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Spatial distribution pattern of *Picea schrenkiana* population in the Middle Tianshan Mountains and the relationship with topographic attributes

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Abstract: The spatial distribution of plant populations is an important feature of population structure and it determines the population's ecological preferences, biological characteristics and relationships with environmental factors. The point pattern analysis method was adopted to study the distribution pattern of *Picea schrenkiana* individuals of different size classes and the correlations between two size classes as well as the impact of topographical attributes on the population distribution. With increasing diameter at breast height, the plant density of the *P. schrenkiana* population showed a declining trend. Old trees showed a random distribution at a small spatial scale (0–12 m), whereas saplings, small trees and big trees all had an aggregated distribution at all scales. With the increase of tree age, the scales at which maximal aggregation occurred gradually increased and the aggregation strength decreased. At a small scale (0–16 m), all size classes showed a negative correlation and the larger the difference between tree size, the more significant the negative correlation. The number of medium, big and old trees had a significantly positive correlation with elevations, whereas the number of saplings and small trees was not significantly correlated with elevations. The numbers of saplings, small and medium trees showed a significant positive correlation with slope gradient, whereas the number of big trees was not significantly correlated, and the number of old trees was negatively correlated with gradient. With the exception of old trees, saplings, small, medium and big trees showed negative correlations with convexity index. The study provides a theoretical basis for the conservation, rehabilitation and sustainable management of forest ecosystems in the Tianshan Mountains.

Keywords: *Picea schrenkiana*; coniferous forest; population structure; spatial correlation; age class; topographic attribute

The spatial distribution pattern of plant populations is an important feature of population structure. In a population, the distribution pattern of different age-class individuals and their mutual relationships are the result of a long-term mutual interaction between the population and environment (Gray and He, 2009). The distribution pattern and relationships reflect the integrity of the population structure and the dynamics and stability of the population (Mateu *et al.*, 1998; Jayapal *et al.*, 2009). The spatial distribution pattern of a plant population differs among species, and the distribution pattern of a single species may vary at different developmental stages and when individuals grow in diverse habitats. Analysis of the

spatial distribution pattern of a plant population is helpful to determine the population's ecological preferences, biological characteristics and relationships with environmental factors (Zhang *et al.*, 2010; Li *et al.*, 2011). Therefore, the analysis of the spatial distribution pattern of plant populations has always been a major focus for ecological research (Haase, 1995; Mateu *et al.*, 1998; Baskent and Keles, 2005). The spatial distribution pattern of plant populations exhibits scale dependence, e.g. a species may show an aggregated distribution at one spatial scale and may change to a random or uniform distribution at a

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different scale. The correlation between two species may be positive at one scale, but negatively or non-significantly correlated at a different scale (Guo *et al.*, 2005; Song *et al.*, 2011). On the basis of the spatial coordinates of plant distribution, the point pattern analysis method of Ripley can be used to study the spatial distribution pattern and interspecific relationships of populations at different scales. The method is especially important for the research on plant spatial distribution patterns (Perry *et al.*, 2006; Li *et al.*, 2011; Lin *et al.*, 2011).

To better understand the distribution patterns, colonization and regeneration mechanisms of forest species, the Smithsonian Institute established the world's first forest dynamic monitoring census plot in Panama. Subsequently, monitoring of plant population spatial distribution and biological diversity based on large-scale fixed sample plots has attracted increasing attention. For example, a 9.2-hm² sample plot was established for the monitoring of the spatial distribution pattern and biological diversity of a *Pinus ponderosa* plant community in southern Colorado (Boyden *et al.*, 2005); a 25-hm² forest sample plot was established to monitor the spatial distribution of trees in natural reserves in northwestern Ecuador (Burton *et al.*, 2009); and in India a 5-hm² fixed sample plot was established to monitor the species composition and distribution characteristics of a deciduous forest (Jayapal *et al.*, 2009). In 2004, the Chinese Academy of Sciences established sample plots to monitor the spatial distribution and dynamics of a number of plant populations, including broad-leaved Korean pine forest in the Changbai Mountains (Hao *et al.*, 2007), subtropical evergreen forests on the Gutian Mountain (Lai *et al.*, 2010; Li *et al.*, 2010), and evergreen forests on the Tiantong Mountain in Zhejiang (Bruehlheide *et al.*, 2011; Song *et al.*, 2011).

Picea schrenkiana in the Tianshan Mountains has important ecological functions, e.g. conservation of water sources, wind prevention, sand stabilization, protection of biological diversity, nitrogen fixation, and oxygen release (Hao *et al.*, 2010; Li *et al.*, 2010; Zhang *et al.*, 2011). Previous researches and reports on the spatial distribution pattern of *P. schrenkiana* were based on a small spatial scale (<4 hm²) and analysis of several quadrats at a single scale (Pan and

Zhang, 1991; Zhang *et al.*, 2011). For example, a 3-hm² forest sample plot which contained 300 subplots (10 m×10 m) and a 2.5-hm² sample plot which contained 250 subplots (10 m×10 m) were respectively established in the middle of the north slope of the Tianshan Mountains by Li *et al.* (2005). While a 0.94-hm² plot which contained 15 subplots (25 m×25 m) was established in the Middle Tianshan Mountains by Song *et al.* (2009). In addition, the effects of topographic attributes on *P. schrenkiana* population distribution were rarely investigated. The present study used the point pattern analysis method to investigate the variation in the spatial distribution pattern of *P. schrenkiana* at different spatial scales and the spatial correlation at different growth stages in an 8-hm² fixed sample plot in the Middle Tianshan Mountains.

1 Materials and methods

1.1 Study area

The study area is located in the State Forestry Bureau Xinjiang Tianshan (Mountains) Forest Ecosystem Research Station (43°24'48"–43°26'18"N, 87°27'29"–87°28'48"E). The elevation ranges from 1,908 to 2,960 m. The station, covering an area of 393 hm², is a member of the National Forest Ecosystem Research Network. The site is characterized by a temperate continental climate. The annual mean temperature is 2.0°C. The mean annual precipitation is 400–600 mm. The mean annual evaporation is 980–1,150 mm; the mean annual relative humidity is 65%; the aridity index is 1.4; and the frost-free period is 89 d (Zhang *et al.*, 2011). The soil is classified as brown forest soil and has a thick humus layer (Forestry of Administration of China, 1989). *P. schrenkiana* secondary forest is distributed in this area, with a vegetation cover of 60%. Grassland covers 8% of the total study area, while bush and bare land covers 6% and 26%, respectively (Forestry of Administration of China, 1989).

1.2 Data collection

During July 2009, an 8-hm² fixed sample plot was randomly established in the forest in State Forestry Bureau Xinjiang Tianshan (Mountains) Forest Ecosystem Research Station following the field protocol of Center for Tropical Forest Science (CTFS) (Condit *et al.*, 2000). The sample plot is 200 m long in the nor-

theast and 400 m long in the southeast (1,958–2,188 m asl, Fig. 1). The sample plot was divided into two-hundred 20 m×20 m subplots. All living and dead woody plants with diameter at breast height (DBH) > 1 cm were tagged, mapped and numbered. In July and August of 2009 and 2010, the species, DBH, height, crown diameter, stem length as well as establishment and germination of all individuals with DBH ≥ 1 cm were recorded. The total number of living individuals in the census was 13,255, which comprised 13,152 *P. schrenkiana*, 31 *Berberis heteropoda*, 31 *Sorbus tianschanica*, 27 *Lonicera hispida*, 5 *Populus davidiana*, 4 *Cotoneaster melanocarpus*, 2 *Crataegus pinnatifida*, 2 *Rosa* spp., and 1 *Betula tianschanica*. The average height, diameter at breast height and height of the first living branch of *P. schrenkiana* were 10.5 m, 3.1 cm and 1.2 m, respectively.

1.3 Data analysis

1.3.1 Classification of age classes

A diameter class structure was adopted in place of the

age structure to analyze the dynamics of population distribution pattern. According to the DBH and life characteristics, all *P. schrenkiana* individuals were classified into five age classes (Li *et al.*, 2005; Zhang *et al.*, 2011): saplings (1 cm < DBH < 2.5 cm), small trees (2.5 cm ≤ DBH < 7.5 cm), medium trees (7.5 cm ≤ DBH < 22.5 cm), big trees (22.5 cm ≤ DBH < 47.5 cm), and old trees (DBH ≥ 47.5 cm).

1.3.2 Calculation of topographic attributes

Topographic attributes, namely elevation (measured by GPS), slope gradient (measured by compass), aspect (measured by compass), and convexity index, were recorded in each quadrat following the method. Quadrat elevation was the mean value of four peak elevations within the quadrat. Convexity index was calculated as the quadrat's elevation minus the mean elevation of eight neighboring quadrats (the convexity index of quadrats on the margins of the sample plot was calculated from the mean elevation of five neighboring quadrats). A positive value meant that the

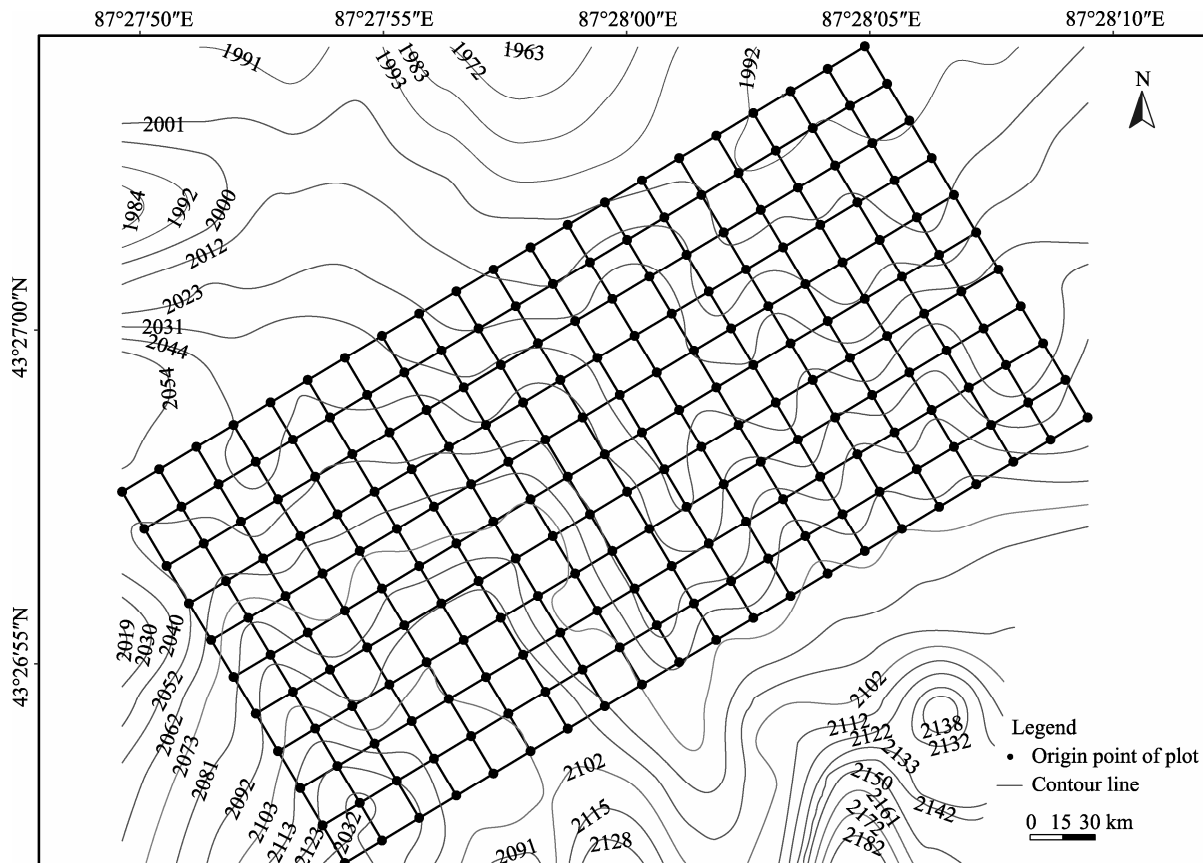


Fig. 1 The map of the 8-hm² sample plot in the Middle Tianshan Mountains of Xinjiang, China

target quadrat was higher than the surrounding quadrats and thus the surface was convex (e.g. located on a ridge), and a negative value meant the surface was concave (e.g. at the floor of a valley). Quadrat aspect was measured by taking four corner points within a quadrat and determining the angle of the plane formed by three of the peaks for each of the four possible combinations, and the mean angle of deviation from due north of these four planes was calculated. With due north as the starting point (0°), eight aspects were recognized: N stands for north slope (337.5–22.5°), NE for northeast slope (22.5–67.5°), E for east slope (67.5–112.5°), SE for southeast slope (112.5–157.5°), S for south slope (157.5–202.5°), SW for southwest slope (202.5–247.5°), W for west slope (247.5–292.5°), and NW for northwest slope (292.5–337.5°). The slope gradient was calculated by considering, in turn, three of the four corner points for each quadrat to form one slope face; the mean value of the four slope face gradients was taken to be the quadrat's gradient.

1.3.3 Point pattern analysis

In this study we adopted Ripley's L function for the analysis of the spatial distribution pattern of *P. schrenkiana*. Ripley's L function is improved from Ripley's K function (Mateu *et al.*, 1998; Martínez *et al.*, 2010; Wang *et al.*, 2010). The latter enables simultaneous analysis of a species' spatial distribution pattern at any scale, and is presently the most important method for the analysis of population spatial distribution patterns. The function analyzes the number of plant individuals appearing in a circle, which is centered on a point within the study area, and r is the radius of the circle. The formula is as follows (Gray and He, 2009):

$$\hat{k}(r) = \frac{A}{n^2} \sum_{i=1}^n \sum_{j=1}^n w_{ij}^{-1} I_r(u_{ij}), \quad (1)$$

where n is the total number of each age class, A the quadrat area, u_{ij} the distance between two points i and j , $I_r(u_{ij})$ an indicator function (when $u_{ij} \leq r$, $I_r(u_{ij})=1$ and when $u_{ij} > r$, $I_r(u_{ij})=0$), and w_{ij} a weight value used for edge correction.

To explain the actual spatial pattern more intuitively, Besag (1977) proposed Ripley's L function:

$$\hat{L}(r) = \sqrt{\hat{k}(r) / \pi} - r, \quad (2)$$

where $\hat{L}(r)=0$ represents a random distribution, $\hat{L}(r)>0$ an aggregated distribution, and $\hat{L}(r)<0$ a uniform distribution.

Analysis of the relation between different age classes is actually the analysis of the point pattern of two species. The formula is:

$$\hat{k}_{12}(r) = \frac{A}{n_1 n_2} \sum_{i=1}^{n_1} \sum_{j=1}^{n_2} w_{ij}^{-1} I_r(u_{ij}), \quad (3)$$

where n_1 and n_2 are the number of individuals (points) of species 1 and species 2, respectively, and i and j represent individuals of species 1 and 2, respectively.

$$\hat{L}_{12}(r) = \sqrt{\hat{k}_{12}(r) / \pi} - r. \quad (4)$$

If $\hat{L}(r)=0$, the two species are not correlated at scale r ; if $\hat{L}(r)>0$, the two species are positively correlated; and if $\hat{L}(r)<0$, the two species are negatively correlated.

Monte Carlo method was used to obtain a 99% confidence envelope. On the assumption the population was distributed at random, a random model was used to fit the coordinate of a group and calculate each r value. Similarly, a random model was used to simulate the coordinate of a new group and calculate the r value under different scales. This process was repeated until specified number of combinations and permutations was reached. The maximum and minimum values were the coordinates of the upper and lower envelope curves, respectively. The fitness time was 100. The analysis was performed with the ADE-4 software package. According to the principle of point pattern formula (Jouquet *et al.*, 2004), the spatial scale was in 1.0 m steps to half of the shortest side length (100 m).

2 Results

2.1 Population structure of *P. schrenkiana*

The 8-hm² fixed sample plot contained 13,152 *P. schrenkiana* individuals growing at an average density of 1,644 individuals/hm². The distribution of the *P. schrenkiana* was not even, such that with increased DBH, the plant density dramatically declined (Fig. 2). The plot contained abundant saplings and small trees, so *P. schrenkiana* population was considered to be in a stable decline.

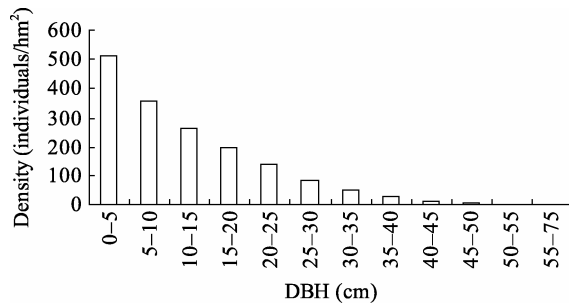


Fig. 2 Diameter distribution of *P. schrenkiana* in an 8-hm² plot in the study area

Figure 3 shows that in the 8-hm² sample plot, the density differences among all age classes in the *P. schrenkiana* population were large: 2,230 saplings, 3,414 small trees, 5,656 medium trees, 1,800 big trees and 52 old trees, respectively.

2.2 Population distribution pattern of all age classes

The point pattern analysis of the five age classes indicated that saplings, small trees, medium trees and big trees all showed an aggregated distribution at all spatial scales, whereas the old ones showed a random

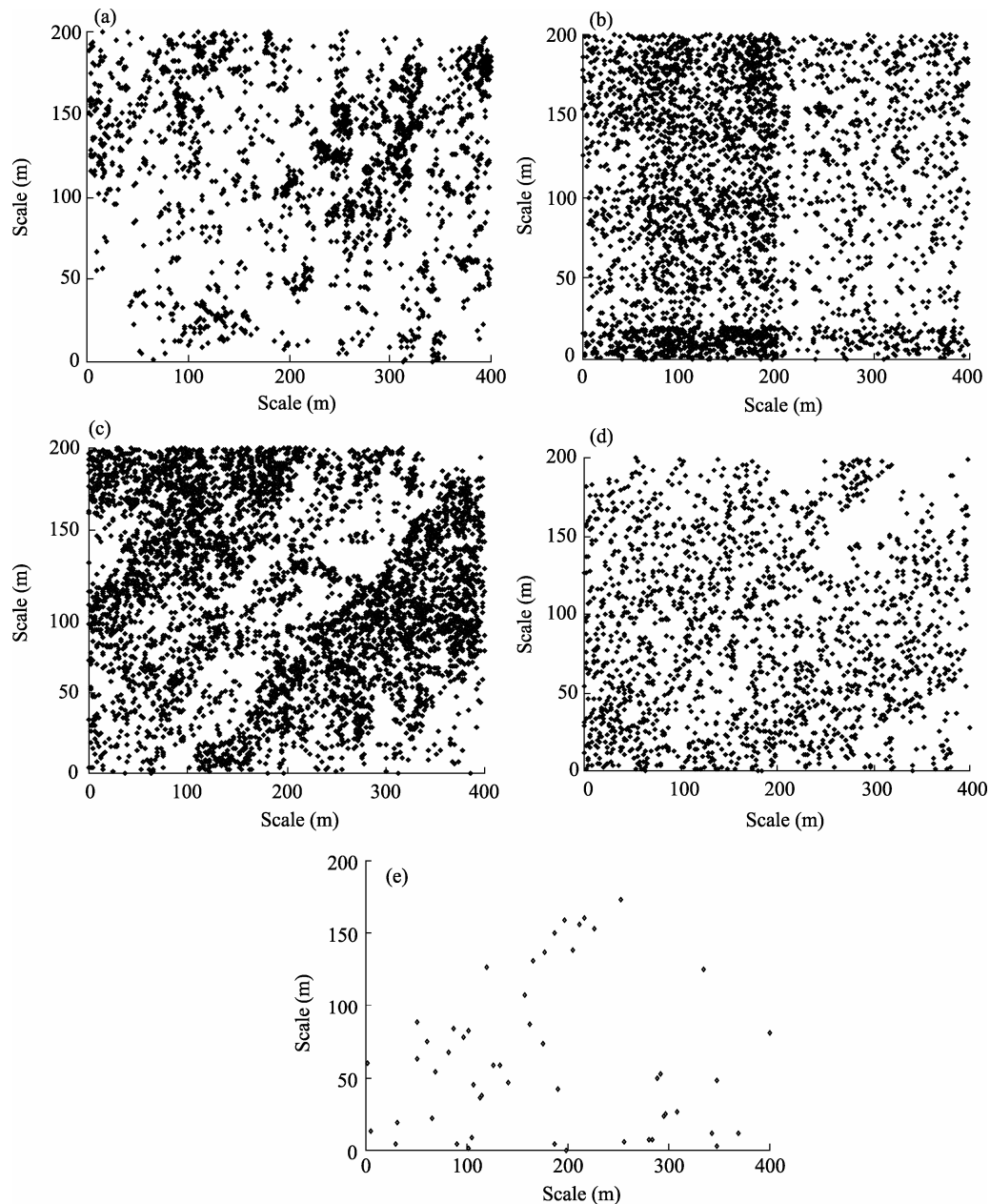


Fig. 3 Distribution points for *P. schrenkiana* of different ages in an 8-hm² sample plot in the study area. (a) Sapling; (b) Small tree; (c) Medium tree; (d) Big tree; (e) Old tree.

distribution at a smaller scale. This random distribution gradually changes into an aggregated distribution as the scale increases (Fig. 4). These data indicated that at the early stages of population development, the pattern of *P. schrenkiana* aggregation did not change, and at later stages of development (mature forest stage) the population only showed a weak random distribution pattern at a small scale which gradually developed a strongly aggregated distribution pattern with in-

creased scales. At the same scale, the order of aggregation strength of all age classes was saplings>small trees>medium trees>big trees. Old trees showed a random distribution at a small scale of <12 m, and a strongly aggregated distribution pattern at 12–100 m. For saplings, the aggregation strength reached a maximum of $L(r)$ 8.02 at $r=25$ m; for small trees it reached a maximum of 5.54 at $r=30$ m; for medium trees it reached a maximum of 4.01 at $r=74$ m;

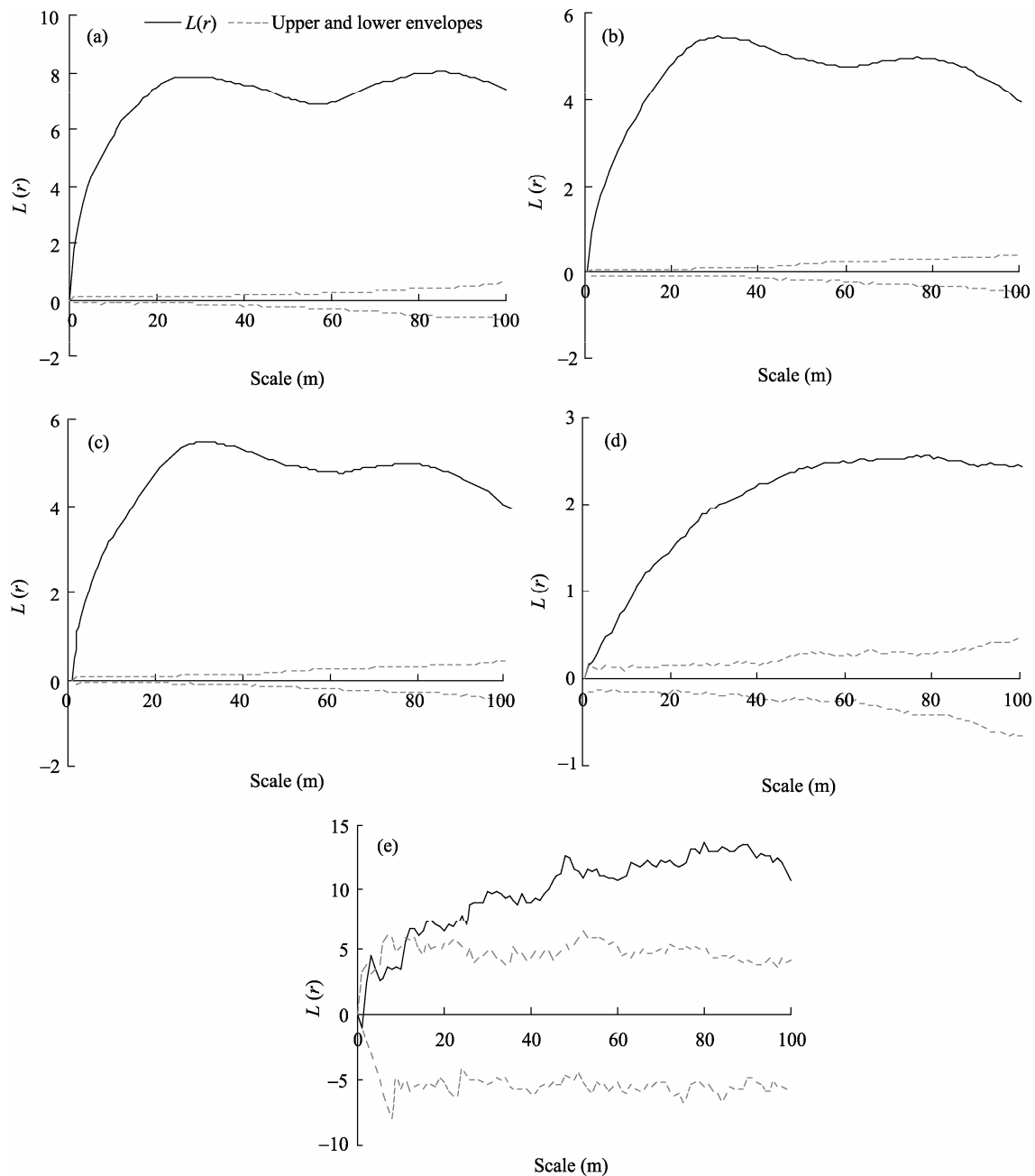


Fig. 4 Point pattern for *P. schrenkiana* of different ages in an 8-hm² plot in the study area. (a) Sapling; (b) Small tree; (c) Medium tree; (d) Big tree; (e) Old tree.

for big trees it reached a maximum of 2.57 at $r=78$ m; and for old trees it reached a maximum of 13.66 at $r=80$ m. These results showed that the aggregation strength of *P. schrenkiana* individuals, except that of old trees, decreased progressively with increasing tree age and the scale for the maximum degree of aggregation increased gradually.

2.3 Spatial correlation of different diameter classes of the *P. schrenkiana* population

In our analyses of the population spatial correlation of different age classes, the more similar the spatial patterns, the more likely that the $L_{12}(r)$ values are higher than the envelope curves, indicating a strong positive correlation. Otherwise, the classes show a negative correlation. Figure 5 showed that saplings were negatively correlated with small trees at the 0–65 m range, were not correlated at the 65–84 m range, and were positively correlated at the 84–100 m range. Saplings were negatively correlated with medium trees at the 0–78 m range, and were not correlated at the 78–100 m range. Saplings were negatively correlated with big trees and old trees at all scales. Small trees and medium trees were negatively correlated at the 0–16 m range, uncorrelated at the 16–64 m range, and significantly positively correlated at the 64–100 m range. The spatial correlation of small trees with big trees and old trees was negative, and the strength of the negative correlation decreased gradually with increased scale. Medium trees were negatively correlated with big trees and old trees at all scales. Big trees were negatively correlated with old trees at the 0–20 m range, and were uncorrelated at the 20–100 m range. Overall, age classes of the *P. schrenkiana* population showed a negative correlation at a small scale and the larger the difference in tree age, the more significant the negative correlation or the weaker the positive correlation between age classes.

2.4 Correlation between topography factors and population distribution

The highest density of *P. schrenkiana* individuals was on north- and northwest-facing slopes, followed by west- and southeast-facing slopes, then northeast- and east-facing slopes, and the lowest density occurred on southwest-facing slopes (Table 1). Compared with

north-facing slopes, the stand density on southwest-facing slopes was decreased by 54.82%. These results indicated that *P. schrenkiana* was preferably distributed on shady and semi-shaded slopes.

With regard to the distribution of age classes in relation to slope aspect, sapling density on northeast- and east-facing slopes was significantly higher than the average density of all saplings in the sample plot. Small, medium and big trees were mainly distributed on north and northwest-facing slopes, and old trees were mainly distributed on west- and north-facing slopes. These results indicate that, although *P. schrenkiana* is a shade-tolerant species, the regeneration and establishment of seedlings required a certain amount of sunlight; thus semi-shaded slopes seemed to be ideal places for regeneration, whereas completely shaded slopes were not suitable.

Saplings and small trees were more frequently distributed on concave surfaces (valleys), whereas medium, big and old trees were mainly distributed on convex surfaces (ridges).

From the overall distribution of *P. schrenkiana* at different slopes, the highest density of *P. schrenkiana* individuals was found within the 30–40° slope gradient range, followed by the 40–50° and 20–30° ranges, and the lowest density occurred on 10–20° slope gradients. The data presented in Table 1 clearly showed that with the increase in slope, the number of saplings also increased, whereas the number of big and old trees decreased. Small and medium trees were distributed most frequently within the 30–40° slope range, followed by the 40–50° and 20–30° slope ranges, and the lowest frequency occurred on 10–20° slopes.

Correlation analysis between the number of *P. schrenkiana* individuals with topography factors (Table 2) showed that within the elevation range of 1,958–2,188 m, the numbers of medium trees, big trees and old trees had a significantly positive correlation with elevations, whereas the numbers of sapling and small trees were not significantly correlated with elevations. The numbers of saplings, small trees and medium trees presented a significant positive correlation with slope gradients, whereas the number of big trees was not significantly correlated with slope gradients, and the number of old trees was negatively

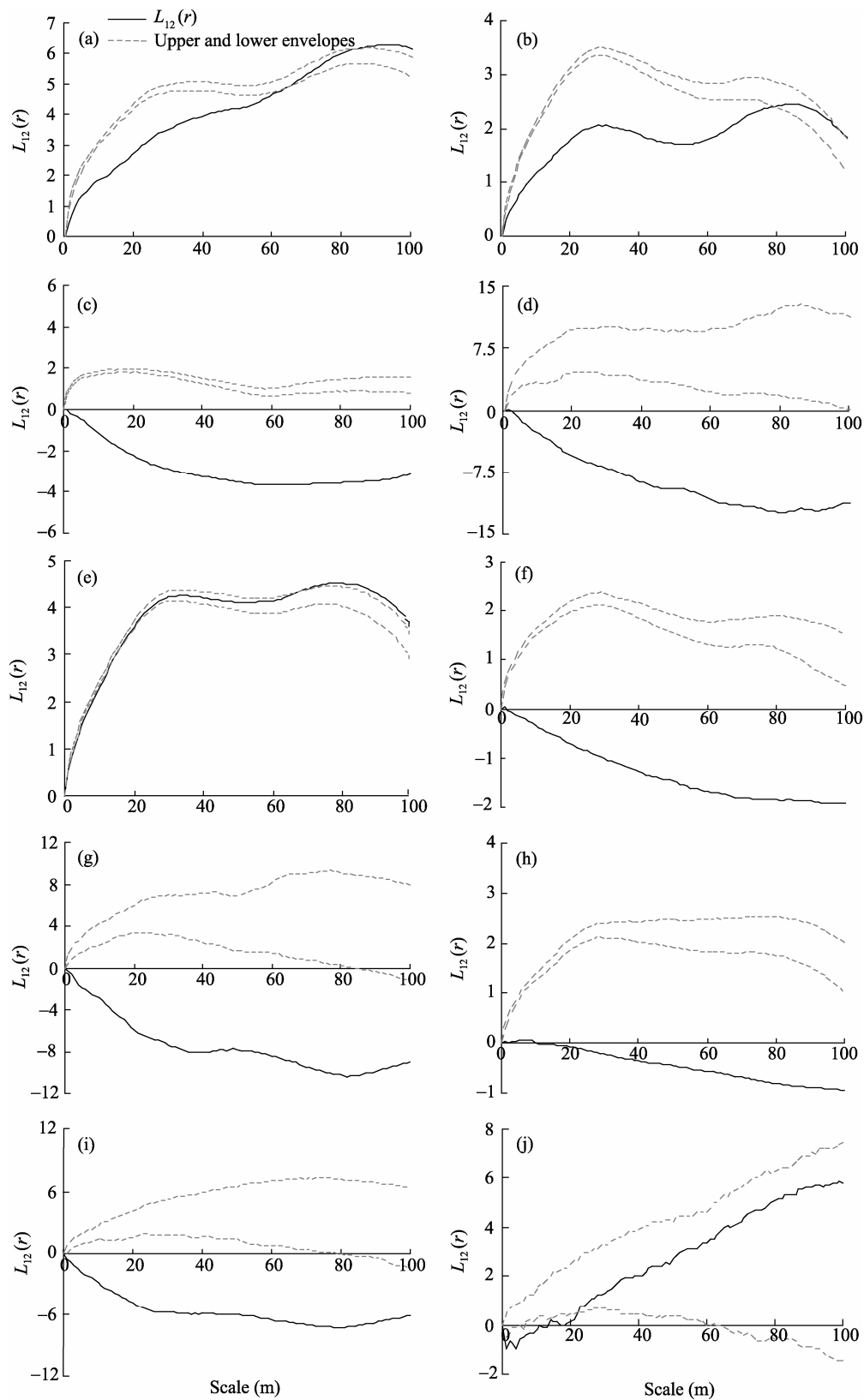


Fig. 5 Spatial correlation of *P. shrenkiana* of different ages in an 8-hm² plot in the study area. (a) Sapling-small trees; (b) Sapling-medium trees; (c) Sapling-big trees; (d) Sapling-old trees; (e) Small trees-medium trees; (f) Small trees-big trees; (g) Small trees-old trees; (h) Medium trees-big trees; (i) Medium trees-old trees; (j) Big trees-old trees.

Table 1 Effects of topography factors on the distribution of *P. schrenkiana* of different ages in an 8-hm² plot

| Topographic attribute | Number of sample plots | Density (individuals/hm ²) | Ratio of density of different age classes and gross stand density of corresponding age classes on gradient of all topographic attributes | | | | | |
|-----------------------|------------------------|---|--|------------|-------------|----------|----------|------|
| | | | Sapling | Small tree | Medium tree | Big tree | Old tree | |
| Slope aspect | N | 59 | 2,373 | 0.90 | 1.65 | 1.56 | 1.46 | 1.56 |
| | NW | 46 | 2,027 | 0.57 | 1.44 | 1.40 | 1.42 | 0.76 |
| | W | 23 | 1,745 | 0.90 | 1.06 | 1.15 | 1.37 | 1.91 |
| | SE | 11 | 1,663 | 0.58 | 1.10 | 1.30 | 0.84 | 0.79 |
| | NE | 39 | 1,373 | 1.30 | 0.66 | 0.63 | 0.96 | 1.18 |
| | E | 15 | 1,233 | 1.86 | 0.57 | 0.35 | 0.42 | 0.00 |
| | SW | 7 | 1,072 | 0.90 | 0.51 | 0.60 | 0.53 | 0.80 |
| | S | 0 | | | | | | |
| Slope degree (°) | 10–20 | 35 | 1,082 | 0.82 | 0.54 | 0.50 | 1.09 | 1.65 |
| | 20–30 | 74 | 1,563 | 1.15 | 0.89 | 0.84 | 1.06 | 1.30 |
| | 30–40 | 77 | 2,054 | 1.14 | 1.34 | 1.28 | 0.97 | 0.55 |
| | 40–50 | 14 | 1,705 | 1.38 | 1.01 | 1.00 | 0.70 | 0.27 |
| Convexity index | Ridge | 106 | 1,363 | 0.65 | 0.78 | 0.83 | 1.12 | 1.40 |
| | Valley | 94 | 1,925 | 1.35 | 1.22 | 1.17 | 0.88 | 0.58 |

Table 2 Correlation between topography factors and the number of *P. schrenkiana* individuals in an 8-hm² sample plot

| | Altitude | Slope | Convexity |
|-------------|----------|---------|-----------|
| Total | 0.386** | 0.352** | −0.222** |
| Sapling | 0.137 | 0.317** | −0.252** |
| Small tree | 0.013 | 0.293** | −0.286** |
| Medium tree | 0.178* | 0.394** | −0.257** |
| Big tree | 0.301** | −0.101 | −0.149* |
| Old tree | 0.339** | −0.172* | −0.102 |

Note: ** and * indicate significant difference at $P < 0.01$ and $P < 0.05$ levels, respectively.

correlated with slope gradients. With the exception of old trees, saplings, small trees, medium trees and big trees had negative correlations with convexity index.

3 Discussion and conclusions

3.1 Spatial distribution pattern of the *P. schrenkiana* population

The forests in the Middle Tianshan Mountains of Xinjiang are mainly composed of secondary *P. schrenkiana* trees which naturally recover again after human disturbance. The individuals of different ages distribute unevenly. The plant density of all size classes decreased with the increase in DBH. This result showed that the *P. schrenkiana* population steadily declines and is essentially in accordance with the findings of

Pan and Zhang (1991), Li *et al.* (2001) and Li *et al.* (2005). The *P. schrenkiana* population structure is similar to that of a natural population of *Pinus tabulaeformis* f. *shekannensis* distributed on the Loess Plateau and *Abies georgei* on the Tibet Plateau (Wang and Shangguan, 2006; Zhang *et al.*, 2008). The *P. schrenkiana* forest district had been greatly disturbed and influenced by grazing and logging before the natural forest protection project was implemented, which destroyed a large number of old-aged individuals and resulted in the steady decline of the population (Li *et al.*, 2005; Zhang *et al.*, 2011b). With the implementation of the natural forest protection project, many seedlings were grown in the forest district, thus the number of saplings has quickly increased.

The spatial distribution pattern of plant populations has a close relationship with spatial scale (Lai *et al.*, 2010; Li *et al.*, 2010). Manabe *et al.* (2000) and Zhang *et al.* (2011) considered that at a smaller scale, a species' spatial pattern and spatial correlation may be influenced by intraspecific competition and the method of seed dispersal, whereas at a larger scale, they may be determined by heterogeneity or patchiness of the species distribution and different environmental conditions (such as terrain and soil moisture). The spatial distribution of *Tilia mandshurica*, *Ulmus laciniata*, *Acer tegmentosum* and *Acer mandshuricum*

were studied by establishing a 25-hm² fixed sample plot in the temperate forests in Northeast China using point pattern method (Hao *et al.*, 2007). Their results indicated that there was a significant correlation between aggregated distribution and topography factors. To analyze the spatial distribution pattern of *Populus tremuloides*, *Populus balsamifera* and *Populus glauca*, Gray and He (2009) established a 1-hm² plot in the Arabian Peace River, and the result indicated that there was an evident shift in spatial distribution from aggregation to randomness (and even to regularity) for the three dominant species. The results of our study showed that saplings, small trees, medium trees and big trees of *P. schrenkiana* all had an aggregated distribution at all spatial scales, whereas old individual trees presented a random distribution only at a smaller scale and it gradually changed to an aggregated distribution with the enlargement in scale. These findings agree with the conclusions of Pan and Zhang (1991) and Liao *et al.* (2008) on *Abies faxoniana*, but differ from the results of Li *et al.* (2001), who found that mature *P. schrenkiana* forests in the Urumqi Nanshan forest district was in a random population distribution. This discrepancy is perhaps related to the small sampling scale (2.5 hm²) used. Seed dispersal, regeneration mode and topographic attributes may be the main factors that cause the aggregated distribution of *P. schrenkiana*. Regeneration of *P. schrenkiana* was weak and just occurred in the forest gap and vacancy, which determines the distribution pattern of *P. schrenkiana*. The cone of *P. schrenkiana* is large; therefore most cones aggregate around the mother tree (Forestry of Administration of China, 1989), and thus saplings and small trees also show an aggregated distribution. In addition, the seedlings of *P. schrenkiana* usually germinate on decaying fallen wood (Forestry of Administration of China, 1989). Outside the research area, we have observed saplings and small trees distributed in rows in a valley with low terrain. The dense growth of saplings is an important means of resisting unfavorable environmental factors and competition with other plant species. The strength of aggregation of *P. schrenkiana* individuals decreased with the increase in age, which may be caused by the increasing demand of an individual for light, water, nutrients, space and other resources as the tree grows. This would result in the strengthening of mutual interactions among *P. sch-*

renkiana individuals and thus cause self-thinning or thinning by other species. For old individuals, the reduction in the degree of aggregation enables them to gain more environmental resources. Hou and Han (1997) considered that the population distribution pattern of *Pinus koraiensis* decreased aggregation strength with the increase of individual age, which was one self-regulatory mechanism in the population.

The negative correlation of different age classes reflects a repelling ecological relationship, which is mainly because big and old individuals of *P. schrenkiana* must compete with saplings, small trees and medium trees for environmental resources. Medium and sapling individuals in forests require adequate sunlight for growth, and because of the limited transmittance of sunlight, most saplings and small trees growing in shade under a crown canopy grow and develop slowly. In addition, the crown canopy intercepts a large quantity of rainfall, therefore the development of saplings and small trees may be affected by a lack of water.

3.2 Relationship between *P. schrenkiana* population distribution and topographic attributes

Terrain is one of the main environmental factors that influence plant distribution and species composition, and forest structure varies with changes in topographic characteristics (Webb *et al.*, 1999; Takyu *et al.*, 2002). Bale *et al.* (1998) established a sample plot in a forest in Australia, investigated the distribution patterns of vegetation on four different slope aspects and found that the slope aspect exerts a major influence on the structure and floristics of forests at upslope positions on steep ridges near the escarpment of north-eastern New South Wales. For example, *Doryphora sassafras* and *Caldcluvia paniculosa* were well represented at all sites than at the northwest-facing slope; *Argyrodendron actinophyllum* was generally well developed at the southwest-facing slope; the numbers of *Dendrocnide excelsa* and *Nothofagus moorei* were not significantly different among four slope aspects. The results in our study indicate that semi-shaded slopes are appropriate for the regeneration of *P. schrenkiana* but shady slopes are not suitable. Chen (1991) discovered that seedlings and saplings can grow at 1–10 years, especially at 6–10 years, and their survival and establishment are positively correlated with sunlight

intensity, which is essentially in accordance with the study of Pan (1991). To analyze the influence of topography factors on the distribution of *Dryobalanops aromatic* and *Dryobalanops lanceolata*, Akira *et al.* (2003) established a 52-hm² forest sample plot in Malaysian tropical rain forests and concluded that *D. aromatica* was significantly more abundant at higher elevations and on convex and steep slopes. In contrast, *D. lanceolata* preferred lower elevations and concavo. Within the elevation range of 1,958–2,188 m, the numbers of medium, big and old trees showed a significant positive correlation with elevation, whereas the numbers of saplings and small trees showed a non-significant correlation with elevations. Liu *et al.* (2011) investigated the variation in *P. schrenkiana* stand factors along an elevation gradient and showed that *P. schrenkiana* stand density increased with increasing elevation within the range of 1,800–2,200 m, but decreased with increasing elevation within the range of 2,200–2,600 m altitude. Our results indicate that *P. schrenkiana* is sensitive to the slope gradient and the total number of plants is significantly, positively correlated with gradient, and saplings and small trees in particular are mainly distributed on steep

gradients. This is because dispersal of cones down a slope is promoted by a gradient, thus causing seedlings and saplings to germinate and grow on steep slopes, whereas big and old trees occupy habitats with a gentle gradient. Saplings and small trees were mainly distributed in valleys, whereas ridges were also mainly occupied by medium, big and old trees. This is because the cones of *P. schrenkiana* accumulate more readily in hollows (valleys). In addition, soil nutrients accumulate in valleys owing to surface runoff, and the soil layer in valleys is thicker, which provides favorable conditions for saplings and small trees to establish. Howe (1986; 1990) and Fisher *et al.* (1991) also found that some species had a close relationship with slope gradient, especially the seedlings and saplings in tropical rain forests, such as *Virola surinamensis*. The similar conclusion was also obtained by Kylee *et al.* (2001).

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