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Assessing the influence of the minimum measured diameter on forest spatial patterns and nearest neighborhood relationships

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Abstract: Forest structure analysis is important for understanding the properties and development of a forest community, and its outcomes can be influenced by how trees are measured in sampled plots. Although there is a general consensus on the height at which tree diameter should be measured [1.3 m: diameter at breast height (DBH)], the minimum measured diameter (MMD) often varies in different studies. In this study, we assumed that the outcomes of forest structure analysis can be influenced by MMD and, to this end, we applied $g(r)$ function and stand spatial structural parameters (SSSPs) to investigate how different MMDs affect forest spatial structure analysis in two pine-oak mixed forests (30 and 57 years old) in southwest China and one old-growth oak forest (>120 years old) from northwest China. Our results showed that 1) MMD was closely related to the distribution patterns of forest trees. Tree distribution patterns at each observational scale (r = 0–20 m) tended to become random as the MMD increased. The older the community, the earlier this random distribution pattern appeared. 2) As the MMD increased, neighboring trees became more regularly distributed around a reference tree. In most cases, however, nearest neighbors of a reference tree were randomly distributed. 3) Tree species mingling decreased with increasing diameter, but it decreased slowly in older forests. 4) No correlations can be found between individual tree size differentiation and MMD. We recommend that comparisons of spatial structures between communities would be more effective if using a unified MMD criterion.

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Introduction

Structure, function, and species composition are the three main characteristics of forest communities. Among these, much attention has been given to the forest structure, which has special significance for understanding the growth and development of forests and for describing their physical state. Tree size is a basic attribute of forest structure and reflects the diversity of community structure (Li et al. 2012). Tree size directly reflects the growth status, degree of maturity, and amount of resources available to an individual tree in a given spatial location within the community, and indirectly reflects its competitiveness and viability. In forest communities, the arrangement of tree size not only directly reflects generational alternations (Podlaski 2016, 2017) and system stability [e.g., a diameter distribution with a reverse J-shape in natural forests is often thought to be stable (Li et al. 2014a)], but also indirectly reflects the history, intensity of external disturbance to which the forest have been exposed (Franklin et al. 2007; Pukkala et al. 2009; Li et al. 2014a), and the habitat quantity and quality (Hui and Pommerening 2014). In addition, tree size is often used as an index of forest economic income, and to evaluate forest ecosystem value (Li et al. 2014b).

Among the indicators that can be used to describe tree size (mainly diameter, diameter at ground height, tree height, leaf area, canopy width, biomass, and volume), diameter is the most widely used because it allows for convenient measurement. Although there is a general consensus on the height at which tree diameter should be measured [1.3 m: diameter at breast height (DBH)], the minimum measured diameter (MMD) used is often different. Many studies have used 5 cm as the MMD (e.g., North et al. 2010; Petritan et al. 2012; Li et al. 2014ab; Li et al. 2017), but some have preferred to use smaller values such as 1.0 cm (Hao et al. 2007; Liu et al. 2014; Lv et al. 2014), 2.5 cm (Polyakov et al. 2008; Nguyen et al. 2016), 3 cm (Chiarucci and Bonini 2005), 4.5 cm (Pastorella and Paletto 2013), and 4.7 cm (Kint et al. 2003), and other larger sizes such as 7.0 cm (Wehenkel et al. 2015; Podlaski 2016, 2017), 7.6 cm (Lin and Augspurger 2008), 10 cm (Janík et al. 2014), and 15 cm (Youngblood et al. 2004). The MMD value depends on the objective of the study (e.g., the stand volume calculation often begins at DBH = 5 cm), but many similar studies such as some forest community spatial pattern analyses, have used different MMD values (e.g., Nguyen et al. 2016; Hao et al. 2007; Lin and Augspurger 2008; Janík et al. 2014; Youngblood et al. 2004; Getzin et al. 2006). Inconsistencies among the results of these studies can lead to a lack of understanding of the underlying mechanisms of species coexistence. To our knowledge, the effect of MMD on forest community spatial structure has not yet been explored.

The distribution patterns and nearest neighborhood relationships (NNRs) are important aspects of the forest community spatial structure. The distribution pattern reflects the distribution of individual plants along the horizontal plane, which subsumes interspecific and intraspecific interactions, as well as adaptations of species to the habitat (Getzin et al. 2006; Getzin et al. 2008; Janík et al. 2014). NNRs describe the fine-scale spatial relationships of a small group of organisms (e.g., trees), including the structural characteristics of several adjacent trees surrounding a reference tree, which are used to assess tree species composition, size differences, and distribution patterns (Kint et al. 2003; Li et al. 2012; Petritan et al. 2012). As natural forests usually contain many trees of different species and sizes, the MMD may be related to the richness and abundance of tree species in the community, such that lower MMD values lead to more species and individuals being recorded and vice versa. The MMD is therefore expected to be associated with distribution patterns and NNRs. However, to date, these relationships have not been examined.

In this study, we hypothesized that the MMD is related to the spatial structures of natural forests that have been free of man-made interference for a long period, and analyzed the characteristics of distribution patterns and NNRs at different measured MMD values. We investigated (1) the influence of the MMD on the distribution patterns of natural forests; (2) the influence of the MMD on NNRs with adjacent trees and (3) the influence of forest age on distribution patterns and NNRs.

1 Materials and Methods

1.1 Study sites

Our plots were established in two pine–oak mixed forests in Guangxi Yachang Orchid National

Nature Reserve in Leye County, Guangxi Zhuang Autonomous Region and one old-growth oak (*Quercus aliena* var. *acuteserrata*) forest in the Baihua forest farm, Xiaolongshan, Tianshui, Gansu Province, PR China. These forests are typical of local vegetation. One of the pine–oak mixed forests in the Nature Reserve is located at the Langquan conservation station, where the old-growth forest was completely destroyed by a wildfire in 1978 (106°19'4.2"N, 24°51'15.9"E), after which it was replaced by a secondary forest (30-year-old forest, 30-YF). The now well-developed stand is situated on a large slope, with canopy cover of about 90% and no obvious vertical stratification. The stand contains 18 tree species, mainly comprising *Pinus yunnanensis* var. *tenuifolia*, *Quercus variabilis* Bl., *Q. glauca* (Thunb.), and a few individuals of *Keteleeria davidiana* (Bertr.) Beissn.; the shrub layer is mainly composed of *Lyonia ovalifolia* (Wall.) Drude var. *elliptica, Myrica rubra* (Lour.) S. et Zucc., *Eurya distichophylla* Hemsl., *Dicranopteris linearis* (Burm.f.) Underw., and *Miscanthus floridulus* (Labnll.) Warb. The herb layer is chiefly distributed on the upper slope and mainly consists of *Dicranopteris linearis* (Burm.f.) Underw. and *Miscanthus floridulu* (Labnll.) Warb. The forest floor contains coarse woody debris and a large amount of pine needle litter. Regenerating oaks are extremely abundant in the forest.

The other pine–oak plot is located at Yigou conservation station (106°14'14.6"N, 24°47'25.4"E). This site is also a secondary forest (57-year-old forest, 57-YF) that had formed following a clear-cut during the "big steel" era (1958–1960). A small part of the *P. yunnanensis* population in this forest was scarified for sap around 1990, but there has been no further interference. This forest shows obvious stratification; there are more than 27 tree species in the plot, ant its canopy cover is approximately 80%. The overstory mainly contains *Q. variabilis*, *Q. glauca*, *Albizia kalkora*, *Q. griffithii* Hook. f. et Thoms ex Miq., and *Mallotus japonicus* (Thunb.) Muell. Arg. var. *ochraceo-albidus* (Muell. Arg.) S. M. Hwang, whereas the understory chiefly contains *Vaccinium bracteatum* Thunb., *Craibiodendron stellatum* (Pierre) W. W. Smith, and *Wendlandia uvariifolia* Hance. The grasses *Miscanthus floridulu* and *Thysanolaena maxima* (Roxb.) Kuntze and four orchid species are also present in the herb layer. The forest floor contains many dead plants, and regeneration is very limited. The litter layer is about 1–3 cm thick, and the humus layer is very thin and consists mainly of putrefying needles.

The old-growth oak forest (OGF, >120 years old) is located in the fourteenth sub-compartment of the nineteenth compartment of Xianping Forest Camp (106°27'12.9"N, 34°14'55.1"E). There are no records of human disturbance at this site since the establishment of the Xiaolongshan Forestry Experimental Bureau in 1962, and therefore it can be considered a virgin forest (Liu et al. 2014; Lv et al. 2015). The forest has a 32° slope and an average elevation of 1857 m, with cinnamon soil. The forest canopy cover is about 90% and the plot contains 53 tree species, with *Q. aliena* being dominant, mainly accompanied by the four associated species: *Carpinus turczaninowii* Hance, *Acer mono* Maxim, *Meliosma cuneifolia* Franch. var. *glabriuscula cufod*, and *Tilia oliveri* Szyszyl. The plot contains 46 shrub species including *Smilax stans*, *Helwingia japonica* (Thunb.) Dietr., *Sinarundinaria nitida*, *Hydrangea longipes* Franch., and *Viburnum betulifolium* Batal. A total of 58 herbaceous plants were recorded including *Chrysosplenium biondianum* Engl., *Urticalotabi folia*, *Oxalis corniculata* Linn., and *Carex breviculmis* var. *fibrillosa*. This stand contains many standing dead trees and felled trees.

1.2 Plot establishment

After selecting the forest stands, we established two permanent fixed plots in each of the reserves in 2016–2017. Their areas were 100 m × 100 m and 80 m × 80 m, respectively (Figure 1a, 1b). First, we used the Total Station apparatus (model NTS-372 R_{10}; Southern Mapping Company) to divide the whole sampling area into 20 m × 20 m grids, and fixed a plastic tube (ø = 12 cm) at each intersection. Then, we used a total station to determine the location (*x, y, z*) of each tree with a DBH of ≥ 1 cm at a height of 1.3 m, and then marked trees having a DBH ≥ 5 cm with an aluminum brand and trees having a DBH < 5 cm with a plastic card. We also measured the DBH, height, and canopy width of each tree, and recorded their species name and marked number. A Global Positioning System (GPS) was used to determine the geographic coordinates and altitude

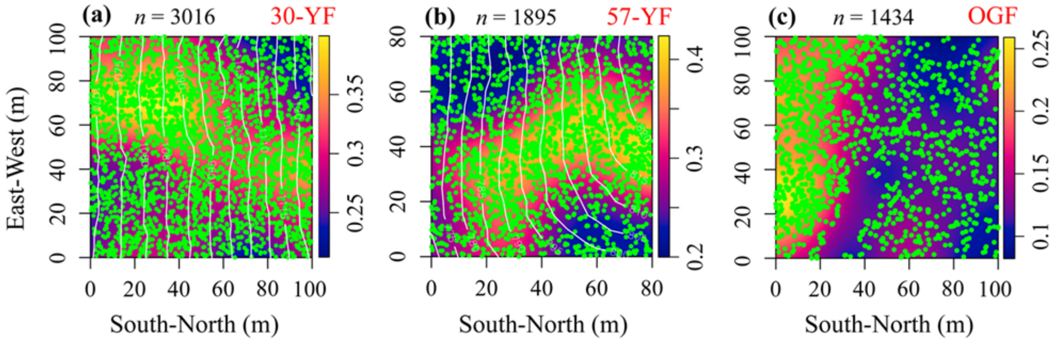

Figure 1 Point patterns of the pine-oak mixed forests (30-year-old forest, 30-YF; 57-year-old forest, 57-YF) and the old-growth forest (OGF). The green dots indicate the relative locations of each individual. The background color of these pictures represents the distribution intensity of all trees. The white lines are contours. *n* is the number of trees measured with a DBH of 1 cm. Distribution intensity is the number of trees per square metre.

Table 1 The main characteristics of the pine-oak mixed forests and *Q. aliena* old-growth forest (SD = standard deviation; OGF means the old-growth oak forest (>120 years old)).

	Parameters	30-YF	57-YF	OGF
Vegetation	Age (years)	30	57	> 120
	Tree species richness	8	9	53
	Shrub species richness	10	18	46
	Density (trees ha^{-1})	3016	2960	1434
	Mean DBH (cm) ±SD	9.6 ± 6.9	8.9 ± 8.6	14.5 ± 11.0
	Basal area (m^2 ha^{-1})	33.84	36.03	37.39
	Canopy cover	80.0%	80.0%	90.0%
	Other herb species richness	4	6	58
	Orchid species richness	1	4	0
Topography	Mean altitude (m)	1068.5	770.3	1857
	Slope position	up	up	up
	Slope aspect	Southeast	Southwest	Northeast
	Mean slope (°)	26	22	32
Litter	Thickness (cm)	5.0-7.0	1.0-3.0	4.0-5.5
	Main composition	Needles	Needles	Broad leaves
Soil	Type	Rendzina	Yellow soil	Cinnamon soil
	Gravel content	40.6%	35.4%	28.7%
	Thickness (cm)	35.7	46.3	52.0
	Nutrition	poor	poor	poor
Climate	Average annual precipitation (mm)	1051.7	1051.7	800.0
	Average annual temperature (°C)	16.3	16.3	10.9

of each sample plot. Using the same methods, a fixed plot was established in the OGF in 2009, but the relative elevation (*z*) of each tree was not recorded. Unfortunately, there was a very large rectangular stone in this plot. We conducted a review of the OGF in 2014 and used the remeasurement data in the analysis undertaken in this study (Figure 1c, Table 1).

1.3 Data analysis

In ecology, Ripley's $K(r)$ function is widely used to analyze the spatial pattern of a forest community; it measures the expected number of points in a circle of radius r centered on an arbitrary point (not counted), divided by the overall intensity of the pattern (Wiegand and Moloney 2004, 2014). The greatest advantage of the $K(r)$ function is that it reflects the characteristics of tree patterns at different scales, enabling investigation of the ecological processes underlying the formation of patterns. However, the cumulative effect at small scales will increase when patterns are analyzed using the $K(r)$ function. An improved model, the $L(r)$ function, keeps the stability of variance, but still can't eliminate the cumulative effect. (Wiegand and Moloney 2014). The pair correction function, $g(r)$, is the probability density function of the $K(r)$ function; it replaces the circle in the analysis of the $K(r)$ function with a ring, which effectively overcomes the deficiency of the $K(r)$ function and can more sensitively distinguish the deviation of the actual distribution of a point on a scale from the expected value, producing a more intuitive graph (Nguyen et al. 2014; Janík et al. 2014; Wiegand and Moloney 2014). Some researchers strongly recommend the univariate model of the $g(r)$ function to analyze the distribution patterns of forest trees (Getzin et al. 2008; Nguyen et al. 2016). Therefore, in this study, the $g(r)$ function was also used to analyze the distribution patterns of pine–oak mixed forests and OGF.

In the analysis of the distribution pattern, it is necessary to judge whether there is habitat heterogeneity in the measured plots, and then to choose an appropriate null model. Habitat heterogeneity driven by environmental factors can be reflected in the distribution of large trees (Getzin et al. 2008; Wiegand and Moloney, 2014). We assumed that the distribution of large trees (DBH ≥ 25 cm) in each sample plot conformed to the homogeneous Poisson process, i.e., the distribution pattern was analyzed by the $g(r)$ and $L(r)$ functions based on the null model of complete spatial randomness (CSR). During the calculation process of the $g(r)$ and $L(r)$ functions, we used the 'spatstat' package (Baddeley and Turner, 2005) with set correction = 'best', *n*rank = 1, and fixed *r* Max = 40 m [half the length of the sample short edge, $r > 20$ m, is used to explain heterogeneity in tropical plant communities (Nguyen et al. 2014)]. We used the Monte Carlo (MC) method to simulate random data at each observation scale 199 times, and obtained the upper and lower 5% envelope traces. We then assessed the distribution pattern by comparing the observed value (black solid line) with the theoretical value [$g_{theo}(r) = 1$, $L_{theo}(r) = 0$]. An observed value that was both greater than its theoretical value and beyond the upper envelope line suggested that large trees (DBH ≥ 25 cm) were in an aggregated state and indicated that there was habitat heterogeneity in the sampled area. However, an observed value that fell within the range of the upper and lower envelope line suggested that large trees (DBH ≥ 25 cm) were randomly distributed and the sample area was not heterogeneous.

NNRs can be described by a set of stand spatial structural parameters (SSSPs): uniform angle index (W), mingling (M), and dominance (U). The SSSPs describe the spatial status of a reference tree *i* and its four nearest neighbors on a small scale. W is defined as the proportion of angles (α) smaller than the standard angle α_o (= 72°) (Eq. 1) and allows for quantification of a situation in which the four nearest neighbors are scattered around *i* and the value range is 0–1; the smaller the value, the more uniform the neighbors surrounding *i*. When the value falls within the interval (0.475–0.517), the neighbors are randomly scattered around *i*. Some researchers have used W to show the distribution patterns of communities (Kint et al. 2003; Szmyt 2014; Wehenkel et al. 2015). M is defined as the proportion of the four nearest neighbors that are different species from *i* (Eq. 2); it also ranges from 0–1, where a higher value suggests a greater difference in species (Hui and Gadow 2003). U is defined as the proportion of the four neighbors that is greater than *i* (Eq. 3), and its value range is the same as that of W and M. A larger U value indicates a more prominent *i* within the structural unit (Li et al. 2012; Liu et al. 2014; Li et al. 2017).

$$W_i = \frac{1}{4}\sum_{j=1}^{4} z_{ij} \tag{1}$$

$$z_{ij} = \begin{cases} 1, \text{ if } \alpha - \text{angle is smaller than } \alpha_0 \\ 0, \text{ otherwise} \end{cases}$$

$$M_i = \frac{1}{4}\sum_{j=1}^{4} v_{ij} \tag{2}$$

$$v_{ij} = \begin{cases} 1, \text{ if neighbor} j \text{ is not the same species as} \\ \qquad\qquad \text{reference tree } i \\ 0, \text{ otherwise} \end{cases}$$

$$U_i = \frac{1}{4}\sum_{j=1}^{4} k_{ij} \tag{3}$$

$$k_{ij} = \begin{cases} 0, \text{ if neighbor } j \text{ is smaller than} \\ \qquad\qquad \text{reference tree } i \\ 1, \text{ otherwise} \end{cases}$$

The spatial relationships of trees within a single structural unit were intuitive and the SSSPs were easy to calculate. A forest community can be composed of *n* (the number of trees) structural units, and the arithmetic mean of the SSSPs can well describe the spatial relationship of the whole forest community (Hui and Gadow 2003; Kint et al. 2003; Li et al. 2012, 2014a). The mean values of SSSPs for all trees in the pine-oak mixed forests and OGF were calculated according to different MMDs, and then the Kolmogorov-Smirnov test was used to check for differences among the three plots. The significance level (alpha) was 0.05. In addition, the changing trend of the mean value of the SSSPs was fitted by models. Data analysis and graphics production were conducted in R (R Core Team 2019), and the distribution pattern was analyzed using the ‘Spatstat’ package (Baddeley and Turner 2005). The R code for calculating SSSPs is described in Li et al. (2017).

2 Results

2.1 Heterogeneity test for secondary and aged forests

The $g(r)$ and $L(r)$ function analyses showed that all observed values (black solid line) for pine–oak mixed forests fell within the 95% MC simulation interval (Figure 2a, b, d, e), indicating that there was no habitat heterogeneity in this community. In the OGF, however, several observed values at scales r = 0–2, 8–12, and 18–20 m were located outside of the upper envelope (Figure 2c), suggesting a clumped pattern, i.e., heterogeneity. The $L(r)$ function analysis results also indicated that the OGF contained habitat heterogeneity (Figure 2f). Therefore, we used the g(r) function to analyze the distribution pattern of the pine–oak mixed forest at r = 0–20 m (1/4 short edge) based on the CSR null model (Figures 3 and 4) and used the heterogeneous Poisson null model for $g(r)$, g_{inhom} (r), to analyze the distribution pattern of the OGF (Figure 5).

2.2 Impact of MMD on the distribution pattern

In the 30-YF, a random pattern only appeared when r = 1–2 m and MMD = 1–5 cm (Figure 3a–f); a clumped pattern was seen at residual scales (r = 3–20 m). With an increase in the MMD (6–8 cm), the distribution pattern at each scale became closer to a random state (Figure 3g–h). However, when the MMD was ≥ 9 cm, there was a regular distribution when r = 1 m, whereas when r = 2–20 m, there was a random distribution (Figure 3i–t). The distribution patterns of the 57-YF showed similar characteristics. Aggregation was observed at all scales (Figure 4a) when the MMD = 1 cm. When the MMD increased to 2–4 cm, the pattern at each scale was significantly closer to a random distribution (Figure 4b–d). There was a regular distribution when r = 3 m and MMD = 8–14 cm (Figure 4h–n), but for the residual MMD (5–7 cm, 15–20 cm), there was a random distribution at all observed scales (r = 0–20 m) (Figure 4e–g, o–t). In the OGF, most MMDs showed a clumped pattern when r = 1 m. When MMD = 1–3 cm, aggregation was also observed when r = 4–5 m, whereas residual scales had a random distribution (Figure 5a–c). Almost all distribution patterns when r = 2–20 m were random when the MMD was ≥ 4 cm (Figure 5d–t).

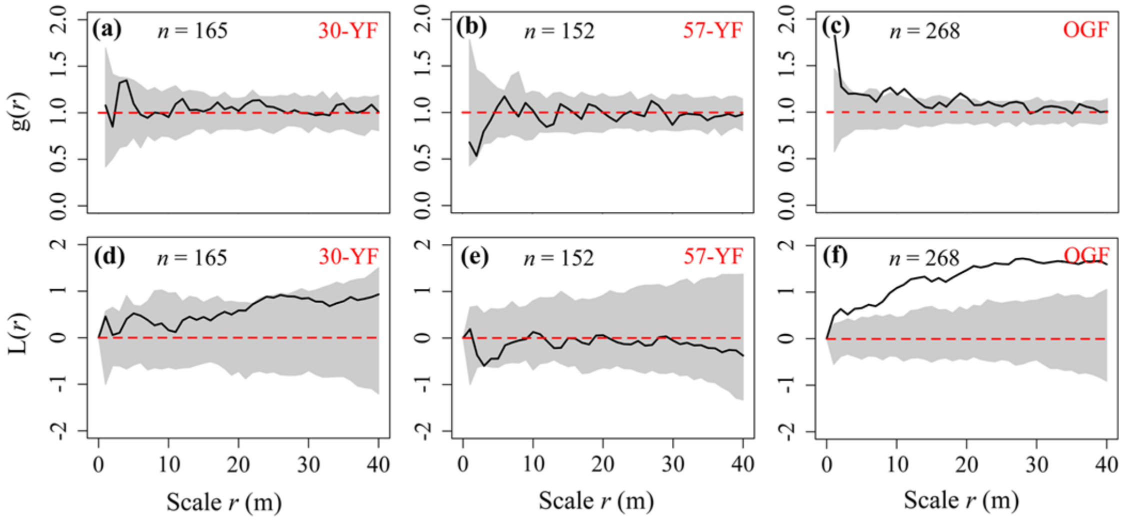

Figure 2 Habitat heterogeneity test of the pine-oak mixed forests (30-year-old forest, 30-YF; 57-year-old forest, 57-YF) and the old-growth oak forest based on the complete spatial randomness (CSR). n is the number of large trees (DBH ≥ 25 cm) referred in test. The red dashed lines represent the theoretical values of the $g(r)$ and $L(r)$ functions.

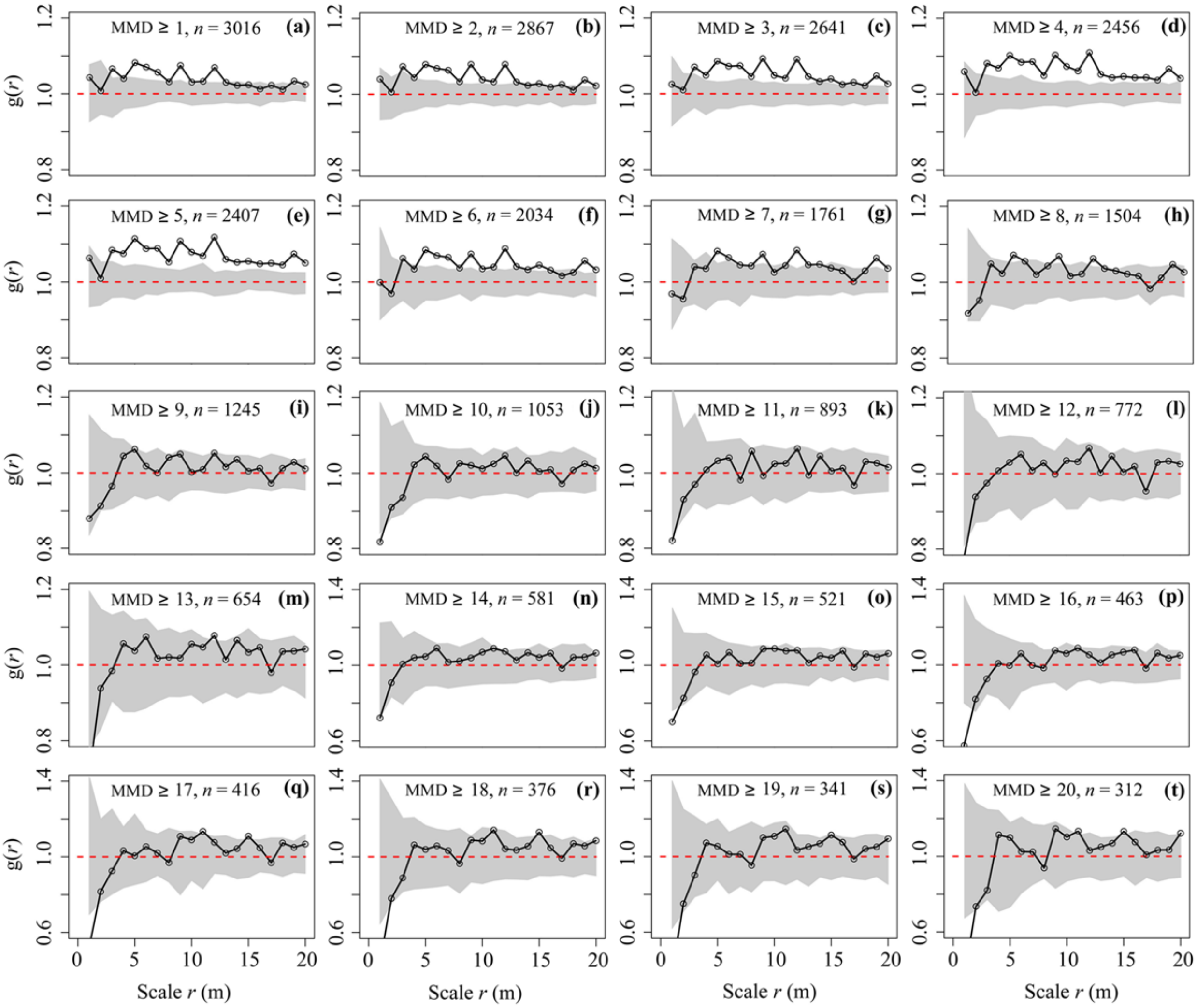

Figure 3 Distribution patterns of the 30-YF (30-year-old forest) with different minimum measured diameter (MMD) values. The red dashed lines represent the theoretical value of the $g(r)$ function.

2.3 Impact of MMD on spatial relationships

The mean W values of the three measured communities displayed a decreasing trend as the MMD increased, which was described well by a linear model; there was a high degree of similarity among each forest (Figure 6a, d, g). For the 30-YF, the mean W value was greater than 0.517 when the MMD was ≤ 5 cm. Its value fell to between 0.475 and 0.517 when the MMD = 6–18 cm. However, when the MMD was increased to 19–20 cm, the W value was < 0.475 (Figure 6a). The W value of the 57-YF deviated slightly from the upper and lower limits of the random distribution when MMD = 1, 3, or 17 cm, whereas the values of the other 17 MMDs fell completely within the range of 0.475–0.517 (Figure 6d). According to the Kolmogorov-Smirnov test ($\alpha = 0.05$), there was no significant difference between the two pine–oak mixed forests ($p_{a\text{-}d} = 0.55$). In the OGF, the W value was significantly greater than 0.517 when MMD = 1–7 cm, and when MMD = 8–18 cm, its value was very close to 0.517. Its value fell to between 0.475–0.517 (Figure 6g) when the MMD was 19–20 cm. This trend was significantly different from those of the other two communities ($p_{a\text{-}g} = 0.0001$, $p_{d\text{-}g} = 2.601 \times 10^{-5}$).

The species mixture of the three plots decreased linearly with increasing MMD, and the value of the pine–oak mixed forests was reduced from 0.69 and 0.58 to 0.36 and 0.28, respectively. There was no difference in the overall distribution ($p_{b\text{-}e} = 0.17$, Figure 6b, e). The degree of mixing of the OGF decreased from 0.73 to 0.52, a small decrease of 0.21, and remained above 0.7 when

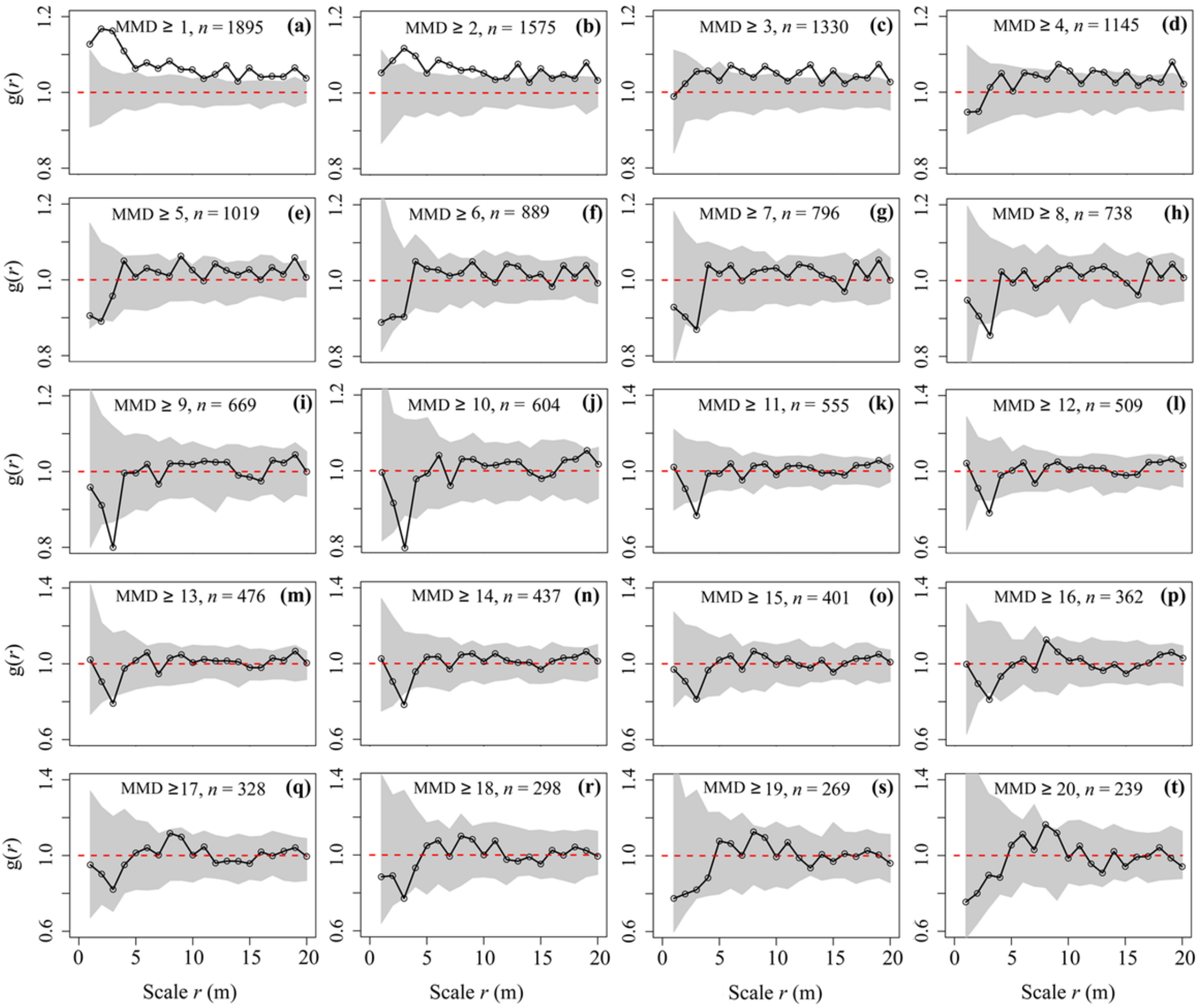

Figure 4 Distribution patterns of the 57-YF (57-year-old forest) with different minimum measured diameter (MMD) values. The red dashed lines represent the theoretical value of the $g(r)$ function.

MMD = 1–10 cm (Figure 6h). When the MMD was ≥ 16 cm, the M value was slightly lower than 0.6, showing a significant difference in distribution compared with the pine–oak mixed forests ($p_{b\text{-}h} = 1.06 \times 10^{-6}$, $p_{e\text{-}h} = 0.0134$). The U values for different MMDs were very similar when plotted (Figure 6c, f, i). The mean U values were 0.493 for both pine–oak mixed forests ($p_{c\text{-}f} = 0.97$), and slightly greater (0.502) in the OGF ($p_{c\text{-}i} = 2.601 \times 10^{-5}$, $p_{f\text{-}i} = 5.522 \times 10^{-6}$).

3 Discussion

Under the condition of habitat heterogeneity exclusion, we explored the impact of the MMD on the distribution patterns and NNRs of two pine–oak mixed forest stands and one old-growth oak forest. The distribution patterns at all scales tended to become or remain random as the MMD increased (Figures 3–5). Previous studies also revealed that the distribution patterns of natural forests tended to be randomly distributed, with an increase in diameter classes, and explained these findings as the result of competition or negative density dependence (e.g., Getzin et al. 2008; Lin and Augspurger 2008; Janík et al. 2014; Nguyen et al. 2014, 2016). However, these studies focused on structural differences among the diameter classes, and did not consider the influence of individual tree size on the community spatial structure in detail. In the pine–oak mixed forests of the current study, when the MMD was ≥ 8 cm, slight repulsion was found at small scales (Figures 3 and 4), which

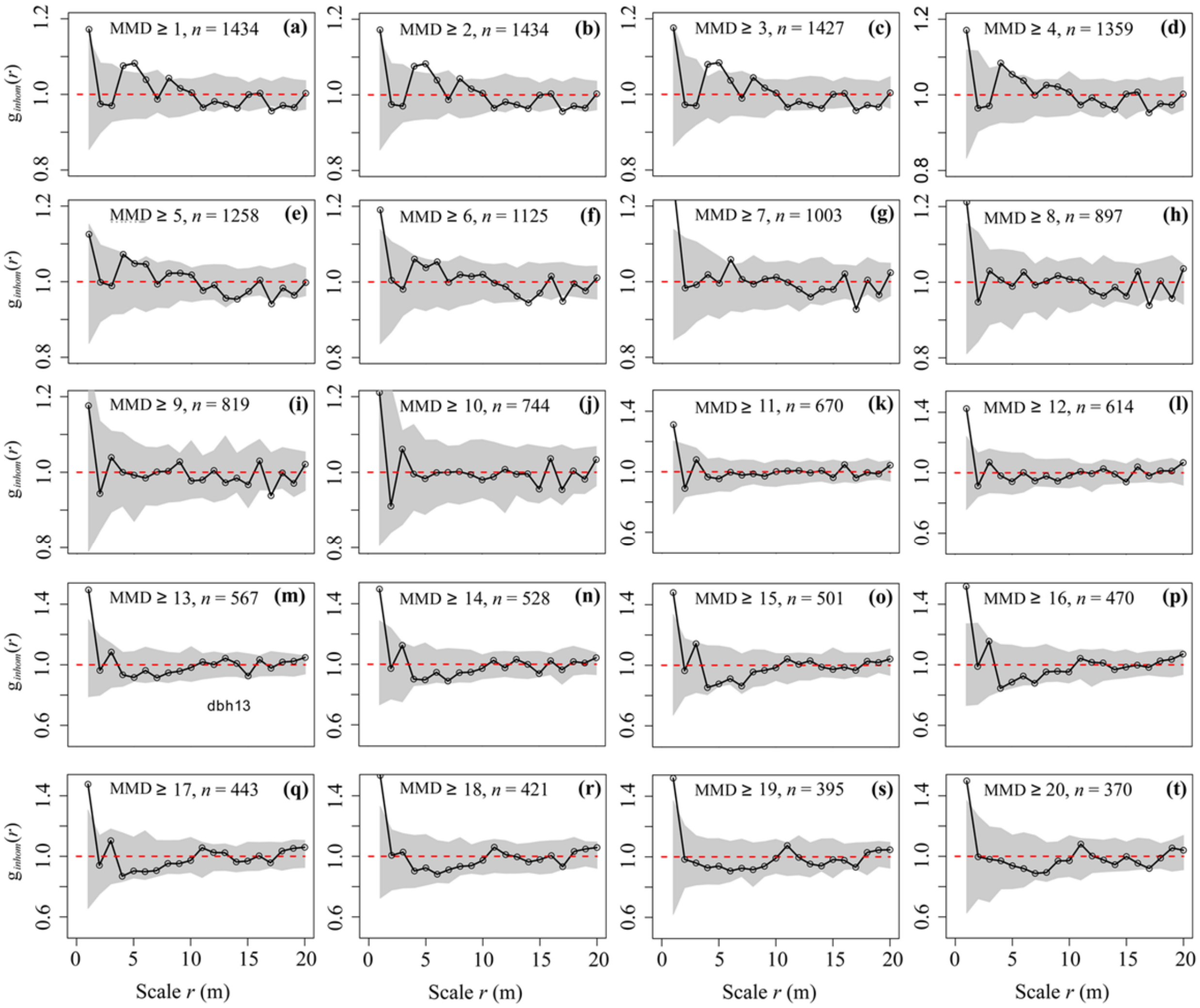

Figure 5 Distribution patterns of the old-growth oak forest with different minimum measured diameter (MMD) values. The red dashed lines represent the theoretical value of the $g_{inhom}(r)$ function.

may be due to autotoxicity causing *P. yunnanensis* individuals to separate from each other at a certain horizontal distance (Fernandez et al. 2008). The scale of the regular distribution of the 30-YF, with a great population density, was smaller than that of the 57-YF, which further indicates the possibility of this phenomenon (Figure 3 *vs.* Figure 4). In turn, the aggregated distribution observed at r = 1 m for each MMD in the OGF may be related to regeneration in gaps. The space left after the death of a single large tree provides a suitable habitat for the growth of many spatially clustered small trees within the gap (Petritan et al. 2012). In addition, the distribution pattern changed from an aggregated to a random distribution with increasing community age, indicating that the relationships among individuals within the community tended to weaken with age (Zhang et al. 1999).

In both the secondary and aged forests, the MMD was closely associated with the nearest neighbors being scattered around the reference tree. The larger the MMD, the more regular the distribution of the neighbors around the reference tree, although the amplitude of variation was not large. In most cases, the reference tree was randomly surrounded by its four nearest neighbors in the pine–oak mixed forests (Figure 6a, d). Random distribution is a common feature among many natural forests (e.g., Zhao et al. 2009; Li et al. 2012; Petritan et al. 2012). Neighbors in the OGF tended to be distributed on one side of the reference tree, and were randomly distributed around the reference tree only when the MMD was

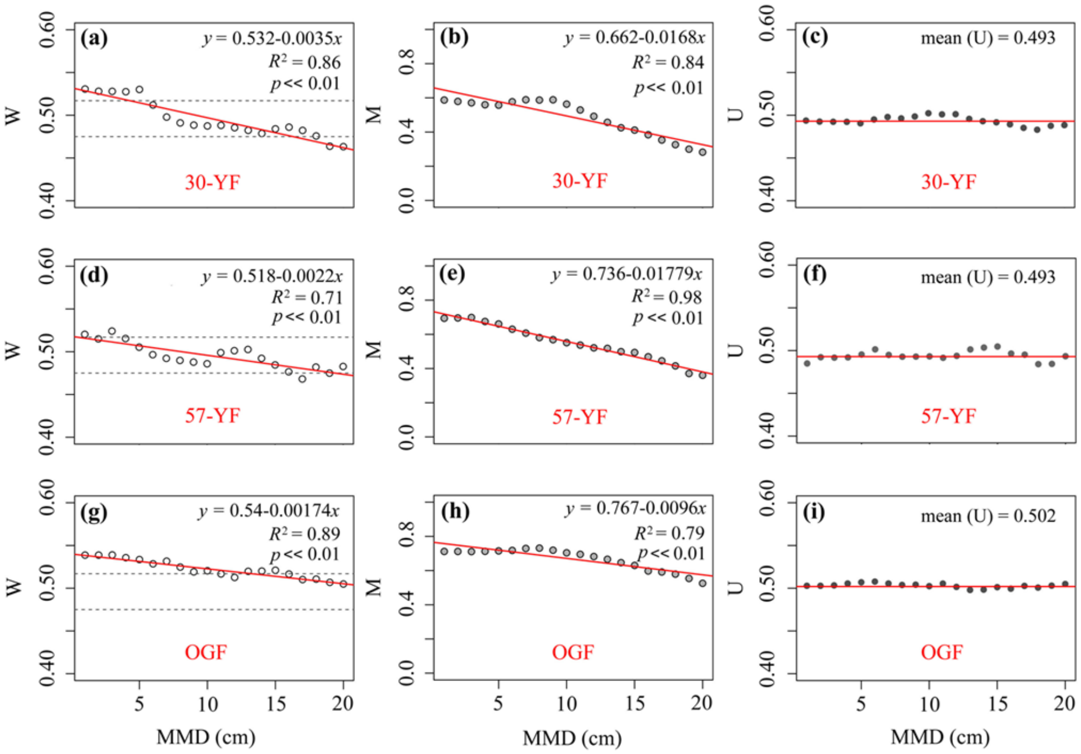

Figure 6 Nearest neighborhood relationships of the pine-oak mixed forests (30-YF, 57-YF) and the old-growth oak forest. R^2 is the fitted goodness of the model. $p << 0.01$ suggests that the fitted model is very good. The dashed lines in the subgraphs a, d and g represent the interval of random pattern [= 0.475-0.517]. The red solid lines in the subgraphs a-b, d-e, g-h are fitted by their linear models and the ones in the subgraphs c, f and i are the mean values of U.

large (Figure 6g). This may be related to the existence of habitat heterogeneity (Figure 2c, f), which often leads to the aggregation of populations and communities (Wiegand and Moloney 2004, 2014; Getzin et al. 2008; Nguyen et al. 2016). In the statistical analysis, habitat heterogeneity could not be excluded when W was used to analyze distribution patterns (cf. Kint et al. 2003), resulting in slight differences between results obtained using W and those obtained using g_{inhom} (r) (Figure 5 *vs.* Figure 6g). That is to say, W showed stronger aggregation than the inhomogeneous model g_{inhom} (r).

There was also a close relationship between the mixture of tree species and the MMD, with the degree of mixing gradually decreasing as the MMD increased (Figure 6b, e, h). This shows that for small trees, there were more species, but fewer large tree species. Both of the pine–oak mixed forests in this study originated from similar forestland. It is believed that only a few species, such as *P. yunnanensis* and *Q. variabilis*, formed pioneer populations in the early stage of succession (Li and Wang 1981), and then gradually formed complex niches to provide suitable habitats for additional species. In the short term, these latecomers remained in the lower layer of the community, whereas the taller trees consisted of only a few species (Li et al. 2017). When the understory heterospecies were excluded, the probability of adjacent trees being of the same species was greatly increased. Increased mixing of tree species can take a long time, sometimes even until the aged forest stage (Kint et al. 2005; Li et al. 2012). In addition to the large number of shrub species, the number of tree species in the OGF was much larger than in the two secondary forests. In a random distribution, an increase in the number of tree species would increase the overall mixing status of the community (Graz 2004; Li et al. 2014a; Li et al. 2017). This may explain why the species mixture in the OGF was greater than that of the secondary forests, and declined with an increase in the MMD.

There was no relationship between the MMD and the size difference among trees, with the size differentiation value remaining around 0.5 regardless of the MMD (Figure 6c, f, i). This means that each tree in the community had a 50% probability of being larger than its four neighboring trees, and a 50% probability of being smaller than its four adjacent trees. The overall size differentiation was therefore very balanced, which is inconsistent with previous hypotheses, thus improving our understanding of the structural diversity of oak and pine-oak mixed forests. Greatly uniform sizes among nearest neighbors have also been reported for other multispecies natural communities (e.g., Petritan et al. 2012; Li et al. 2012; Li et al. 2014b). Even some over-cut forests show this characteristic (e.g., Zhang et al. 2009). Analyses using a second-order statistical function have shown that in natural forests without habitat heterogeneity, tree sizes were randomly distributed at almost all observation scales (Hui and Pommerening 2014; Wang et al. 2017). Long-term monitoring also indicates that tree sizes in natural forests eventually become independent of scale (Suzuki et al. 2008). The size differentiation was similar among the three natural forests in this study, which suggests that tree size differentiation occurs relatively early. Therefore, it may not be necessary to consider the effect of MMD on tree size differentiation when analyzing the spatial structure of a long-undisturbed natural forest.

4 Conclusion

Tree size is an important feature of natural forests. Different-sized individual trees may play different roles within the community. Large trees play a key role in maintaining community structure and functional stability, whereas small-diameter trees are conducive to preserving species diversity. MMD is closely related to accurate measurements of the forest community. If the MMD is too large, then biological information related to seedlings and small trees may be lost, whereas small MMD values indicate higher fieldwork costs. To date, this important issue has been neglected, particularly in studies examining the spatial structure of forest communities. Our results clearly show that the MMD is not related to differences among nearest neighbors, but is closely related to distribution patterns. The MMD also has a significant linear relationship with nearest-neighbor species composition, which can be affected by the stand age. The MMD could therefore be used to predict the spatial structure of natural forests. The adoption of a unified standard MMD for the analysis of spatial structure may be useful in forest community comparisons.

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