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Stand Structural Diversity and Species with Leaf Nitrogen Conservation Drive Aboveground Carbon Storage in Tropical Old-Growth Forests

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Abstract: Tropical old-growth forests are essential for global carbon regulation. Although there is increasing evidence that species and functional diversity, stand structural diversity, functional compositions, and elevation play roles in ecosystem functioning, the relative strengths of these drivers and the underlying mechanisms (mass-ratio hypothesis or niche complementarity hypothesis) are not clear. Aboveground carbon storage, species diversity, stand structural diversity, community-weighted mean (CWM), and functional diversity (FDvar) of 12 leaf traits were analyzed using data from 56 old-growth forest communities in the Dawei Mountain area of Southwest China. Multiple regression models were used to test the relative importance of the predictor variables and the structural equation model was used to explore the direct and indirect influences on aboveground carbon storage. High structural diversity moderately enhanced aboveground carbon storage. CWM leaf nitrogen concentration in young leaves weakly affected aboveground carbon storage. Our final multiple regression model showed that aboveground carbon storage is mostly affected by diameter at breast height (DBH) diversity, followed by FDvar of dry matter concentration in mature leaves and CWM nitrogen concentration in young leaves. The structural equation model indicated that elevation negatively affects aboveground carbon storage via diameter at breast height (DBH) diversity. Our results suggest that niche complementarity effects moderately drive aboveground carbon storage in tropical old-growth forests, but do not fully support the importance of the mass-ratio hypothesis.

Keywords: aboveground carbon storage; functional compositions; stand structural diversity; elevation; niche complementarity; old-growth forest

1. Introduction

Tropical forests play an important role in global carbon (C) regulation [1]. Understanding the relationship between biodiversity and ecosystem functioning is essential for the regulation global climate change and to avoid biodiversity loss caused by anthropogenic activities [2,3]. There is substantial evidence that ecosystem functioning and biodiversity in natural forests are closely related [2–4]. Although numerous studies showed that high species diversity enhances aboveground

C storage [4,5], this is still subject of debate [6–8] and the relationships between ecosystem functioning and biodiversity need to be further clarified [4,8], particularly regarding the multivariate mechanisms simultaneously affecting ecosystem functioning and biodiversity [4]. Since specific resource limitations correspond to plant growth and survival in different forest types; more information about the drivers and mechanisms influencing ecosystem functioning is needed to adequately protect and manage old-growth forests [3,9].

The mass-ratio hypothesis [10] and the niche complementarity hypothesis [11] are the two main mechanisms by which species diversity can influence ecosystem functioning. Based on the niche complementarity hypothesis, functional diversity (FDvar) and species diversity can increase the efficiency of resource use, thereby increasing C storage [12]. Using functional diversity, an index that reflects the variability of traits, is a more mechanistic way to explain ecosystem function compared to species diversity [3]. The mass-ratio hypothesis predicts that the dominant main species in the community determine ecosystem functions, which can be examined by the correlations between ecosystem functioning and community-weighted mean (CWM) functional traits [13]. Species that enhance ecosystem functioning may have conservative or acquisitive traits [9,14,15]. Conservative traits are consistently associated with low C inputs through photosynthesis and low C losses through decomposition; they are a combination of attributes such as low specific leaf area (SLA), low leaf concentrations of nitrogen (LNC) and phosphorous (LPC), high leaf thickness (LT), and high leaf dry matter content (LDMC) [14]. Acquisitive traits have the opposite attributes [14]. Several studies supported either the niche complementarity hypothesis [16–18] or the mass-ratio hypothesis [4,19], which were found to be nonexclusive with each other [4]. However, it is still unclear how these two mechanisms influence ecosystem functioning.

Recently, studies showed that stand structural diversity facilitates niche differentiation and drives ecosystem functions [3,5,20]. Multilayered stand structures promote efficient light use via improved crown space allocation [21], while functional diversity and species diversity indirectly affect ecosystem functioning through stand structural diversity [22–24]. Thus, it is crucial to simultaneously consider species diversity, stand structural diversity, functional dominance, and functional diversity to test the relative importance of the underlying mechanisms and drivers [4,8].

Abiotic factors are important drivers of aboveground C storage as they determine plant survival and growth [4,25]. The microclimate strongly impacts species abundances and distribution [26], which in turn affects both biological and physical stand attributes [27]. Thus, abiotic factors can indirectly affect C storage by affecting biotic factors [4,8]. In general, elevation, a comprehensive factor reflecting climate, affects ecosystem functioning [8]. For example, Cavanaugh [18] reported that elevation was negatively correlated with species diversity and functional diversity, although it had no impact on C storage. However, whether elevation influences aboveground C storage indirectly via biotic factors is still a considerable knowledge gap.

Karst landforms, fragile ecosystems characterized by water deficit and soil erosion, account for 15% of the global land area and are mainly distributed in Southwest China [28]. The authors of a previous study found a significant difference in primary productivity between karst and non-karst areas [29]; however, ecosystem functioning and its influencing factors in old-growth forests in karst and non-karst need to be further investigated.

In this study, we investigated 56 plots in tropical old-growth forests in Southwest China to address the following question: How do biotic (species diversity, stand structural diversity, functional diversity, and functional composition) and abiotic (elevation gradients and karst and non-karst landscapes) factors affect aboveground C storage? We hypothesized that (1) species diversity, stand structural diversity, and functional diversity simultaneously enhance aboveground C storage, and (2) elevation and soil types directly or indirectly affect aboveground C storage via biotic factors.

2. Materials and Methods

2.1. Site Description and Plots

Our study was conducted in the Dawei Mountain area (22°35′–23°10′ N, 103°20′–104°03′ E), located in Yunnan Province, Southwest China. Mean annual rainfall is 1700–1900 mm, at a mean annual temperature of 22.6 °C. Mean temperature of the coldest month (January) is 15.2 °C, while that of the hottest month (July) is 27.7 °C. The area is frost-free throughout the year. Elevation ranges between 225 and 2365 m (the highest peak of Dajian Mountain). The forest types change significantly from the bottom to the top of the mountain [30].

To ensure the comparability of forest communities at different elevation gradients, only old-growth forests, away from human life and almost without anthropogenic disturbance, were selected. Most of the old-growth forests were located in steep terrain, especially in karst areas. Supported by the local forestry department, we established one gradient with four elevations, namely 800, 1200, 1600, and 2000 m, and two soil types (karst and non-karst). Because of the strong heterogeneity of karst habitat, seven 20 × 20 m repeated plots were established, with a distance of more than 100 m between plots for each group to improve representativeness. In total, 56 plots (four elevations × two soil types × seven replicates) were selected. Between 2017 and 2018, all individual trees were identified at the species level in the plot or in the laboratory via samples [4]. Table 1 and Table S1 show the basic information of the plots and the important values of dominant species. Figure 1 shows the locations of the sampling plots. The importance value (IV) was calculated as follows:

$$\text{IV} = (\text{relative density} + \text{relative frequency} + \text{relative dominance})/3 \times 100\% \quad (1)$$

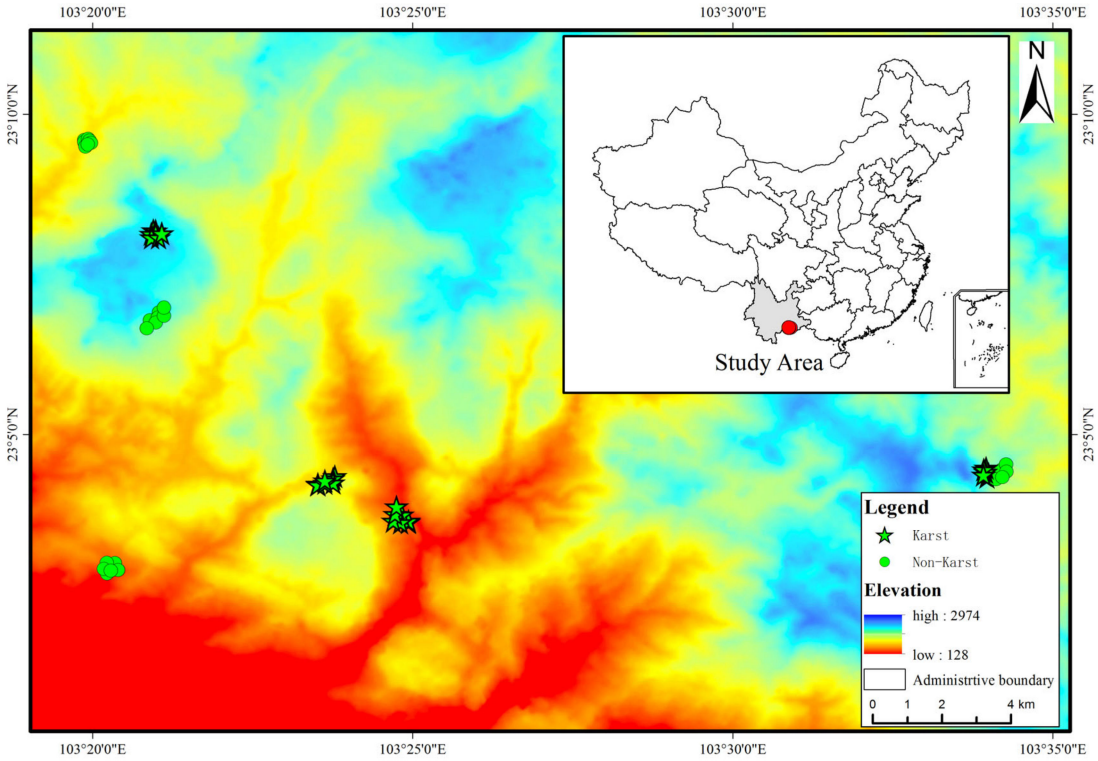


Figure 1. Locations of plots in Dawei Mountain area in Yunnan Province, Southwestern China.

Table 1. Basic vegetation and soil characteristics of the established plots in the Dawei Mountain area in Yunnan Province, Southwestern China.

Elevation	**800 m**		**1200 m**		**1600 m**		**2000 m**	
Region Types	**Karst**	**Non-Karst**	**Karst**	**Non-Karst**	**Karst**	**Non-Karst**	**Karst**	**Non-Karst**
Soil type	Red soils	Brown soils	Red soils	Brown soils	Red soils	Brown soils	Red soils	Brown soils
Slope (°)	25	27	42	35	27	30	36	40
Rock bare rate (%)	70	0	70	0	45	0	55	0
Height (m)	8.77 (3.5, 22.8)	9.78 (4.1, 23.8)	9.08 (3.6, 18.2)	14.57 (3.4, 25.5)	8.34 (3.1, 29)	8.18 (3.2, 25)	6.38 (4.2, 18.9)	11.08 (4, 20)
DBH (cm)	13.25 (5, 116.1)	15.42 (5, 220)	22.03 (4.8, 82.1)	24.19 (5, 166.3)	10.48 (5, 76.2)	9.11 (4.9, 163.8)	8.56 (4.9, 111.5)	21.79 (4.9, 170)
Density (plants/hm^2)	989 (765, 1083)	833 (698, 936)	533 (324, 725)	322 (278, 365)	1500 (1263, 1786)	1622 (1359, 1827)	811 (524, 1254)	411 (316, 625)

Note: DBH, diameter at breast height; mean (minimum, maximum).

2.2. Quantification of Aboveground C Storage

In each plot, we measured the diameter at breast height (DBH) of all trees with a DBH greater than 5 cm. A telescopic pole was used to measure tree height lower than 18 m, and a clinometer was used for the height measurements of taller trees. Because our study areas were relatively widely distributed and there were no species-specific biomass models corresponding to the 152 species in our study sites, the global allometric equation, which considers height, DBH, and wood density, was used to calculate the aboveground biomass of individuals with a DBH greater than 5 cm [31]. Aboveground C storage was calculated by multiplying the aboveground biomass by 0.5 [32]. Wood density values were obtained for 81% of the species, with wood density levels based on average levels for the family or average levels of the corresponding plot for the remaining species [18]. The global allometric equation was calculated as follows:

$$AGB = 0.0673 \times \left(\rho \times DBH^2 \times H\right)^{0.976}, \quad (2)$$

where ρ represents wood density (g cm^{-3}), H represents height (m), and DBH represents diameter at breast height (cm).

2.3. Quantification of Stand Structural and Species Diversity

Species and stand structural (height and DBH) diversity were quantified via the Shannon–Wiener biodiversity index [23]. As recommended by Ali et al. [23], different DBH classes (8, 6, 4, and 2 cm) and height classes (5, 4, 3, and 2 m) were used to calculate stand structural diversity. The proportions of individual species, height class, and DBH class were represented by the relative basal area [23,33]. Because the height and DBH diversity based on different discrete classes may predict aboveground C storage differently, relationships between aboveground C storage and each class of stand structural diversity were evaluated, and the lowest Akaike information criterion (AIC) values were used to select the classes used for the models in Table 2 [34].

Table 2. General linear relationship between aboveground C storage and stand structural (tree diameter at breast height (DBH) and height) diversity of different classes across the plots. The bold discrete classes were selected.

DBH Class (cm)	AIC	R^2	p-Value	Height Class (m)	AIC	R^2	p-Value
2	105.84	0.168	0.002	2	105.84	0.207	<0.001
4	89.37	0.38	<0.001	3	107.16	0.175	0.001
6	87.27	0.402	<0.001	4	108.14	0.133	0.006
8	**85.04**	**0.413**	**<0.001**	5	106.13	0.195	<0.001

Note: AIC, Akaike information criterion; DBH, diameter at breast height.

2.4. Functional Traits

LNC, LPC, N:P ratio, SLA, LDMC, and LT parameters, which are crucial for plant survival and growth [23,33,35], were determined for all species in the plots in both young and mature leaves, considering that central plant trade-offs strongly correlate with leaf longevity [9,36]. In total, 152 species, 1684 trees, and 33,564 leaves were sampled. In the field, three to five healthy mature plants per species were randomly selected in sunlit positions, preferably totally unshaded or minimally shaded (to avoid the effect of the canopy). Five branches were collected as far as possible from five different positions on each tree, i.e., from the four sides and the upper position of the sunlit side of the tree crown. Samples from different branches of one tree were considered as one sample. Moist paper towels were used to cover the samples during transportation. After arriving at the laboratory, the young leaves, mature leaves, and branches were separated, and approximately 10 healthy leaves were selected from each sample to measure average weight, thickness, and specific leaf area. Leaf thickness and weight were measured at an accuracy of 0.1 mm and 0.0001 g, respectively. A leaf area meter (LI-3100C, Li-Cor,

Lincoln, NE, USA) was used to scan the corresponding leaves. Subsequently, leaf samples were oven-dried at 80 °C until constant weight to determine leaf dry mass for the calculation of LDMC and SLA. The LDMC was calculated as the oven-dried mass of a leaf divided by its water-saturated fresh mass, while SLA was calculated as the one-sided area of a leaf divided by its oven-dried mass. Leaf N and P concentrations were measured using a flow injection automatic analyzer (Skalar-1000, The Netherlands).

CWM trait values in each plot were calculated using the following equation [9,14]:

$$\mathrm{CWM}(\mathrm{trait}_X) = \sum_{i=1}^{s} p_i \times x_i, \quad (3)$$

where *CWM (trait$_X$)* represents the CWM *X* trait, *s* represents the species number in each plot, p_i represents the *i*th species' relative abundance in the plot, and x_i represents the *i*th species' trait value.

Functional diversity was calculated as follows [14]:

$$\mathrm{FDvar} = 2/\pi \arctan(5V) \text{ and } V = \sum_{i=1}^{s} p_i (\ln x_i - \ln x)^2, \quad (4)$$

where $p_i = a_i / \sum_{i=1}^{s} a_i$, a_i represents *i*th species' relative abundance in the plot, x_i represents the ith species' trait value, and $\ln x = \sum_{i=1}^{s} p_i \ln x_i$. The variation range of FDvar values was 0 to 1.

2.5. Statistical Analysis

We used one-way ANOVA and least square difference (LSD) multiple comparison tests to determine the differences in aboveground C storage and abiotic factors. The Shapiro–Wilk test was used to examine data normality [17]. Prior to data analysis, non-normal continuous variables were natural-logarithm-transformed to improve normality and linearity [4,17].

Simple and multiple linear regressions were employed to explore the relationships between aboveground C storage and explanatory variables [4]. The bivariate relationships between elevation and exogenous variables were showed in Figure 2. The combination of 28 indices yielded a total of 268,435,455 models, which was beyond the capacity of R [9]. To select the optimal subset of predictor variables of aboveground C storage, ordinary least squares multiple regression analysis was first conducted with all 12 CWM indices (CWM SLA, LDMC, LT, LNC, LPC, and N:P ratio in both young and mature leaves), resulting in 4095 possible models. Subsequently, we used the other 15 biotic indices (FDvar of SLA, LDMC, LT, LNC, LPC, and N:P ratio in both young and mature leaves, species diversity, DBH, and height diversity) to conduct multiple regression analyses, which resulted in 32,367 possible models. Finally, we combined the elevation with the two former best subsets of predictors to conduct multiple analyses, and the eight predicted variables resulted in 255 possible models. All possible models were evaluated with the corrected Akaike information criterion (AICc), and the best-fit regression model was selected based on the lowest AICc values [4,37]. Multicollinearity was diagnosed using the variance inflation factor (VIF); all VIF values were lower than 10 in the best-fit regression model, suggesting that our results were not affected by collinearity among predictor variables [38]. For model selection, we used the "glmulti" package in R 3.6.1 [39].

The structural equation model (SEM), which is widely used to explore the complex relationships between ecosystem functioning and predictor variables [40], was applied to investigate how biotic and abiotic factors affect aboveground C storage (directly or indirectly). The variables retained in the best-fit regression model were used to construct the SEM [9,36]. We hypothesized partial mediation among the variables. The soil types were replaced by categorical variables, the karst area was coded as 1, and the non-karst area was coded as 2. The comparative fit index (CFI), the goodness-of-fit index (GFI), the root mean square error of approximation (RMSEA), the Chi-square (χ^2) test, and the AIC were employed to test the fitness of the SEM [20]. The SEM was implemented using AMOS 21.0 software.

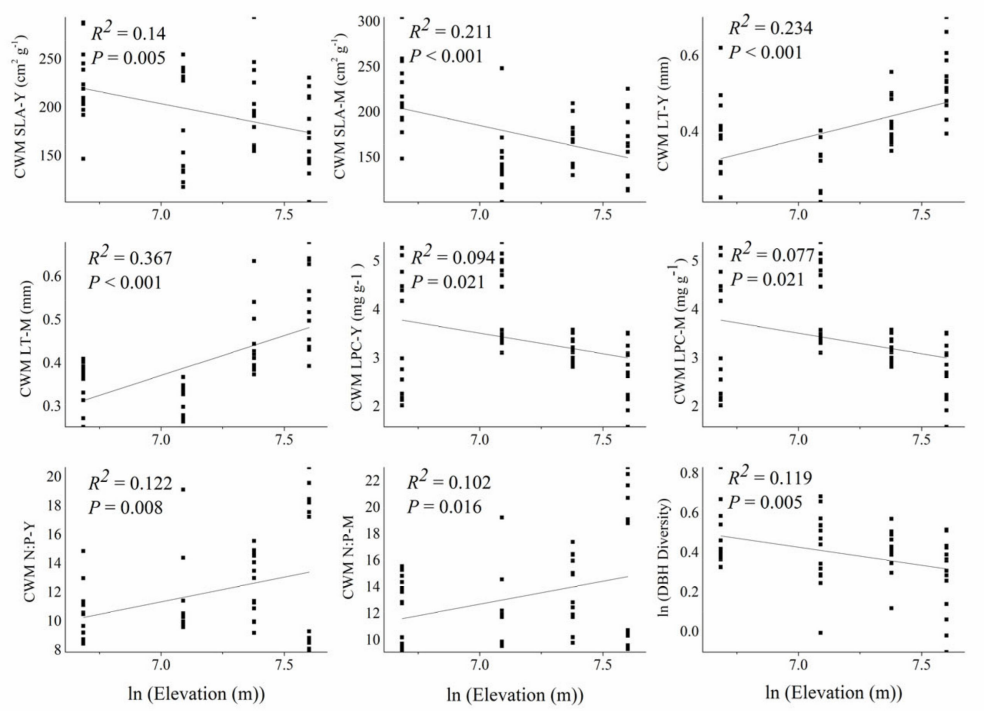


Figure 2. Bivariate relationships between elevation (dependent) and exogenous (independent) variables (n = 56). Only significant relationships are shown ($p < 0.05$). CWM, community-weighted mean; FDvar, functional diversity; SLA-Y, specific leaf area of young leaf; LT-Y, leaf thickness of young leaf; LPC-Y, leaf phosphorus concentration of young leaf; N:P-Y, N:P ratio of young leaf; SLA-M, specific leaf area of mature leaf; LT-M, leaf thickness of mature leaf; N:P-M, N:P ratio of mature leaf; DBH: diameter at breast height.

3. Results

3.1. Effects of Influencing Factors on Aboveground C Storage

Aboveground C storage was moderately affected by DBH (R^2 = 0.413, $p < 0.001$) and height diversity (R^2 = 0.207, $p < 0.001$) (Figure 3). The CWM nitrogen concentration of young leaves weakly affected aboveground C storage (R^2 = 0.08, p = 0.034). Aboveground C storage decreased with FDvar of LDMC and SLA in both young and mature leaves. The FDvar of P concentration in young leaves (R^2 = 0.072, p = 0.045) and elevation (R^2 = 0.067, p = 0.03) also weakly affected aboveground C storage. Carbon storage in the karst area at 2000 m was significantly higher than that in the non-karst area, while no differences were observed for the other three elevations (Table S2).

3.2. Relative Importance of all Predictor Variables for Aboveground C Storage

Only four predictor variables were retained in the optimal multiple regression model, accounting for 57.21% of the total variation in aboveground C storage (Table 3). The DBH diversity still mostly affected aboveground C storage ($p < 0.001$, β = 0.47). The FDvar of leaf dry matter content in mature leaves (p = 0.009, β = −0.27) and the CWM nitrogen concentrations of young leaves (p = 0.011, β = −0.25) both negatively affected aboveground C storage, while height diversity showed no impact on aboveground C storage in the final multiple regression model (p = 0.081, β = −0.18).

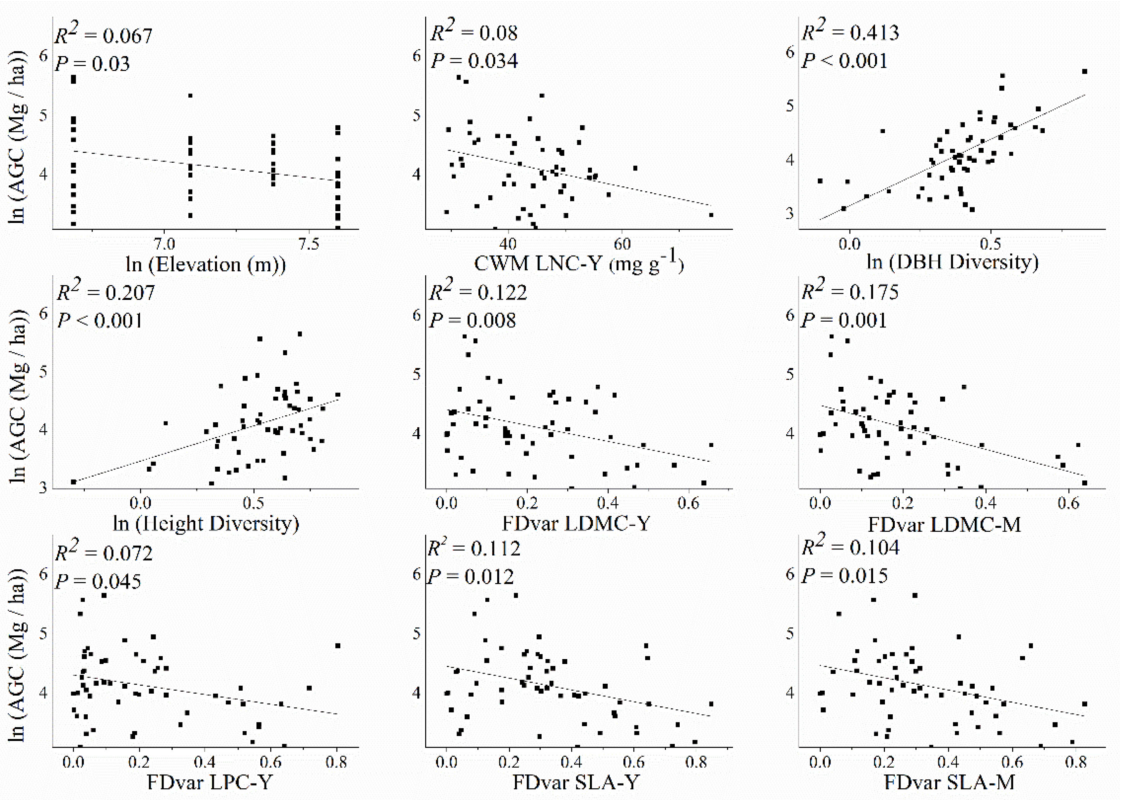


Figure 3. Significant bivariate relationships between aboveground carbon storage (AGC) and predictor variables (n = 56). CWM, community-weighted mean; LNC-Y, young leaf nitrogen concentration; DBH Diversity, diameter at breast height diversity; FDvar, functional diversity; LDMC-Y, leaf dry matter content of young leaf; LDMC-M, leaf dry matter content of mature leaf; LPC-Y, leaf phosphorus concentration of young leaf; SLA-Y, specific leaf area of young leaf; SLA-M, specific leaf area of mature leaf.

Table 3. The optimal model resulted from a sequence of regression analyses of aboveground carbon storage. The regression coefficient (Coeff.), the standardized regression coefficient (Beta), the *t*-test, and the *p*-value are given for each predictor variable. For the model, the coefficient of determination (R^2), the *p*-value, and the Akaike Information Criterion (AICc) are also given. *p*-values of <0.05 are in bold.

Model and Predictor	Coeff.	Beta	*t*	*p*	R^2	AICc
Effects of community-weighted mean (CWM)						
Model[1]				**<0.001**	0.28	105.52
Constant	9.20	0	7.21	**<0.001**		
CWM SLA-Y	−0.01	−0.39	−2.33	**0.024**		
CWM LT-Y	−2.66	−0.46	−3.21	**0.002**		
CWM LNC-Y	−0.02	−0.34	−2.70	**0.009**		
CWM LDMC-M	−5.35	−0.44	−0.28	**0.007**		
Effects of functional diversity (FDvar), species diversity, and stand structural diversity						
Model[2]				**<0.001**	0.51	80.80
Constant	3.35	0	14.36	**<0.001**		
FDvar LDMC-M	−1.17	−0.27	−2.59	**0.012**		
DBH Diversity	1.85	0.49	4.24	**<0.001**		
Height Diversity	0.53	0.17	1.60	0.116		

Table 3. *Cont.*

Model and Predictor	Coeff.	Beta	*t*	*p*	R^2	AICc
Joint effect of all predicted variables						
Model[3]				**<0.001**	0.57	76.18
Constant	4.14	0	11.15	**<0.001**		
CWM LNC-Y	−0.02	−0.25	−2.65	**0.011**		
FDvar LDMC-M	−1.16	−0.27	−2.73	**0.009**		
DBH Diversity	1.78	0.47	4.30	**<0.001**		
Height Diversity	0.56	0.18	1.78	0.081		

Note: CWM, community-weighted mean; FDvar, functional diversity; DBH, diameter at breast height; SLA-Y, specific leaf area of young leaf; LT-Y, leaf thickness of young leaf; LNC-Y, leaf nitrogen concentration of young leaf; LDMC-M, leaf dry matter content of mature leaf; *Model*[1], the optimal model resulted from 12 CWM leaf functional traits; *Model*[2], the optimal model resulted from functional diversity, species diversity and stand structural diversity; *Model*[3], the optimal model resulted from the combination of the elevation and the two former best subsets of predictors.

3.3. Direct and Indirect Impacts on Aboveground C Storage

The optimal SEM accounted for 53, 13, 5, 2, and 1% of the total variation in aboveground C storage, DBH diversity, height diversity, FDvar of LDMC in mature leaves, and CWM nitrogen concentration in young leaves, respectively (Figure 4). Higher DBH diversity directly enhanced aboveground C storage (p = 0.002, β = 0.48), whereas CWM young leaf nitrogen concentration (p = 0.009, β = −0.27) and FDvar of mature leaf dry matter content (p = 0.034, β = −0.27) both showed negative direct effects (Figure 4, Table 4). Elevation negatively and directly affected DBH diversity (p < 0.001, β = −0.37), but demonstrated no direct impact on aboveground C storage (p = 0.906, β = −0.02). However, elevation showed a moderately strong negative indirect effect via DBH diversity (p = 0.002, β = −0.18). The total effect of elevation was significant (p = 0.044, β = −0.30).

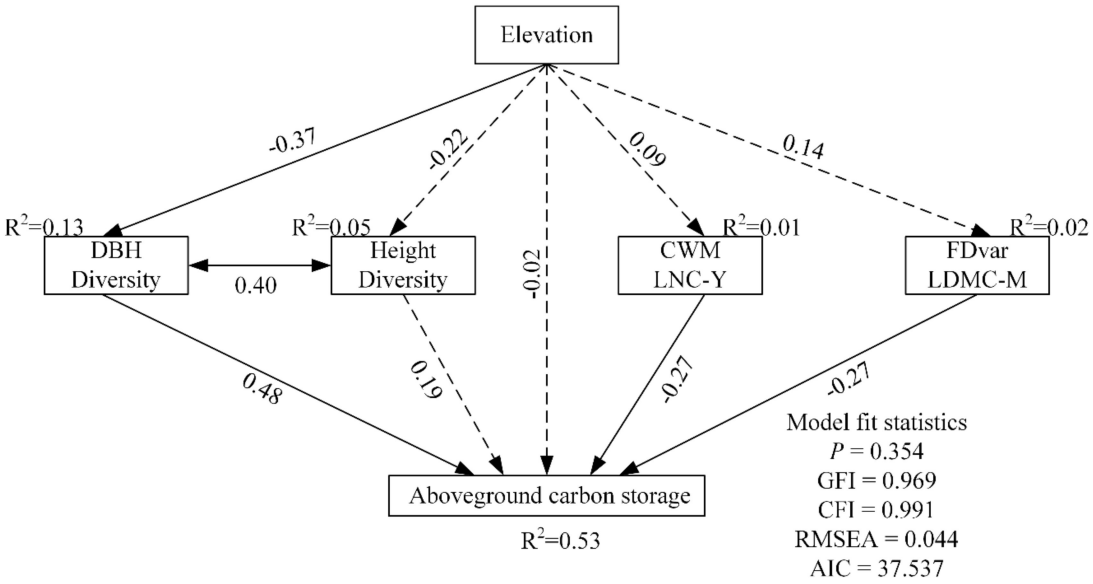


Figure 4. Optimal structural equation model relating aboveground carbon storage to predictor variables. Model-fit statistics and standardized regression coefficients of each path are shown in the figure. Significant and nonsignificant routes at the level of 0.05 are represented by solid arrows and dashed arrows, respectively. The total variation of the explained variable is shown as R^2, which is explained by all explanatory variables. CWM, community-weighted mean; LNC-Y, young leaf nitrogen concentration; DBH diversity, diameter at breast height diversity; FDvar, functional diversity; LDMC-M, mature leaf dry matter content.

Table 4. Direct, indirect, and total standardized effects on aboveground carbon storage based on the structural equation model. The indirect effect of elevation was calculated by multiplying the standardized effects of all paths on one route, from elevation to mediator, and then to aboveground carbon storage, while the total effect was calculated by adding standardized direct and indirect effects.

Predictor	Pathway to Aboveground Carbon Storage	Effect	*p*-Value
Elevation	Direct effect	−0.02	0.906
	Indirect effect via DBH diversity	−0.18	0.002
	Indirect effect via height diversity	−0.04	0.057
	Indirect effect via CWM LNC-Y	−0.02	0.412
	Indirect effect via FDvar LDMC-M	−0.04	0.245
	Total effect	−0.30	0.044
DBH Diversity	Direct effect	0.48	<0.001
Height Diversity	Direct effect	0.19	0.057
CWM LNC-Y	Direct effect	−0.27	0.003
FDvar LDMC-M	Direct effect	−0.27	0.004

Note: CWM, community-weighted mean; LNC-Y, young leaf nitrogen concentration; DBH diversity, diameter at breast height diversity; FDvar, functional diversity; LDMC-M, mature leaf dry matter content.

4. Discussion

Our hypothesis that aboveground C storage is affected by species diversity was not supported by the results, which were consistent with some previous studies [8,20,24]. This may be due to a potent effect of the dominant productive species [8,41,42] or competition exclusion [23,43,44]. In natural forests, species richness may achieve saturation and the ecological niches of most species may overlap, potentially reducing the influence of species diversity on ecosystem functioning [45,46]. As expected, both DBH and height diversity promoted ecosystem functioning, consistent with recent findings [8,23,24,47]. This may have been a result of the multilayered forest structure, enhancing the capture of water, light, and soil nutrients [5,47]. Our outcomes were similar to those of recent European studies [48,49], where structural heterogeneity was not shown to be correlated with tree species diversity in old-growth forests.

Unexpectedly, we found weak negative associations between FDvar of leaf functional traits and aboveground C storage, which was not consistent with the niche complementarity hypothesis and some previous results [8,23]. Low trait diversity may be caused by large dominated species [50]. Such results provide a potential solution to stand structure [8,20,23,24,42] as the niche complementarity mechanism maintaining ecosystem functioning, but not species diversity [6,23] or functional diversity [8,14,18,35].

The CWM nitrogen concentration of young leaves negatively affected aboveground C storage, consistent with our hypothesis and previous studies [9,35]. The only weak effect of CWM LNC in young leaves on aboveground C storage did not fully support the mass-ratio hypothesis. Our results led us to infer that the leaf economic spectrum of plants correlates with aboveground C storage [51]. The high aboveground C storage was accompanied by a low CWM leaf nitrogen concentration, indicating that "slow" forests result in high aboveground C accumulation in old-growth forests [52]. Conservative resource-use syndromes are associated with low C losses through mortality [35] or decomposition [13,53]. In old-growth communities, forests dominated by conservative species might have lower biomass turnover rates and higher aboveground C storage [14]. The insignificant effect of nitrogen concentrations of old leaves on aboveground C storage was inconsistent with previous result in second subtropical forests [9]. However, a previous study [9] showed that CWM leaf nitrogen concentration of young leaves had a stronger effect on aboveground biomass than that of mature leaves, which was similar to our results. This outcome may have resulted from the nutrient transfer efficiency of leaves, which was mainly reflected in the transfer of nutrients from mature branches and leaves to new leaves when there were not enough nutrients for plant growth [54,55].

As expected, aboveground C storage decreased significantly with increasing elevation, which was consistent with previous results [8]. The DBH diversity, CWM SLA, and LPC decreased while CWM LT increased with increasing elevation (Figure 2), indicating that elevation has a significant filtering effect [56]. These leaf conservative resource-use syndromes and the low stand structural diversity at higher elevations may result from adaptations of plants to the harsh environment at higher elevations [57]. As hypothesized, elevation was also shown to indirectly affect aboveground C storage via stand structural diversity, consistent with previous studies where climate factors indirectly affected aboveground C storage via forest composition [4,40]. Unexpectedly, we found no significant difference in AGC between karst and non-karst areas, which was not consistent with Wang [29], who observed differences in net primary productivity between karst and non-karst areas. The outcome of our study may have resulted from the same precipitation and forest types in karst and non-karst areas, which are crucial factors regarding biomass or C storage [3,4].

In our study, stand structure diversity was the most important driver of aboveground C storage, followed by CWM, LNC, and FDvar leaf traits, suggesting that the predicted variables supporting the niche complementarity hypothesis are more important than the variables supporting the mass-ratio hypothesis in enhancing aboveground C storage. These results indicate that niche complementarity may exert a more important effect on the promotion of ecosystem function than the mass-ratio effect. Considering both niche complementarity and the mass-ratio effect simultaneously may lead to an improved understanding of the mechanisms of ecosystem function (Table 3). However, it must be noted that some other functional traits, such as plant diameter [18,33], wood traits [9], and leaf anatomical traits [58], can also affect ecosystem functioning, although these were not measured in this study. The dynamics of other ecosystem functioning parameters (e.g., aboveground productivity) may not be consistent with aboveground C storage [59]. Ecosystem functioning and biotic factors change considerably with succession [2,9,23] and changes in other abiotic factors, such as soil nutrients [3,20] and climate factors [4]. Thus, we encourage further studies investigating the relationships between ecosystem functioning and biodiversity, taking into consideration the predictor variables in communities in different successional stages.

5. Conclusions

Our data, obtained from 56 old-growth forest plots, indicate that the niche complementarity effect is essential in the promotion of ecosystem functioning. Greater complex stand structural diversity moderately enhanced aboveground C storage. Species with leaf nitrogen conservation was shown to drive aboveground C storage. Elevation showed a significant filtering effect on DBH diversity and CWM leaf functional traits, indirectly affecting aboveground C storage via DBH diversity. Our results indicate that complex stand structure and species with leaf nitrogen conservation can maximize aboveground C storage in tropical old-growth forests.

Supplementary Materials: The following are available online at http://www.mdpi.com/1999-4907/11/9/994/s1, Table S1: Importance values of the dominant species of different old-growth forest communities in the Dawei Mountain area in Yunnan Province, Southwestern China, Table S2: Community characteristics of tropical old-growth forest communities in the Dawei Mountain area in Yunnan Province, Southwestern China.

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