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Ecological processes maintaining differential tree species distributions in an Australian subtropical rain forest: implications for models of species coexistence

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ABSTRACT. All stems ≥ 1 cm dbh were measured, tagged, mapped and identified on a 1-ha plot of rain forest at Gambubal State Forest, south-east Queensland, Australia. The spatial patterns and size class distributions of 11 common tree species on the plot were assessed to search for mechanisms determining their distribution and abundance. The forest was species-poor in comparison to many lowland tropical forests and the common species are therefore present at relatively high densities. Despite this, only limited evidence was found for the operation of density-dependent processes at Gambubal. *Daphnandra micrantha* saplings were clumped towards randomly spaced adults, indicating a shift of distribution over time caused by differential mortality of saplings in these adult associated clumps. Ordination of the species composition in 25-m × 25-m subplots revealed vegetation gradients at that scale, which corresponded to slope across the plot. Adult basal area was dominated by a few large individuals of *Sloanea woollsii* but the comparative size class distributions and replacement probabilities of the 11 common species suggest that the forest will undergo a transition to a more mixed composition if current conditions persist. The current cohort of large *S. woollsii* individuals probably established after a large-scale disturbance event and the forest has not attained an equilibrium species composition.

KEY WORDS: density-dependence, spatial distribution, tropical trees, *Sloanea woollsii*, Queensland

INTRODUCTION

Differences in the spatial distribution of coexisting tropical tree species reflect their individualistic responses to biotic and abiotic environmental factors, and

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may play a role in the maintenance of species richness (Aubréville 1971, Chesson 1986, Grubb 1986, Kareiva 1986, Levin 1974, Swaine & Hall 1988, Webb *et al.* 1972). Differences at two spatial scales can be distinguished (Manokaran *et al.* 1992), and these may be determined by separate causes.

At a very localized scale, some species are highly aggregated in their distribution, while others are not. Janzen (1970) and Connell (1971) independently published models to explain the prevention of single species aggregation, and thus the displacement of other species, by host specific predators and pathogens which cause elevated mortality of seeds and seedlings near to the parent trees. Several studies have found evidence to support this type of model, e.g. the density-dependent effects of a canker disease on *Ocotea whitei* at Barro Colorado Island (BCI), Panama (Gilbert *et al.* 1994). The graphical model of Janzen was examined by Hubbell (1980), and by rescaling the axes he adapted it to account for the finding that adult distributions of many tropical forest trees are clumped. The rescaling showed that maximum recruitment was adjacent to the adult, not at intermediate distances, as envisaged by Janzen (1970). This conclusion was supported by Condit *et al.* (1992a) who rejected the Janzen–Connell hypothesis, finding that most species at BCI showed no pattern of distribution, or were attracted to large conspecific adults (as found in several other studies, e.g. Connell 1978, He *et al.* 1997). However, more recent analysis of the BCI data has found significant density-dependent effects on recruitment, many extremely strong, for 67 out of the 84 most common species there (Wills *et al.* 1997). Limited- or clump-dispersal will also result in localized aggregation (Howe 1989), and will interact with density-dependent factors to determine spatial distribution.

At a broader scale, spatial distribution patterns of tropical trees may be determined by gradients in resource availability. Patterns in tropical forest community composition were first documented in the 1960s (e.g. Ashton 1969), and have now been shown to reflect differences in the availability of either water (Newbery *et al.* 1996) or nutrients (Baillie *et al.* 1987, Gartlan *et al.* 1986).

In most cases these scales of spatial variation are readily distinguished, since patchiness determined by the interaction between dispersal and density-dependent mortality would be nested within gradients in distribution determined by resource availability. The exception occurs among species that are strongly dependent on canopy gaps for regeneration. For these species, the scale of patchiness in the critical resource (in this case light) corresponds approximately to the scale of patchiness determined by dispersal limitation in other species. There may also be an interaction between dispersal limitation and response to light, which is reflected in spatial distribution (Augspurger 1983).

The mechanisms determining spatial pattern and maintenance of species richness can be inferred from differences in the spatial distributions of juvenile and adult trees (Hubbell & Foster 1986a, b), and the dispersion of juveniles relative to adults (Hamill & Wright 1986, Hubbell & Foster 1987). Much of the important research on density-dependent processes and spatial pattern analysis in tropical rain forest has been based on data from BCI. Although the species richness of trees at BCI is low by comparison with less seasonal tropical forests (Condit *et al.* 1996), it is considerably higher than that of the subtropical rain forests of Queensland. There is a clear need for more research on the factors determining spatial patterns in these less species-rich forests, where mean stem densities per species are likely to be greater. The compensatory recruitment hypothesis predicts that the incidence of density-dependent processes will be greater in less species-rich forest (Connell *et al.* 1984).

Inferences about the equilibrium status of a forest can be drawn from the size class distributions of the component species and juvenile species composition under adult crowns, and such work has a long history in forest ecology (e.g. Horn 1971). If species replacement probabilities, predicted by either technique, do not reflect current adult composition, we expect to see future changes in species composition, which would imply the forest to be in non-equilibrium, over the short-term at least.

The tropical and subtropical forests of Queensland, Australia, provide case studies of species-poor sites with a long history of research on the spatial distributions of trees and the importance of density dependent processes (Connell *et al.* 1984, Penfold & Lamb 1999, Webb *et al.* 1972). In this paper we report the results of a complete census of all stems ≥ 1 cm diameter at breast height (dbh) on a contiguous 1-ha plot of species-poor subtropical rain forest at Gambubal in south-eastern Queensland (59 species with stems ≥ 10 cm dbh in 5 ha). Working at Gambubal, but using a sampling system of small quadrats, Penfold & Lamb (1999) found evidence of negative density dependence in juvenile abundance in two of the most common species, with several species showing clumped distributions of juveniles close to adults.

In this study we have addressed the following questions: (1) Is there evidence for a greater incidence of density-dependent processes at Gambubal than at more species-rich rain forests? (2) Are the common species distributed at random across the site, or is there evidence for spatial pattern in response to environmental factors? (3) Do the size-class distributions of trees suggest that the forest composition is at equilibrium?

STUDY AREA AND SPECIES

Gambubal State Forest (28°14′ S, 152°24′ E) is located on the upper western slopes of the Great Dividing Range in south-east Queensland, Australia. The study plot was near the end of an east–west ridge (1100 m asl) and sloped at about 8° with a north-west aspect. The climate is cool subtropical. Rainfall and temperature data are available for the Queensland Forest Service (QFS) barracks, 6 km from the study site, at an elevation of 950 m above sea level. Mean annual rainfall is 1284 mm (19-y mean), with maximum falls in the summer months (January – April), varying from a mean monthly minimum of 35 mm in September to a maximum of 210 mm in April (both 6-y means). Annual rainfall at the study plot may be *c.* 200 mm greater than that at the QFS barracks, based on short-term records from both sites. Screen temperatures vary from a mean monthly minimum of 4.9 °C in July to a maximum of 25.2 °C in January. Minimum winter air temperatures cause light frosts most years. Frosts causing injuries to certain susceptible forest species, especially the larger leafed species (such as *Dendrocnide excelsa*) and those found in gaps, occur at intervals of several years (S. Howell, *pers. comm.*; Howell 1993). Prevailing winds are from the south-east, and tend to be moist, influencing the development of epiphytic and epilithic vegetation across the forest, with higher epiphyte loading found on trees of the south-east facing side of the 5-ha research site at Gambubal (Howell 1993). The site's location on the Southern Main Ridge is within Eastern Australia's major Tertiary volcanic province. The soils at the research site are derived from Superbus basalt, with a principal profile form of Gn4.11 (Northcote 1974). They are red in colour with a limited profile development of A1 horizon 20–40 cm deep, red, loam/clay loam enriched with organic matter, and B horizon (no A2 horizon) 2–6 m deep, thick red clay. The soils are acidic and intensive sampling over the 5 ha reveals pH values ranging between 4.3 and 6.1.

In 1989 a plot of just over 5 ha was established by the University of Queensland. All trees ≥ 30.0 cm girth at breast height (gbh) were identified, measured (dbh) and mapped within the research site. During the years 1958–1960 some light logging was conducted over parts of the site, but it is thought unlikely that any logging occurred in the 1 ha surveyed in this study (S. Howell, *pers. comm.*).

The vegetation type of the study plot is described as complex notophyll vine forest (Webb 1959), dominated by *Sloanea woollsii* (consistent with Floyd's [1989] description of a subtropical rain forest), with ecotonal communities (dominated by *Eucalyptus grandis* and *E. dunnii*, with an understorey of rain forest or sclerophyll forest species) and tall open forests (dominated by *Eucalyptus andrewsii* with a grass and low shrub understorey) within 100 m of the plot. Figure 1 shows the hectare surveyed in more detail, and the subdivision into 16 subplots, important for several of the tests conducted in this study.

The 11 species used in this study were ones for which reliable identifications of all individuals were available, and included the six most common species at the research site: *Acmena ingens*, *Daphnandra micrantha*, *Dendrocnide excelsa*, *Diploglottis cunninghamii*, *Doryphora sassafras*, *Melicope micrococca*, *Neolitsea australiensis*, *Orites excelsa*, *Polyosma cunninghamii*, *Sloanea woollsii* and *Zanthoxylum brachyacanthum*. They are described briefly in Table 1, and will be identified hereon by their genus name. *Dendrocnide* requires high light conditions for seed germination and seedling establishment (a pioneer *sensu* Swaine & Whitmore 1988).

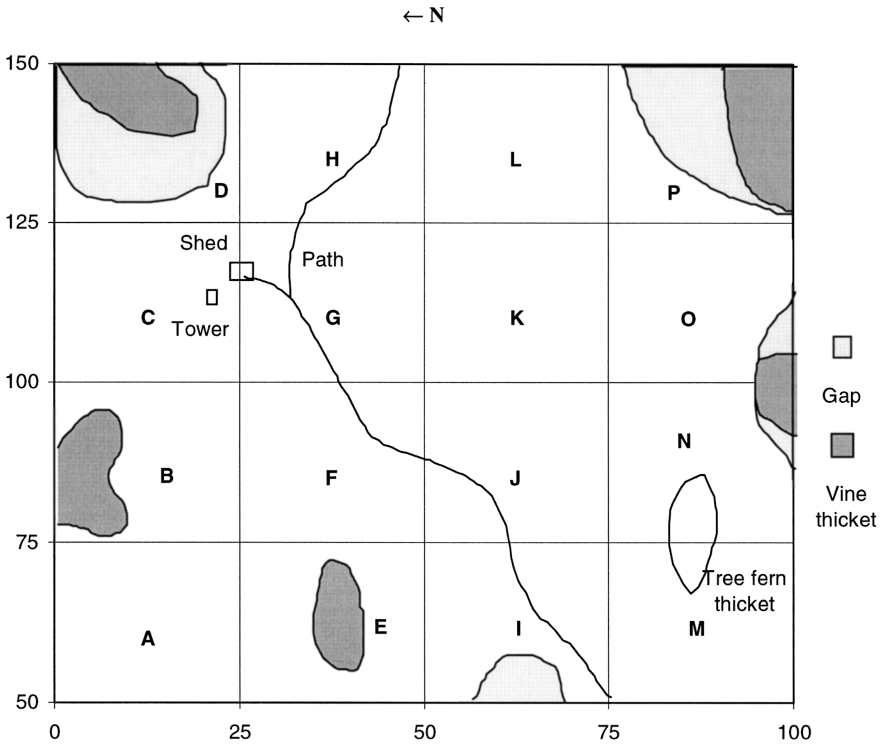


Figure 1. Map of the study plot at Gambubal State Forest, Australia. Features are drawn in approximate location, subplots are lettered A–P. Note the occurrences of the major gaps (light shading) in the north-east and south-east of the plot, and the gap created during the study, in subplot I. Co-ordinates are in metres and refer to the 5-ha research plot.

The other species can be considered as non-pioneers, but they will possess varying degrees of light demand for seedling establishment.

METHODS

A square area of 1 ha of the research site was surveyed, in 25-m × 5-m strips, in each of which all woody stems (excluding vines) 3–32 cm gbh, to encompass all stems 1–10 cm dbh, were tagged (if not already tagged), gbh was measured, identified (in the field or samples of leaf, fruit or flower taken for future identification) and plotted to ± 0.1 m on *x*- and *y*-axes (taking measurements perpendicular from strip-division tapes). Where individual plants were multi-stemmed (i.e. > 1 stem of ≥ 1 cm dbh), each stem was treated separately, but for analyses only the largest stem was considered. Prominent features of the vegetation (e.g. vine thickets), the major gaps (where open sky was visible from the forest floor, as distinguished by eye) and other features (e.g. paths, shed) of the forest were also mapped on the *x*- and *y*-axes. For ordination of species composition across the study plot, the area was divided into sixteen 25-m ×

Table 1. Characteristics of the 11 species studied at Gambubal, including total number of individuals and percentage composition of basal area (sapling and adult) in the 1-ha study plot.

	Family	Number of individuals		Percent basal area	
		≥ 1 < 10 cm dbh	≥ 10 cm dbh	≥ 1 < 10 cm dbh	≥ 10 cm dbh
Acmena ingens (F. Muell. ex C. Moore) Guymer & Hyland	Myrtaceae	281	19	7.4	3.0
Daphnandra micrantha (Tul.) Benth.	Monimiaceae	147	5	3.5	1.0
Dendrocnide excelsa (Wedd.) Chew	Urticaceae	6	18	0.8	2.2
Diploglottis cunninghamii (Hook.) Hook. F.	Sapindaceae	40	13	3.4	1.0
Doryphora sassafras Endl.	Monimiaceae	168	111	13.1	7.0
Melicope micrococca (F. Muell.) T. Hartley	Rutaceae	61	32	5.5	1.4
Neolitsea australiensis Kosterm	Lauraceae	140	23	6.2	1.1
Orites excelsa R. Br.	Proteaceae	168	37	8.0	3.8
Polyosma cunninghamii Bennett	Escalloniaceae	127	46	6.8	1.7
Sloanea woollsii F. Muell.	Elaeocarpaceae	10	70	0.7	60.7
Zanthoxylum brachyacanthum F. Muell.	Rutaceae	119	40	11.0	1.0
Other species		1604	124	33.4	16.2

25-m subplots (see Figure 1). Saplings were defined as individuals with dbh $\geq$ 1 cm $<$ 10 cm, and adults as individuals with dbh $\geq$ 10 cm.

Study plot composition

The distribution of total sapling and adult basal areas are presented as contour plots, using the surface chart function of Microsoft Excel 97 (version 4.10.98, Microsoft Corporation). Basal area density of 10-m × 10-m blocks of forest centred on each intersection of a 10-m × 10-m grid across the 1-ha study plot was used to generate these graphs. To investigate the presence of gradients of floristic composition across the study plot, detrended correspondence analysis using DECORANA (Hill 1979, Hill & Gauch 1980) of saplings and adults of the 11 species in each subplot was conducted, using both numbers and basal area of individuals of each species in each of the 16 subplots (for adults, only basal area data were used as numbers were too low). Although the detrending and rescaling processes of DECORANA have been shown to flatten variation associated with underlying gradients, often represented by axes 2 and greater (e.g. Jongman *et al.* 1995, Minchin 1987), we used DECORANA in this study to investigate only the main gradient of variation in floristic composition, correlated with axis 1. Results are presented as ordination diagrams for species and subplots, which enable comparisons between species distribution and subplot floristic composition.

Investigation of spatial patterns

The spatial distribution of all saplings of the 11 study species across the study plot and all adults of the 11 study species across a 3-ha area totally encompassing the study plot were tested for clumping and over-dispersal using a method of univariate second-order spatial pattern analysis based on Ripley's (1976) *K*-function (methods used follow Haase 1995). This method considers all pairs of trees within a given radius of the focal individual: a circle of radius t is centred on each point and the number of neighbours in that circle are counted. For n points (plants) distributed in an area A, with a density $\lambda = n/A$, $\lambda K(t)$ gives the expected number of further points within the radius t of an arbitrary point. If the points are randomly (Poisson) distributed then $K(t) = \pi t^2$ and a plot of $\sqrt{K(t)}$ vs. t should be linear. The estimator of the function K(t) used is:

$$\hat{K}(t) = n^{-2} A \sum_{i \neq j} \sum w_{ij}^{-1} I_t \, (u_{ij})$$

where n is the number of plants in the plot, A is the area of the plot in m^2, I_t is a counter variable, u_{ij} is the distance between trees i and j, and w_{ij} is a weighting factor to correct for edge effects, the recommended method of edge correction described by Hasse (1995). K(t) was calculated separately for each distance t, for saplings from 0 – 30 m in 1-m increments, and for adults from 0 – 75 m in 3-m increments. Results are displayed as a plot of $\sqrt{[K(t)/\pi]} - t$ vs. t. To test for significant deviation away from a random distribution, Monte

Carlo computer generated data were used. To construct a 99% confidence envelope, 99 simulations were run, and the sample statistic could be compared to this envelope. If the sample statistic is positive and exceeds the confidence envelope, a clumped distribution can be assumed, if it is negative and exceeds the confidence envelope a dispersed or regular distribution can be assumed, and if it does not exceed the confidence limit a random distribution is assumed. These calculations were performed using a program obtained from P. Haase (see Haase 1995 for full details).

A very similar method of bivariate spatial pattern analysis was used to test for positive or negative associations between the distributions of two species, and between saplings and adults of the same species. A program was obtained from M. Moeur (see Moeur 1993) and was used for these analyses. For inter-species analyses data sets of the location of all individuals across the study site for the species concerned were used and for intra-species analyses the input files were locations of all saplings and all adults across the study site for each study species. The K(t) statistic was calculated for t = 0–30 m in 1-m increments, and again results were displayed as a plot of $\sqrt{[K(t)/\pi]} - t$ vs. t. Variation from a random distribution was tested using similar methods to those described above, but a confidence envelope of 95% was used for the intra-specific analyses.

Tree replacement probabilities

Tree replacement probabilities were estimated by calculating the basal area species composition (considering only the 11 species studied) of the sapling cohorts beneath the crowns of adults of each of the 11 species. Saplings associated with any one adult, which is an estimate of the under-crown sapling cohort of that adult, were found by calculating the closest adult neighbour for each sapling, and grouping all saplings that had the same adult as their nearest neighbour. This study considered composition using basal area of saplings, as this integrates the number and size of individuals. We consider this to be the best approximation to replacement probability for relatively small samples collected at only one point in time (as in this study). The association of each adult population with the 11 under-crown sapling cohorts was determined using the chi-squared test on observed counts of sapling basal area (of the 11 species, in cm^2) and expected counts based on the proportion of sapling basal area of each species on the plot. The results are presented as sapling basal area for individual species as a percentage of total sapling basal area for all species.

RESULTS

Structural characteristics of the forest

Within the study plot there were 538 trees ≥ 10 cm dbh, and 2871 stems 1–10 cm dbh, giving a total of 3409 stems ≥ 1 cm dbh. The number of individuals from the 11 species studied is summarized in Table 1. The size-class distribution of all trees in the study plot (Figure 2) shows a logarithmic decline, with some skewing above 80 cm dbh caused by the low numbers of individuals (only *Sloanea* grew to 80 cm dbh or more).

Size-class distributions for the 11 study species (Figure 3) show that the populations of *Acmena*, *Daphnandra*, *Orites* and *Neolitsea* were greatly dominated by saplings. *Diploglottis*, *Doryphora*, *Melicope*, *Polyosma* and *Zanthoxylum*, had a higher proportion of adults but were still dominated by saplings, while *Dendrocnide* and *Sloanea* had more adults than saplings and exhibited bimodial peaks in size.

With abundance expressed as the relative basal area composition of the sapling and adult size-classes (Table 1) the dominance of *Sloanea* (60.7% of adult basal area) and its poor representation among saplings (0.7%) become apparent. The pioneer, *Dendrocnide* was the only other species to have a higher adult percentage. *Polyosma*, *Zanthoxylum* and *Neolitsea* showed the highest sapling basal area relative to adult basal area. This was caused by these three species having the smallest maximum dbh of the 11 species studied.

Distribution of individuals and basal area across the study plot

For stems 1–10 cm dbh, basal area is much higher in the eastern half of the study plot, with a very low basal area in the south-west corner (Figure 4a). Observations at the study plot showed a more closed canopy in the western half of the plot, especially the south-west corner, and the major canopy gaps (distinguished by eye) mapped on the *x*- and *y*-axes (see Figure 1) were in the north-east and south-east corners. For stems ≥ 10 cm dbh, basal area distribution is less variable, with no clear pattern (Figure 4b).

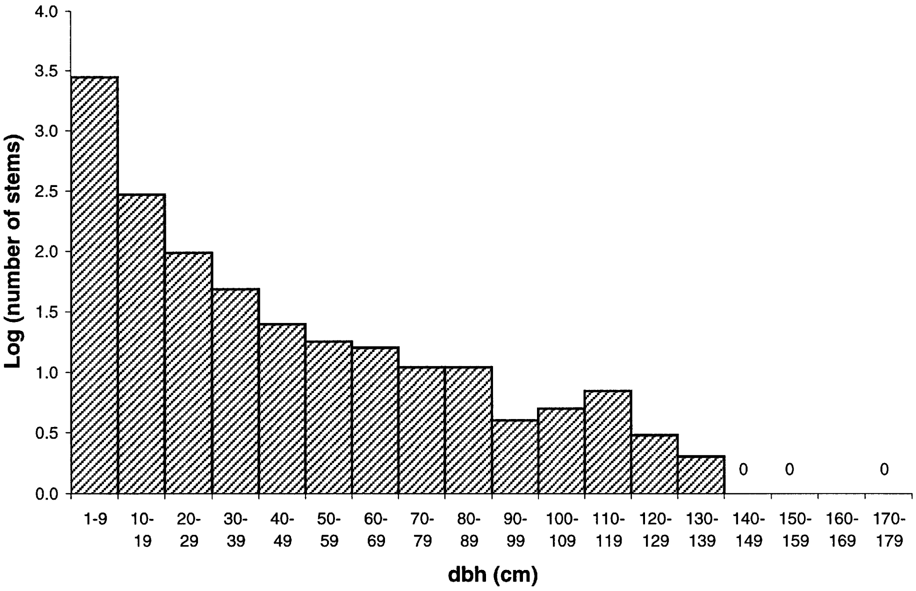


Figure 2. Size-class distribution for all stems ≥ 1 cm dbh in the 1-ha study plot, using a $\log_{10}$ scale.

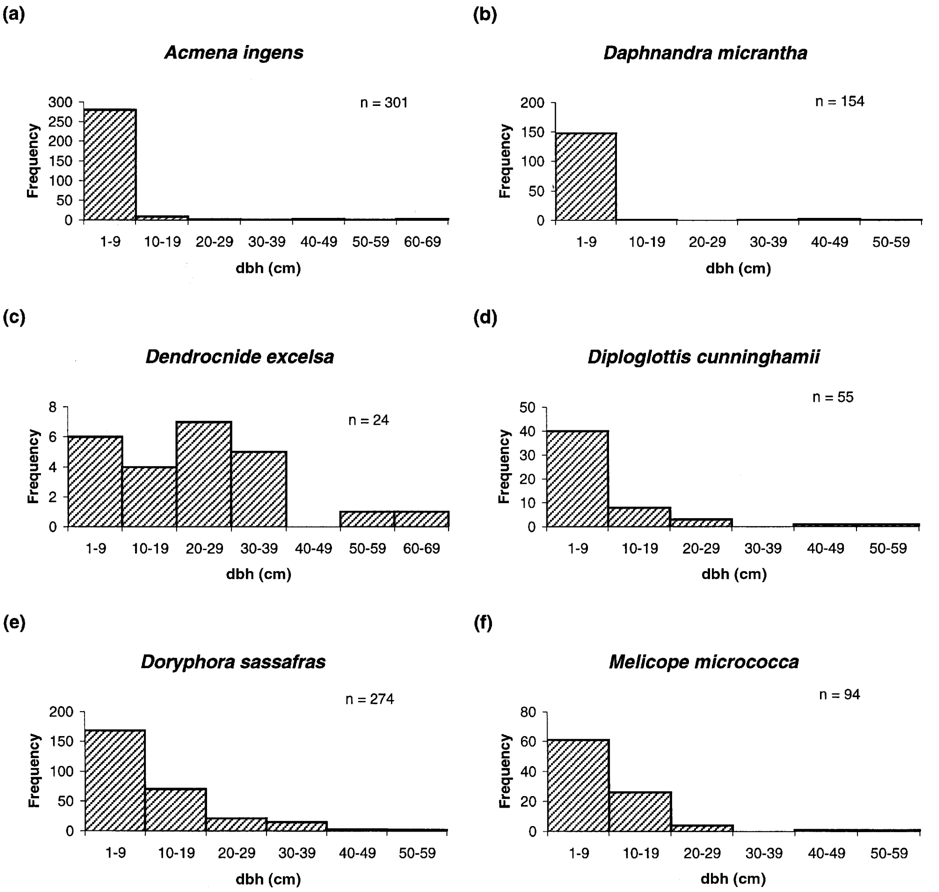


Figure 3. Dbh size-class distributions, and number (n) of individuals ≥ 1 cm dbh, in the study plot for (a) *Amena ingens*, (b) *Daphnandra micrantha*, (c) *Dendrocnide excelsa*, (d) *Diploglottis cunninghamii*, (e) *Doryphora sassafras*, (f) *Melicope micrococca*, (g) *Neolitsea australiensis*, (h) *Orites excelsa*, (i) *Polyosma cunninghamii*, (j) *Sloanea woollsii* and (k) *Zanthoxylum brachyacanthum*.

The species can be grouped according to maximum dbh recorded in this sample, with *Polyosma*, *Zanthoxylum* and *Neolitsea* attaining only 20–40 cm dbh, *Sloanea* attaining 175 cm dbh and the others being intermediate, attaining maximum dbh values between 50 and 70 cm dbh.

Ordination of sapling species composition (using basal area) revealed one major axis of variation (Figure 5a), with *Acmena* and *Polyosma* showing the most contrasting distributions across the plot (Figure 6). Ordination of subplots also revealed one major axis of variation (Figure 5b), which suggests that a north-west to south-east gradient in species composition was present. Similar results were obtained using numbers of individuals.

Ordination of species composition for adults also revealed one major axis of variation (Figure 7a), with *Acmena* and *Melicope* showing the most contrasting distributions (Figure 6). Ordination of subplots revealed A, B, C (and to some

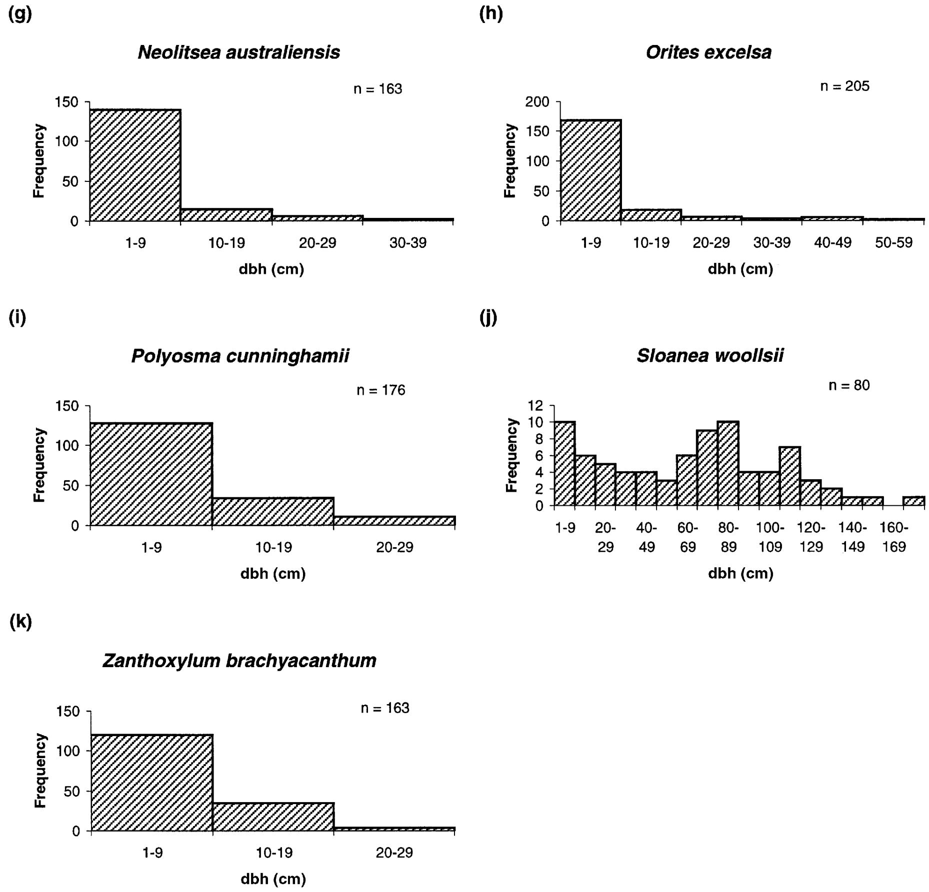


Figure 3. Continued.

extent F), comprising the north(west) of the plot, as outliers on axis 1 of the ordination (Figure 7b) suggesting that axis 1 correlates with some factor (accounting for a high degree of the adult species composition variance across the plot) causing a difference in adult species composition in the north(west) of the plot, while the rest of the plot was very uniform.

Bivariate spatial pattern analysis using Ripley's K(t) of distribution of species pairs supports the findings of the ordination. Examining the plots of $\sqrt{[K(t)/\pi]} - t$ vs. t (Figure 8) for species pairs with contrasting axis 1 scores (*Acmena–Polyosma*, *Daphnandra–Polyosma*, *Acmena–Doryphora* and *Daphnandra–Doryphora*) reveals that significant deviation of the sample statistic at negative values over at least some values of t occurs, suggesting that these species have complimentary distributions. Species pairs with similar axis 1 scores showed no deviation of the sample statistic from the confidence envelope (e.g. *Doryphora–Polyosma*) or a slight positive deviation (e.g. *Acmena–Daphnandra*), suggesting that the species pairs were distributed at random with regard to each other, or somewhat attracted, respectively.

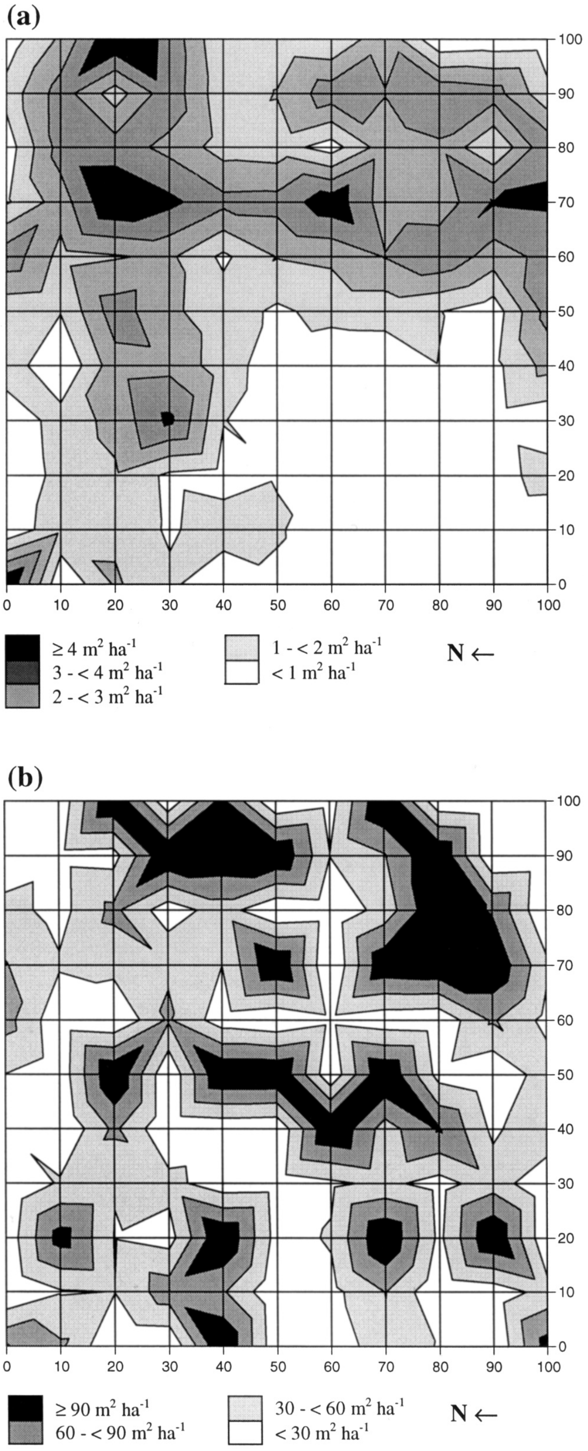


Figure 4. Contour maps of basal area ($m^2 ha^{-1}$) across the study plot for (a) saplings and (b) adults. Orientation (direction of north) indicated.

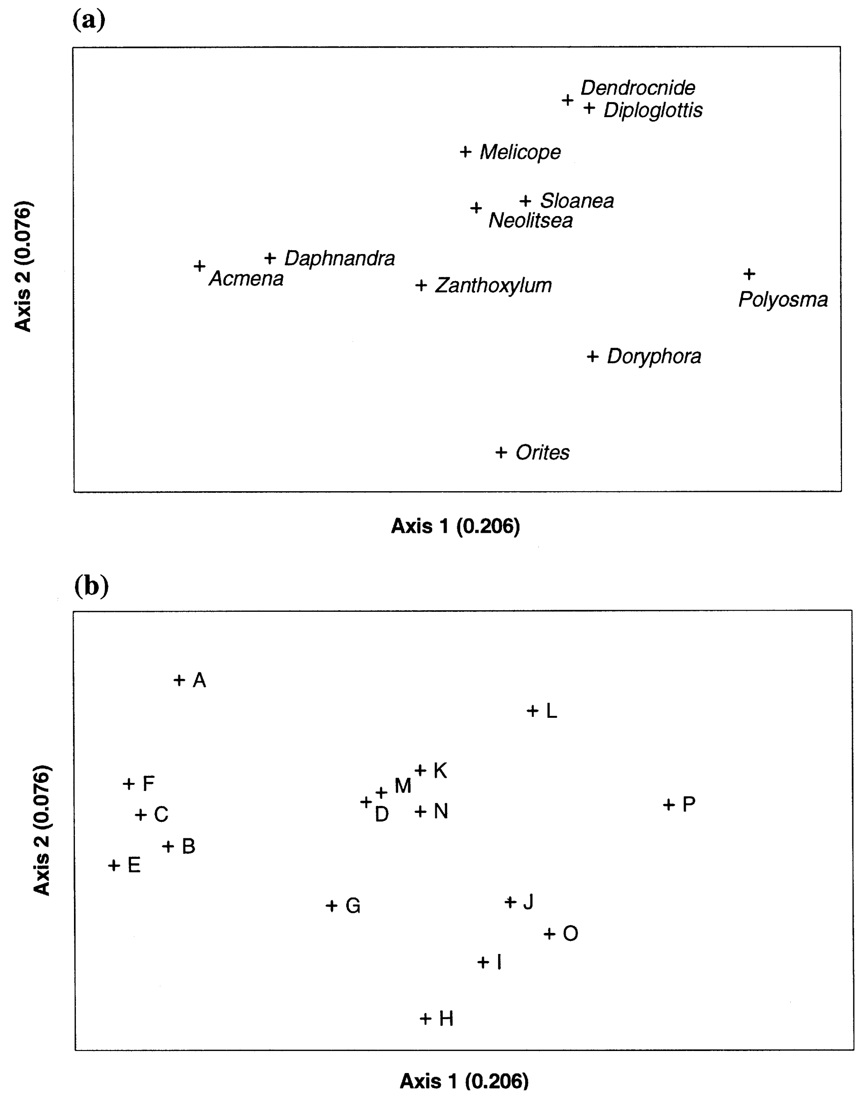
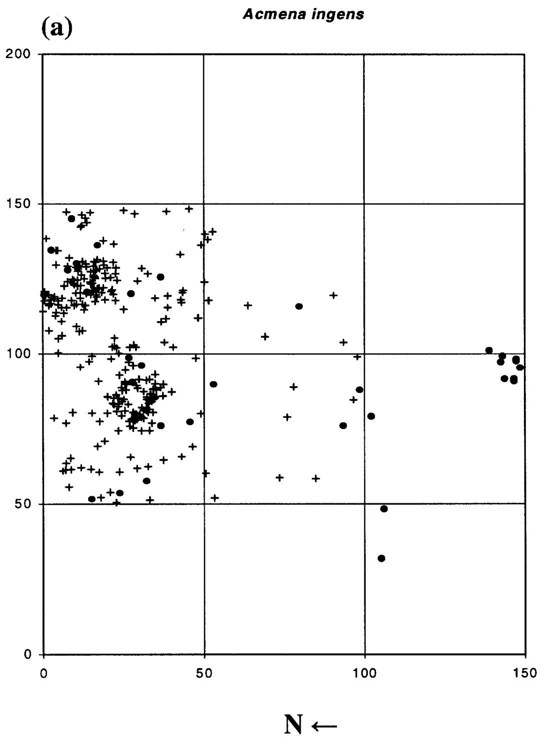


Figure 5. Ordination diagram for (a) species and (b) subplots, using species composition of each subplot based on sapling basal area. Eigenvalues for the axes are shown in brackets.

Dispersion of saplings and adults

Results of the univariate spatial pattern analysis using Ripley's K(t) for adults across a 3-ha area, and saplings across the 1-ha study site are summarized in Table 2. The plotted $\sqrt{[K(t)/\pi]} - t$ values for most species show the sample statistic deviates from the generated confidence envelopes with high positive values, indicating a significantly clumped distribution, over all or most of the range of t considered. The major exceptions were *Sloanea* and *Diploglottis*, for which the sample statistic was almost entirely within the confidence envelope, indicating random distribution patterns for both adults and saplings.



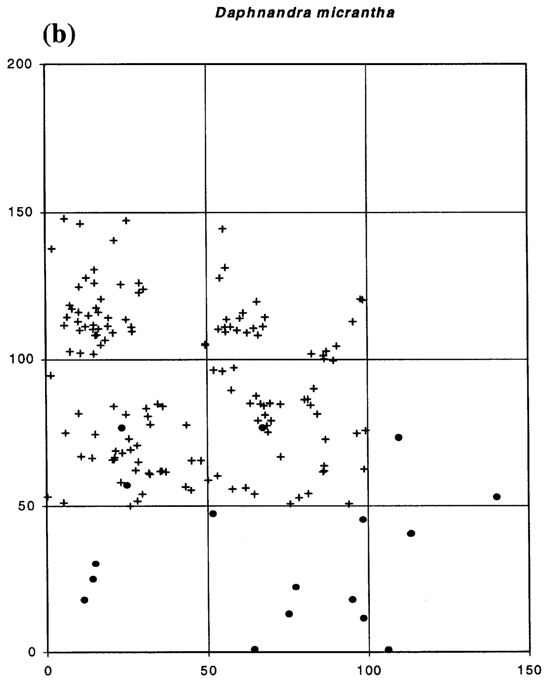


Figure 6. Distribution of all stems ≥ 1 cm dbh within the 1-ha study plot (x = 0–100, y = 50–150) and stems ≥ 10 cm dbh (adults) across a 3-ha area encompassing this study plot for (a) *Amena ingens*, (b) *Daphnandra micrantha*, (c) *Neolitsea autraliensis*, (d) *Polyosma cunninghamii* and (e) *Melicope micrococca*. ● = adults, + = saplings.

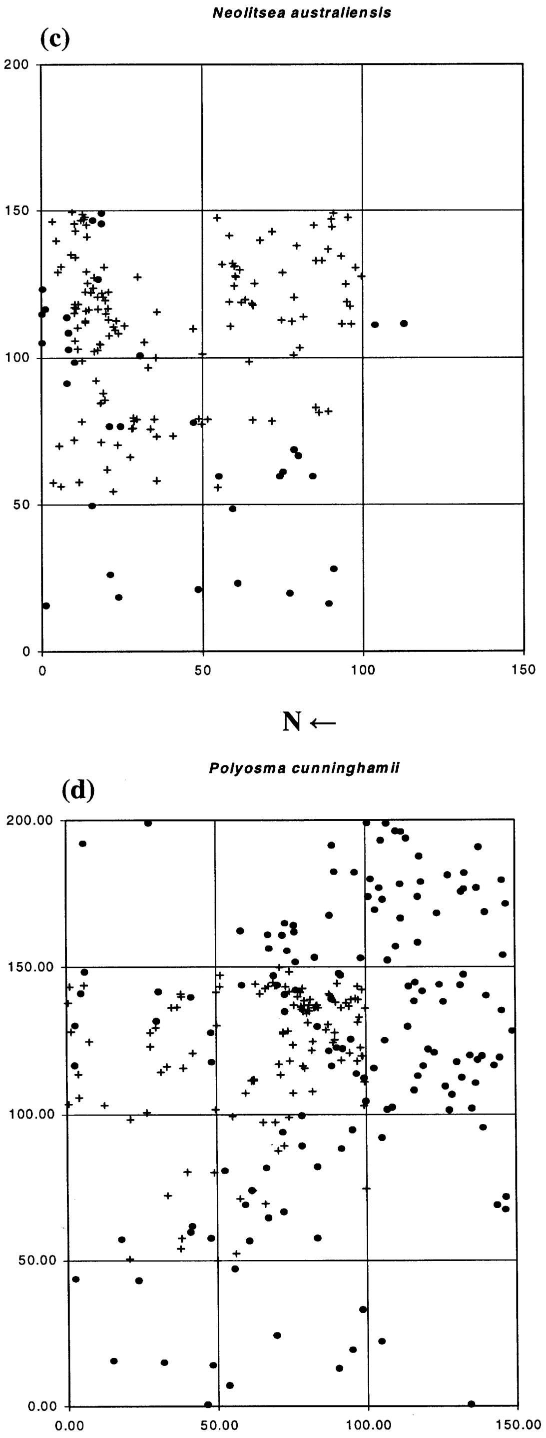


Figure 6 continued.

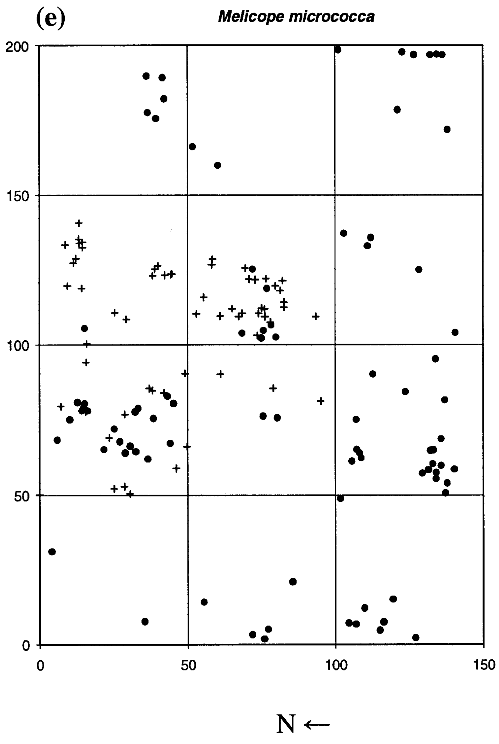


Figure 6 continued.

Dendrocnide also showed a mostly random distribution, but with clumping found at intermediate t values (15–45 m for adults, 9–15 m for saplings), but note should be taken of the small sample sizes for juveniles (n = 6). *Daphnandra* adults were clumped only at t > 30 m, due to its limited distribution on the western half of the 3-ha plot only. All of the seven species with ≥ 100 saplings (i.e. species common in the sapling cohort) showed significantly clumped sapling distributions over the entire range of t tested.

Dispersion of saplings relative to adults

Results of the bivariate spatial pattern analysis using Ripley's K(t) for saplings relative to adults for the 11 study species across the study area, are shown in Figure 9 and summarized in Table 2. Six species rarely or never produced a sample statistic exceeding the confidence envelope, suggesting that saplings and adults were distributed at random with respect to each other, while five species all exceeded the confidence envelope with positive values of the sample statistic over most of the range of t tested, suggesting that sapling distributions were biased towards adults.

Tree replacement probabilities

The composition of the under-crown sapling basal area, considering only saplings and adults of the 11 species studied suggests that most species are

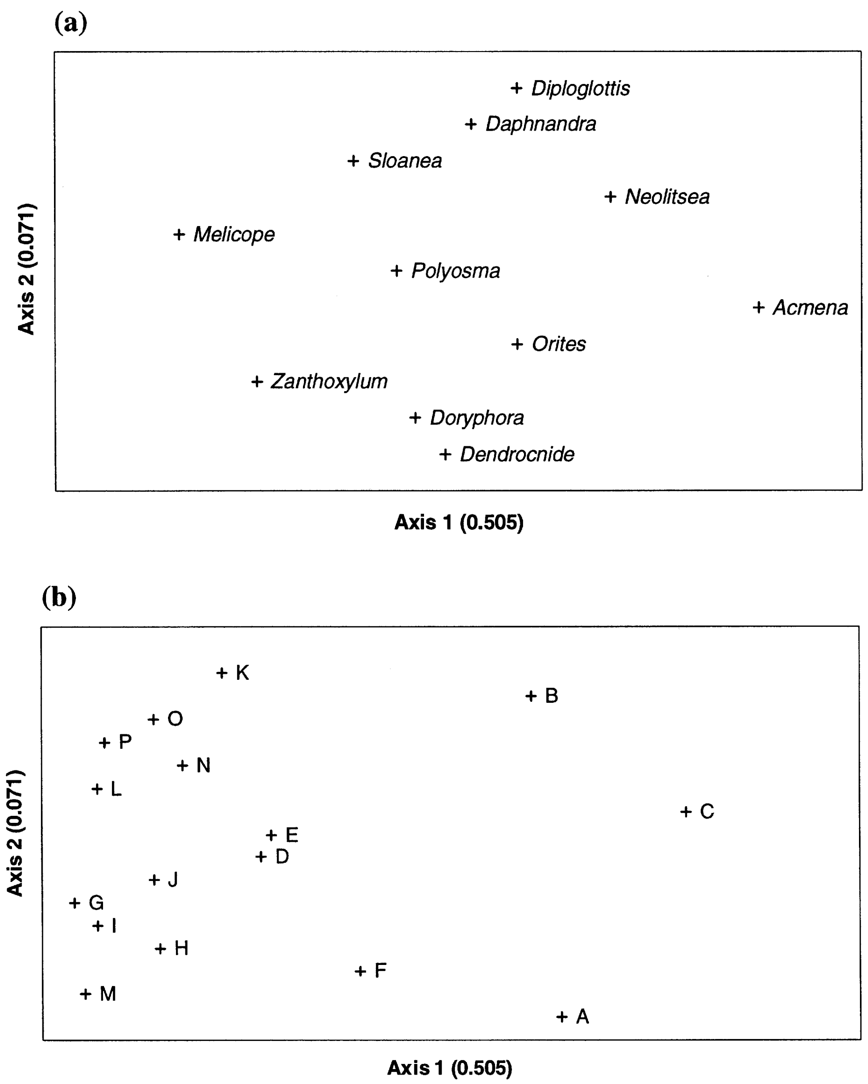


Figure 7. Ordination diagram for (a) species and (b) subplots, using species composition of each subplot based on adult basal area. Eigenvalues for the axes are shown in brackets.

capable of replacing each other except where population sizes are very low (Table 3). Apart from *Melicope*, which has a strong tendency for self-replacement, all the study species are most likely to be replaced by one of *Doryphora*, *Orites*, *Polyosma* or *Zanthoxylum* (as indicated in bold in Table 3). *Acmena* has the highest number of saplings (Table 1), but its lower relative basal area implies saplings of *Acmena* are generally from smaller size-classes.

Table 3 also gives the expected percentage of under-crown sapling basal area, i.e. the per cent of study plot basal area for that species. The chi-square tests suggest that the distribution of saplings is non-uniform throughout the plot, with under-crown sapling cohort basal area composition (considering the

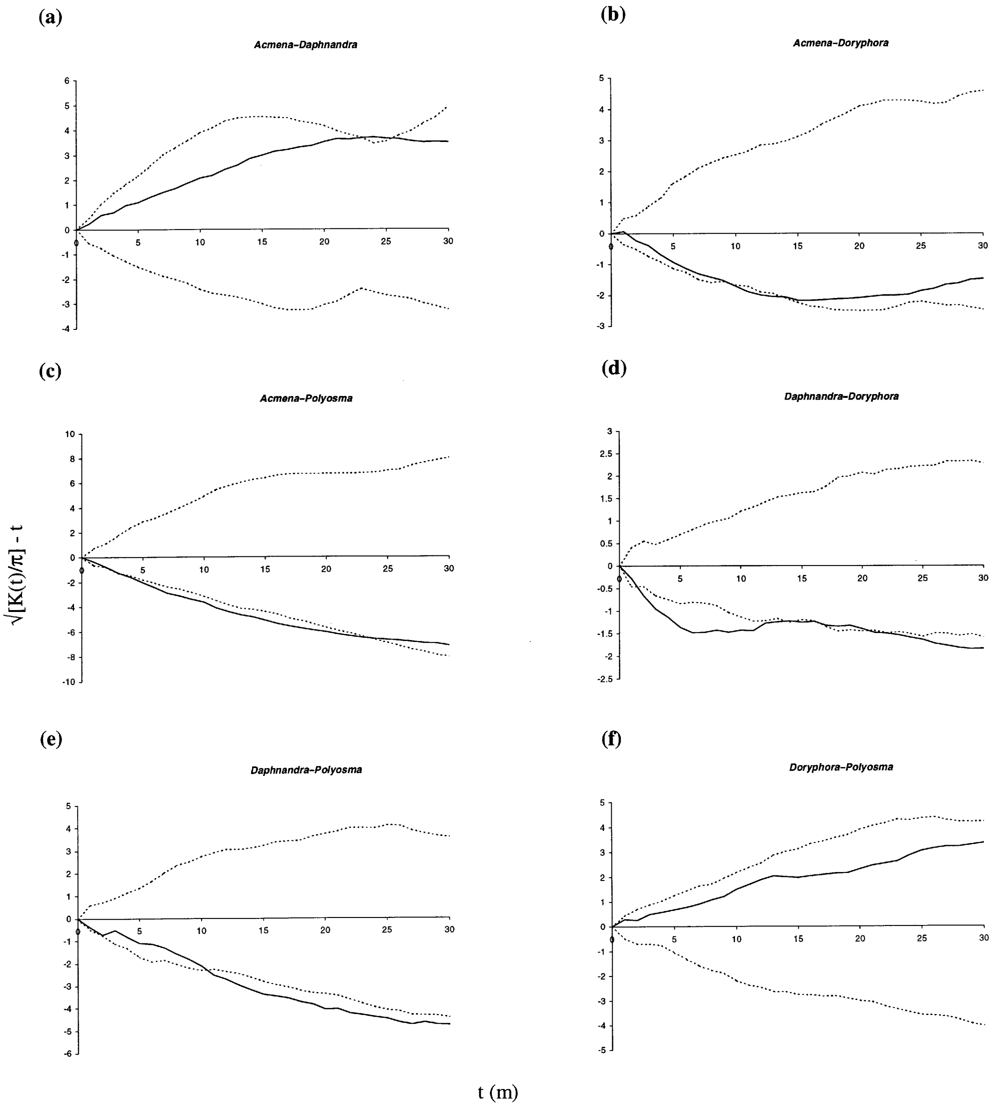


Figure 8. Bivariate spatial pattern analysis using Ripley's K(t) for distribution of selected species pairs across the 1-ha study plot; (a) *Acmena ingens–Daphnandra micrantha*, (b) *Acmena ingens–Doryphora sassafras*, (c) *Acmena ingens–Polyosma cunninghamii*, (d) *Daphnandra micrantha–Doryphora sassafras*, (e) *Daphnandra micrantha–Polyosma cunninghamii* and (f) *Doryphora sassafras–Polyosma cunninghamii*. Continuous lines represent the sample statistic ($\sqrt{[K(t)/\pi]} - t$) and broken lines the 99% confidence envelope over t= 0–30 m.

11 species studied) varying significantly between species. All species except *Daphnandra*, *Orites* and *Zanthoxylum* have significantly higher than expected counts of conspecific sapling basal area in their under-crown sapling cohort (as indicated in italics in Table 3), *Orites* having a significantly lower count. *Melicope* appears to be an extreme case, having the highest under-crown conspecific basal area percentage, but having only a rather low overall proportion of

Table 2. Summary of Ripley's K(t) statistic (univariate) for distribution of saplings across the 1-ha study plot, adults across a 3-ha area encompassing the study plot and (bivariate) saplings in relation to adults across the 1-ha study plot. Range of scales considered (t values) and sample size (n) indicated.

Species	Saplings (t = 0 – 30 m)	n	Adults (t = 0 – 75 m)	n	Saplings in relation to adults (t = 0 – 30 m)
Acmena	Clumped at all scales	281	Clumped at all scales	34	Attracted > 5 m
Daphnandra	Clumped at all scales	147	Clumped > 30 m	18	Attracted 8–17 m and 19–21 m
Dendrocnide	Clumped 9–15 m	6	Clumped 15–45 m (and 9 m)	36	Random (except attracted at 1 m)
Diploglottis	Random (except clumped at 20 and 24 m)	40	Random	36	Random
Doryphora	Clumped at all scales	168	Clumped > 3 m	348	Attracted > 2 m
Melicope	Clumped > 2 m	61	Clumped < 45 m	86	Random (except attracted at 5–6 m)
Neolitsea	Clumped at all scales	140	Clumped at all scales	35	Random (except repelled at 5–6 m)
Orites	Clumped at all scales	168	Clumped at all scales	182	Attracted 9–13 m and 15 m
Polyosma	Clumped at all scales	127	Clumped > 3 m	144	Attracted > 4 m
Sloanea	Random	10	Random	202	Random
Zanthoxylum	Clumped at all scales	119	Clumped > 3 m	68	Random

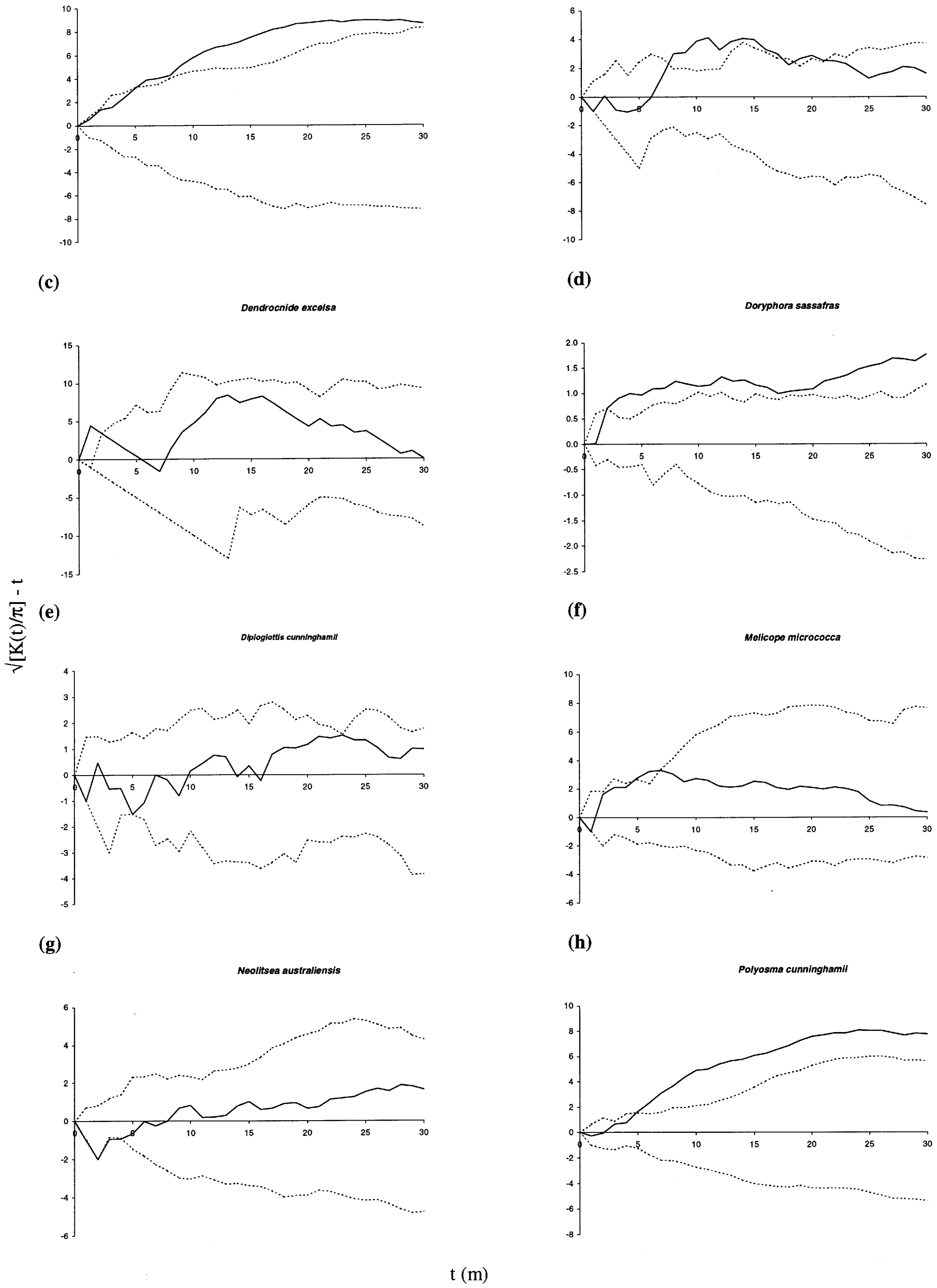


Figure 9. Bivariate spatial pattern analysis using Ripley's K(t) for juvenile and adult distribution across the 1-ha study plot for (a) *Acmena ingens*, (b) *Daphnandra micrantha*, (c) *Dendrocnide excelsa*, (d) *Diploglottis cunninghamii*, (e) *Doryphora sassafras*, (f) *Melicope micrococca*, (g) *Neolitsea australiensis*, (h) *Orites excelsa*, (i) *Polyosma cunninghamii*, (j) *Sloanea woollsii* and (k) *Zanthoxylum brachyacanthum*. Continuous lines represent the sample statistic ($\sqrt{[K(t)/\pi]} - t$) and broken lines the 95% confidence envelope over t = 0–30 m.

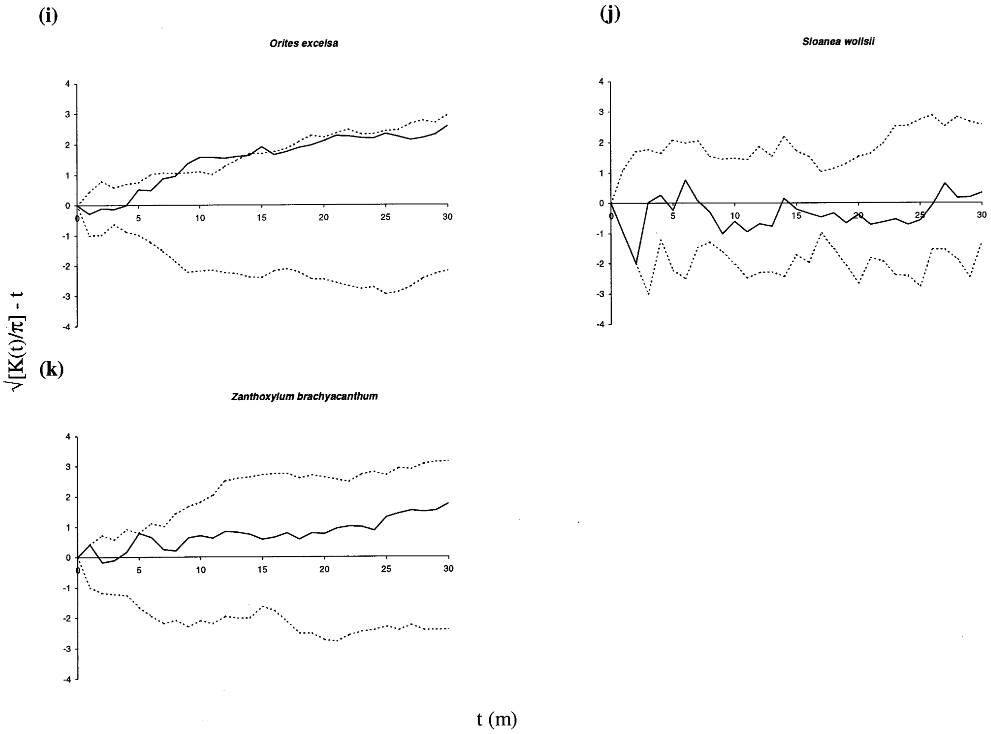


Figure 9 continued.

sapling basal area within the plot, suggesting a strong capability for self-replacement. This is probably an artefact caused by the relative scarcity of saplings and a few larger saplings found close to adult trees.

DISCUSSION

Gambubal compared to other sites

The density of stems within the study plot at Gambubal is roughly similar to many other tropical and subtropical rain forests, and although the basal area (64.6 m^2) is higher than the range for the 18 tropical forests (28–52 m^2 ha^{-1}) compared by Swaine *et al.* (1987), it is very similar to the values obtained at Lamington National Park, south Queensland (61.5/63.4 m^2 ha^{-1}) by Connell *et al.* (1984). The high basal area at Gambubal reflects the abundance of large trees of *Sloanea*. As the tree species richness is lower at Gambubal than in many tropical forests, average density per species is greater. Under these circumstances we expect density-dependent recruitment to be more frequent at Gambubal than in the more species-rich equatorial forests.

Is there evidence for density-dependence?

1 – Spatial distribution of saplings and adults

Saplings of most species were found to be clumped at all or most spatial scales

Table 3. Basal area species composition (percentage) of sapling cohorts beneath crowns of 11 species studied, and their expected percentage based on their relative basal area density on the whole plot. The significance of the observed values from the expected values is indicated as follows: *, $P < 0.05$, **, $P < 0.01$, ***, $P < 0.001$. Values in bold represent the highest percentage for each species, and those in italics are conspecifics.

		Adults										
Saplings	Whole plot	*Acmena*	*Daphnandra*	*Dendrocnide*	*Diploglottis*	*Doryphora*	*Melicope*	*Neolitsea*	*Orites*	*Polyosma*	*Sloanea*	*Zanthoxylum*
Acmena	**7.4**	*11.9****	0.0**	10.7***	13.0***	6.7*	7.6	4.2**	5.6**	5.0***	4.6***	5.2***
Daphnandra	**3.5**	3.9	*4.5*	3.6	1.2***	1.7***	5.7***	1.8*	2.6*	1.2***	2.0***	3.2
Dendrocnide	**0.8**	2.4***	0.0	*2.1****	0.0**	0.1***	0.0***	0.0*	0.0***	0.0***	0.0***	0.0***
Diploglottis	**3.4**	1.2***	0.0	0.1***	*5.2***	2.1***	3.4	6.0***	9.6***	6.8***	8.1***	1.7***
Doryphora	**13.1**	5.7***	0.0***	**16.8*****	1.9***	***18.3*****	6.8***	15.7*	6.2***	**22.4*****	11.0***	**15.0****
Melicope	**5.5**	4.3	0.0*	4.0**	7.5*	0.3***	***22.3*****	6.4	4.4*	4.7	5.4*	5.1
Neolitsea	**6.2**	6.7	0.0**	8.4***	3.3***	3.9***	6.1	*10.0****	6.2	4.5**	4.3***	5.4
Orites	**8.0**	5.0***	0.0**	14.0***	3.1***	13.2***	1.8***	0.0	*6.5***	12.2***	**11.4*****	6.9
Polyosma	**6.8**	3.4***	**16.4****	0.4***	5.0*	7.6*	5.4*	1.6***	**17.9*****	*13.1****	4.5***	10.2***
Sloanea	**0.7**	4.1***	0.0	0.3*	0.0*	0.0***	0.3*	0.0	2.1***	0.0***	*1.5****	0.0***
Zanthoxylum	**11.0**	**17.7*****	0.0***	7.3***	**13.6***	10.3	7.7***	**18.1*****	4.3***	6.4***	10.3	*11.7*
Other species	**33.6**	33.8	79.1	32.3	46.2	35.8	32.9	36.1	34.7	23.6	36.8	35.5

tested, except for those of *Dendrocnide*, *Diploglottis* and *Sloanea*, which were distributed mainly at random (Table 2). Over the 3-ha plot used, adults of most species were also clumped at all or most spatial scales tested, except for *Diploglottis* and *Sloanea*, which were randomly distributed at all scales, *Daphnandra* which was clumped at larger scales only and *Melicope* at smaller scales only (Table 2). Since *Daphnandra* was clumped as saplings, but distributed at random as adults at $t \leq 30$, some factor(s) must be causing differential mortality of small trees in relation to the density of conspecifics in this species. Similar patterns have been observed at other rain forest sites, where a trend of spatial pattern change, with increasing age, from closer to looser aggregation or randomness has been found (e.g. Connell *et al.* 1984, He *et al.* 1997). Further research is required to determine the causal factors determining this shift in spatial distribution for *Daphnandra* at Gambubal.

2 – Dispersion of saplings relative to adults

Comparisons between the univariate analyses of sapling and adult distributions and the bivariate analyses of distribution of saplings in relation to adults (Table 2) allow a number of patterns of spatial distribution to be distinguished: clumped saplings attracted to clumped adults (*Acmena*, *Daphnandra*, *Doryphora*, *Orites*, *Polyosma*); clumped saplings randomly distributed with respect to clumped adults (*Dendrocnide*, *Melicope*, *Neolitsea*, *Zanthoxylum*); and randomly distributed saplings and adults (*Diploglottis*, *Sloanea*). A probable cause of the first pattern is limited dispersal, with seeds falling close to adults, producing clumps of saplings, around clumps of adults. Penfold & Lamb (1999) found juveniles of *Acmena* and *Polyosma* were seldom found more than 10 m and 15 m away from conspecific adults respectively, supporting our findings. As already noted, *Daphnandra* is only clumped as adults at larger spatial scales, not at the scale of 0 – 30 m, the scale considered for saplings. We therefore observe a shift in spatial pattern over the life-span of *Daphnandra* from saplings clumped close to adults, to randomly dispersed adults, indicating high mortality in adult-associated clumps. *Zanthoxylum* and *Neolitsea* (and to a lesser extent *Melicope*) are some of the smallest species considered in this study, and we suggest the pattern of saplings clumped at random with respect to clumped adults may be an artifact of 'missed' adults, i.e. trees that reached reproductive maturity before the 10 cm dbh threshold for adults used in this study. Indeed, some evidence for attracted distributions is found for *Neolitsea* and *Melicope*. As *Dendrocnide* is known to be gap-dependent for regeneration we would expect a non-associated distribution of clumps of saplings in current gaps, and clumps of adults in old gaps, presuming gaps are formed at random spatially. *Sloanea* is extremely rare as a sapling, but very common as an adult, so we would not expect to find a pattern, although this difference in abundance suggests high density-dependent mortality in seedlings.

3 – Tree replacement probabilities

The six most common species as adults (stems ≥ 10 cm dbh) on the 5-ha research site (O'Donnell 1993), both as number of individuals and per cent of total basal area are *Doryphora* (723, 11.7%), *Orites* (425, 8.1%), *Sloanea* (330, 51.6%), *Polyosma* (278, 2.1%), *Melicope* (139, 1.1%) and *Zanthoxylum* (91, 0.5%). Our results show the sapling basal area to be dominated by *Doryphora*, *Orites*, *Polyosma* and *Zanthoxylum*, with a very minor contribution by *Sloanea* (only 0.7%). Under the presumption that the future adult composition of the forest is mirrored by the present sapling composition, our results suggest that the composition of the forest will shift in the future away from the dominance by *Sloanea*. The evidence of transition on our study plot is particularly compelling: the seven species *Acmena*, *Doryphora*, *Melicope*, *Neolitsea*, *Orites*, *Polyosma* and *Zanthoxylum* make up 58% of the sapling basal area but only 19% of the adult basal area (most of the balance is *Sloanea*).

We have found possible evidence for density-dependent juvenile mortality in only two species (*Daphnandra* and *Sloanea*), while most species show no evidence that sapling distributions are over-dispersed in relation to adults, as predicted by the compensatory recruitment hypothesis. This implies that density-dependent processes were not widely operating even amongst some of the most common tree species at Gambubal. Hubbell & Foster (1987) used a method for considering juvenile cumulative distribution of distance to nearest conspecific adult to seek for evidence of density-dependent recruitment in the five most common tree species on Barro Colorado Island (BCI), Panama, and found significant over-dispersion of saplings of the two most abundant species (*Trichilia tuberculata* and *Alsies blackiana*) relative to conspecific adults. More recently, significant density-dependent effects on recruitment, many extremely strong, have been found for 67 out of the 84 most common species at BCI (Wills *et al.* 1997). It should be noted that the densities of the commonest species at Gambubal are mostly higher than those for which evidence was found for over-dispersion at BCI, which suggests that high density due to low species diversity does not predispose trees to density-dependent mortality as we hypothesized for this study.

Penfold & Lamb (1999) found evidence for reduced juvenile abundance in the vicinity of adult trees (i.e. negative density-dependence) for two species at Gambubal. The phenomenon was marked in *Sloanea* and also occurred for *Doryphora*, although we found no evidence for such processes in the latter species in this study. Penfold & Lamb (1999) found *Sloanea* to be the second most abundant species in the juvenile size class, which consisted of individuals of four leaves or greater but with very few over 1 cm dbh, due to small sample areas. Our current observation of very low sapling abundance in this species is therefore the manifestation of high early juvenile mortality.

The two mechanisms for clumping of saplings close to adults are restricted seed dispersal and the occurrence of permanent patches of high resource availability (Hamill & Wright 1986). Although most of the 11 species studied at Gambubal are known to be bird-dispersed, it is likely that a high proportion of seeds fall beneath the parent crown. In the absence of density- or distance-dependent mortality, clumping of saplings relative to adults is the inevitable consequence of limited- or clump-dispersal (Howe 1989). We found that all species (except *Orites*) show a higher than expected sapling basal area beneath conspecific adult crowns (Table 3). On BCI, the species with explosively-dispersed seeds have the most clumped sapling distributions (Condit *et al.* 1992b). At Gambubal the aggregation of saplings and adults as a result of patchiness in resource availability is a possible mechanism for the species that had a non-uniform distribution across the plot (Figure 6). The differences in these distributions suggests that the critical resource varies between species (Figure 8).

Floristic composition across the plot

Ordination of floristic composition across the plot showed a pattern of variation, with a gradient of sapling (and adult) species composition running from the south-east to the north-west of the plot (Figure 5). Bivariate spatial pattern analysis by Ripley's K(t) function supported this finding, suggesting that species that were widely separated on axis 1 of the ordination have repelled distributions, whilst species with similar axis 1 scores were distributed at random with respect to each other, or showed some evidence that their distributions were attracted (Figure 8). The gradient of species composition between the 16 subplots correlates with a slope (of about 8°) running downhill from south-east to north-west.

It is possible that there is a gradient in the soil conditions (i.e. a catena), or variation in water availability at different positions on this slope. Fog-stripping, or interception of cloud and fog, by the canopy, makes a significant contribution to annual precipitation at Gambubal (Hutley *et al.* 1997). Such a pattern can be observed at a larger scale across the research site at Gambubal – the south-east facing side of the ridge has a higher epiphyte loading than the north-west facing side, the side on which the study plot used here is located, due to fog stripping (Howell 1993). Adults showed much less variation in subplot species composition, perhaps because of the scale of the study, i.e. larger areas are needed to see differences in the composition of adults, although the species composition of the north-west corner is also well separated on axis 1 of the subplot ordination for adults (Figure 7). Water availability is known to affect species composition, even at very local scales, e.g. at Danum Valley (Sabah, Malaysia) the distributions of trees $\geq$10 cm gbh on 4 ha of a ridge showed spatial variability in understorey tree composition at a scale of 0.25 ha, this response being related to variation in water availability on the ridge (Newbery *et al.* 1996).

Size class distributions: implications for forest dynamics

The size class distributions of the 11 species within the study plot showed *Dendrocnide* and *Sloanea* to be the only species with more adults than saplings, suggesting that they are not regenerating *in situ* (Figure 3). This population structure can be explained for *Dendrocnide* by its dependence on canopy gaps for seedling establishment (Floyd 1989), and the closed canopy over most of the study plot (all saplings were found in subplots D, N and O, within the three gaps, excluding the recently created gap in subplot I, shown in Figure 1). For *Sloanea*, the relatively few saplings were located at random across the study plot, and not just in gaps in the manner of *Dendrocnide*. Germination of recently-dispersed *Sloanea* fruits was, however, occurring commonly within the study plot (I. Debski, *pers. obs.*), and small *Sloanea* juveniles (i.e. < 1 cm dbh) were found to be common within the research site (Penfold & Lamb 1999). The dominance of adult basal area (but not of number of adult stems) within the study plot by *Sloanea* (60.7%) is equivalent to the examples of monodominance reviewed by Connell & Lowman (1989). Two types can be distinguished, i.e. rain forests with a persistent dominant, and rain forests with a non-persistent dominant. The former have seedlings that are tolerant of conditions below conspecific adults, while the latter are described as colonizers of large scale disturbance with shade-intolerant seedlings. The small number of saplings in the study plot, consisting of only 0.7% of the sapling basal area, but the presence of germinating seedlings, suggests that *Sloanea* seedlings suffer high mortality before they reach the 1 cm dbh size class. This may be caused by some density-dependent effect (e.g. host-specific predation of seedlings as envisaged by Connell 1971), some density-independent effect (e.g. reduced irradiance reaching the forest floor), or some combination of different effects. The results of this study suggest that *Sloanea* is a non-persistent dominant. Similar conclusions were drawn at Woopen Creek, Queensland, where *Backhousia bancroftii* (Myrtaceae) formed 68% of the canopy trees but was represented by only a few seedlings in the forest (Connell & Lowman 1989).

Three major life-history attributes among tropical trees were distinguished by Denslow (1987); ruderal species, small-gap species and large-gap species. Large-gap species exhibit rapid establishment and growth when large (multi-tree fall) gaps are created, then show a scarcity of saplings when the canopy closes. A possible explanation for the observed size class distribution of *Sloanea* at Gambubal is that it is a large-gap species. We suggest that a catastrophic disturbance event one *Sloanea* generation ago, such as a severe cyclone (Gambubal is situated at the southern edge of the southern cyclone belt), would have destroyed most adult trees and enabled *Sloanea* to establish and become the dominant species. This study suggests sapling establishment of *Sloanea* is very low after canopy closure.

This interpretation suggests that the composition of the forest at Gambubal is partly determined by a rare (and random) disturbance event. For non-equilibrium forests the consideration of such large-scale events, rather than replacement probabilities and density-dependent factors, will be required to predict future forest composition (e.g. Condit *et al.* 1992a). As pointed out by

LaFrankie (1996), the critical events determining the structure and regulation of tropical forest communities may be exceedingly rare, and much of what we often see, the 'day-to-day affairs', may not be the key. We suggest that only if the forest remains undisturbed will the changes in species composition predicted by the tree replacement probabilities actually occur. There is evidence of past large-scale disturbance in most tropical forests studied, and evidence that forests where the current species composition is controlled by small patch-scale canopy disturbance may be in the minority (Swaine *et al.* 1987, Whitmore & Burslem 1998). We suggest that Gambubal provides additional support for this conclusion.

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