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Distribution patterns of tree species
in a Malaysian tropical rain forest

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Abstract. Spatial patterns of tree species were studied in a 50-ha tropical rain forest plot in the Pasoh forest, Malaysia. This forest is characterized by a high diversity and very high number of rare species. Out of the 745 species occurring with > five individuals, 80.4 % had an aggregated distribution, 19.5% were randomly distributed and one species had a regular distribution. The spatial patterns of rare vs. common species, juvenile vs. adult trees, and coarse vs. fine scales were compared. Rare species are generally less aggregated than common ones and most of the randomly distributed species are rare. Spatial patterns shift from high clumping to looser intensity or random distribution when moving from juveniles to adults for the same species. No adult tree species display a regular pattern, however. Regular distributions were rarely found; this is probably due to intraspecific competition at a local scale. There is a negative correlation between per capita death rate and population density.

This study suggests that the Pasoh forest and its high diversity are subjected to multiple controlling factors, e.g., topography, spacing effect, density-dependent processes and species rarity. The importance of any factor changes across spatial and temporal scales.

Keywords: Donnelly statistic; Pasoh Forest; Spatial pattern; Species diversity.

Nomenclature: Ng (1978, 1979); Whitmore (1972, 1973).

Introduction

Point pattern analysis of species in a community can be used to detect the spatial arrangement of individuals and to generate hypotheses as to the possible underlying processes controlling the observed structure. In some communities, such as temperate forests and tundra, a single dominant regime may drive the forest towards a single type of spatial pattern (Pielou 1960; Chapin et al. 1989). However, such cases have rarely, if ever, been observed in tropical rain forests. Instead, these forests are subjected to multiple controlling mechanisms, for instance intra and interspecific competition, predation, niche differentiation, suitability of locations, disturbance and stochastic recruitment (Janzen 1970; Connell 1971, 1978; Hubbell 1979; Chesson & Warner 1981; Newbery et al. 1986; Denslow 1987).

Among the many processes that contribute to the spatial patterning of species is the well-known Janzen-Connell model which generated a debate among ecologists (Janzen 1970; Connell 1971; Hubbell 1979; Clark & Clark 1984; Schupp 1992; Burkey 1994). Janzen (1970) and Connell (1971) demonstrated that host-specific seed and seedling enemies (herbivores or pathogens) play the role of 'spacing agents' by preferentially attacking seeds or seedlings near conspecific adults; seeds or seedlings some distance away from adults can escape attack or may be subject to fewer attacks. Consequently, tree mortality is spatially organized, which causes the adult trees to be less strongly aggregated and reduces the possibility of finding conspecific neighbours. Given the large number of species present in tropical forests, the gaps are more likely to be occupied by some other species; this in turn tends to maximize the number of species present in any given area. However, many facts about spatial patterns in tropical rain forests do not support this hypothesis (Hubbell 1979, 1980; Fleming & Heithaus 1981). Considering the complexity of these forests, it would be more realistic to expect the mechanisms maintaining high diversity to differ from between species, from time to time, and from location to location, just as the resulting spatial patterns of species differ between species, times and locations. Some process may dominate in a specific location and time while others play minor roles, depending on the biology of the species in presence, the environmental constraints, and the spatial and temporal scales of the observations (He et al. 1994).

In this paper, we analyse univariate spatial patterns of conspecific trees in a Malaysian tropical rain forest. The purposes of this study are to investigate how

conspecific trees are spatially organized in the forest; to demonstrate that in a tropical rain forest community various spatial distributions can occur depending on the spatial and temporal scales of the observations; and to propose mechanisms to explain the observed spatial distributions. We will attempt to demonstrate that multiple rather than single controlling mechanisms are working together to organise the structure and maintain the high diversity of this forest. We fully realise that the analysis of multivariate spatial patterns (i.e. patterns of non-conspecific trees) would also be important to gain insight into the coexistence and competition of species. Since such a study would certainly be more difficult, both theoretically and methodologically, given the 825 species found in our tropical forest plot, we limit the present paper to univariate analyses.

Material and Methods

Study site

A tract of mapped forest, located at 102° 18' W and 2° 55' N, was established in the Pasoh Reserve, Negeri Sembilan, Malaysia, to monitor long-term changes in a primary forest (hereafter called the Pasoh forest). The vegetation falls within the south-central subtype of the red meranti-keruing forest type of Wyatt-Smith (1987). The upper canopy is dominated by red meranti, *Shorea* section *Muticae*, especially *S. leprosula*, *S. acuminata*, and *S. macroptera*. Other important emergent canopy species are *Dipterocarpus cornutus* (keruing), *Shorea maxwelliana* (balau) and *Neobalanocarpus heimii* (chengal).

Mean annual rainfall at Pasoh is ca. 2000 mm, one of the lowest figures for peninsular Malaysia.

The forest tract under study is a plot of 50 ha forming a rectangle 1 km long and 0.5 km wide. The plot lies in a mostly level plain of relatively uniform terrain between two meandering streams. About half of the plot lies within a range of 2 m of topographic change; a hill rises in the centre of the plot to ca. 24 m above the lowest point. The survey consisted of enumerating all free-standing trees and shrubs at least 1 cm in diameter at breast height (DBH), positioning each one by geographic coordinates on a reference map and identifying it to species. The initial census of 1987 was repeated in 1990. The data from the 1990 survey are used in this study for spatial analysis. Whenever necessary, both surveys will be used, for example when comparing the per capita death rates between rare and common species.

Data analysis

Relationship between tree locations and elevation

To evaluate the relationship between species distributions and elevation, the number of individuals of a species was counted in each of 1250 (20 m × 20 m) quadrats, and the elevation in each quadrat was measured. Spearman rank correlation was used to evaluate this relationship. To reduce computations, 100 of the 825 species (totalling 45 201 individuals), were selected at random; of these, only the species with over 300 individuals were included in the analysis. This restriction was made to minimize the number of quadrats missing representatives of a species included in the analysis. 36 species were retained using this criterion.

Donnelly statistic and clumping index

Several statistics have been proposed and patterns detected have been interpreted in terms of species interactions (see Haase 1995 for a recent survey of methods and Haase et al. 1996 for examples of interpretation). We applied the nearest-neighbour distance statistic to detect whether a point pattern departs from an assumed random Poisson point pattern (Clark & Evans 1954). The method is biased if there is a strong edge effect. Donnelly (1978) modified the statistic after simulation experiments to account for edge effects; the figures in the following equations are empirical constants derived by simulation.

$$r_c = r_e + \left(0.051 + \frac{0.041}{\sqrt{n}}\right)\left(\frac{L}{n}\right) \tag{1}$$

$$s_r = \frac{\sqrt{\left(0.07A + 0.037L\sqrt{\frac{A}{n}}\right)}}{n} \tag{2}$$

where r_c is the Donnelly nearest-neighbour distance statistic corrected for edge effect; it is computed for each species separately; s_r is the standard error of the Donnelly statistic; $r_e = 0.5 / \sqrt{\rho}$ is the expected distance to the first nearest neighbour without considering edge effect, with ρ = point density in the study area (trees per m²); A is the surface area of the study plot (m²); L is the length of the boundary around the study area (m); n is the number of individuals of the species under consideration in the study area.

The value of the Donnelly statistic is transformed into a standard normal deviate z which is amenable to a z-test:

$$z = \frac{r_a - r_c}{s_r} \tag{3}$$

where r_a is the observed mean distance to the 1st nearest neighbour. Spatial randomness is rejected in favour of

clumping or regularity, for extreme values in the upper and lower tails respectively (Kenkel 1988). Donnelly suggested that this z-test is unbiased if the number of points is larger than seven in a study area of smooth boundaries, like a square, rectangle or circle.

The ratio of the mean observed first nearest-neighbour distance (r_a) to the Donnelly statistic defines a clumping index $CI = r_a/r_c$. However, r_a is subject to sampling error, which is computed as $z_\alpha \times s_r$ at the α significance level, based on Eq. 3; here $\alpha = 0.05$. Hence, we define the following patterns:

(a) Aggregated pattern if
$$CI < \frac{r_a - z_\alpha s_r}{r_c},$$

(b) Random pattern if
$$\frac{r_a - z_\alpha s_r}{r_c} \leq CI \leq \frac{r_a + z_\alpha s_r}{r_c},$$

(c) Regular pattern if
$$CI > \frac{r_a + z_\alpha s_r}{r_c}.$$

In the Pasoh forest, the Donnelly statistic and the clumping index were used to determine the spatial patterns of all species, except those whose abundances in the whole plot were less than five individuals; 745 species were retained for the analysis.

Death rate, abundance and local abundance

To evaluate and compare the death rates of rare and common species, we used the per capita death rates of the species, obtained by comparing the censuses of 1987 and 1990. Because the study area is constant (50 ha) for all species, abundances were used instead of densities to correlate with per capita death rates. Since competition usually occurs among neighbours, it seems more informative to compare the per capita death rates to the local abundances of conspecific neighbours. Augspurger (1984) has shown that the 'effect distance' of conspecific adults on seedling survival can be as far as 25 - 50 m, while other studies showed that neighbourhood effect is less than 20 m (Clark & Clark 1984; Schupp 1988). 20 m was chosen as an eclectic cutoff in the present study. The local abundance for each species was calculated by counting conspecific trees within a 20-m radius circle centred around each individual of that species. The average of the counts was used as the local abundance for that species. In following sections local abundance as defined here will be called 'local density'. Edge effect was eliminated by including only individuals whose distances to the boundaries were at least 20 m.

Since randomly relocating the trees of all 825 species would be computationally burdensome, the same randomly selected 100 species as mentioned above were used to compare the difference between the observed local abundance and its counterpart after all trees in the plot were randomly relocated. Conspecific densities of

three species were not calculated because they were represented by a single tree each.

Spatial patterns at different growth stages

The spatial patterns of tree groups at different growth stages from juveniles to adults were evaluated by dividing individuals of a species according to diameter (DBH) size, based on the assumption that younger trees have smaller diameters than adult trees (Sterner et al. 1986). He (1993) used diameter size and abundance to classify the Pasoh forest species into six groups: treelet-shrub, understory, understory-midstory, dominant midstory, sparse overstory and dominant overstory species. The three most abundant species from each of the six groups are used in the present study. The diameter criteria (in DBH) corresponding to the growth stages are:

	A	B	C	D
DBH	4 cm	5- 9 cm	10-25 cm	> 25 cm.

Species are divided in two or more stages as follows:

Treelet-shrub species – A: juvenile; B: adult:
Ardisia kunstleri, *Ardisia* spp., *Diospyros nutans*;

Understory species – A: juvenile; B: premature; C: mature:
Anaxagorea javanica , *Aporusa microstachya* , *Ardisia crassa*;

Understory-midstory species – A - C as above category:
Dacryodes rugosa, *Rinorea anguifera*, *Xerospermum noronhianum*;

Dominant midstory – A - C as above; D: overmature:
Gluta malayana, *Shorea guiso*, *Sindora coriacea*;

Sparse overstory – A - D as above:
Canarium littorale var. *rufa*, *Mesua ferrea*, *Pimelodendron griffithianum*;

Dominant overstory – A - D as above:
Ixonanthes icosandra, *Neobalanocarpus heimii*, *Shorea maxwelliana*.

Our interest is to detect changes in spatial patterns of species through age rather than through an accurate developmental period. Therefore, we do not assume that the DBH criteria used to define the growth stages are biologically meaningful; the terms 'juvenile','mature', etc. are used only for convenience.

Spatial behaviour within a patch

An aggregated pattern may exhibit a regular distribution at local scale because of competition within a crowded patch (Pielou 1962; Campbell 1992). Therefore, a clumping pattern may be composed of two spatial components: an overall aggregation, combined with regular distribution within patches. Competition occurs at very local scales in this situation. Pielou (1962) has formulated a test for local scale competition using a truncated sample which consists of nearest-neighbour

distances smaller than an arbitrarily chosen upper limit. In this test, the observed mean nearest-neighbour distance for the truncated sample is substituted for the expected mean in an equation for a truncated random distribution, and a new local density for the crowded individuals is estimated. A goodness-of-fit test is then applied to the truncated sample which is divided into classes of equal expected frequencies, assuming spatial randomness; a significant deficiency of individuals in the first class indicates regularity. The key step is to determine the density λ per unit circle (radius = 1 m; q, the density per m^2, is calculated by dividing λ by π) and the largest nearest-neighbour distance (x_o) of the truncated sample; x_0 is the radius of the patch.

Campbell (1992) modified Pielou's method using a graphical analysis to determine the size of the truncated sample x_0. The expected first nearest-neighbour distance of each point in ascending order, under the assumption of randomness, is calculated from the equation:

$$y_i = \sqrt{-\ln\left(1 - \frac{i - 0.5}{n}\right)} \qquad (4)$$

where $i = 1, 2, ..., n$; n is the number of points. This equation enabled us to directly compare the observed nearest-neighbour distances (x) with the counterparts (y) of a random distribution. If the observed point pattern is random, then it is expected that the relationship between the ascending observed and expected distances computed by eq. 4 follows a straight line running through the origin. Hence, a straight line with the expected equation $y = \beta x$ indicates a random distribution; otherwise, either a convex curve (aggregation) is produced, as shown in Fig. 1, or a concave curve (regular pattern). The tangent intercept x_o between the curve and the expected straight line under the random model is a convenient non-arbitrary truncation level when applying Pielou's method since it marks the turning point of the overall aggregation in the observed distribution of nearest-neighbour distances; the squared slope of this line (β^2) is the estimated density λ of the truncated sample. Instead of Campbell's second order polynomial regression equation, we find that the best and most stable function, to establish the relationship between observed and expected nearest-neighbour distances by regression, is:

$$y^2 = a + bx + cx^2 \qquad (5)$$

Using the values estimated for parameters a, b and c, the slope (β) and the tangent intercept (x_o) of the expected straight line ($y = \beta x$), which is the tangent to the Eq. 5, are found to have the following equations:

$$\beta = \frac{\sqrt{4c - \dfrac{b^2}{a}}}{2} \qquad (6)$$

$$x_o = -\frac{2a}{b} \qquad (7)$$

The density q of the truncated sample is β^2/π at size x_o.

Object pairs falling below the regression line for distances smaller than x_o are those that have an observed nearest-neighbour distance larger than expected. These pairs of points may have a regular distribution within the patch. To test whether the deviation differs significantly from randomness at x_o, a one-tailed standard normal deviate test was applied, explained in more detail in Pielou (1962) and Campbell (1992).

Results

The diversity of the plot is high: there are 334 077 individuals, belonging to 825 species. There is no clearly dominant species. The most abundant one, *Xerospermum noronhianum*, accounts for only 2.5 % of the total number of trees.

Species abundance relation: rarity vs. commonness

The relationship between abundance and the number of species possessing that abundance, i.e., the species abundance distribution, illustrates the diversity pattern of a community. Fig. 2 shows the frequency distribution of abundance categories in log-base 2.

Species abundances in the 50-ha Pasoh forest range from 1, i.e. a single individual, as found in 32 species, to 8959 individual trees of *Xerospermum noronhianum*, the most abundant species. In the Barro Colorado Island forest Hubbell & Foster (1986) proposed that the species whose densities are equal to or less than one tree per ha be considered rare; this corresponds to 50 individuals in our 50-ha plot. By virtue of this criterion, there are 300 rare species, accounting for 36 % of all species of the Pasoh forest.

Species distributions: tree locations vs. elevation

In the Pasoh forest, elevation is the only abiotic variable from which we are able to evaluate the effects of the environmental conditions on species distributions. The relationships between elevation and the distributions of 36 randomly selected species, with the abundance of each species $\geq$ 300, vary widely. Spearman rank correlations vary from -0.256 to 0.408. Ca. 33 % of the species show no significant relation with elevation;
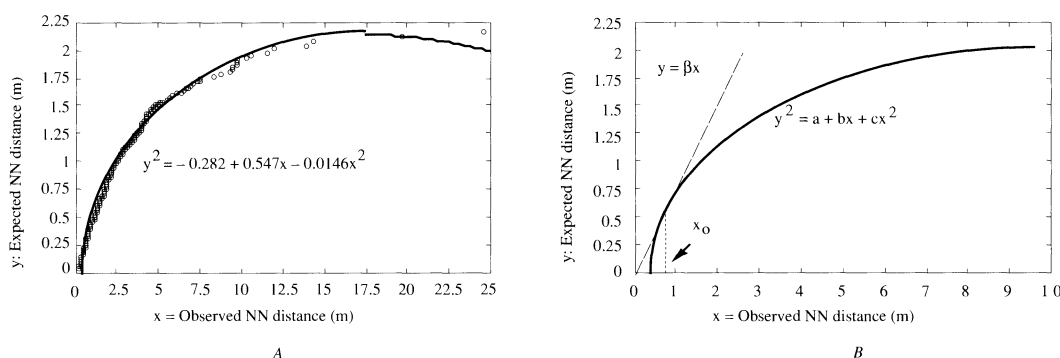
Fig. 1. Graphical analysis of within-patch spacing pattern of *Mallotus leucodermis* whose point location map is shown in Fig. 6. **A.** Equation and curve, modelling the relationship between observed nearest-neighour (NN) distances and expected NN distances under the assumption of randomness. There are four points excluded from the graph because of their remoteness from the other points, which impairs curve adjustment. **B.** Determination of the slope β and distance size (x_o) of a truncated sample.

among the remaining 67 %, half of them are positively correlated with elevation (preference for positions higher up the slope), and half negatively (preference for the valley) ($p \leq 0.01$). The distributions of some of the species could be well predicted by elevation. For example, logistic regression on elevation of the presence/absence (in 20 m × 20 m quadrats) of the species *Anisophyllea corneri* (723 trees in the Pasoh plot) showed that 71 % of the quadrats are correctly predicted by the logistic regression equation (the Spearman rank correlation between species distribution and elevation being 0.594.
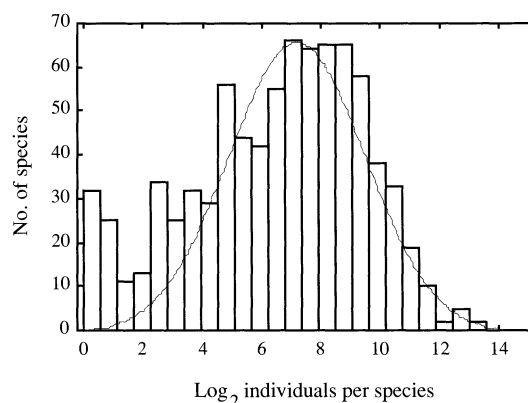
Spatial patterns of tree species: overall analysis

Among the 825 tree species in the Pasoh forest, 80 species with abundances < 5 trees were excluded from our spatial pattern analysis. Based on the z-test (Eq. 3), there is only one (*Galearia maingayi*, 8 trees) among the remaining 745 species, showing a significantly regular distribution ($p = 0.018$); 145 species are classified as having a random distribution (i.e. no significant departure from the null hypothesis of the z-test), accounting for 19.5 % of these 745 species; 599 others (80.4 %), have significantly aggregated distributions. Table 1

summarises the relationship between spatial distributions and species abundances. Most of the randomly distributed species are rare (≤ 50 trees), while most of the common species have aggregated distributions. The most abundant of the randomly distributed species is *Pometia pinnata* var. *alnifolia* (646 trees).

Population densities in tropical rain forests are usually low and nearest-neighbour distances among conspecific trees are relatively large. The density of the most abundant species, *Xerospermum noronhianum*, in the Pasoh forest is only 179 trees/ha, while its average conspecific nearest-neighbour distance is 3.5 m. The largest average nearest-neighbour distance, for species represented by at least five trees, is that of *Sterculia macrophylla*

Table 1. Relationship between spatial distribution pattern and species abundance for the 745 species in the Pasoh forest. A species with < 50 trees is classified as rare species.

| | Spatial distribution | | | |
	Regular	Random	Aggregated	Total
Rare	1	103	116	220
Common	0	42	483	525
Total	1	145	599	745

Fig. 2. Frequency distribution of species abundances in the Pasoh forest. The horizontal axis is the abundance in logarithm base 2. The number of intervals is 25. The fitted curve is a log-normal distribution, $S(R) = 66 \exp(-0.02174\, R^2)$ fitted to the right part of the frequency distribution, where $S(R)$ is the number of species in the R-th octave.
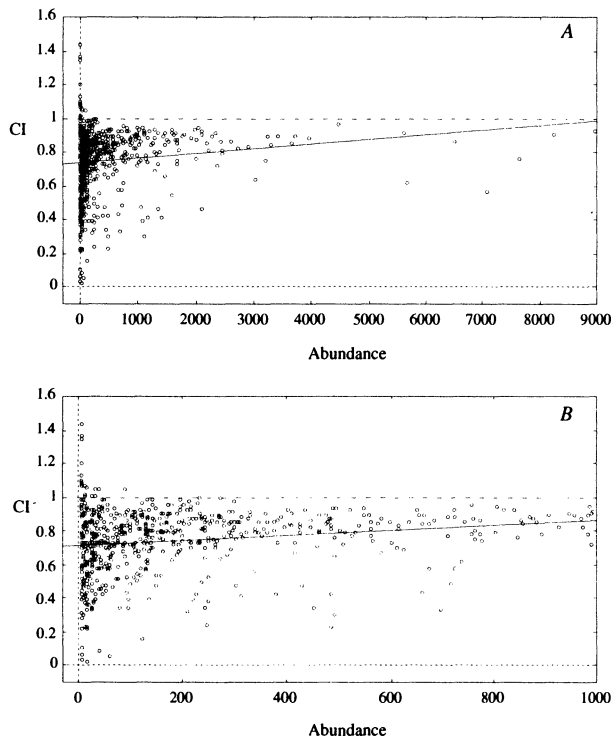
Fig. 3. Relation between abundance and clumping index CI of species in the Pasoh forest. **A.** All 745 tree species. The dashed line corresponds to CI = 1, the solid line is the regression line. **B.** Enlargement showing the 659 species with abundances < 1000.

(5 trees, nearest-neighbour distance = 272 m), while the smallest average nearest-neighbour distance is 2.5 m in *Pentace strychnoidea* (627 trees).

The regression line in Fig. 3 indicates that the clumping index slightly increases with the abundance of the species in the Pasoh forest. The coefficient of determination (r^2) between clumping index and abundance is 0.0177 ($p = 0.0003$). Clumping index values in Fig. 3 are more scattered among rare species (left of the graph) than among common species.

Local conspecific densities: observed vs. randomized

The distances among conspecific trees are generally large in the Pasoh forest; this decreases chances of intraspecific interactions. The Donnelly statistic of the last section allowed testing of the null hypothesis that an observed pattern is random over the whole plot. Here we compare the observed local densities of conspecific trees to the densities after randomly relocating the trees on the map. This comparison provides an intuitive insight into the local behaviour of tree aggregation. The observed to randomized local conspecific densities, computed in a 20-m radius circle, is shown in Fig. 4 for 97

randomly selected species (see Methods). The observed conspecific densities for all species are higher than the randomized, which suggests that the distributions of species are aggregated. Of course, the measure of local density changes with the size of the radius, but the relationship shown in Fig. 4 remains.

The local density of a species not only depends on the total abundance of the species in the whole study area, but also on the intensity of aggregation. For 740 species, Pearson's r^2 between local density and total abundance is 0.332 ($r = 0.576, p = 0.0001$), and 0.089 ($r = -0.298$, $p = 0.0001$) between local density and clumping index. However, the r^2 for the multiple correlation between local density and total abundance plus clumping index is 0.474 ($p = 0.0001$), which is larger than the sum of the r^2 values of the two simple regressions.

Per capita death rates: rarity vs. commonness

No positive correlation is found between per capita death rate and density, either over the whole plot or at a :20 m circle) ($p > 0.231$) for all species in t, although the relation is weakly signifi- .... of abundance ≥ 500 at a small scale (172 species, $r^2 = 0.0235$, $p = 0.0448$). On the contrary, the per capita death rate is significantly higher among rare than among common species (Table 2). Mean per capita death rate over all species of the Pasoh forest is 0.048. The per capita death rate of the most common species (≥ 3000 trees) is below that mean, while for half of the rare species it is above. Although the death of an individual may result from many factors, competition among neighbouring trees may be important.

Spatial patterns: juveniles vs. adults

Spatial patterns change over ages (diameter size) for the 18 species investigated. 12 of the 18 species are shown in Fig. 5. The general trend of the change is that with increasing age, the spatial pattern shifts from closer to looser aggregation or randomness, i.e. from lower to

Table 2. Comparison of the per capita death rates between rare and common species. The number of species in rare (≤ 50 trees) and common (> 50 trees) species groups is less than the ones listed in Table 1 because death data are not available for all species.

	Rare species	Common species
No. of species	218	522
Mean death rate	0.056	0.045
Standard deviation	0.087	0.030

t-test for the difference of per capital death rate:
$t = 2.69$, d.f. $= 738, p = 0.0074$
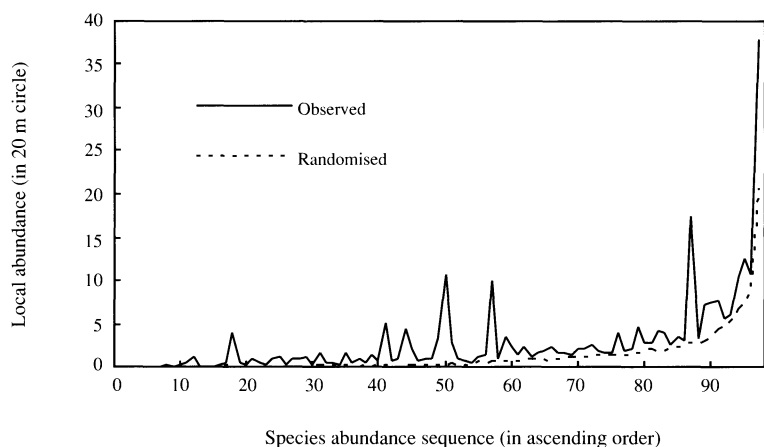
Fig. 4. Comparison between the observed local densities of conspecifics (upper line), for 97 tree species, to their local densities (within 20 m circle, lower line) after random relocation of the corresponding 45201 trees.

higher *CI* values. When including all trees (the T groups in Fig. 5), most species display patterns of medium-size aggregation, higher than in A but lower than in B, C or D. The final growth stage of each species presents itself either with a slightly aggregated or a random pattern.

Spatial patterns: coarse versus fine scales

A test for the overall pattern of a population would not reveal localized spatial behaviour, because competition usually occurs at the scale of nearest neighbours. 10 populations were selected to detect the local spatial patterns of the species by the truncated sampling method. These 10 species represent two distinct characteristics, i.e, highly aggregated or very abundant; this is where intraspecific competition is most likely to occur. The point location maps of four of the 10 species are shown

in Fig. 6 which compares the distributions of the species. *Anacolosa heptandra* and *Mallotus leucodermis* have similar abundances, but very different spatial distributions. A similar situation is found between *Aporusa microstachya* and *Anaxagorea javanica*.

Overall, these populations are aggregated with greater or lesser intensity ($CI = 0.224 - 0.964$). According to the truncated sample test *Mallotus leucodermis*, *Shorea pauciflora*, *Aporusa microstachya*, *Anaxagorea javanica*, *Rinorea anguifera* and *Xerospermum noronhianum* show within-patch regularity ($p \leq 0.05$), while *Anacolosa heptandra*, *Pimelodendron griffithianum* and *Gironniera parvifolia* do not. On the other hand, *Knema laurina* displays more aggregation at small scales (≤ 3.19 m; $p = 0.012$). This may be because of the biological characteristics of this species, such as its reproductive system (dioecious), or some special environmental requirements.

Fig. 5. Spatial pattern changes of 12 abundant species, belonging to four of the six groups corresponding to different strata in the vertical profile of the Pasoh forest (He 1993). Each species is divided in different growth stages according to dbh size:
A: dbh ≤ 4 cm;
B: 4 < dbh ≤ 9 cm;
C: 9 < dbh ≤ 25 cm;
D: dbh > 25 cm.
T : the whole population.
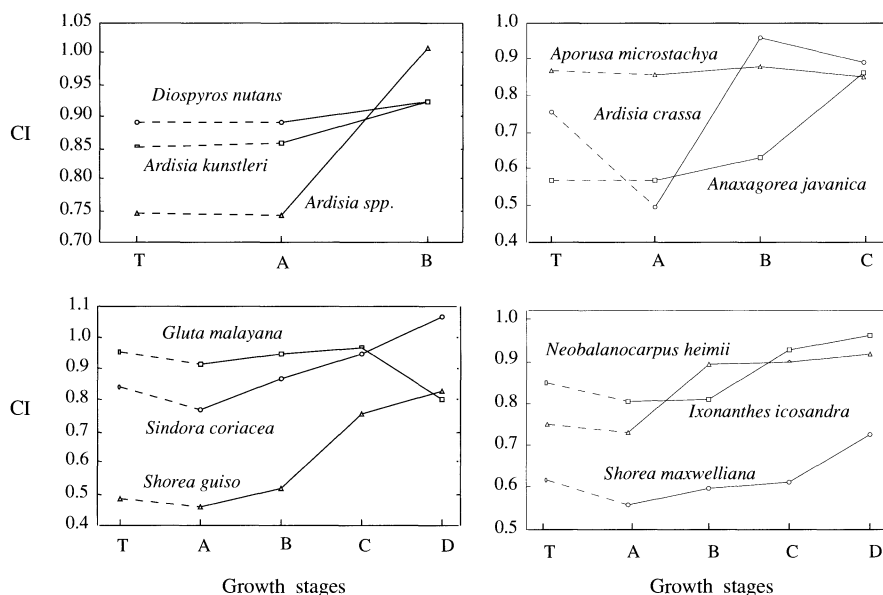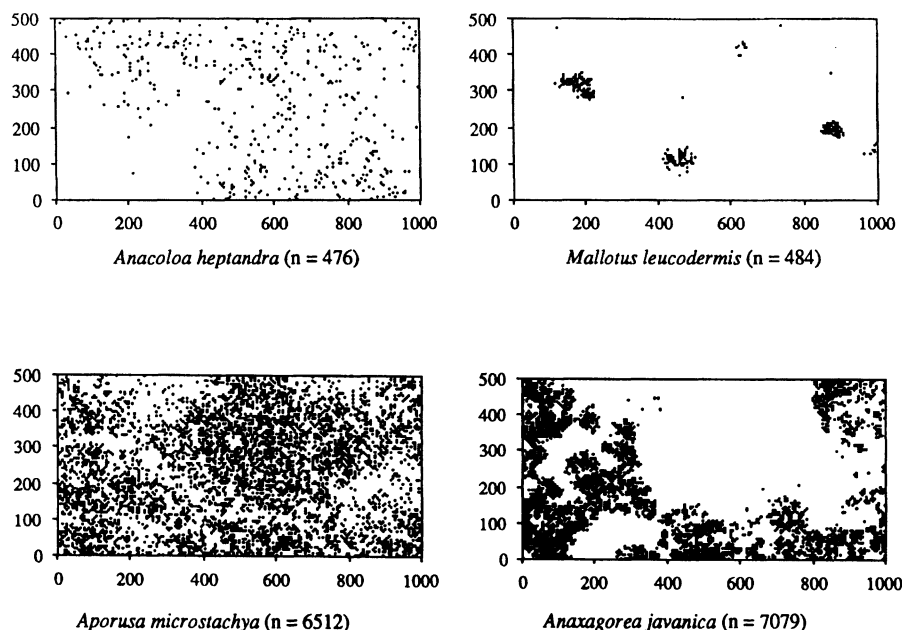
Fig. 6. Comparison of point patterns for four species. *Anacolosa heptandra*, *Mallotus leucodermis*, *Aporusa microstachya*, *Anaxagorea javanica*. They demonstrate that similar abundant species can have very different spatial distributions. n denotes the abundance.

Discussion

Species-abundances relation

The species-abundance distribution in many temperate and boreal plant communities have been described by a theoretical distribution such as the lognormal or logarithmic series. The species-abundance distribution in the Pasoh forest is poorly fitted by them because of the over-abundance of rare species. The same situation was found in the Barro Colorado Island forest (Hubbell & Foster 1986). Apparently, the underlying processes determining the abundance relations between species are different in tropical rain forests. A model which can accommodate and explain the extraordinary number of rare species is required.

Spatial patterns of tree species

Any population in a community, at a given scale of observation, presents one of three distributions: aggregated, random, or regular, depending on the underlying processes. It has been found that few species in nature are distributed in a regular way; on the contrary, most of them are clumped, or appear to be randomly distributed at some given observation scale (Greig-Smith 1983). Species in the Pasoh forest follow this general pattern. Only *Galearia maingayi* is regularly distributed; aggre-

gated patterns are dominant at the scale of the whole plot. The spatial patterns of rare species are more variable than for common species.

Different factors may be at work in different types of species distributions. An aggregated pattern may occur if seeds are randomly dispersed over a heterogeneous environment, which in turn makes germination vary from site to site; or in a homogeneous environment, if individual trees grow in family groups due to vegetative reproduction, or by seeds with small dispersal distance (Feller 1943). Hubbell (1979) showed that in a tropical dry forest, different reproductive systems do not necessarily lead to different spatial patterns, while the methods of seed dispersal result in different clumping intensities of populations. Spatially heterogeneous environmental conditions, such as topography, can also lead to patchy distributions for some species (Hubbell & Foster 1983). Of course, the factors that are responsible for the spatial pattern of one species may not influence another one.

Maintaining high diversity

Several hypotheses or theories, such as niche differentiation, disturbance, frequency-dependent mortality, Janzen-Connell spacing, and lottery recruitment, are frequently used to explain the high species richness of tropical rain forests (e.g. Janzen 1970; Connell 1971,

1978; Hubbell 1979; Chesson & Warner 1981; Connell et al. 1984; Denslow 1987). These models differ in that they assume alternative underlying mechanisms. However, tests of these models do rarely involve whole communities (but see Connell et al. 1984). A mechanism at work for one species need not control a community. The Janzen-Connell spacing model is applicable to some abundant species in a rain forest in Costa Rica, but it is not certain that the same model is also valid for the less abundant, let alone the rare species (Sterner et al. 1986). Hence, we would rather expect that any single model is unlikely to explain the high diversity of tropical rain forests. It is more likely that these forests are subjected to multiple mechanisms, and that the importance of each one waxes and wanes depending on the biological properties of species and the spatial and temporal scales of a study. The results in the present study seem to support this point of view. The following processes seem to play roles in maintaining the high diversity in the Pasoh forest.

Environmental conditions. The spatial segregation of species is due in this case to topographical variation, providing conditions that meet the requirement of different species. This is the basis for the mechanism of niche differentiation.

Spacing effect. It is generally stated that as succession proceeds, spatial patterns of populations shift from high to lower aggregation intensity, i.e. towards either more random or regular distributions (Greig-Smith 1961; Laessle 1965; Christensen 1977; Hutchings 1978). For different reasons, Janzen (1970) and Connell (1971) found a similar spacing effect in tropical rain forests, which was also observed for most abundant species in the Pasoh forest. However, as far as spacing agents are concerned, the situation is complicated. Herbivores and pathogens are not the only density- or distance-responsive spacing agents; environmental factors may also modulate the action of seedling predators (Thomson et al. 1996). Other mechanisms such as competition (both intra- or inter-specific), as well as gap dynamics, can also be density-responsive. We have shown that in very abundant species (e.g. *Xerospermum noronhianum*) or highly patchy ones (e.g. *Mallotus leucodermis*), intraspecific competition is obvious at the local scale of patches. Condit et al. (1994) also found that density dependence exists for two abundant understory species on the Barro Colorado Island. But one should not expect density-dependence effects to be overwhelming in tropical rain forests because most species are sparsely distributed. In any case, changes in the spatial pattern of conspecific trees of different ages can result from both density-independent and density-dependent processes.

Rare species. Rare species are crucially important to understand the high diversity of tropical rain forests.

There are several reasons for a species to be rare; for example, declining population (unsuccessful reproductive or high death rate), recent immigration, or a small proportion of suitable habitat. Hubbell & Foster (1986) found that most rare species are specialists either in habitat utilization (topography or edaphic conditions) or in regeneration niche (relatively ephemeral or regenerative conditions in gap openings). It implies that a high heterogeneity of environmental conditions is necessary to accommodate so many specialist species. In the Pasoh forest, we found that the environment and its associated diversity pattern are highly unpredictable (He et al. 1994) . On the other hand, we also showed that rare species had significantly higher per capita death rates than common species. This means that rare species have higher turnover rates, which may allow them to use regeneration niches and occupy new gap openings more quickly. This also indicates that rare species are not favoured over common ones in the Pasoh forest, i.e., frequency-dependent mortality does not work for this forest. The same result was also observed for other forests (Connell et al. 1984). The high per capita death rates of the rare species suggest that the maintenance of rare species is generally difficult in the Pasoh forest.

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