Density-dependent and distance-dependent effects in a 60-ha tropical mountain rain forest in the Jianfengling mountains, Hainan Island, China: Spatial pattern analysis

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ABSTRACT

To understand the density-dependent and distance-dependent effects on the spatial patterns of trees in tropical mountain rain forest, we used the recent developed O-ring statistic, which is a point pattern analysis method, to explore spatial distribution patterns and spatial associations of trees of different size-classes in a 60-ha tropical mountain rain forest plot in the Jianfengling Nature Reserve, Hainan Island, China. We describe four main findings. (1) As the size-classes of live trees increased, the live trees became more regular. (2) Densities of saplings, small trees, and dead trees tended to decrease with increasing distances, while densities of medium trees, big trees, and old-growth trees initially increased and then decreased at greater distances, showing a skewed inverted *V*-shaped pattern. (3) Densities of saplings, small trees, and medium trees first increased rapidly from 0 m to 5 m to 7 m radius (distance from old-growth trees) and then decreased continuously away from old-growth trees, showing consistent patterns expect from the distance-dependent effect. (4) Mortality was non-random, and dead trees were significantly aggregated with live trees at scales < 2 m, showing clustering of dead (or surviving) trees and clear density dependence where stems with more neighbors had a higher risk of mortality. We concluded that size and spacing effects play important roles in determining spatial distribution patterns of the trees in the Jianfengling tropical mountain rain forest plot.

1. Introduction

Generally, spatial patterns and interactions are expected to be especially important for plants which cannot move (except via births and deaths) and are, therefore, likely to respond directly to their immediate neighborhood (Miriti, 2007; Das et al., 2008; Raventós et al., 2010). Different ecological processes may leave a particular signature on the spatial arrangement of individuals; therefore, studying spatial patterns may help to reveal the importance of underlying mechanisms (McIntire and Fajardo, 2009). At a community scale, spatial patterns of trees are determined by multiple controlling factors, which vary across spatial and temporal scales, related to disturbance (Nagel et al., 2006; Franklin et al., 2007; Yu et al., 2009; Castilla et al., 2012), competition (Stoll and Bergius, 2005; Getzin et al., 2006; Berger et al., 2008; Gray and He, 2009; Das et al., 2011), density-dependent processes (He and Duncan, 2000; Gray and He, 2009; Yu et al., 2009; Chen et al., 2010;

Comita et al., 2010; Lin et al., 2012), dispersal limitation (Albani et al., 2005; Hu et al., 2012; Shen et al., 2013), etc. Among those factors, density-dependent and distance-dependent effects have been commonly studied in specific species, and, in most cases, the tree species studied were dominant species (He and Duncan, 2000; Getzin et al., 2006; Gray and He, 2009; Yu et al., 2009; Hu et al., 2012). However, in tropical forests, where there are many tree species with few or no obvious dominant species, density-dependent and distance-dependent effects remain unclear. Current research has emphasized general distance-dependent effects and density-dependent effects of large-size trees on seeds and/or seedlings (Harms et al., 2000; Getzin et al., 2008; Fajardo and McIntire, 2011; Lin et al., 2012). Those results are discussed in light of seeds and seedling ecology, especially with regard to seedling and sapling gap-dependence, which likely has affected the recruitment of juvenile trees, and, therefore, the spatial patterns of the resultant older trees. However, there are few studies on distance-dependent effects and
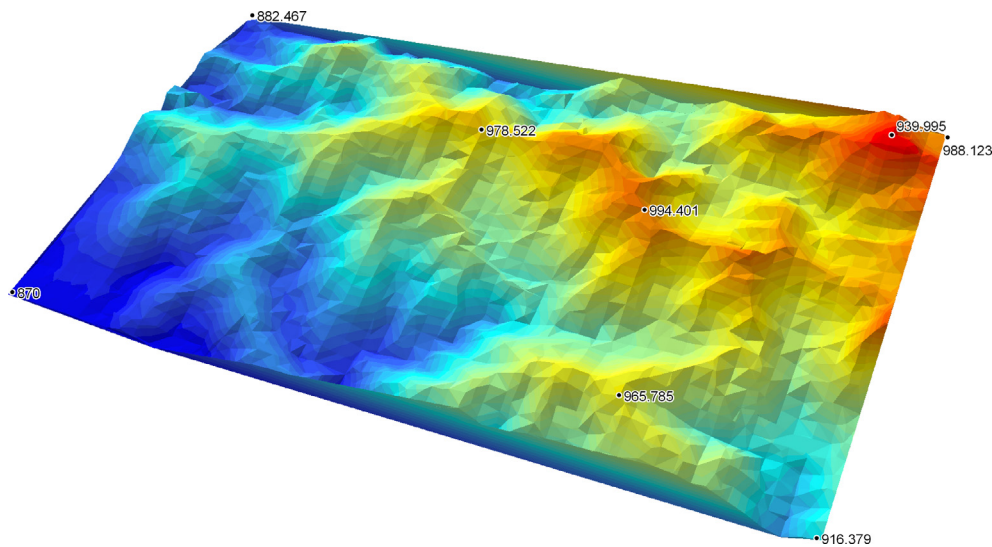

Fig. 1. Topographical image of the 60 ha tropical mountain rain forest plot in the Jianfengling Nature Reserve.

density-dependent effects across multiple life stages (Zhu et al., 2015, 2018).

Tropical forests play an important role in conserving global biodiversity and maintaining the functions of the earth's ecosystems (Deng et al., 2008). The Jianfengling Mountains, located in southwestern Hainan Island, is one of few areas in China where there are well-protected primary tropical forest. The mountain rain forest in the Jianfengling Mountains corresponds to subtropical/warm-temperate zones. Floristically, subtropical/warm-temperate elements dominated, especially Fagaceae and Lauraceae, while tropical elements were subordinate. Plant species richness in the Jianfengling mountain rain forest was lower than in typical Indo-Malayan tropical rain forests but somewhat higher than dry tropical forests with low rainfall. Thus, the Jianfengling mountain rain forest is a transitional forest type from tropical to subtropical/warm-temperate rain forests (Fang et al., 2004).

In this study, we used spatial pattern analysis to reveal spatial distribution patterns and spatial associations of different tree size-classes in a 60-ha plot in the tropical mountain rain forest of Hainan Island, China. Our analyses are guided by the following hypotheses. First, increasing size-classes will be expected to show more regular patterns. With the increasing of size-classes, stems in a natural primary stand should show more regular spatial patterns at small scales, due to thinning caused by competition (Kenkel, 1988; Barot et al., 1999; Getzin et al., 2006; Li et al., 2009; Wang et al., 2010; Guo et al., 2013) (analysis 1). Second, smaller trees are positively associated with large dead trees. In general, mortality is higher for trees at higher densities and for smaller sized trees, regardless of the relative species mix. Large dead trees showed positive associations with juveniles (Franklin et al., 2002; Salas et al., 2006). Saplings were significantly aggregated and positively correlated with dead trees, which suggests that regeneration mostly occurred in canopy gaps (Wolf, 2005). Therefore, we hypothesized that saplings and small trees will show aggregative patterns with large dead trees (analysis 2). Third, for the distance-dependent hypothesis (Hu et al., 2012; Miao et al., 2014), we tested the distance-dependence effect by sizes (~age). Because independence may indeed be a good approximation in the limit of very species-rich communities (Wiegand et al., 2012), we hypothesize that young individuals are expected to show higher densities within close proximity to (i.e., under the canopy of) old-growth trees. However, beyond the canopy of old-growth trees, we would expect to see a typical gradual decline with distance as a result of distance-dependence effect (analysis 3). Fourth, for the random mortality hypothesis (Kenkel, 1988; He and Duncan, 2000; Getzin et al., 2006; Yu et al., 2009), we expect that dead trees are more clumped than expected under random mortality. Additionally, we

expect mortality to be spatially correlated in a density-dependent way where stems located in areas of higher stem density have a higher mortality (analysis 4). Our findings may contribute to the conservation and management of the ecosystem and biodiversity of the tropical mountain rain forests over their historical range in China.

2. Materials and methods

2.1. Data collection

We conducted this study in the 60-ha (1000 m × 600 m) Jianfengling montane rain forest plot located in the Jianfengling Nature Reserve, Ledong County, Hainan province, South China, with latitude N 18.73079° and longitude E 108.90491°. This tropical mountain rain forest is located at the northern edge of the Indo-Malayan rain forest, and has relatively distinct species composition and community structure from typical Asian tropical forests. This forest plot was established in 2011, and the first census was completed in 2012. At the time, this plot was established, it was the largest plot and had the highest number of tree stems by one census (in 2012) of all large-scale permanent plots recorded by the Center for Tropical Forest Science (CTFS) of the Smithsonian Tropical Research Institute (http://www.ctfs.si.edu) (Xu et al., 2015a).

The elevation of the Jianfengling plot ranges from 866.3 m to 1016.7 m above sea level and includes valleys and a low mountain peak. Slopes vary from 1.74° to 49.25° at the 20 m × 20 m spatial scale (Fig. 1). The climate is strongly seasonal with distinct alternations between the dry season (November 1–April 30) and the wet season (May 1–October 31), as this area is situated at the north edge of the tropics and has a typical monsoon climate. The National Forest Ecosystem Research Station's meteorological station in the Jianfengling Mountains was just 4 km from the Jianfengling study plot and at a similar elevation (893 m). Based on the records at the meteorological station from 1980 to 2005, the annual precipitation (rain fall) in this montane rain forest varied from 1305 mm to 3686 mm with an annual average of 2449.0 mm. The precipitation fell mainly in the wet season, which accounts for an average of 86.7% of the entire annual precipitation (Zhou et al., 2013). The annual average temperature was 19.8 °C from 1980 to 2005, with the coldest and warmest monthly average temperatures being 10.8 °C and 27.5 °C, respectively. The Jianfengling Mountains is one of the areas with highest biodiversity in China. The total number of plant species in the Jianfengling area is 2849, consisting of 1250 genera from 244 families, including 562 alien species (Li et al., 2012).

All free-standing tree stems ≥ 1 cm diameter at breast height (DBH)

(henceforth referred to as trees) in the plot have been measured, mapped and identified to species from October 2010 to January 2012, following a standard field protocol (Martíneza et al., 2010). All trees were classified according to the following age/size classes: saplings (≥ 1 cm– < 2.5 cm DBH, 203,667 stems); small trees (≥ 2.5 cm– < 7.5 cm DBH; 118,365 stems); medium trees (≥ 7.5 cm– < 15 cm DBH; 34,922 stems); big trees (≥ 15 cm– < 30 cm DBH; 23,350 stems); old-growth trees (≥ 30 cm DBH; 11,566 stems); dead trees (≥ 1 cm DBH standing dead trees; 10,254 stems); large dead trees (≥ 15 cm DBH, standing dead trees; 2136 stems).

2.2. Methods

2.2.1. Spatial pattern analysis

A powerful tool to characterize the spatial patterns and interactions of plant communities is point patterns analysis, which allows comparative estimates of the spatial distributions of individuals mapped in a given study area (Diggle, 2003; Wiegand and Moloney, 2004, 2014; Illian et al., 2008; Law et al., 2009). We used the O-ring statistic (Wiegand and Moloney, 2004) and the pair-correlation function (Stoyan and Stoyan, 1994) as summary statistics to describe the spatial correlation structure of the bivariate point patterns observed at our study site. Since there were apparent topological heterogeneities in our study transect (Fig. 1), we used methods for inhomogeneous point patterns.

The O-ring statistic gives an intuitive interpretation of a neighborhood density and is especially sensitive to small-scale effects (e.g., within 1 m increments in the radiuses of subsequent circular plots) (Wiegand and Moloney, 2004; Illian et al., 2008). The bivariate O-ring statistic, $O_{12}(r)$, is the expected density of points at a distance r from type 1 individuals in a ring of radius r and width dw centered on arbitrary type 2 individuals (Wiegand and Moloney, 2004, 2014). Type 1 represents individuals of one tree size-class and type 2 represents individuals of another tree size-class. The bivariate pair-correlation function $g_{12}(r)$ is the intensity normalized version of $O_{12}(r)$ (i.e., $O_{12}(r) = g_{12}(r)\lambda$), where λ is the intensity of type 2 individuals in the study transect (i.e., the number of points of pattern 2 divided by the area of the study plot) (Stoyan and Stoyan, 1994; Wiegand and Moloney, 2004). We used the bivariate O-ring statistic for analysis of the relationship of different size-classes of trees in the plot where the direct interpretation of density is of interest, and the pair correlation function for analysis of recruitment mortality.

2.2.2. Analyses

Analysis 1: Univariate spatial patterns to test hypothesis 1

We aimed to assess whether the basic patterns of different size-classes of trees (saplings, small trees, medium trees, big trees, old-growth trees, and dead trees) would become more regularly distributed. In order to make such an assessment, we used the O-ring statistic as the test statistic and implemented a null model based on a heterogeneous Poisson process. A heterogeneous Poisson process was chosen because our plots were partly influenced by the first-order heterogeneity (Fig. 1), hence the intensity, λ varies with the location (x, y). We used a circular moving window with a fixed radius (R) to estimate λ (x, y); hence, patterns may be interpreted up to a radius of $R = 30$ m only (Wiegand and Moloney, 2004). We used the heterogeneous Poisson null model to test univariate patterns.

Analysis 2: Associations of different size-classes of trees to test hypothesis 2 and 3

The intertype function $O_{12}(r)$ and an independence null model (Wiegand and Moloney, 2004) were used to analyze the spatial association between different size-classes of trees (saplings, small trees, medium trees, big trees, old-growth trees, and large dead trees).

Analysis 3: Test of the random mortality hypothesis to test hypothesis 4

To explore possible non-random spatial structures in tree mortality, we used random labeling as a null model (Kenkel, 1988; Goreaud and

Pélissier, 2003; Illian et al., 2008). The framework of 'marked point patterns' is required to identify the spatial structures in the process that assigned a label 'mortality' to the trees (Goreaud and Pélissier, 2003). This null model assumes that mortality acted as a random process over a given tree pattern, i.e., the n_2 dead trees of a stand are assumed to be a random subset of the joined pattern of the n_2 dead and n_1 live trees (1 referring to live and 2 to dead trees) (Kenkel, 1988; Getzin et al., 2006; Jacquemyn et al., 2010; Raventós et al., 2010). The test of the random mortality hypothesis was conducted by using a Monte Carlo implementation of random labelling from the observed data, then randomly re-sampling sets of n_2 trees from the joined pattern of dead and live trees to generate simulation envelopes of the test statistic.

Tests of aggregation among live trees and of aggregation among dead trees. We used univariate random labelling (Wiegand and Moloney, 2004) to explore the patterns of tree aggregation. If the $g_{11}(r)$ was above the simulation envelopes, live trees showed additional clustering, whereas, live trees are more regularly distributed, if $g_{11}(r)$ was below the simulation envelope. Under density-dependent competition, we expect that clumps of interacting trees should die together, thus dead trees should be spatially aggregated. If $g_{22}(r)$ shows a positive departure from the random labelling null model, dead trees are significantly clustered at scale r, conditioned on the joint pattern of dead and live trees.

Test of attraction vs. segregation of dead and live trees. We used the test statistic $g_{12}(r)$ (Goreaud and Pélissier, 2003) to explore spatial patterns of tree survival and mortality. The test statistic $g_{12}(r)$ is below the simulation envelopes if there are less dead neighbors at distance r from an arbitrary live tree than expected under random labeling (Goreaud and Pélissier, 2003). This indicates that live and dead trees tend to be negatively correlated at distance r (i.e., segregated). Conversely, live and dead trees are positively correlated if the test statistic $g_{12}(r)$ is above the simulation envelopes.

Test for possible departures from the random mortality. We adopted the test statistic, $g_{1,\,1+2} - g_{2,\,1+2}$, specifically to provide a direct test of density-dependent effects in mortality (see also Yu et al. 2009). The difference, $g_{1,\,1+2} - g_{2,\,1+2}$, compares the density of dead and live trees (i.e., $1 + 2$) around dead trees (i.e., pattern 1) with the density of dead and live trees (i.e., $1 + 2$) around live trees (i.e., pattern 2). The expected value of this test statistic is zero under random labelling, but, under density-dependent mortality, we expect that dead trees would occur more frequently in areas with high live tree densities, i.e., $g_{1,\,1+2} - g_{2,\,1+2} > 0$.

2.2.3. Computation and significance of patterns against null models

All analyses were done using the software *Programita* (Wiegand and Moloney, 2004, 2014; Wiegand et al., 2006; Wiegand et al., 2007). Since the use of radius of the rings greater than half the shortest plot side introduces bias due to edge effects, the maximal radius was set less than half the shortest plot side at the starting ring width of 1 m. We use the model of the Programita that works without grid, distance bins are 1 m. Statistical significance of the functions above was determined with Monte Carlo simulations (Diggle, 1983). Details on the estimators of the summary statistics and edge correction used in *Programita* can be found in Wiegand and Moloney (2014).

To assess departures from the null model, we compared the pair correlation functions of the observed spatial patterns with approximately 95% simulation envelopes being the fifth lowest and highest values of the pair correlation functions of data created by 199 simulations of the heterogeneous Poisson null model (Wiegand and Moloney, 2014). Note that the simulation envelopes cannot be interpreted as confidence intervals for formal hypothesis testing because type I error inflation may occur due to simultaneous inference (i.e., tests at many spatial scales (Diggle, 2003)); however, this is of minor concern for our exploratory data analysis.
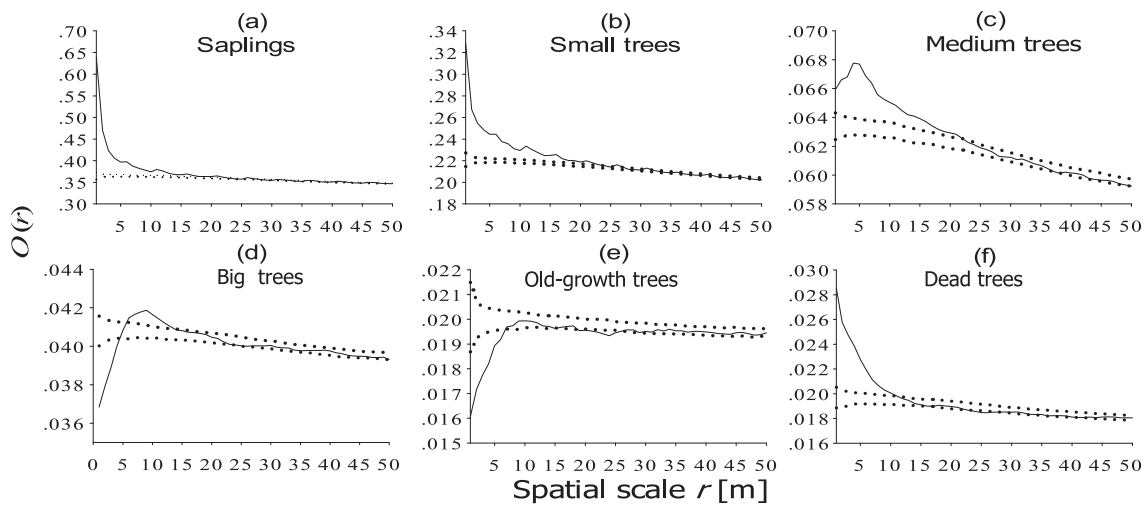
Fig. 2. Univariate point pattern analyses.

3. Results

3.1. Stand composition

The total number of live trees in the census of the 60-ha plot was 402,069, consisting of 290 species of 155 genera from 62 families and also included 61 unidentified trees. There were 10,254 standing dead trees. Mean stand density was 6701 trees/ha with a mean basal area of 30.6 m^2/ha. Abundance and importance values of species can be seen in Xu et al. (2015a). Species abundance and spatial distributions can be seen in Xu et al. (2015b).

3.2. Univariate spatial patterns

Saplings, small trees, medium trees, and dead trees showed significantly aggregated patterns at scales ≤ 23 m, ≤ 22 m, ≤ 21 m, and ≤ 12 m, respectively (Fig. 2A, B, C and F). The live trees became more regular, that is, the maximum $O(r)$ values (density) of saplings, small trees, medium trees, big trees, and old-growth trees decreased at increasingly larger size-classes (Fig. 2A–E). In contrast, big trees and old-growth trees showed a significantly regular pattern at scales ≤ 4 m and at scales ≤ 6 m (Fig. 2D and E). Those analyses supported our first hypothesis.

Densities of saplings, small trees, and dead trees tended to decrease with increasing distances (Fig. 2A, B, and F). Densities of medium trees, big trees, and old-growth trees initially increased and then decreased at greater distances, showing a skewed inverted V-shaped pattern, indicating that the densities of medium trees, big trees, and old-growth trees reached their minimum at the smallest distance and reached their maximum at somewhat greater distances (Fig. 2C–E).

In each graph, the O-ring function of the data is shown as a solid line and the simulation envelopes, being the fifth smallest and fifth largest values of the 199 simulations of the null model, are shown as dotted lines.

3.3. Associations of different size-classes of trees

The densities of saplings, small trees, and medium trees were at minimums next to the old growth trees and reached maximums at distances of about 10 m (Fig. 3A, B, and C). Densities of saplings tended to decrease with increasing distances from small, medium, and big live trees (Fig. 3D, E, F, and G). Large dead trees tended to decrease with increasing distances from saplings, small trees, and medium trees (Fig. 3H–J). With increasing distances from old-growth trees, the densities of saplings, small trees, and medium trees initially increased

(from 0 to 5 or 10 m) and then decreased at greater distances (beyond 5 or 10 m), showing an inverted, skewed, V-shaped pattern confirming our third hypothesis.

Large dead trees showed (1) significantly positive associations with saplings, small trees, and medium trees at scales < 7 m, (2) spatial independence with saplings, small trees, and medium trees at scales of 7–11 m, 7–9 m, and 7–11 m, respectively, and (3) significantly negative associations with saplings, small trees, and medium trees at scales > 11 m, > 9 m, and > 11 m, respectively (Fig. 3H–J) confirming our second hypothesis. With increasing distances from big trees and old-growth trees, large dead trees initially increased and then decreased beyond a distance of about 10 m, showing an inverted, skewed, V-shaped pattern. The densities of large dead trees were at minimums next to big trees and old-growth trees and reached maximums at distances of about 10 m (Fig. 3K, and L).

3.4. Test the random mortality hypothesis

There was a significant effect of neighborhood density on mortality, i.e., dead trees were significantly aggregated with live trees at scales ≤ 2 m (Fig. 4A) as expected under self-thinning (e.g., Kenkel, 1988). This result suggested aggregation of dead trees and a clear density-dependent mortality of dead trees that were located in areas with higher densities of live trees. This result was strengthened by the analysis with the test statistic difference $(g_{2,1+2} - g_{1,1+2})$, which revealed density-dependent effects at scales ≤ 2 m where dead trees had more dead neighbors than live ones (Fig. 4D). The dead trees were significantly regularly distributed at scales ≤ 2 m (Fig. 4B). Live trees were significantly aggregated at scales ≤ 15 m (Fig. 4C). Analysis of the spatial pattern of mortality using random labeling clearly rejected the random mortality hypothesis (Kenkel, 1988) (hypothesis 4).

4. Discussion

4.1. Size effects on spatial patterns

Different size-classes of trees located in different layers of the forest showed different spatial distribution patterns (Condit et al., 2000; Dovciak et al., 2001). Spatial patterns differed in different size-classes of trees, suggesting that the pattern of each size-class is due to differing responses to varying sets of environmental factors (Dovciak et al., 2001; Zhu et al., 2015).

At small scales, live trees became less aggregated at increasingly larger size-classes (Fig. 2A–E), indicating that the spacing effect among different trees increases with tree size, with the density of trees
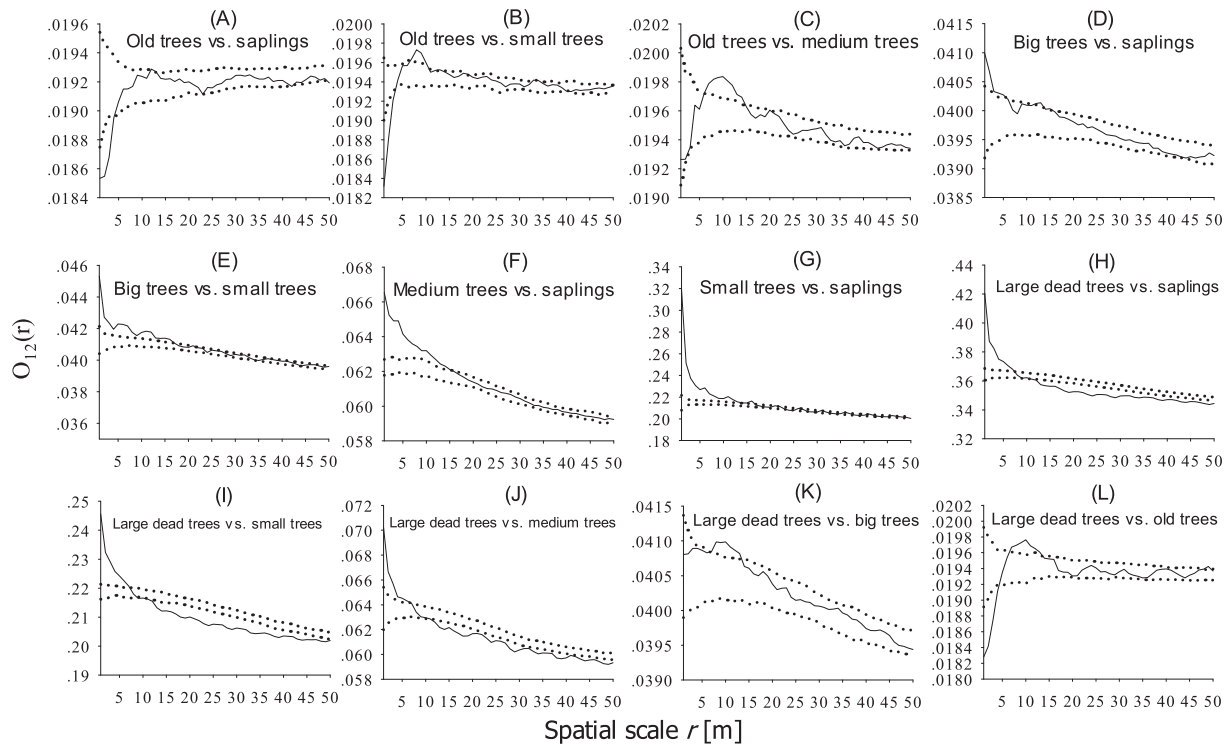
Fig. 3. $O_{12}(r)$ values of spatial associations between different tree size-classes within the 60-ha forest plot. Solid lines indicate ring statistics $O_{12}(r)$; dotted lines indicate the upper and lower limits of the 95% simulation envelope of the heterogeneous Poisson null model. Points above the upper envelope indicate positive associations, points between the envelopes indicate spatial independence, and points below the lower envelope indicate negative associations.

decreasing at increasingly larger size-classes. Densities of saplings, small trees, and dead trees tended to decrease with increasing distances (Fig. 2A, B, and F), while densities of medium trees, big trees, and old-growth trees initially increased and then decreased at greater distances, indicating that the densities of medium trees, big trees, and old-growth trees reached their minimum at the smallest distance and reached their maximum at greater distances (Fig. 2C–E). Our results are consistent with the former research, that spatial patterns shift from high aggregation to lower densities, and from random distribution to regular

distribution with increasing size-classes (Kenkel et al., 1997; Moeur, 1997; Wolf, 2005; Getzin et al., 2006; Li et al., 2009; Wang et al., 2010; Guo et al., 2013).

Big trees and old-growth trees showed a regular pattern at scales ≤ 4 m and ≤ 6 m, respectively, which suggest that big trees and old-growth trees which survived had fewer neighboring trees within 4 m and 6 m than trees at distances > 4 m and > 6 m, respectively. Small-scale initial patterns were regular rather than random or clumped. We suggest that these small-scale regularities may have been in part
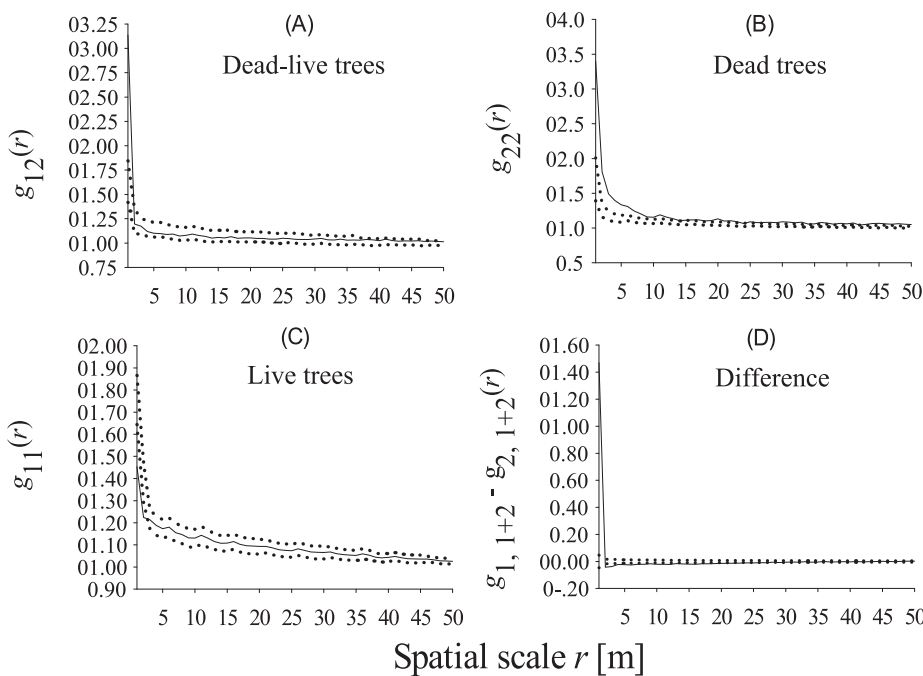

Fig. 4. Analysis of random mortality. Dead-live trees: test statistics to reveal density dependence in mortality. The test statistic showed positive values if tree density around dead trees is greater than expected under random mortality. Dead trees and live trees: test statistic to reveal aggregation of dead trees or live trees. If $g_{11}(r)$ or $g_{22}(r)$ is above (or below) the simulation envelopes, then dead (or live) trees are more aggregated than expected under random mortality. Difference: The expected value of this test statistic is zero under random labeling, but, under density-dependent mortality, we expect that dead trees would be found more frequently in areas with high living tree densities, (i.e., $g_{2,1+2} - g_{1,1+2} > 0$).

influenced by competitive interactions and subsequent density-dependent mortality at small-scales (Kenkel, 1988; Barot et al., 1999; Getzin et al., 2006; Lutz et al., 2014).

4.2. Distance-dependence effect of old-growth trees

Saplings, small trees, and medium trees showed similar patterns: they are distributed within a particular range of annuli around the old-growth trees, with the densities of these three size-classes reaching their maximums within 5–7 m from old-growth trees (the peak of the inverted V). Small trees show a narrow zone of aggregation around the old-growth trees (~6–10 m), and medium trees show a broader zone of aggregation around the old-growth trees (~7–15 m) (Fig. 2A–C). The pattern appears to be creating a neighborhood distance-dependent effect where the zone of aggregation begins at 6–7 m and expands its area as the larger size-class trees increase in density. This distance-dependent effect was consistent with the spatial relationship between young trees and big trees (Miriti, 2007; Das et al., 2008; Raventós et al., 2010; Larson et al., 2015). Densities of saplings, small trees, and medium trees first increased rapidly from 0 m to 5 m to 7 m radius (distance from old-growth trees) and then decreased continually away from old-growth trees, consistent in part with the conclusions that saplings, small trees, and medium trees tended to be distributed within a particular range of annuli around the old-growth trees (Miao et al., 2014).

By treating all the trees together, regardless of species differences, we were able to show not only the strong spatial influence that old-growth trees exert on the regeneration of four different size-classes of trees, but, also, we were able to show how that influence changes with distance from the immediate vicinity of an old-growth tree over a range of distances measured in step-wise 1 m increments from 0 m to 50 m away from the old-growth trees. We found that null patterns of association dominated at intermediate to large scales in our study site.

4.3. Mortality of trees in mountain rain forests of Hainan Island

Spatial pattern analyses of combined living and dead stems showed an increase in uniformity of living trees (Fig. 4A), suggesting that mortality was non-random in this primary mountain rain forest stand. There was a significant effect of neighborhood density on mortality, that is, dead trees were significantly aggregated with live trees at scales < 2 m (Fig. 4A) as expected under self-thinning (Kenkel, 1988). The results suggested aggregation of dead trees and a clear density-dependent mortality of dead trees that were located at scales < 2 m where dead trees had more dead neighbors than live trees (Fig. 4B and D).

In a different environment with a much higher tree density, Kenkel (1988) found a mean "area of influence" of a 3.5 m radius in a pure stand of jack pine (*Pinus banksiana*) in a boreal forest near Elk Lake, Ontario, Canada, suggesting that trees may compete directly only with their immediate neighbors. The mean "area of influence" radius value was 4 m in an old-growth Douglas fir (*Pseudotsuga menziesii*) forest on Vancouver Island, British Columbia, Canada. Similarly, the equivalent radius value was 5 m in a natural pine forest (*Pinus sylvestris* var. *mongolica*) in the Hulun Buir sandland of Inner Mongolia, China. Also, Ward et al. (1996) found that regeneration of trees was inhibited within a 6 m zone in a 4 ha interior study area on the Davis-Purdue Research Forest in east-central Indiana. However, in the tropical mountain rain forest of the Jianfengling, Hainan Island, China, we found the area of influence of only 2 m, which was less than other forest types. We hypothesize that this may be explained by the higher density of trees in this montane rain forest (Xu et al., 2015a) that is expected to show higher levels of competitive interactions which is expected to result in subsequent density-dependent mortality (Lutz et al., 2014; Larson et al., 2015). Our results were consistent with the conclusions that individuals are likely to respond directly to their immediate neighbours (Kenkel et al., 1997; Miriti, 2007; Das et al., 2008; Raventós et al., 2010; Zhu

et al., 2015).

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