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Forest dynamics of a subtropical monsoon forest in Dinghushan, China: recruitment, mortality and the pace of community change

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Abstract: Structure and demographics in many tropical forests is changing, but the causes of these changes remain unclear. We studied 5 y (2005–2010) of species turnover, recruitment, mortality and population change data from a 20-ha subtropical forest plot in Dinghushan, China, to identify trends in forest change, and to test whether tree mortality is associated with intraspecific or interspecific competition. We found the Dinghushan forest to be more dynamic than one temperate and two tropical forests in a comparison of large, long-term forest dynamics plots. Within Dinghushan, size-class distributions were bell-shaped only for the three most dominant species and reverse J-shaped for other species. Bell-shaped population distributions can indicate a population in decline, but our data suggest that these large and long-lived species are not in decline because the pattern is driven by increasing probabilities of transition to larger size class with increasing size and fast growth in saplings. Spatially aggregated tree species distributions were common for surviving and dead individuals. Competitive associations were more frequently intraspecific than interspecific. The competition that induced tree mortality was more associated with intraspecific than interspecific interactions. Intraspecific competitive exclusion and density-dependence appear to play important roles in tree mortality in this subtropical forest.

Key Words: forest dynamics, population trends, size-class distributions, spatial patterns, subtropical forest, tree mortality

INTRODUCTION

Knowledge of the dynamics of plant community composition is fundamental to understanding numerous ecological processes (Sheil *et al.* 2000). Growth and mortality are the most important factors that influence plant community dynamics and species composition (Lewis *et al.* 2004, Manokaran & Kochummen 1987, Rüger *et al.* 2011). Analysis of community dynamics has been especially important in ecological studies of species-rich ecosystems, such as tropical forests (Feeley *et al.* 2011, Lewis *et al.* 2004, Rüger *et al.* 2011). For example, Condit *et al.* (1999) compared the dynamics of tropical forest communities from Pasoh, Malaysia, with Barro Colorado Island (BCI), Panama, and concluded that

growth, recruitment and mortality rates were higher in Panama. In this study, we evaluate the forest population dynamics of 195 species over 5 y in the Dinghushan (DHS) subtropical forest dynamics plot in Southern China, with the goal of understanding population and community structure, and determining the effects of inter- and intraspecific spatial associations on tree mortality.

Analysis of size-class distributions of plant populations combined with dynamic transition probabilities between size classes is a valuable tool for predicting population stability and understanding community dynamics. If the number of juveniles is much larger than the number of adults, the population could be considered stable. Yet, few juveniles may be a warning of low recruitment and population decline (Condit *et al.* 1998), unless there is a high probability of individuals moving into intermediate size classes, resulting in a bell-shaped size-class distribution. Large and long-lived species may be

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especially prone to bell-shaped size-class distribution because their size-class distribution are also affected by long-term demographic factors such as episodic recruitment or mortality events, which vary greatly across different species and with time (Condit *et al.* 1998, Venter & Witkowski 2010). In previous studies at Dinghushan, nearly all species exhibited a reverse J-shaped size-class distribution, which may be interpreted as a stable population. However, the three most dominant species were the only exceptions. They showed a bell-shaped size-class distribution, with a peak of individuals concentrated in the intermediate diameter at breast height (dbh) classes (Ye *et al.* 2008), raising questions of whether these three species could lose their dominance in the near future due to a lack of recruits.

Tree mortality is another of the most important processes in determining forest dynamics (Rüger *et al.* 2011), and involves many factors which can be mainly divided into biotic and abiotic factors (Das *et al.* 2008). Relating tree mortality to biotic versus abiotic factors is challenging because of the long-term nature of tree growth. However, through temporal and spatial demographic patterns, it is possible to determine the ecological and environmental processes that contribute to mortality and community structure (Boyden *et al.* 2005). Therefore, we also evaluate mortality in the context of spatial inter- and intraspecific tree associations using a second-order point pattern analyses, Ripley's K function (Ripley 1977).

Forest dynamics are slow-acting (Gaines & Denny 1993), and thus require long-term data to accurately determine the rates of processes. Much of our current knowledge of long-term forest dynamics is derived from tropical forest, especially from large-scale and stem-mapped permanent forest dynamics plots (Condit *et al.* 1993, 1995; Feeley *et al.* 2011). Many of these plots have now logged multi-decadal demographic datasets, which are critical for understanding temporal variation in ecological processes. Demographic data, such as recruitment, growth and mortality offer keys to understanding directional changes in forest processes such as community composition (Hubbell & Foster 1992). We measured the 5-y dynamics of a 20-ha subtropical forest plot in South China based on a census conducted in 2005 and again in 2010, and compared these data to other forest dynamics plots to test three hypotheses. First, we hypothesized that the bell-shaped size-class distributions for dominant species at Dinghushan indicate a declining population. Second, we hypothesized that demography of the subtropical forest at Dinghushan will be more dynamic than a temperate forest at Changbaishan, China, and less dynamic than tropical forests at Barro Colorado Island, Panama and Pasoh, Malaysia, consistent with greater dynamism towards the equator. Finally, we hypothesized that tree mortality

will be more related to intraspecific spatial associations than to interspecific spatial associations, due to common aggregated distributions within species at Dinghushan (Li *et al.* 2009).

METHODS

Study site

The study was conducted in the Center for Tropical Forest Science 20-ha forest dynamics plot in the Dinghushan Man and the Biosphere Reserve, Guangdong Province, China (23°09'21"–23°11'30"N, 112°30'39"–112°33'41"E). The 20-ha (400 × 500 m) plot was established within the 1155-ha reserve in 2004–2005 (Ye *et al.* 2008), and re-censused in 2010, all stems ≥ 1 cm dbh were measured, mapped and tagged. For individuals with multiple stems, all stems were measured and tagged, so that all demographic calculations could be made on the basis of individuals or on the basis of stems. The zonal vegetation is low subtropical evergreen broadleaved forest more than 400 y old. The altitude in the plot ranges from 230 to 470 m asl (Li *et al.* 2009). The site has a subtropical monsoon climate with a mean annual temperature of 20.9 °C, mean relative humidity of 85%, and mean annual precipitation of 1927 mm, most of which occurs between April and September (Bin *et al.* 2011).

Demographic rates

We calculated demographic rates from the 2005–2010 census interval. The rate of species turnover was calculated using species presence/absence census data as $((N_l + N_n)/2N_a t) \times 100\%$ where N_l is the number of species lost from the census, N_n is number of new species appearing since the last census, N_a is the number of all species at the first census, and t is the time interval between the first and last census. Relative growth rate (RGR) was calculated as $(\log(dbh_t) - \log(dbh_o))/t$, where dbh_o and dbh_t are the stem diameter at breast height (dbh) from first and last measurements, respectively. Exponential mortality coefficients were calculated as $(\log(N_o) - \log(N_s))/t$, where N_o and N_s are the number of stems at the first measurement and number of surviving stems at the last measurement, respectively (Sheil *et al.* 1995). Recruitment rate was calculated as $(\log(N_t) - \log(N_s))/t$ where N_t is number of stems at the last measurement. Rate of population change (Condit *et al.* 1999), was calculated as $(\log(N_o) - \log(N_t))/t$. We calculated the demographic rates for the 101 species with at least 20 stems in the plot. We compared demographic rates in Dinghushan Forest with data collected at similar

long-term forest dynamics plots, including the tropical 50-ha plots on Barro Colorado Island, Panama and Pasoh, Malaysia, and the temperate 25-ha plot in Changbaishan, China, using published sources (Condit *et al.* 1999, Wang *et al.* 2011).

Size-class distributions

We constructed size-class distributions with 5-cm dbh intervals for all stems in 2005 and dead stems during 2005–2010 for the three most common species (dominant species: *Castanopsis chinensis*, *Schima superba* and *Engelhardia roxburghiana*), and calculated the mean annual RGR of each size class. The same methods were used for the three next-most-common species (co-dominant species: *Cryptocarya chinensis*, *Syzygium rehderianum*, *Acmena acuminatissima*) to analyse differences in size-class distributions. We used the quotient of successive size-classes which examines the population stability (Venter & Witkowski 2010), and the permutation index to evaluate population trends between dominant species and co-dominant species. Quotients approach a constant value in a stable population, but fluctuate in an unstable population (Botha *et al.* 2004). The permutation index was used to measure the deviation from a monotonic distribution using size-classes ranked from smallest (most frequent) to largest (least frequent) (Venter & Witkowski 2010), and is calculated as:

$$P = \sum_{i=1}^n |j_i - i|; j_i = 1, 2, \dots, n$$

where n is the number of size-classes, and j_i is the rank of size-class i ($i = 1$ for the smallest size-class), with highest rank ($j_i = 1$) given to the most frequent size-class. Populations with discontinuous size-class distributions will have a permutation index greater than zero, except in undisturbed populations (Botha *et al.* 2004, Wiegand *et al.* 2000). Finally, we calculated transition probabilities of successive size-classes for three dominant species and co-dominant species using data from two census periods in the DHS plot. The probability of an individual remaining in the same size-class (P_{xx}) or growing to the next consecutive size-class (P_{xy}) was calculated as in Caswell (1989).

Spatial patterns of tree mortality

We used Ripley's K function with isotropic correction for edge effects for comparing the spatial distributions of surviving and dead individuals over the measurement interval in order to assess differences in aggregation. Ripley's K function is defined as the mean number of

points within a distance r from a sampled point (Barot *et al.* 1999). In our study, $K_1(r)$ and $K_2(r)$ are univariate K functions of surviving and dead individuals, respectively (de la Cruz *et al.* 2008), and we used an r value of 50 m from each focal tree for our analyses. If $K_1(r) - K_2(r) > 0$, surviving individuals are more aggregated than dead individuals, and if $K_1(r) - K_2(r) < 0$, dead individuals are more aggregated than surviving individuals. $K_1(r) - K_{12}(r)$ and $K_2(r) - K_{12}(r)$ are derived from the function $K_1(r) K_2(r)$, where $K_{12}(r)$ is a bivariate K function for surviving and dead individuals. These functions are based on the property that every individual pattern would be a random thinning of the corresponding bivariate pattern under the null model of random labelling. The two functions are thus used to evaluate whether one type of point tends to be surrounded by other points of the same type or not. $K(r)$ has an expected value of 0 for all r distances under random labelling. If $K_1(r) - K_{12}(r) > 0$, we can conclude that surviving individuals are surrounded by more surviving individuals than expected by chance, but if $K_1(r) - K_{12}(r) < 0$, surviving individuals are surrounded by more dead individuals than expected by chance. The complementary function $K_2(r) - K_{12}(r)$ is similar; when $K_2(r) - K_{12}(r) > 0$, dead individuals are surrounded by more dead individuals than are surviving individuals. The analyses were performed with 99 point process simulations.

We also investigated the spatial associations between all individuals in the first census and individuals that were dead in the second census to understand how intra- and interspecific relationships influenced tree mortality. We used $K_{12}(r)$, which counts the expected number of points of all individuals within a given distance ($r = 100$ m) of a dead individual to implement the analyses (de la Cruz *et al.* 2008). To facilitate the visualization and interpretation of the results, we transformed the function K_{12} to an L_{12} function calculated as:

$$L_{12}(r) = \sqrt{\frac{K_{12}(r)}{\pi}} - r$$

If the observed L function lies upon the upper simulated envelope, all individuals significantly positively associate with dead individuals, indicating competitive associations between all individuals and dead individuals. In contrast, if the observed L function lies below the lower simulated envelope, all individuals have a significant negative association with dead individuals and this would denote facilitative associations. Such associations often occur in harsh conditions such as arid and semi-arid environments when plant recruitment sometimes requires safe sites under the canopy of nurse plants which provide shelter from high temperature and radiation (Flores & Jurado 2003). A total of 199 simulations of the selected null models were computed. Spatial distributions of tree

Table 1. Forest structure and change between 2005–2010 in the 20-ha Dinghushan Forest Dynamics Plot, China.

Forest structure	2005	2010	Net change	Average annual change rate (% y ⁻¹)
Number of species	195	178	-17	-1.82
Number of individuals	71 458	61 125	-10 333	-3.12
Number of stems	80 504	68 467	-12 037	-3.24
Basal area (m ² ha ⁻¹)	30.1	26.6	-3.53	-2.49

mortality and spatial associations of conspecifics were performed for 74 common species with 50 or more individuals in the Dinghushan plot.

Twenty species with population sizes ≥ 1000 individuals were selected for spatial association analyses among all individuals of a species and dead individuals of another species, and we evaluated type and frequency for the $20 \times 19 = 380$ species pairs. Spatial pattern analyses were conducted using 'ecspa' and 'Spatstat' packages in R (2.13.2, 2011).

RESULTS

Demographic rates

The total number of species in the Dinghushan plot decreased from 195 to 178 over a 5-y period with 20 lost species and three new species (Table 1, Appendix 1). Species turnover rate was 1.2% y⁻¹. The total number of stems decreased from 80 504 in 2005 to 68 467 in 2010, including mortality of 20 424 stems (25.3% of total stems in 2005) and recruitment of 8387 stems (12.2% of total stems in 2010). Size-class distributions for all stems in 2005 and dead stems during 2005–2010 were both close to reverse-J shaped, and the number of dead stems decreased as size-classes increased. There were 71 458 individuals in the 2005 census, but only 61 121 individuals left after the 2010 census, representing a loss of 17 101 individuals (23.9% of total individuals in 2005) and recruitment of 6764 individuals (11.1% in total individuals in 2010) into the ≥ 1 cm dbh size class between 2005–2010. Basal area was 30.1 m² ha⁻¹ in 2005, and decreased to 26.6 m² ha⁻¹ in 2010, resulting in a decrease of 4.16 m² ha⁻¹ due to mortality and an increase of 0.64 m² ha⁻¹ due to dbh growth and recruitment (0.39 m² ha⁻¹ and 0.25 m² ha⁻¹, respectively). The mean RGR for 101 species was 0.032 cm cm⁻¹ y⁻¹, and it ranged from 0.005 to 0.1713 cm cm⁻¹ y⁻¹. The average exponential mortality coefficient was 8.01% y⁻¹, and ranged from 0 to 43.3% y⁻¹ among species. Over 5 y, mean recruitment rate was 3.17% y⁻¹, and ranged from 0 to 20.2% y⁻¹ among species. Number of stems in the plot decreased for 86 out of 101 species (Figure 1, Appendix 1),

resulting in a mean annual population change rate of -4.80% y⁻¹, for example, *Mallotus paniculatus* stems increased by 13.7% y⁻¹ and *Garcinia oblongifolia* decreased by 42.0% y⁻¹.

Size-class distributions

Size-class distributions of stems of the three co-dominant species were reverse J-shaped (Figure 2a–c). The size-class distributions for their RGR decreased gently with increasing size class (Figure 2d–f). Size-class distributions for stems of the three dominant species showed a bell-shaped curve, with *Castanopsis chinensis* showing a tendency toward positive skew (Figure 3a–c). This indicates that for these three dominant species, most stems were concentrated in the intermediate dbh size range, with fewer stems in the small and large dbh size classes (Figure 3a–c). The RGR of these species were much greater in small dbh stems, and decreased sharply with increasing dbh (Figure 3d–f).

Quotients calculated between successive size-classes for all six populations were not constant, but the amplitude of fluctuation of dominant species was much larger than co-dominant species (Figure 4), indicating that co-dominant species appear more stable than dominant species. Moreover, the permutation index values of co-dominant species were equal to zero, but permutation index values were much larger than zero for dominant species (36, 20 and 48, respectively), demonstrating that the size-class distributions of dominant species were discontinuous, and recruitment and mortality were episodic events.

The mean probability of an individual remaining in the same size-class (P_{xx}) for three dominant species was 0.62 ± 0.4 (1 SE), whereas the mean P_{xx} for co-dominant species was larger than dominant species (0.74 ± 0.3). The mean probabilities of an individual growing to the next consecutive size-class (P_{xy}) for the three dominant species was larger than co-dominant species (0.20 ± 0.2 versus 0.11 ± 0.3). No clear patterns of P_{xy} were observed for three co-dominant species (Figure 5a). Interestingly, P_{xy} tended to increase as size-class increased (Figure 5b), and had a peak at the size-class of 5–9.9 cm for *Castanopsis chinensis* and *Schima superba*.

Spatial patterns of tree mortality

Spatial distributions for surviving and dead individuals of 32 species (43.2%) significantly departed from the null model at different scales (Figure 6), with surviving individuals significantly more aggregated than dead individuals for 13 species (17.6%). However, dead individuals were significantly more aggregated than

Figure 1. Histogram of rates of population change from 2005–2010 in the 20-ha forest dynamics plot at Dinghushan, China; 101 species that had at least 20 stems at the first measurement were included.

surviving individuals for 19 species (25.6%). The results derived from the function $K_1(r) - K_{12}(r)$ showed that surviving individuals tended to be surrounded by more surviving individuals than expected by chance for 25 species (33.8%), with four species (5.4%) showing the opposite pattern. For dead individuals, 33 species (44.6%) tended to be surrounded by more dead individuals than expected by chance, whereas four species (5.4%) tended to be surrounded by more surviving individuals than expected by chance. Spatially aggregated tree species

distributions were dominant across the plot for surviving and dead individuals.

Tree mortality showed significant positive associations with intraspecific individuals for all 74 species, but at different scales. Our interspecific association analyses for all 20 species indicated that all 380 species pairs departed from the null model in different directions and different scales (Figure 7). A total of 170 species pairs (44.7%) showed a significant positive association, 184 species pairs (48.4%) showed a significant negative

Figure 2. Size-class distributions (diameter at breast height; dbh) in 5-cm intervals of all stems at the first measurement (solid lines) and size-class distributions of dead stems from 2005–2010 (dashed lines) for three co-dominant species (*Cryptocarya chinensis*, *Syzygium rehderianum* and *Acmena acuminatissima*) in the 20-ha forest dynamics plot at Dinghushan, China (a–c). Size-class distributions of average annual relative growth rate (RGR) for three co-dominant species (d–f).

Figure 3. Size-class distributions (diameter at breast height (dbh) in 5-cm intervals) of all stems at the first measurement (solid lines) and size-class distributions of dead stems during 2005–2010 period (dashed lines) for three dominant species (*Castanopsis chinensis*, *Schima superba* and *Engelhardia roxburghiana*) in the 20-ha forest dynamics plot at Dinghushan, China (a–c). Size-class distributions for average annual relative growth rate (RGR) for three dominant species (d–f).

association, and two species pairs showed significant positive associations at small scales and significant negative associations at large scales. The rest of the 24 species pairs had no clear pattern.

DISCUSSION

Our analysis of forest dynamics reveals the pace of important ecological processes. The study over a 5-y census interval in a subtropical forest in Southern China allowed us to compare the forest dynamics of several forest types that range across tropical, subtropical and temperate latitudes. We found that the subtropical forest plot in Dinghushan was much more dynamic than the tropical and temperate forests used for comparison (Table 2). Our results also indicate that although nearly all of the species in the Dinghushan plot exhibited a reverse J-shaped curve, suggesting a stable population with recruitment, the three most dominant species showed

a bell-shaped curve, suggesting a declining population resulting from a lack of recruitment. Therefore, we examine the implications of size-class distributions on long-term forest dynamics and explore whether other factors, such as population size, demographic rates or transition probabilities can be used to further inform interpretations of size-class distributions. Our study suggests that comparing population structures, transition probabilities and the rates of demographic processes is useful for evaluating contrasting species and forest types.

Contrary to our hypothesized results, we found Dinghushan forest to be substantially more dynamic than tropical forest plots in BCI and Pasoh and the temperate plot in Changbaishan, with 50% of the species at Dinghushan showing an annual population change rate greater than 5% (Table 2). The pace of forest dynamics integrates numerous factors, including topography (Bellingham & Tanner 2000), geology and climate (Condit *et al.* 1999), organisms present and the stage of succession, and anthropogenic factors in lands

Table 2. Comparison of demographic rates among forest dynamics plots of 50 ha at Barro Colorado Island, Panama (BCI), 50 ha at Pasoh, Malaysia, 20 ha at Dinghushan (DHS), China and 25 ha at Changbaishan (CBS), China.

Plot	Species turnover rate (% y ⁻¹)	Exponential mortality coefficient (% y ⁻¹)	Recruitment rate (% y ⁻¹)	Population change rate > 5% y ⁻¹ (% y ⁻¹)
BCI	0.10	1.46	1.65	2
Pasoh	0.33	2.55	2.87	10
DHS	1.18	5.85	2.61	50
CBS	0.96	2.31	2.24	0

Figure 4. Quotients between successive size-classes (diameter at breast height; dbh) in 5-cm intervals for three co-dominant species (a–c) and three dominant species (d–f) in the 20-ha forest dynamics plot at Dinghushan, China. *Cryptocarya chinensis* (a); *Syzygium rehderianum* (b); *Acmena acuminatissima* (c); *Castanopsis chinensis* (d); *Schima superba* (e); *Engelhardia roxburghiana* (f).

surrounding the reserve (Laurance *et al.* 2012). Of these, topography most distinguishes Dinghushan from the other forest dynamics plots. The elevation of Dinghushan plot varies from 230 m to 470 m and contains numerous extremely steep slopes (Wang *et al.* 2009). Topography is therefore considerably more complicated than the other forest plots, with elevation differences of less than 40 m in Changbaishan, Pasoh and BCI plots. We suggest that greater topographic variation in the Dinghushan plot may

contribute to greater demographic dynamism than the other forest dynamics plots. Comparison of demographic rates among forest dynamics plots also indicates that Dinghushan has a relatively low basal area of 26.6 m² ha⁻¹ compared with approximately 30 m² ha⁻¹ in Pasoh and Barro Colorado, and 44.5 m² ha⁻¹ in Changbaishan. Dinghushan also had the fastest species turnover rate and largest exponential mortality coefficient of the forest plots compared (Table 2). Aside from recruitment, which was

Figure 5. Transition probability of an individual grow to the next consecutive size-class (P_{xy}) for three co-dominant species, *Cryptocarya chinensis*, *Syzygium rehderianum* and *Acmena acuminatissima* (a) and dominant species, *Castanopsis chinensis*, *Schima superba* and *Engelhardia roxburghiana* (b) during 2005–2010 period in the 20-ha forest dynamics plot at Dinghushan, China.

Figure 6. Examples of differences between the spatial pattern of surviving and dead individuals of species in the 20-ha forest dynamics plot at Dinghushan, China. The solid line indicates the observed difference and the dashed lines indicate the 2.5% and 97.5% percentiles of the distribution of the difference computed on 99 random assignments of the labels surviving and dead. K_1 : univariate K function for the pattern of surviving individuals. K_2 : univariate K function for the pattern of dead individuals. K_{12} : bivariate K function for the bivariate pattern of surviving and dead individuals. Difference of aggregation between surviving and dead individuals (a and b, *Neolitsea umbrosa* and *Aporosa yunnanensis*). Positive departures denote surviving individuals are more aggregated than dead individuals, vice versa. Evaluation of the tendency of surviving individuals to be surrounded by other surviving individuals of the same species (c and d, *Blastus cochinchinensis* and *Cryptocarya chinensis*). Evaluation of the tendency of dead individuals to be surrounded by other dead individuals of the same species (e and f, *Syzygium rehderianum* and *Cryptocarya concinna*). A positive departure represents individuals that are surrounded by more of the same type of individuals than expected by chance, and a negative departure represents individuals that are surrounded by more of the other type of individuals (c–f).

the only demographic rate that was fairly similar among the forest plots, the subtropical forest at Dinghushan is highly dynamic.

Our data revealed sharply contrasting size-class distributions between dominant and co-dominant species. Although a reverse J-shaped size-class distribution is normally considered to be stable, and a bell-shaped size-class distribution is normally considered to be a warning of population decline (Condit *et al.* 1998), there is some evidence that this may not hold true for some species and must be considered in combination with recruitment of individuals into successive size classes. For example, Venter & Witkowski (2010) reported that the large and long-lived South African *Adansonia digitata*, albeit from a

very different forest type, exhibits an approximately bell-shaped size-class distribution. Yet they also reported that there was no significant reduction of fruit production in large trees, and that mortality rate was extremely low. In addition, young individuals had much higher RGR than old individuals (Dhillon & Gustad 2004). These authors reasoned that bell-shaped size-class distributions may not be a concern for large and long-lived species because they can maintain current populations with only a few recruits. Bell-shaped size-class distributions thus may signify episodic recruitment rather than a declining population. Our calculated quotients between successive size-classes and permutation index values suggest unstable results for dominant species (Figure 4).

Figure 7. Examples of interspecific spatial associations between all individuals and dead individuals in Dinghushan plot. The dotted line is the observed $L(r)$ and the solid lines represent the simulations envelopes under the null model. Significant associations occur at scales where the observed $L(r)$ exceeds the simulated envelopes. The observed positive departure of $L(r)$ from the envelopes indicates that dead individuals of a species tend to be surrounded by more interspecific individuals than expected by chance within a given distance, and a negative departure of $L(r)$ from the envelopes indicates that dead individuals of a species tend to be surrounded by less interspecific individuals than expected by chance within a given distance. *Lindera chunii*–*Blastus cochinchinensis*, positive association (a); *Memecylon ligustrifolium*–*Blastus cochinchinensis*, negative association (b); *Sarcosperma laurinum*–*Blastus cochinchinensis*, positive association at small scales and negative association at large scales (c); *Craibiodendron kwangtungense*–*Blastus cochinchinensis*, negative association at small scales but positive association at large scales (d).

However, individual sizes of dominant species were much larger than other species and they appear to survive for several hundred years. In addition, seed traps indicate that adult fruit production by dominant species is much greater than sub-dominant species (Ye *et al.* unpubl. data), and seedling recruitment was not deficient (Ye *et al.* unpubl. data). Therefore, dominant species in Dinghushan may successfully maintain a stable bell-shaped size class distribution.

Other factors that could contribute to stable bell-shaped size class distributions among dominant species are the very high RGR found in saplings (Figure 3d–f) and the increasing P_{xy} with increasing size-classes (Figure 5b) at Dinghushan. Thus RGR may be one of the causes of the bell-shaped size class distribution because stems of dominant species had high RGR during the sapling phase, but it decreased rapidly once they entered the intermediate size classes (Figure 3d–f). This is consistent with other

studies demonstrating rapidly declining growth rates of tropical trees (Condit *et al.* 1998, Dhillon & Gustad 2004), and offers an explanation for the peak in intermediate-size stems. If stems pass fleetingly through the sapling phase, but have less of a chance of growing into the largest dbh class, a bell-shaped size-class distribution would develop. Size-class distributions for dead stems were also close to bell-shaped for dominant species, and the number of dead stems was positively significantly correlated with the number of stems in each size-class ($R = 0.615$). Thus recent mortality does not appear to be a reason for the bell-shaped size-class distribution. Rather, our data points to variation in RGR among size classes that reinforces the bell-shaped size-class distribution. The transition probabilities among dominant species also contributed to maintaining a stable population with a bell-shaped size-class distribution. Mean P_{xy} of dominant species were larger than co-dominant species, and P_{xy} increased as

size-class increased (Figure 5b), which indicates that the population can retain a certain amount of individuals, particularly large individuals. For *Castanopsis chinensis* and *Schima superba*, P_{xy} had a peak in the second size class. Saplings can quickly grow to the next size class for these species, which supports our conclusion that dominant species can maintain current populations with only a few recruits.

Tree mortality is one of the most important factors influencing forest dynamics (Lewis *et al.* 2004). Spatial pattern analysis is considered an effective tool to research tree mortality because it reveals many of the processes and mechanisms of forest dynamics (de la Cruz *et al.* 2008). The spatial segregation hypothesis can be used for explaining species coexistence mechanisms through spatial analyses (Chesson 2000). This hypothesis suggests that intraspecific aggregation leads to interspecific segregation, and as a result, competition occurs mostly among intraspecific individuals in the community rather than interspecific individuals. Furthermore, this hypothesis predicts that competitively superior species will be suppressed, preventing the elimination of competitively inferior species and promoting species coexistence in the community (Chesson 2000, Tilman 1994). Our results supported this hypothesis. In the analysis of spatial associations between all individuals and dead individuals, we found very strong spatial associations between all individuals and dead individuals in both intra- and interspecific cases with 100% and 93.7% of cases significantly departing from null models in intra- and interspecific cases, respectively. However, positive associations, which indicate competitive relationships, were more frequent in intraspecific (100%) than interspecific cases (44.7%). This suggests that any competition that induced tree mortality occurred more frequently in intraspecific rather than in interspecific associations, and that the death of the majority of individuals resulted from intraspecific competitive exclusion.

Previous studies in two tropical forest communities showed that tree mortality is regulated by intraspecific density-dependent processes not only for the earliest stage of plant establishment but also for large trees (Peters 2003), consistent with our results. We propose that conspecifics share pests and pathogens, but also resource requirements, and therefore experience intense competition among conspecifics for obtaining resources, which contributes to mortality (Burkey 1994, Janzen 1970, Nathan & Casagrandi 2004). Tree mortality reveals that interspecific relationships are more complicated than intraspecific relationships. In temperate forest, species of the same family, fruit type or habitat association had more frequent competitive associations than expected by chance, with facilitative associations more frequent for species sharing the same

canopy layer (Wang *et al.* 2010). This finding is not completely consistent with our results because we found that competitive associations were more frequent than facilitative associations for species sharing the same canopy layer (57.9% vs. 36.9%). We suggest that in Dinghushan species sharing the same canopy layer have similar resource requirements and tree mortality was associated with competition among the individuals in the same layer.

Our data also demonstrate that facilitative associations were more frequent than competitive associations between all individuals of species in upper layers and dead individuals of species in lower layers (53.5% vs. 38.3%). There is a possibility that upper-canopy species create a suitable environment for lower-stature species, and if canopy individuals die, the environment can become less hospitable and lead to death of subcanopy individuals (Flores & Jurado 2003). However, ontogenetic factors could also affect the outcome of facilitative interactions (Callaway & Walker 1997), and spatial scales should be included in the analyses because spatial processes and mechanisms may act on different scales (Wiegand *et al.* 2009).

In summary, Dinghushan forest appears more dynamic than Changbaishan, BCI and Pasoh based on comparisons of their demographic rates, but more studies are required to understand the mechanisms of differences in vital rates. Our data also indicate that it is not appropriate to predict population dynamics using size-class distribution alone, because other factors such as relative growth rate, individual size, transition probabilities and longevity should be considered for a complete picture. Finally, we found that tree mortality was much more frequently associated with intraspecific competitive exclusion and density dependence than interspecific interactions. Overall, the intraspecific effects observed in these forests appear to contribute to species coexistence.

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Appendix 1. Species list in the 20-ha Dinghushan Forest Dynamics Plot, China. Status a, b and c indicate species that were present in the two censuses (2005–2010), absent in the last census and present in the last census, respectively. Abundance 1 and Abundance 2 indicate the number of stems for each species in the first and the last census, respectively, 101 species that had at least 20 stems at the first measurement are included.

Species	Status	Abundance 1	Abundance 2	Rate of population change (% y ⁻¹)
<i>Aidia canthioides</i> (Champ. ex Benth.) Masamune	a	6396	8513	5.7
<i>Syzygium rehderianum</i> Merr. & Perry	a	6259	5411	–2.9
<i>Blastus cochinchinensis</i> Lour.	a	4712	3567	–5.6
<i>Cryptocarya concinna</i> Hance	a	4552	3990	–2.6
<i>Ardisia quinqueгона</i> Bl.	a	4198	3658	–2.8
<i>Aporosa yunnanensis</i> (Pax & Hoffm.) Metc.	a	4098	3078	–5.7
<i>Cryptocarya chinensis</i> (Hance) Hemsl.	a	3588	3318	–1.6
<i>Craibiodendron kwangtungense</i> S. Y. Hu	a	3390	1835	–12.3
<i>Ormosia glaberrima</i> Y. C. Wu	a	2859	2458	–3.0
<i>Castanopsis chinensis</i> Hance	a	2844	2701	–1.0
<i>Schima superba</i> Gardn. & Champ.	a	2545	2086	–4.0
<i>Lindera metcalfiana</i> Allen	a	2491	1175	–15.0
<i>Lindera chunii</i> Merr.	a	2305	1048	–15.8
<i>Xanthophyllum hainanense</i> Hu	a	2014	1956	–0.6
<i>Acmena acuminatissima</i> (Bl.) Merr. & Perry	a	1982	1831	–1.6
<i>Sarcosperma laurinum</i> (Benth.) Hook. f.	a	1727	1501	–2.8
<i>Rhododendron henryi</i> Hance	a	1712	1357	–4.6
<i>Neolitsea umbrosa</i> (Nees) Gamble	a	1482	574	–19.0
<i>Memecylon ligustrifolium</i> Champ.	a	1362	1337	–0.4
<i>Mischocarpus pentapetalus</i> (Roxb.) Radlk.	a	1352	1336	–0.2
<i>Machilus breviflora</i> (Benth.) Hemsl.	a	1209	1023	–3.3
<i>Psychotria rubra</i> (Lour.) Poir.	a	955	486	–13.5
<i>Engelhardia roxburghiana</i> Wall.	a	909	734	–4.3
<i>Rapanea nerifolia</i> (S. & Z.) Mez	a	820	727	–2.4
<i>Macaranga sampsoni</i> Hance	a	793	766	–0.7
<i>Carallia brachiata</i> (Lour.) Merr.	a	753	996	5.6
<i>Garcinia oblongifolia</i> Champ.	a	661	81	–42.0
<i>Ilex ficoidea</i> Hemsl.	a	651	685	1.0
<i>Canthium dicoccum</i> (Gaertn.) Teysm. & Binnend.	a	624	416	–8.1
<i>Eurya macartneyi</i> Champ.	a	582	432	–6.0
<i>Machilus chinensis</i> (Champ. ex Benth.) Hemsl.	a	543	450	–3.8
<i>Syzygium levinei</i> (Merr.) Merr. & Perry	a	446	426	–0.9
<i>Artocarpus styracifolius</i> Pierre	a	427	414	–0.6
<i>Syzygium championii</i> (Benth.) Merr. & Perry	a	420	350	–3.6
<i>Canarium album</i> (Lour.) Raeuch.	a	385	409	1.2
<i>Diplospora dubia</i> (Lindl.) Masam.	a	367	342	–1.4
<i>Elaeocarpus dubius</i> A. DC.	a	350	480	6.3
<i>Pithecellobium lucidum</i> Benth.	a	328	272	–3.7
<i>Gironniera subaequalis</i> Planch.	a	318	328	0.6
<i>Euonymus laxiflora</i> Champ. ex Benth.	a	317	308	–0.6
<i>Neolitsea cambodiana</i> Merr. & Chun	a	316	233	–6.1
<i>Diospyros eriantha</i> Champ. ex Benth.	a	301	151	–13.8

Appendix 1. Continued

Species	Status	Abundance 1	Abundance 2	Rate of population change (% y ⁻¹)
<i>Diospyros morrisiana</i> Hance	a	301	283	-1.2
<i>Castanopsis fissa</i> (Champ.) R. & W	a	291	505	11.0
<i>Machilus velutina</i> Champ. ex Benth.	a	267	119	-16.2
<i>Acronychia pedunculata</i> (Linn.) Miq.	a	251	174	-7.3
<i>Litsea verticillata</i> Hance	a	230	139	-10.1
<i>Schefflera octophylla</i> (Lour.) Harms	a	206	188	-1.8
<i>Meliosma rigida</i> Sieb. & Zucc.	a	201	155	-5.2
<i>Ilex triflora</i> Bl.	a	193	169	-2.7
<i>Reevesia thyrsoidea</i> Lindl.	a	192	161	-3.5
<i>Elaeocarpus sylvestris</i> Poir.	a	181	113	-9.4
<i>Pinus massoniana</i> Lamb.	a	174	148	-3.2
<i>Nephelium chryseum</i> Bl.	a	170	105	-9.6
<i>Chrysophyllum lanceolatum</i> (Bl.) A. DC. var. <i>stellatocarpon</i> P. Royen	a	169	149	-2.5
<i>Mallotus paniculatus</i> (Lam.) Muell. Arg.	a	162	321	13.7
<i>Photinia prunifolia</i> (Hook. & Arn.) Lindl.	a	161	75	-15.3
<i>Ilex chapaensis</i> Merr.	a	139	127	-1.8
<i>Microdesmis caseariifolia</i> Planch.	a	139	132	-1.0
<i>Symplocos wikstroemiifolia</i> Hayata	a	136	94	-7.4
<i>Pygeum topengii</i> Merr.	a	121	143	3.3
<i>Antidesma japonicum</i> Sieb. & Zucc.	a	108	54	-13.9
<i>Melastoma sanguineum</i> Sims.	a	105	72	-7.5
<i>Itea chinensis</i> Hook. & Arn.	a	86	50	-10.8
<i>Bridelia fordii</i> Hemsl.	a	85	92	1.6
<i>Ficus variolosa</i> Lindl. ex Benth.	a	76	59	-5.1
<i>Helicia reticulata</i> W. T. Wang	a	73	39	-12.5
<i>Rhododendron mariae</i> Hance	a	70	40	-11.2
<i>Archidendron turgidum</i> (Merrill) I. C. Nielsen	a	70	53	-5.6
<i>Evodia lepta</i> (Spreng.) Merr.	a	63	60	-1.0
<i>Litsea cubeba</i> (Lour.) Pers.	a	62	39	-9.3
<i>Ficus esquiroliana</i> Levl.	a	58	54	-1.4
<i>Sterculia lanceolata</i> Cav.	a	58	67	2.9
<i>Croton lachnocarpus</i> Benth.	a	57	51	-2.2
<i>Pterospermum heterophyllum</i> Hance	a	56	55	-0.4
<i>Machilus kwangtungensis</i> Yang	a	50	31	-9.6
<i>Enkianthus quinqueflorus</i> Lour.	a	50	39	-5.0
<i>Ilex championii</i> Loes.	a	50	43	-3.0
<i>Syzygium jambos</i> (Linn.) Alston	a	50	43	-3.0
<i>Lasianthus chinensis</i> (Champ.) Benth.	a	49	28	-11.2
<i>Machilus phoenicis</i> Dunn	a	49	36	-6.2
<i>Homalium cochinchinense</i> (Lour.) Drucc	a	46	28	-9.9
<i>Antidesma microphyllum</i> Hemsley	a	43	30	-7.2
<i>Mangifera indica</i> Linn.	a	43	34	-4.7
<i>Tarenna mollissima</i> (Hook. & Arn.) Rob.	a	41	27	-8.4
<i>Casearia villilimba</i> Merr.	a	38	27	-6.8
<i>Caryota ochlandra</i> Hance	a	38	48	4.7
<i>Memecylon nigrescens</i> Hook. & Arn.	a	37	36	-0.5
<i>Ormosia semicastrata</i> Hance	a	33	24	-6.4
<i>Gardenia jasminoides</i> J. Ellis	a	32	30	-1.3
<i>Macaranga bracteata</i> Merr.	a	31	31	0.0
<i>Schoepfia chinensis</i> Gardn. & Champ.	a	28	19	-7.8
<i>Laurocerasus phaeosticta</i> (Hance) Schneid.	a	28	36	5.0
<i>Calophyllum membranaceum</i> Gardn. & Champ.	a	27	11	-18.0
<i>Aquilaria sinensis</i> (Lour.) Gilg	a	26	18	-7.4
<i>Canthium horridum</i> Bl.	a	26	34	5.4
<i>Sapium discolor</i> (Champ. ex Benth.) Muell. Arg.	a	25	17	-7.7
<i>Magnolia paenetaluma</i> Dandy	a	25	19	-5.5
<i>Rhododendron simsii</i> Planch.	a	23	17	-6.0
<i>Pavetta hongkongensis</i> Bremek.	a	21	14	-8.1
<i>Glochidion wrightii</i> Benth.	a	20	10	-13.9

Appendix 1. Continued

Species	Status	Abundance 1	Abundance 2	Rate of population change (% y ⁻¹)
<i>Mallotus apelta</i> (Lour.) Muell. Arg.	b	—	—	—
<i>Ficus vasculosa</i> Wall. ex Miq.	a	—	—	—
<i>Ficus superba</i> (Miq.) Miq. var. <i>japonica</i> Miq.	a	—	—	—
<i>Microcos paniculata</i> Linn.	a	—	—	—
<i>Pseudosasa amabilis</i> (McClure) Keng f.	a	—	—	—
<i>Litsea rotundifolia</i> Hemsl.				
var. <i>oblongifolia</i> (Nees) Allen	a	—	—	—
<i>Ehretia longiflora</i> Champ. ex Benth.	a	—	—	—
<i>Euonymus kwangtungensis</i> C.Y. Cheng	b	—	—	—
<i>Podocarpus fleuryi</i> Hickel	a	—	—	—
<i>Syzygium buxifolium</i> Hook. & Arn.	a	—	—	—
<i>Aralia spinifolia</i> Merr.	a	—	—	—
<i>Mallotus hookerianus</i> (Seem.) Muell. Arg.	a	—	—	—
<i>Ficus hirta</i> Vahl	a	—	—	—
<i>Clerodendrum cyrtophyllum</i> Turcz.	a	—	—	—
<i>Zanthoxylum myriacanthum</i> Wall. ex Hook. f.	a	—	—	—
<i>Rhododendron tingwuense</i> Tam	b	—	—	—
<i>Elaeocarpus decipiens</i> Hemsl.	a	—	—	—
<i>Garcinia multiflora</i> Champ.	a	—	—	—
<i>Ormosia fordiana</i> Oliv.	a	—	—	—
<i>Citrus reticulata</i> Blanco	a	—	—	—
<i>Eurya groffii</i> Merr.	b	—	—	—
<i>Hovenia acerba</i> Lindl.	b	—	—	—
<i>Pittosporum glabratum</i> Lindl.	a	—	—	—
<i>Symplocos lancifolia</i> Sieb. & Zucc.	a	—	—	—
<i>Syzygium kwangtungense</i> (Merr.) Merr. & Perry	a	—	—	—
<i>Lindera kwangtungensis</i> (Liou) Allen	a	—	—	—
<i>Clerodendrum fortunatum</i> Linn.	a	—	—	—
<i>Adenanthera pavonina</i>				
var. <i>microsperma</i> (Teijsm. Binnend.) Nielsen	b	—	—	—
<i>Alchornea trewioides</i> (Benth.) Muell. Arg.	a	—	—	—
<i>Syzygium hancei</i> Merr. & Perry	a	—	—	—
<i>Archidendron clypearia</i> (Jack) Nielsen	a	—	—	—
<i>Sloanea sinensis</i> (Hance) Hemsl.	a	—	—	—
<i>Ternstroemia gymnanthera</i> (Wight. & Arn.) Deddome	a	—	—	—
<i>Daphniphyllum oldhami</i> (Hemsl.) Rosenth.	a	—	—	—
<i>Euonymus nitidus</i> Benth.	b	—	—	—
<i>Antidesma fordii</i> Hemsl.	a	—	—	—
<i>Cratoxylum cochinchinense</i> (Lour.) Bl.	b	—	—	—
<i>Casearia glomerata</i> Roxb.	a	—	—	—
<i>Viburnum sempervirens</i> K. Koch	a	—	—	—
<i>Michelia foveolata</i> Merr. ex Dandy	a	—	—	—
<i>Zanthoxylum avicennae</i> (Lam.) DC.	a	—	—	—
<i>Litchi chinensis</i> Sonn.	a	—	—	—
<i>Machilus robusta</i> W. W. Sm.	a	—	—	—
<i>Wikstroemia indica</i> (Linn.) C. A. Mey.	a	—	—	—
<i>Maesa salicifolia</i> Walker	a	—	—	—
<i>Ixora chinensis</i> Lam.	a	—	—	—
<i>Dimocarpus longan</i> Lour.	b	—	—	—
<i>Rhododendron latoucheae</i> Franch. & Finet	a	—	—	—
<i>Ilex pubescens</i> Hook. & Arn.	a	—	—	—
<i>Glochidion eriocarpum</i> Champ. ex Benth.	a	—	—	—
<i>Eustigma balansae</i> Oliver	a	—	—	—
<i>Toxicodendron succedaneum</i> (Linn.) O. Kuntze	a	—	—	—
<i>Cordia dichotoma</i> Forst. f.	a	—	—	—
<i>Ficus pandurata</i> Hance	a	—	—	—
<i>Ficus variegata</i> Bl. var. <i>chlorocarpa</i> (Benth.) King	a	—	—	—
<i>Elaeocarpus japonicus</i> Siet. & Zucc.	b	—	—	—
<i>Ormosia pachycarpa</i> Champ. ex Benth.	a	—	—	—
<i>Trema tomentosa</i> (Roxb.) Hara	a	—	—	—
<i>Vitex quinata</i> (Lour.) Will.	a	—	—	—

Appendix 1. Continued

Species	Status	Abundance 1	Abundance 2	Rate of population change (% y ⁻¹)
<i>Eriobotrya fragrans</i> Champ. & Benth.	b	—	—	—
<i>Meliosma thorelii</i> Lecomte	a	—	—	—
<i>Catunaregam spinosa</i> (Thunb.) Tirv.	a	—	—	—
<i>Glycosmis parviflora</i> (Sims) Little	a	—	—	—
<i>Michelia maudiae</i> Dunn	b	—	—	—
<i>Raphiolepis indica</i> (Linn.) Lindl.	b	—	—	—
<i>Styrax suberifolius</i> Hook. & Arn.	b	—	—	—
<i>Ficus fistulosa</i> Reinw. ex Bl.	a	—	—	—
<i>Glochidion puberum</i> (Linn.) Hutch.	c	—	—	—
<i>Rhodomyrtus tomentosa</i> (Ait.) Hassk.	a	—	—	—
<i>Ilex rotunda</i> Thunb.	a	—	—	—
<i>Ficus nervosa</i> Heyne ex Roth	a	—	—	—
<i>Bridelia tomentosa</i> Bl.	c	—	—	—
<i>Canarium pimela</i> Leenh.	a	—	—	—
<i>Nauclea officinalis</i> (Pierre ex Pitard) Merr. & Chun	a	—	—	—
<i>Pentaphylax euryoides</i> Gardn. & Champ.	b	—	—	—
<i>Antidesma bunius</i> (Linn.) Spreng.	a	—	—	—
<i>Eurya nitida</i> Korth.	b	—	—	—
<i>Wikstroemia nutans</i> Champ.	a	—	—	—
<i>Trema angustifolia</i> (Planch.) Blume	a	—	—	—
<i>Symplocos adenopus</i> Hance	a	—	—	—
<i>Meliosma fordii</i> Hemsl.	a	—	—	—
<i>Lindera communis</i> Hemsl.	b	—	—	—
<i>Ilex micrococca</i> Maxim.	a	—	—	—
<i>Lasianthus attenuatus</i> Jack.	a	—	—	—
<i>Neolitsea aurata</i> (Hay.) Koidz.	a	—	—	—
<i>Neolitsea chuii</i> Merr.	a	—	—	—
<i>Artocarpus tonkinensis</i> A. Chev. ex Gagnep.	a	—	—	—
<i>Adinandra millettii</i> (Hook. & Arn.) Benth. & Hook.f. ex Hance	a	—	—	—
<i>Michelia skinneriana</i> Dunn	c	—	—	—
<i>Ilex cochinchinensis</i> (Lour.) Loes.	a	—	—	—
<i>Symplocos cochinchinensis</i> (Lour.) S. Moore	b	—	—	—
<i>Helicia cochinchinensis</i> Lour.	a	—	—	—
<i>Pterospermum lanceaefolium</i> Roxb.	a	—	—	—
<i>Clerodendrum japonicum</i> (Thunb.) Sweet	a	—	—	—
<i>Linociera ramiflora</i> Roxb.	a	—	—	—
<i>Elaeocarpus chinensis</i> Hook. ex Benth.	b	—	—	—
<i>Oreocnide frutescens</i> (Thunb.) Miq.	b	—	—	—