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Interaction Effect of Stand Age and Diversity on Aboveground Wood Carbon Accumulation in Subtropical Mixed Forests of the Zhejiang Province (China)

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Abstract: Aboveground wood carbon (AWC) stocks in forest ecosystems are mediated by biotic and abiotic variables. Understanding the internal regulatory mechanisms of forests is important for future forest management and global climate change mitigation. However, how these factors affect AWC in subtropical mixed forests remains poorly understood. Using a database from the National Forest Inventory (NFI) from China, we observed the effects of climate variables (temperature and precipitation), stand structure indices (stand density and DBH coefficient of variation and diversity), stand diversity indices (taxonomic diversity, functional diversity, and phylogenetic diversity), and stand functional indices on coniferous mixed forests (CMF), coniferous–broadleaf mixed forests (CBMF), and broadleaf mixed forests (BMF). Meanwhile, we examined the AWC based on a linear mixed model and a structural equation model for each mixed forest. We found that both stand structure and stand diversity can affect the AWC through their indirect effects on the stand function, aligning with the niche complementarity effect. Stand age is an important factor affecting AWC because it interacts with stand structure and stand diversity. Our study highlights that AWC is dependent on the regulation of stand age and structure, which can be crucial for boosting high carbon stocks in subtropical forests.

Keywords: mixed forests; aboveground wood carbon; stand age; forest structure; stand diversity

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1. Introduction

As an important component of the global terrestrial ecosystem carbon cycle, forests store about 80% of aboveground biomass carbon and about 40% of belowground biomass carbon in terrestrial ecosystems [1,2]. Forest ecosystems can reduce the concentration of carbon dioxide (CO_2) in the atmosphere, which mitigates global warming and has a large environmental and economic impact [3], as well as promoting the functions, services, and sustainability of trees [4]. Subtropical forest ecosystems occupy a large area in China, and this was estimated to be 0.72 ± 0.08 Pg C yr^{-1}, which contributes to about 8% of the global net ecosystem productivity of forest ecosystems [5], therefore, their ecological value cannot be ignored. At present, Zhejiang Province, which is located in a typical subtropical region, has carried out a 5 year afforestation and reforestation project, and there are plans to afforest 120,000 hectares and for the province's forest coverage rate to reach 60.8% [6]. Therefore, it is necessary to monitor the effect of the driving factors on forest carbon accumulation.

However, forest carbon accumulation is driven by multiple abiotic and biotic factors, such as stand structure [7,8], stand diversity [9–13], stand function [10,14,15], and abiotic factors (topographic and environmental factors) [16–20]. Aboveground wood carbon

(AWC) is another way to characterize the living tree biomass, which is an indicator of the active capacity of the carbon pool [21].

Many studies have highlighted the importance of stand diversity for most forest ecosystem functions and services [22–24]. Longer evolutionary divergence and richer functional traits can be the main mechanisms by which stand diversity indices affect the forest ecosystem's stability and productivity [11,13,25]. Biodiversity (taxonomic, phylogenetic, and functional diversity) can explain the main driving mechanism for the direct or indirect effects on AWC [13]. Previous studies [26] found that during the succession of subtropical forests, biodiversity was significant for explaining biomass. Two ecological hypotheses (the niche complementarity effect and the mass ratio effect) explain this mechanism [27]. The niche complementarity hypothesis suggests that more tree species, a better stand structure, and functional diversity can promote forest functioning because of niche differentiation and facilitation [7,27]. The mass ratio effect hypothesis states that the forest community function is driven by the dominant, high-functioning tree species [18,28]. The positive relationship between the community-weighted mean (CWM) of trait values and AWC also indicates the mass ratio hypothesis [29]. A high CWM of acquisitive traits (e.g., maximum tree height and specific leaf area) could result in high photosynthetic rates [9,15,30,31]. Previous studies [12,14,32] have shown that the community-weighted mean of leaf traits could predict the aboveground biomass.

In addition to stand diversity, stand structure is also an important factor affecting AWC [11,33,34]. Stand structural complexity, which is typically characterized by the coefficient of variation of individual trees diameters at breast height (DBH), trees heights, and stand density [20,35,36], increases the niche complementarity effect to boost the forest's productivity [7,27]. Therefore, as competition intensifies, individual tree sizes become unequal, and coexisting mixed tree species in the forest ecosystem can make more efficient use of the resources and perform efficient light capture to promote the forest's biomass [7,25,37].

Topographic factors (e.g., elevation, slope, and aspect) could influence the AWC, especially on a large scale [19,37,38]. Previous studies have indicated that climatic factors (e.g., precipitation and temperature) can indirectly and directly mediate the aboveground biomass by changing the plant growth patterns, which in turn affects the stand diversity and structure [38]. Previous studies have shown that appropriate precipitation and light can regulate the plant growth rates [39,40]. Therefore, abiotic variables must be considered when one is studying the driving mechanisms of AWC in different forest types.

It is generally clear that stand age increases the AWC stock, which might be due to the large-size tree effect [41,42]. In different forest types, the redundant biodiversity and structure of forests change, however, the internal regulation effect of stand age as the main factor driving biomass/carbon storage has seldom been studied. Meanwhile, exploring the mechanisms in subtropical forests is crucial for future forest management decision making. Therefore, in this study, our objective was to integrate stand age along with climatic, stand structure, and stand function indices to assess the drivers of AWC in subtropical mixed forests across Lishui city, Zhejiang Province, south-eastern China, using a dataset from 268 permanent sample plots. We hypothesized that: (1) abiotic factors (topographic and environmental factors) and biotic factors (stand structure, diversity, and function) have direct and indirect effects on the AWC; (2) stand age is a key factor of the AWC through an interaction effect with other factors (stand structure and diversity). Meanwhile, based on this study of the driving mechanisms of each forest type, it provides an empirical basis for forest management in the region.

2. Materials and Methods

2.1. Study Area and Forest Inventory Data

This study was conducted in Lishui (118°41′–120°26′ E and 27°25′–28°57′ N), Zhejiang Province, south-eastern China. The area covers approximately 17,300 km^2, of which 80.79% is forested (Figure 1). This area is typical of the subtropical monsoon region, with a mean annual temperature of 17.2 °C and a mean annual precipitation of 1468 mm. Lishui is rich in forest resources, and the main vegetation types are coniferous, coniferous–broadleaf, broadleaf, and bamboo forests.

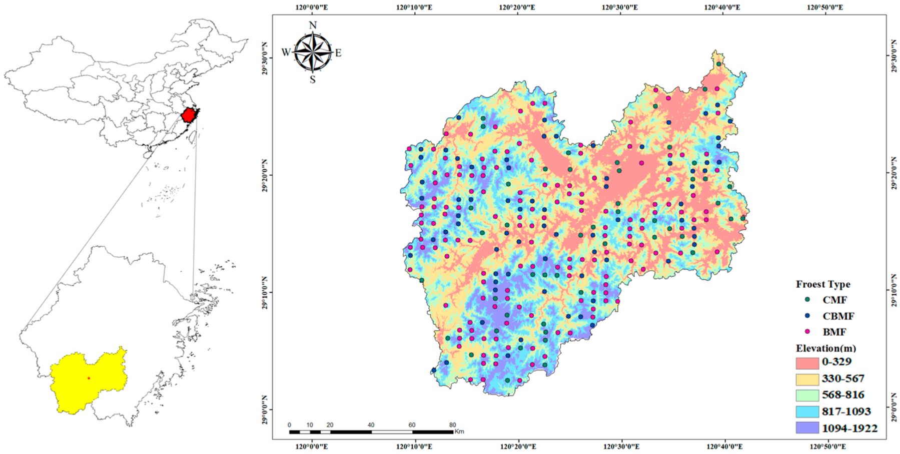

Figure 1. The distribution of sample plots in Lishui, Zhejiang Province, China. Abbreviations refer to forest type: coniferous mixed forest (CMF), coniferous–broadleaf mixed forest (CBMF), and broadleaf mixed forest (BMF).

The dataset of the stand characteristics used in this study was retrieved from permanent sample plots of the 10th National Forest Inventory (NFI) from 2019. The east–west interval distance between the adjacent plots was 6 km, the south–north interval was 4 km, and each plot covered an area of 800 m^2 (28.28 m × 28.28 m). The selected forest types were coniferous mixed forest (CMF), coniferous–broadleaf mixed forest (CBMF), and broadleaf mixed forest (BMF) (48, 71, and 149 plots, respectively). Location (longitude and latitude), elevation, slope, tree species, forest type, and individual trees with DBH > 5.0 cm were recorded according to the protocols of the National Forest Inventory standards issued by the State Forestry Administration of China. For the age of the forest, this can be obtained by consulting historical information from the Zhejiang Forest Resources Monitoring Centre or local forestry departments. However, for a few sample plots in remote mountainous areas, it is necessary to obtain information manually in the field, for example, by drilling the wood cores of three standard trees in the sample plots, obtaining their annual rings and calculating their average value to conservatively estimate the age of the sample plots. The stand characteristics of the forests in Lishui are listed in Table S1.

The aboveground biomass estimation model [43,44] was used to calculate the aboveground wood biomass of the sample plots. The total AWC stocks were calculated by multiplying the carbon conversion coefficients for each of the tree species [44]. The carbon stocks of all of the individual trees in the sample plots were summed to obtain the AWC for each sample plot, and these were converted to tons per hectare (Mg ha^{-1}).

2.2. Environment Variables

In this study, we chose two topographic variables as predictors to explain the aboveground forest carbon stocks, the elevation, and the slope for the plots. Furthermore, elevation (0–300 m, 301–600 m, 601–900 m, 901–1200 m, and 1201–1500 m) and slope (0–5°, 6–14°, 15–24°, 25–34°, 35–44°, 45–54°) were classified in five categories.

The mean annual temperature (MAT), mean annual precipitation (MAP), and annual heat-moisture index (AHM) were used as climatic data for the sample sites. Based on the latitude, longitude, and elevation of the sample sites, we extracted the climatic data from ClimateAP v2.30 [45]. Furthermore, we obtained the mean values of the variables from 1981 to 2019.

2.3. The Stand Diversity, Structure, and Functional Variables

We calculated three components of the tree diversity indices in the sample plots: taxonomic, phylogenetic, and functional diversity. Taxonomic diversity was determined using Shannon's tree diversity index. Phylogenetic diversity was determined using Faith's phylogenetic diversity [29], which was calculated as the sum of branch lengths of the phylogeny among the tree species in each sample plot (Figure S10). Functional diversity was determined as the functional dispersion index, which was calculated as the functional divergence of the species in each sample plot. The functional diversity indices included three functional traits: the tree wood density (WD, g cm^{-3}), the specific leaf area (SLA, m^2 kg^{-1}), and the maximum tree height (H, m). These functional traits profoundly affect the trees' growth, survival, reproduction, and carbon storage [32,46–48]. Furthermore, wood density values were extracted from a global wood density database [49]. The specific leaf area values were obtained from the study by Wang et al. [50]. The database compiles the functional traits of Chinese land plants and contains information on the locations where the data were collected, and the data we extracted were all from relevant species in the Zhejiang region. The maximum tree height values were obtained from the Flora of China [51] (http://www.iplant.cn/foc, accessed on 15 August 2022), a database of real values obtained from specific areas, reflecting the regional variability of the habitats and stands. Functional composition was defined as the mean community weight (CWM) of each trait. We calculated three functional traits: CWM_{WD}, CWM_{SLA}, and CWM_{H}.

We calculated three components of the stand structure indices in the sample plots: the DBH coefficient of variation, the structural diversity, and the stand density (stem ha^{-1}). The DBH coefficient of variation values were calculated from the trees in the plot. The structural diversity values were quantified based on the Shannon index of DBH [52], as follows:

$$Shannon_{DBH} = -\sum_{i=1}^{d} p_i \times \ln(p_i) \quad (1)$$

where p_i is the proportion of the ith DBH class, and the diameter class width was set to 2 cm.

2.4. Statistical Analysis

A one-way analysis of variance (ANOVA) and an LSD test were used to test for differences in the AWC at a significance level of 0.05. Prior to the following analysis, the values of the aboveground wood carbon were log transformed to meet the normal distribution of the residuals. All of the variables were standardized to have a mean of 0 and a standard deviation of 1. Linear regression analyses were used to test the bivariate relationships between the AWC and all of the variables in the three forest types. Furthermore, to reduce multiple correlations and collinearity among the variables (Figures S4–S6), we performed a principal component analysis (PCA), as suggested by previous studies on diversity indices, stand structure indices, and stand functional traits of each forest type, respectively [37,53]. The first principal component of the results of the principal component analysis (*PC1*) was used as an independent variable and in the statistical analysis. A summary of the variables used in this study is provided in Table S1. We used a multiple linear mixed-effects model to examine the effect of diversity*PC1*, stand structure*PC1*, stand function*PC1*, stand age and climate*PC1* on the AWC of CMF, CBMF, and BMF. Additionally, diversity*PC1*, stand structure*PC1*, stand function*PC1*, stand age and climate*PC1* were fixed effects, and elevation and slope were random effects. We used the Akaike information criterion (AIC) to correct and select the best-fit model (the lowest AIC). The model as follows:

$$\ln AWC = \beta_0 + \beta_1 * diversity\mathit{PC1} + \beta_2 * structure\mathit{PC1} + \beta_3 * function\mathit{PC1} + \beta_4 * age + \beta_5 * climate\mathit{PC1} + b_{elevation} + c_{elevation} + \varepsilon \quad (2)$$

where AWC is aboveground wood carbon; diversity*PC1* is the first multivariate axis of the three diversity indices of the PCA; structure*PC1* is the first multivariate axis of the three stand structure indices of the PCA; function*PC1* is the first multivariate axis of the three

CWM trait indices of the PCA; climate*PC1* is the first multivariate axis of the three climate indices of the PCA; age is stand mean age; elevation and slope are candidate variables, as mentioned above; β_0 is the estimated fixed intercept; β_1, β_2, β_3, β_4, and β_5 are the model coefficients estimated for diversity*PC1*, structure*PC1*, function*PC1*, age, and climate*PC1*, respectively; ε represents the error term.

Based on our conceptual model (Figure 2), we used structural equation modelling (SEM) to test the direct and indirect effects of the drivers mentioned above on the AWC. The model was evaluated using the chi-squared (χ^2) test, the comparative fit index (CFI), the goodness-of-fit index (GFI), and the standardized root mean square residuals (SRMR). We selected the best SEM with CFI > 0.95, GFI > 0.95, SRMR < 0.08, the lowest AIC value, and the highest explained variation (R^2) [54,55].

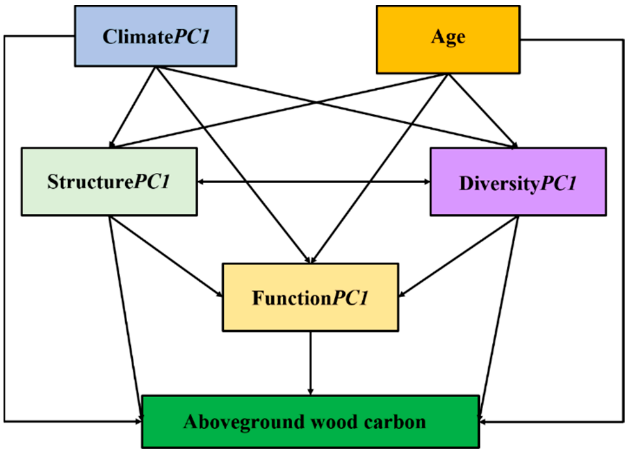

Figure 2. Conceptual models indicating how diversity*PC1*, structure*PC1*, function*PC1*, stand age and climate*PC1* affect aboveground wood carbon. PC1 refers to the first principal component of the results of principal component analysis.

All of the analyses were performed using R 4.1.2 [56]. Diversity indices were calculated using the vegan package [57]. The PCA was performed using the Stat software package. Multiple linear mixed-effects models were evaluated using the nlme package, and the SEM was performed using the lavaan package [58].

3. Results

3.1. The Bivariate Relationships between Abiotic Factors and AWC in Three Different Kinds of Mixed Forests

The AWC stock in the BMF (63.44 Mg ha^{-1}) was significantly higher compared to the those of CBMF (45.82 Mg ha^{-1}) and CMF (46.44 Mg ha^{-1}) ($p < 0.01$) (Figure 3). However, the AWC values in the CMF were not significantly different from those in the CBMF (Figure 3). Of all of the variables, only the mean annual temperature and stand age were not significantly different across the forest types, while all of the other variables showed differences (Figure 4).

When the bivariate relationships between the abiotic variables and the AWC were examined, the stand age and elevation were significantly positively correlated with the AWC (Figure 5, $p < 0.05$) but not with the slope (Figure 5, $p > 0.05$). Furthermore, the relationship between the AWC and the stand age increased in three different kinds of mixed forests ($R^2 = 0.126$, $p < 0.05$; $R^2 = 0.525$, $p < 0.001$; $R^2 = 0.483$, $p < 0.001$, Figure 5). The slope displayed a weaker/non-significant linear fit with the AWC. For the correlation between the other variables and the AWC, please refer to the Supplementary Material (Figures S1–S3).

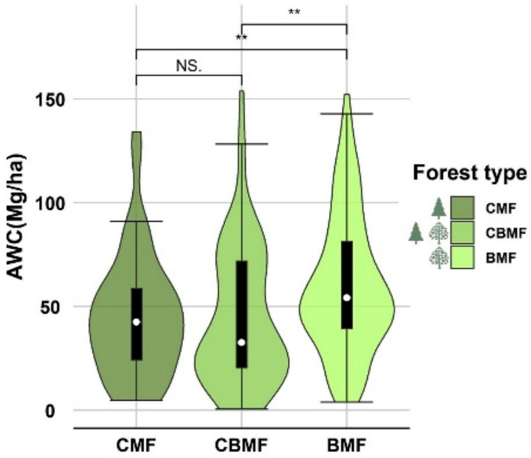

Figure 3. Kernel density estimation of aboveground wood carbon (AWC) in three different kinds of mixed forests. CMF, CBMF, and BMF represent coniferous mixed forests, coniferous–broadleaf mixed forests, and broadleaf mixed forests, respectively. The white points represent the mean values and the height and width of the graph represent the range and frequency of the distribution, respectively. The white points represent the mean values and the black lines represent the standard deviations. One-way analysis of variance (ANOVA) followed by the LSD test was used to analyze the differences of AWC among in three different kinds of mixed forests. The symbols ** denote significant differences in the different forest types at $p < 0.01$. NS represents no significance in the different forest types at $p > 0.05$.

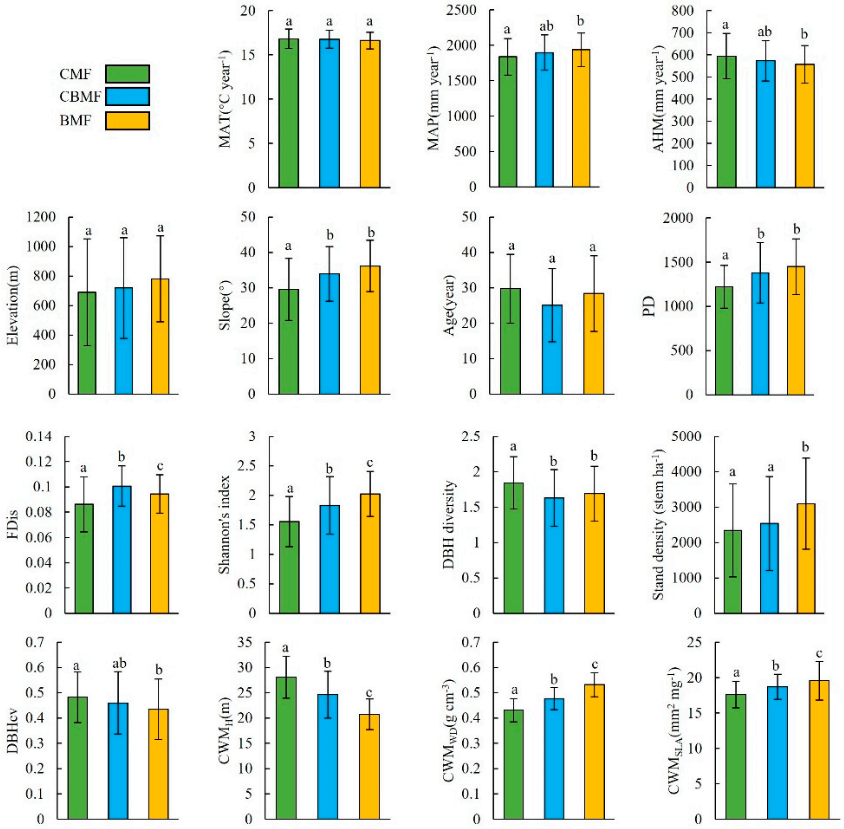

Figure 4. One-way analysis of variance (ANOVA) and LSD tests were used to analyze the differences between the variables in the three different types of mixed forests. CMF, CBMF, and BMF represent mixed coniferous, mixed conifer-broadleaf, and mixed broadleaf forests, respectively.

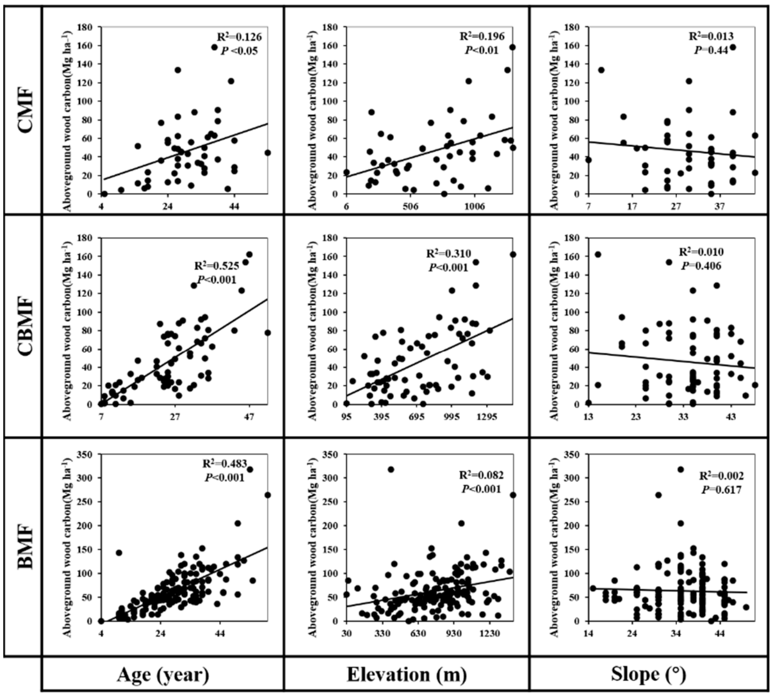

Figure 5. Bivariate relationships between abiotic variables and aboveground wood carbon. CMF, CBMF, and BMF represent coniferous mixed forests, coniferous–broadleaf mixed forests, and broadleaf mixed forests, respectively.

3.2. Changes and Interactions of Drivers in Three Different Kinds of Mixed Forests

In each mixed forest type, we performed a PCA on the stand diversity indices, stand structural indices, functional indices, and climate indices (Figures S7–S9). We selected the best-fit model (Table 1). Furthermore, we constructed a linear mixed model with the first principal components (diversity*PC1*, structure*PC1*, function*PC1,* and climate*PC1*) in each forest type.

Table 1. SEMs of aboveground wood carbon (AWC) of mixed coniferous forests (CMF), coniferous–broadleaf mixed forest (CBMF), and broadleaf mixed forests (BMF). Model in bold font represents the final causal model used in this study.

Forest Type	Models	df	Model Fit Statistics Summary						
			CFI	GFI	RMSEA	SRMR	Chi-Square	AIC	*p* Value
CMF	Model 1 (Full model)	0	1	1	0	0	0	714.534	0.083
	Model 2 [Model 1: (Climate*PC1*→Function*PC1*)]	**1**	**1**	**1**	**0**	**0.002**	**0.008**	**712.542**	**0.927**
	Model 3 (Model 1: (Age→Function*PC1*))	1	0.965	0.967	0.296	0.04	5.219	717.753	0.022
	Model 4 (Model 1: (Climate*PC1*→Function*PC1*&Age→Function*PC1*))	2	0.973	0.966	0.185	0.04	5.274	715.808	0.072
CBMF	Model 5 (Full model)	0	1	1	0	0	0	1032.232	0.096
	Model 6 (Model 5: (Climate*PC1*→Function*PC1*))	1	0.987	0.983	0.197	0.04	3.744	1033.976	0.053
	Model 7 (Model 5: (Age→Function*PC1*))	**1**	**0.998**	**0.994**	**0.072**	**0.016**	**1.373**	**1031.605**	**0.241**
	Model 8 (Model 5: (Climate*PC1*→Function*PC1*&Age→Function*PC1*))	2	0.989	0.98	0.133	0.039	4.502	1032.734	0.105
BMF	Model 9 (Full model)	0	1	1	0	0	0	2232.194	0.079
	Model 10 (Model 9: (Climate*PC1*→Function*PC1*))	**1**	**1**	**0.999**	**0**	**0.008**	**0.265**	**2230.459**	**0.607**
	Model 11 (Model 9: (Age→Function*PC1*))	1	0.95	0.971	0.296	0.054	14.084	2244.278	0.243
	Model 12 (Model 9: (Climate*PC1*→Function*PC1*&Age→Function*PC1*))	2	0.947	0.967	0.216	0.064	15.951	2244.145	0.135

Note: the minus sign means that this path relationship goes out in SEMs. CMF, CBMF, and BMF represent coniferous mixed forests, coniferous–broadleaf mixed forests, and broadleaf mixed forests, respectively.

In the results of the linear mixed model of the CMF (Table 2), structure*PC1* and age significantly affected the AWC ($p < 0.001$), while diversity*PC1*, function*PC1*, and climate*PC1* also exhibited significant effects on the AWC ($p < 0.01$). Furthermore, we found that stand age and the interaction between stand age and structure*PC1* influenced the AWC ($p < 0.01$). In the results of the linear mixed model of the CBMF (Table 3), we found that diversity*PC1* was a new component that was capable of significantly and strongly interacting with stand age, thus influencing the AWC ($p < 0.001$). In the results of the linear mixed model of the BMF (Table 4), we found that stand age, structure*PC1*, and diversity*PC1* significantly affected the AWC ($p < 0.001$). Furthermore, the interaction of stand age with structure*PC1* and diversity*PC1* significantly affected the AWC ($p < 0.001$). Our results reveal a change in the driving factors in three different kinds of mixed forests.

Table 2. Summary of the linear mixed-effect model of the effects of age, diversity*PC1*, structure*PC1*, function*PC1*, and climate*PC1* on aboveground wood carbon, which were analyzed for coniferous mixed forests (CMF). *PC1* refers to the first principal component of the results of principal component analysis. The colons represent interactions between the components. Only significant components ($p < 0.05$) are reported, and the green areas are the highly significant influence components.

	numDF	denDF	F Value	*p* Value	Remark
(Intercept)	1	12	4757.35	$p < 0.001$	***
Structure*PC1*	1	12	132.45	$p < 0.001$	***
Age	1	12	89.44	$p < 0.001$	***
Age: Structure*PC1*	1	12	15.79	0.0018	**
Function*PC1*	1	12	15.14	0.0021	**
Diversity*PC1*	1	12	12.98	0.0036	**
Climate*PC1*	1	12	10.97	0.0062	**
Diversity*PC1*: Climate*PC1*	1	12	8.38	0.0134	*
Age: Structure*PC1*: Function*PC1*: Climate*PC1*	1	12	8.09	0.0148	*
Age: Diversity*PC1*	1	12	7.04	0.0211	*
Age: Climate*PC1*	1	12	6.25	0.0279	*
Diversity*PC1*: Structure*PC1*	1	12	5.24	0.0410	*

Note: The symbols * denotes significant at the 0.05 alpha level, ** denotes significant at the 0.01 level and *** denotes significant at the 0.001 level

Table 3. Summary of the linear mixed-effect model of the effects of age, diversity*PC1*, structure*PC1*, function*PC1*, and climate*PC1* on aboveground wood carbon, which were analyzed at for coniferous–broadleaf mixed forests (CBMF). *PC1* refers to the first principal component of the results of principal component analysis. The colons represent interactions between the components. Only significant components ($p < 0.05$) are reported, and the green areas are the highly significant influence components.

	numDF	denDF	F Value	*p* Value	Remark
(Intercept)	1	35	2356.02	$p < 0.001$	***
Age	1	35	219.37	$p < 0.001$	***
Diversity*PC1*	1	35	58.66	$p < 0.001$	***
Structure*PC1*	1	35	33.64	$p < 0.001$	***
Age: Diversity*PC1*	1	35	27.01	$p < 0.001$	***
Climate*PC1*	1	35	14.22	0.0006	***
Function*PC1*: Climate*PC1*	1	35	4.59	0.0392	**

Note: The symbols ** denotes significant at the 0.01 level and *** denotes significant at the 0.001 level

3.3. The Direct and Indirect Effects of Driving Factors on AWC

The best SEMs for testing the direct and indirect effects of stand age, diversity*PC1*, structure*PC1*, function*PC1*, and climate*PC1* on the variables showed that all of the predictor variables together explained 73.8%, 77%, and 66.7% of the variance in the AWC, respectively (Figure 6). However, the pathways of these effects in three different kinds of mixed forests were different. There was a clear pattern in the strength of the stand age effect on the AWC after controlling for stand diversity, structure, function, and climate within the mixed forests. The climate*PC1* factor had a negative direct effect on the AWC, and its strength decreased with the change in the forest type ($\beta = -0.174$, $\beta = -0.237$, and $\beta = -0.081$ in CMF, CBMF, and BMF types, respectively; Figures 6 and 7). Meanwhile, the direct effect of stand age on the AWC increased with the change in the forest type ($\beta = -0.022$, $\beta = 0.151$, and $\beta = 0.425$ in CMF, CBMF, and BMF types, respectively; Figures 6 and 7). Additionally, the positive effect of stand structure*PC1* on the AWC decreased with the change in the forest type ($\beta = 0.744$, $\beta = 0.534$, and $\beta = 0.228$ in CMF, CBMF, and BMF types, respectively; Figures 6 and 7).

Table 4. Summary of the linear mixed-effect model of the effects of age, diversity*PC1*, structure*PC1*, function*PC1*, and climate*PC1* on aboveground wood carbon, which were analyzed for the broadleaf mixed forests (BMF). *PC1* refers to the first principal component of the results of principal component analysis. The colons represent interactions between the components. Only significant components ($p < 0.05$) are reported, and the green areas are the highly significant influence components.

	numDF	denDF	F Value	*p* Value	Remark
(Intercept)	1	114	2221.85	$p < 0.001$	***
Age	1	114	440.65	$p < 0.001$	***
Diversity*PC1*	1	114	66.17	$p < 0.001$	***
Age: Diversity*PC1*	1	114	55.77	$p < 0.001$	***
Structure*PC1*	1	114	33.42	$p < 0.001$	***
Age: Structure*PC1*	1	114	16.39	$p < 0.001$	***
Structure*PC1*: Climate*PC1*	1	114	11.09	0.0012	**
Age: Diversity*PC1*: Structure*PC1*: Climate*PC1*	1	114	11.08	0.0012	**
Structure*PC1*: Function*PC1*	1	114	10.26	0.0018	**
Age: Climate*PC1*	1	114	7.32	0.0079	**
Age: Diversity*PC1*: Structure*PC1*	1	114	6.73	0.0107	*
Age: Diversity*PC1*: Climate*PC1*	1	114	6.27	0.0137	*
Climate*PC1*	1	114	6.00	0.0158	*
Function*PC1*	1	114	5.27	0.0235	*
Age: Function*PC1*	1	114	4.20	0.0427	*
Age: Structure*PC1*: Function*PC1*: Climate*PC1*	1	114	4.10	0.0452	*

Note: The symbols * denotes significant at the 0.05 alpha level, ** denotes significant at the 0.01 level and *** denotes significant at the 0.001 level

In addition, stand diversity*PC1* directly and indirectly affected the AWC via stand function*PC1*, and the total effect increased with the change in the forest type. Meanwhile, function*PC1* had a direct effect on the AWC, and its strength increased with the change in the forest type ($\beta = -0.270$, $\beta = 0.144$, and $\beta = 0.078$ in CMF, CBMF, and BMF types, respectively; Figures 5 and 6). Interestingly, climate*PC1* had a significant negative effect only on stand diversity*PC1*, and stand age had a significant negative effect only on stand function*PC1* in the BMF (Figure 6).

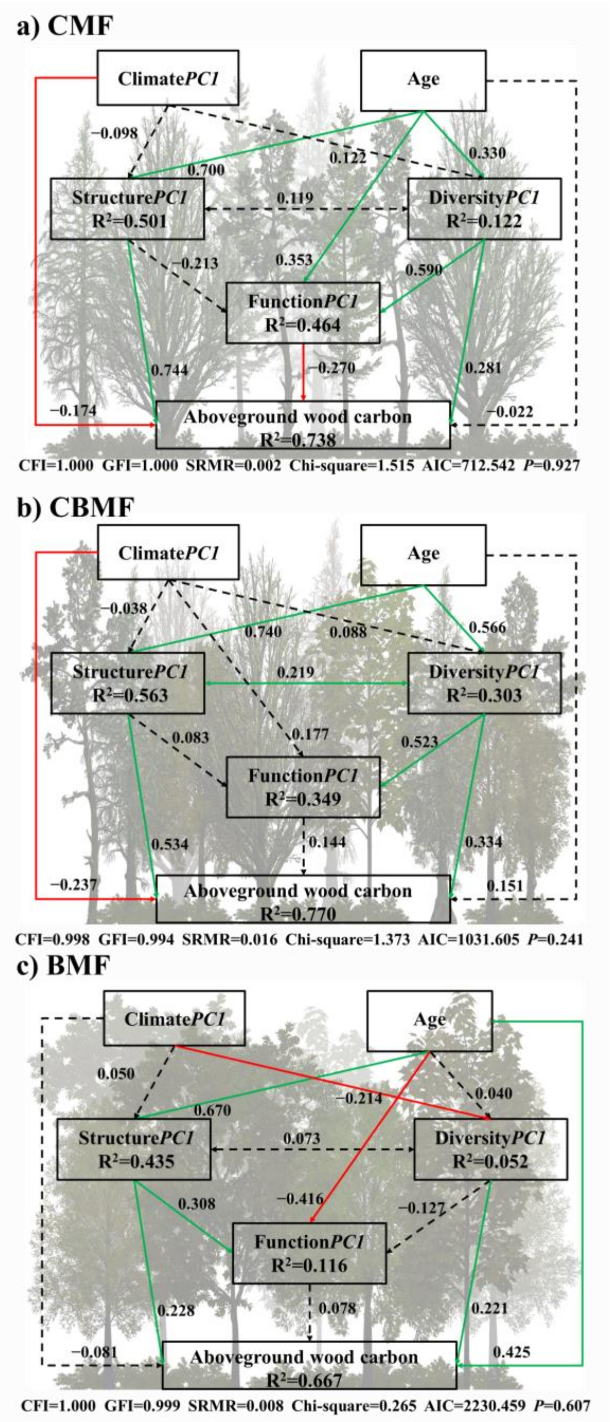

Figure 6. Structural equation models for testing the direct effects of climate and stand age versus indirect effects mediated by stand structure, stand diversity, and stand function on aboveground wood carbon with the change in forest types. CMF, CBMF, and BMF represent coniferous mixed forests, coniferous–broadleaf mixed forests, and broadleaf mixed forests, respectively. *PC1* refers to the first principal component of the results of principal component analysis. Numerical values under each graph refer to comparative fit index (CFI), goodness-of-fit index (GFI), standardized root mean square residuals (SRMR), and Akaike information criteria (AIC). The dashed lines represent non-salient paths ($p > 0.05$), while the solid lines represent significant paths ($p < 0.05$). The standardized coefficients are marked (see Table S2 for statistics). Positive and negative pathways are shown in green and red colors, respectively. R^2 represents the proportion of explained variance.

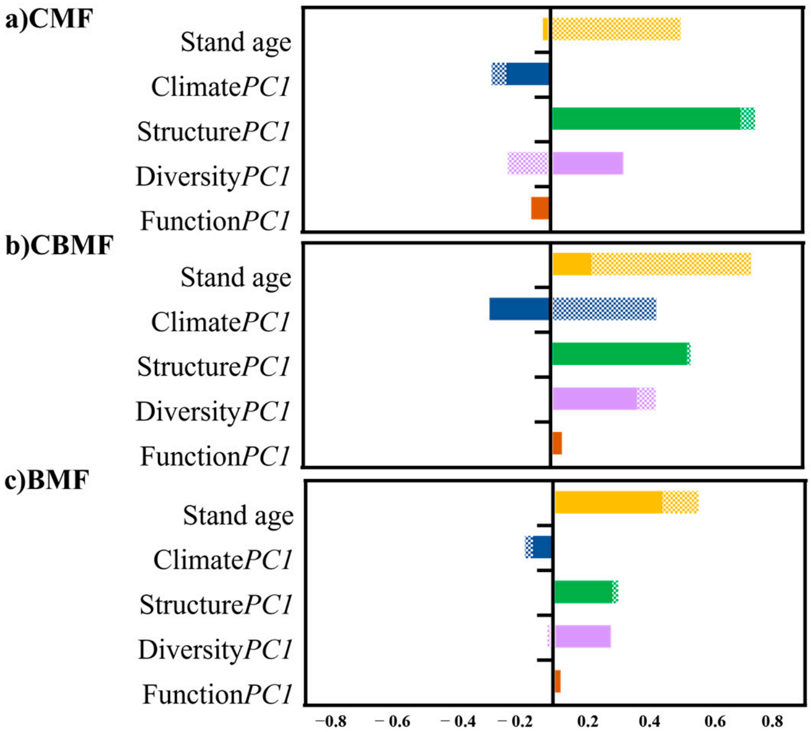

Figure 7. Beta coefficients of stand age, climate*PC1*, structure*PC1*, diversity*PC1*, and function*PC1* on aboveground wood carbon. CMF, CBMF, and BMF represent the coniferous mixed forests, coniferous–broadleaf mixed forests, and broadleaf mixed forests, respectively. *PC1* refers to the first principal component of the results of principal component analysis. Filled and dotted bars indicate the direct and indirect effects of abiotic and biotic factors on aboveground wood carbon, respectively.

4. Discussion

4.1. Different Effects of Abiotic Factors on AWC in Three Different Kinds of Mixed Forest Types

We found that the AWC stock of the broad-leaved mixed forest (BMF) was significantly higher than those of the coniferous mixed forest (CMF) and coniferous–broadleaf mixed forest (CBMF), which is consistent with the results of previous studies [43,59]. In our results, evergreen broad-leaved mixed forest as the dominant forest community in the subtropical region had the highest mean AWC value (63.44 Mg ha^{-1}), which was already higher than the mean AWC values of Zhejiang Province (55.70 Mg ha^{-1}), but it was lower than the global mean AWC values (94.2 Mg ha^{-1}) [60,61]. Tree species conversion is recognized as an important factor affecting the soil properties with the change in the forest type [32,62]. Changes in the composition of tree species (from coniferous species dominated to broadleaf species dominated) with different functional traits may result in different carbon stocks [63–65]. Broadleaf trees species (e.g., *Cyclobalanopsis glauca* and *Cinnamomum camphora*) are considered to be suitable for planting in Lishui because it is located in the subtropical monsoon region [66]. Previous studies suggest that an increase in the number of highly productive tree species may lead to an increased community AWC [67]. This indicates that changes in the tree species can promote niche complementarity, improve nutrient utilization, and enhance the influence of niche differentiation on AWC [28,68,69].

Topography (elevation and slope) is a common factor influencing both the tree species and the environmental patterns [19,38,70]. Our results indicate that elevation has a significant positive effect on the AWC in three different kinds of mixed forests. This suggests that the AWC increases along an altitudinal gradient. In contrast to our results, many studies have reported a decreasing trend in the forest AWC along an altitudinal gradient [8,70–72]. At higher altitudinal gradients, less human disturbance is assumed to be a possible reason for the increasing trend of AWC along the altitudinal gradients because forest growth is promoted by less human disturbance [16,28,73]. Previous studies evaluating the effects of elevation on AWC partly agree with our results [17,74]. However, we found that slopes had no significant positive effect on the AWC. The reason for this could be that the relationship between slopes and the AWC is not simple or linear; rather, it may be influenced by other factors. Previous studies have reported that slopes play a significant role in changing the soil properties [62,75], as slopes affect the growth of trees by indirectly altering the soil physicochemical properties and microenvironments [38,76]. However, the impact of steep and gentle slopes on forest carbon storage remains controversial. Forests on steep slopes experience fewer human disturbances since the site environment is harsh and difficult to access. Forests on gentle slopes are often disturbed or managed since they are easily accessible. Furthermore, the influence of slopes on the AWC may be masked by spatial and temporal heterogeneity [43].

The forest environment (MAT, MAP, and AHM) can significantly influence the mixture of tree species, which indirectly affects the AWC [77,78]. As noted in previous studies, the water availability can have a significant influence on the AWC because it can directly affect tree growth, seedling recruitment, and survival [79]. We found that the climate had a significant negative total effect on the AWC in broadleaf mixed forests (BMF), which is consistent with previous findings [20], in that climate change will have an impact on the stand structure as the forest types change. Similarly, the climate regulates large-scale patterns of AWC and productivity through direct effects, as well as indirect effects, such as stand structure, stand diversity, and function [80]. Based on our results, we found that the impact of climate*PC1* on the AWC gradually weakened with the change in the forest type, which suggests that more advanced forest ecosystems are less affected by the climate.

4.2. *The Effects of Stand Age on AWC Depends on Interactions with Stand Structure and Diversity*

Our study provides comprehensive evidence for the importance of stand age as a driver of the AWC in three mixed forests. This is consistent with the results of previous studies, which found that the relative contribution of stand age to the forest aboveground biomass was 31% [81]. Stand age can promote biomass and carbon stock via an increase in the tree size variation (indirect effect) [14,25,82].

In three mixed forests, we found that stand structure*PC1* significantly affected the AWC directly, which is consistent with Ullah et al. [8], who reported that stand structure (stand density, species richness, and tree size variation) determined the aboveground biomass. However, we found that the impact of stand structure*PC1* on the AWC gradually weakened in the BMF. This may be because BMF are still in the stage of young and middle-aged forests, and the internal structure of the forest ecosystem has not yet been established.

Meanwhile, we also found the stand diversity*PC1* can enhance the AWC, which is consistent with Kunwar et al. [30], who reported that evolutionary diversity boosts the aboveground biomass across the tropical forests in Nepal. In large-scale studies, the mass ratio hypothesis suggests that dominant tree species also dominate the forest ecosystem's properties [54]. Meanwhile, we found the AWC is also correlated with the stand function*PC1* because of the dominant tree species' functional variables [14].

We also found that the interaction between the factors increased from a single variable to multiple variables, with the interaction between the factors being the main influencing factor [22,25]. Furthermore, the interactions between stand age and stand structure emerged in the BMF. The introduction of broad-leaved tree species changes the stand structure and promotes light capture and light-use efficiency within the forest community [9,25,83]. Stand age stimulates the niche complementarity effect to increase the biomass with the change in the forest type in our study, which resulted in high AWC values in the BMF. The interaction of stand age and diversity*PC1* can significantly positively affect carbon stocks in the CBMF and BMF, which is consistent with the results of Ren et al. [28], who reported that superior competitive tree species dominate the community and significantly limit the relative abundance of other tree species.

Our findings suggest that stand age can increase the AWC by increasing the stand diversity*PC1*, not only through niche complementarity effects, but also selection effects, which is consistent with previous studies [77,81,84]. Similar results were reported for the productivity or aboveground biomass in subtropical forests [9,10,82], indicating that the selection effect also caused a positive relationship between diversity*PC1* and the AWC in three mixed forests. A higher species diversity increases the probability of high-functioning tree species, which in turn improves community productivity [28].

4.3. Implications for Management of Subtropical Forest

We found that the climatic factors can influence the AWC, which could inform forest management practices in the future [40]. With the change in the forest type, the environmental impact on the AWC gradually decreases, which means that the ability of the BMF to resist climate change is relatively high [26]. Future studies should test how forest structure boosts the aboveground biomass or carbon of subtropical forests among different ecological gradients [75,83], which could have crucial implications for promoting a high biomass, especially considering the climate change that will occur in the future.

The results of this study show that stand age improved the stand structure and diversity. Moreover, stand structure and stand diversity simultaneously and indirectly drive the AWC through the stand function [40,82,85]. Our results provide additional evidence regarding the significance of stand age in boosting the AWC in subtropical forests. Further studies are needed to test whether these variables (stand age, structure, diversity, function, and climate) drive mature subtropical broadleaf mixed forests [9,24,86].

The findings of this study revealed that both stand structure and stand diversity play an important role in enhancing the AWC stocks [80]. These results provide inspiration for future forest management projects, particularly in plantation forests where the artificial replanting of multiple species should be practiced to benefit from multi-species mixing [19,20,22]. In natural forests, tending management should be practiced, weak trees should be felled over time, and the dominant trees should be protected [61,74]. In subtropical forests, our results suggest that management should be directed towards a mix of broad-leaved species and a complex forest structure [53,75]. Therefore, the implementation of multi-species afforestation can adjust the internal control mechanism of the forest, and this should be considered as an essential part of future forest management plans [74]. Extending the stand age and protecting the dominant tree species is essential for meeting the goals of increasing the forest carbon sinks and biodiversity conservation of subtropical forests in China [9,12].

5. Conclusions

This study suggests that stand age improves the link with stand structure and diversity, promotes the interaction of the three components, and positively promotes the AWC in broadleaf mixed forests more than other stands do. Meanwhile, stand age in our study was the dominant variable of mixed forest ecosystems, probably because the study site is located in the subtropical forest of Zhejiang Province, China, and most of these forests are still in the middle and young stand age stage. Meanwhile, both the stand structure and stand diversity can affect the AWC indirectly through their effects on the stand function. The mechanisms regulating the AWC in broadleaf mixed forests are more complex than those in the other two forest types are. Our results suggest that broadleaf mixed forests reserve more biodiversity, a more complex stand structure, and a greater ability to tolerate the challenges of climate warming. Therefore, our findings provide a new sight for policy makers and highlight the importance of the biodiversity of forests, especially stand structure and stand diversity, to achieve sustainable forest management goals in the future.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/f14020262/s1. Table S1: Summary of biotic and abiotic variables used in our study. Table S2: The direct, indirect, and total standardized effects of climatePC1, Age, structurePC1, functionPC1, diversityPC1 and aboveground wood carbon based on the structural equation models (SEMs); Figure S1: Relationship between aboveground wood carbon and all variables in coniferous mixed forest (CMF); Figure S2: Relationship between aboveground wood carbon and all variables in coniferous and broadleaf mixed forest (CBMF); Figure S3: Relationship between aboveground wood carbon and all variables in broadleaf mixed forest (BMF); Figure S4: Pearson's correlation matrix of aboveground wood carbon (AWC) in coniferous mixed forest (CMF); Figure S5: Pearson's correlation matrix of aboveground wood carbon (AWC) in coniferous and broadleaf mixed forest (CBMF); Figure S6: Pearson's correlation matrix of aboveground wood carbon (AWC) in broadleaf mixed forest (BMF); Figure S7: Principal Component Analysis (PCA) for diversity variables, structure variables, CWM function traits and Climate variables in coniferous mixed forest (CMF); Figure S8: Principal Component Analysis (PCA) for diversity variables, structure variables, CWM function traits and Climate variables in coniferous and broadleaf mixed forest (CBMF); Figure S9: Principal Component Analysis (PCA) for diversity variables, structure variables, CWM function traits and Climate variables in broadleaf mixed forest (BMF); Figure S10: Phylogenetic trees used for the quantification of phylogenetic diversity indices.

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