Encroachment order and spatial patterns of broad-leaf tree species in the naturalization of a *Cunninghamia lanceolata* plantation

Xiaoxia Zeng [a], Lin Chen [b], Zacchaeus G. Compson [c], Jiejun Li [b], Qiaohua Peng [b], Chao Gong [a], Renquan Wen [a], Jun Liu [a], Xiong Fang [a], Fenggang Luan [a], Qingni Song [a], Qingpei Yang [a,*]

[a] *Jiangxi Province Key Laboratory for Bamboo Germplasm Resources and Utilization, Jiangxi Agricultural University, Nanchang 330045, China*
[b] *Administration of Jiangxi Guanshan National Nature Reserve, Yichun 336000, China*
[c] *Department of Biological Sciences, Advanced Environmental Research Institute, University of North Texas Denton, TX, 76201, USA*

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ABSTRACT

The aim of this study was to understand the encroachment order, spatial patterns, interspecific associations, and species diversity of a *Cunninghamia lanceolata* plantation and to provide context for how to improve the spatial structure of *C. lanceolata* plantations. We investigated a Guanshan (*C. lanceolata*) Plantation in the Jiangxi Province. The *C. lanceolata* plantation was divided into three developmental stages (early, middle and late), with a space-for-time substitution method, according to their diameter at breast height (DBH) measurements. Across these plots, we analyzed encroachment patterns of the species and their interspecific associations with *C. lanceolata* according to the coordinates of trees in the plot, as well as the variation of species diversity after the encroachment of broad-leaf tree species. Our results show that the encroachment of broad-leaf trees into the *C. lanceolata* plantation followed a clear successional sequence of tree community assembly: intolerant tree species encroachment first, such as *Alniphyllum fortunei* and *Liquidambar formosana*, encroached; neutral tree species then encroachment, such as *Daphniphyllum oldhamii* and *Schima superba*, and shade-tolerant tree species encroachment last, such as *Castanopsis eyrei* and *Castanopsis tibetana*. Further, the spatial pattern of species establishment differed based upon when they encroached on the plantation. Intolerant and neutral tree species of early and middle developmental stages were distributed randomly. However, intolerant and some shade-tolerant tree species of the late developmental stage were aggregated on a scale of about 0–3 m. In addition, the interspecific associations between broad-leaf species encroachment into the *C. lanceolata* plantation were mainly negative, among which the most competitive ones were *A. fortunei*, *D. oldhamii* and *Machilus thunbergii*. However, with the development of the community, some species with negative correlations changed to having no correlation with *C. lanceolata*. We found that species diversity in the plantation gradually increased by nearly-five times from the early to the late developmental stage. Based on our collective results, we conclude that the encroachment and assembly of tree species show obvious order and pattern, which has a strong competitive effect with *C. lanceolata* in the naturalized plantation. Additionally, the community biodiversity has been significantly improved. Therefore, this successional process is important in the transformation of the *C lanceolata* plantation and different tree species should be replanted according to *C. lanceolata* plantation developmental stages with priority given to competitive species, such as *A. fortunei*, *D. oldhamii*, and *M. thunbergii*, so as to promote the *C. lanceolata* plantation change to *C. lanceolata* and broadleaf mixed forest.

1. Introduction

Cunninghamia lanceolata is a commercially important, fast-growing species useful for timber production in China (Bi et al., 2007). Currently, *C. lanceolata* plantations cover about 9.9 million hectares, which accounts for more than 17.33 % in the total area of plantation forests of China (Zhang, 2019). However, long-term management of pure forests has generated a series of ecological problems, such as simple stand structure, soil degradation, and biodiversity reduction (Farooq, 2019; Wu et al., 2017; Xia et al., 2018). The *C. lanceolata* plantation has become a critical part of the ecological welfare of public forests, since the implementation of national forest classification management policy

in China (Li et al., 2016). Therefore, improving the ecological function of *C. lanceolata* plantation has already become an important management goal.

Close-to-nature forest management was approaches to utilize and conserve plantation forests (O'Hara, 2016), which is an effective way for improving the ecological benefits of plantation (He et al., 2018; Ming et al., 2020; Zhou et al., 2016). Previous studies have mainly evaluated the ecological benefits of close-to-nature transformation, such as carbon stock (Zhang et al., 2019), species diversity (Ming et al., 2020), and soil physicochemical properties (Jiang et al., 2019). However, the processes and mechanisms of enhancing ecological benefits are not well understood, such as encroachment order, spatial patterns of broadleaf species, and interspecific relationships between broadleaf species and *C lanceolata* during the natural development of *C lanceolata* plantations.

Encroachment order is the successional sequence of other species (non-plantation species) that encroach into the community during the naturalization of the plantation. Relevant research showed that intolerant tree species encroach into the community first, followed by neutral species, and then shade tolerant species (Zhang and Chen, 2000). Generally, Encroachment order was related to the forest environment and ecological characteristics of the species (Xue, 2006). First, the early development stage community is relatively open, which is conducive to the growth of intolerant broad-leaved tree species with sun-loving and fast-growing characteristics (Abbas et al., 2019). Next, with the development of the community, increasing canopy density is not conducive to the renewal of intolerant tree species, and the neutral tree species that are more shade tolerant and hydrophilic begin to encroach. Finally, other shade-tolerant tree species gradually encroach (Zhang and Chen, 2000). According to the order of tree species encroachment into *C lanceolata* naturalizing plantations, these added encroaching species are beneficial for stand development and shortening the succession time of the forest (Li et al., 2014). Therefore, understanding the process of tree species encroachment into *C lanceolata* plantations is crucial for transforming them into close-to-nature forests.

Spatial distribution patterns are the result of long-term interactions between tree communities and the environment (Gu et al., 2019; Zhang et al., 2020), which play a decisive role in the survival, growth, and reproduction of individual plants in the community (He et al., 2018). In the natural state, spatial distribution patterns influence many ecological community processes, such as intraspecific interspecific competition, seed dispersal (Watt, 1947), the pattern of tree species replanting is rarely considered an important feature of close-to-nature transformation of plantation forests, and replanting often follows a uniform or random distribution pattern (Lan, 2014; Liu, 2014). During the development of a stand, the spatial distribution pattern of trees is influenced by biotic and abiotic factors (Whitfeld et al., 2015). In the early stages of community development, they often show a random distribution, due to the seed source is mainly derived from external dispersal (Xue, 2006). As the community develops, the source of seedlings gradually changes from external dispersal to internal renewal, and tree species often show an aggregated distribution, due to the influence of seed dispersal limitation (Condit, 2000). Therefore, we supposed that the pattern of tree encroachment in *C lanceolata* plantations should follow a random distribution in the early stages of encroachment and an aggregated distribution in the late stages of encroachment.

Interspecific associations are often assessed as the correlation of the spatial distribution of different species within a community (Sfenthourakis and Giokas, 2010) and are drivers of community assembly and development. The broad-leaf tree species niche of encroachment in *C lanceolata* plantations are often similar to *C lanceolata* (Xu et al., 2017), implied that broad-leaf tree species will be negatively correlated with *C lanceolata* when they are resource-limited because of competition. However, some studies have found that a variety of trees, such as *Daphniphyllum oldhamii* and *Castanopsis fargesii*, are positively correlated or unrelated to *C lanceolata* (Tang et al., 2008; Xu et al., 2018a), probably because interspecific relationships are related to the developmental

stage of the community (Gu et al., 2017; Tu et al., 2019). At the early stage of community development, a few successful encroaching broadleaf tree species will compete with *C lanceolata* for the same resources, which creates a negative association. As the community develops, various groups occupy further differentiated ecological niches, and the interspecific relationships gradually change from negative to positive or unrelated. Therefore, we speculated that there may be differences in the interspecific correlation between broad-leaf tree species and *C lanceolata* at different developmental stages. Specifically, we hypothesized that broad-leaf species will have a negative correlation with *C lanceolata* in early stages of succession, gradually changing to positive association or no association as the community develops.

Jiangxi Guanshan Mountain has widely distributed *C. lanceolata* plantation on a large scale. Since the establishment of the provincial nature reserve in 1981, the *C. lanceolata* plantation has entered the natural broad-leaf state, which provides a good experimental platform to study the natural development process of a *C. lanceolata* plantation. Thus, we used Guanshan Nature Reserve as the study site and hypothesized that: (1) the order of broad-leaf tree species encroaching *C. lanceolata* plantations would be intolerant broad-leaf species, neutral broad-leaf species, and shade-tolerant broadleaf species; (2) the pattern of broad-leaf tree species encroaching *C. lanceolata* plantations would be randomly distributed in the early stage of succession and would exhibit a clustered distribution in the late stage of succession; and (3) broad-leaf trees would be negatively correlated with *C. lanceolata* after encroachment, and the degree of negative correlation would gradually decrease as the community developed, changing to a positive correlation or no correlation in the late stage of community development. Testing these hypotheses would illuminate the natural development process of *C. lanceolata* plantations and provide important successional reference points for the close-to-nature management of *C. lanceolata* in order to maximize the ecological health and public benefit of these forests.

2. Material and methods

2.1. Study site

Jiangxi Guanshan Nature Reserve is located in the western part of the Jiuling Mountains in northwestern Jiangxi ($28°30'{\sim}28°40'$N; $114°29'{\sim}114°45'$E). It has four distinct seasons and full sunshine, with an average annual air temperature of 16.2 °C and an average annual precipitation of approximately 1950 mm to 2100 mm. The soil is clay loam, composed of 16.75–19.37 % clay (<0.002 mm), 31.04–35.07 % silt (0.02 – 0.002 mm), 45.49–48.7 % sand (2 – 0.02 mm), and is classified as a red and yellow soil according to the Chinese soil classification system (State Soil Survey Service of China, 1998). This area has 5 vegetation type groups and 11 vegetation types, and the evergreen broad-leaved forest is a zonal climax vegetation with 2344 species of wild higher plants (Cao et al., 2012; Xu et al., 2018b). However, Jiangxi Guanshan Mountain has a tradition of prescribed burning and afforestation, and part of the forests have historically been burned, so there are secondary forests, such as *C. lanceolata*, left in some areas.

2.2. Survey methods and forest plot data

To monitor the changes of vegetation composition, structure and function of *C. lanceolata* plantation, three 1 hm^2 *C. lanceolata* plantation monitoring plots (GS-1, GS −2 and GS-3) were established in Guanshan, according to the CTFS (Centre for Tropical Forest Science) sample plot survey method of 2014 (Condit, 1995). From 1954 to 1956, seedlings of *C. lanceolata* were planted as follows: 5000 seedlings of *C. lanceolata* were planted at 2.5 m intervals; saplings were nurtured continuously for 10 years (including fertilizer application, weed removal, pest control and other tending measures). With the establishment of the nature reserve in 1981, *C. lanceolata* completely entered the stage of natural broad-leaf succession.

All woody plants with diameter of a cross-section of a tree trunk 1.3 m above the ground (DBH) greater than 1 cm in the 3 plots were investigated, include tree species name, DBH, coordinates, other indicators, in 2014. For individuals with DBH $\geq$ 5 cm, the DBH was measured with enclosed ruler, and for individuals with 1 cm $\leq$ DBH < 5 cm, the DBH was measured with a vernier caliper. Survey results show that there are 14,612 trees belonging to 54 families, 109 genera, and 227 species: 4882 deciduous trees and 9731 evergreen trees. 2602 of these trees were *C. lanceolata*, and the *C. lanceolata* largest DBH was 35.2 cm. Based on the relative abundance, relative height, and relative dominance of the species, we calculated the IV (Importance Value) for each tree species (Table 1). We then selected 12 species as research target according to IV and shade tolerance, including *Alniphyllum fortunei, Daphniphyllum oldhamii, Liquidambar formosana, Choerospondias axillaris, Machilus thunbergii, Padus buergeriana, Schima superba, Castanopsis fargesii, Castanopsis carlesii, Castanopsis eyrei, Cyclobalanopsis myrsinifolia, and Castanopsis tibetana*.

2.3. Data processing and analysis

2.3.1. Succession stages division

In this study, we substituted DBH for age class because there are positive correlations between DBH and age for most of tree species (Frost and Rydin, 2000). We divided the *C. lanceolata* plantation into three developmental stages (Fig. 2), according to the DBH of broad-leaf trees: 1) early developmental stage (S1), the assembly of all broad-leaf tree individuals with DBH greater than 20 cm and all existing *C. lanceolata* in *C. lanceolata* plantation, 2) middle developmental stage (S2), the assembly of all broad-leaf tree individuals with DBH less than or equal to 20 cm and greater than 5 cm and all existing *C. lanceolata* in *C. lanceolata* plantation and 3) late developmental stage (S3), the assembly of all broad-leaf tree individuals with DBH less than or equal to 5 cm and greater than 1 cm and all existing *C. lanceolata* in *C. lanceolata* plantation.

Table 1
IV of the species in arbor layer of *Cunninghamia lanceolata* plantation.

Species	Abundance/ind.	Maximum of diameter/cm	Mean of diameter/cm	IV/%	IV of rank
Cunninghamia lanceolata	1470	35.20	12.91	23.75	1
Alniphyllum fortunei	676	63.50	16.04	15.45	2
Daphniphyllum oldhamii	313	32.70	14.03	6.16	3
Liquidambar formosana	91	54.70	23.16	3.34	5
Choerospondias axillaris	82	61.00	17.63	2.66	6
Pinus massoniana	53	53.00	17.63	2.66	7
Rhododendron latoucheae	192	31.00	31.74	2.45	8
Machilus thunbergii	117	20.10	8.52	2.21	9
Padus buergeriana	76	47.60	12.75	1.86	10
Schima superba	64	35.00	13.50	1.86	11
Castanopsis fargesii	80	26.30	7.89	1.72	12
Castanopsis carlesii	80	18.90	8.02	1.63	13
Castanopsis eyrei	48	21.8	8.53	1.14	17
Cyclobalanopsis myrsinifolia	17	38.10	12.57	0.48	35
Castanopsis tibetana	3	9.80	8.73	0.09	78
Others	1037	–	–	28.02	–

2.3.2. Spatial distribution pattern and interspecific relationship analysis

We analyzed the spatial distribution pattern of trees by adopting the method of Heterogeneous Poisson null model point-pattern analysis. The Ripley's K function, K(r), is critical in point pattern analysis; it is a cumulative distribution function within the distance of r (Ripley, 1977). An alternative approach uses rings (or annulus) instead of circles, with a pair correlation function, $g_{11}(r)$, or the O-ring statistic $O_{11}(r)$ (Wiegand et al., 1999).

In our study, the univariate function, $g_{11}(r)$, was used to analyze spatial distribution patterns in the categories of broad-leaf tree species in three successional stages of the *C. lanceolata* plantation. The function, g (r), is related to Ripley's K function, where r is the distance (ring in g(r)) in rad, *n* is the number of points of the pattern in the study region of area A, d_{ij} is the distance between the focal tree (i) and its neighboring tree (j), *Ir* is a counter variable [$Ir(d_{ij}) = 1$, if $d_{ij} \leq r$; and $Ir(d_{ij}) = 0$, if $d_{ij} > r$], and w_{ij} is a weighting factor to account for edge effects. The weight, w_{ij}, is the proportion of the area of a circle centered at the *i*th point, with radius d_{ij}, that lies within the study region.

To analyze relationships between broad-leaf trees and *C. lanceolata* in different successional stages of the *C. lanceolata* plantation, we used the bivariate pair correlation function, $g_{12}(r)$, by using the antecedent condition model of pattern 1 (*C. lanceolata*), which was fixed, and pattern 2 (broad-leaved tree species), which was random. In the formula, d_{ij} is the distance between the focal tree of pattern 1 and its neighboring tree of pattern 2, and n_1 and n_2 are the total numbers of trees in the patterns 1 and 2, respectively.

The analyses were performed up to 50 m with a 1 m lag distance. We used a ring width of one meter and used 99 Monte Carlo simulations of complete spatial randomness (CSR) to acquire pointwise critical envelopes (Zhang et al., 2020), and the significance level was 0.01. If the value of $g_{11}(r)$ was within the envelope of the Monte Carlo test, the spatial pattern at distance *r* was assessed to be entirely random, and if the value was above the upper or below the lower envelopes of the Monte Carlo test, this indicated an aggregated or regular pattern. If the value of $g_{12}(r)$ was within the envelope of the Monte Carlo test, there was no interspecific association at the distance *r*. If $g_{12}(r)$ was above the upper or the below the envelopes of Monte Carlo test, then there was a positive or negative interspecific association between broad-leaf trees and *C. lanceolata* (Stoyan and Penttinen, 2000). Statistical analyses were conducted using Programita 2008 software and plotted with MATLAB (2018a). (Because of the small number of individuals of some species in different developmental stages of *C. lanceolata* plantation, the distribution patterns of only six species of *Alniphyllum fortunei, Daphniphyllum oldhamii, Machilus thunbergii, Castanopsis fargesii, Castanopsis carlesii, Castanopsis eyrei* were analyzed, and interspecific relationships between these six broad-leaf species and *C. lanceolata* were also analyzed.).

$$k_{11}(r) = \frac{A}{n^2} \sum_{i=1}^{n} \sum_{j=1}^{n} \frac{I_r(d_{ij})}{w_{ij}} \tag{1}$$

$$g_{11}(r) = \frac{1}{2\pi r} \frac{dK_{11}(r)}{dr} \tag{2}$$

$$K_{12}(r) = \frac{A}{n_1 n_2} \sum_{i=1}^{n_1} \sum_{j=1}^{n_2} \frac{I_r(d_{ij})}{w_{ij}} \tag{3}$$

$$g_{12}(r) = \frac{1}{2\pi r} \frac{dK_{12}(r)}{dr} \tag{4}$$

2.3.3. Species diversity analysis

Individual plants and 20 m × 20 m plots were taken as statistical by randomly selecting quantitative individuals or sub-quadrats to construct a rarefaction curve, respectively, (Gotelli and Colwell, 2001), and using MATLAB (2018a) programming, 499 times were randomly selected. The rarefaction curve can reflect the functional relationship between the number of samples and species richness in the natural succession process
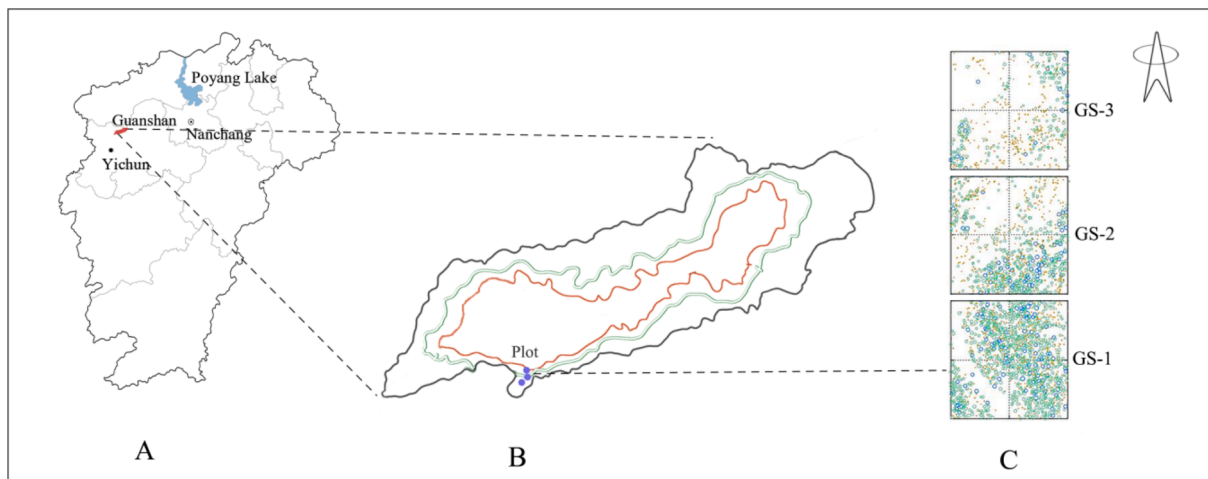
Fig. 1. The location of the study area and spatial distribution of *Cunninghamia lanceolata.* Locations of Guanshan National Nature Reserve (A) and the Guanshan *Cunninghamia lanceolata* plantation monitoring plot (B) are pictured, as well as the spatial distribution of *C. lanceolata* (C). DBH values are indicated by the size of circles.
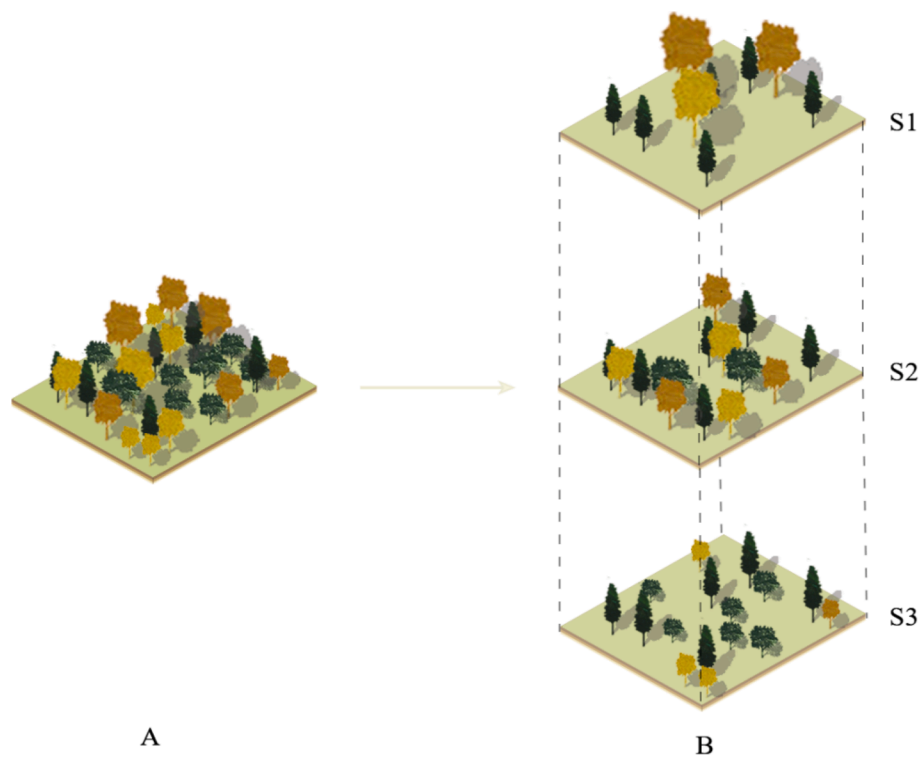

Fig. 2. Schematic diagram of succession stage division of the *Cunninghamia lanceolata* plantation. The current situation of *C. lanceolata* plantation (A) and, the division result of the development stage of *C. lanceolata* plantation (B), as well as, the B-S1, B-S2 and the B-S3 means the early, middle and late developmental stage respectively.

of the *C. lanceolata* plantation. In these calculations, individuals with DBH < 20 cm were not included in S1, individuals with DBH ≤ 5 cm were not included in S2, and all individuals were included in S3. Furthermore, we calculated species diversity of S1, S2, and S3 of the *C. lanceolata* plantation in three sample plots (GS-1, GS-2 and GS-3), including species abundance, Margarlef index, Shannon-wiener, and Pielou's Evenness (Ma, 1994). We used one-way analysis of variance (ANOVA) to compare the difference of biodiversity index in different developmental stages of the *C. lanceolata* plantation, and used the Duncan method to test for differences among groups (Romanyà et al., 2005). These calculations were performed using SPSS 22.00 statistical

software.

$$\text{Margalef} (M)\ M = \frac{(S-1)}{ln(N)} \tag{5}$$

$$\text{Shannon} - \text{wiener} (H^{'})\ H^{'} = - \sum_{i=1}^{s} Pi ln(Pi) \tag{6}$$

$$\text{Pielou}^{'}\text{s Evenness} (J)\ J = \frac{H^{'}}{lnS} \tag{7}$$

For Eqs. 5–7, *S* represents species richness, *N* is species abundance, and *Pi* means the proportion of the abundance of the *i*th species in the

total number.

3. Results

3.1. Process of broad-leaf tree species encroachment on a Cunninghamia lanceolata plantation

We found that broad-leaf trees encroached upon the *C. lanceolata* plantation after anthropogenic tending of these trees stopped, as demonstrated by the increased relative abundance and decreased size of different tree species (Table 2). *A. fortunei, L. formosana, C. axillaris* and *P. buergeriana* were the first species to encroach the *C. lanceolata* plantation, as their number of individuals were more than other trees, especially the *A. fortunei*, which had the higher DBH of broad-leaf species, reaching up to 203 trees and was 51.7 % of the 12 broad-leaf species' total in S1 (early developmental stage). Four species (*D. oldhamii, S. superba, C. myrsinifolia, C. fargesii*) in S2 (middle developmental stage) were comparatively large, and were the second group of species to encroach the *C. lanceolata* plantation. Individuals of *D. oldhamii* were 75 trees in S1, while its maximum DBH was only 32.7 cm, which was far less than *A. fortunei, L. formosana, C. axillaris*, and *P. buergeriana*, justifying its placement in the second group. *M. thunbergii, C. carlesii, C. eyrei*, and *C. tibetana* individuals were 0 to 1 tree in S1, and the number of individuals in S3 (late developmental stage) was much higher than that in S2; furthermore, the maximum DBH of trees in this group was<20 cm, making them the last group that encroached the *C. lanceolata* plantation (Fig. 3).

3.2. Pattern of broad-leaved tree species encroachment on a Cunninghamia lanceolata plantation

Broad-leaf tree species encroached into the *C. lanceolata* plantation in both random and aggregation modes (Fig. 4). In the S1 and S2 stages, six tree species were randomly distributed in the scale of 0–50 m. Yet in the S3 stage, *A. fortunei, M. thunbergii* and *C. eyrei* were aggregated at 0–3 m, 0–2 m, and 0–2 m, respectively. Collectively, these results indicated that broad-leaf trees mainly encroached randomly in the early and middle stages of *C. lanceolata* plantation development, but that species expressed an aggregated distribution in the later successional stage.

3.3. Interspecific association between broadleaved tree species and Cunninghamia lanceolata

In the process of natural development of *C. lanceolata* plantation, the great majority broad-leaf trees showed negative associations with *C. lanceolata*; only *C. eyrei* and *C. carlesii* were not associated with *C. lanceolata* (Fig. 5). Among them, the first and second batch of encroachment species of *C. lanceolata* plantation were the highly competitive in S1 stage, such as *A. fortunei* and *D. oldhamii*, which were negatively associated with *C. lanceolata* at the scales of 1–26 m and 2–21 m, respectively, while they were barely correlated with *C. lanceolata* at the scale of 0–50 m in S3 stage. And the third batch of encroachment species such as *M. thunbergia* had the most competitive in S2 and S3 stage, which were negatively correlated with *C. lanceolata* at the scales of 1–29 m and 1–26 m, respectively. This indicates that the current driving force affected the growth and regeneration process of *C. lanceolata* mainly came from competition with *A. fortunei, D. oldhamii* and *M. thunbergii*, and the competition between the first and second batch of broad-leaf tree species into the *C. lanceolata* plantation and *C. lanceolata* weakened gradually.

3.4. Species diversity in three succession stages

Individual-species and quadrat-species rarefaction curves of different successional stages demonstrates clear increases in diversity at the different successional stages (Fig. 6). The curves at the 3 stages of natural development of the *C. lanceolata* plantation displayed rapid growth at first, the curves became flatten later, while the growth was much more rapid and the equilibrium point was also higher at progressively later successional stages (Fig. 6 A, B). When the number of individuals was 800, species richness values were 44(S1), 79(S2) and 110(S3), which indicated that species diversity of the *C. lanceolata* plantation increased substantially with the encroachment of broad-leaf tree species.

The change of species diversity index also reflects this rule from another perspective (Table 3). The species richness, number of individuals and Magarlef index in S3 stage were significantly higher than those in S1 and S2 stage (P < 0.05), and the number of individuals increased from 268 in S1 stage to 4871 in S3 stage, an increase of 1717.53%. In addition, the Shannon Wiener index and Pielou were the highest at S3, which indicated that the encroachment of broad-leaved trees not only increases the number of species in *C. lanceolata* plantation, but also makes the interspecific distribution of individual numbers tend to be even.

4. Discussion

4.1. Successional sequence of broad-leaf tree species encroachment into a Cunninghamia lanceolata plantation

We found an obvious sequence in *C. lanceolata* plantation encroachment by broad-leaf tree species via the process of natural succession. Specifically, shade-intolerant tree species encroached into the plantation first, followed by neutral tree species, and then shade-tolerant tree species, a pattern supporting hypothesis 1 (Table 2). Through stem date analysis of broad-leaf tree species in the monitored plot and using allometric growth equations documented in other studies (Hou et al., 2018; Li et al., 2011; Liu et al., 2014; Song et al., 2011), we found that the maximum individual age of *A. fortunei* and *C. axillaris* (two shade-intolerant tree species) was ~50 years, *C. fargesii* (the neutral tree species) was ~30 years, and *C. carlesii* and *C. tibetana* (two shade-tolerant tree species) was ~20 years. This suggests that DBH reflects the order of broad-leaf tree species encroachment into the *C. lanceolata* plantation. According to the theory of community succession (John and Frederic, 1933), the success of species encroachment (settlement) was affected by the environment and ecological
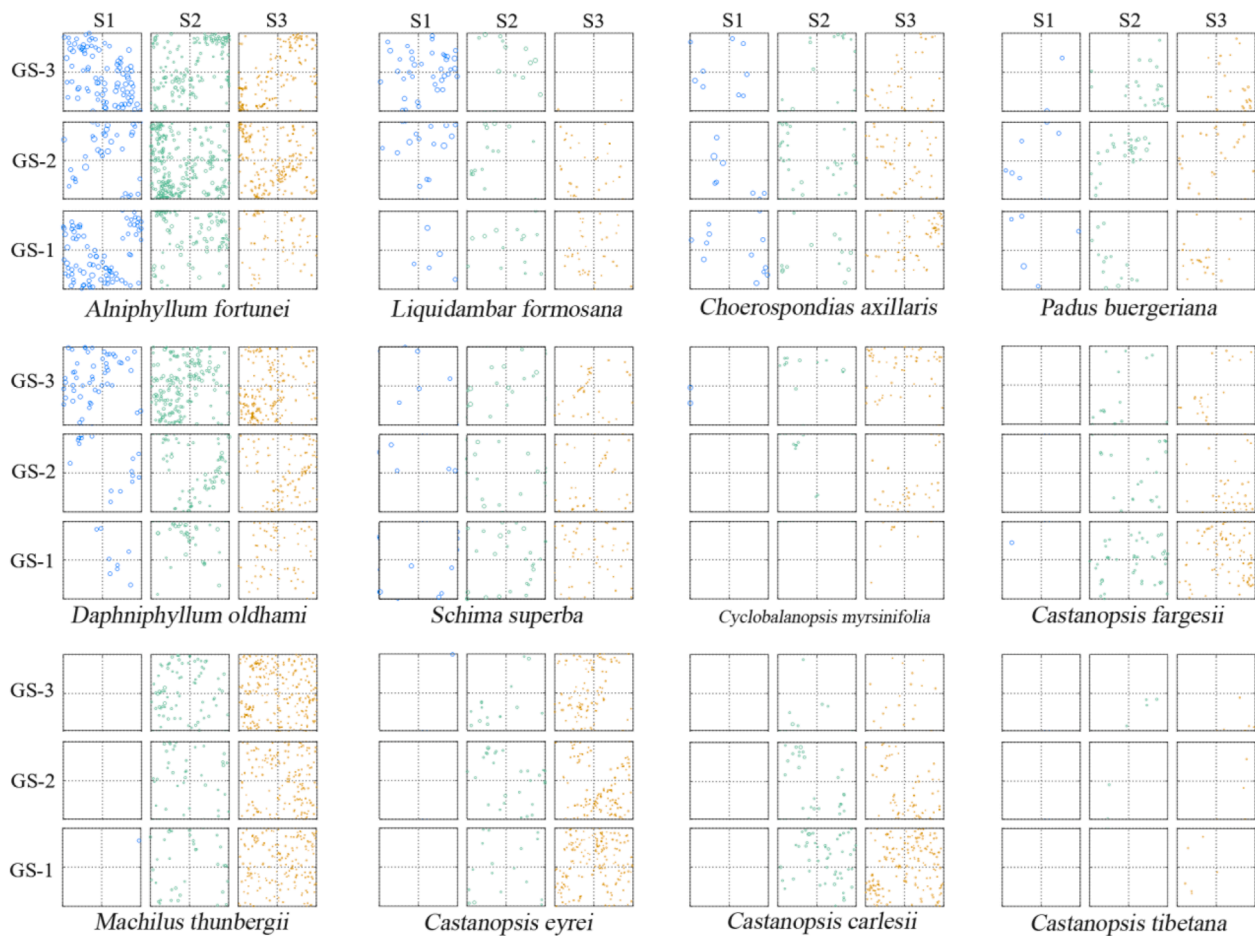
Table 2
Abundance and DBH of 12 established broad-leaf trees in three succession stages of the *Cunninghamia lanceolata* plantation.

Tree species	Abundance/ind			Max-DBH/cm	Mean-DBH/cm
	S1 (Stage1)	S2 (Stage2)	S3 (Stage3)		
Alniphyllum fortunei	203	480	451	63.5	10.8
Choerospondias axillaris	28	57	156	61	7.6
Liquidambar formosana	57	40	71	54.7	13.8
Padus buergeriana	12	65	73	47.6	7.7
Daphniphyllum oldhamii	75	266	366	32.7	7.9
Schima superba	13	52	124	35	6.2
Cyclobalanopsis myrsinifolia	2	19	94	38.1	4.2
Castanopsi fargesii	1	79	145	26.3	4.5
Machilus thunbergii	1	146	619	20.1	3.5
Castanopsis eyrei	1	60	432	21.8	3.0
Castanopsis carlesii	0	82	273	18.9	3.9
Castanopsis tibetana	0	6	12	9.8	4.4

The S1, S2 and the S3 means the early, middle and late development stage respectively (same below).

Fig. 3. Spatial distribution of 12 broad-leaved tree species in three successional stages of *Cunninghamia lanceolata* plantation. Tree DBH is indicated by the size of the circle. Blue: DBH greater than 20 cm individual, green: 5 cm < DBH ≤ 20 cm individual, yellow: 1 cm < DBH ≤ 5 cm individual. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

characteristics of plants. Therefore, the sequence of broad-leaf tree encroachment was closely related to the environment in different developmental stages of the *C. lanceolata* plantation, as well as the ecological characteristics of broad-leaved tree species.

Initially, the *C. lanceolata* plantation was relatively empty and the light is comparatively abundant, which provided an open niche for the encroachment of broad-leaf trees, after which the *C. lanceolata* plantation grows to 10 years after anthropogenic tending. Shade-intolerant broad-leaf tree species are light-loving and exhibit rapid growth (Chen et al., 2017); including *A. fortunei*, *C. axillaris*, *L. formosana*, and *P. buergeriana*, which can quickly occupy the vacant niche in the *C. lanceolata* plantation and become the first batch of encroaching broad-leaf tree species. In addition, the number of individuals encroached by intolerant tree species was not equal: the number of *A. fortunei* was much higher than other tree species (Table 2). We suspected that this was due to a robust seed bank of *A. fortunei*, as *A. fortunei* individuals was more than 2000 around the *C. lanceolata* plantation, providing more seeds than others species (e.g., *C. axillaris* had only ~400 individuals, and *L. formosana* and *P. buergeriana* had only ~200 individual). Furthermore, the amount of encroachment by individual species was likely affected by the seed dispersal mode, as *A. fortunei* encapsulates its fruit with wings at both ends, and the weight of seeds is relatively light (1000 seeds weigh only 0.6–0.8 g) (Li et al., 2011), which mode of dispersal is mainly wind propagation. However, fruits and seeds of *C. axillaris* and *P. buergeriana* are relatively large, and their dispersal depend on animals (i.e., beasts or birds). The seeds of *L. formosana* fall around the mother plant, within cones, and the seedlings are poorly regenerated under their parental trees (Wang et al., 2011) (Fig. 3).

With the development of the community and the encroachment of shade-intolerant broad-leaf tree species, the canopy density of the stand gradually increased, neutral and shade-tolerant tree species encroachment to the *C. lanceolata* plantation one after another, after about 30 and 40 years of *C. lanceolata* planting. Therefore, the possible relationship between the order of broad-leaf tree encroachment and the developmental stage of the *C. lanceolata* plantation can be predicted based on our encroachment results (Fig. 7). However, the close-to-nature management of artificial forest mainly takes "Matching Tree Species with Site" as the basic principle, and selects local tree species with fast growth speed and strong shade tolerance as supplementary planting, (Ding et al., 2013). There is a lack of understanding of the relationship between the order of broad-leaved tree encroachment and the development stage of plantation, while the stage of stand development is the key to close-to-nature management (Wang et al., 2018), and different species have different reforming abilities in different succession stages of the community (Dutta and Agrawal, 2003).Therefore, in the transforming process of *C. lanceolata* plantation, the selection of planting tree species should not only focus on local tree species, but also fully reflect the development process, with focus on replanting different broad-leaf tree species according to their associations with respective successional stages. Moreover, these successional patterns can give insights of development process of plantation forests, possibly providing ways for how human efforts to naturalize and restore these areas post-plantation could be expedited.
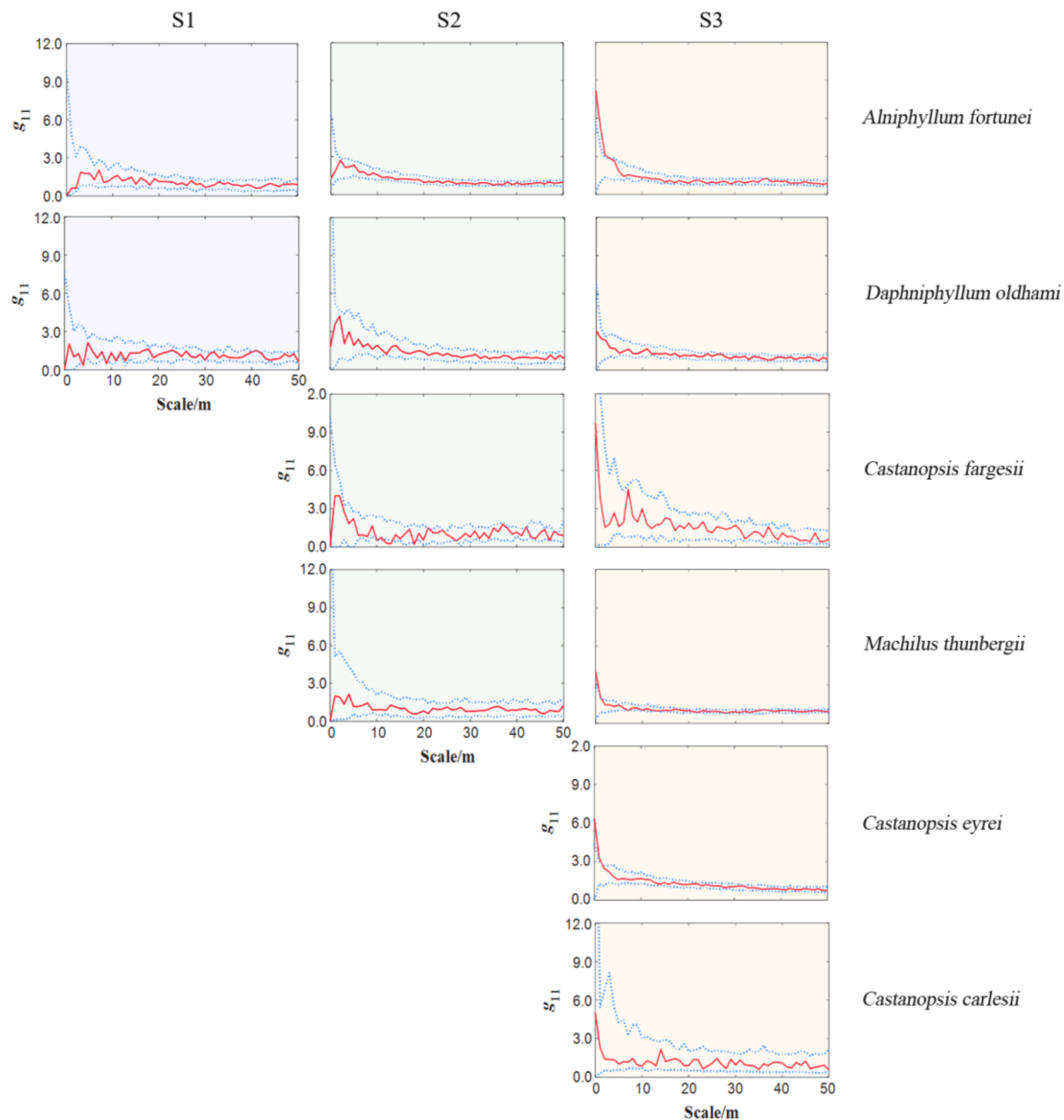
Fig. 4. Spatial point patterns of six broad-leaf tree in three developmental stages of the *Cunninghamia lanceolata* plantation. The red solid line indicates point analysis results. The blue dashed line indicates the upper and lower envelops of Monte Carlo test. If *g11(r)* (red line) is within envelops of the Monte Carlo test, the spatial pattern at distance *r* is random. If *g11(r)* is above the upper or below the lower envelops of Monte Carlo test, the spatial pattern is aggregated or regular, respectively (*p* < 0.01). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4.2. Spatial patterns of broad-leaf tree species encroachment into a Cunninghamia lanceolata plantation

Our findings demonstrated that the broad-leaf tree species were randomly distributed in the early (S1) and middle (S2) stages of the *C. lanceolata* plantation, and some species in the late stage (S3) showed aggregated distribution on a small scale (i.e., <3 m), which supported hypothesis 2 (Fig. 4). The distribution pattern of species is the consequence of their own traits, interspecific associations, and environmental conditions (Yang et al., 2018). In the early stage of development, plants mainly spread from outside of the community, and often show random distributions (Xue, 2006; Zhang et al., 2020). Similar to our study, with the development of the tree assemblage, the source of population-regenerating seedlings has been shown to gradually change from external diffusion to internal renewal, with the species showing an aggregated distribution on small scales, due to the limitation of seed dispersal (Condit, 2000).

Broad-leaf tree species in this study were randomly distributed in S1.

However, after about 30 years of development of the *C. lanceolata* plantation (S2), the distribution pattern of broad-leaf trees was still random, which was related to the distribution pattern of *C. lanceolata*. The distribution pattern of *C. lanceolata* changed from a regular distribution to a random distribution throughout this period, which provided random forest gaps for the encroachment of broad-leaf tree species due to the influence of intraspecific competition (Fig. 1C). The result is similar the findings of Zhao et al., (2015), which the encroaching species, *Ulmus pumila*, was mainly randomly distributed. However, with the individual encroachment in S1 and S2 of broad-leaf trees, the canopy density of the stand became progressively higher, and some *C. lanceolata* died due to the alien-thinning by interspecific competition, causing sprouting and regeneration to become more difficult. Thus, forming a large, spare niche provided an opportunity for the encroachment of broad-leaf trees in the S3 stage. At the same time, some broad-leaf trees' population regeneration from seedlings changed from external renewal to internal renewal. Thus, some species formed aggregated distributions on a small scale (Fig. 4), and we predict that the number of species with
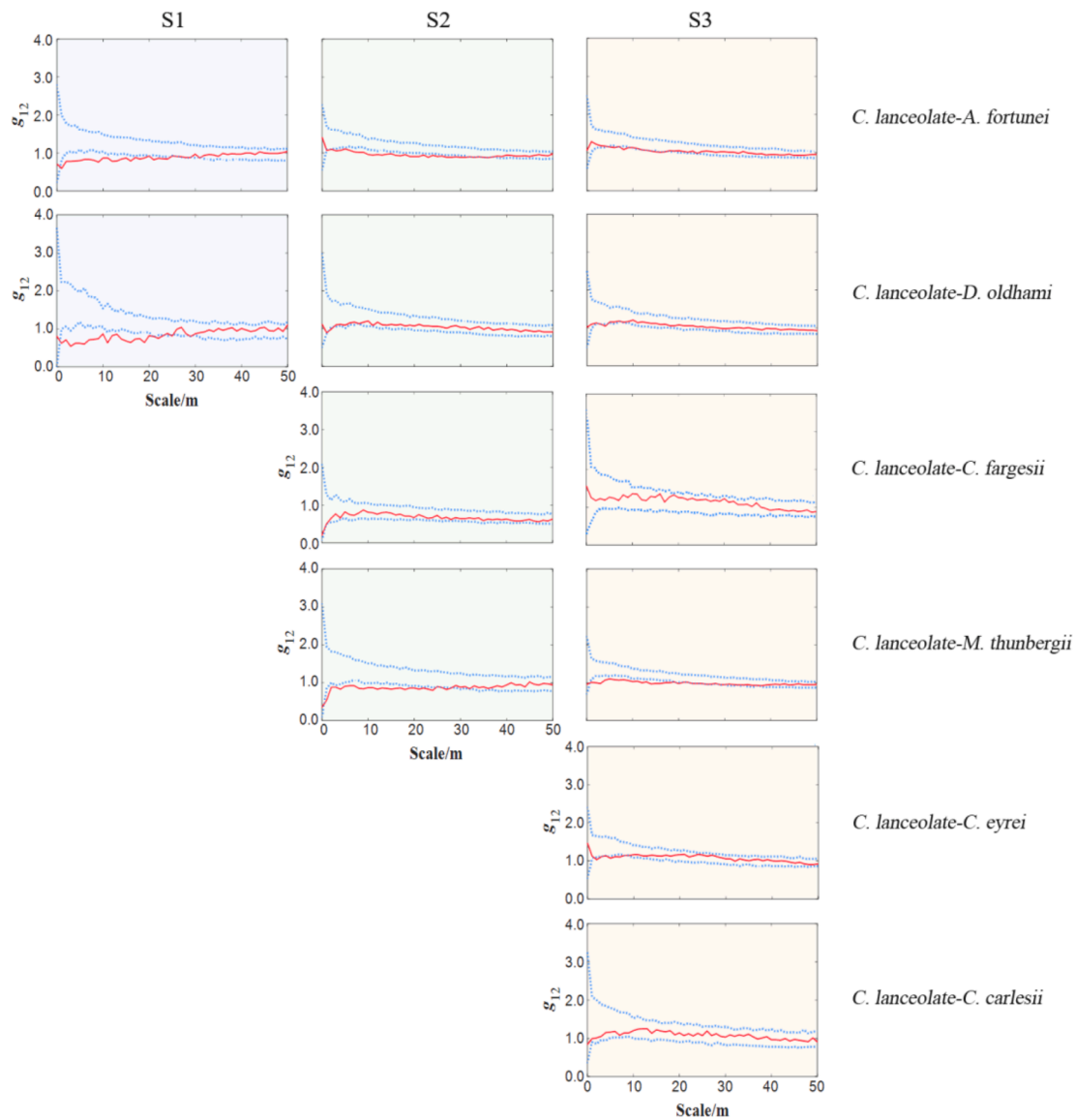
Fig. 5. Association patterns between *Cunninghamia lanceolata* and six borad-leaf tree species in the three successional stages of the *Cunninghamia lanceolata* plantation. If *g12(r)* is within the envelops of Monte Carlo test, there is no interspecific association at the distance *r*. If *g12(r)* is above the upper or the below the envelops of Monte Carlo test, then there are positive or negative interspecific association, respectively ($p < 0.01$).
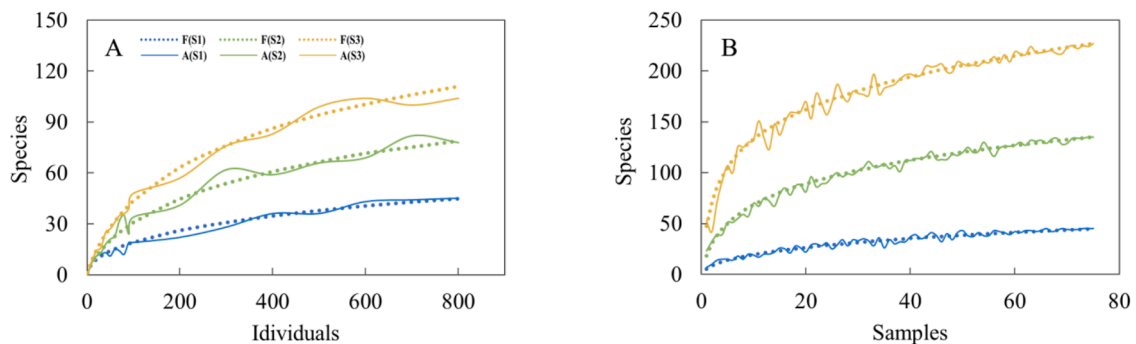

Fig. 6. Individual- and Sample-based rarefaction curves, indicating the species richness of plants in the *Cunninghamia lanceolata* plantation. A and B indicate species richness with the number of individuals and sample plots, respectively. A$_{(S1)}$, A$_{(S2)}$ and A$_{(S3)}$ are cumulative curves of species richness in the early (solid blue line), middle (solid green line), and late (solid gold line) developmental stages, respectively. F$_{(S1)}$, F$_{(S2)}$, F$_{(S3)}$ are rarefaction curves of species richness in the early (dotted blue line), middle (dotted green line) and late (dotted gold line) developmental stages, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 3

Variation of species diversity indexes of tree species in the *Cunninghamia lanceolata* plantation.

Stage	S	N	Magarlef index Dm	Shannon-Wiener index H'	Pielou index E
S1	28 ± 1.000c	268 ± 32.230c	4.84 ± 0.159c	2.29 ± 0.113b	0.69 ± 0.035b
S2	92 ± 1.528b	1627 ± 61.656b	12.31 ± 0.260b	2.79 ± 0.278b	0.62 ± 0.060b
S3	162 ± 7.860a	4871 ± 226.475a	19.01 ± 0.966a	3.72 ± 0.018a	0.73 ± 0.004b

Different letters indicate significant differences in species diversity among three successional stages (n = 3 per stage). The same letter means no significant difference among groups (Duncan test).
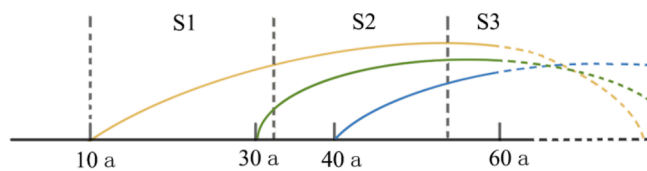

Fig. 7. Encroachment order of broad-leaved trees in successional stages of *Cunninghamia lanceolata* plantation. The yellow line depicts intolerant tree species, the green line depicts neutral tree species, and the blue line depicts shade-tolerant tree species. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

aggregated distributions may increase in the future, which was consist with other studies. For example, Li et al., (2019) found that species distribution patterns of a subtropical secondary forest over 57 years, and showed that all populations were aggregated in the range of 14 m.

However, the distribution pattern of broad-leaved tree replanting is rarely regarded as an important feature of *C. lanceolata* transformation (Mccallum et al., 2018), and the difference of distribution pattern will affect the close-to-nature process of plantation, such as pollination and competition. Therefore, according to the conclusions of this study, we suggest that broad-leaf trees should be replanted in a random arrangement if the goal was to transform the *C. lanceolata* plantation in the early and middle stage into close-to-nature forest. This would not only promote seed transmission and reduce intraspecific competition, but also increase the encroachment opportunities of other broad-leaf trees, promoting the development of plantation forest while shortening its development time. For the *C. lanceolata* plantation in the late stage of development, the planting trees with an aggregated distribution should be more conducive to the establishment of broad-leaf trees. This is because, in late-stage *C. lanceolata* plantation forest, a large forest gap is formed with the withdrawal of *C. lanceolata*, and so planting individuals together could weaken the role of interspecific competition and promote species coexistence (Stoll and Prati, 2001).

4.3. Community development effects on interspecific correlations between broad-leaf tree species and Cunninghamia lanceolata

Our results revealed that the interspecific association between broad-leaf tree species and *C. lanceolata* was usually negative at scales from 0 to 20 m in the early development stage of the *C. lanceolata* plantation, and some species were not correlated with *C. lanceolata* in the late development stage (Fig. 5), which supports hypothesis 3. The negative, interspecific association indicates that the two species are likely competitive or have different resource requirements (Allouche et al., 2012; Kylee et al., 2001; Zhou et al., 2019). Xu et al. (2017) demonstrated that broad-leaf trees, such as *C. fargesii* and *C. lanceolata*, have high niche similarity. Thus, we infer that the negative relationship between broad-leaf tree species and *C. lanceolata* was due to interspecific

competition. This idea was further supported by the fact that the number of *C. lanceolata* individuals decreased from more than 5000 initially to ~2600 currently, while the number of broad-leaf tree species increased to more than 12,000 individuals over the same time interval. Competition between broad-leaf tree species and *C. lanceolata* has been identified as the main driving factor of natural succession after cessation of anthropogenic maintenance of *C. lanceolata* plantations (Kraft and Ackerly, 2010; Yang et al., 2014).

Another interesting pattern in our findings was that the first and second batch of encroaching species into the *C. lanceolata* plantation forest was the most competitiveness in S1 stages. Further, the third batch of encroaching species was the most competitiveness in S2 and S3 stages (Fig. 5). Collectively, these findings suggested that with the development of the tree assemblage, the competitiveness of the first and second batch of broad-leaf trees encroaching upon the *C. lanceolata* plantation was decreasing, while the competitiveness of the last batch of encroaching broad-leaved trees was increasing. However, the interspecific relationship between the replanted species (broad-leaved trees) and the original species (plantation tree species) is rarely considered in the close-to-nature transformation. The interspecific competitive relationship between species is the driving factor of community development (Martorell and Freckleton, 2014), and the replanted broad-leaved trees with strong competitiveness are more conducive to the positive succession of the community. Therefore, human-assisted transformations of *C. lanceolata* plantations should consider selection of target tree species based not only on encroachment order of broad-leaf tree species, but also with the intent to fully reflect the interspecific relationship of the tree assemblage, with intentional replanting according to the interspecific relationships between broad-leaf tree species and *C. lanceolata*. Replanting competitive broad-leaf trees at the corresponding development stage, such as *A. fortunei, D. oldhamii, M. thunbergia,* and other tree species, might promote more rapid transformation of *C. lanceolata* plantations into close-to-nature forests (Liu et al., 2015).

4.4. Encroachment of broad-leaved tree species as a tool to increase species diversity of Cunninghamia lanceolata plantations

Our results showed that species diversity increased with the natural development of the *C. lanceolata* plantation. Species richness increased nearly 5-fold, from the S1 stage (28 species / hm²) to the S3 stage (149species / hm²). This substantial increase in species richness was related to environmental conditions. Firstly, there was a large species bank around the *C. lanceolata* plantation, including 304 species of broad-leaf trees in GSP (Guanshan Evergreen Broad-Leaved Forest Monitoring Plot, unpublished) and 1896 species of angiosperms documented in the reserve (Liu and Wu, 2005); thus, the huge regional species bank provides rich provenances for the development of the *C. lanceolata* plantation into mature, close-to-nature forest. At the same time, *C. lanceolata* plantation composition of species is relatively simple, with low canopy density and thus a lot of available niche space, which created optimal conditions for the encroachment of intolerant tree species. In turn, the encroachment of intolerant tree species creates conditions for the encroachment and establishment of neutral and shade-tolerant tree species (Abbas et al., 2019; Xiang et al., 2017). Therefore, the species diversity increases greatly.

Diversity of species composition is essential for maintaining the structure and function of forest ecosystems (Lawton and Brown, 1994). With the increasing species diversity, it would improve the ecological problems such as soil erosion and soil fertility decline caused by single tree species of plantation (Jiang et al., 2019), and promote the self-regulation and ecological restoration ability of plantation ecosystem (Naeem et al., 2000), gradually realize the virtuous cycle of nutrients and the sustainable utilization of forest land, and finally realize the sustainable utilization of artificial forest. Thus, the plant diversity has important function for the effectiveness of sustainable forest management (Schulze et al., 2016; Yu et al., 1997).

5. Conclusion

The *C. lanceolata* plantation studied on the Guanshan Nature Reserve has developed from entirely natural processes, with broad-leaf trees establishing in a clear successional pattern after humans stopped artificial tending it. Broad-leaf tree species encroached into the *C. lanceolata* plantation in order of shade tolerance, establishing random and aggregated distributions in the process of natural development, and competition exclusion with *C. lanceolata*. With the encroachment of broad-leaf trees, *C. lanceolata* dominance gradually waned within the forest, and species diversity increased by degrees. In this study, the developing process of the *C. lanceolata* plantation was speculated by substituted DBH for age class, but there were differences in growth rates among different species. Thus it is necessary to make full use of dynamic forest monitoring plots to observe the process of seed propagation, germination, and growth of different species as they undergo successional processes. Furthermore, it is important to document the process and mechanism of broad-leaf tree species interspecific competition dynamics with *C. lanceolata*, so as to provide a better reference for the formulation of spatial structure optimization measures and a comprehensive assessment of ecological and anthropogenic benefits of *C. lanceolata* close-to-nature, post-plantation forests.

CRediT authorship contribution statement

Xiaoxia Zeng: Data curation, Formal analysis, Writing – original draft. **Lin Chen:** Investigation, Resources. **Zacchaeus G. Compson:** . **Jiejun Li:** Investigation. **Qiaohua Peng:** Investigation. **Chao Gong:** Investigation, Data curation. **Renquan Wen:** Data curation. **Jun Liu:** Supervision, Funding acquisition. **Xiong Fang:** . **Fenggang Luan:** Conceptualization. **Qingni Song:** Investigation, Funding acquisition. **Qingpei Yang:** Conceptualization, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data that has been used is confidential.

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