Quantitative division of succession and spatial patterns among different stand developmental stages in Changbai Mountains

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Abstract: Broadleaf-Korean pine forests exhibit high species richness and distinctive species composition, which are currently becoming more dominant among natural forests in Changbai Mountains of north-eastern China. Understanding the ecological process of restored vegetation is quite important for ecosystem reconstruction. Distinguishing stand development stages and analyzing the dynamic spatial patterns could provide insights into significant community coexistence mechanisms. In the present study, eight permanent study areas were established according to the substituting space for time method in Changbai Mountains of north-eastern China. The optimal division method was used to quantify the successional series into different stand development stages, and the point pattern analysis method ($L(r)$ function) was used to analyse the dynamic changes in spatial patterns and interspecific associations. Our results suggested that: (1) The stand development process was divided into five stages: the first three stages were poplar-birch secondary forests in different stages of recovery, the fourth stage was the spruce-fir mixed forest, and the last stage was the primary broadleaf-Korean pine forest; (2) The spatial pattern showed an aggregated distribution at a small scale and changed to a random distribution as the scale increased in poplar-birch secondary forests, but the spatial pattern appeared to be randomly distributed in spruce-fir mixed forest and broadleaf-Korean pine forest; (3) The interspecific associations between pioneer species and climax species changed from negative to positive among the different stand stages, and environmental resources were shared among these species. Interspecific differences in shade tolerance among the tree species were key determinants of forest dynamics and structure. Our study is vital to the understanding of the forest development; thus, the spatial change features should receive greater attention when forest management is being planned and restoration strategies are being developed for the Changbai Mountains.

Keywords: Dynamic spatial patterns; Interspecific association; Optimal division method; Stand developmental stages; Space for time substitution

Introduction

Stand development refers to the changes in ecological processes that lead to a qualitative change from one community to another community (Huber et al. 2018; Boyden et al. 2005; Hao et al. 2007), and different stages of stand development have their own stand structures and have varying influence on the relations between the stages (Collins and Carson 2004). Accurate vegetation classification based on stand development processes is important to understand the roles and relations of ecosystem changes (Grau 2000), and this knowledge would serve as the basis for predicting and planning for vegetation changes over time. Intensive research focused on stand development analyses has been conducted and has attracted great interest; unfortunately, the classification methods focused on distinguishing stand development stages are qualitative, but the stage of the succession stages is very complicated, which have been hindered by complex stand structure and species composition (Stefano et al. 2013). Therefore, how to quantify different succession stages is a key issue. The division of the community succession stage at the quantitative level could overcome the defects of the subjective judgment, and the division results can reflect the development process of the community more realistically, and make the quantitative division more reasonable and more scientific (Lua et al. 2003). Vegetation age is the most straightforward method used for the identification of stand development stages (Ripley et al. 1977; Uhl et al. 1988), but age alone is not a suitable forest stand parameter for use in predicting the different stand development stages, because many factors influence the structural differences among sites within the same age class (Tucker et al. 1998). Average stand height and basal areas are also used to define the different stages of stand development, but classifying different forest sites with overlapping basal areas and average stand heights is difficult (Lua et al. 2003). Remote-sensing technology, especially Lidar data, has recently been used extensively to analyse the different stand development stages (Henareh et al. 2012; van Ewijk et al. 2011). These methods of dividing different stand development stage are based on qualitative analyses but not on quantified aspects.

Spatial patterns are ecologically significant attributes of vegetation and provide essential clues to understanding the dynamics of stand development (O'Hara 2014; Firm et al. 2009; Larson et al. 2016; Duncan and Stewart 2011); these patterns can preserve an imprint of past ecological processes and interactions in the neighbourhood, including forest establishment, growth, competition, reproduction, and mortality (Yousef and Krzysztof 2017; Harpole and Tilman 2007). Spatial patterns could clarify coexistence mechanisms, such as interspecific associations and principal community factors (Janík et al. 2016). The debate concerning species associations has been central in succession theory, and several models of succession implicitly assume that interspecific associations are of primary importance in determining stand development patterns (Martíneza et al. 2010; Rousset and Lepart 2000; Zhao et al. 2012). Generally, spatial distribution is divided into three groups: random, clustering and uniform (Miura et al. 2001), and the change in spatial distribution often begins with the aggregation of individuals in young stands that develops into random or evenly uniform patterns in more mature stands (Martíneza et al. 2010). Intense discussions have focused on defining the deterministic process of spatial structures because both exogenous and endogenous factors can impact the spatial and temporal distributions (Nakashizuka 2001; Lei et al. 2007). The spatial autocorrelation of tree sizes is expected to decrease over time due to competition among similarly sized individuals (Wright 2002). Assessing spatial patterns at a given point in time may, of course, be insufficient for detecting ongoing processes but provides a necessary first step (Schleicher et al. 2011). We thus believe that forest spatial patterns could illuminate and quantify the mechanisms of population development in natural forests.

The forests in Changbai Mountains experienced relatively little human disturbance before the 19th century (Barnes et al. 1992), but during the 20th century, human disturbance became more frequent and severe, and from 1950 to 1986, the area of primary forest decreased by 70.4% (Shao et al. 2005; Dai et al. 2011). The broadleaf-Korean pine forest is a primary forest and a unique ecosystem because it is the most productive and biodiverse ecosystem in north-

eastern China and is endangered by unsustainable forest management practices (Miura et al. 2001; Liu et al. 2014a). After suffering from a serious disturbance, the natural forest can be divided into secondary, deforested and primary forest, according to the level of degradation (Zhang et al. 2014). It also can be classified to four different stand development stages—primary, tree rejection, lower wood restoration and old stage (also called a stable stage)—or five stages— contained construction, competitive growth, quality selection, near natural, and continuous forest (Kang 2011). In general, the methods existing for classifying the stand development stages in this area were not quantitative. Although forest spatial pattern analyses had been performed by some researchers (Chen and Bradshaw 1999; Zhang et al. 2014b; Zhang et al. 2010; Guo et al. 2017), but studies linking the spatial patterns with different stand development processes in these forests were rare.

In this study, we attempted to outline a new method for distinguishing the different stand development stages and for analysing spatial patterns and intra- and interspecies associations among different stand development stages that often existing in a chronosequence in Changbai Mountains. The aims were to explore how spatial patterns or aggregation changes occur in the stand development process and to gain insight into tree coexistence and development trends. These results could provide the basis for future ecological restoration research and forest reconstruction in Changbai Mountains.

1   Materials and Methods

1.1 Study area

The study area is on the Jingouling Forest Farm Wangqing County (43°22'N, 130°10'E) (Figure 1), which is located in the middle-lower hill region of the Changbai Mountains, Jijin province, China (Zhang et al. 2014b). The annual precipitation along this gradient ranges from 600 mm to 700 mm and the average relative humidity is 66%. The annual mean temperature varies from 7.3°C at the low elevations (700 m a.s.l.) to 2.8°C at the mountain summit (2691 m a.s.l.). The accumulated temperature above 10°C is approximately 2473°C. The growth period is 120 days. The topography of the area below 1700 m is gentle with slope inclinations of less than 5°. Above 1700 m, the slope is relatively steep with an average angle greater than 20°. Volcanic soils overlaying a deep layer of volcanic ash are common across the study area, and the soil type is a dark brown podzol, with an average thickness of ~40 mm. The elevation of the study plot is approximately 700 m, and the gradient is moderate.

1.2 Experimental design

Substituting space for time had been a widely used method for evaluating vegetation change, and this technique was initially used to distinguish different stand development stages in woody vegetation by assuming that time was the only difference (Pickett 1989). To meet the requirement for comparative analyses, secondary succession was determined based on measurements obtained in eight permanent field study areas that were designated broadleaf-Korean pine forest, spruce-fir mixed forest and poplar-birch forest. These areas represented different stand development stages.

Korean pine forest, also called primary forest (plot 20), was located in sub-compartment 4, compartment 44, in Jingouling Forest Farm; this plot was established in 1986 and had an area of 0.2 hm², which was continuously re-measured for 24 years from 1986 to 2010. At present, the primary forest, which shows limited effects of human disturbance, has maintained its basic primitive forest form. The spruce-fir mixed forest was
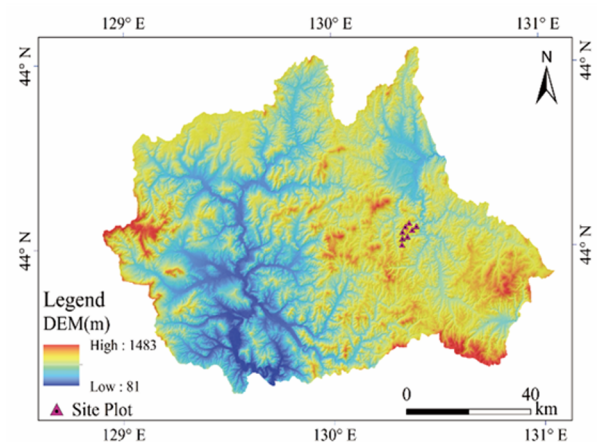

Figure 1 Location of the forest farm (in Northeast China).

formed after two highly intense selective cuttings in the primary forest in 1990 and 1995 (Kang 2011). Plot 28, located in sub-compartment 5, compartment 37, in Jingouling Forest Farm, was established in 1987, with an area of 0.02 hm². The poplar-birch forest was the first pioneer community in the secondary bare land of the broadleaf-Korean pine forest after destruction (e.g., fire, clear, fallow, etc.), which represented one of the most important transition stages of the natural pattern of restoration succession of broadleaf-Korean pine forest (Ni et al. 2014). The poplar-birch forest (plot 33) was located in sub-compartment 8, compartment 65, in Jingouling Forest Farm, which was established in 1989, with an area of 0.025 hm².

In addition, in Aug. 2007 and Aug. 2008, five permanent sample plots (plots *A*, *B*, C, *E*, *F,* and Plot *D* was damaged by the thinning in the later period, so it was not included in the statistics in this paper.) were established based on the average DBH of the pioneer species (poplar and birch) in different recovery stages after burning in the poplar-birch community, the main species were *birch (Betula platyphylla Suk.), poplar (Populus davidiana Dode.), linden (Tilia tuan Szyszyl.),* and *Momo maple species (Acer mono Maxim.)*. In each plot, the coordinates (x and y), diameter at breast height of 1.3 m (DBH), height (h), and the crown width of adult trees (DBH >3.0 cm) were measured. In addition, five 2 m × 2 m bush quadrats and five 1 m× 1 m plant quadrats were respectively arranged at the four corners and at the center of the subplot. The basic information on the plots was shown in Table 1. The density of the plots varied from 724 to 2055 stems/hm², and each plot had a basal area from 9.1 to 26.9 m²/hm².

1.3 Data analysis

1.3.1 Importance value

Importance value is a comprehensive quantitative indicator used to characterize the status and role of each species in the community, and the larger the importance value of a species, the greater the dominance of the species, which was calculated with the following equation (Feroz et al. 2008):

$$IV = \frac{\frac{n_i}{\sum_{i=1}^{S} n_i} \times 100 + \frac{a_i}{\sum_{i=1}^{S} a_i} \times 100 + \frac{f_i}{\sum_{i=1}^{S} f_i} \times 100}{3} \quad (1)$$

where n_i is the number of individuals of the i_{th} species, a_i is the basal area at the height of 1.3 m belonging to the i_{th} species, f_i is the number of quadrats in which the i_{th} species appeared, and S is the total number of species.

1.3.2 Interspecific Association

Interspecific associations comprise positive association, negative association and no association (Ofomata et al. 1999). We used chi-square (χ^2) statistics based on a 2×2 contingency table to examine the interspecific associations (Zhang et al. 2015). The formula is as follows:

$$\chi^2 = \frac{(|ad - bc| - 0.5n)^2 n}{(a + b)(a + c)(b + d)(c + d)}$$

$$\chi^2 = \frac{(|ad-bc|-0.5n)^2 n}{(a+b)(a+c)(b+d)(c+d)} \quad (2)$$

where n is the total number of quadrats, a is the number of quadrats with both species I and species II present, b indicates the number of quadrats with species I only, c indicates the number of quadrats with species II only, and d indicates the number of quadrats without species I and species II. When $\chi^2 < 3.841$, no interspecific association exists; when $3.841 \leq \chi^2 < 6.635$, certain associations exist among

Table 1 Basic information of the plots

ID	Area (ha)	Slope (°)	No of trees (/m²)	Age group	DBH (cm) Max.	DBH (cm) Aver.	Basal area (m²/hm²)	SDD	Skewness
A	0.2 (40 m×50 m)	15	1730	Mature	52.3	13.9	26.9	7.42	2.14
B	0.2 (40 m×50 m)	16	1735	Mature	45.9	13.0	23.0	6.44	2.20
C	0.2 (40 m×50 m)	16	2055	Mature	44.8	11.5	21.6	5.21	2.35
E	0.2 (40 m×50 m)	13	1115	Near-mature	41.1	16.3	23.2	9.13	1.11
F	0.12 (30m×40 m)	13	1933	Near-mature	41.8	8.8	11.8	3.35	2.22
20	0.2 (40 m×50 m)	15	805	Mature	100.1	29.5	17.6	18.72	1.59
28	0.2 (40 m×50 m)	16	980	Near-mature	47.0	23.3	13.4	9.14	0.32
33	0.25 (50 m×50 m)	14	724	Mature	54.6	22.4	9.1	10.8	0.56

Notes: DBH = Diameter at breast height; SDD = Standard deviation of diameter.

the species; and when $\chi^2 \leq 6.635$, significant associations exist among the species. When $ad>bc$, the interspecific association is positive, and when $ad<bc$, the interspecific association is negative.

1.3.3 Optimal partitioning method

The optimal segmentation method was used to divide the stand development stages (Tang 1984):

A class is set for: $\{X_i, X_{i+1}, \cdots\cdots, X_j\}$ $1 \leq i \leq j \leq n$,

so, the vector is: $\overline{X} = [1/(j-i+1)]\sum_{i=1}^{j} X_i$

and the class diameter is: $D(i,j) = \sum_{i=1}^{j}(X_i - \overline{X}_{ij})'(X_i - \overline{X}_{ij})$.

According to the definition of the objective function, the n-ordered plots are divided into categories. The method is set to $P(n,k)$. The objective function is as follows:

$$e[P(n,k)] = \sum_{i=1}^{n} D(i_1, i_{i+1} - 1) \qquad (3)$$

where i_i, i_{i+1} is the plot number, which represents the corresponding plot. Next, the sum of squares of deviations is found, and then the following recursive formula is used:

$$e[P_0(n,k)]$$
$$= k \leq \overset{min}{j} \leq n\{e[P_0(j-1, k-1) + D(j,n)]\} \qquad (4)$$

1.3.4 Spatial point process analysis

The pair correlation function $K(t)$ (also known as spatial point process analysis) is an important spatial pattern statistic and is a cumulative distribution function within the distance of t (Getis et al. 1987; Ripley 1977; Greig-Smith 1952). The $L(t)$ function, a transformation of Ripley's K-function (Besag 1977), can linearize the $K(t)$ function and stabilize the variables, make the assumption close to 0 under a random distribution:

$$K(t) = \varepsilon \sum_{i=1}^{n} \sum_{j=1}^{n} \frac{\delta_{ij}(t)}{n^2}; i \neq j \qquad (5)$$

$$L(t) = \sqrt{\frac{K(t)}{\pi}} - t \qquad (6)$$

where ε is the area of sample plot, t is the scale of the distance, n is the stem number of the analysed trees, and δ_{ij} is the reciprocal of the proportion of the perimeter of a circle centred on event i, passing through event j, and lying within the plot. The value of $\delta_{ij}(t)$ is equal to 1 for a circle wholly contained within the plot area and greater than 1 when the edge correction is required (Koukoulas and Blackburn 2005). The maximum value (t) for the rectangular plots is restricted to half of the short sides of a rectangle (Moeur 1993).

Under the null model of complete spatial randomness (CSR), the value of $L(t)$ is 0, whereas values of $L(t) <0$ indicate a regular distribution and values of $L(t) > 0$ indicate an aggregated distribution at scale t. A Monte-Carlo simulation was conducted to test the statistical significance of $L(t)$ deviations from zero under the null hypothesis of CSR (Getzin et al. 2006). Confidence intervals (99%) were generated using the high and low $L(t)$ values obtained from 1,000 random permutation simulations.

An analysis of the relation between two species is actually the point pattern analysis of the two species, which is also called a multivariate point pattern analysis. The analysis of the Ripley's $\hat{K}_{12}(t)$ index was made by its transformation in $\hat{L}_{12}(t)$ (Greig-Smith 1952):

$$\hat{K}_{12}(t) = \frac{A}{n_1 n_2} \sum_{i=1}^{n_1} \sum_{i=2}^{n_2} w_{ij}^{-1} I_r(u_{ij}) \qquad (7)$$

$$\hat{L}_{12}(t) = \sqrt{\hat{K}_{12}(t)/\pi} - t \qquad (8)$$

where n_1 and n_2 are the numbers of the two classes of points per tree and w_{ij} is the probability that the plant can be observed. $\hat{L}_{12}(t) = 0$ indicates that the two groups are spatially independent at t scale, $\hat{L}_{12}(t) > 0$ indicates a positive association, and $\hat{L}_{12}(t) < 0$ indicates a negative association. To test the statistical significance of $\hat{L}_{12}(t)$ deviations from zero, the random labelling hypothesis was tested to analyse the relations among the species and the different growth stages.

All calculations and simulations were computed using the ADE-4 package (Thioulouse et al. 1997).

2 Results

2.1 Quantitative division

2.1.1 Interspecific association among pairs

When the interspecific association coefficient was calculated, species with an importance value of at least 1% were included in this study (Table 2). We can see that the important values of the same tree species were still different in different plots, i.e., *Betula platyphylla* and *Tilia mandshuricum* in poplar-birch plot were obviously larger than other forest types, but for *Abies nephrolepis* and *Picea*

Table 2 Importance values of dominant tree species in different plots (Unit: %)

Species	Importance values for different plots							
	A	B	C	E	F	20	28	33
Betula platyphylla	14.3	25.5	26.8	10.6	31.7		2.1	3.0
Tilia mandshuricum	20.2	11.2	6.2	21.3	1.0	21.7	5.5	23.8
Betulla costata	13.1	1.3	1.1	17.2	2.0	3.8	2.6	0.8
Pinus koraiensis	5.5	2.6	6.4	2.4	2.4	9.7	19.4	15.0
Phellodendron amurense			1.4				0.6	0.6
Abies nephrolepis	5.1	4.3	0.4	6.1	1.9	22.1	40.1	30.3
Larix gmelini	2.3		3.1	4.8			4.0	
Acer mono	8.4	17.1	16.5	13.2		9.9	2.7	6.2
Fraxinus mandshurica	8.5	7.3		4.7	4.3	3.3		
Maackia amurensis			2.8					
Populus ussuriensis	2.5	0.4	18.9	0.7	33.0			
Ulmus propinqua	2.3	10.9	1.5	4.0	1.1	1.3		
Picea jazoensis	3.4	3.1	3.0	1.3		18.0	22.3	11.5
Xylosma racemosum			1.3					9.3
Hardwood ligna	14.2	16.2	10.6	13.8	22.5	10.2	0.6	0.6

Table 3 Half matrix of inter-specific association among dominant tree species

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
2	-0.01													
3	12.60	4.95												
4	2.32	27.50	3.80											
5	0	-20.60	-14.00	-27.51										
6	0.04	-9.42	-1.08	-12.60	17.80									
7	-0.32	-14.24	-7.74	-23.12	54.94	21.10								
8	14.21	7.60	2.25	6.81	0.09	0	-1.04							
9	6.24	6.12	6.91	35.69	-53.00	-8.00	-33.10	-1.90						
10	2.43	27.51	17.00	4.34	-9.03	-7.91	-2.04	0.02	0.29					
11	0.18	23.38	1.23	3.45	0	-0.60	-1.03	2.75	-4.90	10.24				
12	-3.46	-2.40	-0.17	-8.15	3.81	0.15	3.75	0	-1.00	-0.10	-0.01			
13	0.42	-1.67	-0.01	6.90	0	0.39	1.06	-2.23	0.90	-0.09	-0.70	-0.10		
14	-2.74	-0.49	0.61	2.76	-2.40	-3.63	0.02	-1.96	11.50	0.026	-0.92	-0.01	0.01	
15	-0.07	-0.10	1.59	0.01	-4.30	2.02	-2.27	0.16	9.03	-0.84	-0.70	-0.02	-0.01	-0.31

Notes: 1) *Tilia mandshuricum,* 2) *Hardwood ligna,* 3) *Acer mono,* 4) *Betula platyphylla,* 5) *Abies nephrolepis,* 6) *Pinus koraiensis,* 7) *Picea jazoensis,* 8) *Betulla costata,* 9) *Populus ussuriensis,* 10) *Ulmus propinqua,* 11) *Fraxinus,* 12) *Larix gmelini,* 13) *Xylosma racemosum,* 14) *Phellodendron,* 15) *Maackia amurensis* $X^2_{0.05(1)}=3.841$; $X^2_{0.01(1)}=6.635$.

jazoensis in poplar-birch plot, the important values were obviously smaller than other forest types. Among the total of 105 species pairs, 14 dominant species were observed. A total of 51 pairs showed positive associations, 53 pairs showed negative associations, and 1 pair showed no association (Table 3). When the pioneer species of *birch* trees was used as a reference, a clear negative relation was observed among the *Korean Pinus (Koraiensis Siebold et Zuccarini), spruce (Picea asperata Mast.), fir (Abies fabri (Mast.) Craib), larch* and other mixed trees, so they should be classified as the climax species group. In addition, a clear positive relation was observed among *poplar, oak trees and ribbed birch,* so they should be categorized as the pioneer species group. *Linden,*

maple, elm (Ulmus pumila Linn.), Manchurian ash (Fraxinus mandschurica Rupr.), Amur cork (Phellodendron amurense Rupr.) and mountain locust (Robinia pseudoacacia L.) did not show an apparent association, and therefore, they should be assigned to the group for other species. When the climax species of *Korean pine and spruce* were used as references, neither *Larix Larix gmelinii (Ruprecht) Kuzeneva)* nor *ribbed birch* showed a clear relation with *Korean pine* or with *Picea,* so *ribbed birch* and *larch* should be assigned to the other species group.

By considering biology and ecology in the process of stand development, the species *birch, poplar and oak* were classified as pioneer species; *Korean Pine, spruce and fir* were classified as

climax species; and *ribbed birch, larch, linden tree, maple, elm, Manchurian ash, Amur cork tree and mountain locust* were classified as the other species group. The proportions of the 3 species groups in each stand development stage were considerably different (Table 4), with more pioneer species observed in the early stand development stage, reaching up to 66.37%. As the forest developed, the pioneer species gradually withdrew and nearly completely disappeared in the spruce-fir forest, whereas the proportion of climax species was greater than 60%. The stand development series were formed by the size of the importance values of pioneer species (Table 5).

2.1.2 Arrangement of secondary succession series

According to the principal component analysis (PCA), the first principal component variable (y_1) indicated that the importance value of pioneer species declined during the process of stand development, and the importance values of the climax species increased. The second principal component variable (y_2) represented the transition variable. The contribution rate of the first principal component variable (y_1) was 64.019% (Table 6);

therefore, it was more prominent variable and demonstrated the progress of forest development based on the other variables. After calculating the coordinates of the first principal component variables (y_1), the value of y_1 in plots were arranged from small to large (Table 7). The stand development series belonged to the non-linear process, and the proportion of the other species increased in the early stand development stage.

2.1.3 Optimal division of secondary succession stage

The stand development series was divided into five stages with minimal variance (Table 8). The first two stages were the *poplar-birch* secondary forest community, and these stages showed different degrees of recovery after the fire. The first stage was in the early period of the *poplar-birch* forest (including plot *F*), the climax species had not yet invaded the forest, and the pioneer species (consisting of *birch* and *poplar*) presented a great advantage and had the highest *IVs* among the canopy components. However, the forest was mainly in the middle and young stage and had an average diameter of approximately 8.8 cm. The

Table 4 Basic structure characteristics of dominant tree species in different plots

Plot ID	Climax tree species			Pioneer tree species			Other tree species		
	Numbers (n/m²)	%	Diameter (cm)	Numbers (n/ha)	%	Diameter (cm)	Numbers (n/m²)	%	Diameter (cm)
A	185	10.69	14.4	220	12.72	18.6	1325	76.59	12.8
B	135	7.80	12.2	305	17.60	20.7	1395	74.60	10.4
C	110	5.35	16.9	1010	49.15	12.0	935	45.50	9.9
E	75	6.73	20.9	90	8.07	23.4	950	85.20	14.9
F	/	/	/	1283	66.37	9.1	650	33.63	7.7
20	475	59.01	27.3	/	/	/	330	40.99	33.9
28	820	83.67	24.7	/	/	/	160	16.33	14.0
33	460	62.54	20.3	48	6.63	37.6	216	29.83	22.1

Table 5 Importance values of species groups in different plots, which is based on the division results of the succession groups.

species	Plot ID							
	F	*C*	*A*	*B*	*E*	33	28	20
Pioneer species (x_1)	62.54	37.48	21.60	21.27	16.11	14.18	3.42	0
Other species (x_2)	31.16	49.99	61.24	60.53	72.04	33.10	19.63	49.66
Climax species (x_3)	6.29	12.53	17.17	18.20	11.85	52.76	76.94	50.34

Table 6 Results of the Principal Component Analysis (PCA) for the species groups.

Principal component	Feature vector			Feature root	Contribution rate (%)	Cumulative contribution rate (%)
	x_1	x_2	x_3			
y_1	0.381	0.323	-0.521	1.921	64.019	64.019
y_2	-0.631	0.726	-0.110	1.079	35.981	100

Note: y_1 was the first principal component variable, which was determined by x_1 and x_3; y_2 was the second principal component variable, which represented the transition variable, was determined by x_2.

Table 7 The value of main component coordinates in each plot, arranged from small to large according to the coordinates of the first principal component variable (y_1)

Coordinate Axis	F	C	A	B	E	33	28	20
y_1	-1.44	-1.05	-0.77	-0.71	-0.66	1.26	1.86	2.65
y_2	-2.12	-0.40	0.66	0.53	1.34	-0.37	-0.61	0.37

Table 8 The division results of minimum variance function.

Plot No.	Division 2 stage	Division 3 stage	Division 4 stage	Division 5 stage
2	0 (1)	-	-	-
3	440.9546 (1)	0 (2)	-	-
4	994.7024 (3)	440.9546 (3)	0 (3)	-
5	1094.4190 (3)	540.6599 (3)	99.7144 (3)	0 (4)
6	1120.097 (3)	566.3392 (3)	125.393 (3)	0.8373 (5)
7	1526.1510 (3)	972.3920 (7)	531.4464 (3)	125.3937 (6)
8	3477.1120 (3)	1526.1510 (7)	972.3920 (7)	531.4482 (7)

Note: The plot numbers (1-8) in the table was 20, 28, 33, *E, B, A, C, F;* and (1)-(7) represented the divided interval.

second stage was in the middle period of the *poplar-birch* forest (including plots *E, A, C,* and *B*), the pioneer species and climax species co-existed, other species were generally stable, and the *DBH* of the pioneer species was greater than 12.0 cm. The third stage was the late period of the *poplar-birch* forest (including plot 33). *Fir* and *spruce* had invaded the forest and gradually occupied the main forest layer. The fourth stage was the *spruce-fir* mixed forest (including plot 28). In this stage, the *DBH* was small and the ecological system was sensitive; therefore, the stability of the whole ecosystem could be gradually restored via scientific management, with the goal of optimizing the community structure. The fifth stage was the primary forest (including plot 20), which was less damaged and maintained a primary forest form.

2.2 Spatial pattern dynamics

The spatial pattern showed an aggregated distribution at a small scale and changed to a random distribution as the scale increased in plots *E, A, C,* and *B* (Figure 2). In plot 33, 10 m was the boundary scale at which the trees transitioned from an aggregated to random pattern. In addition, the spatial pattern appeared to be randomly distributed across plot 28, because the *L(t)* value fluctuated around 0. The amplitude did not break the fitting lines, and the trees mainly showed a random distribution. In the primary forest, the spatial pattern was the most random, and the *L(t)* value was positive at a scale of <13 m, deviated far from 0 m at a scale above 12.5 m, and then

strengthened the rectangular distribution, although the amplitude was within range of breaking the fitting line. The aggregated distributions were typical for pioneer species in the *poplar-birch* secondary forests (Figure 3). Pioneer species in the spruce-fir mixed forest and primary forest had almost withdrawn from the stands and were scattered and few. Climax species were few in plot *F* and presented an aggregated distribution in the early stage of the *poplar-birch* secondary forests (Figure 4). Subsequently, this distribution transitioned to a random pattern in the late stage of poplar-birch secondary forests (plot 33), and the intensity gradually decreased with the expansion of the spatial scale range. In the spruce-fir mixed forest, the climax species showed a random distribution. In the primary forest, climax species developed from random (0 m to 12 m) to regular distribution (scale >12 m). The distribution pattern of other species in each stand development stage was from an aggregated pattern to a random pattern. The spatial scale varied in the different plots but demonstrated an aggregated pattern at a small scale and a random pattern at a large scale (Figure 5).

2.3 Spatial associations

Climax species in the early *poplar-birch* forest (plot *F*) were rare, and almost no pioneer species were observed in the *spruce-fir* mixed forest (plot 28) and primary forest (plot 20); therefore, the interspecies associations between pioneer and climax species were not analysed because the small
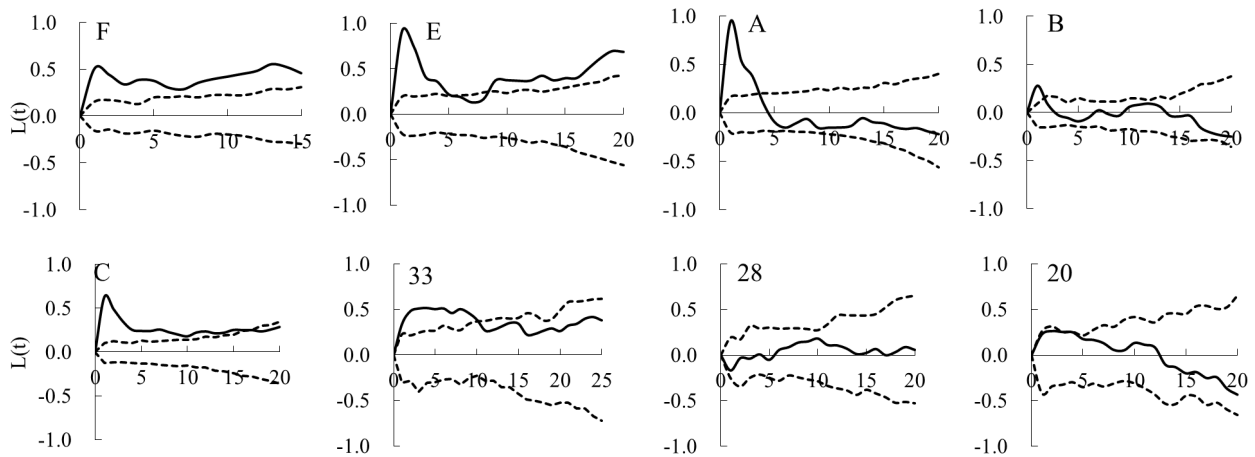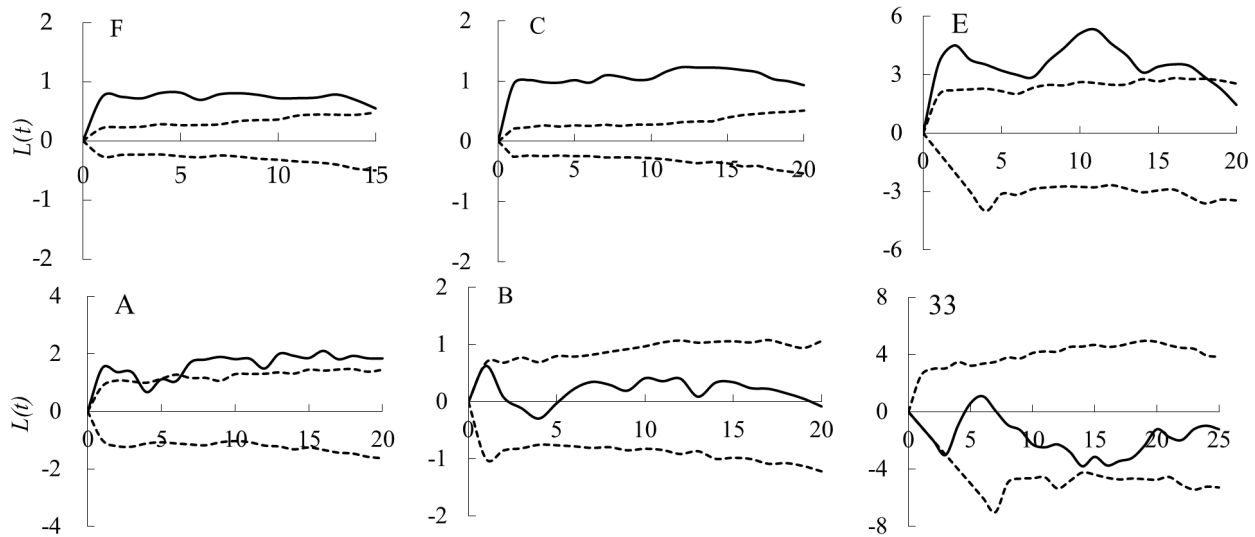
Figure 2 Spatial patterns of all trees in the different forest development stages using point pattern analysis method $L(t)$. The Y axes represents the $L(t)$ values, which is an index of spatial pattern; the X axes represents the spatial distance; the solid line shows actual $L(t)$ value, and dotted line correspond to 99% confidence intervals generated from 1,000 Monte Carlo simulations under the null hypothesis of complete spatial randomness. If $L(t)$ within confidence intervals, then the spatial pattern at distance t is entirely random; if $L(t)$ is above the upper confidence interval and below the lower confidence interval, then indicate aggregated pattern and regular pattern, respectively ($p < 0.01$).

Figure 3 Spatial patterns of pioneer species in the different forest development stages using point pattern analysis method $L(t)$. The Y axes represents the $L(t)$ values, which is an index of spatial pattern; the X axes represents the spatial distance; the solid line shows actual $L(t)$ value, and dotted line correspond to 99% confidence intervals generated from 1,000 Monte Carlo simulations under the null hypothesis of complete spatial randomness. If $L(t)$ within confidence intervals, then the spatial pattern at distance t is entirely random; if $L(t)$ is above the upper confidence interval and below the lower confidence interval, then indicate aggregated pattern and regular pattern, respectively ($p < 0.01$).

number of trees would affect the calculation precision. Similarly, the associations between pioneer species and other species were not analysed in the *spruce-fir* mixed forests (plot 28) and primary forests (plot 20), and the associations between climax species and other species were not analysed in the early *poplar-birch* secondary forest (Plot *F*).

The interspecies associations between the pioneer and climax species showed negative associations, and the associations were not significant at all scales (plot *C*) (Figure 6). However, positive associations at small scales and negative associations at large scales were observed in the other stand development stages (plot *A* and *B*). Negative associations were observed at all scales between pioneer species and other species in the early and middle *poplar-birch* forest (plot *F* and *C*)
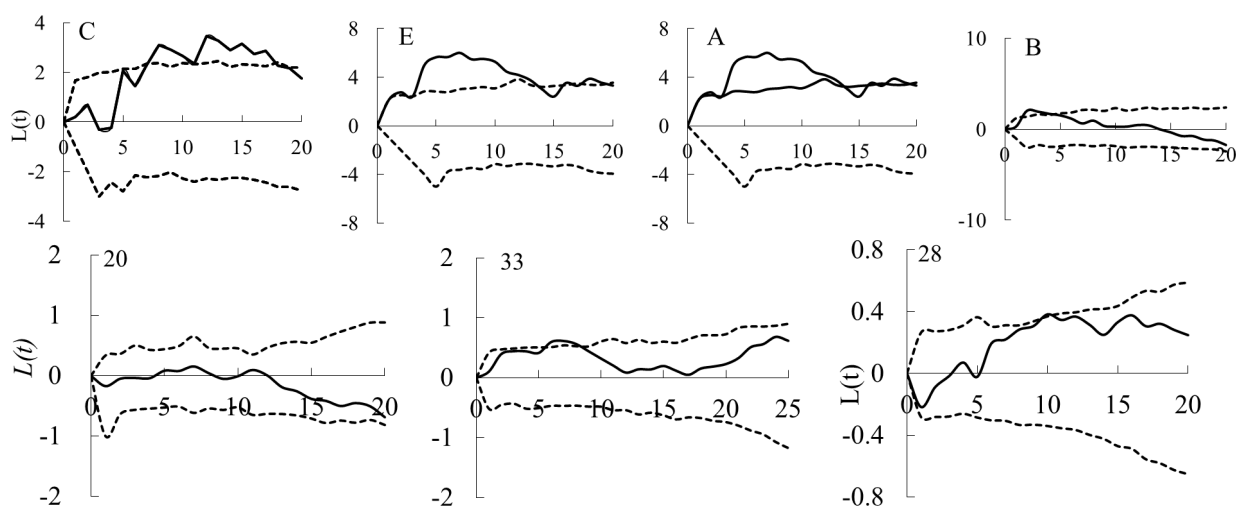
Figure 4 Spatial patterns of climax species in the different forest development stages using point pattern analysis method *L(t)*. The *Y* axes represents the *L(t)* values, which is an index of spatial pattern; the *X* axes represents the spatial distance; the solid line shows actual *L(t)* value, and dotted line correspond to 99% confidence intervals generated from 1,000 Monte Carlo simulations under the null hypothesis of complete spatial randomness. If *L(t)* within confidence intervals, then the spatial pattern at distance t is entirely random; if *L(t)* is above the upper confidence interval and below the lower confidence interval, then indicate aggregated pattern and regular pattern, respectively ($p<0.01$).

(Figure 7). Pioneer species in other stand development stages of the *poplar-birch* forest (plot *E*, *A*, *B*) were also negatively related with other species, although this relation was not significant. The $\hat{L}_{12}(t)$ value in plot 33 fluctuated around 0 and indicated mutual independence. A negative association was observed in plot *A* and *B*, a positive association was observed in plot 33, and a remarkable negative association was observed in the *spruce-fir* mixed forest (plot 28) (Figure 8).

3　Discussions

3.1 Division of stand development stages

Tree size was an important factor that affected stem growth and could be used to explain the spatial pattern and provide insight into forest dynamics (Jang et al. 2013). In this research, the seedlings and saplings of climax species showed an almost linear increase and finally accounted for the majority of species from the poplar-birch secondary forest that advanced to the different stand development stages. This result implied that pioneer species rapidly decreased with the stand development. A positive association showed that a close relation occurred between resource utilization and niche overlap (Hubbell et al. 2011); for example, the pioneer species between *poplar* and

birch had a negative association, which reflected species exclusion and indicated niche separation (e.g., the *birch* and *Korean pine*). Because a clear indicator was observed ($p <0.01$ and $p <0.05$), the χ^2 test represented a more accurate and objective expression of the interspecific associations. The climax species (consisting of *Korean pine*, *fir* and *spruce*) were shade-tolerant and found under their own canopy or that of pioneer species and other species (consisting of *linden* and *Acer mono*) (Zhang 2004). Classifying the stand development group was convenient for arranging the succession series and provided conditions for quantitative division (Whitfeld et al. 2014). According to the species association of χ^2 coefficient statistics, different stand development stages were divided into three groups: failing, transition and progressing in the northern mountains of Fujian Province. The series was rearranged, and five stages were defined using optimal division methods (Zhang et al. 2004). Subsequently, the interspecies associations were combined with the tree characteristics and used to classify the tree species, and the stand development stages were divided by using the optimal division method (Petritan et al. 2014). Accurate and quantitative divisions could overcome the defects of subjective judgement to provide more flexible and scientific divisions (Ishizuka et al. 1998; Yang et al. 2005).
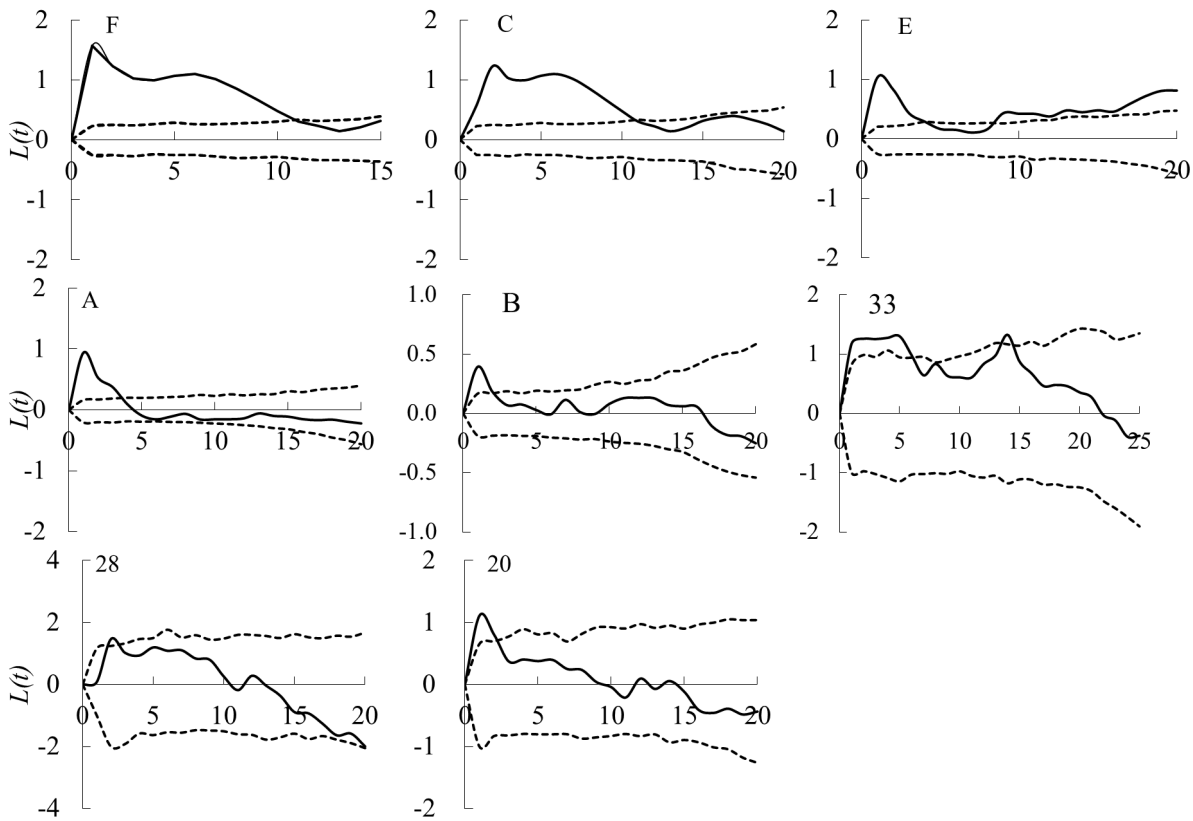
Figure 5 Spatial patterns of other species in the different forest development stages using point pattern analysis method *L(t)*. The *Y* axes represents the *L(t)* values, which is an index of spatial pattern; the *X* axes represents the spatial distance; the solid line shows actual *L(t)* value, and dotted line correspond to 99% confidence intervals generated from 1,000 Monte Carlo simulations under the null hypothesis of complete spatial randomness. If *L(t)* within confidence intervals, then the spatial pattern at distance t is entirely random; if *L(t)* is above the upper confidence interval and below the lower confidence interval, then indicate aggregated pattern and regular pattern, respectively (*p*<0.01).

Based on studies and observations in the northern United States, Oliver (1981) proposed a pattern of forest development that consists of four stages (stand initiation, stem exclusion, understory re-initiation, and old growth), and those stages were used to guide our discussion. Dansereau et al. (1982) proposed that stand development was composed of four stages: pioneer, reinforcement, sub-top, and top. By comparing those stages with our division results, the five stages were divided with minimal variance, and they were consistent with each other in the last three stages. However, the pioneer stage in our study was divided into two parts, and the first and second stages represented different *poplar-birch* secondary forest communities that were in different degrees of recovery after a fire.

Our research consistently showed a progressive decline in the importance of shade-intolerant species and an accompanying increase in the more shade-tolerant hardwoods, especially *fir* and *spruce* species (Schurr et al. 2004). Cain and Shelton (1995) examined understory dynamics over a period of 38 years in a mature, closed-canopy and found trends similar to those reported in the present investigation of *pine-oak* forest in south-eastern Arkansas. In that earlier study, the relative importance of woody understory species tended to increase over time for shade–tolerant genera and decrease for shade–intolerant genera. In contrast, the stand development pattern for old-field sites with no existing woody vegetation showed a high contribution of light-seeded hardwoods that became established either with or shortly after the shade–intolerant genera (Theodore et al. 2012).

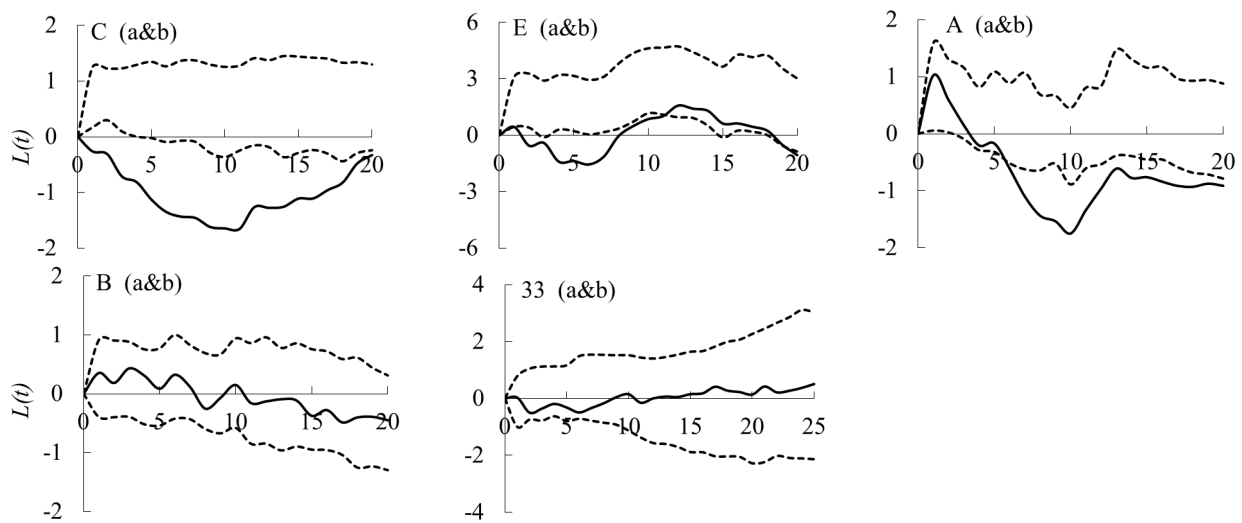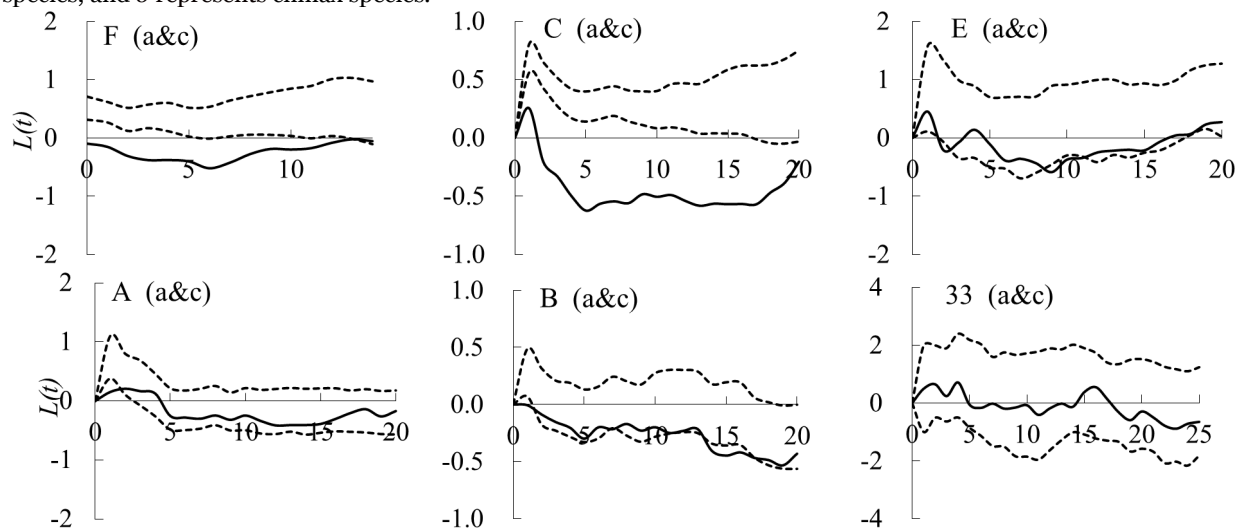**Figure 6** Inter-and interspecies spatial associations between pioneer species and climax species in each forest types. The Y axes represents the $\hat{L}_{12}(t)$, which is the value of multivariate point pattern; the X axes represents the spatial distance; the solid line shows actual $\hat{L}_{12}(t)$ value, and dotted line correspond to 99% confidence intervals generated from 1,000 Monte Carlo simulations under the null hypothesis of complete spatial randomness, a represents pioneer species, and b represents climax species.

Figure 7 Inter-and interspecies spatial associations between pioneer species and other species in each forest types. The Y axes represents the $\hat{L}_{12}(t)$, which is the value of multivariate point pattern; the X axes represents the spatial distance; the solid line shows actual $\hat{L}_{12}(t)$ value, and dotted line correspond to 99% confidence intervals generated from 1,000 Monte Carlo simulations under the null hypothesis of complete spatial randomness, a represents pioneer species, and c represents other species.

3.2 Spatial pattern analysis

Our comparisons of spatial patterns among the different stand development stages suggested that stages differed greatly in their spatial patterns, as had been observed in forests elsewhere (Zhang et al. 2015). The spatial pattern differences among various changed stages could inform mechanistic hypotheses explaining succession development. In

this paper, the spatial patterns transitioned from clustered distribution to random distribution as stand development progressed, and population distribution patterns depended significantly on the spatial scale, as has been reported elsewhere (Levin 1992; Chen et al. 1999). The spatial pattern of the *birch* population (pioneer species) changed from clustered to random, which was similar to the species of *birch* population at the *Mao'er*
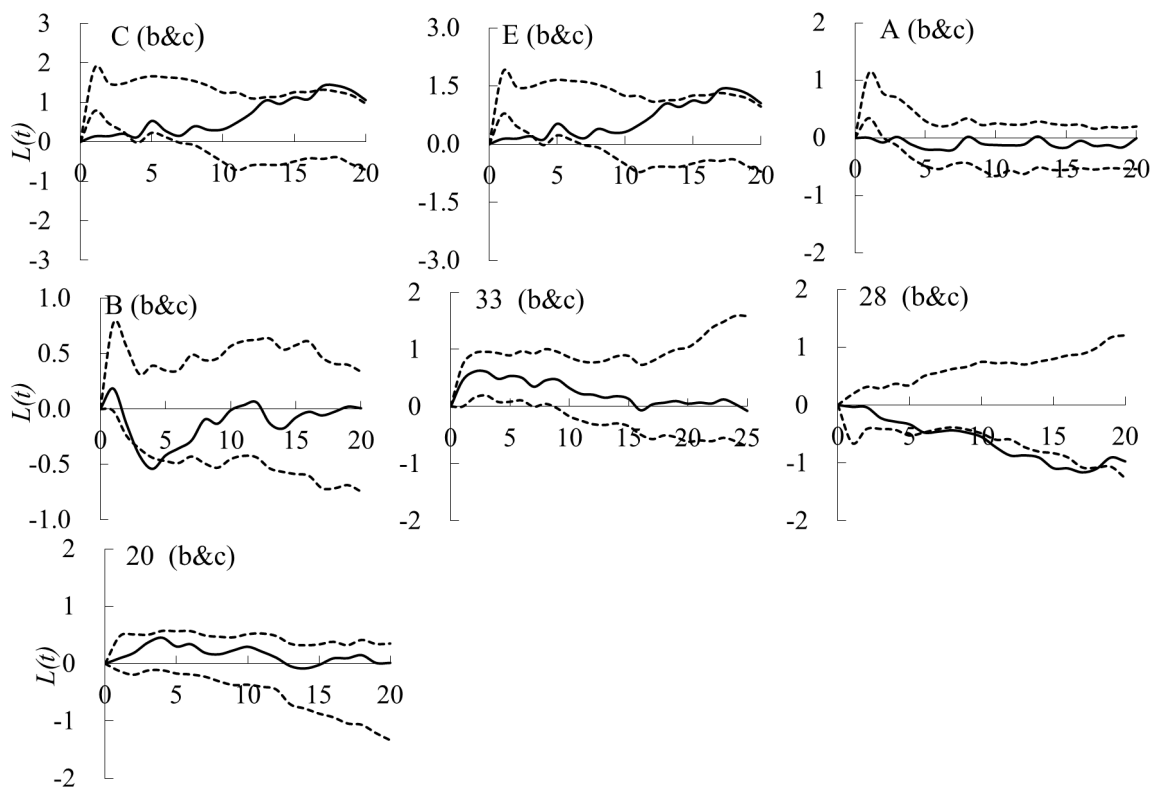
Figure 8 Inter-and interspecies spatial associations between climax species and other species in each forest types. The Y axes represents the $\hat{L}_{12}(t)$, which is the value of multivariate point pattern; the X axes represents the spatial distance; the solid line shows actual $\hat{L}_{12}(t)$ value, and dotted line correspond to 99% confidence intervals generated from 1,000 Monte Carlo simulations under the null hypothesis of complete spatial randomness, b represents climax species, and c represents other species.

Mountains Ecological Station in Heilongjiang Province (Sun et al. 1994). The clustered patterns may have been caused by regeneration. Regeneration typically occurred near seed sources and was influenced by habitat heterogeneity (Jang et al. 2013; Ishizuka et al. 1998). The random patterns may have been caused by intraspecific thinning due to high resource requirements and competition (Halpin and Lorimer 2016; Tiphaine et al. 2014). Species that showed clustered patterns as young trees tend to present random patterns as the forest became more stable (Larson et al. 2016; Wang et al. 2007). Our results indicated that density-dependent mortality of offspring was common. When dense plant communities were subject to intense competition, density-dependent mortality occurs in the process known as self-thinning (Yoda et al. 1963). The action of competition had been shown to decrease cluster and promoted shifting towards more regular or random patterns (Martíneza et al. 2010; López et al. 2010).

For spatial associations, both ecological habits and updated strategies would lead to different reactions (Levin, 1992). In the poplar-birch forest, pioneer species and other species at any scale were spatially negatively related and showed significant relations at a scale of 15 m, thus providing indirect evidence of habitat differentiation (Yang et al. 2005). Climax species and other species exhibited intraspecific positive associations at all scales, which probably could be attributed to prompt growth reactions to spatially limited light availability, which was suggested by Hubbell et al. (2001). Additionally, Pacala (1997) suggested that intraspecific competition effects should be much more important than interspecific competition, which could promote species coexistence (Martíneza et al. 2010; Carson and Pickett 1990; Zhao et al. 2012). Interestingly, the forests demonstrated an intraspecific self-thinning process, which could create favourable conditions for the invasion and settlement of other species. Our findings were somewhat expected, as interspecific

differences in shade tolerance among tree species were key determinants of forest dynamics and structure, and the shade under the canopy of shade-intolerant species was expected to facilitate establishment and growth of shade-tolerant species (Oliver 1996). Therefore, saplings recruit beneath the canopies of large parent trees must be shade tolerant to support long-term persistence, where young individuals of climax species would gradually dominate the natural space after a period of competition and elimination.

Stand structure played an important role in population renewal and community dynamics in the succession process from secondary forest to primary forest. At present, secondary forests in China account for 46.2% of the country's forest area and the mainstay of forest resources. The results of variation trend of spatial distribution in this paper could enhance the understanding of population dynamics and interspecific relationships among different forest stages, and which could be determined with reference to the local forests management, and provide silviculture principles might accelerate this process and improve the internal forest structure to be conducive to forest development.

and finally accounted for the majority, whereas pioneer species consistently showed a progressive decline. Our results suggested that under current conditions in non-intervention stands, climax species, although common, would tend towards replacement of pioneer species, and knowledge of this pattern could have helped to improve silvicultural practices.

Stand development was difficult to evaluate because of its long timescale. Nevertheless, the length and structure of each stage in this study contributed to the site conditions, vegetation, and disturbance characteristics. Achieving a simple, intuitive and large-scale method for forest ecosystem management was important, which could provide scientific basis for the sustainable and stable realization of multiple benefits of forest ecosystems. But due to the limited experimental conditions, the data in this study did not include trees with the $DBH < 5.0$ cm. Therefore, discrepancies with other studies in the spatial distribution patterns and associations may be observed. Future research should investigate how these environmental factors affect spatial patterns and prioritize the assembly of long-term monitoring data and scientific design.

4 Conclusions

Comparisons of spatial structure among the five stages suggested that population distribution patterns depend significantly on spatial scale and that interspecific differences in shade tolerance among the tree species were key determinants of forest dynamics and structure. Additionally, during the succession process, the seedlings and saplings of climax species showed an almost linear increase

Acknowledgements

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