

TREE MORTALITY AND RECRUITMENT IN A SUBTROPICAL BROADLEAVED MONSOON FOREST IN SOUTH CHINA

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BIN Y, LIAN J, WANG Z, YE W & CAO H. 2011. Tree mortality and recruitment in a subtropical broadleaved monsoon forest in south China. Mortality and recruitment are key factors influencing forest succession. Using spatial pattern and neighbourhood analyses, effects of conspecifics and heterospecifics upon mortality and recruitment of some locally dominant tree species were investigated in a 1-ha forest plot. Specifically, we were interested in how species in different layers of the forest responded to such effects in a subtropical forest in China. During a seven-year period (1992–1999), mortality rates of the studied species ranged from 2 to 7% per year while recruitment rates ranged from 0 to 3% per year. At this small spatial scale, mortality of all but one species was random in space. Unlike mortality, however, recruitment into the ≥ 1 -cm size class consistently occurred where local conspecific density was high. This suggests that this process may be limited by seed dispersal. Heterospecific individuals did not influence recruitment significantly for any species. Both canopy species had difficulty recruiting into the ≥ 1 -cm size class during the study period. In conclusion, tree mortality in this patch of forest was random and recruitment for six non-canopy species and two canopy species was possibly limited by seed availability and ecological needs respectively.

Keywords: Density dependence, spatial pattern, neighbourhood analysis

BIN Y, LIAN J, WANG Z, YE W & CAO H. 2011. Kematian serta perekrutan pokok di hutan monsun daun lebar subtropika di selatan China. Kematian serta perekrutan merupakan faktor utama yang mempengaruhi penggantian hutan. Kesan konspecies dan heterospecies terhadap kematian dan perekrutan beberapa spesies pokok dominan dikaji dalam plot 1 ha dengan menggunakan corak analisis ruang serta analisis jiran. Tujuannya adalah untuk melihat bagaimana spesies dalam lapisan hutan yang berbeza bergerak balas terhadap kesan tersebut di hutan subtropika di China. Sepanjang tempoh tujuh tahun (1992–1999), kadar kematian spesies yang dikaji berjudat antara 2% hingga 7% sementara kadar perekrutan berjudat antara 0% hingga 3% setiap tahun. Pada skala ruang yang kecil ini, kematian semua spesies, kecuali satu, adalah secara rawak. Tidak seperti kematian, perekrutan dalam kelas saiz ≥ 1 cm wujud secara konsisten apabila kepadatan konspecies tempatan adalah tinggi. Ini mencadangkan bahawa proses ini mungkin terhad oleh penyebaran biji benih. Individu heterospecies tidak mempengaruhi perekrutan secara signifikan untuk mana-mana spesies. Bagaimanapun, dalam tempoh kajian, kedua-dua spesies kanopi menghadapi kesukaran perekrutan dalam kelas saiz ≥ 1 cm. Sebagai kesimpulan, didapati bahawa kematian pokok di tapak hutan ini adalah rawak dan perekrutan mungkin dihadkan oleh penyebaran biji benih. Juga keperluan ekologi untuk enam spesies bukan kanopi serta dua spesies kanopi masing-masing dihadkan oleh kewujudan biji benih dan keperluan ekologi.

INTRODUCTION

Mortality and recruitment are key factors influencing the dynamics and structure of forest tree populations (Lewis et al. 2004) and the succession and composition of forest communities. Consequently, an understanding of these processes is important for ecologists and forest managers (Silk et al. 2003).

Conspecific density-dependent mortality is one possible mechanism responsible for

the maintenance of species diversity in forest communities (He & Duncan 2000, Peters 2003). Negative conspecific density-dependent mortality, possibly resulting from the enhanced propagation of pests and species-specific herbivores and pathogens, is defined as an inverse relationship between plant survival and conspecific density. Under the regulation of this negative feedback, rare species can achieve a higher rate of population

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growth than common species and, thus, maintain species diversity (Janzen 1970, Connell 1971). Some researchers have pointed out that high conspecific density and/or basal area results in low survival for conspecific trees, especially for seedlings and saplings (Peters 2003, Pigot & Leather 2008). Others have suggested that distance from conspecific trees has little impact on seed survival but may increase seedling survival (Hyatt et al. 2003), or that performances of plants are negatively related to the overall density irrespective of the species of their neighbours (Sletvold 2005). Therefore, the extent of density-dependent mortality most likely varies within and across forest ecosystems.

Dispersal limitation is another mechanism for maintenance of species diversity. Dispersal limitation refers to the phenomenon that seed density declines rapidly with distance away from the maternal tree (Muller-Landau et al. 2008). Under this hypothesis, seeds of superior competitors may fail to arrive at suitable microsites and less competitive species will have more chances to take their places, thus, slowing competitive exclusion and promoting species coexistence (Hurt & Pacala 1995). Scientists have found some indirect support for this, for example, in a meta-analysis, seedling recruitment increased in response to seed addition for about half of the species tested (Turnbull et al. 2000), and in tropical forest communities, several field studies from Panama have shown that the composition of seedlings in canopy gaps closely reflected that of the adult communities around them (Dalling et al. 1998, Hubbell et al. 1999). An analysis of the relations between recruit density and conspecific density in the neighbourhood of recruits and how spatial pattern is influenced by recruits may thus provide further indirect information on the relationship between dispersal limitation and recruitment patterns in forests.

Mortality and recruitment have been studied extensively in tropical forests, especially in search of density dependence and limited dispersal (Condit et al. 1994, Peters 2003, Uriarte et al. 2005, Wright et al. 2005, Queenborough et al. 2007). The conspecific negative density-dependent effect and limited dispersal may also play a role in maintaining the species diversity in a subtropical area. Yet there is a lack of comparative information for subtropical forest systems for which mortality and recruitment are little explored and thus poorly understood.

We speculate that the conspecific negative density-dependent mortality also exists in this subtropical forest but the effects differ among species, and that although heterospecifics can also affect survival, the effect is relatively weak compared with conspecifics. We also speculate that recruits may gather around conspecifics because of limited dispersal of seeds and fruits, and with regard to seedling stage before severe competition takes place, heterospecifics generally do not influence the seedling recruitment pattern. In this study, we aimed to test the above speculations on recruitment and mortality with data obtained from a forest plot in a subtropical area.

MATERIALS AND METHODS

Study site

A 1-ha permanent plot was set up in November 1992 in Dinghu Mountain, a nature reserve located in Zhaoqing (112° 30'–112° 33' E, 23° 09'–23° 11' N), Guangdong province, China. The reserve occupies an area of 1155 km², covered mostly by hills and valleys at an altitude ranging from about 14 to 1000 m above sea level (asl). This area has a typical monsoonal climate with an annual average precipitation of 1927 mm. April till September is the main rainy season. The mean annual temperature is 21 °C. The lowest monthly average temperature is 12.6 °C in January and the highest is 28 °C in July. The annual mean relative humidity is 80%.

The soil in Dinghu Mountain is composed mainly of lateritic red and mountain yellow-brown soil. The lateritic red soil occurs in hilly land below an altitude of 300 m, and in hills and low mountains at an altitude of 300 to 900 m asl, whereas the mountain yellow-brown soil occurs partially on the top of overlying hills.

The plot was constructed in November 1992. To map the stems accurately, the 1-ha plot was subdivided into 25 subplots, each measuring 20 × 20 m, that we further divided into sixteen 5 × 5 m quadrates. All trees and shrubs with diameters at breast height (dbh) ≥ 1 cm were tagged, measured for dbh with callipers and identified to species. Using a measuring tape with a precision of 1 dm, coordinates inside each quadrate and a detailed map of all stem positions in the 1-ha plot were obtained. New recruits and mortality were recorded in a subsequent census

in November 1999. Recruits were defined here as trees that were less than the 1-cm dbh threshold in November 1992 but had reached 1 cm or more in November 1999. Sprouts were excluded from the analysis.

The structure of the forest is complex. There are five layers in the forest from the top of the canopy to the ground floor, namely, three tree layers (top: height above 15 m, middle: 10–15 m and low: 3–9 m), one shrub layer (0.5–2 m) and one herb layer (below 0.5 m). Based on the importance value (IV), which is the sum of relative abundance, relative dominance and relative frequency (Song 2001), *Castanopsis chinensis* and *Schima superba* are the two most dominant species in the top tree layer (i.e. the canopy). *Cryptocarya chinensis* and *Cryptocarya concinna* are the two most dominant species in the middle layer, *Acmena acuminatissima*, *Aporosa yunnanensis* are the two most dominant species in the low layer, and *Blastus cochinchinensis* and *Psychotria rubra* dominate the herb/shrub layer. These eight species—as opposed to only canopy species—were chosen because they likely have important ecological roles in different layers of forest and this approach provided a more comprehensive description of forest dynamics.

Neighbourhood analysis

We used the logistic regression model to study the relationship between the mortality probability of an individual tree and its neighbourhood density (He & Duncan 2000, Suzuki et al. 2003). Predictive variables were the number of conspecifics (Cons-N), basal area of conspecifics (Cons-BA), number of heterospecifics (Het-N) and basal area of heterospecifics (Het-BA) within 5, 7.5 and 10 m from the focal tree. Each predictive variable was used alone in the logistic regression model.

The significance of the logistic regression cannot be tested in the usual way because our sample violates the assumption of statistical independence (He & Duncan 2000, Suzuki et al. 2003). Instead, a randomisation procedure was used to remove the distortion resulting from any spatial pattern of plants. By holding the number of dead trees the same as observed, the fate of a tree was randomly assigned to the predictive variable. One thousand randomisations were conducted, generating the null distribution of log-likelihood ratio. The observed log-likelihood

ratio was then compared with the null distribution under the assumption that tree mortality was independent of the predictive variable. If the observed log-likelihood ratio was outside the 95% confidence level of the null distribution, the effect was judged to be significant.

To determine whether recruitment was related to density, Cons-N, Cons-BA, Het-N and Het-BA within 5, 7.5 and 10 m of recruits of the eight dominant species were compared with those of 500 randomly generated points. If their 95% confidence intervals did not overlap they were considered to be significantly different. Data were analysed using the statistical computing program R 2.6.0 (2008).

Spatial pattern analysis

Second order point pattern analyses were used to detect the relative importance of density-dependent and density-independent processes. $K(r)$ is defined as the expected number of points within distance r from randomly chosen points (He & Duncan 2000). $K(r)$ was calculated at 1-m intervals until a maximum of 25 m. The transformation $L(r) = (K(r)/\pi) \times 0.5 - r$ is expected to be zero when the pattern is spatially random. An L value greater than zero reveals clustering whereas an L value less than zero indicates regular distribution.

We tested the random mortality hypothesis by determining whether the spatial pattern of individuals in 1992 with ≥ 1 -cm dbh that were still alive in 1999 differed from that expected if the mortality of living trees in 1992 had occurred randomly. Random mortality was simulated by randomly deleting individuals from the original data set. The number of individuals removed was set to be equal to the number of individuals that died from 1992 till 1999. This procedure was repeated 1000 times and the significant difference from randomness was tested as above. Also tested in the same way was whether recruits occurred randomly in space. The only difference was that trees were not randomly deleted but rather the number of recruited was added into the original data set. This procedure was also conducted on R 2.6.0.

RESULTS

In 1992, 3535 trees ≥ 1 -cm dbh were mapped in the 1-ha forest plot. In 1999 census, 2597 of them

were alive and 602 recruits were observed. The eight species accounted for 58.7% of the total number of stems, 71.3% of the total basal area, 60.2% of the dead trees and 34.1% of the recruits. Annual death rates ranged from 2.04 to 7.55% and recruitment rates, from 0 to 3.57% among the eight species (Table 1). *Castanopsis chinensis* and *S. superba* accounted for 35.04% of the total basal area. Almost all standing *C. chinensis* and *S. superba* were above 10 m tall and the majority of them were about 20 m tall (Zhou, personal communication).

Mortality

Cons-N had significantly positive impact on the mortality of *A. acuminatissima* across all three neighbourhood radii (Table 2). At the 5-m neighbourhood distance, mortalities of *C. concinna* and *B. cochinchinensis* were significantly negatively related to Het-N and Het-BA respectively. Mortality of *A. yunnanensis* was significantly positively associated with Het-BA at 7.5 and 10 m (Table 2). Regression could not be conducted for three species because of their too small sample sizes.

The L(r) lines of the live trees of *C. chinensis*, *S. superba*, *C. chinensis*, *C. concinna*, *A. yunnanensis* and *P. rubra* were inside the 95% confidence envelopes, indicating that mortality of these species occurred randomly during the time interval 1992–1999 (Figures 1a–d, f and h). The

curve of live trees of *A. acuminatissima* exceeded the lower envelope at small scales, indicating that mortality of this species was possibly negatively density-dependent (Figure 1e), and part of the L-curve for *B. cochinchinensis* exceeded the upper envelope at scales around 2 to 5 m, indicating that mortality of this species was possibly related to habitat heterogeneity (Figure 1g).

Recruitment

Except for Cons-N of *C. concinna* at the 7.5-m radius, the recruits of six of the eight species studied had larger observed Cons-N and Cons-BA means than randomly generated points did at all three neighbourhood radii although most of the differences were not significant (Table 3). Tests were not conducted for *S. superba* as it had no recruits and for *C. chinensis* as it had only one recruit.

The density and basal area of heterospecifics did not show a clear trend among species across all neighbourhood radii (Table 3). The observed Het-N and Het-BA were significantly larger than random points only for *P. rubra* at radii 7.5 and 10 m. *Castanopsis chinensis* had all observed points lower than random points at all three radii, except for Het-BA at 5 m. The rest of the species did not show any significant difference between observed and simulated random points at any radius (Table 3).

Table 1 Survey summary of the eight species studied in a 1-ha plot at Dinghu Mountain reserve in China

| Species | Forest layer | No. 1992 ^a | No. 1999 ^b | No. died ^c | No. recruited ^d | Annual mortality rate ^e (%) | Annual recruitment rate ^f (%) |
|--------------------------------|--------------|-----------------------|-----------------------|-----------------------|----------------------------|--|--|
| <i>Castanopsis chinensis</i> | Top | 12 | 10 | 3 | 1 | 3.57 | 1.19 |
| <i>Schima superba</i> | Top | 35 | 30 | 5 | 0 | 2.04 | 0.00 |
| <i>Cryptocarya chinensis</i> | Middle | 22 | 19 | 7 | 4 | 4.55 | 2.60 |
| <i>Cryptocarya concinna</i> | Middle | 201 | 146 | 84 | 29 | 5.97 | 2.06 |
| <i>Acmena acuminatissima</i> | Low | 111 | 94 | 25 | 8 | 3.22 | 1.03 |
| <i>Aporosa yunnanensis</i> | Low | 1100 | 950 | 184 | 34 | 2.39 | 0.44 |
| <i>Blastus cochinchinensis</i> | Shrub | 373 | 269 | 197 | 93 | 7.55 | 3.57 |
| <i>Psychotria rubra</i> | Shrub | 220 | 196 | 60 | 36 | 3.90 | 2.34 |

^aAbundance in 1992 census; ^babundance in 1999 census; ^cnumber of individuals died from 1992 till 1999; ^dnumber of individuals recruited into the ≥ 1 cm dbh size class from 1992 till 1999; ^eproportions of trees died and recruited per year from 1992 till 1999; ^fproportions of trees recruited per year from 1992 till 1999

Table 2 Results of the analysis of the relationships between neighbourhood density and tree mortality for five species studied in a 1-ha plot at Dinghu Mountain reserve in China

| Species | Parameter | Neighbourhood distance | | |
|--------------------------------|-----------|------------------------|----------|----------|
| | | 5 m | 7.5 m | 10 m |
| Regression coefficient | | | | |
| <i>Cryptocarya concinna</i> | Cons-N | -0.0441 | -0.0543 | -0.0400 |
| | Het-N | -0.0341* | -0.0077 | -0.0023 |
| | Cons-BA | -0.0002 | -0.0002 | -0.0001 |
| | Het-BA | -0.0001 | 0.0000 | 0.0001 |
| <i>Acmena acuminatissima</i> | Cons-N | 0.4526** | 0.3634** | 0.2550** |
| | Het-N | -0.0362 | -0.0157 | -0.0161 |
| | Cons-BA | 0.0017 | 0.0003 | 0.0001 |
| | Het-BA | 0.0000 | -0.0001 | -0.0001 |
| <i>Aporosa yunnanensis</i> | Cons-N | 0.0038 | 0.0003 | 0.0023 |
| | Het-N | 0.0097 | 0.0049 | 0.0049 |
| | Cons-BA | 0.0010 | 0.0002 | 0.0002 |
| | Het-BA | 0.0000 | 0.0001* | 0.0001** |
| <i>Blastus cochinchinensis</i> | Cons-N | -0.0024 | 0.0076 | 0.0243 |
| | Het-N | -0.0093 | 0.0014 | 0.0065 |
| | Cons-BA | -0.0030 | 0.0003 | 0.0051 |
| | Het-BA | -0.0001** | 0.0000 | 0.0000 |
| <i>Psychotria rubra</i> | Cons-N | 0.0078 | 0.0022 | 0.0065 |
| | Het-N | 0.0303 | 0.0145 | 0.0043 |
| | Cons-BA | 0.0008 | 0.0001 | 0.0006 |
| | Het-BA | 0.0001 | 0.0001 | 0.0000 |

Cons-N = number of conspecifics; Het-N = number of heterospecifics; Cons-BA = basal area of conspecifics; Het-BA = basal area of heterospecifics; * = $p < 0.05$; ** = $p < 0.01$

Recruits increased spatial aggregations of the six species analysed but did so at different spatial scales (Figure 2). Recruitments of *A. acuminatissima* and *C. concinna* significantly increased the spatial aggregation at scales greater than 10 and 20 m respectively (Figures 2c and b). Recruitment contributed to spatial aggregation of *C. chinensis* at scales up to 10 m (Figure 2a), but beyond 10 m, recruitments seemed to be random (Figure 2a). The recruits of *B. cochinchinensis*, *A. yunnanensis* and *P. rubra* significantly increased spatial aggregation at all the scales studied (Figures 2d, e and f).

DISCUSSION

Whether a given forest community is regulated by density-dependent processes has been debated for a long time. Some have found evidence consistent with density-dependent tree mortality (Wills et al. 1997, Peters 2003). However, in a study on tree survival in an old-growth temperate forest in north-eastern China, significant negative density-dependent mortality was not detected when trees reached 1-cm dbh (Zhang et al. 2009). In our research, mortality of *A. acuminatissima* was positively related to the number of conspecifics

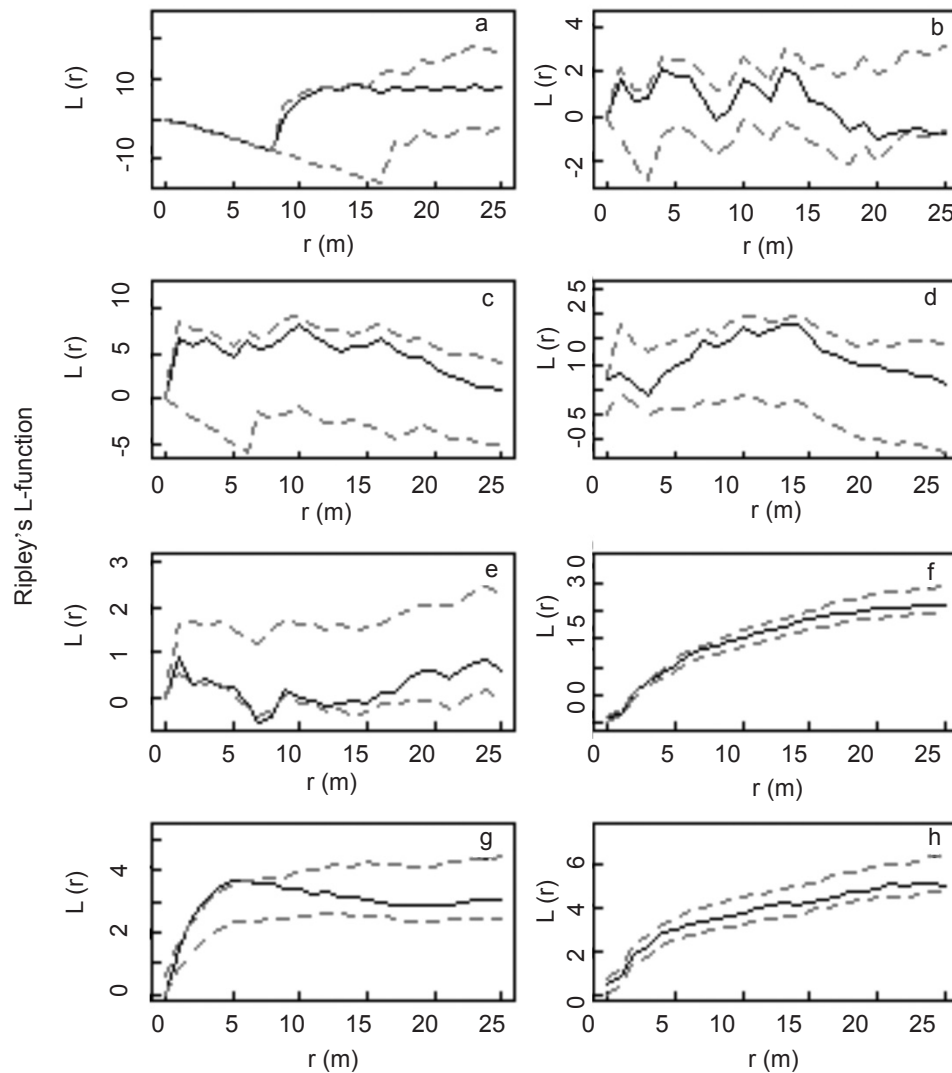


Figure 1 Tests of random mortality by spatial pattern analysis in a 1-ha plot at Dinghu Mountain reserve in China. The solid line is the observed $L(r)$ after excluding trees that died in 1992 and 1999; the dash lines are the 95% confidence envelopes for $L(r)$ if mortality is random. a: *Castanopsis chinensis*, b: *Schima superba*, c: *Cryptocarya chinensis*, d: *Cryptocarya concinna*, e: *Acmena acuminatissima*, f: *Aporosa yunnanensis*, g: *Blastus cochinchinensis*, h: *Psychotria rubra*. If the solid line is above the dash lines, mortality has enhanced the original spatial aggregation and mortality possibly results from habitat heterogeneity. If the solid line is below the dash lines, mortality alleviated the spatial aggregation of the original pattern, and mortality is possibly due to the negative effect of conspecific individuals. If the solid line is within the two dash lines, spatially random mortality is observed.

up to 10-m neighbourhood radius analysed. However, we did not find such a consistent density-dependent mortality in the other five species. Therefore, generally, we believe that mortality is not dependent on density of the conspecifics in our study. Our results also suggested that mortality of individuals of the studied species occurred, generally, at random, although it seemed that *A. acuminatissima* and *B. cochinchinensis* deviated from this at up to 5- and 10-m neighbourhood radii respectively.

On the other hand, a more plausible explanation for why we did not detect conspecific density-dependent mortality in our species, except possibly for *A. acuminatissima*, might be due to the small sample sizes of our species and limited spatial scale of 1 ha. For example, stems lying near plot borders could have been affected by trees lying outside the plot. In order to obtain more reliable results, a 20-ha forest plot was established in Dinghu Mountain reserve in 2005 (Li et al. 2009). Seed traps and seedling plots have

Table 3 Conspecific and heterospecific neighbourhood densities of observed recruits of the six studied species and the randomly selected points at three radii (r) in a 1-ha plot at Dinghu Mountain reserve in China

| | r = 5m | | r = 7.5m | | r = 10m | |
|--------------------------------|------------------|----------------|------------------|----------------|-------------------|-----------------|
| | Observed | Random | Observed | Random | Observed | Random |
| <i>Cryptocarya chinensis</i> | | | | | | |
| Cons-N | 1.0 ± 0* | 0.2 ± 0.1 | 1.3 ± 0.7* | 0.3 ± 0.7 | 1.3 ± 0.7 | 0.7 ± 0.1 |
| Het-N | 18.0 ± 6.9* | 27.0 ± 1.2 | 31.3 ± 2.7* | 57.8 ± 2.5 | 54.0 ± 6* | 102.3 ± 4.4 |
| Cons-BA | 1819.8 ± 1309.7* | 102.6 ± 36.5 | 1875.6 ± 644.6* | 161.4 ± 51.2 | 1875.6 ± 644.6* | 390.2 ± 79.8 |
| Het-BA | 926.8 ± 1324.7 | 2170.2 ± 227.9 | 3398.6 ± 621.7* | 5164.6 ± 391.0 | 4847.0 ± 885.1* | 8820.7 ± 484.7 |
| <i>Cryptocarya concinna</i> | | | | | | |
| Cons-N | 1.7 ± 2.0 | 1.6 ± 0.2 | 3.2 ± 0.6 | 3.3 ± 0.3 | 6.1 ± 0.8 | 5.6 ± 0.4 |
| Het-N | 26.7 ± 17.0 | 25.4 ± 1.2 | 60.1 ± 5.8 | 56.3 ± 2.4 | 104.4 ± 9.0 | 95.8 ± 4.0 |
| Cons-BA | 442.8 ± 680.5 | 305.9 ± 34.6 | 687.0 ± 177.5 | 641.5 ± 54.4 | 1204.1 ± 241.3 | 1126.8 ± 80.0 |
| Het-BA | 2229.8 ± 5805.7 | 1851.0 ± 215.7 | 5219.4 ± 1567.3 | 5124.1 ± 387.7 | 10057.2 ± 1771.8 | 8023.5 ± 507.7 |
| <i>Acmena acuminatissima</i> | | | | | | |
| Cons-N | 1.0 ± 2.0 | 0.8 ± 0.1 | 2.7 ± 1.2 | 2.0 ± 0.2 | 4.9 ± 1.9 | 3.8 ± 0.3 |
| Het-N | 17.1 ± 22.2 | 26.5 ± 1.2 | 42.0 ± 17.2 | 57.8 ± 2.5 | 73.7 ± 29.4 | 102.5 ± 4.3 |
| Cons-BA | 253.0 ± 482.6 | 98.3 ± 25.5 | 346.9 ± 139.9 | 220.1 ± 36.6 | 459.9 ± 219.7 | 416.6 ± 50.3 |
| Het-BA | 2341.0 ± 3102.6 | 2223.9 ± 240.7 | 3830.5 ± 1130.3 | 4954.6 ± 342.1 | 10666.4 ± 3412.8 | 9110.0 ± 495.0 |
| <i>Aporosa yunnanensis</i> | | | | | | |
| Cons-N | 12.4 ± 10.6 | 8.8 ± 0.6 | 27.1 ± 4.2* | 19.7 ± 1.2 | 46.4 ± 5.4* | 35.1 ± 1.8 |
| Het-N | 16.6 ± 17.0 | 17.5 ± 0.9 | 40.3 ± 8.2 | 41.0 ± 2.0 | 70.2 ± 14.7 | 69.7 ± 3.4 |
| Cons-BA | 264.8 ± 222.4 | 194.1 ± 12.8 | 621.3 ± 91.2* | 448.5 ± 23.8 | 1089.8 ± 108.7* | 822.3 ± 38.7 |
| Het-BA | 1698.4 ± 3272.4 | 2255.1 ± 242.9 | 4156.4 ± 1212.9 | 4876.1 ± 370.5 | 9162.2 ± 1679.3 | 8792.5 ± 471.5 |
| <i>Blastus cochinchinensis</i> | | | | | | |
| Cons-N | 4.4 ± 8.4 | 2.6 ± 0.3 | 8.0 ± 1.6 | 5.5 ± 0.6 | 12.0 ± 2.0 | 9.6 ± 1.0 |
| Het-N | 24.4 ± 23.4 | 24.3 ± 1.1 | 54.6 ± 5.6 | 55.4 ± 2.4 | 101.0 ± 9.3 | 96.3 ± 4.0 |
| Cons-BA | 12.1 ± 25.3 | 7.6 ± 1.0 | 22.8 ± 5.4 | 15.8 ± 1.8 | 35.2 ± 6.6 | 27.2 ± 3.0 |
| Het-BA | 2069.0 ± 4142.3 | 2167.4 ± 230.1 | 4594.8 ± 856.9 | 5324.4 ± 379.1 | 9713.2 ± 1207.3 | 9332.2 ± 487.7 |
| <i>Psychotria rubra</i> | | | | | | |
| Cons-N | 3.6 ± 5.0 | 1.6 ± 0.2 | 8.5 ± 1.7* | 3.8 ± 0.4 | 13.4 ± 1.9* | 6.9 ± 0.7 |
| Het-N | 31.5 ± 15.4 | 25.3 ± 1.1 | 74.1 ± 5.0* | 54.6 ± 2.2 | 131.4 ± 7.0* | 98.1 ± 3.7 |
| Cons-BA | 19.6 ± 28.4 | 9.7 ± 1.7 | 46.8 ± 10.3* | 23.0 ± 3.2 | 78.4 ± 15.0* | 40.0 ± 5.0 |
| Het-BA | 3276.8 ± 6078.7 | 2253.5 ± 216.5 | 7187.2 ± 1519.4* | 4879.0 ± 327.7 | 13167.0 ± 1580.5* | 10115.0 ± 523.6 |

Mean ± 2SE; Cons-N = number of conspecifics; Het-N = number of heterospecifics; Cons-BA = basal area of conspecifics; Het-BA = basal area of heterospecifics; * = p < 0.05; ** = p < 0.01

been constructed and monitored since late 2007. However, the only results obtained from the 20-ha plot currently are from two-year-old seedlings and thus are not comparable with results obtained for seedlings from the current study. The 20-ha plot is due for another census in 2011. Nonetheless, the present study provided the first preliminary information of tree mortality and recruitment

for this region. Future studies from the 20-ha plot should provide robust information on local forest dynamics and either verify or possibly contradict our results. In this study, significant effects of heterospecific density on mortality only occurred positively for basal areas at 7.5- and 10-m neighbourhood radius in *A. yunnanensis* and negatively at 5 m in *B. cochinchinensis*, and

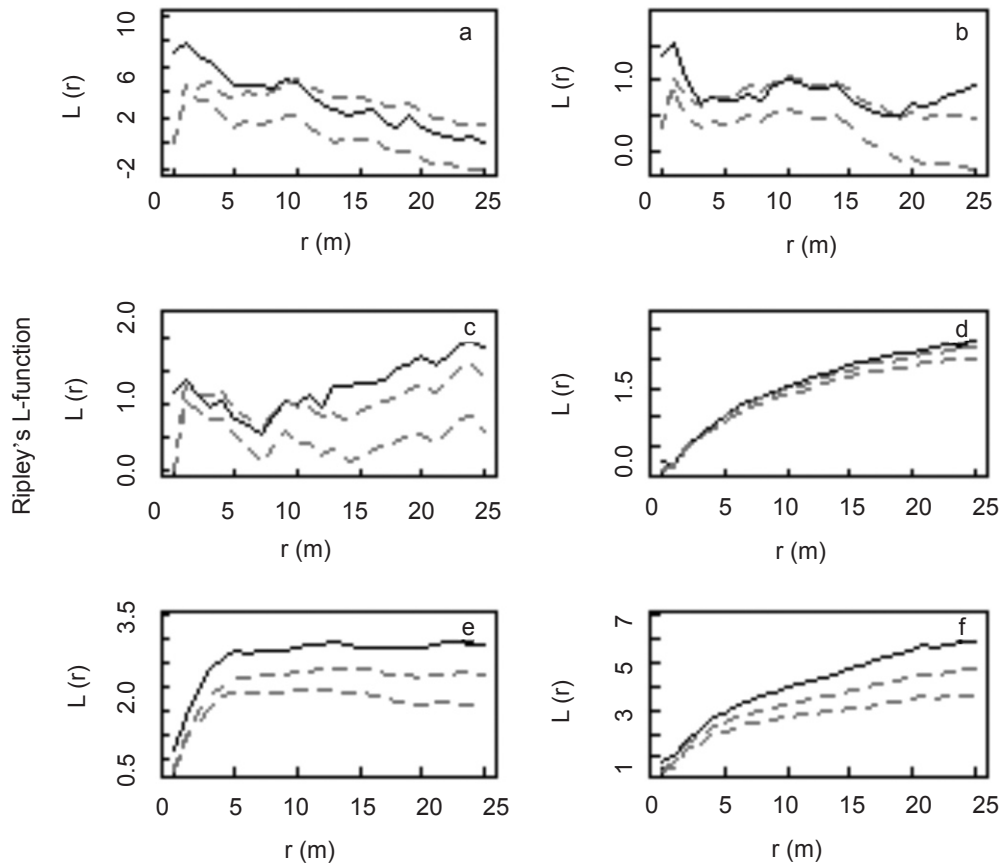


Figure 2 Tests of random recruitment by spatial pattern in a 1-ha plot at Dinghu Mountain reserve in China. The solid line is the observed $L(r)$ for trees recorded in 1992 and recruits found in 1999, the dash lines are the 95% confidence envelopes for $L(r)$ if recruitment is random. a: *Cryptocarya chinensis*, b: *Cryptocarya concinna*, c: *Acmena acuminatissima*, d: *Aporosa yunnanensis*, e: *Blastus cochinchinensis*, f: *Psychotria rubra*. If the solid line is above the dash lines, recruitment enhanced the spatial aggregation of the original pattern, possibly due to limited dispersal. If the solid line is below the dash lines, recruitment alleviated the spatial aggregation of the original pattern, possibly due to habitat heterogeneity. If the solid line is within the two dash lines, spatially random recruitment is observed.

negatively for number of heterospecifics at 5 m for *C. concinna*, but not in other combinations of species and neighbourhood radius. These inconsistent relationships between density of heterospecifics and mortality among species are similar to those reported by Zhang et al. (2009) and Queenborough et al. (2007). Though plants all consume a set of similar resources such as light, water and soil nutrient, different species may differ in the amount they require, and when they need it. Adjacent heterospecific plants can influence each other by facilitation and competition. When the positive effect of facilitation exceeds that of competition, the net direction of plant–plant interaction is positive, and vice versa.

The two canopy species, *C. chinensis* and *S. superba*, had few recruits in the 1-ha plot we surveyed in 1999. One possible cause for this poor regeneration is that the relatively mature forest cannot meet the ecological needs of these species. *Castanopsis chinensis* and *S. superba* are considered to be moderately light-demanding or shade-intolerant species (Huang et al. 1998). The climax of this forest is supposed to be a *C. chinensis*–*C. concinna* community; at the time of census the forest was approaching climax based on results from a 12-year study at the same site (Peng et al. 1998). Thus, perhaps it is not all that surprising that *C. chinensis* and *S. superba* now exhibit some signs of *in situ* population decline, such as severe difficulty in recruitment to the

1-cm dbh size class. Similarly, in an African wet forest, a dominant light-demanding canopy tree, *Microberlinia bisulcata*, also had scarce recruits > 1-cm dbh (Newbery et al. 2010). Another possible explanation for poor regeneration in *C. chinensis* is related to the biology of its seeds. Before dispersal, the seeds are predated by *Curculio davidi*, a weevil, and then after dispersal by rats and birds (Du et al. 2006). Furthermore, pathogens threaten the survival of seeds in both pre- and post-dispersal periods (Du et al. 2006). Collectively, potentially severe losses of seeds may partially contribute to the few recruits of *C. chinensis* in the 1-ha plot. Alternatively, however, recruits of these canopy species may be occurring at some distance away from maternal trees where canopy gaps are more prevalent (e.g. Newbery et al. 2010). If these were indeed the case, such recruits outside of our 1-ha plot would have been missed out in our 1999 survey.

Although much work has been done monitoring tree recruitment and mortality in this region of China, more studies over a larger area and longer time span are needed to elucidate whether the forest is at equilibrium in the short term, and what factors are driving the succession process in this subtropical forest and other forests around the world.

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