduous forest (DF)
		Rich (EBR)	Medium (EBM)	Poor (EBP)	Very poor (EBG)	
<i>Anisoptera costata</i> Korth.	EN	2	2	–	–	–
<i>Hopea recopei</i> Pierre ex Laness	EN	15	40	–	3	–
<i>Parashorea chinensis</i> Hsie Wang	EN	–	1	16	–	–
<i>Pterocarpus macrocarpus</i> Kurz	EN	2	–	–	–	2
<i>Sindora siamensis</i> Miq.	LR	6	3	8	–	–
<i>Amesiodendron chinense</i> (Merr.) Hu	NT	–	–	5	–	–
<i>Dipterocarpus obtusifolius</i> Teijsm.ex Miq.	NT	5	31	23	1	88
<i>Dipterocarpus tuberculatus</i> Roxb.	NT	9	32	29	1	96
<i>Shorea obtusa</i> Wall.	NT	–	–	–	–	4
<i>Swietenia mahagoni</i> (L.) Jacq.	NT	14	17	4	–	–
<i>Dalbergia tonkinensis</i> Prain	VU	–	4	–	–	–
<i>Dipterocarpus scaber</i> Buch.-Ham.	VU	7	16	17	5	4
<i>Dipterocarpus costatus</i> C.F.Gaertn.	VU	1	–	–	1	–
<i>Hopea odorata</i> Roxb.	VU	12	33	30	4	–
<i>Madhuca pasquieri</i> (Dubard) H.J.Lam	VU	–	–	–	–	8
<i>Shorea stellata</i> (Kurz) Dyer	VU	–	24	8	4	–
<i>Shorea roxburghii</i> G.Don	VU	2	12	1	10	144
<i>Vitex ajugiflora</i> Dop	VU	6	24	73	18	1

IUCN – International Union for Conservation of Nature Red List; LR – Lower risk species; NT – Near threatened species; VU – Vulnerable species; EN – Endangered species.

Table 2. List of dominant tree species (IVI $\geq 50\%$), mean diameter (d -mean, in cm), BA ($\text{m}^2 \text{ha}^{-1}$), above-ground woody biomass (AGB, Mg ha^{-1}) and their relative contribution to living above-ground carbon storage (AGC, Mg ha^{-1}) in four evergreen broad-leaved forest categories and deciduous forest in Southeast Vietnam

Forest type	Dominant species	IVI (%)	d -mean	BA	AGB	AGC
Evergreen broad-leaved rich forest (EBR)	<i>Syzygium cumini</i> (L.) Skeels	103.23	23.63	5.84	38.66	18.17
	<i>Litsea cambodiana</i> Lecomte	73.43	25.47	3.09	14.54	6.83
	<i>Lagerstroemia speciosa</i> Pers.	66.28	36.46	6.47	46.49	21.85
	<i>Irvingia malayana</i> Oliv. ex A.W.Benn	62.5	42.06	4.45	51.30	24.11
	<i>Millettia ichthyochtona</i> Drake	51.75	20.01	0.63	2.91	1.37
Evergreen broad-leaved medium forest (EBM)	<i>Syzygium cumini</i> (L.) Skeels	116.33	18.98	3.79	19.18	9.02
	<i>Dipterocarpus obtusifolius</i> Teijsm.ex Miq.	58.44	18.27	0.59	3.28	1.54
	<i>Millettia ichthyochtona</i> Drake	57.13	19.24	0.90	3.80	1.79
	<i>Dipterocarpus tuberculatus</i> Roxb.	53.01	20.83	0.88	6.02	2.83
Evergreen broad-leaved poor forest (EBP)	<i>Syzygium cumini</i> (L.) Skeels	113.38	15.48	1.94	8.92	4.19
	<i>Vitex ajugiflora</i> Dop	60.43	17.83	0.92	3.96	1.86
	<i>Catunaregam tomentosa</i> (Blume ex DC.) Tirveng	52.91	17.23	0.32	1.49	0.70
	<i>Litsea cambodiana</i> Lecomte	52.26	14.84	0.62	2.03	0.95
	<i>Cratoxylon formosum</i> (Jacq.) Benth. & Hook.f. ex Dyer	51.3	18.02	0.86	6.10	2.87
	<i>Neonauclea sessilifolia</i> (Roxb.) Merr.	50.43	17.03	0.28	1.56	0.73
Evergreen broad-leaved very poor forest (EBG)	<i>Syzygium cumini</i> (L.) Skeels	105.19	18.12	1.63	3.29	7.00
	<i>Terminalia franchetii</i> Gagnep.	50.00	17.67	0.47	0.73	1.54
Deciduous forest (DF)	<i>Dipterocarpus tuberculatus</i> Roxb.	121.41	21.14	4.75	19.98	9.39
	<i>Dipterocarpus obtusifolius</i> Teijsm.ex Miq.	118.31	20.82	4.39	16.67	7.84
	<i>Shorea roxburghii</i> G.Don	116.42	14.56	3.14	9.28	4.36
	<i>Careya aborea</i> Roxb.	59.81	26.09	0.94	2.90	1.36
	<i>Syzygium cumini</i> (L.) Skeels	57.44	13.84	0.76	1.57	0.74
	<i>Terminalia calamansanay</i> Rolfe.	56.89	20.03	1.13	3.11	1.46
	<i>Baccaurea ramiflora</i> Lour.	53.41	13.83	0.46	0.79	0.37

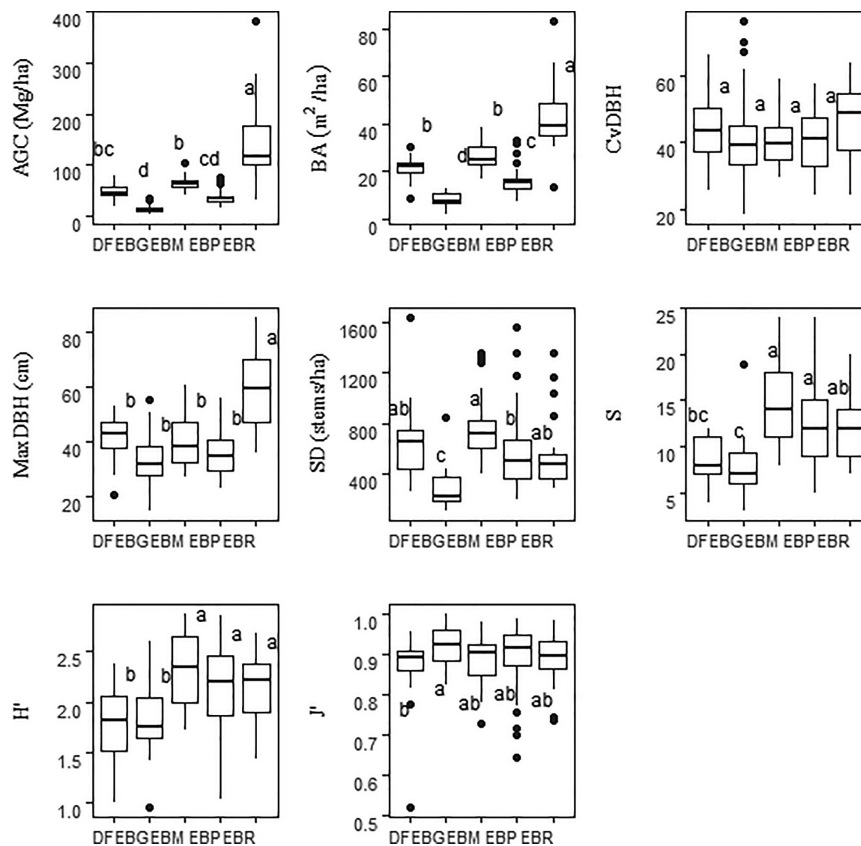


Fig. 2. Boxplots of AGC storage and multiple metrics of taxonomic diversity and forest structural attributes for the five forest vegetation types. Different letters (a–d) indicate significant differences at $p < 0.05$ (Wilcoxon rank-sum test). Factors are above-ground C storage (AGC), species richness (S), Pielou's evenness index (J'), Shannon index (H'), coefficient of variation in DBH ($CvDBH$), stand basal area (BA), maximum diameter ($MaxDBH$) and stem density (SD). Horizontal lines inside the boxes = median values, boxes = 25% and 75% quartiles, vertical lines = 10% and 90% percentiles, dots = outliers

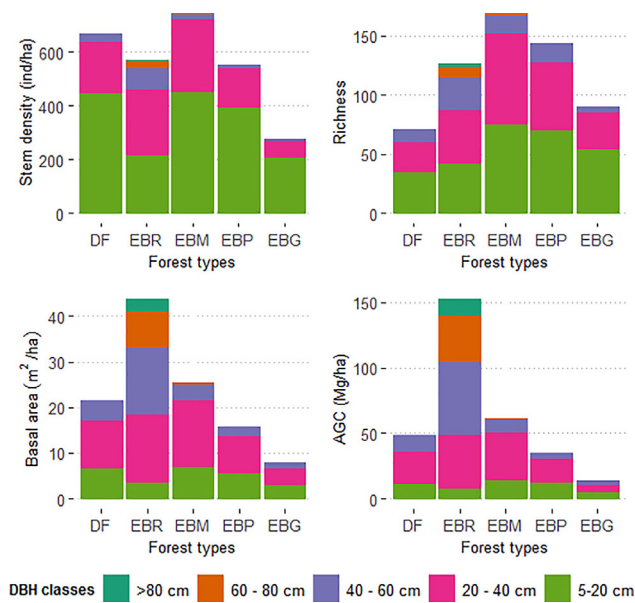


Fig. 3. Distribution of stem density (SD), species richness (S), basal area (BA) and above-ground carbon storage (AGC) among five different DBH classes for five different forest types in Southeast Vietnam

in the larger DBH classes. In terms of BA, the most important DBH class was between 20 and 40 cm, accounting for more than half of the total BA. Similarly,

there was higher AGC in the lower diameter class (20–40 cm) in all forest types except for EBR which had the highest amount of AGC contained within individuals of 40–60 cm in diameter (Figure 3).

Bivariate relationships between AGC storage and forest attributes

Results showed that correlation coefficients ranged from -0.22 (J') to 0.9 (BA) throughout all predictor variables. All predictor variables except Pielou's evenness showed a significant positive relationship with $\log_{10}(AGC)$ ($p < 0.05$) (Figure 4).

The multiple regression models were used to explore the relationship between the aforementioned explanatory variables and AGC storage. These models showed nonsignificant multicollinearity because the VIFs of structural attributes, taxonomic diversity and forest types were less than 5. Multiple linear regression analysis integrating stem density, maximum diameter ($MaxDBH$), Pielou's evenness (J'), Shannon diversity (H) and forest types explained more than 80% of the total variation in AGC storage. Maximum diameter, stem density and forest types showed a significant ($p < 0.05$) relationship to AGC (Table 3).

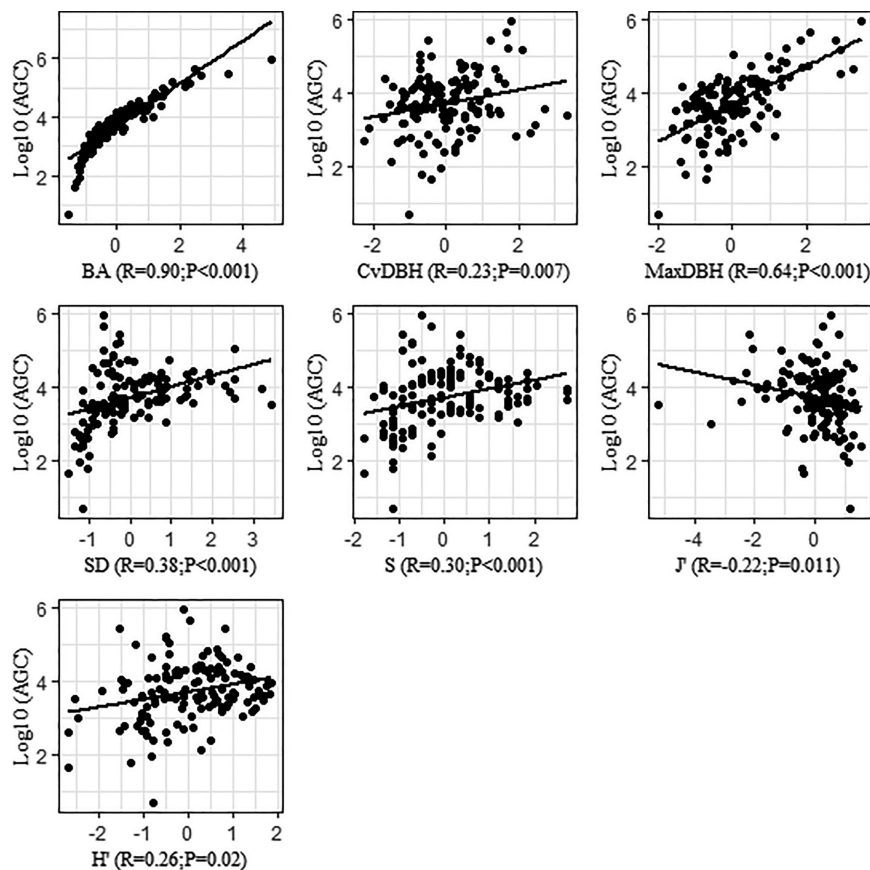


Fig. 4. Bivariate relationships between forest attributes and AGC storage (log-10-transformed) using pooled data

Table 3. Multiple linear regression showing the relationships between tree above ground carbon (AGC) storage and forest attributes in the five forest vegetation types studied in Southeast Vietnam

Explanatory variables	Estimate	Std. error	t	VIF	P value
Intercept	3.762	0.086	43.87		<0.001
Shannon diversity (H')	0.064	0.050	1.266	1.800	0.208
Pielou's evenness (J')	-0.095	0.051	-1.872	1.821	0.063
Maximum diameter	0.369	0.044	8.363	1.582	<0.001
Stem density (SD)	0.179	0.053	3.395	1.891	<0.001
Forest types				1.194	<0.001
EBG	-0.767	0.122	-6.284		<0.001
EBM	0.194	0.110	1.766		0.080
EBP	-0.127	0.104	-1.22		0.225
EBR	0.518	0.129	4.017		<0.001
Model statistics	R^2	R^2_{Adjusted}			
	0.85	0.84			

Std. error – the standard error of the multiple linear regression, t – the coefficient divided by its standard error, VIF – variance inflation factor.

Linear mixed effect models and structural equation models: testing for the direct and indirect effects of forest types on AGC storage

The best multiple linear mixed model showed that tree AGC was best explained by maximum diameter ($MaxDBH$), stem density (SD) and forest type. As indicated by the marginal R^2 , sites had a weak direct effect on AGC, as it only explained less than 1% of the total variation in AGC. Among these predictors, maximum diameter ($MaxDBH$) had the highest effect size, followed by stem density. Pielou's evenness had the lowest effect size and its direct

effect was negative. When accounting for the variation caused by the sites, forest type has an impact on AGC, showing that EBR and EBM have a positive effect (Table 4).

The best pSEM model showed that AGC storage was positively affected by forest structure (stem density and $MaxDBH$), after accounting for the strongest positive direct effects of disturbance intensity (forest type). Forest type had the strongest total positive effect on AGC storage through the summation of direct ($\beta = 0.179$, $p < 0.001$) and indirect ($\beta = 0.271$, $p < 0.001$) positive effects via $MaxDBH$. While Pielou's evenness had a nonsignificant direct negative effect on AGC storage ($\beta = -0.052$, $p = 0.294$) (Figure 5).

Table 4. Summary statistics of the best linear mixed effect model for predicting above-ground tree carbon, where the best model was selected using Akaike Information Criteria (AIC)

Explanatory variables	Estimate	Std. Error	t	P
Intercept	3.820	0.125	30.671	<0.001
Stem density	0.146	0.031	4.680	<0.001
Maximum diameter	0.254	0.039	6.463	<0.001
Pielou's evenness	-0.042	0.028	-1.512	0.133
Forest types				<0.001
EBG	-0.952	0.146	-6.530	<0.001
EBM	0.196	0.128	1.531	0.1284
EBP	-0.272	0.137	-1.991	0.0487
EBR	0.695	0.162	4.277	<0.001
Spatial autocorrelation	Range (km)	Nugget		
	1.22	0.066		
Model statistics	R^2_m	R^2_c	AIC	AICc
	0.81	0.82	75.35	77.9

Standardized regression coefficient (Estimate), the standard error (Std.Error), t test, P value, conditional (c) and marginal (m) R^2 (both fixed and random effects (R^2_c) and fixed effects only (R^2_m)) and a corrected Akaike Information Criterion for small data sets (AICc) are given.

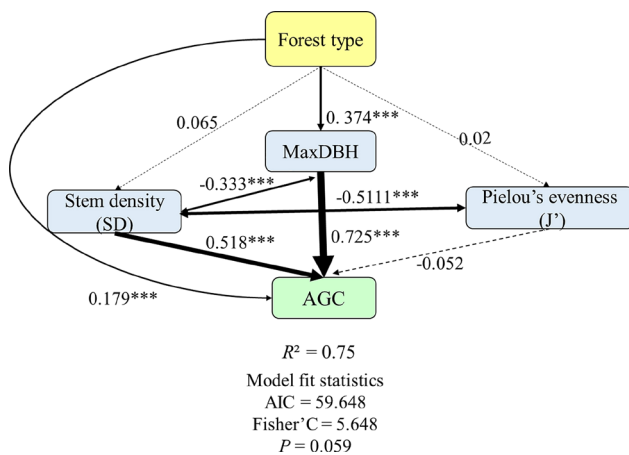


Fig. 5. The best-fit structural equation model for linking forest types, diversity (Pielou's evenness), forest structural attributes (*MaxDBH* and stem density) and AGC storage in evergreen broad-leaved and deciduous forests in Southeast Vietnam. Solid arrows represent significant paths, while dashed arrows represent non-significant effects. For each path, the standardized regression coefficient is shown. R^2 indicates the total variation explained for the dependent variable (AGC) that is explained by the combined direct and indirect effects of the independent variables. Arrow width is proportional to the path coefficient. Bidirectional arrows indicate correlated errors. Significance of coefficient is shown on each path: *** $p < 0.001$

Discussion

Taxonomic diversity, species composition and the relationship with forest disturbances

In this study, we identified 110 tree species with $DBH \geq 5$ cm belonging to 46 families and 18 orders in 6.85 hectares. Shannon Weiner diversity scores ranged from 1.79 to 2.34. Similar scores (1.5–3.5) were found by Con et al. (2013) in six ecological regions in Vietnam (Northeast, Central North, Northwest, North Central Coast, Mid-Central Coast and Central Highland) but not higher than those found by Van et al. (2017) with 3.44–4.11 in the Central highlands of Vietnam. Our findings suggest that tree species diversity in the study area was significantly affected by anthropogenic disturbances. Although the outcome of the effects of disturbance on tree species likely differs based on the intensity of disturbance. Since 1980s, selective logging with different intensities had widely been applied in Vietnam leading to an extreme decrease of forest cover in natural forest areas. In 1993, the Vietnamese government promulgated a logging ban in protected areas known as 'special use forests', and in 2014, it prohibited the cutting of trees from natural forests. However, the consequences of past logging have created different

forest states in Vietnam (Hai et al., 2015). For instance, very poor and poor forests were highly selectively logged and/or highly disturbed by cultivation that extracted timber, this resulted in 30–50% of the forest cover area being removed. Medium intensity selective logging (medium disturbances) that extracted timber was from 10% to less than 30% for the medium forest. Low intensity selective logging (low disturbances) that extracted timber was less than 10% of total standing volume for the rich forest. Neither signal of selective logging or rare stumps was found from selective logging for very rich forest (Le, 1996; Hai et al., 2015). In general, we found that species richness declined markedly from medium intensity of disturbance in EBM to high intensity of disturbance in EBG.

The IVI and the relative contribution of tree species to living above-ground carbon storage indicate that the overall dominance of the fast - growing and light - demanding species (*Syzygium cumini*, *Litsea cambodiana*, *Millettia ichthyochtona* and *Grewia nervosa*) in four categories of evergreen broad-leaved forest. These species are wood of low quality and of non-commercial value, so it is rarely selectively logged. Their intense reproduction in forest gap after forest canopy damage due to selective logging is one of the reasons these species are so dominant. Similarly, Cochard et al. (2018) reported that previous logging impacts persisted and continued to influence seedling establishment, sapling growth/survival, and ultimately species composition. In summary, species composition, taxonomic diversity are modulated by the lasting imprints of logging operations.

Standing trees in the large-diameter classes override AGC

We highlight how forest carbon is affected by forest structure. In our study, the contribution of small-diameter trees (5–20 cm) to overall stem density was 59.5%, and 44% for species richness in all forest types, but they only contributed to 18.6% of total stand BA and 11.8% to AGC (Figure 2). These findings are similar to that of Keeling & Phillips (2007), who detected a negative diversity-biomass carbon storage relationship in high productive stands consisting of smaller, lighter-wooded trees. Similarly, several studies have shown that most AGC is stored in large-diameter trees (≥ 50 or ≥ 70 cm) (Marshall et al., 2012; Bastin et al., 2015; Shirima et al., 2015; Van et al., 2017). In this study, trees > 20 cm in diameter contributed to 96.9% of BA and 97.6% of AGC in EBR. In addition, the multiple linear mixed model and piecewise structural equation modeling (pSEM) suggested that *MaxDBH* was the stronger predictor of AGC storage compared to taxonomic diversity

and other forest structural attributes, which aligns with the findings of other studies (Slik et al., 2013; Stephenson et al. 2014). Other studies also found that the 1% of largest trees override the other 99% of trees in explaining the variation in AGC storage in subtropical forests (Lutz et al., 2018; Ali et al., 2019). Van et al. (2020) also found that trees ≥ 30 cm in diameter accounted for 76% of AGC when studying ecoregional variations of above-ground biomass and stand structure in evergreen broad-leaved forests of Vietnam. In order to reduce time and resources, it has been recommended that field surveys should only focus on large-diameter trees to quantify productivity and carbon stocks of EBR in Southeast Vietnam, as trees ≥ 20 cm in diameter tend to contribute to the majority of AGC storage. However, we found higher species richness and stem density within individuals of 5–20 cm in diameter across the five forest types studied, suggesting that this second-growth forest is still under regeneration.

Drivers of AGC while accounting for forest disturbance

In this study, SEM results indicated that forest type had a significant direct effect on AGC and indirect on AGC via maximum diameter (Figure 5). The variation in AGC between forest types is potentially linked to past disturbance. Lower *MaxDBH* was observed in EBP and EBG plots, suggesting that past logging activities have decreased the proportion of large individuals. Different forest categories for the evergreen broad-leaved forests in the present study resulted from past human disturbances mainly due to selective logging and shifting cultivation. Human disturbances have significantly influenced carbon stocks in tropical forests of Vietnam. For instance, Stas et al. (2020) showed that large reductions in AGC were the result of medium and heavily logged lowland forests of Vietnam. In our study, AGC showed significant differences among the five different vegetation types studied, being higher in EBR ($146.74 \text{ Mg ha}^{-1}$) but lower in EBG (14.81 Mg ha^{-1}). The same pattern of carbon contribution was found in a evergreen broad-leaved forest in Central, Vietnam (Avitabile et al., 2016), where total AGC stock increased exponentially from very poor forest (18.2 Mg ha^{-1}) to poor forest (44.5 Mg ha^{-1}), to medium forest (83 Mg ha^{-1}), and to rich forest (166.8 Mg ha^{-1}). Similar results were found in Central Highland, Northeast, Central North, Northwest, North Central Coast and Mid-Central Coast of Vietnam (Con et al., 2013; Luong et al., 2015; Nguyen & Kappas, 2020; Van et al., 2020; Vu et al., 2021) (Appendix B). However, these values are lower than that of the tropical evergreen broad-leaved forests of Central Highland, Vietnam, which

were reported total carbon stock increased from very poor forest (75.2 Mg ha^{-1}), to medium forest (198.9 Mg ha^{-1}), and to very rich forest (254.8 Mg ha^{-1}) (Hai et al., 2015). Collectively, these findings support the view that AGB in the Central Highland is the highest among Vietnam's ecoregions (Le, 1996; Hai et al., 2015). This may be explained by the difference in species composition, edaphic factors, climatic variables and past human disturbance. The general trend in AGB and/or total basal area show an increase with increasing annual temperature and precipitation in old-growth forests of Vietnam (Van et al., 2020). This could be associated with the relatively high rainfall in Central Highland (1924 mm y^{-1}) compared to that of Southeast (1804 mm y^{-1}).

Taxonomic diversity is a weak proxy of AGC

Taxonomic diversity and above-ground carbon (AGC) relationships are commonly found in herbaceous grasslands (Mittelbach et al., 2001) and also in tropical forests (Zimudzi & Chapano, 2016; Filqisthi & Kaswanto, 2017). Interestingly and contrary to the general view, we found diversity metrics are a weak proxy of AGC. Taxonomic diversity (Shannon diversity and Pielou's evenness) showed different relationships with AGC in the bivariate and multiple regression models. Shannon diversity showed a non-significant positive relationship with AGC, while Pielou's evenness had a weak negative relationship with AGC in the bivariate linear regression ($p=0.063$). Our mixed effect model showed that Pielou's evenness had a weak negative relationship with tree AGC, while Shannon diversity and species richness did not show any relationship with it. Similarly, another study that also analyzed the relationship between tree AGC and different taxa found a very weak relationships between AGC and species richness in European forests (Sabatini et al., 2019). Similarly, species richness and Shannon-Wiener diversity index were also found to be weak proxies of tree AGC in the Himalayas (Måren & Sharma, 2021). At small spatial scales, we hypothesized that tree diversity enhances tree carbon storage because there is usually a higher number of stems and consequently a higher species richness. As expected, we found that species richness had a positive effect on tree AGC (Figure 4), which is consistent with other studies conducted in other tropical forests (Cavanaugh et al., 2014; Poorter et al., 2015). Similarly, Chisholm et al. (2013) found that species richness was generally positively related to productivity and biomass, with a doubling of species richness corresponding to an average of 48% increase in productivity and 53% increase in biomass at very small spatial scales ($20 \text{ m} \times 20 \text{ m}$). This may be

explained by higher species richness leading to niche complementarity that enhances resource capture, efficient resource use and higher productivity (Poorter et al., 2015). In addition, our results also showed that medium forests had higher values of Shannon diversity, species richness and stem density than rich forests but have lower biomass values which results in the nonsignificant relationship between taxonomic diversity and carbon stocks in the mixed model (Figure 2; Table 4). One possible mechanism underlying the negative relationship is the successional process following disturbance. Horn (1974) suggested that disturbed patches of forests have lower biomass and are also likely to have higher species richness, first because they contain a higher abundance of juvenile and sub - adult trees, and secondly because they may contain a mix of early- and late successional species; while in older patches, a few high-biomass individuals of late-successional species may dominate.

Finally, our results suggest that tree species composition rather than biodiversity have a greater effect on AGC storage. Total AGC was largely determined by the biomass of the 16 dominant species out of 110 recorded within the study area. Only five species (out of 52 species recorded; in order of importance: *Syzygium cumini*, *Litsea cambodiana*, *Lagerstroemia speciosa*, *Irvingia malayana*, *Millettia ichthyochtona*) contributed to 49.3% of plot AGC, and the remaining 47 species present within the plots, contributed to a further 50.7% in EBR. Notably, *Syzygium cumini* and *Terminalia franchetii* contributed to 57.7% of AGC in EBP (Table 2).

Conclusion

Although the tropical forests of Vietnam have experienced intense human pressure for years, we found that the remnant tropical forests of South-east Vietnam store an important amount of carbon (14.81–146.74 Mg ha⁻¹) and have a large biodiversity pool (110 tree species), contributing substantially to global change mitigation through its carbon sequestration and storage. We found that forest structural attributes, particularly stem density and maximum diameter had the strongest effect on AGC across the five forest types studied, while taxonomic diversity had a nonsignificant effect on AGC. The present study suggests that anthropogenic disturbance is an important factor to account for when determining the association between AGC, taxonomic diversity and forest structural attributes in the tropical forests of Vietnam. Therefore, maintaining the abundance distributions of remnant tree species, particularly that of large trees, as well as protecting remnant natural forest areas, is one important method to enhance AGC storage in these tropical forests of southern Vietnam.

Author contributions

N.T.T. conceived the study, did all analysis and led the writing; V.C.T. conducted the fieldwork; N.T.T, M.C.O and N.V.Q contributed to study methodology; N.T.T. and D.I.R.-H wrote the manuscript, with inputs of J.H.

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Conflict of interest

The authors declare that they have no conflict of interest.

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Appendix A.

Table A1. List of 110 tree species identified in the study area

ID	Species name	ID	Species name	ID	Species name
1	<i>Aglaia spectabilis</i> (Miq.) S.S.Jain & S.Bennet	38	<i>Dipterocarpus scaber</i> Buch.-Ham.	75	<i>Peltophorum pterocarpum</i> (DC.) K.Heyne
2	<i>Albizia lebbek</i> (L.) Benth.	39	<i>Dipterocarpus tuberculatus</i> Roxb.	76	<i>Pentacme siamensis</i> (Miq.) Kurz
3	<i>Albizia myriophylla</i> Benth.	40	<i>Dysoxylum cyrtobotryum</i> Miq.	77	<i>Peponidium horridum</i> Arènes
4	<i>Alstonia scholaris</i> (L.) R. Br.	41	<i>Elaeocarpus macroceras</i> (Turcz) Merr.	78	<i>Phyllanthus emblica</i> L.
5	<i>Amesiodendron chinense</i> (Merr.) Hu	42	<i>Engelhardtia roxburghiana</i> Lindl.	79	<i>Prunus Arborea</i> (Blume) Kalkman
6	<i>Anisoptera costata</i> Korth.	43	<i>Erythrina variegata</i> L.	80	<i>Pterocarpus macrocarpus</i> Kurz
7	<i>Aporosa sphaerosperma</i> Gagnep.	44	<i>Garcinia oblongifolia</i> Champ. ex Benth.	81	<i>Pterospermum diversifolium</i> Blume
8	<i>Aporosa villosa</i> Aubl.	45	<i>Gironniera parvifolia</i> Planch.	82	<i>Pterospermum heterophyllum</i> Hance
9	<i>Aquilaria crassna</i> Pierre ex Lecomte	46	<i>Gironniera subaequalis</i> Planch.	83	<i>Quercus kerrii</i> Craib
10	<i>Artocarpus gomezianus</i> Wall. ex Trécul	47	<i>Gleditsia fera</i> (Lour.) Merr.	84	<i>Rhamnus crenatus</i> Sieb
11	<i>Artocarpus lacucha</i> Buch.-Ham.	48	<i>Grewia nervosa</i> (Lour.) Panigrahi	85	<i>Samanea saman</i> (Jacq.) Merr.
12	<i>Baccaurea ramiflora</i> Lour.	49	<i>Holarrhena pubescens</i> Wall. ex G.Don	86	<i>Sandoricum koetjape</i> (Burm.f.) Merr.
13	<i>Barringtonia acutangula</i> (L.) Gaertn	50	<i>Hopea odorata</i> Roxb.	87	<i>Scaphium macropodium</i> (Miq.) Beumée ex K.Heyne
14	<i>Barringtonia macrostachya</i> (Jack) Kurz	51	<i>Hopea recopei</i> Pierre ex Laness	88	<i>Schefflera heptaphylla</i> (L.) Frodin
15	<i>Bauhinia malabarica</i> Roxb.	52	<i>Irvingia malayana</i> Oliv. ex A.W.Benn	89	<i>Schima crenata</i> Korth.
16	<i>Bombax ceiba</i> L.	53	<i>Knema lenta</i> Warb.	90	<i>Schrebera swietenoides</i> Roxb.
17	<i>Bridelia balansae</i> Tutcher	54	<i>Lagerstroemia calyculata</i> Kurz	91	<i>Semecarpus</i> sp.
18	<i>Buchanania latifolia</i> Roxb.	55	<i>Lagerstroemia speciosa</i> Pers.	92	<i>Senna siamea</i> (Lam.) H.S.Irwin & Barneby
19	<i>Caesalpinia sappan</i> L.	56	<i>Lepisanthes rubiginosa</i> (Roxb.) Leenh.	93	<i>Shorea obtusa</i> Wall.
20	<i>Canarium subulatum</i> Guillaumin	57	<i>Litsea cambodiana</i> Lecomte	94	<i>Shorea roxburghii</i> G. Don
21	<i>Careya aborea</i> Roxb.	58	<i>Macaranga denticulata</i> (Blume) Müll. Arg.	95	<i>Shorea stellata</i> (Kurz) Dyer
22	<i>Castanopsis piriformis</i> Hickel. & A Camus.	59	<i>Machilus odoratissima</i> Benth.	96	<i>Sindora siamensis</i> Miq.
23	<i>Catunaregam tomentosa</i> (Blume ex DC.) Tirveng	60	<i>Madhuca pasquieri</i> (Dubard) H.J.Lam	97	<i>Spondias pinnata</i> (L. f.) Kurz
24	<i>Cinnamomum bejolghota</i> (Buch.-Ham.) Sweet	61	<i>Magnolia conifera</i> (Dandy) V.S.Kumar	98	<i>Stereospermum cylindricum</i> Pierre ex Dop.
25	<i>Citharexylum spinosum</i> L.	62	<i>Mallotus pallidus</i> (Airy Shaw) Airy Shaw	99	<i>Strychnos nux-blanda</i> A.W.Hill
26	<i>Clausena excavata</i> Burm.f.	63	<i>Mangifera</i> sp.	100	<i>Swietenia mahagoni</i> (L.) Jacq.
27	<i>Cratoxylum formosum</i> (Jacq.) Benth. & Hook.f. ex Dyer	64	<i>Melia azedarach</i> L.	101	<i>Syzygium cumini</i> (L.) Skeels
28	<i>Cryptocarya annamensis</i> C.K.Allen	65	<i>Millettia ichthyochtona</i> Drake	102	<i>Syzygium lanceolatum</i> (Lam.) Wight & Arn.
29	<i>Dalbergia tonkinensis</i> Prain	66	<i>Millingtonia hortensis</i> L.f.	103	<i>Terminalia alata</i> Wall.
30	<i>Delonix regia</i> (Hook.) Raf.	67	<i>Morinda citrifolia</i> L.	104	<i>Terminalia calamansanay</i> Rolfe.
31	<i>Dillenia</i> SP	68	<i>Muntingia calabura</i> L.	105	<i>Terminalia chebula</i> Retz.
32	<i>Diospyros ehretioides</i> Wall. ex A. DC.	69	<i>Neonauclea sessilifolia</i> (Roxb.) Merr.	106	<i>Terminalia corticosa</i> Pierre ex Laness.
33	<i>Diospyros eriantha</i> Champ. ex Benth.	70	<i>Nephelium chryseum</i> Blume	107	<i>Terminalia franchetii</i> Gagnep.
34	<i>Diospyros maritima</i> Blume	71	<i>Nephelium lappaceum</i> L.	108	<i>Vitex ajugiflora</i> Dop
35	<i>Diospyros venosa</i> Wall. ex A.DC.	72	<i>Ormosia pinnata</i> (Lour.) Merr.	109	<i>Wrightia arborea</i> (Dennst.) Mabb.
36	<i>Dipterocarpus costatus</i> C.F.Gaertn.	73	<i>Parashorea chinensis</i> Hsie Wang	110	<i>Xylia xylocarpa</i> (Roxb.) Taub.
37	<i>Dipterocarpus obtusifolius</i> Teijsm.ex Miq.	74	<i>Parinari annamense</i> Hance		

Table A2. List of 44 family names found in the study area

ID	Family name	ID	Family name	ID	Family name	ID	Family name
1	Anacardiaceae	13	Elaeocarpaceae	25	Loganiaceae	37	Rosaceae
2	Apocynaceae	14	Euphorbiaceae	26	Lythraceae	38	Rubiaceae
3	Araliaceae	15	Eurylaimidae	27	Magnoliaceae	39	Rutaceae
4	Bignoniaceae	16	Fabaceae	28	Malvaceae	40	Sapindaceae
5	Burseraceae	17	Fagaceae	29	Meliaceae	41	Sapotaceae
6	Cannabaceae	18	Hypericaceae	30	Moraceae	42	Sterculiaceae
7	Chrysobalanaceae	19	Irvingiaceae	31	Muntingiaceae	43	Theaceae
8	Clusiaceae	20	Juglandaceae	32	Myristicaceae	44	Thymelaeaceae
9	Combretaceae	21	Lamiaceae	33	Myrtaceae	45	Ulmaceae
10	Dilleniaceae	22	Lauraceae	34	Oleaceae	46	Verbenaceae
11	Dipterocarpaceae	23	Lecythidaceae	35	Phyllanthaceae		
12	Ebenaceae	24	Leguminosae	36	Rhamnaceae		

Table A3. List of 18 order names found in the study area

ID	Orders	ID	Orders	ID	Orders
1	Dilleniales	7	Gentianales	13	Myrtales
2	Ebenales	8	Lamiales	14	Rosales
3	Ericales	9	Laurales	15	Rutales
4	Euphorbiales	10	Magnoliales	16	Sapindales
5	Fabales	11	Malpighiales	17	Theales
6	Fagales	12	Malvales	18	Urticales

Appendix B.

Table B1. Study area, minimal DBH (in cm), above-ground carbon (AGC, in Mg ha⁻¹) and Shannon diversity index of several studies that have been carried out in Tropical Vietnam

ID	Study area	Plot size (ha)	Minimal DBH	Evergreen forest AGC (Mg ha ⁻¹)	Deciduous forest AGC (Mg ha ⁻¹)	Shannon Index	Reference
1	Central, Vietnam	0.04	≥5 cm	EBR = 166.8; EBM = 83; EBP = 44.5, EBG = 18.2			(Avitabile et al., 2016)
2	Highland, Vietnam	0.25	≥10 cm	104–175		3.44–4.11	(Do et al., 2017)
3	Xuan Lien Nature Reserve, Thanh Hoa, Vietnam	0.05	≥5 cm	42.78–118.35			(Nguyen & Kappas, 2020)
4	Highland, Vietnam	0.05–0.1	≥5 cm	EBR = 149.64; EBM = 117.49; EBP = 47.5	25.75–77		(Luong et al., 2015)
5	Highland, Vietnam	0.25	≥5 cm	EBR = 227.8; EBM = 198.9; EBP = 138.2, EBG = 75.2			(Hai et al., 2015)
6	North-central Vietnam	0.25	≥5 cm	EBR = 111; EBM = 60; EBG = 56			(Stas et al., 2020)
7	Six ecoregions of Vietnam	1	≥10 cm	93.53–122.62			(Do et al., 2017)
8	Central Highland of Vietnam	1	≥10 cm	172.2			(Nam et al., 2018)
9	Six ecoregions of Vietnam	1	≥10 cm	50.76–181	39.95–64.86	1.5–3.5	(Con et al., 2013)