

Article

Partitioning Tree Species Diversity and Developmental Changes in Habitat Associations in a Subtropical Evergreen Broadleaf Secondary Forest in Southern China

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Abstract: The classical environmental control model assumes that species diversity is primarily determined by environmental conditions (e.g., microclimate and soil) on the local scale. This assumption has been challenged by the neutral theory that assumes that the maintenance of biodiversity mainly depends on the ecological drift and dispersal limitation. Understanding the mechanisms that maintain biodiversity depends on decomposing the variation of species diversity into the contributions from the various components that affect it. We investigated and partitioned the effects of the biotic component (productivity, forest spatial structure) and the environmental component (topography and soil fertility) on the distribution of tree species richness jointly (the combined effect of environment and biotic process) and separately (the effect of environment or biotic process alone) in 25 permanent plots of 600 m² in a subtropical evergreen broadleaf secondary forest in southern China. The analysis was also completed for trees at different growth stages based on diameter breast height (young trees: 5 cm ≤ DBH < 10 cm, mature trees: 10 cm < DBH ≤ 20 cm, old trees: DBH > 20 cm) within each plot. Our results indicated that (1) tree species richness had significant negative relationship with productivity and a unimodal relationship with its spatially structured distribution; (2) biotic and environmental factors both have significant influence on species richness and jointly explain ~60% of the variation for the overall tree assemblage, and the variation explained by the two components jointly increased across growth stages (34%, 44%, and 75%, respectively); (3) additive variation partitioning revealed that the tree species richness was dominantly controlled by environmental factors (32%), while the biotic component also independently contributed a non-negligible effect (16%); and (4) the dominant fraction changed from the biotic component to the environmental component across growth stages. Results suggest that the tree species richness may be governed from neutral process to environmental control during tree life span in subtropical evergreen broadleaf secondary forests.

Keywords: tree species richness; above ground biomass; spatial structure; evergreen broadleaf secondary forest; variation partitioning

1. Introduction

Understanding the connection between maintaining biodiversity and ecosystem processes has long been a major focus of research in ecology [1,2]. Existing studies in forests have obtained equivocal results of the factors affecting community species richness, and most are attributed to four major processes: selection, drift, speciation, and dispersal [3]. Niche differentiation has traditionally been used as an explanation for the maintenance of local diversity in multispecies communities [4].

Focusing on the selection process, the variation in environmental conditions may be responsible for the species diversity through species–habitat associations. This is the classical environmental control model [5]. Studies of niche differentiation in tree species communities focus on species' partitioning along gradients of environment heterogeneity, especially on topography and soil nutrient on local scales in forests [6].

An important driver of habitat diversification is topography, which controls spatial variation of hydrological conditions [7,8]. Variation of species richness along the topography gradient has been observed in previous studies. Richerson et al. [9] studied the diversity patterns of vegetation in California and found that they can be explained statistically by topographic variables. Homeier et al. [10] studied the spatial heterogeneity of tree diversity in a highly diverse tropical mountain area in southern Ecuador and found a significant correlation between richness and elevation and topography gradients. In addition, species diversity may also be driven by edaphic factors (e.g., nutrients). Relationships between changes in richness and a gradient of nutrient availability have been found in many studies. John et al. [11] tested the variation of soil nutrients in three diverse neotropical forest plots in Colombia, Ecuador, and Panama and found that ~40% of tree species showed strong associations with soil nutrient distributions. However, the results of the edaphic–diversity relationship can vary in different ecosystems. Braakhekke et al. [12] found that high species diversity occurred at intermediate values of nutrient ratios of N, P, and K in 25 grasslands, while de Oliveira and Mori [13] observed high tree species richness on poor soils in a central Amazonian forest. Based on the niche theory, with similar abiotic conditions, such as topography and soil nutrient, different species can coexist within habitat types.

It has been proposed that where a species is found may be also affected by some biotic factors. Among the many biotic components that control the variation in diversity, productivity and spatial aggregation have been identified as important factors. Understanding the relationship between species diversity and productivity is of long-standing interest to ecology research and unraveling the mechanisms driving this relationship is important in understanding determinants of biodiversity [14]. Despite the attention focused on this problem, considerable controversy remains [15]. Species richness is often hypothesized to produce a unimodal relationship with productivity [16,17]; positive and negative correlations have also been observed [18]. Most experiments were conducted in ecosystems with simple community structure and how this relationship changes in forest ecosystems is worth discussing [19]. Moreover, in terms of spatial distribution, the relationship between species diversity and horizontal distribution of trees is of great interest to ecology. The horizontal distribution of trees in a forest, as a result of competition, mixture, and position, influences the spatial variation in resource availability, indirectly affecting tree diversity [20]. Spatial structure in the forest has been used to define the spatial aggregation conditions [21] and is largely influenced by the relationship within neighborhood groups of trees [22]. Indices based on neighborhood conditions have been widely used to analyze the spatial structure of plant communities and species diversity [23].

The niche differentiation theory predicts species coexistence in heterogeneous environments where the species are suited to a specific habitat [24]. However, in many species-rich communities, all plants depend on the same few resources and acquire them in similar ways, which makes it difficult to explain coexistence of species through niche differentiation [25]. A possible hypothesis in the niche context is that coexistence of species may be through the partitioning of the 'regeneration niche' [26]. If niche differentiation takes place during regeneration, tree species in early growth stages may experience the environment more heterogeneously in terms of some physical factors, such as soil moisture [8] and light availability [27]. In addition, environmental or biotic requirements may change with size and in that case species' ecological preferences may differ across growth stages [28,29]. Most studies of species–habitat associations are based on static distribution of old trees which are insufficient to detect such changes in ecological preferences; studies at multiple growth stages are rare [30]. In each growth cycle, if we assume that the habitat with which a species is associated is different at the young, mature, and old stages, the species–habitat associations may follow one of

three patterns: (1) young trees less strongly associated with habitat than mature trees than old trees; (2) young trees more strongly associated with habitat than mature trees than old trees; (3) young trees, mature trees, and old trees similarity associated, or no regular pattern. Even though many studies have been done on the species–habitat associations, it still remains unclear when these observed associations form and how these associations change across growth stages [31].

It has been proposed that species–habitat associations alone cannot demonstrate that habitat partitioning is the only hypothesis of species coexistence in many species-rich communities where habitat may not provide enough niches for species [32]. An alternative hypothesis is that coexistence of species may be explained by the unified neutral theory which assumes that individuals of every species have the same set of demographic rates [33]. According to neutral theory, species diversity may be generated by the species assemblages themselves due to dispersal limitation. High tree species diversity does not necessarily depend on habitat partitioning and the coexistence of many species is through random walk dynamics. Differences in dispersal or other random ‘neutral process’ may lead to species differing in their observed patterns of coexistence across growth stages [30].

Revealing why these patterns of species’ coexistence are observed and the mechanisms of how the patterns change across growth stages are of great importance in maintaining species diversity. In this study, we evaluate the role of environmental or biotic factors in maintaining tree species diversity in evergreen broadleaf forests, which are now recognized as an important resource that contributes to the biodiversity of the subtropical regions of China [34,35]. A hotspot of the subtropical evergreen broadleaf forests in southern forests in the Jiangle region, Fujian Province presents an ideal location to assess how ecosystem processes, such as biotic and environmental process, affect tree species diversity. In our study, we examined four inter-related questions as follows: (1) How does productivity influence tree species diversity in subtropical secondary evergreen broadleaf forests? (2) Does tree spatial aggregation have a significant role in explaining tree species diversity? (3) How do biotic and environmental factors jointly affect the tree species diversity and what is the relative influence of either factor? (4) How do the above relationships change across growth stages within a forest?

2. Materials and Methods

2.1. Site Description

This study was conducted in Jiangle County, Sanming City, Fujian Province of China on the southeast slope of the cordillera Wuyi. Within this area, two sites covered by subtropical evergreen broadleaf secondary forests were chosen for the plots (Figure 1). The study site above 500 m a.s.l. is located in Longqishan National Nature Reserve (LQS). Due to igneous rocks such as granite, quartzite, and metamorphic rocks, two main soil types were formed. The mountain soil was mainly composed of red earths, while yellow-brown earth was the major type in the low mountains. The mean annual temperature is below 14 °C in LQS. The evergreen broadleaf forest is mainly distributed under 1200 m a.s.l., and the forest at 1100–1300 m a.s.l. is composed of a mixed broadleaf deciduous forest. The site below 500 m is located in Guangming Township, 46 km away from LQS. Similar to low mountains in LQS, yellow-brown earth was the major soil type of Guangming plots. The mean annual temperature is between 14.6 and 18.8 °C, while the mean annual precipitation is 1797 mm (range 799–1859 mm, data from the Jiangle County meteorological station, collected from 1943 to 2005). The Jiangle plots contain secondary forest that was disturbed by agriculture and charcoal production approximately 50 years ago. Since that time, no obvious human disturbance is evidenced in our forest plots because of the NFPP (Natural Forest Protection Project) in China. At the present time, most of the forest is in the early successional stage.

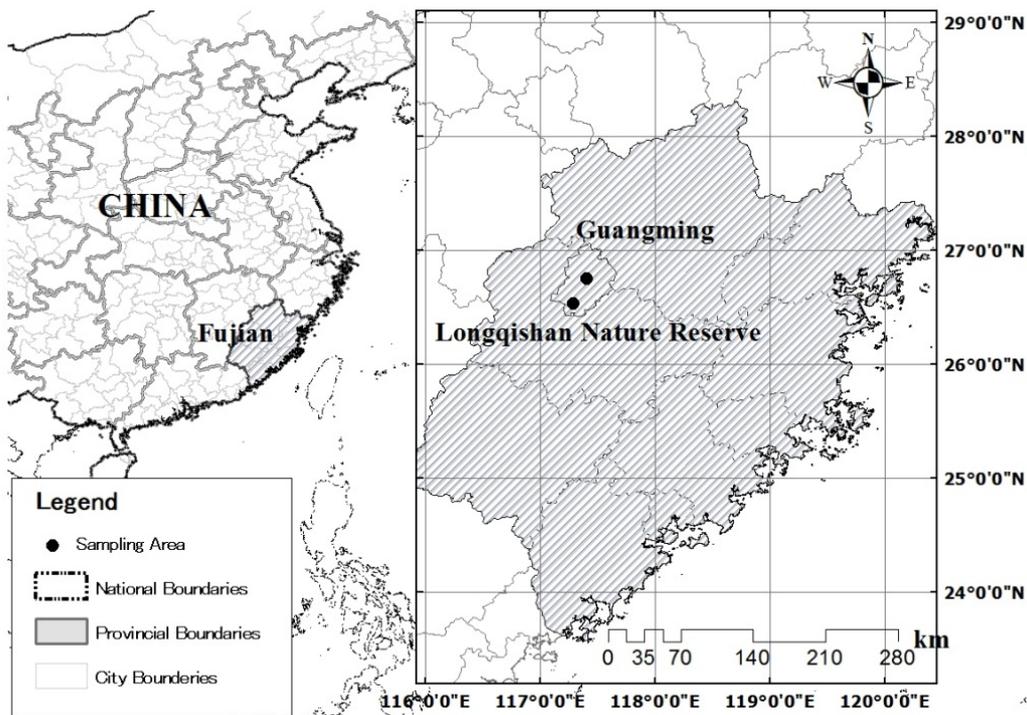


Figure 1. Location of study area and sampling sites.

2.2. Plot Establishment and Data Collection

From June to September in 2012, 2013, and 2015, we installed 25 permanent plots of 20 m × 30 m with an elevation gradient of 240–1190 m a.s.l. The area of evergreen broadleaf forest in LQS was generally between 400 and 600 m² [36], and we chose the same plot size in two study sites to make sure our study plots were covered by homogeneous evergreen broadleaf forest patches in this heterogeneous environment. To avoid spatial autocorrelation among plots, the horizontal distance of the nearest two plots was over 1000 m. All stems with diameter at breast height (DBH) ≥ 5 cm were tagged to ensure accurate measurement. All the individual trees were identified to the species level, and total tree species richness was assessed within each of the 25 plots.

2.2.1. Biotic Parameters

A band was painted on each trunk at breast height (1.3 m), and DBH was measured. Tree height was measured using an ultrasound instrument of Vertex IV (Haglof Inc., Avesta, Sweden). The spatial coordinates of each individual tree were recorded to calculate spatial structure index.

2.2.2. Environmental Parameters

In the field, elevation and slope were measured at the center of each plot using a portable GPS. In each plot, three randomly selected locations were used to collect one 100 cm³ sample along the soil profile at five depths (0–10, 10–20, 20–40, 40–60, 60–80 cm) using the cutting ring method. Soil water content (%), organic matter (%), total nitrogen (N %), available potassium (K %), and available phosphorous (P %) were assessed for each sample in the laboratory and averaged among the three profiles for analyses following [37]. Soil organic matter (%) was assessed using K₂Cr₂O₇ solution, total nitrogen (N %) was assessed by the Semi-micro Kjeldahl method. Available potassium (K %) and available phosphorous (P %) were assessed by neutral CH₃COONH₄ solution and NaHCO₃ solution separately.

2.3. Statistical Analyses

2.3.1. Biotic Variables

Productivity refers to the rate of energy flow in a system (average over some time scale), while this rate rarely is measured in nature. Instead, in small-scale studies plant biomass (peak standing stock during the growing season) is generally used as an indirect measure that correlates with productivity for fast-growing ecosystems, such as forests in early stage of secondary succession [13]. The above ground biomass (AGB) of each live tree was calculated using species specific allometric equations of evergreen broadleaf tree species of Fujian Province in Southern China following Zuo et al. [38], which is expressed in Equation (1) as:

$$W = a(D^2H)^b \quad (1)$$

where W is the above ground biomass (AGB, m^3), D is the DBH (cm), H is the tree height (m), and a and b are coefficients. The AGB of each tree in a plot was summed up to obtain the AGB of each plot.

In order to evaluate the relationship between the spatial structure and tree species richness, neighborhood-based indices (uniform angle index and DBH dominance index) were used to describe the horizontal distribution of trees. For a five-tree group as an example (Figure 2), selecting a tree as reference tree i , starting randomly with a tree number 1 and moving clockwise around tree i , the angle α between the two adjacent neighbors is observed. In this method, α_{12} , α_{23} , α_{34} , and α_{41} are obtained.

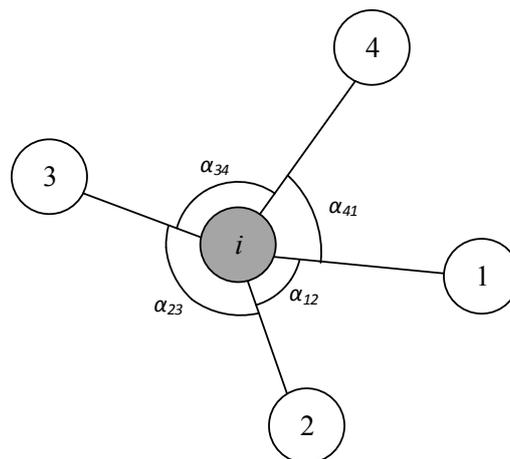


Figure 2. Angles between two adjacent neighbors in a five-tree group.

It has been suggested that four is the most appropriate number of nearest neighbors for calculating uniform angle index [39,40]. By comparing the four angles mentioned with the standard angle α_0 ($\alpha_0 = 360^\circ / n$, $\alpha_0 = 90^\circ$ when $n = 4$), the uniform angle index was obtained following Equation (2) as [22]:

$$W_i = \frac{1}{4} \sum_{j=1}^n Z_{ij} \quad (2)$$

where W_i is the uniform angle index, $Z_{ij} = 1$ if the α angle is smaller than α_0 (90°), otherwise $Z_{ij} = 0$. The W_i value falls in the interval $[0, 1]$. The distribution pattern of trees tends to be regular when value of the uniform angle index is below 0.5. On the other hand, the distribution tends to be clumped when this value is over 0.6.

Similar to concepts of the uniform angle index, the DBH dominance reflects the four nearest neighbors that are larger or smaller than the reference tree and is defined as:

$$U_i = \frac{1}{4} \sum_{j=1}^n k_{ij} \quad (3)$$

where U_i is the DBH dominance index, $k_{ij} = 1$ if neighbor tree j is smaller than reference tree i , otherwise $k_{ij} = 0$.

DBH dominance index explains the differentiation between a reference tree and its nearest neighbors. The two indices could provide habitat information for trees with some common characters (e.g., niches of dominant trees, intermediate-size trees or short, mixed trees) compared to the traditional index such as the Clark and Evans aggregation index [22]. The mean value of W_i and U_i within a plot reflects the overall aggregation patterns in a small-scale structural unit [22]. To avoid border effects, a buffer of 3 m was set in each plot before calculating the spatial structure index.

The relationship via regression between tree species richness (dependent variable) and AGB, uniform angle index and DBH dominance index (independent variables) were examined separately in our study site. The regression model included a linear and a quadratic term. The Type III sums of squares were used in our study so that priority was not assigned to the linear or quadratic components [41]. A relationship was considered to be quadratic if it had a significant quadratic coefficient. Then, the Mitchell-Olds and Shaw (MOS) test was executed to determine if the relationship was unimodal or saturating. If the vertex of the curve occurs between the minimum and maximum independent variable in the data, the relationship is unimodal or U-shaped. If not, the relationship is nonlinear but monotonic [42].

2.3.2. General Linear Model and Variation Partitioning

We used a general linear model (GLM) to explain tree species richness as a function of biotic (AGB, spatial structure,) and environmental factors. The spatial structure included: the uniform angle index and dominance. The environmental factors included: elevation (the difference in elevation between the highest and lowest plot was 950 m), slope (with values from 20° to 41°), and soil properties (including the soil water content, % K, % N, % P and organic matter). The variables were squared if the relationship was quadratic. To avoid multicollinearity between the biotic and environmental factors, variance inflation factors among all factors were calculated. The values of variance inflation factors ranged between 1.43 and 4.89, which suggested that no significant multicollinearity existed among all variables.

Variation partition was used to examine how biotic factors and environmental parameters influence tree species richness separately and jointly. It is based on Redundancy Analysis (RDA), which examines how much of the variation is explained by a set of variables, allowing the isolation of the effect of a component on tree species richness. The variance explained uniquely by either biotic or environmental variables and their joint effect was extracted and partitioned into the following components: (1) independent effect of biotic factors controlled by environmental factors; (2) the independent effect of environmental factors controlled by biotic factors; and (3) the shared effect of biotic and environmental factors, which is the intersection (not the interaction) of the amounts of variation explained by the linear models of the two explanatory tables [43]. Variation partition and partial RDA were computed in R 3.2.5 [44] using the varpart function in the vegan package [45]. For unbiased variance estimation, adjusted R^2 was computed [46] and significance of the two independent components was tested using partial RDA.

In order to reveal how biotic and environmental factors influence the maintaining of tree species diversity across growth stages, three tree growth stages in each plot were classified: (1) young trees: trees which $5 \text{ cm} \leq \text{DBH} < 10 \text{ cm}$; (2) mature trees: trees which $10 \text{ cm} \leq \text{DBH} < 20 \text{ cm}$; and (3) old trees: trees which $\text{DBH} \geq 20 \text{ cm}$. To examine how the above process changed across growth conditions, GLMs and variation partitioning were also used for each growth stage. If a component (biotic or environmental fraction) was insignificant, the other fraction was tested using a redundancy analysis to see if the variation of richness can significantly be explained by one of the components alone.

3. Results

3.1. Relationship of Tree Species Richness with AGB (above Ground Biomass) and Spatial Structure

A total of 2209 stems belonging to 103 species representing 47 plant families were recorded from the 25 plots. Among all the 103 species, 103, 77 and 43 species belonged to young, mature, and old trees separately. Relationships between the AGB and richness were shown for different sizes of trees and the entire trees (Figure 3). For trees of different growth stages, species richness evinced a unimodal relationship with the AGB (Figure 3a,c), except in mature trees, where the relationship was positive and linear (Figure 3b). In particular, for old trees, the positive linear regression was also significant ($p < 0.01$), while it explained less variation ($R^2 = 0.651$) than the quadratic model ($R^2 = 0.708$). The AGB values of maximum richness of the quadratic models for young and old trees were 1.687 and 27.82, respectively. For all trees, there is a non-significant negative linear relationship between tree species richness and AGB ($p = 0.014$) (Figure 3d). Due to insignificant linear and quadratic components ($p = 0.497$ and 0.183 , respectively), the quadratic model was not selected even though the overall model was significant ($p = 0.021$).

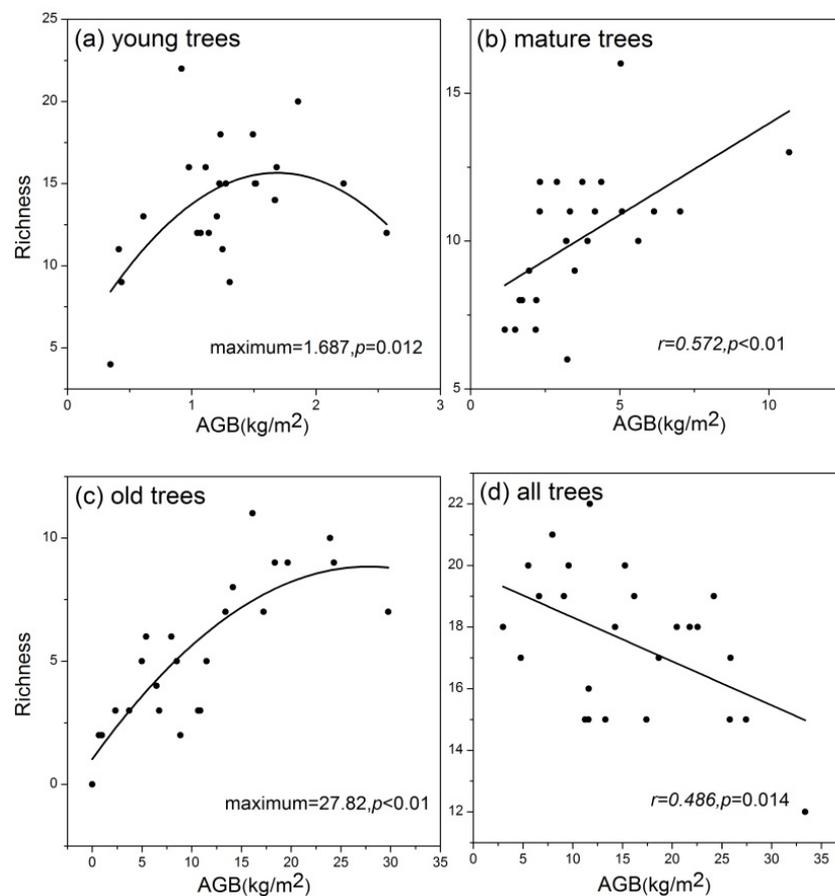


Figure 3. Relationship between tree species richness and above ground biomass (kg/m^2) for all trees and different growth stages: (a) young trees; (b) mature trees; (c) old trees; (d) all trees. The regression line is plotted if the relationship is significant ($p < 0.05$), with the unimodal relationship examined by the Mitchell-Olds and Shaw (MOS) test.

In 25 plots, the uniform angle index was between 0.46 and 0.69, with an average value of 0.55 and a standard deviation of 0.049. For trees of various growth stages, a significant relationship between richness and uniform angle index was detected, except for old trees (Figure 4c). For young trees, the species showed a unimodal relationship with the uniform angle index (Figure 4a) but a

significant positive linear correlation for mature trees ($r = 0.578$, $p < 0.01$) (Figure 4b). The uniform angle index value of maximum richness of the quadratic models for young and all trees were 0.578 and 0.567, respectively. For the entire trees, a unimodal relationship was observed between richness and the uniform angle index, and both the linear and quadratic component were significant ($p < 0.01$). (Figure 4d)

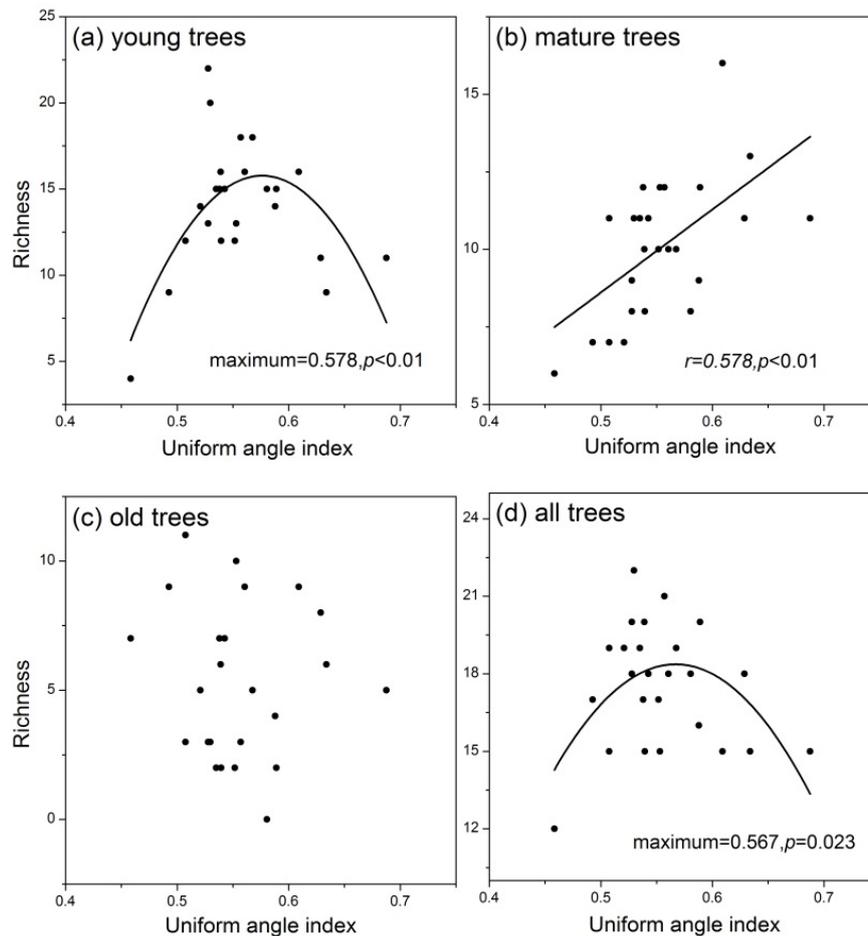


Figure 4. Relationship between the tree species richness and the spatial aggregation index of uniform angle index for all trees and different growth stages: (a) young trees; (b) mature trees; (c) old trees; (d) entire trees. If the relationship is significant ($p < 0.05$), the regression line is plotted, with the unimodal relationship examined by the Mitchell-Olds and Shaw (MOS) test.

The value of DBH dominance index ranged between 0.45 and 0.55, with an average value of 0.50 and a standard deviation of 0.27. For trees of various growth stages, only richness of mature trees is significantly explained by DBH dominance index (Figure 5b) with a unimodal relationship. The DBH dominance index value of maximum richness of the quadratic models is 0.567 (MOS test). The relationship between richness and DBH dominance index was non-significant in young and old trees (Figure 5a,c). DBH dominance index showed a unimodal relationship with richness in all trees ($p = 0.021$) with both linear and quadratic components significant ($p = 0.019$ and $p = 0.02$ separately).

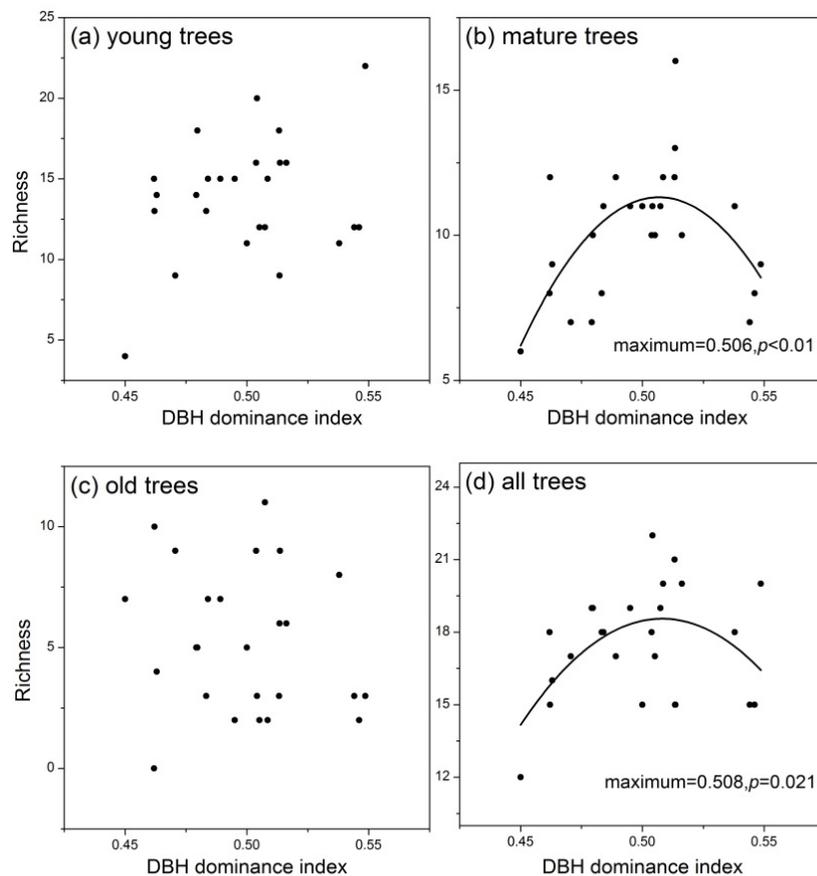


Figure 5. Relationship between tree species richness and spatial aggregation index of DBH dominance index for all trees and different growth stage: (a) young trees; (b) mature trees; (c) old trees; (d) all trees. If the relationship is significant ($p < 0.05$), the regression line is plotted, with unimodal relationship examined by the Mitchell-Olds and Shaw (MOS) test.

3.2. General Linear Model and Variation Partitioning

The general linear model (Table 1) suggests that AGB also had a significant effect on tree species richness when all variables were included in the model ($F_{1, 10} = 16.51, p = 0.001$). The uniform angle index appeared to have a significant effect ($F_{1, 10} = 5.04, p = 0.04$), while the DBH dominance index had no significant effect on species richness. Among the seven environmental factors, elevation ($F_{1, 10} = 7.68, p = 0.01$), slope ($F_{1, 10} = 5.35, p = 0.04$), and N % ($F_{1, 10} = 6.12, p = 0.03$) had significant influence. The soil water content, organic matter, P %, and K % had no significant impact on tree species richness. Overall, the model explained 58.42% of the total variation.

The results of the GLMs for trees of different growth stages are shown in Table 2. When both biotic and environmental factors were included, tree species richness has a significant effect with the AGB in all three growth stages. The DBH dominance index has a significant influence on richness for young ($F_{1, 10} = 5.27, p = 0.03$) and mature trees ($F_{1, 10} = 6.24, p = 0.026$). In addition, soil water content and elevation had significant influence on richness for young and old trees. The whole GLM was significant except for young trees ($p = 0.055$). Overall, the model of mature and old trees explained 43.47% and 75.39% of corresponding total variation.

Table 1. Summary of general linear models for the effects of biotic and environmental factors on richness.

	Term	DF	F Value	<i>p</i>
Biotic factors	AGB	1	16.51	0.001 ***
	Uniform angle index	1	5.04	0.041 *
	DBH dominance index	1	0.0064	0.937
Environmental factors	Elevation	1	7.68	0.015 *
	Slope	1	5.35	0.037 *
	Soil water content	1	1.08	0.316
	Organic matter	1	0.53	0.478
	N %	1	6.12	0.027 *
	P %	1	0.098	0.759
	K %	1	2.31	0.151
	Whole model ^a	10	4.47	0.006 **

Note: ^a Whole model adjusted $R^2 = 0.5842$; DF: degree of freedom; * $0.05 > p > 0.01$; ** $0.01 \geq p > 0.001$; and *** $p \leq 0.001$.

Table 2. Summary of general linear models for the effects of biotic and environmental factors on the richness of young trees, mature trees, and old trees.

Growth Stage	Factors	DF	F Value	<i>p</i>
Young ($5 \leq \text{DBH} < 10$)	AGB	1	5.62	0.033
	DBH dominance index	1	5.27	0.038
	Soil water content	1	5.18	0.039
	Whole model ^b	10	2.53	0.055
Mature ($10 \leq \text{DBH} < 20$)	AGB	1	13.87	0.002
	DBH dominance index	1	6.24	0.026
	Whole model ^c	10	2.85	0.036
Old ($\text{DBH} \geq 20 \text{ cm}$)	AGB	1	46.50	<0.001
	Elevation	1	25.71	<0.001
	Whole model ^d	10	8.35	<0.001

Note: ^b Whole model adjusted $R^2 = 0.3410$; ^c Whole model adjusted $R^2 = 0.4347$; ^d Whole model adjusted $R^2 = 0.7539$; DF: degree of freedom; Only factors with significant correlations ($p < 0.05$) are shown in each growth stage (For details of other insignificant variables, see Tables A1–A3 in Appendix A).

The results of variation partitioning across growth stages for tree species richness are shown in Table 3. The variation of saplings was not partitioned because the relationship was not significant ($p = 0.055$) which suggested that variation of tree species richness in the young stage cannot be explained by the combination of the environmental and biotic factors. For all trees, the variation in richness was decomposed. The variation explained by the two fractions was statistically significant ($p = 0.014$ and $p = 0.027$, respectively). The adjusted R^2 showed that the biotic and environmental factors collectively explained 58.4% of the richness data. The environmental component alone accounted for over half of this explained variation (55.6%) and 27.3% was explained by the biotic fraction. For mature trees, both components explained 43.5% of the variation. The biotic component had a significant effect on richness ($p = 0.008$) and explained the most (41.5%), while the environment had little influence on richness (2.02%) and was not significant ($p = 0.407$). The pure effects of the two fractions were 41.5% and 1.94%. The variation of the old trees was found to have a significant canonical relationship with both the biotic and environmental factors ($p = 0.003$ and $p = 0.001$, respectively) and 75.4% was explained. When decomposing the variation, 5.89% and 40.9% of the explained variation was caused by the biotic and environment components, respectively. Redundancy Analysis was used additively for biotic component of mature stage and environmental fraction for old trees and the results were both significant ($p = 0.006$ and $p = 0.001$, separately) (For details, see Appendix Table A4).

Table 3. (A) Overall variance explained; and (B) Variance partitioning results of the individual fractions.

DBH Size	Variance Partitioning	DF	R ²	Adjusted R ²	p
All	(A) Overall variance explained				
	Biotic	3	0.352	0.259	0.027 *
	Environment	7	0.591	0.421	0.014 *
	All	10	0.757	0.584	
	(B) Individual fractions				
	Biotic controlled by environment	3		0.162	0.047 *
	Environment controlled by biotic	7		0.324	0.024 *
Young (5 ≤ DBH < 10)	(A) Overall variance explained				
	Biotic	3	0.189	0.073	0.195
	Environment	7	0.432	0.198	0.144
	All	10	0.616	0.341	
	(B) Individual fractions				
	Biotic controlled by environment	3		0.414	0.008 **
	Environment controlled by biotic	7		0.019	0.388
Mature (10 ≤ DBH < 20)	(A) Overall variance explained				
	Biotic	3	0.488	0.415	0.005 **
	Environment	7	0.306	0.020	0.407
	All	10	0.670	0.435	
	(B) Individual fractions				
	Biotic controlled by environment	3		0.414	0.008 **
	Environment controlled by biotic	7		0.019	0.388
Old (DBH ≥ 20)	(A) Overall variance explained				
	Biotic	3	0.515	0.446	0.003 **
	Environment	7	0.794	0.709	0.001 ***
	All	10	0.856	0.754	
	(B) Individual fractions				
	Biotic controlled by environment	3		0.044	0.136
	Environment controlled by biotic	7		0.308	0.007 **
	Unexplained			0.246	

Note: Adjusted R² = 1 - ((1 - R²) × (total degrees of freedom/residual degrees of freedom)); DF: degrees of freedom; * 0.05 > p > 0.01; ** 0.01 ≥ p > 0.001, and *** p ≤ 0.001.

4. Discussion

4.1. Relationship of Biotic and Environmental Factors with Tree Species Diversity

The relationship of each biotic factor with diversity alone was analyzed with two classifications: productivity (AGB) and tree aggregation conditions (spatial structure index). A significant negative linear relationship exists between tree species diversity and above ground biomass as a measure of productivity in the evergreen broadleaf subtropical secondary forest of Jiangle (Figure 3d). The relationship is strong for the entire dataset, but changes among growth stages (Figure 3a–c). A unimodal relationship was found in young trees, similar to results observed in most fast-growing ecosystems [16,47]. Interestingly, the richness–productivity relationship in mature and old growth stages was almost positive (old curve decrease with a maximum DBH of 28), however, the relationship was significantly negative with all stages combined. The maximum richness of the sapling curve appeared at nearly the middle of the curve, followed by an obvious decrease. It is notable that the number of young tree individuals was the largest class. Also, species richness was highest at the sapling stage and lowest at the old stage. Old trees dominated the composition of entire productivity in a forest with the lowest richness. On the contrary, young trees were the major class affecting tree species diversity but made least contribution to productivity. This might be an explanation which led to the different richness–productivity relationships between growth stages and the entire data that, with the increment of productivity, abundance of young trees decreased following an obvious downtrend of the overall richness.

The biophysical structure of forests plays a major role in ecosystem diversity [48]. The analysis of neighborhood-based index provided a powerful tool for analyzing the spatial variation in species

composition. The two indices provided the competition and aggregation conditions of trees in a plot, and the regression results showed that both the uniform angle index and the dominance index evinced a unimodal relationship with richness for the entire dataset (Figures 4 and 5). This phenomenon may be explained by the traditional niche theory that, with the growing abundance of individuals, diversity increased rapidly until a lack of resources was reached (e.g., light conditions). Interactions of plants in a similar niche lead to the competitive exclusion process until the limiting of the similarity between the coexistent species [49,50]. Then, the divergence of species traits influences the decrease of diversity [51,52]. Trees in early growth stages seem to be constrained by the horizontal spatial arrangement of tree position. Three categories of environmental factors were added into general linear models for diversity regression: micro-topography (elevation and slope), soil fertility (organic matter, % N, % K, % P), and water condition (soil water content). For all the data, two biotic factors (AGB and uniform angle index) and three environmental factors (elevation, slope, and % N) showed significant relationship with richness when all the variables were contained (Table 1). Despite a non-significant relationship for the entire model ($F_{3, 10} = 2.531, p = 0.054$), the factors that control young and mature trees are similar, with the AGB and DBH dominance index playing dominant roles. Additionally, the soil water content had a weak effect on young trees. It seems that both microclimate (elevation) and productivity (AGB) have significant influence on the maintenance of diversity for old trees.

Edaphic factors were considered important for maintaining local diversity [53]. However, it is notable that a non-significant relationship with richness was found for soil fertility when assessing the relationships within each growth stage (Table 2). This suggests that soil fertility is not essential for maintaining diversity in our study sites. This non-significant relationship was also observed in forty-six Costa Rican forest sites, which suggests that the highest species richness often is observed under poor growth conditions [54].

4.2. Diversity Partitioning

The importance of niche vs. neutral assembly mechanisms in tree communities remains a controversial question [55]. Traditionally, plant ecologists have recognized that environmental conditions are key to determining species distribution [5]. For all the data in our study, the additive partitioning of variation in tree species richness revealed that a large proportion (58%) is determined by biotic and environmental factors (Table 3). Pure effect of biotic (16%) and environmental factors (32%) indicated that environment is the dominant component. The combination of the two fractions cannot be neglected, with a proportion of 10%, and it may be due to the influence of the environment on plant growth. It is not surprising that ~41% of the variation is not explained for the entire dataset. Several reasons may be considered to explain this high proportion of unaccounted variation, e.g., other unmeasured environmental factors or biotic disturbances [26]. This variation can be connected to the niche theory, in which resources and competition determine the species distribution [4]. Another conceivable explanation is that the variation may be due to stochastic processes and can be explained by the neutral theory, which assumes that species diversity is driven by ecological drift and dispersal limitation and is not habitat dependent [32]. The unexplained variation decreased from young to old trees. Trees of small size within forest stands are vulnerable to natural interference and resource competition (e.g., light availability) [56], and the larger proportion of unexplained variation may be determined by the unmeasured parameters.

For the three growth stages examined here, we detected a significant environment–diversity association only in old growth stage and significant biotic–diversity associations in the latter two stages (mature and old stages). Species that were significantly associated with a habitat at one stage were not associated with that habit at the other stages in our study sites. Similarly, Webb & Peart [30] found that the species richness–habitat associations changed between adults and seedlings in a Bornean forest. Wiegand et al. [31] observed a different richness–habitat association during the transition from juvenile to reproductive stages in a Panamanian lowland forest. All the 103 species were observed in the young stage in our results. However, it is noted that both biotic and environmental factors were

not significantly associated with young tree species' richness. The non-significant species–habitat association in young stages could be explained by the unified neutral theory. Species distribution patterns of young trees may be largely influenced by seed dispersal patterns [32]. Most seeds fall close to parent trees and the richness of young trees will therefore tend to be higher in the preferred habitat of adult trees compared with other habitats [30]. In that case, young trees may show association with the same habitat as mature or old trees. Random process, such as ecological drift combining with dispersal limitation, form coexistence of species of young stage in our study sites.

The variation explained by the two components (environment and biotic) jointly increased across three growth stages (34%, 44%, and 75%, respectively). This result would suggest that the seed dispersal out of the optimal habitat should regenerate young trees distributions with weaker habitat associations than those of mature and old. Interestingly, results from the variation partitioning suggest that mature trees were apparently more influenced by biotic conditions than by the environment. For mature trees, the partial redundancy analysis revealed that the environmental fraction was insignificant ($p = 0.39$), and it was controlled by the biotic matrix. In the mature growth stage, the species–biotic association forms and many species disappear from young to mature stages (from 103 to 77). The biotic processes (productivity and spatial structure) could be recognized as indirect factors which result from the variation in resource availability and influence changes in tree species diversity. However, the explanatory power of the environment matrix was higher than the biotic matrix for old trees. The biotic matrix was also non-significant ($p = 0.136$) when controlled by the other fraction. Even though young and mature trees were dispersing and establishing widely, but suffering higher mortality outside the optimal habitat, leading to the observed species–habitat associations of old trees. Our result revealed that habitat associations of trees do not form at the early two (young and mature) growth stages. Similar results were observed by Comita et al. [57] when comparing species–environment associations in different growth stages of tree species in a Panamanian lowland forest. Also, according to the regeneration niche hypothesis, the advantages of species differ among life stages and this results from the coexistence of species [25]. As a consequence, our results support the idea that both the neutral process and the niche process may affect richness for trees for growing life stages. With the lack of these types of data, our future studies should therefore focus on how the neutral process will affect trees in the early stages.

5. Conclusions

Our results suggest that both biotic (productivity, spatial structure) and environmental (micro-topography, water availability, soil fertility) processes are substantial determinants of the distribution of tree diversity in Jiangle evergreen broadleaf forest plots. The productivity of all trees shows a significant negative relationship with diversity; moreover, both the two spatial structure indices (uniform angle index and dominance index) prove to be unimodal with diversity. When examining trees of different growth stages, both the productivity–diversity and spatial–diversity relationships changed. Variation partitioning revealed that the environmental process was the dominant fraction that controlled diversity for the entire forest and old trees. On the contrary, biotic conditions were more powerful for trees of early growth stages (young and mature trees). It seems that the decisive factors changed from biotic process to environmental conditions as the trees grew within a stand. A un-negligible proportion of unexplained variation may be driven by the unmeasured factors or by stochastic processes, the proportion of which decreased along with the growing stage, which was probably due to the greater number of unmeasured resources (e.g., microclimate and light availability) required for small trees, or the neutral process such as dispersal limitation. Unfortunately, because of the lack of reliable stand climate or light availability data, we were not able to fully account for the entire variability among study sites. In summary, both biotic and environmental processes make contributions to tree species diversity in our evergreen broadleaf forest plots, while the relative attribution changes across the growth stages within plots.

When managing a forest stand, an adjustment of species interaction should be considered to maintain species diversity.

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Appendix A

Table A1. Summary of general linear models for the effects of biotic factors and environmental factors on the richness of young trees.

Saplings	Term	DF	F Value	<i>p</i>
Biotic factors	AGB	1	5.62	0.033 *
	Uniform angle index	1	0.01	0.942
	DBH dominance index	1	5.27	0.038 *
Environmental factors	Elevation	1	1.42	0.253
	Slope	1	3.41	0.086
	Soil water content	1	5.68	0.032 *
	Organic matter	1	0.04	0.852
	N %	1	0.97	0.340
	P %	1	0.65	0.432
	K %	1	2.24	0.156
	Whole model	10	2.53	0.055

Note: DF: degrees of freedom; * 0.05 > *p* > 0.01.

Table A2. Summary of general linear models for the effects of biotic factors and environmental factors on the richness of mature trees.

Mature Trees	Term	DF	F Value	<i>p</i>
Biotic factors	AGB	1	13.87	0.002 **
	Uniform angle index	1	0.63	0.441
	DBH dominance index	1	6.24	0.026 *
Environmental factors	Elevation	1	3.60	0.079
	Slope	1	1.35	0.265
	Soil water content	1	0.65	0.432
	Organic matter	1	0.16	0.902
	N %	1	0.03	0.856
	P %	1	1.75	0.210
	K %	1	0.31	0.584
	Whole model	10	2.85	0.036

Note: DF: degrees of freedom; * 0.05 > *p* > 0.01 and ** 0.01 ≥ *p* > 0.001.

Table A3. Summary of general linear models for the effects of biotic factors and environmental factors on the richness of old trees.

Old Trees	Term	DF	F Value	<i>p</i>
Biotic factors	AGB	1	46.50	<0.001 ***
	Uniform angle index	1	2.25	0.156
	DBH dominance index	1	1.47	0.246
Environmental factors	Elevation	1	25.71	<0.001 ***
	Slope	1	0.04	0.846
	Soil water content	1	0.60	0.453
	Organic matter	1	0.88	0.364
	N %	1	1.91	0.188
	P %	1	0.04	0.847
	K %	1	4.11	0.062
	Whole model	10	8.35	<0.001 ***

Note: DF: degrees of freedom; *** *p* ≤ 0.001.

Table A4. Results of Redundancy Analysis of Mature trees controlled by biotic factors and old trees by environmental factors.

Growth Stage	Controlled Factors	DF	F Value	p
Mature	Biotic factors	3	6.6825	0.006 **
Old	Environmental factors	7	9.3718	0.001 ***

Note : DF: degrees of freedom; ** $0.01 \geq p > 0.001$ and *** $p \leq 0.001$.

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