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Spatial pattern of diversity in a tropical rain forest in Malaysia

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Abstract. The diversity of trees (species richness, abundance and Shannon diversity) in a tropical rain forest of Malaysia has been studied from the point of view of its spatial organization in order to formulate hypotheses about the origin of the observed spatial patterns. The question that motivated this study is whether tropical forests communities are in a state of equilibrium or non-equilibrium. Three aspects have been examined: (1) changes in diversity were studied with respect to sampling area and sampling designs. A minimum area of 5–10 ha is recommended by the species–area curves, while 2–5 ha seem appropriate based on the Shannon diversity–area curves. Different sampling designs significantly affect the species–area curves. The power function, which can be derived under the equilibrium assumption, is not appropriate to fit the observed diversity–area curves. (2) The spatial features of diversity variables were then studied. Variograms showed that there are dominant short-range effects (around 150 m), obvious anisotropic distribution, and high random variation in the diversity data. (3) Partitioning the variation of the diversity measures into environmental (topographic) and spatial components indicated that the spatial organisation of that community was mostly unpredictable. There may be many processes controlling the formation of the spatial patterns in the tropical rain forest. Unidentified causes, affecting mainly the small-scale processes (<20 m), seem responsible for the large amount of undetermined variation in the diversity data sets. The study suggests that the Pasoh forest of Malaysia may not be in a state of equilibrium.

Key words. Diversity, Malaysia, non-equilibrium, rain forest, spatial structure.

Résumé. La diversité des arbres (richesse spécifique, abondance et diversité de Shannon) d'une forêt tropicale de Malaisie fut étudiée sous l'aspect de son organisation spatiale, afin de formuler des hypothèses quant à l'origine des patrons observés. La question à l'origine de cette étude est de savoir si les communautés des forêts tropicales sont, ou non, en état d'équilibre. Trois aspects de la question furent considérés. (1) Nous avous d'abord examiné comment les différentes mesures de diversité changent en fonction de la superficie échantillonnée et du plan d'échantillonnage. Les courbes décrivant la relation entre le nombre d'espèces et la superficie échantillonnée indiquent que la surface minimale à échantillonner est de 5 à 10 ha; les courbes décrivant la relation entre la diversité de Shannon et la superficie échantillonnée suggèrent, pour leur part, une superficie minimale de 2 à 5 ha. Des plans d'échantillonnage différents conduisent à des courbes différentes du nombre d'espèces en fonction de la superficie. La fonction de puissance, dont la dérivation théorique peut se faire sous l'hypothèse d'équilibre, ne s'ajuste pas convenablement aux courbes calculées de la diversité en fonction de la superficie. (2) Nous avous ensuite étudié l'organisation spatiale des variables décrivant la diversité spécifique. Les variogrammes montrent la grande importance des effets à petite échelle (environ 150 m), l'anisotropie des distributions, ainsi que la variabilité aléatoire élevée des données. (3) Une partition de la variation des mesures de diversité en leurs composantes environnementale (topographie) et spatiale a indiqué que l'organisation spatiale de cette communauté est en grande partie imprédictible. Plusieurs processus peuvent être concurremment en action pour former les patrons de répartition spatiale de cette forêt tropicale humide. Des causes non-identifiées, agissant principalement à petite échelle (moins de 20 m), semblent responsables d'une grande partie de la variation non-déterminée des données de diversité. L'étude suggère que la forêt Pasoh de Malaisie serait dans un état de non-équilibre.

Mots clés. Diversité, forêt tropicale, Malaisie, non-équilibre, structure spatiale.

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INTRODUCTION

One of the salient properties of the tropical rain forest is its high diversity. Ecologists have spent treasures of imagination to explain why the tropical habitat could accommodate so many species and individuals, and how the species are distributed (Ashton, 1969; Hubbell, 1979; Hubbell & Foster, 1983, 1987; Newbery, Renshaw & Brünig, 1986). The traditional explanation is that the great age of the tropics and its benign and stable climate have permitted speciation and a consequent slow accumulation of species. Niche differentiation (Ashton, 1969), species competition (MacArthur, 1969), host-specific predation (Connell, 1970; Janzen, 1970), gap disturbance (Denslow, 1987), etc. are among the driving mechanisms most often invoked. Rosenzweig (1992) has proposed a convincing model explaining why species diversity is much higher in the tropics than anywhere else, and has validated it by showing that various predictions of the model are supported by facts. This model applies to evolutionary times, however, and it remains to be explained how individuals, species and populations behave at shorter time and spatial scales: how species adapt to ecological niches and how individuals find, in the landscape, the environmental conditions to which they are best adapted; without that, populations disappear. The present work is devoted to this last question: describing how individuals of local populations of different species do apportion the space available to them in a tropical rain forest, this apportioning representing a mechanism at work in ecological (opposed to evolutionary) time. Spatial structures should emerge in the tropical rain forest communities, as the consequence of any and all of these mechanisms. Therefore, studying its spatial organization should help understand the mechanisms that have generated the diversity of the tropical rain forest.

Diversity of a community usually refers to species richness, abundance, or a combination of these (various diversity indices), in a community. It is regarded as the result of species interaction or community adaptation to its environment over evolutionary time (Rice & Westoby, 1982). The bewildering diversity of tropical forests has triggered the interest of several authors. Poore (1968) described the diversity of a rain forest in Malaysia. Hubbell (1979) studied the distribution patterns of tree species in a neotropical dry forest. Hubbell & Foster (1983) studied the canopy tree diversity in Barro Colorado Island, Panama. Rice & Westoby (1982) compared the richness of different communities, parts of which are rain forest communities. Although these studies have led ecologists to better understand the community structure of some tropical forests, not much has been done towards understanding how species diversity is distributed spatially over a tropical rain forest, and to what extent local-style diversity patterns are regulated by environmental factors or by intrinsic community dynamics. These questions are directly related to the equilibrium and non-equilibrium hypotheses about the formation of tropical communities (Connell, 1970, 1978; Hubbell, 1979, 1980).

Until the late 1970s, the widely accepted paradigm was that tropical communities are mostly in equilibrium, because of their stable environment and seemingly stable community composition. One should not, however, claim that a community is stable simply because it is composed of long-lived individuals (Frank, 1968). Connell (1978) and Hubbell (1979) opened a Pandora's box when they claimed that it is very likely that tropical communities may not be in equilibrium, simply because there are so many other mechanisms acting on the community besides the stable climatic conditions; this is especially true at the local scale. Much of ecological theory has been developed under the assumption that natural communities are at or near equilibrium. Equilibrium means predictability, which implies that historical effects, chance factors and occasional environmental perturbations play but a small role (Chesson & Case, 1986). By opposition, a non-equilibrium community is more unpredictable in terms of its compositional structure, with high stochastic effects, and it should generally lack clear and consistent spatial patterns (Wiens, 1984); so, predictability of its spatial structure and of its species–environment relationships should be low. If a community is in equilibrium, its species-area model should best be fitted by a power function $S=\alpha A^{\beta}$ (S: the number of species; A: area; and α, β: the parameters of the model; Preston, 1960; MacArthur & Wilson, 1967); this assertion has been questioned by Connor & McCoy (1979), however. Conversely, if the species–area relation is not well-fitted by a power function, this would indicate that the community may not be in equilibrium.

In summary, equilibrium/nonequilibrium theory makes the following predictions about the diversity of communities that are not in equilibrium: (1) their species–area relations are unlikely to follow a power function; (2) their spatial patterns of diversity should be relatively unclear and inconsistent, demonstrating for instance high random variation; (3) their diversity patterns should not be well-predicted by environmental factors, and they should generally lack clear large-scale spatial patterns.

Since most ecological processes are structure-generating (Legendre & Fortin, 1989; Legendre *et al.*, 1989; Legendre, 1993), analysing the resulting spatial structures may provide important clues as to the processes that have generated them (Borcard & Legendre, 1994). Several methods of spatial investigation, such as spatial autocorrelation analysis, geostatistics, fractal dimensions and mapping techniques, may be used to detect the variation and scale effect of ecological variables. Multiple and partial regression analysis (for a single dependent variable), or canonical and partial canonical analyses (for multivariate dependent datasets), may also be used to partition the variability into environmental and spatial components, and relate observed spatial patterns to environmental factors (Borcard, Legendre & Drapeau, 1992; Dutilleul & Legendre, 1993; Borcard & Legendre, 1994).

In this paper, we will study the spatial structure of species diversity in a tropical rain forest of Malaysia and investigate the causes for the formation of spatial patterns, to help decide whether this tropical rain forest is in equilibrium. To fulfil these purposes, the following three groups of questions will be addressed specifically, in order to test predictions of equilibrium/non-equilibrium theory: (1) how do the richness, abundance and Shannon diversity change with plot size? Will the sampling locations in that tropical rain forest affect the relations between richness, abundance, Shannon diversity and area? (2) How are richness, abundance and Shannon diversity spatially distributed in the study area? What are their distributional features: are they distributed in patches, or in a regular or random fashion? In an isotropic or anisotropic way? (3) What are the underlying processes that govern the spatial distribution of richness, abundance and Shannon diversity? To what extent do the environmental factors and the large-scale spatial structure contribute to the observed spatial patterns? All in all, what is the implication of these findings to the equilibrium and non-equilibrium hypotheses in that tropical rain forest? Although abundance and Shannon diversity were not directly used, in the literature, as evidences to test the hypothesis of equilibrium in tropical environments, they represent important aspects of the diversity of a community; investigation of these two indices should give us a more complete insight into the diversity patterns of the community under study.

MATERIALS 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. The vegetation is primary rain forest and 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* Miq., *S. acuminata* Dyer and *S. macroptera* Dyer. Other important canopy emergents are keruing, *Dipterocarpus cornutus* Dyer, balua, *Shorea maxwelliana* King and chengal, *Neobalanocarpus heimii* (King) Ashton. Mean annual rainfall at Pasoh is about 2000 mm, which is among the driest stations in Peninsular Malaysia.

The forest tract under study was a plot of 50 ha forming a rectangle 1 km long and 0.5 km wide (Fig. 1a). The survey consisted of enumerating all free standing trees and shrubs at least 1 cm diameter at breast height (d.b.h.), positioning each one by geographic coordinates on a reference map and identifying it to species. The plot was divided into 1250 quadrats of 20 × 20 m. The diversity of the plot was quite high: there were 334,077 trees, belonging to 825 species. There was no obvious dominant species. The most abundant one, *Xerospermum norohianum* (Sapindaceae), accounted for only 2.5% of the total number of trees (Kochummen, LaFrankie & Manokaran, 1991). Relative elevation and slope were also measured in each 20 × 20 m quadrat; these were used as synthetic environmental factors in the variation partitioning analysis of the diversity datasets.

Data analyses

Species diversity may be understood in different ways, depending on the operational definition we give of this concept. In this paper diversity refers to richness, abundance and their combination of the Shannon diversity index. More specifically, richness is defined as the number of species in a specified study area, while abundance is the number of individuals all species confounded. The Shannon diversity index has been advocated by Margalef (1958, 1974) as a synthetic measure of community structure. It is widely used by ecologists for this purpose. Its computation is described in any text of quantitative ecology.

To answer the various questions stated in the Introduction, different methods will be applied. For question 1, richness, abundance and Shannon diversity were measured after sampling areas of increasing sizes, from five starting locations of the map (a, b, c, d and e in Fig. 1b), doubling the quadrat size from 10 × 20 m until the 50-ha tract was covered. The expected species–area curve (null model) was also computed under the assumption that all species in the study area were randomly distributed (Coleman *et al*., 1982). The different species–area curves were compared. If the community was in equilibrium, then the species–area curves should be best fitted by a power function; the contrary would indicate that it may not be in equilibrium. The statistical criterion for the fit of a species–area curve is the sum of squares of the residuals, as in regression analysis.

For question 2, there are several methods available to detect the spatial distribution of diversity (Legendre & Fortin, 1989; Dutilleul & Legendre, 1993). Spatial autocorrelograms and variograms, combined with maps, are the two most widely used means of assessing spatial heterogeneity in ecology. A variogram is a graph of the semi-variance as a function of distance lags. There are three basic parameters in variograms used to interpret the spatial features of a variable: (1) the range, if present, is the distance where the spatial influence disappears (the semi-variance ceases to increase); (2) the sill is the semi-variance value that the variogram reaches at the range; in theoretical variograms, the sill equals the overall variance of a variable; and finally (3) the nugget effect is the ordinate value of the variogram at distance zero; it need not be equal to zero. Several factors such as sampling error or short-scale spatial variability may result in a nugget effect. The ratio of the nugget effect to the sill is referred to as the relative nugget effect; it can be used to evaluate sampling error and short-scale spatial effect. Variograms are computed to examine the hypothesis that a non-equilibrium community generally lacks clear and consistent spatial patterns. Variogram analysis was preferred in this study because the semi-variance, which is evaluated from the differences between pairs of observations over predetermined distance classes, emphasizes heterogeneity, in contrast to the Pearson-type autocorrelation measured by Moran's I coefficient, which emphasizes correlation. Another reason was that the stationarity requirement of a surface pattern for variogram, called the intrinsic hypothesis, is weaker than for autocorrelograms (Burrough, 1987). More information on these methods can be found in the review paper by Legendre & Fortin (1989) and in the book by Isaaks & Srivastava (1989), for instance. To aid in the interpretation of variograms, maps of richness, abundance and Shannon diversity will be drawn.

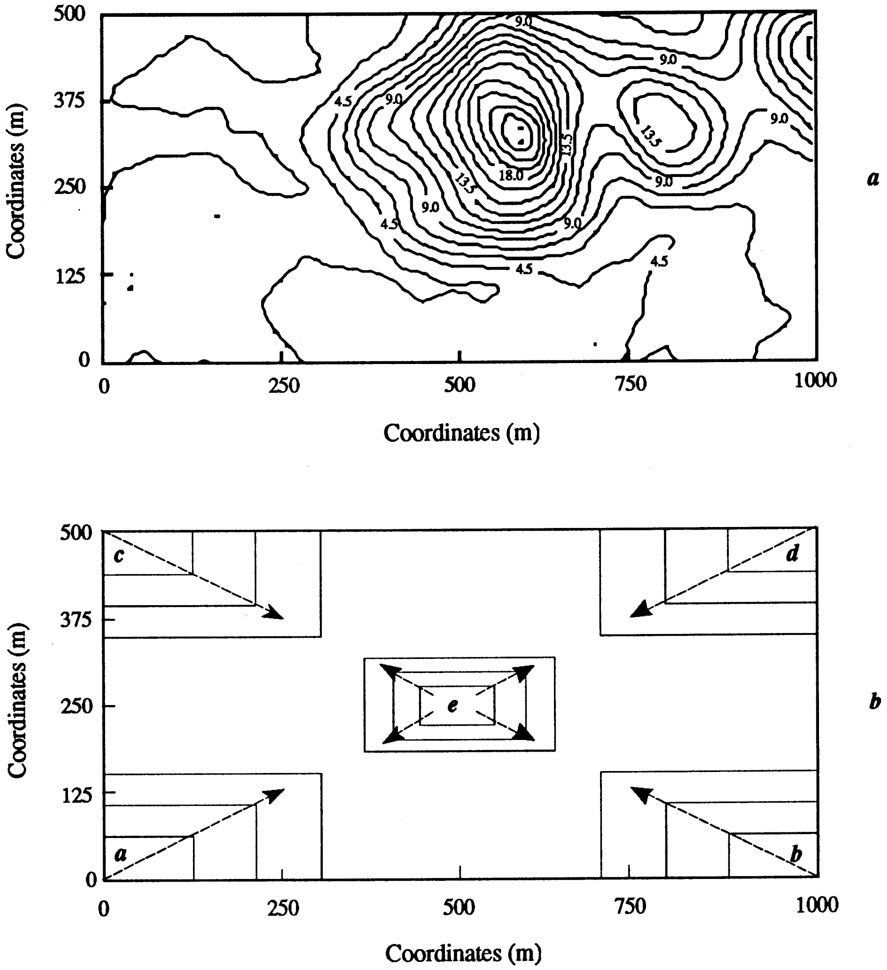


FIG. 1. *a*. Contour map of the 50-ha Pasoh forest plot, Malaysia. *b*. The sampling designs for the study of diversity–area relations are the following: starting from a 20 × 10 quadrat at five different locations (*a* to *e*), quadrat size is doubled until it covers the whole plot.

Let us turn to question 3. Ecologists are always interested to know how the observed structure of a community has been formed, and to what extent do the environmental or biotic factors, or the identifiable large-scale spatial structure, are responsible for the patterns. Borcard *et al.* (1992) proposed a method to evaluate to what extent different factors control the spatial patterns of ecological (dependent) variables. The total variation of a variable, or a multivariate dataset, is decomposed into four fractions, as described in the next paragraph. In the present study, topographical data (elevation and slope) are the only synthetic environmental variables available; they are related to and indicators of several abiotic factors, such as drainage condition, nutrient flow, etc. There are no independent biotic variables, because all the species of the Pasoh forest data base are included among the dependent variables. All variables are measured at the scale of 20 × 20 m quadrats in the 50-ha plot. The 'spatial' data matrix is constructed from the locations (x and y coordinates) of all quadrats in the Pasoh plot, plus the various quadratic and cubic terms that can be constructed by combining them, as originally proposed by Legendre (1990) (see Results for details). Partial regression analysis allows one to measure the amount of variation in each of the three vectors of diversity data in turn (richness, abundance and Shannon diversity) that can be explained by the environmental variables while controlling for the large-scale spatial structure (extracted by regressing on the spatial coordinate data table). One would use partial canonical analyses instead of partial regression when studying a multivariate dependent dataset.

The computations involve the three partial regressions or three canonical ordinations for each dependent variable (or set of dependent variables); these can be computed in various ways, as explained by Borcard *et al.* (1992). The following contributions to the diversity datasets can then be evaluated (presented as percentages in Fig. 10):

(a) *Pure environmental contribution*. This is the proportion of the diversity variation that can be explained as a linear model of the 'pure' environmental factors, independently of any spatial structure.

(b) *Evironmental + spatial contribution*. This is the spatially structured variation of the dependent variable(s) that can be explained by the spatial structure of the independent

environmental or biotic variables in the model. This proportion of variation is explained both by the environmental and the spatial regression models. Two types of situation may be responsible for this fraction of variation: first, diversity may vary spatially as a function of the environmental factors in the model; or there may exist other processes, unidentified in the regression model under study, which control both the species diversity and the environmental factors in the model.
(c) *Pure spatial contribution*. This is the large-scale spatial effect that cannot be attributed to the environmental or biotic variables in the model. It refers to spatially structured processes, affecting the dependent ecological variable(s) under study, that are not adequately described by the environmental or biotic variables explicitly used as independent variables in the model.
(d) *Undetermined contribution*. This fraction, which measures the unexplained fraction of variation, does not possess large-scale spatial structure which would have come out in fractions (b) or (c). It may be the consequence of stochastic fluctuations, or sampling error, or it may reflect some spatially structured variation which exists at small scale in the study, given the sampling scale. Legendre & Borcard (1994) discussed this small-scale spatial variation and how it could eventually be included in the model.

Partitioning the variation of the diversity vectors helps one to understand what the community structure is, and what the processes are that may have contributed to its formation. If diversity varies as a function of the environmental variables in the regression model, the amount of explained variation in fraction (a + b) is expected to be high and significant; if it possesses a large-scale spatial structure, fraction (b + c) is similarly expected to be significantly different from zero. According to our hypothesis, if the community is under equilibrium, then the predictable proportion should be high (a, b and c) and the undetermined component (d) low; otherwise it is plausible to conclude that the community does not seem in equilibrium.

All the statistical tests of significance and confidence intervals in this paper were computed at the $\alpha = 0.05$ level.

RESULTS AND DISCUSSION

Richness, abundance and Shannon diversity versus quadrat size

Diversity is the outcome of the co-evolution of species in a biogeographic region. It is often considered to be a synthetic measure of the structure, complexity and stability of a community. Abundance is an extensive variable, meaning that in a spatially homogeneous system its value changes proportionally (linear relation) to the size of the sampling units (Margalef, 1974); abundance values are additive through space, but not necessarily through time. Species richness and diversity, on the other hand, are not extensive, because they are not additive in the first place (i.e. values of richness or diversity cannot be added across quadrats and retain meaning). Diversity measures have been used for a variety of purposes. For instance, the minimum sampling area to be used in an ecological study has often been defined as the minimum area where the diversity spectrum stabilizes. Diversity has been widely investigated in tropical rain forests (Poore, 1968; Ashton, 1969; Hubbell, 1979; Hubbell & Foster, 1983), either as richness or as Shannon diversity. The relations between diversity and area in the Pasoh forest were intensively investigated.

(1) *Richness* (*S*) The species–area curves are displayed in Fig. 2. Several models were applied to fit the species–area relations, including the power model (log species/log area), the exponential model (species/log area) and others. Among them, the logistic model proved to be best suited for the species–area curves, with the lowest sums of residuals; see Fig. 3 and Table 1 where the three models are compared. In Fig. 2g, it can be seen that in the Pasoh forest the minimum sampled area should be between 5 and 10 ha (containing 79–86% of all species). A minimum area of 7 ha is recommended (containing 82% of all species).

Species–area curves may be altered depending on the group of species (see below) included in a survey list. In general, the minimum area decreases with number of species from one vegetation type to another, for instance from tropical to temperate continents (Rice & Westoby, 1985), but no generalization about the minimum area and the number of species within a local area could be reached in the present study. Taking into account canopy species only, Poore (1968) proposed that a sampling area of 2–5 ha is adequate in a Malaysian rain forest. If only the large tree species are taken into account (mean d.b.h. of a species $\geqslant 6.0$ cm, or the largest individual of a species $\geqslant 60$ cm), the species–area curve for the Pasoh forest is quite different from the all-species-included curve (compare curves *a* and *g* in Fig. 2h), but the minimum area estimated is very similar. This also confirms the conclusion of Webb *et al.* (1967), that big tree species retain most of the information about the structure of a rain forest.

The species–area curves may be influenced by the spatial patterns of species distributions (Hubbell & Foster, 1983). The empirical species–area curves are compared to the null model, under the assumption that all species are randomly distributed, to evaluate the effect of species spatial patterns on the species–area relations. One may ask whether there is any difference among the empirical species–area curves themselves and the null model, shown in Figs 2f and 3f. The simplest way to test whether models are significantly different is to check the confidence intervals of the model parameters (Sokal & Rohlf, 1918). If there is no overlap in the confidence intervals for corresponding parameters, then they are significantly different. For example, in Table 1 the limits of the 95% confidence intervals for parameter α in the logistic model for sample designs a and b are (799.206, 870.442) and (1054.523, 1136.825), respectively, which indicates a significant difference. The same can be found for other parameters, or when comparing models or sampling designs in Table 1, which shows that different sampling designs significantly affect the parameters of a model. Note, however, that since samples are not independent of one another (because the data are autocorrelated), the confidence intervals of the parameters are likely to be narrower than they should for the normal $\alpha = 5\%$ level

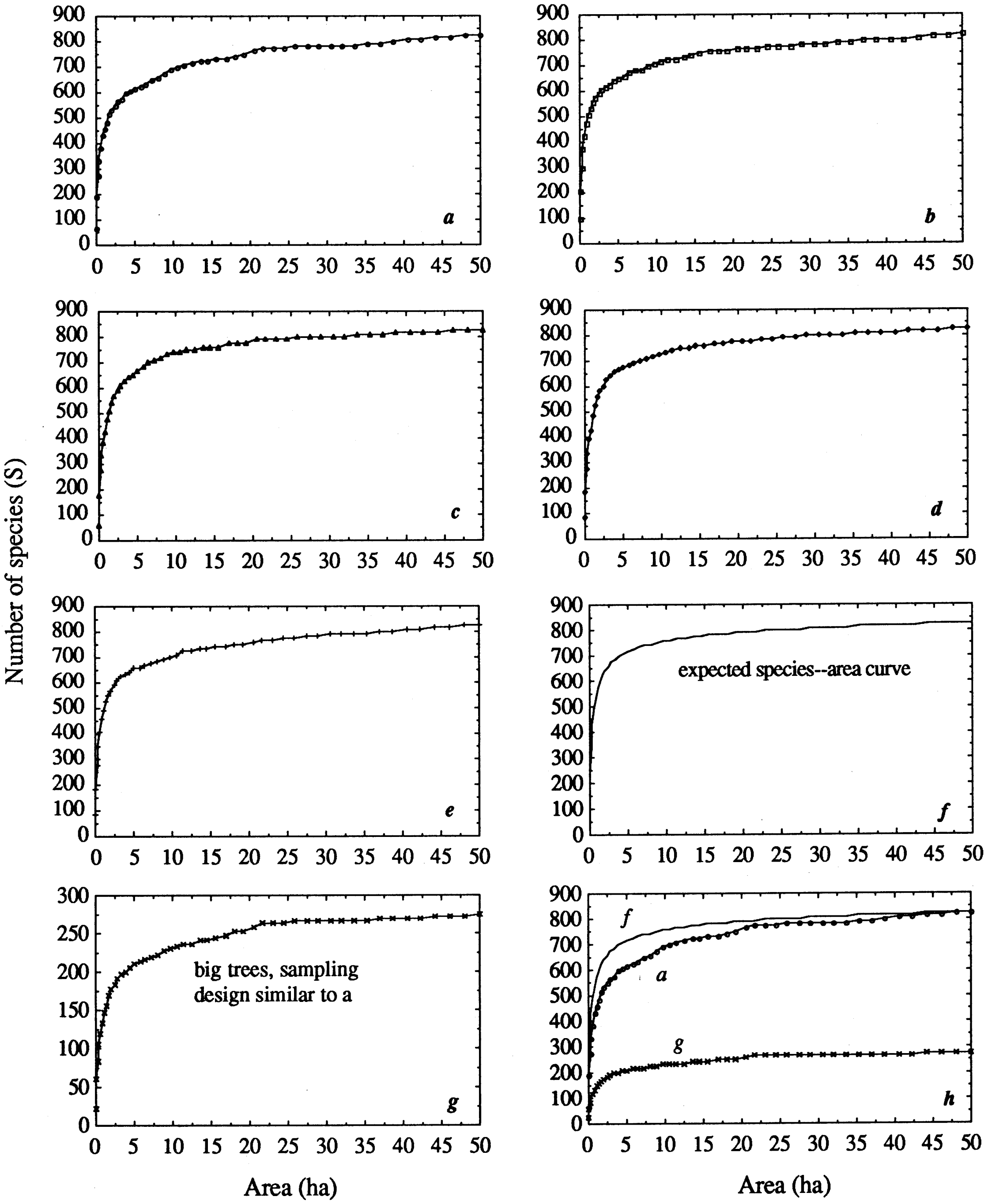


FIG. 2. Species richness–area curves. The abscissa is in ha while the ordinate represents the number of species; *a* to *e* correspond to the different sampling designs of Fig. 1*b*. *f* is the expected richness–area curve under the assumption that all species are randomly distributed over the study area. *g* is for the large-tree group only. *h* compares curves *a*, *f* and *g*.

(Legendre, 1993), so that apparently significant differences should be interpreted liberally; only well-separated confidence intervals should lead to conclude that parameters, and thus models, differ.

Not only are the expected and the large-tree species–area curves (curves *f* and *g* in Fig. 3h) significantly different from the observed all-tree-included species–area curves (Fig. 3a–e), but there are also differences among the all-tree-included curves themselves. At least three points can be extracted from the study of these species–area relations:

(a) Both the number of species and the spatial patterns of species distributions influence the species–area curves. This implies that it is important to take spatial patterns into

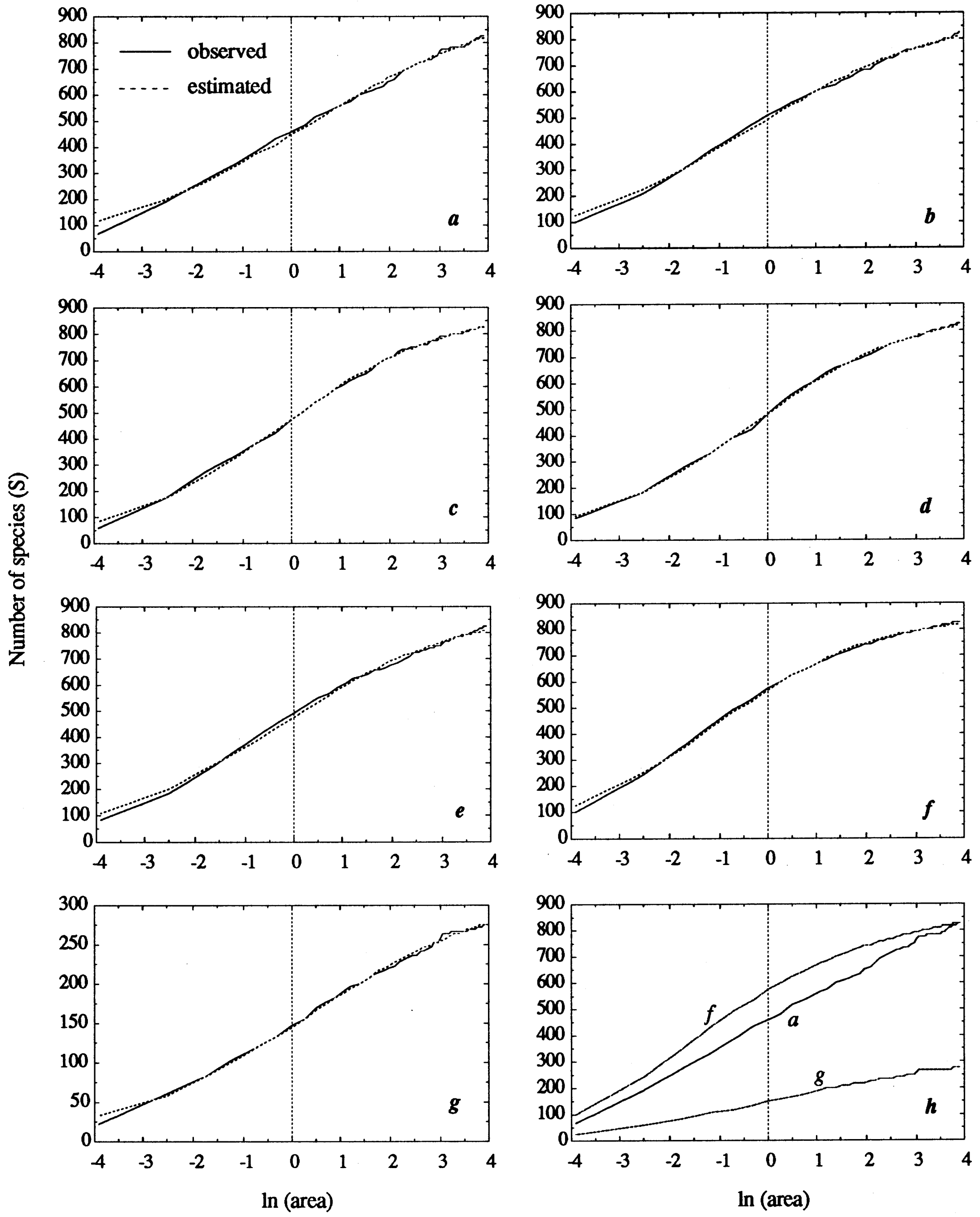


FIG. 3. Logistic models (dotted curves) fitted to the species richness (S)-logarea ($x = \ln(A)$) relations: $S = \alpha/(\beta + \exp(-\gamma x))$. The model parameters are listed in Table 1; *a* to *g* correspond to the richness–area curves of Fig. 2. Fig. 3*h* compares curves *a*, *f* and *g*.

account when studying diversity properties of communities, since in the real world most species are not randomly distributed through space. When tropical surveys take only some size classes into account (e.g. Poore, 1968, only recorded trees with d.b.h.$\geqslant$91 cm), the conclusions of such studies do not apply to the whole community.

(b) The location of the survey may also influence the species–area curves. With different sampling designs (Fig. 1b), the same theoretical models display significant differences (Table 1). This implies that in the same study plot different samplings may lead to different conclusions. For instance, when $A = 7$ ha (minimum area), the predicted richness, based on the logistic model (Fig. 3a), is 661 ± 7 for design *a*, while for design *c* (Fig. 3c) it is 705 ± 4.

(c) The power model can be derived from the dynamic equilibrium assumption. Not only is the power function model of the species–area relationship construed by many as evidence of equilibrium, but equilibrium is also considered to imply the power function (Preston, 1960; MacArthur & Wilson, 1967). In our study, this leads us to suggest that

TABLE 1. Comparison of three species–area models: logistic, exponential and power. Species richness is represented by S while A is the area in hectares; *a* to *e* correspond to the different sampling designs of Fig. 1*b*. *f* is the expected species–area curve, and *g* is the large-tree group. 'Residual' is the sum of squared residuals after fitting the given model, and 'conf. interval' is the half-width of the 95% confidence intervals of the parameter values. From these confidence intervals, it is clear that the parameters of a given model may be significantly different for different starting points.

Models sampling	$S=\frac{\alpha}{\beta+\exp(-\gamma\ln(A))}$		$S=\alpha+\beta\ln(A)$		$S=\alpha A^{\beta}$	
	Parameters ± conf. interval	Residual	Parameters ± conf. interval	Residual	Parameters ± conf. interval	Residual
a	$\alpha=834.824\pm35.618$ $\beta=0.861\pm0.0642$ $\gamma=0.468\pm0.0307$	6365.82	$\alpha=457.406\pm4.248$ $\beta=97.467\pm1.582$	4604.92	$\alpha=450.886\pm18.368$ $\beta=0.167\pm0.0137$	70990.54
b	$\alpha=1095.674\pm41.151$ $\beta=1.222\pm0.066$ $\gamma=0.513\pm0.0255$	3959.32	$\alpha=489.170\pm8.282$ $\beta=90.262\pm3.085$	17508.72	$\alpha=486.590\pm20.790$ $\beta=0.460\pm0.0145$	91164.98
c	$\alpha=1029.041\pm20.952$ $\beta=1.158\pm0.0317$ $\gamma=0.615\pm0.0167$	1459.02	$\alpha=477.853\pm11.589$ $\beta=99.762\pm4.317$	34283.98	$\alpha=477.820\pm25.996$ $\beta=0.159\pm0.0183$	142215.94
d	$\alpha=1087.026\pm23.509$ $\beta=1.237\pm0.0357$ $\gamma=0.605\pm0.0170$	1588.73	$\alpha=483.518\pm11.571$ $\beta=96.316\pm92.007$	34176.13	$\alpha=483.103\pm25.047$ $\beta=0.153\pm0.0175$	132117.78
e	$\alpha=1037.289\pm40.641$ $\beta=1.164\pm0.0650$ $\gamma=0.543\pm0.0287$	4869.90	$\alpha=477.267\pm8.610$ $\beta=93.983\pm3.207$	18921.78	$\alpha=474.963\pm22.0264$ $\beta=0.153\pm0.0157$	102168.31
f	$\alpha=1696.382\pm52.999$ $\beta=1.988\pm0.0751$ $\gamma=0.626\pm0.0202$	2044.73	$\alpha=540.167\pm15.667$ $\beta=84.339\pm5.835$	62651.59	$\alpha=543.149\pm26.696$ $\beta=0.123\pm0.0169$	151810.49
g	$\alpha=268.743\pm8.706$ $\beta=0.841\pm0.0447$ $\gamma=0.514\pm0.0261$	491.36	$\alpha=150.412\pm2.208$ $\beta=34.072\pm0.823$	1245.02	$\alpha=148.348\pm6.789$ $\beta=0.174\pm0.0153$	9705.72

the tropical forest under study would not be in a state of equilibrium.

(2) *Abundance* (N) The relations between abundance and sampling area are illustrated in Fig. 4. The data are extremely well fitted by linear models. The confidence intervals of the parameters of the linear models also indicate that with different sampling designs, the linear models are significantly different. For example, the limits of the confidence intervals of slope β for designs *a* and *b* are (6656.16, 6766.22) and (6540.81, 6588.63), respectively. The predicted values of abundance would certainly vary for different sampling designs.

When abundance is divided by sample size, a density (individuals/unit area) to area curve can be obtained (Fig. 5). This allows us to answer the question of the minimum quadrat size that is large enough to estimate abundance in a given plot or region. Abundance would be estimated in an unbiased way by any sample size if trees were randomly distributed throughout the plot. In reality, there are two main alternative sampling designs. One is to sample many small-size quadrats and the another is to consider fewer

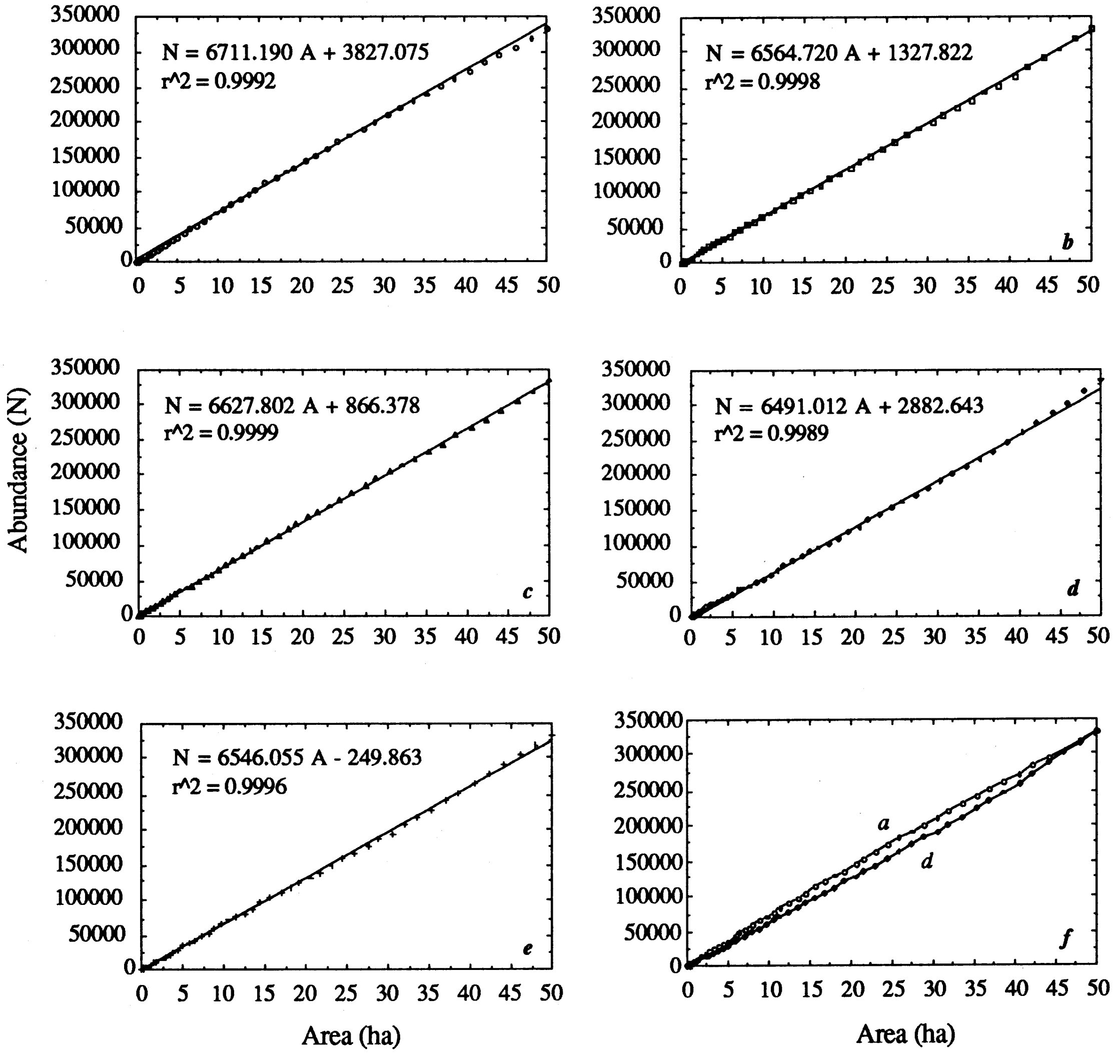


FIG. 4. Abundance–area curves (points) and linear models (lines) for the different sampling designs of Fig. 1*b*. *f* compares the two most different curves, *a* and *d*.

quadrats of larger size. Based on Fig. 5, a minimum continuous sampling unit of 5 ha is recommended to estimate the abundance of trees in the Pasoh forest; with smaller samples, the variance of the estimates would be very large.

(3) *Diversity* (*H*) Fig. 6 shows the relationship between Shannon diversity and area. Considering this figure alone, one may conclude that 2–5 ha would be the sufficient minimum sampling area; this is quite different from the minimum area derived from the species–area curves. The reason is that the Shannon diversity index reduces the effect of rare species, compared to richness (Hill, 1973; Peet, 1974). Considering regression residuals, the Shannon diversity–area curves are best fitted neither by the power nor by the exponential model, but by a parabolic model (Fig. 7 and Table 2). Again, the confidence intervals of corresponding parameters for the same model show that for different sampling designs, the model parameters may be significantly different.

The spatial structure of richness, abundance and Shannon diversity

In contrast to spatial homogeneity, which means absence of spatial variation, spatial heterogeneity refers to variability of quantitative or qualitative variables over a study area (Dutilleul & Legendre, 1993). The spatial heterogeneity of diversity may be the result of some underlying pattern or process such as environmental heterogeneity, biotic control (habitat selection, predation and competition, etc.), abiotic/biotic coupling processes (Hunter, 1987; Pringle, 1990), or even historical or chance events (Hubbell & Foster, 1986; Borcard & Legendre, 1994).

Fig. 8 shows the variograms of richness, abundance and Shannon diversity in the Pasoh forest. Empirical variograms were computed in four geographic directions: 0° (south–north: SN), 90° (west–east: WE), 45° (SW to NE) and 135° (SE to NW). The variograms show that the distributions of abundance and Shannon diversity are

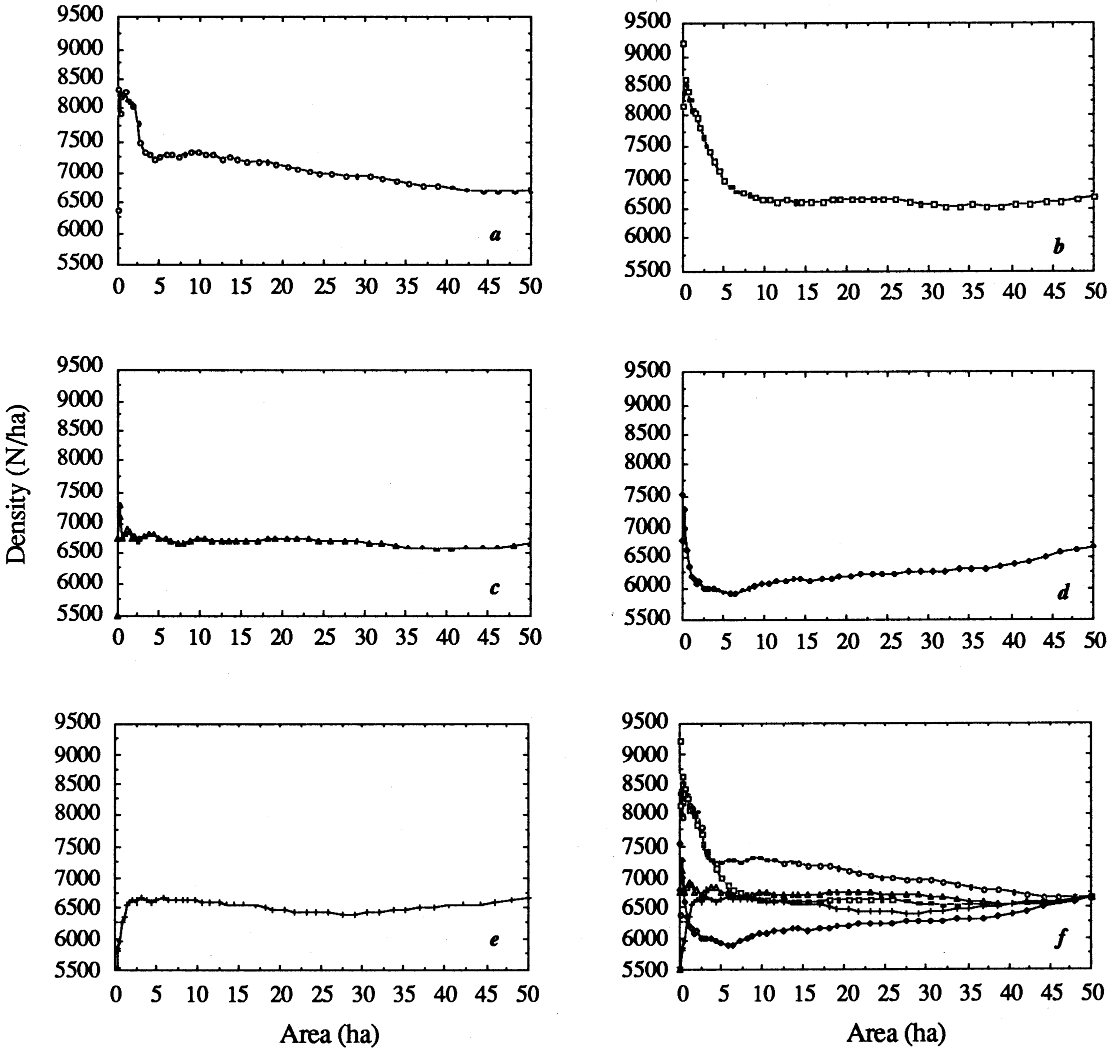


FIG. 5. Density–area curves. Density estimates (individuals/unit area) are a function of sampling location and sample size; *a* to *e* correspond to the different starting sampling locations shown in Fig. 1*b*. The curves suggest that, in order to avoid large bias in abundance estimates, a sampling size of 5–10 ha should be adequate.

anisotropic. On the other hand, the quick increase in semivariance in the short distance classes indicates that random variation dominates the distributions of richness and Shannon diversity. Considering the four directions, richness displays similar spatial structures, with the range around 150 m (Fig. 8a,b), although the nugget effects of the 45° and 135° variograms seem higher than for the 0° and 90° directions. The same phenomena can be observed for the other two variables. The relative nugget effect is 43% in Fig. 8.1a, while in Fig. 8.2a it is about 63%. The distribution map of richness is shown in Fig. 9a. In such a complex rain forest, it is no surprise to observe high nugget effects. Given the complexity and high species diversity over the study area, the possibility is high for sampling errors during the process of data transcription or species identification. The high observed nugget effects may also be due to small-scale processes that may dominate the tropical rain forest. Since the density for each species is low, species morphologies are highly specialized, and their niches are narrow (Ashton, 1969), some interesting spatial features may be detected at finer scales than the scale used here (= 20 m). A clear gradient structure is present for tree abundances (Fig. 8, 1b and 2b). The long-range effect is strong in all directions, though stronger in the 0° and 135° directions. This feature can also be seen from Fig. 9b. The relative nugget effect for the 0° and 90° cases is 21%, and 28% for the other two directions. The spatial structure of Shannon diversity shows a dominant short-range effect ($\leqslant 150$ m), and a clear large-scale patchiness in the 0°, 45° and 90° directions; this is confirmed by Fig. 9c. The relative nugget effect for the 0° and 90° directions is about 44%, and 63% for the other two directions.

The Shannon diversity index is a non-linear combination of both richness and abundance. It does not necessarily mean that the spatial structure of the Shannon index has to follow richness or abundance. In this study where we

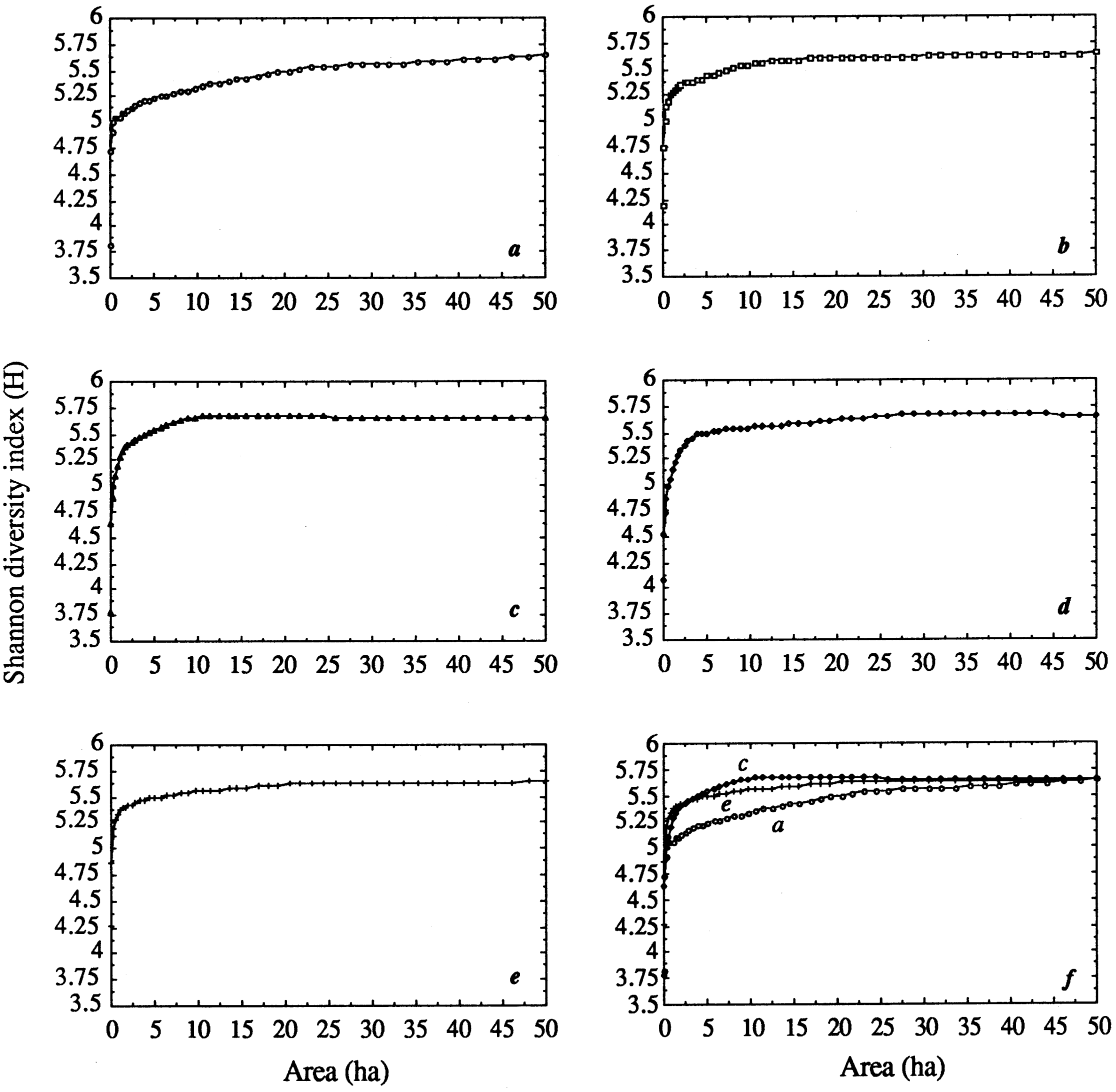


FIG. 6. Shannon diversity–area curves. The minimum area suggested by these curves is 2–5 ha. *a* to *e* correspond to the different sampling designs of Fig. 1*b*; *f* compares curves *a*, *c* and *e*.

evaluate the spatial structure of the Pasoh forest, it can be seen that richness is closer to Shannon diversity than is abundance.

Spatial patterns and controlling processes

There are several theories available to explain the spatial heterogeneity observed in plant and animal communities. The environmental and the biotic control models are two of them (Whittaker, 1956 and Bray & Curtis, 1957 for the former; Lindeman, 1942; MacArthur, 1969 and Southwood, 1987 for the latter). In the Pasoh forest the spatial patterns of diversity are explained by topographic and spatial factors, following the approach proposed by Borcard *et al.* (1992).

(1) *Richness* The total variance of richness is 2699 and the coefficient of variation is 19.4%. The matrix of x and y coordinates has been constructed as suggested by Legendre (1990), by including all terms of a cubic trend surface polynomial equation (the x and y geographic coordinates were centred on their respective means before computing the other terms of the geographic polynomial). A backward selection procedure was used to discard the terms of the trend surface equation whose contribution to richness is not significant ($P \leqslant 0.001$). The following terms were retained for the richness trend surface equation:

$$S = b_1x^2 + b_2xy + b_3y^2 + b_4y^3 + b_5x^2y + b_6xy^2$$

The same elimination procedure was applied to the environmental data and their combination (relative elevation z_1 and slope z_2), which resulted in the following equation:

$$S = c_1z_2 + c_2z_1z_2$$

Variance partitioning can be done by multiple regression since there is only one dependent variable (S); the R^2 of the multiple regression is equivalent to the sum of canonical

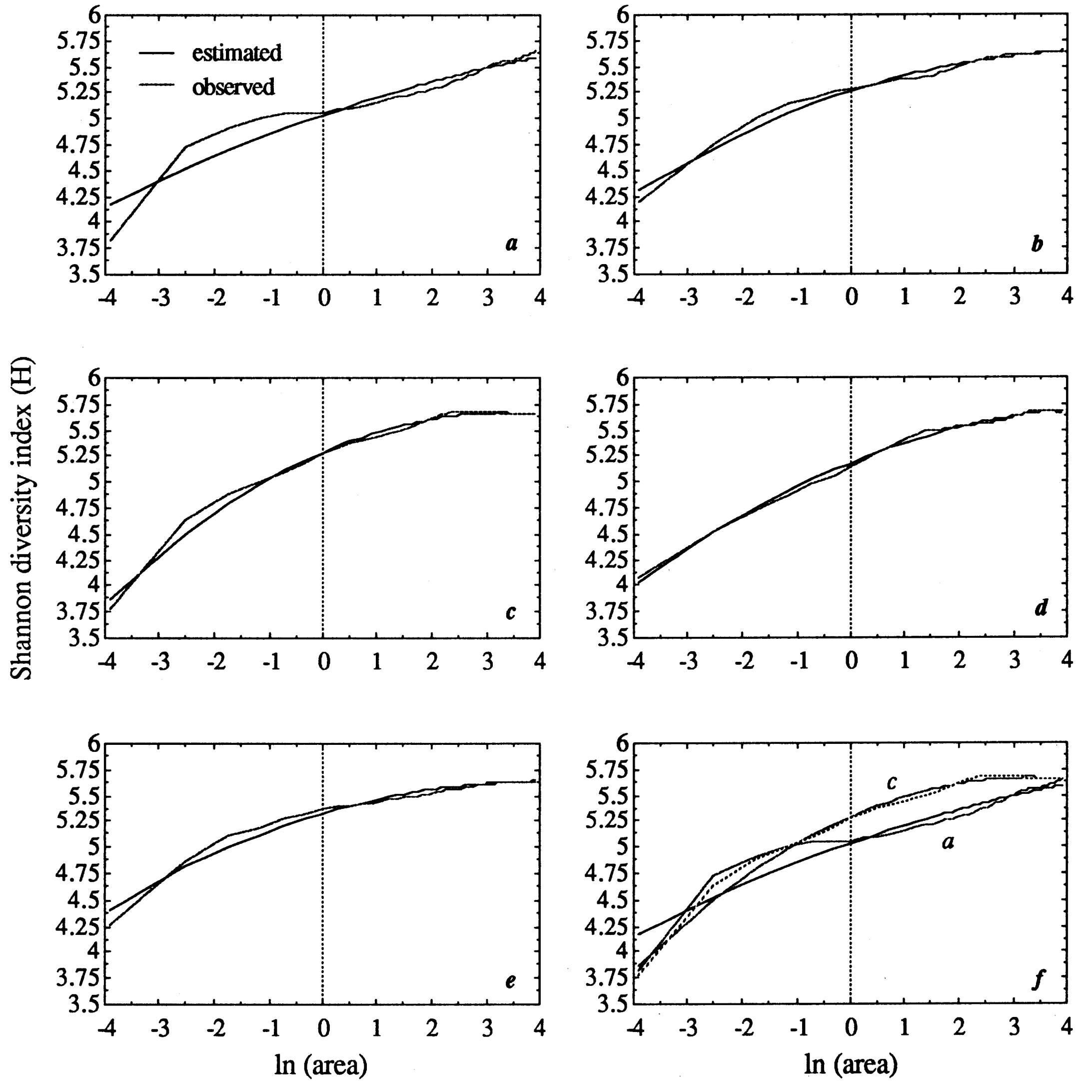


FIG. 7. Parabolic model (smooth curves) fitted to the Shannon diversity (H)-logarea ($x=\ln(A)$) relation (broken lines): $H=\alpha+\beta x+\gamma x^2$. The parameters of the model are listed in Table 2. *a* to *e* correspond to the different diversity–area curves of Fig. 6; *f* compares curves *a* and *c*.

eigenvalues in canonical analysis. The resulting partition of the variation is shown in Fig. 10. The explained portion of variation (a+b+c) is 10.1% of the total variation in the richness data; this is not high. The undetermined proportion (d), on the contrary, is very high. Although all these contributions (a, b and c) are significant, their contribution to the spatial patterns of diversity are simply very low. This is not surprising if we keep in mind the complexity of tropical rain forests. There are certainly many processes contributing to the formation of tropical communities, but a lack of one dominant force (Ashton, 1969; MacArthur, 1969; Connell, 1970; Janzen, 1970; Hubbell, 1979, 1980; Hubbell & Foster, 1986; Denslow, 1987); this is also one of the reasons why tropical environment can accommodate so many species. Faction (d) is the unexplained and not spatially structured fraction of variation; its large size agrees with the results of the variograms (Fig. 8, 1a and 2a) which, in the last section, evidenced little large-scale structuring. A high fraction (d) may result from sampling error, or from processes acting at finer local scales, or from some other important biotic or abiotic control factors that have not actually been included in the analysis (Borcard & Legendre, 1994). The surprise was to find a negative (b) fraction. Although this proportion is small in value, it remains statistically significant. Theory allows for a negative (b) fraction (Whittaker, 1984), but 'In ecological practice, however, this is unlikely to occur' (Borcard *et al.*, 1992). Its ecological interpretation is that the two processes of environmental and 'spatial' control probably behave in opposite directions, one process hindering the contribution of the other.

(2) *Abundance* The total variance of the abundance data is 227 and the coefficient of variation is 11.9%. The trend surface equation was constructed following the same

TABLE 2. Comparison of three Shannon diversity–area models: parabolic, exponential and power. Shannon diversity is represented by H while A is the area in hectares. 'Residual' is the sum of squared residuals after fitting the given model, and 'conf. interval' is the half-width of the 95% confidence intervals of the parameter values. The parabolic model is the best one to fit the Shannon diversity–area curves, while the power model is the worst. From the confidence intervals, it is clear that the parameters of a same model for different sampling designs (*a* to *e*) may be significantly different.

Models sampling	$H=\alpha+\beta\ln(A)+\gamma\ln(A)^2$		$H=\alpha+\beta\ln(A)$		$H=\alpha A^{\beta}$	
	Parameters ± conf. interval	Residual	Parameters ± conf. interval	Residual	Parameters ± conf. interval	Residual
a	$\alpha=5.037\pm0.0453$ $\beta=0.181\pm0.0173$ $\gamma=-0.0104\pm0.00616$	0.359	$\alpha=4.996\pm0.0419$ $\beta=0.164\pm0.0155$	0.447	$\alpha=4.750\pm0.0503$ $\beta=0.05\pm0.0388$	1.806
b	$\alpha=5.260\pm0.0184$ $\beta=0.168\pm0.0071$ $\gamma=-0.0189\pm0.0025$	0.0602	$\alpha=5.186\pm0.0371$ $\beta=0.138\pm0.0138$	0.351	$\alpha=5\pm0.0686$ $\beta=0.05\pm0.0502$	3.352
c	$\alpha=5.291\pm0.0183$ $\beta=0.227\pm0.00703$ $\gamma=-0.0344\pm0.0025$	0.0592	$\alpha=5.156\pm0.0633$ $\beta=0.171\pm0.0236$	1.023	$\alpha=4.945\pm0.0558$ $\beta=0.0418\pm0.0472$	2.144
d	$\alpha=5.182\pm0.0138$ $\beta=0.211\pm0.00535$ $\gamma=-0.0211\pm0.00189$	0.0338	$\alpha=5.100\pm0.0394$ $\beta=0.177\pm0.0146$	0.395	$\alpha=5.000\pm0.0557$ $\beta=0.050\pm0.0407$	2.210
e	$\alpha=5.333\pm0.0192$ $\beta=0.155\pm0.00739$ $\gamma=-0.0208\pm0.00263$	0.0653	$\alpha=5.252\pm0.0404$ $\beta=0.122\pm0.0151$	0.417	$\alpha=5\pm0.0734$ $\beta=0.05\pm0.0538$	3.847

procedure as for the richness data. With centred data, the following terms were retained for the abundance trend surface equation:

$$A=b_1x+b_2y+b_3x^2+b_4y^2$$

The following equation was obtained for the environmental data (relative elevation z_1 and slope z_2):

$$A=c_1z_1+c_2z_1^2$$

The resulting partition of the variation is shown in Fig. 10. The explained portion (a + b + c) accounts for 24.9% of the total variation of the abundance data. The spatially structured environmental contribution (b) is very low, although significant, which means that the relation of the abundance data to the spatially structured environmental factors is weak. As with richness, the undetermined proportion (d) is very high (75.1%).

(3) *Diversity* The total of variance for Shannon diversity is 0.0272; its coefficient of variation is only 3.7%, which may imply that the spatial variation of Shannon diversity is basically random. The following terms were retained for the Shannon diversity trend surface equation:

$$D=b_1x+b_2y+b_3x^3+b_4xy^2$$

The following equation was obtained for the environmental data (relative elevation z_1 and slope z_2):

$$D=c_1z_1+c_2z_2+c_3z_1z_2+c_4z_1z_2^2$$

The resulting partition of the variation is shown in Fig. 10. The explained portion (a + b + c) accounts for only 10.4% of the total variation of the Shannon diversity data, although all contributions (a, b and c) are significant. The spatially structured environmental contribution (b) is higher than for the abundance data. Again, the undetermined proportion (d) is high.

There are several common features to the variation partitions of the richness, abundance and Shannon diversity data; they imply similar underlying controlling processes in the Pasoh forest. In all cases, we observe fairly large pure spatial components (c) and small pure environmental components (a), as well as very high undetermined proportions (d). High (c) may result either from spatially structured environmental factors not included in the analysis, from spatially structured historical processes, or from environment-independent processes, such as growth (architecture and root system), reproduction, predation and competition with neighbours acting to shape the community.

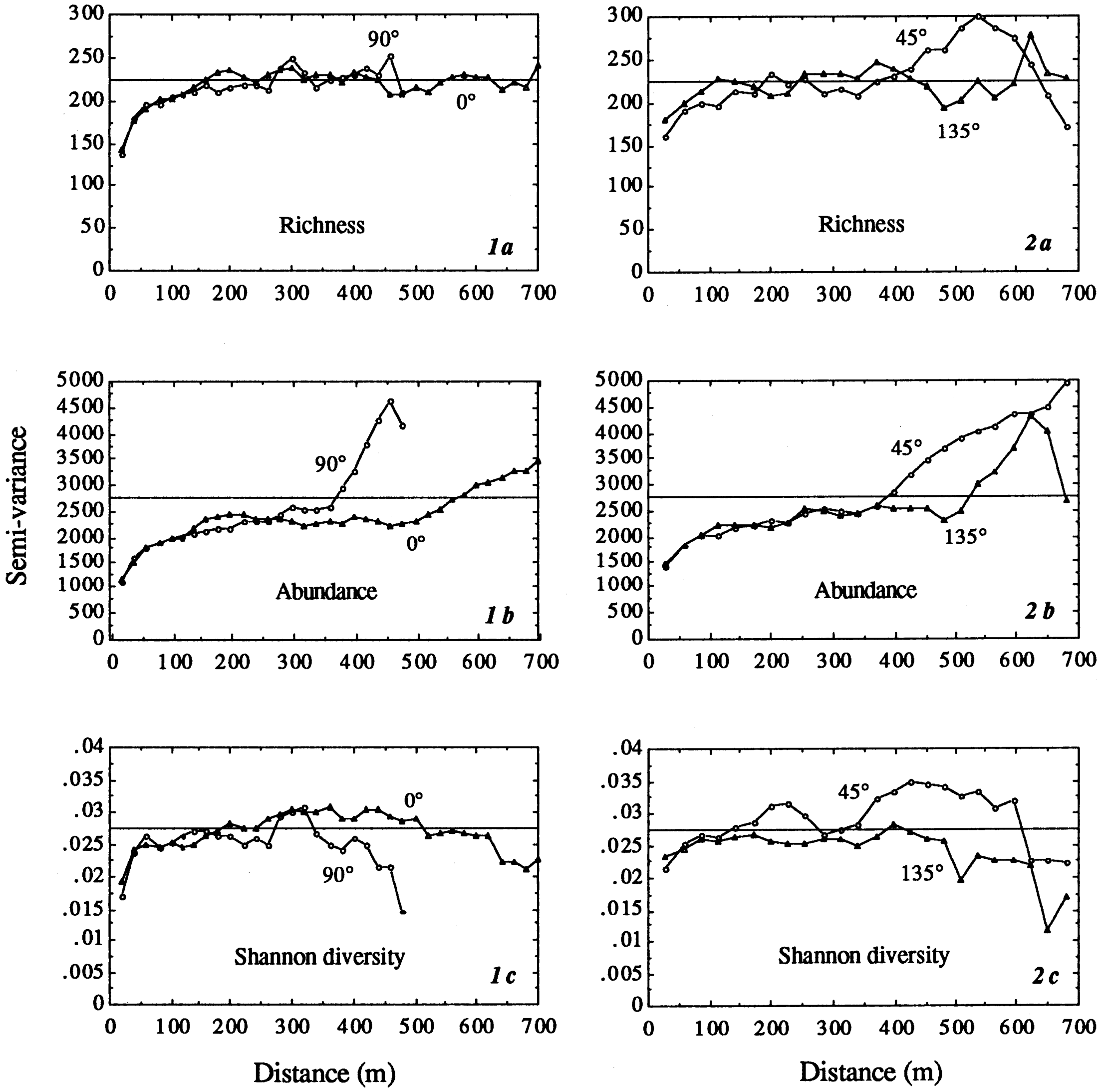
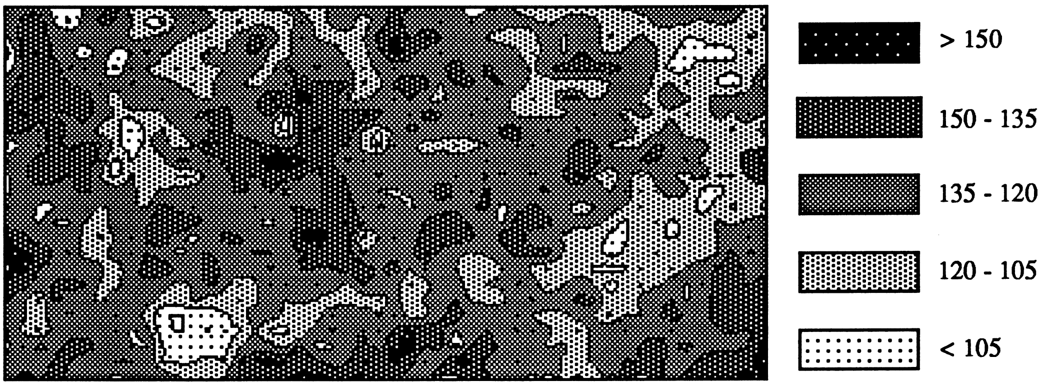


FIG. 8. Empirical variograms of richness (1a–2a), abundance (1b–2b) and diversity (1c–2c) in four geographic directions: 0° is east–west (horizontal), 90° is south–north (vertical), 45° is SE–NW and 135° is NE–SW. The horizontal lines show the overall variance of the variables in the whole Pasoh plot.

Low environmental explanation (a) may be attributed, on the one hand, to the relative flat topography of the study area (Fig. 1a) which is also typical in lowland tropical rain forests; on the other hand, it may result from the absence of dominant environmental controlling factors in this study area. There are some possible explanations for the high unexplained proportions (d). One is that there is only a small amount of variability to be explained in this relatively homogeneous forest (small coefficient of variation), considering that trend–surface equations are not appropriate to capture small-scale variability. Another possible explanation is high sampling error, but this is certainly not the case here since the survey has been exhaustive in the Pasoh plot. Finally, niche differentiation, species specificity and the lack of dominant controlling forces (many processes controlling the structure of tropical communities, each one playing but a small role) may be invoked. Most of these act at very local scales; this is corroborated by the high nugget effects of the variograms in Fig. 8. The diversity of forces controlling the development of tropical forest communities and acting at small spatial scales emerges as the likely cause for the high observed species diversity. If this holds true, then fraction (d) would be expected to be lower for tropical forest communities dominated by a single species (Connell, 1978; Hart, 1990).

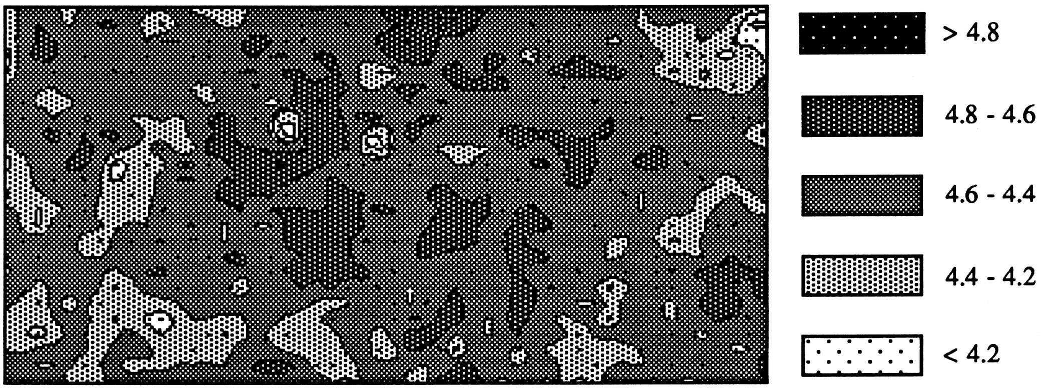
CONCLUSION

This study is basically a spatial analysis approach to understand the community organization of the Pasoh forest. Some conclusions concerning the spatial structure of diversity and community organisation can be reached in this study, corresponding to the questions raised in the Introduction.



a. **Richness**

b. **Abundance**



c. **Shannon diversity index**

FIG. 9. Maps of the diversity data showing the distributions of richness, abundance and Shannon diversity in the 50-ha Pasoh plot, Malaysia. The maps are interpolated by the inverse-distance method based on a 20 × 20 m sampling grid.

(1) The diversity–area relations found in the Pasoh forest differ with sampling locations. The observed species–area curves differ markedly from the one derived from the null hypothesis that the individuals are randomly distributed over the study area, which suggests that spatial patterns of species dramatically affect the diversity–area relation. From the species–area curves, a minimum sampling area of 5–10 ha is recommended, while 2–5 ha seems appropriate based on the Shannon diversity–area relations.

(2) The species–area curves are better fitted by the logistic model than by the power or exponential models, while the parabolic model is the best one to fit the Shannon diversity–area curves. Among the models that we studied, the power function is the least appropriate to describe the

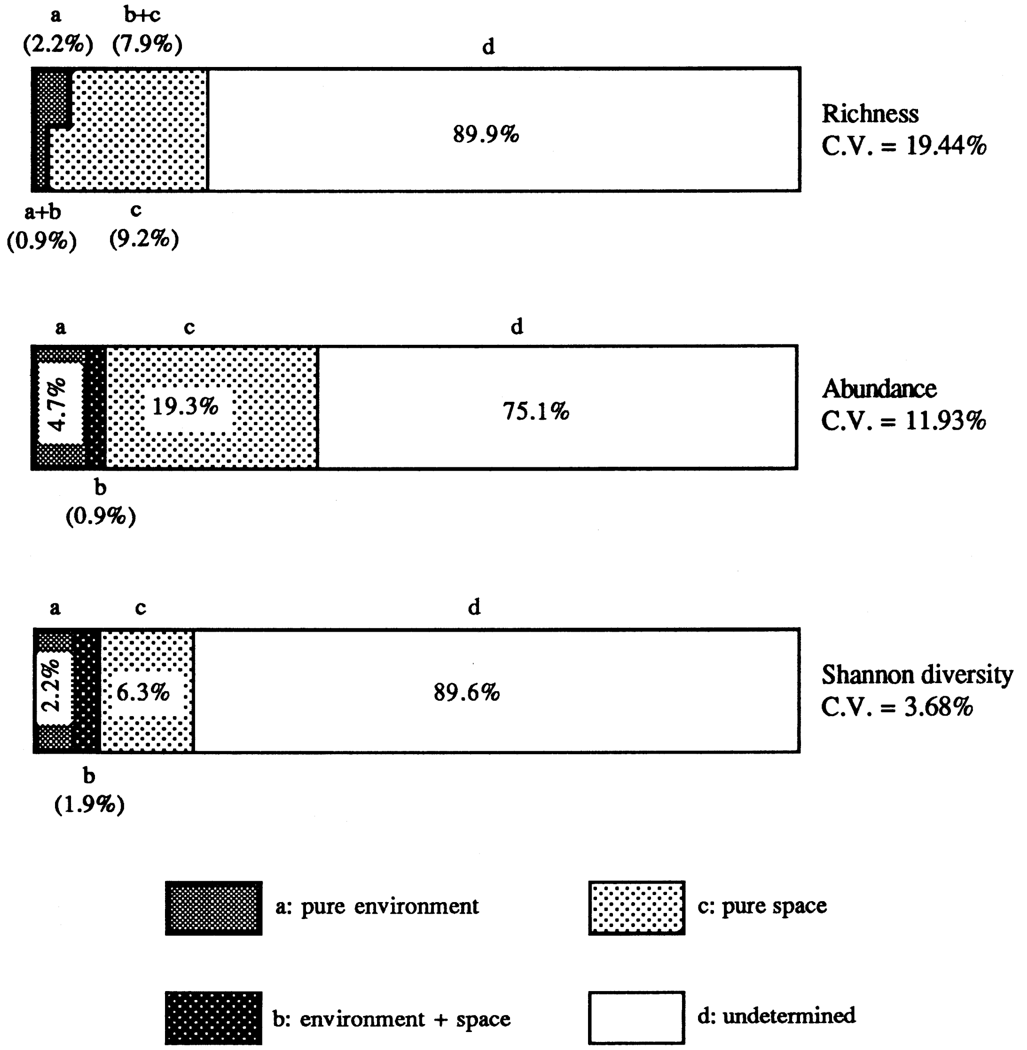


FIG. 10. Variation partitioning of the diversity data vectors (richness, abundance and Shannon diversity); (a) is the pure environmental contribution, (b) is the joint environmental and spatial contribution, (c) is the pure spatial contribution, and (d) is the undetermined effect (shortened in the three pictures). C.V. is the coefficient of variation of each dependent variable. Notice that in the case of richness, (b) = −1.3%.

species–area relation. This suggests that the community may not be in equilibrium.

(3) The spatial structure of diversity, as captured by the semi-variograms, displays short-range effects (around 150 m) in the cases of richness and Shannon diversity, and high nugget effects in all three diversity variables (richness, abundance and Shannon diversity). Semi-variograms of the diversity data generally demonstrate clear anisotropy and high random variation, except for abundance which forms a gradient in the Pasoh plot. Absence of a clear and consistent spatial structure of diversity also suggests that the Pasoh forest may not be in equilibrium.

(4) Only a small proportion of variation contained in the diversity data could be explained by the topographic (relative elevation and slope) and spatial variables. High undetermined, non-spatially structured effects remain in the diversity data, which indicates that the community is relatively unpredictable, and thus may not be in equilibrium.

(5) Local-scale processes (<20 m) play an important role in the organization of the Pasoh forest. High community complexity, lacking long-range dominant forces, niche differentiation and other specific requirements to species, as well as contagious biological processes (reproduction, predation, competition and growth) are among the fine-scale processes possibly in operation. These processes may account for the high unexplained variation and high nugget effects of the variograms; they have also been described by authors, cited in the references (Ashton, 1969; Connell, 1970, 1978; Janzen, 1970; Hubbell, 1979, 1980; Hubbell & Foster, 1986; Denslow, 1987), as the major causes for the high diversity of tropical forests.

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