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Temporal Changes in Community Structure over a 5-Year Successional Stage in a Subtropical Forest

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Abstract: In the context of global warming, the changes of forest structure, diversity, and productivity along with forest succession have always been a topic of interest for many researchers. Studying the changes in community structure, biomass, and diversity of different diameter at breast height (DBH) classes in subtropical mountainous forests during forest succession can provide data in support of future forest succession predictions and forest management. We analyzed the changes of three DBH classes in a 10-ha plot while studying subtropical mountainous forest succession in 2012 and 2017. The results showed that during forest succession, the community abundance and richness significantly decreased while biomass increased slightly. Among the three DBH classes, changes were the greatest in small trees, followed by large trees, and then medium-sized trees. The abundance, biomass, richness, and Shannon–Wiener index of small trees all decreased significantly. In forests with medium-sized trees, biomass decreased significantly and abundance did not change significantly. In large trees, abundance and biomass increased significantly. Changes were observed in environmental driving factors during forest succession. In 2012, driving factors with significant effects included total phosphorus, transmitted direct solar radiation, organic matter, and capillary water capacity. In 2017, two driving factors were total phosphorus and total potassium while the main driving factor was still total phosphorus. The results showed that during forest succession the abundance and diversity of small trees were principal components of community abundance and diversity. A reduction in small-tree abundance and diversity will decrease community abundance and diversity. Large-tree biomass was a principal component of community biomass; accumulation of large-tree biomass will increase community biomass. *Schima superba* Gardner and Champ. and *Castanopsis carlesii* (Hemsl.) Hayata are the main dominant species in this area, which can quickly form stable communities. *S. superba* is also a fire-resistant tree species. Therefore, in natural forest management, planting of *S. superba* and *C. carlesii* in the secondary bare land can be considered. In addition, the evergreen broad-leaved forest can be recovered to the forest structure and productivity level before selective cutting, which provides important inspiration for forest management in the region.

Keywords: biomass; DBH class; mixed forests; productivity; species diversity

1. Introduction

Under global climate change, the development dynamics of forest structure, diversity, and productivity have always been the focus of researchers [1]. Climate warming changes the structure and diversity of the original forests [2–4]. Many studies have been carried out on this aspect in boreal forests and rainforests [5–8], but there are few studies on this aspect in subtropical forests [1]. Some studies have shown that the species distribution and productivity of subtropical evergreen broad-leaved forests have changed under the interference of climate change, such as the decline of forest biomass, the change of dominant species, the death of non-vascular epiphytes, and the migration of species [1,9,10]. However, the response of trees of different diameter at breast height (DBH) classes to climate change during forest succession is not clear.

Mountainous subtropical forests are composed of distinct layers, namely a canopy consisting of large trees, a subcanopy consisting of medium-sized trees, and an understory consisting of small trees [11]. Ecological succession in these forests is jointly determined by the canopy, subcanopy, and understory layers. During forest succession, changes in phylogenetic diversity [12], community structure and diversity [13], and forest carbon stock [14,15] occur, which result in varying effects on forest biodiversity, the carbon sink, and other ecological effects. Changes in stand structure occur in different forest layers during forest succession [16]. This inevitably leads to differences in forest diversity and biomass within the forest [11]. However, how the structure, diversity, and biomass of different forest layers change during forest succession is still not completely clear.

The canopy of our sample plot mainly consisted of mature *Castanopsis carlesii* (Hemsl.) Hayata and *Schima superba* Gardner and Champ., which are both tall trees and typical representatives of canopy tree species in our region [17,18]. The subcanopy mainly consists of immature and small trees while the understory is composed of juvenile trees, small juvenile trees, and shrubs. Due to differences in growth stages and microenvironments between the different forest layers, plants have different survival strategies at each stage. Canopy plants will compete for resources with the understory layer by reducing effective solar radiation and soil temperature, increasing soil moisture, and affecting soil nutrients [19–22]. Therefore, small trees tend to die during competition with large trees. However, the small-diameter class is major contributor towards community abundance and diversity [23]. Therefore, the death of small trees directly affects community structure and diversity [16]. Soil is the carrier of tree growth, and light is an essential resource for photosynthesis [24]. In many studies, light is a limiting factor for undergrowth [25,26]. The pioneer species and heliophytic tree species need to grow in a well-lit environment. At the mid–late stage of succession, insufficient light in the forest will cause the death of the pioneer species and heliophytic tree species [27]. Soil chemical factors, such as total nitrogen, total phosphorus, and total potassium, can provide the chemical elements needed for growth of trees [24], and play a key role in the survival, growth, and species distribution [28,29]. Soil physical factors, such as bulk density and natural moisture content, indirectly affect the water absorption of trees by affecting the water content and state in soil [7,30].

Many studies have shown that changes in forest community structure, diversity, and biomass vary during succession [11,31]. During different stages of succession, community species diversity does not increase or decrease monotonically but typically reaches a maximum at the middle stage of succession [32]. Changes in community biomass differ at different succession stages [33]; during the early stage, biomass will increase as trees grow, although while succession progresses the death of dominant species will decrease total biomass [34]. Similarly, community abundance is intimately associated with successional stages and will increase or decrease during different stages of succession [27]. Are changes in various forest layers during forest succession consistent with the community? There is currently no clear answer to this question. The contributions of various forest layers toward community structure, diversity, and biomass are still unclear.

The subtropical forest succession is a long-term process. Some studies have shown that needle-leaved forest, needle-leaved and broad-leaved mixed forest, and evergreen broad-leaved forest can be formed in the secondary succession of bare land in subtropical areas after 25, 50, and 75 years of succession, respectively [35]. Although 5 years is a short time for forest succession, we hypothesized that the stand structure will be appreciably different, although the type and the nature of the forest community remains unchanged over a 5-year successional stage. In this paper, we studied the changes in different DBH classes in a 10 ha mountainous forest in the Dongyuan Kanghe Nature Reserve during forest succession in 2012–2017 to answer the following questions: (1) What is the composition and distribution of different DBH classes during subtropical mountainous forest succession? (2) Are there significant changes in the composition and distribution of different DBH classes during mountainous subtropical forest succession? Is so, what changes occur? (3) What are the changes in major environmental driving forces in different DBH classes during forest succession? Answering these questions is helpful to understand forest succession stage and succession direction. Under global warming, it can provide data support and theoretical guidance for forest managers to make better forest management plans.

2. Materials and Methods

2.1. Study Area

The study area was located at the Kanghe Provincial Nature Reserve (115°04′–115°09′ E, 23°44′–23°53′ N) in the southeastern part of Guangdong Province, China (Figure 1). The nature reserve has a subtropical monsoon climate, with an annual mean temperature of 20–21 °C, annual mean rainfall of 2143 mm, and annual mean humidity of 77%. Major vegetation in the region includes secondary evergreen broad-leaved forests and mixed coniferous–broad-leaved forests [36]. Selective cutting was carried out in 1993 (DBH >13 cm). Since then, any form of cutting has been banned, and human interference has been excluded. At the first survey in 2012, the forest developed well, the canopy was closed, and the forest structure and productivity were greatly restored. *C. carlesii*, *S. superba*, *Ardisia quinquegona* Blume, *Castanopsis fargesii* Franch, and *Itea chinensis* Hook. and Arn were the main dominant species in the plot [37]. The dominant species in the community were mainly heliophytic tree species such as *C. carlesii*, *S. superba*, and *C. fargesii*, indicating that the forest was in the stage of succession dominated by heliophytes, that is, the early-to-mid stage of subtropical secondary succession [35].

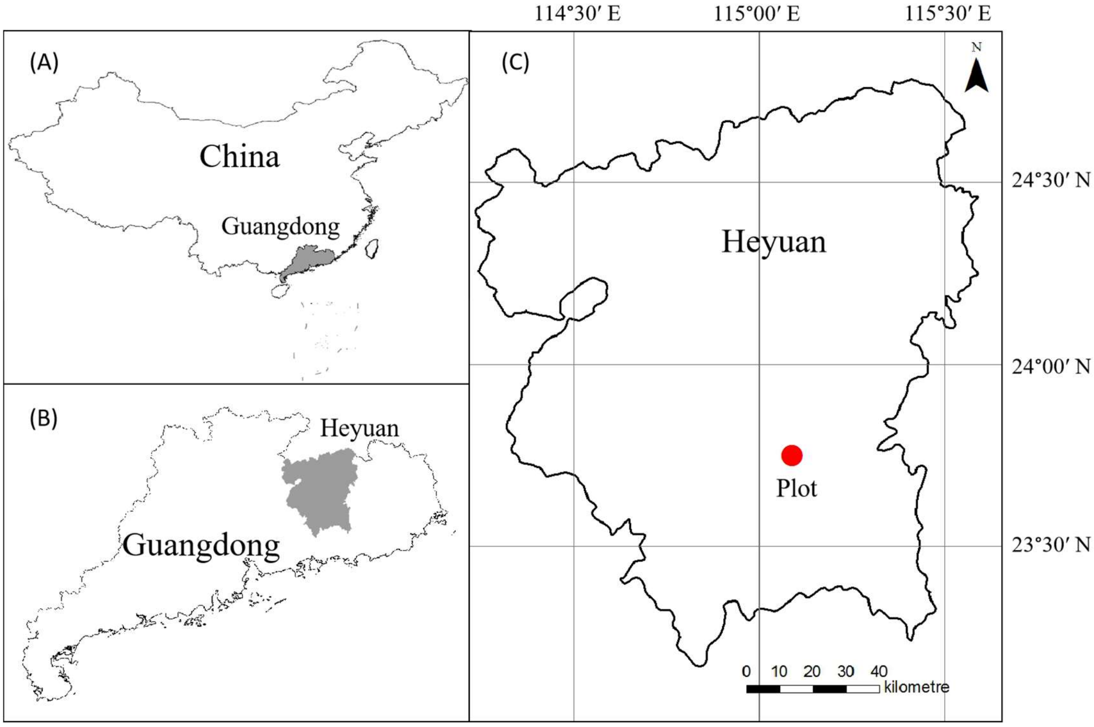

Figure 1. Geographic location of the study area in Guangdong, China (**A**,**B**) and the plot (**C**).

2.2. Sampling Design

A 10 ha fixed sample area was established according to the standards of the Center for Tropical Forest Science (CTFS) [38]. The sample area was a 200 m × 500 m rectangle. An initial survey was conducted in 2012, and the area was resurveyed in 2017.

2.3. Data Collection and Measurements

All trees with a diameter at breast height (DBH) ≥1 cm in the sample plots were surveyed. The surveyed data included species, DBH, and tree height. In this paper, three different DBH classes were used to represent different forest layers as follows: small trees, 1 cm ≤ DBH < 7.5 cm; medium-sized trees, 7.5 cm ≤ DBH < 22.5 cm; and large trees, 22.5 cm ≤ DBH [36].

Surface soil was collected at the center and at 1/4 and 3/4 of the diagonals of every 20 × 20 m quadrat; five subsamples from each quadrat were mixed for analysis of soil chemical characteristics. At the same locations, a soil cutting ring was used for the collection of soil samples for analysis of physical characteristics. Eight soil factors such as organic matter, total nitrogen, and total phosphorus were used for measurement of soil physiochemical characteristics [39,40]. The physical characteristic of each quadrat was the mean value of five cutting ring samples collected in each quadrat.

A Nikon 4500 Coolpix®camera (Tokyo, Japan) equipped with a Nikon FC-E8 fish-eye lens was used for canopy photography at the center and at 1/4 and 3/4 of the diagonals of every quadrat. During photography, the camera was mounted on a tripod that was 1.65 m above the ground. The image resolution was 2272 × 1704 pixels, and images were stored in JPEG format. All photography was carried out on cloudy and windless days [41]. Gap Light Analyzer 2.0 [42] image processing software was used to analyze canopy photographs and measure four solar radiation factors (canopy openness, leaf area index, transmitted direct solar radiation, and transmitted diffuse solar radiation). The solar radiation factor of each quadrat was the mean value of five values collected in the quadrat.

2.4. Data Analysis

The binary standing tree volume formula in the Common Forest Tree Volume Tables for Forest Inventory drafted by the Guangdong Provincial Forestry Bureau and Guangdong Academy of Forest Inventory and Planning [43] was used. The specific formulas are as follows.

The formulas for binary standing tree volumes for coniferous, hardwood broad-leaved, and softwood broad-leaved trees are shown in Equations (1), (2), and (3), respectively:

$$V = 7.98524 \times 10^{-5} D^{1.74220} H^{1.01198} \tag{1}$$

$$V = 6.01228 \times 10^{-5} D^{1.87550} H^{0.98496} \tag{2}$$

$$V = 6.74286 \times 10^{-5} D^{1.87657} H^{0.92888} \tag{3}$$

where V is the standing stock of a single plant (m^3), D is DBH (cm), and H is tree height (m).

The biomass expansion factor method recommended in Methodologies for Forestry Carbon Sequestration Projects [44] was used as a reference. The specific formula and biomass estimation factors (Table 1) are as follows. The single-tree biomass is calculated as

$$B = V \times D \times BEF \times (1 + R) \tag{4}$$

where B is the single-tree biomass ($t \cdot individual^{-1}$), V is the single-tree volume ($m^3 \cdot individual^{-1}$), D is the basic wood density ($t \cdot m^{-3}$), BEF is the biomass expansion factor that is dimensionless and is used to convert tree volume to aboveground biomass, and R is the ratio of belowground biomass/aboveground biomass and is dimensionless.

Table 1. Estimation of biomass factors.

Species Group	D (g/cm^2)	BEF (t)	R
Cunninghamia lanceolata (Lamb.) Hook.	0.307	1.634	0.246
Pinus massoniana Lamb.	0.380	1.472	0.187
Mixed broad-leaved trees	0.482	1.514	0.262

The richness and Shannon–Wiener indices were used for quantitative analysis of the species diversity of different forest layers [45].

One-way analysis of variance was used to analyze the differences in diversity, structure, and biomass of different forest layers during forest succession. The Kruskal–Wallis test was used for testing as it is a non-parametric test method that is suitable for field ecological data analysis [46]. The multiple response permutation procedure (MRPP) was used to analyze differences in species distribution in the various forest layers during forest succession and between various forest layers in 2012 and 2017. The MRPP is a non-parametric statistical method that is widely used in the analysis of ecological data to test the differences in species distribution between two or more groups [47]. The higher the absolute T value, the greater the inter-group differences.

Indicator species analysis was used to study changes in indicator plants and indices in different forest layers during forest succession [47]. Redundancy analysis (RDA) was used to study the major driving factors during forest succession and changes in these factors.

Statistica 8.0 (Statsoft, Inc. Tulsa, OK, USA) was used for histograms, box plots, one-way analysis of variance, and the Kruskal–Wallis test of species abundance and biomass. PC-ORD (MjM Software, Gleneden Beach, OR, USA) was used to calculate the MRPP and for indicator species analysis. CANOCO 5.0 [48] was used for redundancy analysis.

3. Results

3.1. Characteristics of DBH Classes during Forest Succession

Significant changes were observed in the abundance of the community and three DBH classes in 2012–2017 (Table 2). At the plot-level, small trees showed the greatest change, with mean abundance decreasing from 152.40 to 113.66. Large trees showed the smallest change. Changes in biomass also occurred with large trees having the greatest change in biomass, which increased from 6.98 Mg to 7.89 Mg in each quadrat, while small trees had the smallest change. Changes in species diversity were relatively low, with small trees showing the largest change because its richness index decreased from 22.62 to 19.64, while medium-sized trees showed the smallest change. At the community-level, abundance and biomass of small and medium trees decreased, and abundance and biomass of large trees increased. The degree and trend of change at the community-level were consistent with the plot-level. However, in terms of species diversity index, small, medium, and large trees all decreased. The abundance of the community decreased, which was mainly affected by the large decrease in the abundance of small trees. The biomass of the community increased, mainly due to the increase in the biomass of the large trees.

Table 2. Community characteristics of different diameter at breast height (DBH) classes during forest succession.

Index	DBH Classes (2012)				DBH Classes (2017)			
	All	Small	Medium	Large	All	Small	Medium	Large
Plot-Level								
Abundance	200.28	152.40	36.79	11.09	160.46	113.66	34.10	12.70
Species Richness	25.14	22.62	8.05	3.10	22.83	19.64	7.98	3.34
Shannon–Wiener index	2.37	2.35	1.55	0.75	2.30	2.25	1.55	0.81
Biomass (Mg)	11.70	0.43	4.29	6.98	12.05	0.37	3.80	7.89
Community-Level								
Abundance	50,070	38,100	9198	2772	40,115	28,415	8524	3176
Species Richness	153	138	99	55	147	127	95	47
Biomass (Mg)	2925.4	107.0	1072.3	1746.1	3012.9	91.6	949.5	1971.8

During forest succession, the community size-structure changed significantly, especially the small trees (Figure 2A,B). In 2012, the community size-structure showed an inverted "J" shape, indicating a good community renewal status. In 2017, the community size-structure still showed an inverted "J" shape, but there was a large decrease in small trees, which indicated that the small trees were undergoing drastic changes. This may result in insufficient numbers of small trees to supplement future forest succession after the death of the medium and large trees.

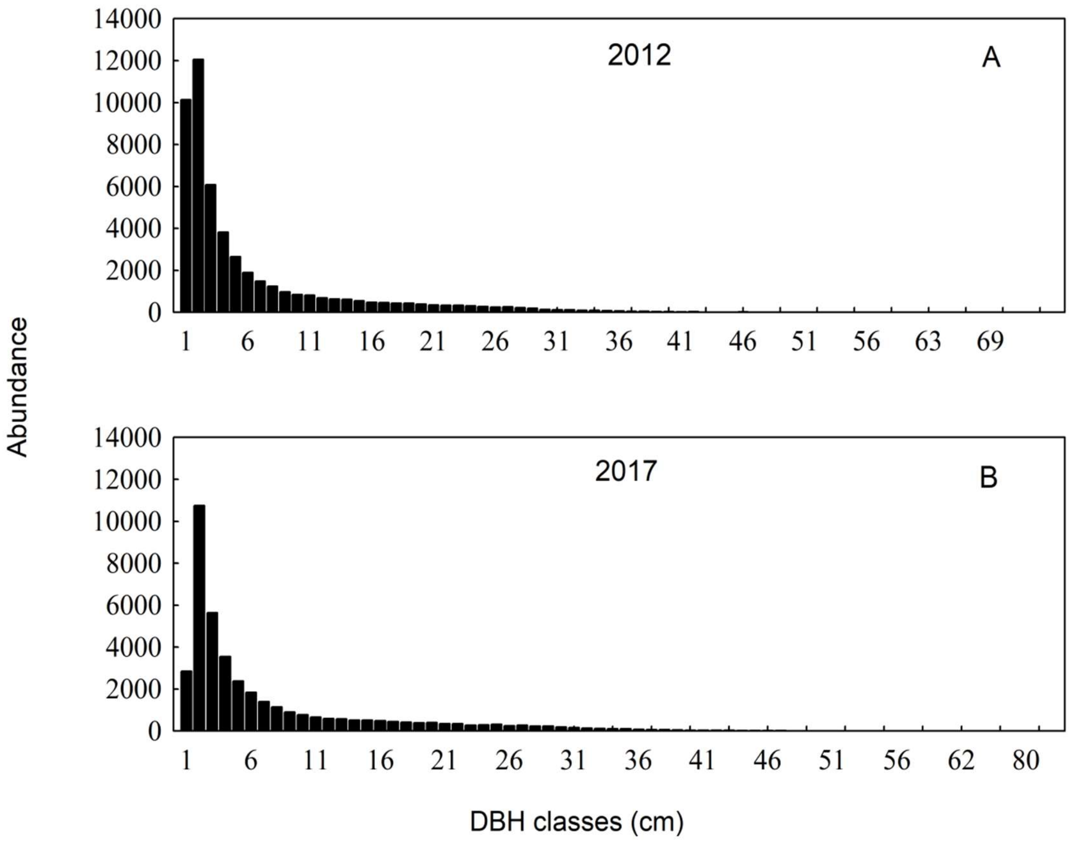

Figure 2. The dynamic changes of size-structure during forest succession from 2012 (**A**) to (2017) (**B**).

The top ten species with changes in abundance all showed reductions, of which the top three species with the largest reductions were *C. carlesii* (−2289 plants), *Cratoxylum cochinchinense* (Lour.) Blume (−665), and *S. superba* (−644) (Figure 3A). The top ten species with changes in absolute abundance all showed reductions, of which the top three species with the highest reductions were *Alchornea trewioides* (Benth.) Müll. (−88.89%), *Vitex negundo* (−86.36%), and *Pinus massoniana* Lamb. (−83.02%) (Figure 3B). The top ten species with changes in biomass mainly showed increases, except for decreased biomass in *P. massoniana* and *Cunninghamia lanceolata* (Lamb.) Hook. The top three species with the greatest change in biomass were *S. superba*, (+36.34 Mg), *C. carlesii* (+26.41 Mg), and *Engelhardtia roxburghiana* Lindl. (+19.92 Mg) (Figure 3C). The top ten species with changes in absolute biomass included increases and decreases in biomass (Figure 3D).

3.2. Plot-Based Differences in Community Characteristics during Forest Succession

Diversity indices changed in different ways between different DBH classes during forest succession. The richness index of the entire community and the richness and Shannon–Wiener indices of small trees all decreased significantly (Figure 4A,C,D), while other indices experienced no significant change. Medium-sized trees showed the lowest change in diversity (Figure 4E,F), and large trees showed no significant change (Figure 4G,H).

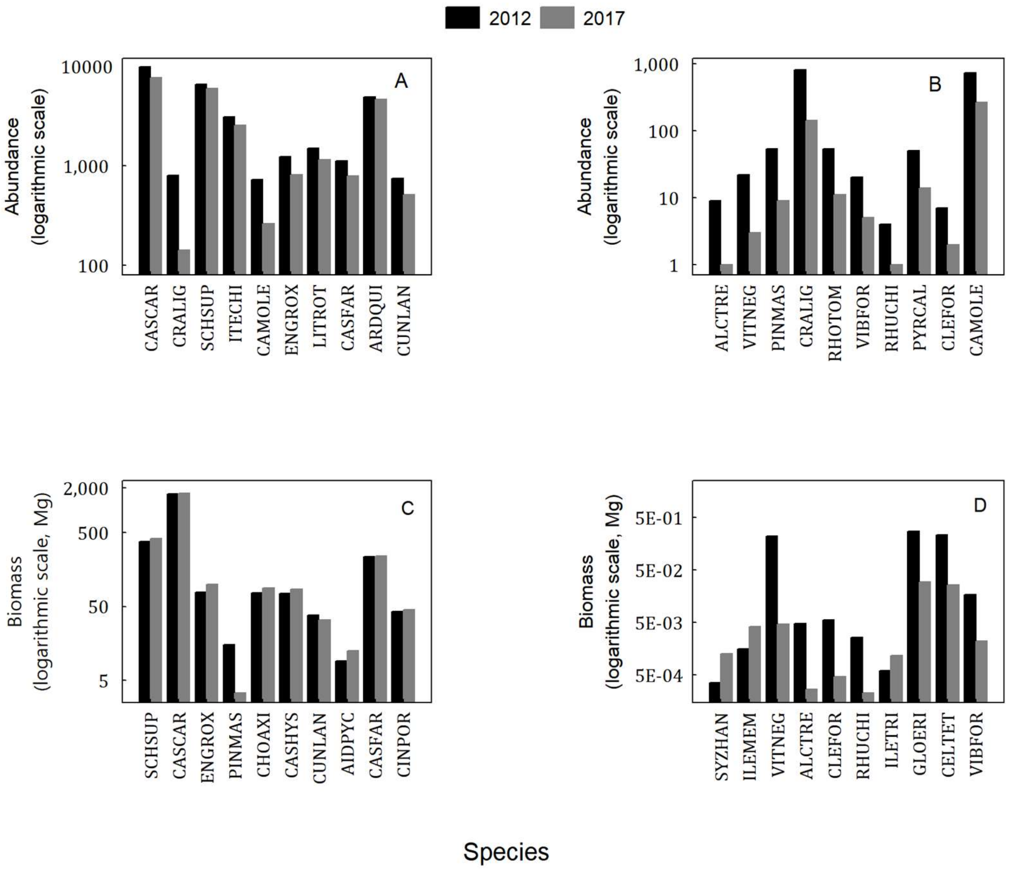

Figure 3. Changes in abundance (**A** and **B**) and biomass (**C** and **D**; logarithmic scale) of ten dominant species during forest succession. Species code: AIDPYC, *Aidia pycnantha* (Drake) Tirveng.; ALCTRE, *Alchornea trewioides* (Benth.) Müll. Arg.; ARDQUI, *Ardisia quinquegona* Blume; CAMOLE, *Camellia oleifera* Abel; CASCAR, *Castanopsis carlesii* (Hemsl.) Hayata; CASFAR, *Castanopsis fargesii* Franch.; CASHYS, *Castanopsis hystrix* Hook. f. and Thomson ex A. DC.; CELTET, *Celtis tetrandra* Roxb.; CHOAXI, *Choerospondias axillaris* (Roxb.) B.L. Burtt and A.W. Hill; CINPOR, *Cinnamomum porrectum* (Roxb.) Kosterm.; CLEFOR, *Clerodendrum fortunatum* L.; CRALIG, *Cratoxylum cochinchinense* (Lour.) Blume; CUNLAN, *Cunninghamia lanceolata* (Lamb.) Hook.; ENGROX, *Engelhardtia roxburghiana* Lindl.; GLOERI, *Glochidion eriocarpum* Champ. ex Benth.; ILEMEM, *Ilex memecylifolia* Champ. ex Benth.; ILETRI, *Ilex triflora* Blume; ITECHI, *Itea chinensis* Hook. and Arn.; LITROT, *Litsea rotundifolia* Hemsl.; PINMAS, *Pinus massoniana* Lamb.; PYRCAL, *Pyrus calleryana* Decne.; RHOTOM, *Rhodomyrtus tomentosa* (Aiton) Hassk.; RHUCHI, *Rhus chinensis* Mill.; SCHSUP, *Schima superba* Gardner and Champ.; SYZHAN, *Syzygium hancei* Merr. and L.M. Perry; VIBFOR, *Viburnum fordiae* Hance; VITNEG, *Vitex negundo* L.

With regard to abundance, except for medium-sized trees that showed no significant changes (Figure 5E), groups of all, small, and large trees showed significant decreasing, decreasing, and increasing trends, respectively (Figure 5A,C,G). Except for all trees that showed no significant change in biomass (Figure 5B), the biomass in groups of small, medium, and large trees showed significant decreasing, decreasing, and increasing trends, respectively (Figure 5D,F,H).

The MRPP was carried out on the differences in species composition and distribution in different DBH classes during succession (Table 3). The results showed that significant differences existed in species composition and distribution in all trees and small trees during forest succession although no significant differences were observed in medium-sized and large trees. The absolute T-value for small trees was large, indicating large changes occurred in the species composition and distribution of small trees during succession.

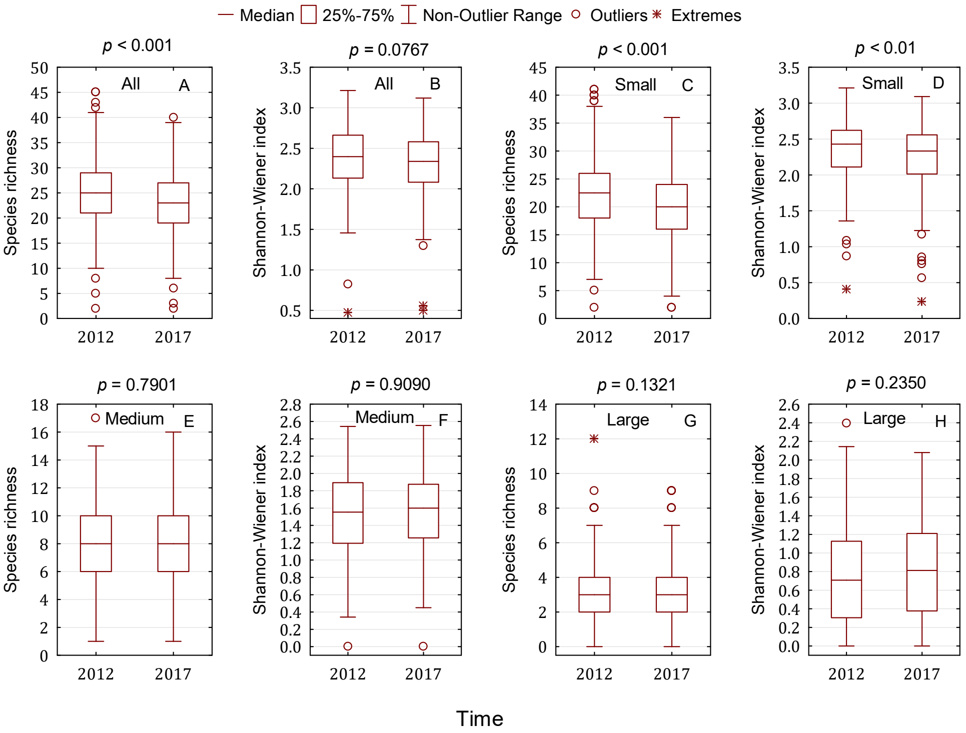

Figure 4. Changes in community diversity parameters in relation to forest succession. DBH classes are defined according to the tree size, as follows: All (**A** and **B**), All trees; Small (**C** and **D**), 1 cm ≤ DBH < 7.5 cm; Medium (**E** and **F**), 7.5 cm ≤ DBH < 22.5 cm; Large (**G** and **H**), 22.5 cm ≤ DBH.

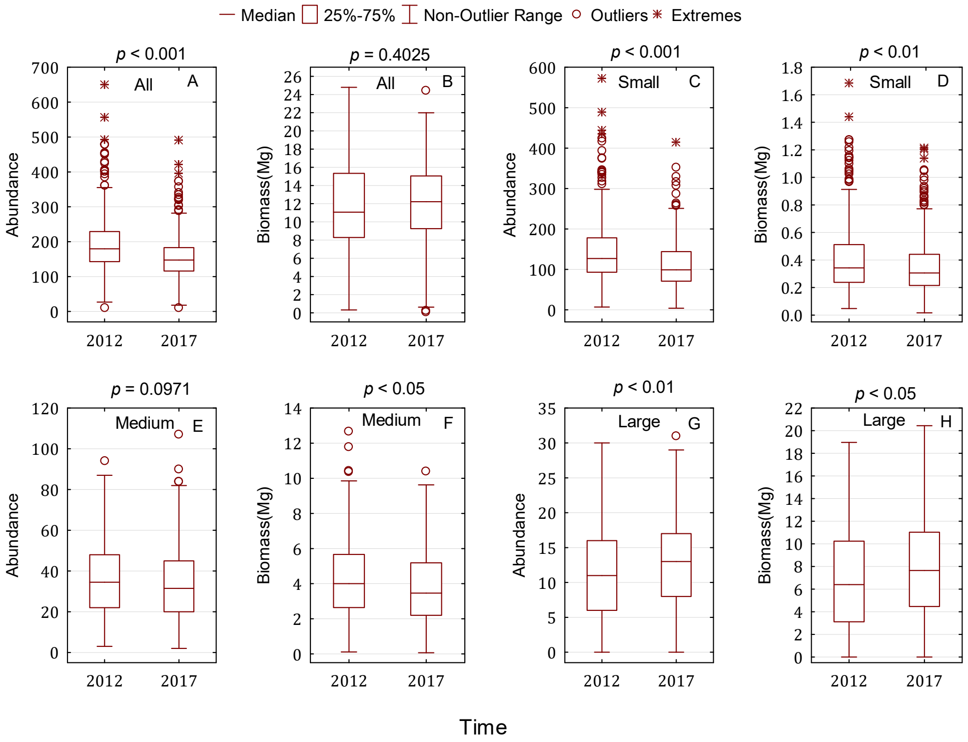

Figure 5. Changes in community biomass parameters in relation to forest succession. DBH classes are defined according to the tree size, as follows: All (**A** and **B**), All trees; Small (**C** and **D**), 1 cm ≤ DBH < 7.5 cm; Medium (**E** and **F**), 7.5 cm ≤ DBH < 22.5 cm; Large (**G** and **H**), 22.5 cm ≤ DBH.

Table 3. Multi-response permutation procedures (MRPP) to test for significance of variation in species composition of different DBH classes during forest succession. The DBH classes are as follows: All, All trees; Small, 1 cm ≤ DBH < 7.5 cm; Medium, 7.5 cm ≤ DBH < 22.5 cm; Large, 22.5 cm ≤ DBH.

Groups Compared	*T*	*A*	*P*
All (2012) vs. All (2017)	−4.98	0.003	0.002
Small (2012) vs. Small (2017)	−7.22	0.005	0.000
Medium (2012) vs. Medium (2017)	−1.00	0.001	0.131
Large (2012) vs. Large (2017)	−0.37	0.001	0.231

In addition, significant differences were observed in the species distribution and composition between different DBH classes (Table 4). A pairwise comparison of different DBH classes in 2012 by MRPP showed that the difference in the composition and distribution between all trees in the community and large trees was the greatest (|T| = 242.39) and the difference in the composition and distribution between all trees in the community and small trees was the least (|T| = 28.79). This indicates the composition and distribution of all trees is mainly affected by small trees. In addition, the inter-group differences between small trees and large trees (|T| = 216.30) were greater than between small and medium-sized trees (|T| = 147.58), showing that similar DBH classes have similar species composition and distribution. The 2017 results are consistent with the 2012 results.

Table 4. Multi-response permutation procedures (MRPP) to test for significance of variation in different years plant species composition across different DBH classes. The DBH classes are as follows: All, All trees; Small, 1 cm ≤ DBH < 7.5 cm; Medium, 7.5 cm ≤ DBH < 22.5 cm; Large, 22.5 cm ≤ DBH.

Groups Compared	2012			2017		
	T	*A*	*P*	*T*	*A*	*P*
Overall Comparison	−253.01	0.171	$< 10^{-7}$	−254.56	0.168	$< 10^{-7}$
Pairwise Comparison						
All vs. Small	−28.79	0.019	$<10^{-7}$	−42.74	0.029	$<10^{-7}$
All vs. Medium	−184.74	0.140	$<10^{-7}$	−176.13	0.134	$<10^{-7}$
All vs. Large	−242.39	0.221	$<10^{-7}$	−244.07	0.217	$<10^{-7}$
Small vs. Medium	−147.58	0.099	$<10^{-7}$	−136.61	0.093	$<10^{-7}$
Small vs. Large	−216.30	0.172	$<10^{-7}$	−211.61	0.167	$<10^{-7}$
Medium vs. Large	−99.01	0.096	$< 10^{-7}$	−88.23	0.080	$< 10^{-7}$

3.3. Changes in Indicator Species in Different DBH Classes during Forest Succession

With the exception of one indicator plant in the medium-diameter class in 2017 (*Cinnamomum porrectum*), all other indicator plants were in the small-diameter class during forest succession (Table 5). The results showed that the small-diameter class had high species diversity and included species present in medium-sized and large-diameter classes. The numbers of indicator plant species in the small-diameter class in 2012 and 2017 were 28 and 23, respectively. The indicator values of indicator plants in the small-diameter class in 2017 showed varying degrees of decrease compared with 2012, of which *C. porrectum* showed the greatest decrease in indicator value by 50.6% and changed from an indicator plant to a non-indicator plant, while its abundance decreased by 52.9%. *Aidia canthioides* showed the greatest increase in indicator value (4.4%) and the lowest change in abundance (−3.7%).

Table 5. Plant species with a significant indicator value (IV) ≥ 20 for different DBH classes from both 2012 and 2017 communities. The DBH classes are as follows: Small, 1 cm ≤ DBH < 7.5 cm; Medium, 7.5 cm ≤ DBH < 22.5 cm; Large, 22.5 cm ≤ DBH. * indicates significant at $p < 0.05$. Species code: ADIMIL, *Adinandra milletii* (Hook. and Arn.) Benth. and Hook.f. ex Hance; AIDCAN, *Aidia canthioides* (Champ. ex Benth.) Masam.; AIDPYC, *Aidia pycnantha* (Drake) Tirveng.; ARDQUI, *Ardisia quinquegona* Blume; BEITSA, *Beilschmiediatsangii* Merr.; CAMOLE, *Camellia oleifera* Abel; CASCAR, *Castanopsis carlesii* (Hemsl.) Hayata; CASVIL, *Casearia villilimba* Merr.; CINPOR, *Cinnamomum porrectum* (Roxb.) Kosterm.; CRYCHI, *Cryptocarya chinensis* (Hance) Hemsl.; DAPOLD, *Daphniphyllum oldhamii* (Hemsl.) K.Rosenthal; DIOMOR, *Diospyros morrisiana* Hance; ELACHI, *Elaeocarpus chinensis* (Gardner and Champ.) Hook. f. ex Benth.; ENGROX, *Engelhardtia roxburghiana* Lindl.; EURBRE, *Eurya brevistyla* Kobuski; EURMAC, *Eurya macartneyi* Champ.; FICVAR, *Ficus variolosa* Lindl. ex Benth.; ILEPUB, *Ilex pubescens* Hook. and Arn.; ITECHI, *Itea chinensis* Hook. and Arn.; LITROT, *Litsea rotundifolia* Hemsl.; MACCHI, *Machilus chinensis* (Benth.) Hemsl.; MACVEL, *Machilus velutina* Champ. ex Benth.; PHOPRU, *Photinia prunifolia* (Hook. and Arn.) Lindl.; SCHOCT, *Schefflera heptaphylla* (L.) Frodin.; SCHSUP, *Schima superba* Gardner and Champ.; STYODO, *Styrax odoratissima* F.B. Forbes and Hemsl.; STYSUB, *Styrax suberifolius* Hook. and Arn.; TARMOL, *Tarenna mollissima* (Walp.) Rob.

Species Code	2012			2017			Rate of Abundance Change (%)	Rate of IV Change (%)
	DBH Class	IV	Abundance (Small)	DBH Class	IV	Abundance (Small)		
ITECHI	1	86.4 *	3052	1	81.8 *	2454	−19.6	−5.3
ARDQUI	1	73.2 *	4918	1	73.1 *	4636	−5.7	−0.1
ELACHI	1	65.7 *	792	1	61.6 *	664	−16.2	−6.2
EURMAC	1	65.7 *	628	1	64.6 *	567	−9.7	−1.7
ILEPUB	1	65.7 *	775	1	63.1 *	609	−21.4	−4
DIOMOR	1	64 *	589	1	59.4 *	496	−15.8	−7.2
MACVEL	1	61.9 *	774	1	57.8 *	596	−23	−6.6
SCHSUP	1	59.8 *	4283	1	53.3 *	3489	−18.5	−10.9
BEITSA	1	55.9 *	895	1	51.4 *	804	−10.2	−8.1
PHOPRU	1	52.8 *	700	1	45.3 *	529	−24.4	−14.2
MACCHI	1	52 *	519	1	41 *	319	−38.5	−21.2
STYODO	1	49.4 *	457	1	43.2 *	342	−25.2	−12.6
FICVAR	1	46.4 *	280	1	35.6 *	192	−31.4	−23.3
AIDCAN	1	45.7 *	1421	1	47.7 *	1368	−3.7	4.4
EURBRE	1	44.0 *	327	1	40.5 *	270	−17.4	−8
ADIMIL	1	42.7 *	565	1	37.2 *	335	−40.7	−12.9
SCHOCT	1	42.6 *	376	1	37.1 *	325	−13.6	−12.9
CASCAR	1	42.2 *	4826	2	31	2813	−41.7	–
TARMOL	1	39.5 *	298	1	34 *	237	−20.5	−13.9
ENGROX	1	34.2 *	783	1	16.9	369	−52.9	−50.6
CASVIL	1	33.8 *	251	1	28.3 *	195	−22.3	−16.3
CRYCHI	1	31.8 *	252	1	29.5 *	231	−8.3	−7.2
AIDPYC	1	31.7 *	1699	1	31.5 *	1598	−5.9	−0.6
CAMOLE	1	30.8 *	730	1	22.4 *	264	−63.8	−27.3
CINPOR	1	28.2 *	329	2	25.7 *	181	−45	–
STYSUB	1	23.2 *	340	1	17.4	244	−28.2	−25
DAPOLD	1	22.2 *	153	1	12.2	80	−47.7	−45

3.4. Major Drivers for Community Succession

In the RDA analysis of 2012, 12 environmental factors explained 36.6% of the changes in species distribution, of which the first four axes in the RDA ordination graph explained a total of 78.97% of the variation. This shows that the first four axes could explain most of the effects of these environmental factors on species distribution but only axes 1 and 2 had significant explanatory effects ($p < 0.05$). Pseudo-canonical correlation reflects the effects of environmental factors on species distribution; the species–environment correlations of the four axes were high (Table 6). Only four environmental factors had significant explanatory effects on species distribution (p (adj) < 0.05), which included total phosphorus, transmitted direct solar radiation, organic matter, and capillary water capacity. Total phosphorus had the strongest explanatory effect and contributed 21.1% to the explained variation

(Table 7). From the ordination graph (Figure 6A), we can see that total phosphorus and transmitted direct solar radiation had greater effects on species distribution than other environmental variables. In seen in Axis 1 from right to left, as total phosphorus increased, species abundance decreased.

Table 6. Eigenvalues and explained variations of the first four axes in redundancy analysis (RDA) ordination of species distribution and environmental variables.

Statistic	Axis 1	Axis 2	Axis 3	Axis 4
2012				
Eigenvalues	0.1457	0.0739	0.0377	0.0314
Cumulative explained variation (%)	14.57	21.97	25.74	28.88
Pseudo-canonical correlation	0.8074	0.7611	0.7432	0.8244
Cumulative explained fitted variation (%)	39.86	60.08	70.38	78.97
p value	0.001	0.028	0.675	0.797
2017				
Eigenvalues	0.1703	0.0477	0.0354	0.0295
Cumulative explained variation (%)	17.03	21.8	25.34	28.29
Pseudo-canonical correlation	0.8563	0.6435	0.7476	0.7901
Cumulative explained fitted variation (%)	47.63	60.97	70.89	79.14
p value	0.001	0.559	0.838	0.919

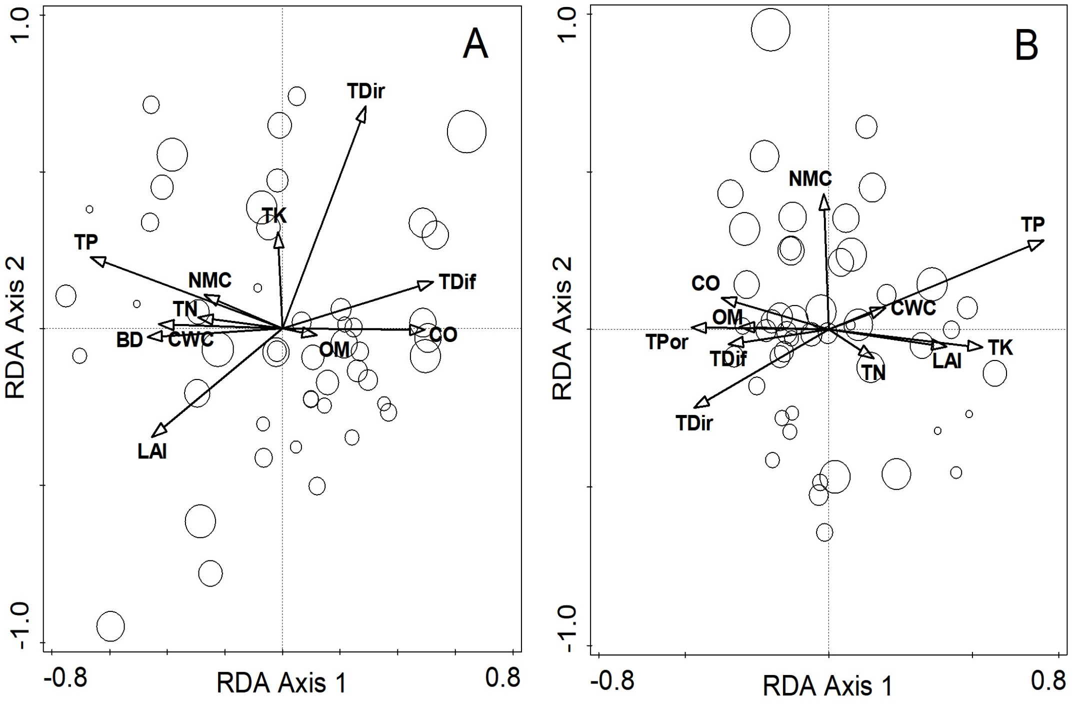

Figure 6. RDA ordination of species distribution and environmental variables in 2012 (**A**) and 2017 (**B**). Environmental variables: OM = organic matter; TN = total nitrogen; TP = total phosphorus; TK = total potassium; NMC = natural moisture content; BD = bulk density; CWC = capillary water capacity; TPor = total porosity; CO = canopy openness; LAI = leaf area index; TDir = transmitted diffuse solar radiation; TDif = transmitted diffuse solar radiation (mols·m^{-2}·d^{-1}).

In the RDA analysis of 2017, 12 environmental factors explained 35.7% of the changes in species distribution, of which the first four axes in the RDA sequence explained a total of 79.14% of the variation but only axis 1 has significant explanatory effects ($p < 0.05$) (Table 6). Only two environmental factors had significant explanatory effects on species distribution (p(adj) < 0.05), which were total phosphorus and total potassium. Total phosphorus had the strongest explanatory effect and contributed 29% to the explained variation (Table 7). From the ordination graph (Figure 6B), we can see that total phosphorus and total potassium had greater effects on species distribution. As seen in Axis 1 from left to right, as total phosphorus increased, species abundance decreased.

Table 7. Effects of environmental variables on species distribution.

Environmental Variables	Explained Variation	Explained Fitted Variation (%)	*p* (adj)
2012			
Total phosphorus (g/kg)	7.7	21.1	0.012
Transmitted direct solar radiation (mols·m^{-2}·d^{-1})	5.6	15.3	0.012
Organic matter (g/kg)	4.7	12.9	0.024
Capillary water capacity (g/kg)	3.8	10.4	0.024
2017			
Total phosphorus (g/kg)	10.4	29.0	0.012
Total potassium (g/kg)	5.1	14.2	0.024

4. Discussion

By analyzing the changes of the small-diameter class, medium-diameter class, and large-diameter class during forest succession and combined with the biological characteristics of dominant species, we speculated that the forest succession tended to the mid–late stage of succession. Our results will help forest managers to understand the forest succession stage and succession direction and make forest management plans. For example, in natural forest management, forest managers may consider planting heliophytic tree species such as *S. superba* and *C. carlesii* on secondary bare land, which is conducive to rapid forest growth, increased forest productivity, and effective resistance of forest fires [18,49].

When compared with other measurements, community abundance showed the greatest change during succession, of which the small-diameter class showed the greatest change. A drastic reduction in the abundance in the small-diameter class may be due to environmental screening [50] and density limitations [51]. The abundance of large trees showed a slight increase, showing that large trees are more adapted to the existing environment during forest succession and occupy more environmental resources, such as solar radiation, than smaller trees. The large trees will form a closed canopy and dominate the stand structure, resulting in sparse solar radiation resources for smaller trees and will affect the growth and death of understory plants [52]. Changes in diversity during succession were relatively low, of which the small-diameter class showed the greatest change, followed by large trees, and then medium-sized trees. Changes in diversity may be related to changes in species abundance [53]. Changes in biomass were low, of which the largest change was in large trees, followed by medium-sized trees and then small trees. However, biomass increased in large trees but decreased in medium-sized and small trees. This indirectly shows that large trees absorb more solar radiation and soil nutrient resources than smaller trees [54].

Small trees usually experience a rapid growth phase, with high resource utilization rates and demands [55]. Hence, the abundance and diversity of the small-diameter class is dependent on the amount of available resources [23]. Large and medium-diameter classes are resource allocators, particularly for solar radiation [11], while small trees are at a weaker position in resource competition. In addition, small trees have relatively low vitality, stress tolerance, and survival probability. These conditions result in a drastic decrease in abundance in the small-diameter class [56] and decreased diversity over time during ecological succession. In addition, the community succession stage also has important effects on changes in the small-diameter class. The foundation species, *C. carlesii*, is a heliophytic tree species. The death of a large number of *C. carlesii* trees shows that it is not a mesophytic or sciophytic tree species that is adapted for the mid−late stage of succession [27]. *C. carlesii* had a cluttered distribution in the plot, and it was subject to high intra- and inter-specific competition in the community with rich diversity and limited resources [37]. In adaptive strategy theory [57,58], this type of heliophytic tree species should be a C-type strategy species that employs a competitive strategy to adapt to a resource-rich habitat. Successful competitors allocate most of their resources to aboveground vegetative growth organs and can fully utilize abundant resources in the environment, which makes it difficult for other plants to compete with it, thereby increasing its own fitness [59]. However, competition with S-type strategy species during the mid−late stages of succession causes many members of this species group to degrade and die [60]. This fits the phenomenon of *C. carlesii*, a C-type strategy species that will die in large numbers. Because small-tree abundance and diversity are principal components of abundance and diversity of the community [23], the abundance and diversity of the community decreases significantly due to the effects of the small-diameter class. In addition, changes in species distribution were the greatest for the small-diameter class during succession. This also results in significant changes in species distribution in the community.

Large trees occupy a significantly dominant position in resource acquisition, such as solar radiation [11]. This allocation of resources by large trees will affect resource acquisition by small trees and limit their growth [22]. In addition, the strong vitality and stress tolerance of large trees enables them to have a high survival probability. Additionally, medium-sized trees ultimately grow into large trees. Therefore, the abundance of biomass and diversity of large trees all increased. The foundation species, *C. carlesii*, is a C-strategy species in adaptive strategy theory [57,58] that is adapted to a resource-rich environment. During the mid−late stages of succession, environmental resources become limiting with competition from other mesophytic tree species [27,60]. However, as large *C. carlesii* trees possess abundant resources that can satisfy their own growth demands, they will not die as a result of resource deficiency over a short period of time. At this time, S-strategy species still did not show resource dominance and are unable to threaten large C-strategy trees. In initial floristic composition theory [61,62], plant species substitution does not necessarily occur in an orderly manner, and every species will tend to exclude and inhibit any new colonizing plants. Therefore, the large amount of resources possessed by large *C. carlesii* trees will exclude and inhibit all other plants directly, particularly small trees. Therefore, there will be a sufficient number of medium-sized *C. carlesii* trees to replenish the population of large *C. carlesii* trees, so that when large *C. carlesii* trees have not entered the decline stage, the latter will occupy a dominant position for a long period of time. Changes in canopy structure are primarily determined by the lifespan of dominant canopy species [63]. After large *C. carlesii* trees have entered the decline stage, changes in the canopy may be caused by the replacement by large trees (such as *S. superba*) with a longer lifespan, which then become the dominant tree species of the canopy. Large tree biomass is a principal component of community biomass [36]. Therefore, the biomass of the community increases because of the effects of an increase in large tree biomass.

Medium-sized trees lie between large and small trees in terms of dominance. Medium-sized trees will continue to grow into large trees while small trees grow into medium-sized trees. Currently, the growth rate for the abundance of medium-sized trees is negative, showing that the growth rate of small trees into medium-sized trees is lower than the growth rate of medium-sized trees into large trees. The speeds of death for *C. carlesii* and *C. fargesii* are relatively fast while those of sciophytic tree species (such as *Itea chinensis* Hook. and Arn and *Aidia pycnantha* (Drake) Tirveng) increase greatly. Among this increase and decrease, medium-sized trees showed the lowest change. In adaptive strategy theory [57,58], C-type strategy species such as *C. carlesii* and *C. fargesii* are gradually replaced by S-strategy species such as *A. pycnantha*.

In the small-diameter class, heliophytic tree species such as *C. carlesii*, *C. fargesii*, and *C. lanceolata* die off in large numbers while mesophytic tree species such as *A. quinquegona* and *A. canthioides* show a lower decrease in numbers. From this, we can see that forest succession was at the mid–late stage in the present study area, which fits the adaptive strategy theory [57,58] in which C-strategy species change into S-strategy species [60]. From the stable increase in the foundation species, *C. carlesii*, and the large increase in mesophytic and sciophytic tree species such as *A. canthioides* and *Schefflera octophylla* (Lour.) Harms, we can see that this also matches the initial floristic composition theory [61,62]. Large *C. carlesii* trees dominate the community, have already incorporated many resources, and will retain their dominant position for a long period of time. However, in small- and medium-diameter class, mesophytic and sciophytic tree species will gradually replace pioneer species and heliophytic tree species to ultimately occupy a dominant position [27].

The community in which the canopy remains stable reflected this in that the subcanopy gradually becomes sparse over time and the understory layer experiences drastic changes, showing significant self-thinning [56]. As the community reaches the mid–late stage of succession in which environmental resources are very limited [60], sample plots with high abundance and number of species will result in better resource absorption. Therefore, total phosphorus and total potassium in the soil will decrease as the number of species increases. As forest succession progresses, mesophytic and sciophytic tree species in the small-diameter class will gradually occupy a dominant position with increased resistance against environmental stress. Therefore, the effects of environmental resources on the species distribution in the small-diameter class decreases, which also decreases the distribution of species in the community. This can be seen in the redundancy analysis of the explanatory power of environmental factors in 2017. In this paper, major environmental factors that affected species distribution were total phosphorus, total potassium, and organic matter, which is consistent with Satdichanh et al. [64]. Their study found that soil nutrients show a strong correlation with stand structure during short-term forest succession but species interaction has important effects on stand structure when forest succession occurs over a longer period.

The trend of community succession has important implications for forest managers. Forest managers can carry out appropriate anthropic disturbances to ensure sustainable development of the forest [6,65]. For example, forest managers should pay attention to the collocation of tree species during the afforestation period. Pioneer species and heliophytic tree species can quickly form forests and give full play to the ecological efficiency of forests. Mesophytic and sciophytic tree species can grow in the understory of shaded forests to enrich community levels and replace pioneer species and heliophytic tree species in the middle and late stage of succession to promote forest succession [27,66]. From selective cutting in 1993 to the first survey in 2012, after 19 years of recovery, the community biomass reached 292.5 t/ha, which was similar to the biomass of the 400-year-old forest in the Dinghushan Biosphere Reserve (our study land is located at the same latitude with the Dinghushan Biosphere Reserve, and the vegetation types of both are evergreen broad-leaved forests) [1], indicating that the forest productivity had been close to or fully recovered. The stand density was 5007 plants per hectare, which was also similar to the stand density of the old forest in the Dinghushan Biosphere Reserve [1], indicating that the forest structure had been recovered to the level of the old forest. The recovery of forest structure and biomass indicates that the evergreen broad-leaved forest can be recovered to the forest structure and productivity level before selective harvesting after a certain number of years. However, in the forest species composition, heliophytic tree species were the main dominant species and the main component of the community, while mesophytic tree species were the secondary component of the community, which indicated that the forest species composition and distribution were quite different from the old forest [27,35].

We only conducted 5 years of dynamic monitoring; as a result, our understanding of the long-term direction of various forest layers during succession in subtropical mountainous forests is still not deep enough. In the next study, a longer monitoring period will be used in combination with further refinement of forest layers and DBH classes to expand the study of the characteristics of each species. This will enable us to explain forest succession patterns at the species or even the individual level. In particular, we wish to examine the direction of forest succession under climate change. Will forest succession be affected? The answers to these questions will provide valuable supporting data and guidance for understanding the direction of forest succession under climate change.

5. Conclusions

Studying the differential changes of plants at different stages of growth during forest succession will aid in exploring the direction of future succession in forests and provide data in support of forestry management. During forest succession, different types of changes occur in the community structure, diversity, and biomass of different DBH classes. Many individuals in the small-diameter class tend to die off as a result of environmental stress and stress from other individuals, resulting in changes in community structure and diversity. Large-diameter class trees were relatively stable and their biomass increased significantly over time, resulting in an increase in biomass of the community. Significant differences were observed in the species distribution of different DBH classes; small-diameter class have the highest abundance and diversity along with the lowest biomass, exhibiting a trend that is reversed in large trees, while medium-sized trees lay in the middle. Significant differences were found in species distribution patterns between different DBH classes, of which the small-diameter class has the most indicator plants. Changes were seen in major environmental driving factors during forest succession, and the explanatory power of environmental factors decreases over time. The large-diameter class will maintain a stable state and large *C. carlesii* trees will maintain a dominant position. In the medium-diameter class, heliophytic tree species such as *C. carlesii* were gradually replaced by mesophytic and sciophytic tree species, while the replacement rate increased in small-diameter class. Adaptive strategy theory can better explain changes in medium-and small-diameter classes while the initial floristic composition theory can better explain changes in the large-diameter class. The two theories showed that the existing community is at the early-to-mid stage of succession and tends to the mid–late stage of succession in the study area. After 19 years of recovery, the forest structure and productivity have been greatly improved, indicating that the evergreen broad-leaved forest can be recovered to the forest structure and productivity level before a selective cutting level after a certain number of years.

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