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Scale dependence of tree abundance and richness in a tropical rain forest, Malaysia

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Abstract

Abundance and richness are the two fundamental components of species diversity. They represent two distinct types of variables of which the former is additive when aggregated across scales while the latter is nonadditive. This study investigated the changes in the spatial patterns of abundance and richness of tree species across multiple scales in a tropical rain forest of Malaysia and their variations in different regions of the study area. The results showed that from fine to coarse scales abundance had a gradual and systematic change in pattern, whereas the change in richness was much less predictable and a 'hotspot' in richness at one scale may become a 'coldspot' at another. The study also demonstrated that different measures of diversity variation (e.g., variance and coefficient of variation) can result in different or even contradictory results which further complicated the interpretation of diversity patterns. Because of scale effect the commonly used measure of species diversity in terms of unit area (e.g., species/m^2) is misleading and of little use in comparing species diversity between different ecosystems. Extra care must be taken if management and conservation of species diversity have to be based on information gathered at a single scale.

Introduction

Species diversity is usually measured on the basis of area. Different areal samples likely produce different values of diversity, i.e., diversity depends on the sampling unit size (or scale) at which it is observed. Worse is that diversity pattern and scale are rarely found to follow a linear or other proven mathematical forms. As a result, there are no simple or reliable rules that can be used to extrapolate studies conducted at one scale up or down to other scales, so that parameters or conclusions derived as such are only of limit use. Such a scale effect was recognized long ago in ecology (Tillyard 1914; Arrhenius 1921; Greig-Smith 1952; Bormann 1953) and continues to be a challenging issue, although much advancement has been made over the past two decades (Turner et al. 1989; Wiens 1989; Jelinski and Wu 1996; Legendre and Fortin 1989; Peterson and Parker 1998; Dungan et al. 2002). Of the many scale issues, scale effect on species diversity patterns has attracted particular attention, in a large part because of its significance for biodiversity studies and conservation applications.

Scale may be defined differently in different studies, but it mainly refers to the components in sampling designs, such as sampling unit size (or grain size), the shapes of sampling units, directional layout of sampling units (or zoning effect), the intervals between sampling units (or spatial lag), or the extent area of a study (Palmer 1988; Legendre and Fortin 1989; Turner et al. 1989; Wiens 1989; Jelinski and Wu 1996; Dungan et al. 2002). Research on the effect of scale on diversity patterns and their interpretation has concentrated on a number of important problems, including (1) determining optimal sampling unit size, shape and sample size (Hall et al.

1998; Condit et al. 1996; Mouillot and Leprêtre 1999), (2) identifying "characteristic area" for studying the structure and dynamics of plant communities (Juhász-Nagy and Podani 1983; Podani 1984; Podani et al. 1993; Bartha et al. 1998; Fortin et al. 1999), (3) investigating the scale dependence of diversity measures and patterns (Condit et al. 1996; He and Legendre 1996; Wilson et al. (1998, 1999); Fortin et al. 1999; Crawley and Harral 2001), and (4) evaluating the effect on diversity mapping (Stoms 1994; Stohlgren et al. 1997).

Regardless how species diversity is measured, individual abundance (defined as the total number of individuals pooled across species in an area) and species richness (defined as the total number of species in an area) are the two most fundamental diversity variables. In this study we investigated these two variables individually rather than some combined indices of abundance and richness although such indices capture an important aspect of community structure (Juhász-Nagy and Podani 1983; Podani 1984; Podani et al. 1993). Abundance and richness represent two categories of variables that have a very different spatial property. Abundance (or equivalently density) is additive when aggregated across scales, while species richness is nonadditive (He and Legendre 1996; Legendre and Legendre 1998). For example, assume n_1 and n_2 are the abundance in two adjacent subplots, and s_1 and s_2 are the corresponding species richness. When the subplots are aggregated, the abundance in the combined plot $n = n_1 + n_2$, whereas the total number of species $s \leqslant s_1 + s_2$, the equal sign holds only if the two subplots have distinct species composition. Because of the nonadditivity of species richness, high species richness at a smaller scale does not guarantee high richness at a larger scale; all depend on the similarity in species composition. (Nonadditive variables are not uncommon in life; ratio variable such as the number of TV sets or cars per household in a city block is another example.) For nonadditive variables, many spatial analysis techniques and modeling approaches, e.g., quadrat agglomeration (Greig-Smith 1952), autocorrelation (Cliff and Ord 1973), semivariogram (Burrough 1987), analysis of variance (Moellering and Tobler 1972) cannot be applied. A species in an area will be repeatedly counted if the area is divided into smaller units and the species occurs in more than one unit. This inevitably leads the units to have a certain degree of species overlapping, a phenomenon not readily described by the above techniques (Stoms 1994).

This study presented an analysis about scale effect on abundance and richness of tree species in a tropical rain forest of Malaysia. Here scale refers to the sampling unit size (i.e., grain size) unless defined otherwise. The objectives of the study were: (1) to map the distributions of abundance (additive) and richness (nonadditive), (2) to investigate the spatial variation of these two types of variables and their differences across scales, and (3) to assess the "regional" differences in abundance and richness, i.e., to determine if diversity patterns are consistent in different regions of the study area. The study followed with a discussion on how to interpret the diversity patterns across scales, to determine if abundance and richness are robust to scale change and to precaution the use of information collected at a single scale for the purposes of diversity management and conservation.

Study site and methods

Study site

The forest tract under study is a rectangular plot of 50 ha (500 × 1000 m) established in 1987 at the Pasoh Forest Reserve, Negeri Sembilan, Malaysia (102°18′ W, 2°55′ N). The plot has a mostly level plain of relatively uniform terrain, a hill rising in the center of the plot to about 25 m above the lowest point (Figure 1), see Kochummen et al. (1990) for a further detailed description of the site. The field survey (census) consisted of enumerating and identifying all free-standing trees and shrubs $\geqslant$ 1 cm in diameter at breast height, positioning each one by geographic coordinates on a reference map. The initial census of 1987 was repeated in 1990 and 1995. The data from the 1987 survey was used in this study (Manokaran et al. 1999). There were a total of 335,356 individual stems belonging to 814 species. The most abundant species had 8962 stems.

Methods

The 50 ha Pasoh forest plot was divided into grid systems using eight quadrat sizes (i.e., grain sizes): 5 × 5 meters (20,000 quadrats), 10 × 10 (5000), 20 × 20 (1250), 25 × 25 (800), 50 × 50 (200), 100 × 100 (50), 250 × 250 (8), 500 × 500 (2). The total tree abundance (the number of stems pooling across all

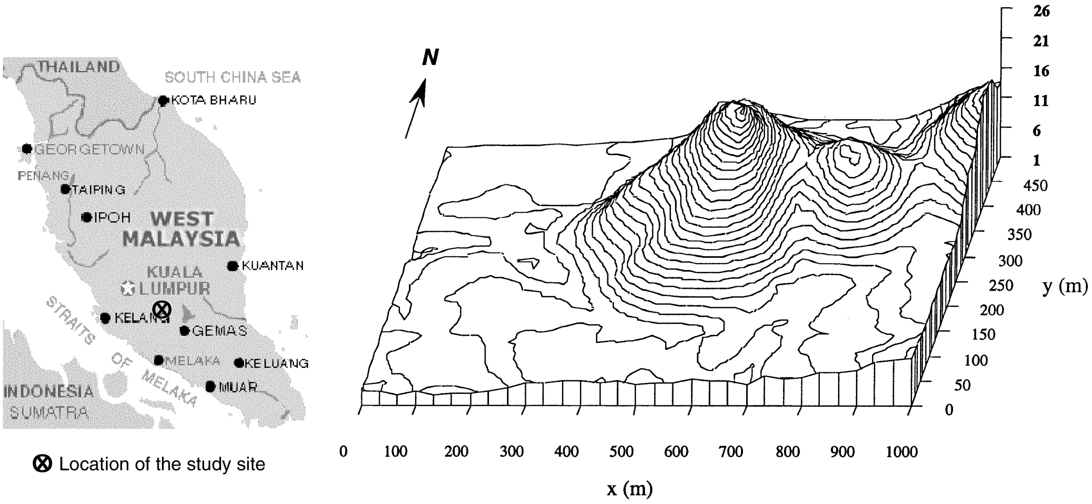


Figure 1. Topography of the 50 ha Pasoh forest plot, Malaysia.

species) and the number of species were then counted in each quadrat for each grain size.

The abundance and richness data so obtained were used to produce abundance and richness maps for the eight grain sizes. Spearman rank correlation coefficients were calculated to assess the association between the maps. In the meantime, spatial variance and coefficient of variation (CV) of abundance and richness were also calculated. The variance and CV were then plotted against the grain size, so as to examine the effect of scale on the spatial variability in abundance and richness and to identify possible breaks or peaks in the variability across scales. It is suggested that such breakpoints or peaks may be useful for identifying a certain underlying physical or ecological process or a characteristic area for a community (Juhász-Nagy and Podani 1983; Horne and Schneider 1995).

To assess the dependence of abundance and richness patterns on regions, an abundance-area curve (or called individuals-area curve) and a species-area curve were constructed for each of the four 250 × 250 m subplots of the Pasoh forest, i.e., divide the entire 500 × 1000 m Pasoh plot into eight 250 × 250 m subplots, four of them were examined, see the 250 × 250 m maps of Figures 2 and 3. The abundance-area and species-area curves were computed for each subplot using six sampling grain sizes: 5 × 5 m (2500 quadrats), 10 × 10 (625), 20 × 20 (144), 25 × 25 (100), 50 × 50 (25), 100 × 100 (4). The curves were the average of the quadrat counts for each grain size.

Results

Abundance and richness maps

Six of the eight distribution maps of tree abundance and species richness are shown in Figures 2 and 3, respectively. It is clear that at small sampling scales $\leqslant$ 25 m), the maps capture the detailed variation in abundance and richness, but these variations are averaged out at coarser scales. At the scales $\leqslant$ 25 m it is discernible that the northeastern region has the lowest values of abundance and richness, whereas the western region has the highest values, this trend is also evident at 2-dimensional grey-scaled maps (not shown). With the increase of scale, abundance shows a gradual and consistent change, while the change in richness appears erratic. The southwestern region becomes most depauperate in species richness at scales $\geqslant$ 100 m, although it is not so at small scales $\leqslant$ 25 m).

These visual findings are confirmed by the Spearman rank correlation coefficients among the maps at different scales (Tables 1 and 2), although caution is needed for interpreting the significance test in the tables because of the possible dependence in the data points between neighbouring quadrats. The positive Spearman rank correlation coefficients among the abundance maps suggest the consistency in the distribution of abundance across scales, although the monotonic decrease in the correlation along the column of Table 1 indicates the attenuation in the correlation from fine to coarse scales. In contrast, the cor-

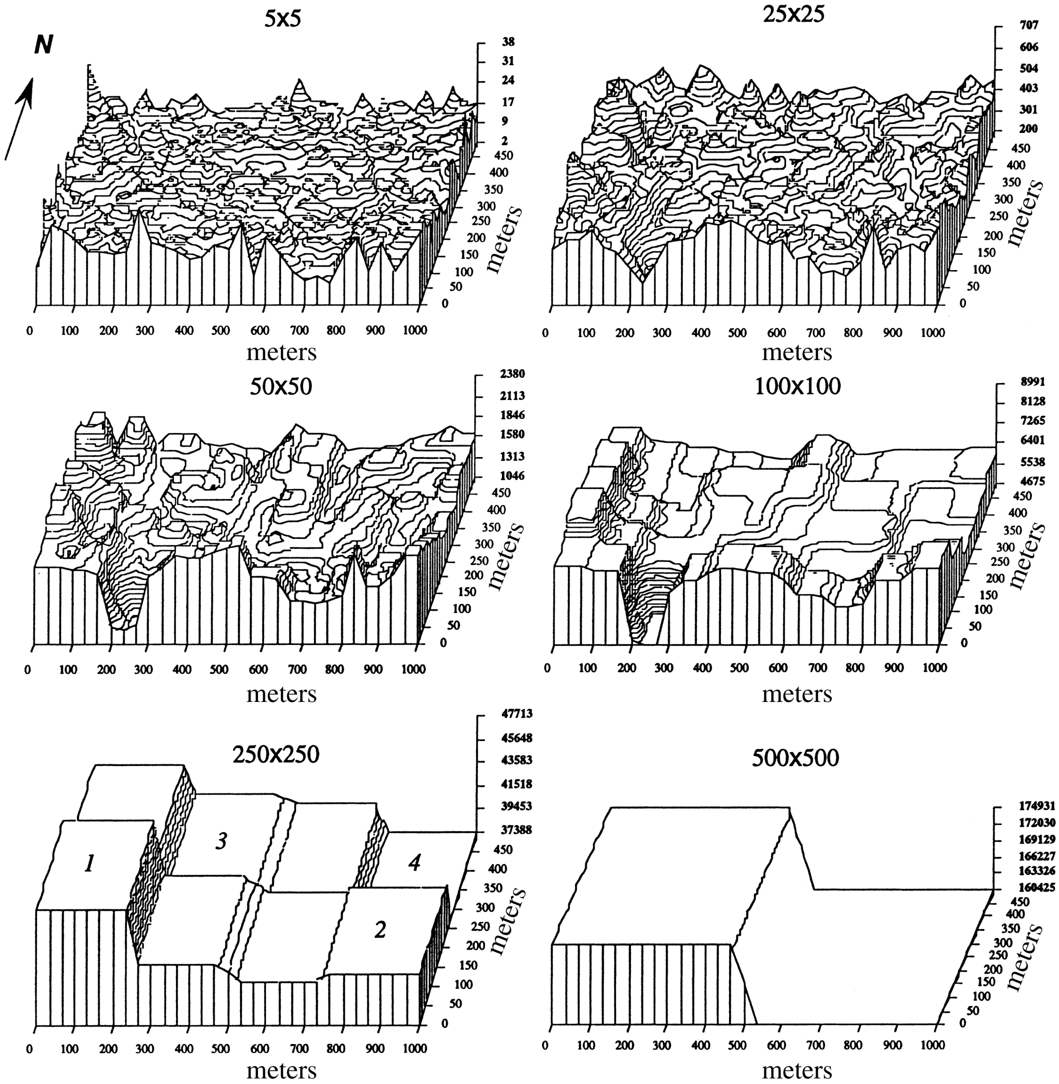


Figure 2. Maps of tree abundance in the Pasoh forest plot at six grain sizes (5×5, 25×25, 50×50, 100×100, 250×250 and 500×500 m). The vertical axis is the abundance (number of stems). Four numbered subplots in the 250×250 m map are used to evaluate regional effect on diversity pattern in a later analysis.

relation coefficients among the richness maps are so erratic that their direction of correlation even changes, despite that adjacent scales show a higher correlation than scales farther apart (Table 2). This inconsistency is also visually evident in Figure 3 (e.g., the changes at the southwestern corner). The correlation between abundance and richness is also subjected to scale effect (Table 3). At fine scales ($\leqslant$ 25 m), there is a very strong association between abundance and richness, but such an association vanishes at coarse scales.

Although it seems that there is a higher variation in abundance and richness at small scales (Figures 2 and 3), this is an illusive impression if variance is used to measure the variation. Contrary to the visual effect, both variables have low spatial variance at small scales (Figure 4a). It is clear that these two variables have a striking difference in spatial variance across scales. Variation in abundance linearly increases with scale (in the log-log transformation), whereas variation in richness is unimodal, maximizing at 250 × 250 m grain size (Figure 4a). In contrast, if CV is used to measure the variability in abundance and richness, the results are however consistent with the visual observations as shown in Figures 2 and 3, the CVs of abundance and richness in Figure 4b are monotonically decreased with scale.

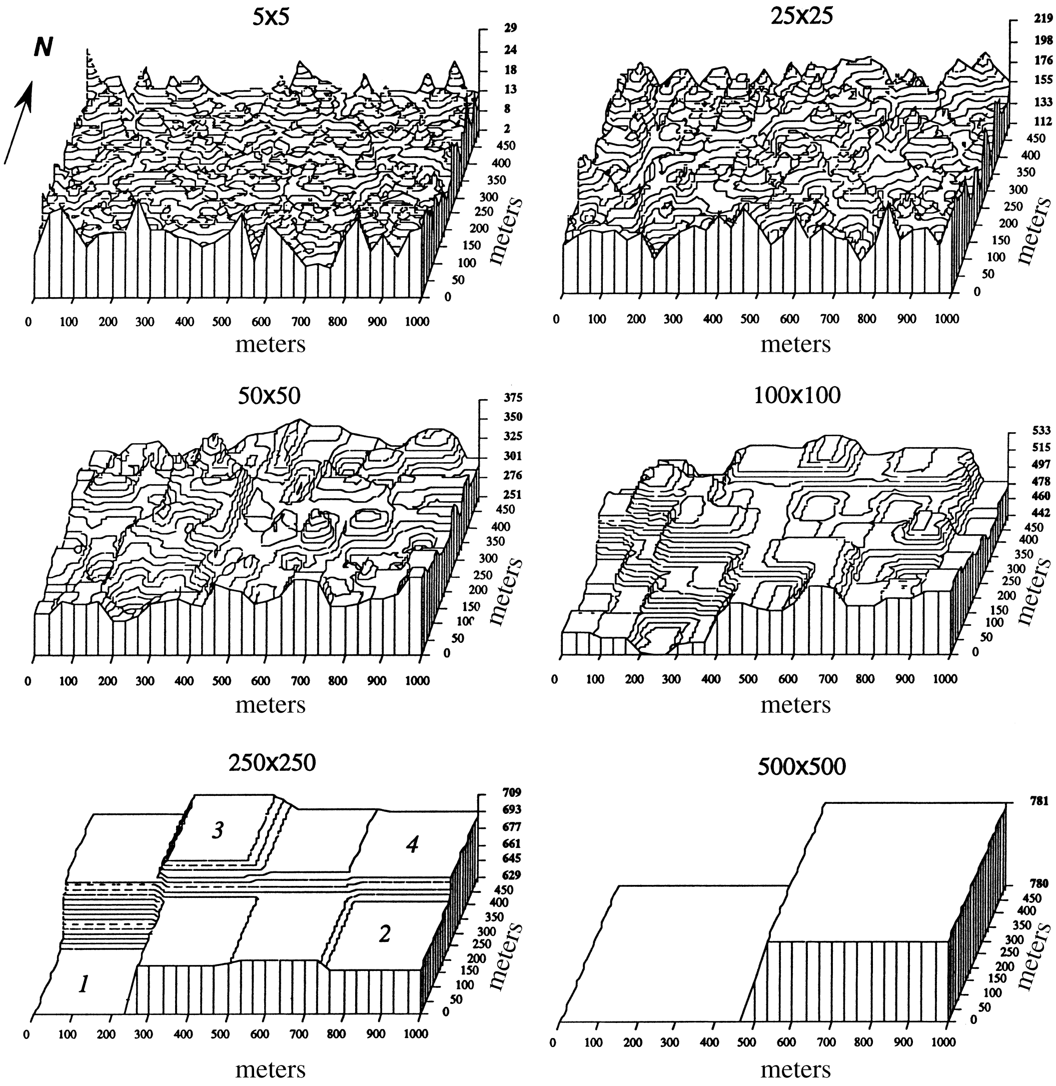


Figure 3. Maps of species richness in the Pasoh forest plot at six grain sizes (as Figure 2). The vertical axis is the number of species. Four numbered subplots in 250 × 250 m map are used to evaluate regional effect on diversity pattern in a later analysis.

Abundance-area and species-area curves

From the maps shown in Figures 2 and 3, it is obvious that abundance and richness not only depend on scale but also on region. The abundance-area and species-area curves constructed for the four subplots chosen from the Pasoh plot (see the numbers marked in the 250 × 250 m maps in Figures 2 and 3) are shown in Figure 5. It is obvious that abundance and area form a linear relationship, but the lines for different subplots have different slopes with no lines intersecting each other (Figure 5a). Subplot 1 always has the highest abundance across the scale, subplot 4 has the least, whereas subplots 2 and 3 have the intermediate values.

Similarly, species-area curves also show a strong dependence on region (Figure 5b), but different from abundance the species-area curves have a considerable interaction across scales, suggesting that a location with high richness does not necessarily retain the high value if spatial scale is changed. At small scales $\leqslant$ 20 m) subplot 1 has the highest number of species, while at larger scales $\geqslant$ 50 m) its number is the lowest among the four subplots (in fact it is the lowest in the entire 250 × 250 m map shown in Figure 3). Subplot 3 has the intermediate number of species at small scales (< 20 m) but the highest number of spe-

Table 1. Spearman rank correlation coefficients (corrected by ties) for abundance map pairs at different grain sizes (see Figure 2 for six of the eight maps). Because different grain sizes had different number of samples (quadrats), the coarse scale map was divided into the same number of quadrats to match the finer scale map (e.g., the 100 × 100 m map was divided into 20000 quadrats to match the 5 × 5 m map). For those maps whose quadrats cannot be exactly overlaid, both maps were divided by the largest common scale (e.g., for the 50 × 50–20 × 20 m map pair, both maps were divided using 10 × 10 m grain size, resulting in 5000 quadrats). The number in the parenthesis is the sample size. All coefficients are significant at *p*-value < 0.001 level.

	5 × 5	10 × 10	20 × 20	25 × 25	50 × 50	100 × 100	250 × 250
10 × 10	0.667 (20000)						
20 × 20	0.463 (20000)	0.753 (5000)					
25 × 25	0.473 (20000)	0.664 (20000)	0.787 (20000)				
50 × 50	0.385 (20000)	0.565 (5000)	0.709 (5000)	0.797 (800)			
100 × 100	0.322 (20000)	0.471 (5000)	0.350 (1250)	0.658 (800)	0.806 (200)		
250 × 250	0.164 (20000)	0.247 (5000)	0.321 (5000)	0.344 (800)	0.417 (200)	0.567 (200)	
500 × 500	0.115 (20000)	0.175 (5000)	0.227 (1250)	0.248 (800)	0.291 (200)	0.420 (50)	0.655 (8)

Table 2. Spearman rank correlation coefficients (corrected by ties) for richness map pairs at different grain sizes (see Figure 3 for six of the eight maps). The number in the parenthesis is the sample size, the determination of the sample size followed the same method as in Table 1. All coefficients are significant at *p*-value < 0.001 level except those identified by *NS*.

	5 × 5	10 × 10	20 × 20	25 × 25	50 × 50	100 × 100	250 × 250
10 × 10	0.617 (20000)						
20 × 20	0.401 (20000)	0.638 (5000)					
25 × 25	0.337 (20000)	0.504 (20000)	0.657 (20000)				
50 × 50	0.084 (20000)	0.183 (5000)	0.344 (5000)	0.490 (800)			
100 × 100	−0.052 (20000)	−0.019^{NS} (5000)	−0.168 (1250)	0.170 (800)	0.599 (200)		
250 × 250	−0.079 (20000)	−0.067^{NS} (5000)	−0.010^{NS} (5000)	0.058^{NS} (800)	0.329 (200)	0.484 (200)	
500 × 500	−0.083 (20000)	−0.089 (5000)	−0.064 (1250)	0.048^{NS} (800)	0.124^{NS} (200)	0.132^{NS} (50)	0.109^{NS} (8)

Table 3. Spearman rank correlation coefficients (corrected by ties) between the maps of abundance and richness at different grain sizes. *n* is the number of quadrats for each grain size.

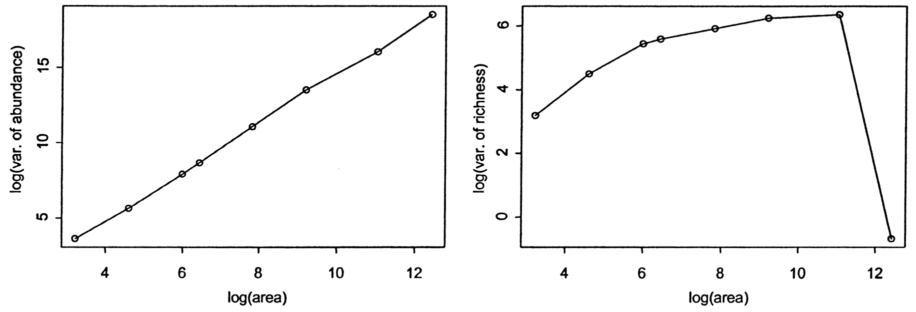
	5 × 5	10 × 10	20 × 20	25 × 25	50 × 50	100 × 100	250 × 250
Corr. coef.	0.948	0.876	0.742	0.664	0.153	−0.238	−0.738
n	20000	5000	1250	800	200	50	8
p-value	0.0001	0.0001	0.0001	0.0001	0.0312	0.0957	0.0508

cies at scales $\leqslant$ 20 m. Of all, the expected species-area curve for random distribution of species is always higher than the observed ones (Figure 5b).

Discussion

Ecological patterns and processes depend on the scale at which they are examined, and different variables likely respond differently to scale changes. Abundance and richness represent two categories of variables that are commonly found in reality. Abundance is additive when aggregated across scales while richness is nonadditive. This distinction leads to a profound difference in spatial distribution for the two variables. Abundance in the Pasoh forest shows a relatively consistent change across scales (Figure 2, Table 1): high abundance remains high when data are scaled up, and low abundance remains low when scaled down. This suggests that the identification of ‘hotspot’ (high value) and ‘coldspot’ (low value) in abundance is independent of scale, although the degree of spatial variability in abundance changes substantially (Figure 4, left panels). The approximately linear relationship between abundance and scale further suggests that abundance as an additive variable be likely robust to scale change. Here, we may conclude that the scale effect on abundance is topologi-

a) Spatial variance



b) Coefficient of variation

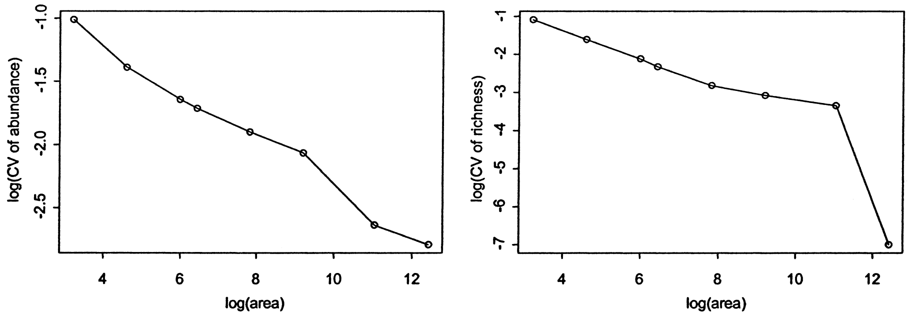


Figure 4. (a) Upper row: Spatial variances of tree abundance and species richness in the Pasoh forest across eight grain sizes (5 × 5, 10 × 10, 20 × 20, 25 × 25, 50 × 50, 100 × 100, 250 × 250 and 500 × 500 m). (b) Low row: Coefficients of variation of tree abundance and species richness across the same eight grain sizes.

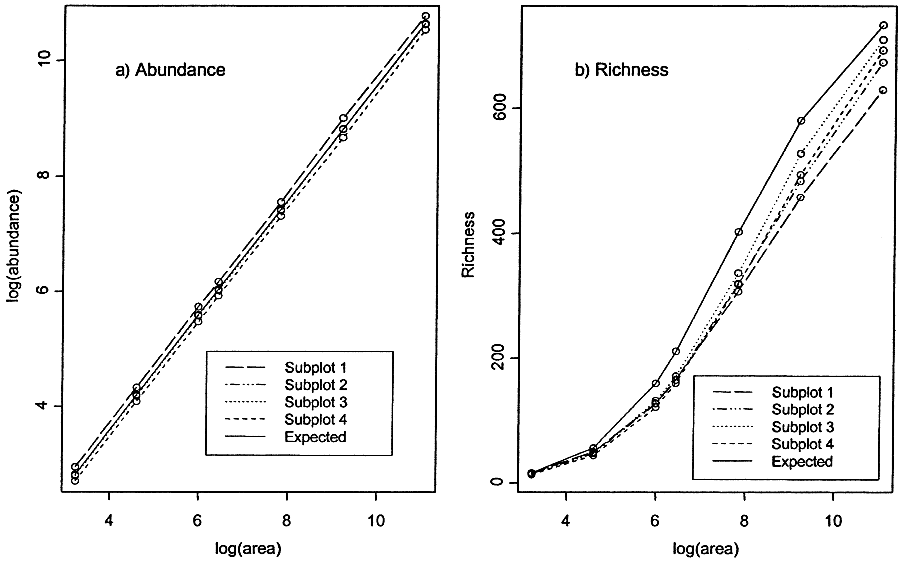


Figure 5. (a) Abundance-area curves at four subplots identified in Figure 2, showing regional effect on abundance-area relationships. The dashed lines are the observed values, whereas the solid line is the expectation under the assumption of random distribution of species in the plot. (b) Species-area curves at four subplots identified in Figure 3, showing regional effect on species-area curves. The dashed lines are the observed values, whereas the solid line is the expectation under the assumption of random distribution of species in the plot.

cally invariant, i.e., there are quantitative changes in spatial variance across scales but not in patterns (Figure 2, Table 1).

Contrary to abundance, species richness shows changes both in the shape of the maps (Figure 3, Table 2) and in spatial variability (Figure 4, right panels). The correlation coefficients in Table 2 among the richness maps change from positive to negative at certain scales, indicating the inconsistency in scale effect. These results together with the species-area curves (Figure 5b) clearly show that a 'hotspot' in species richness identified at a particular scale may become a 'coldspot' at another scale. This is because that species richness cannot simply be added up when aggregated from fine to coarse scales. This inconsistency makes it difficult to extrapolate species richness over scales and suggests that diversity management and conservation plans based on the concept of 'hotspot' or 'coldspot' may not be solid. In practice, a multi-scale evaluation (at least at the stage of pilot study) for identifying conservation priority of 'hotspots' is necessary.

It is obvious that although the spatial variance and CV of abundance are linearly dependent on scale (by the log-log transformation, see Figure 4, left panels), spatial variations measured by variance and CV are not in accordance. The ever increasing variance suggests that information about abundance is progressively less precise as scale becomes coarser (Figure 4a, left panel). This seems reasonable because abundance is aggregated and averaged out at the coarse scale, resulting in the loss of information. On the contrary, the CV suggests that the finer scales always have higher variability than the coarser scales (Figure 4b, left panel). This difference between the variance and CV is also observed for species richness as shown in Figure 4 (right panels), although the similar linear relationship as for abundance does not hold for richness. Instead, the spatial variance of richness and scale form a hump-shaped curve with a maximum occurring at 250 × 250 m (Figure 4a, right panel). Similar hump-shaped curves are also observed in other studies (Juhász-Nagy and Podani 1983; Podani 1984; Podani et al. 1993; Bartha et al. 1998) although in our case it is not yet clear why the maximum in variance occurs at 250 × 250 m. Some authors suggest that CV be a more reliable measurement than variance because it normalizes variance by the mean (Taylor 1977). Although such a suggestion may be valid, the problem is that variance is usually more useful, particularly when statistical inference about an estimate is the interest of a study.

In terms of the measurement of CV, spatial variability in both richness and abundance decreases more rapidly at smaller scales (< 25 m); abundance decreases from 0.36 to 0.19 from 5 × 5 to 25 × 25 m, and richness drops from 0.34 to 0.12 (these numbers can be read from the anti-log transformation from Figure 4b). Therefore, scales smaller than 25 × 25 m are supposed to capture most of the spatial variations in abundance and richness in the Pasoh forest. Within this scale range (i.e., up to 25 m) the richness distribution maps do show a relatively consistent change (Figure 3, Table 2). The occurrence of the highest spatial variation at the fine scales may have ecological interpretations according to the proximal neighborhood spacing processes (e.g., Janzen-Connell process; Janzen (1970) and Connell (1971)). It should be emphasized however that an appropriate scale should be determined in terms of a specific ecological inquiry rather than by spatial variation, as we have seen that breakpoints in spatial variation may not occur at all. Different inquiries require different scales, e.g., local neighboring scale may be adequate for investigating competition, intermediate scale is appropriate for studying pollination, while large (regional) scale is useful in studying climatic effect on species diversity. No single scale is able to meet the objectives of all studies, as have been demonstrated by many studies such as the role of density-dependent processes in regulating populations (Antonovics and Levin 1980; Ray and Hastings 1996), the importance of herbivores in structuring plant communities (Brown and Allen 1989), the mechanisms in maintaining species diversity in the tropics (Augspurger 1983; Clark and Clark 1984; Schupp 1992), and sampling design in ecology (Fortin et al. 1989; Hall et al. 1998).

A measure that is often used to describe and compare species richness of different ecosystems is the number of species per unit area or given areal size (e.g., the well-known Whittaker's 0.1-ha standard plot) (Grime 1973; Westoby 1993; Gaston 1994; Gross et al. 2000). Unlike additive variables that are often expressed by density and are invariant to scale change (see the stem density in Table 4), the density for species richness in Table 4 shows that different sampling grain sizes produce dramatically different values: the number of species per m^2 is 0.585 at 5 × 5 m sampling quadrat, and the density is 0.267 at 25 × 25 m quadrat, whereas it is 0.0016 (= 814 species/500,000 m^2) if the entire plot is considered. Yet, all these different values are supposed to represent the same community! Clearly, the use of species richness per unit area should be avoided in comparing different ecosystems.

Table 4. Number of stems and number of species per square meter for different grain sizes in the Pasoh forest. The densities at each grain size were computed as follows: (1) divide the plot into a grid system using a given grain size (e.g., 5 × 5 m), (2) count the total number of stems and the number of species in each quadrat, respectively, (3) average these two quantities across all the quadats, and (4) then divide the averages by the grain size.

Grain size (m)	No. stems/m^2 (std. error)	No. species/m^2 (std. error)
5 × 5	0.671 (0.244)	0.585 (0.197)
10 × 10	0.671 (0.167)	0.475 (0.095)
20 × 20	0.671 (0.130)	0.318 (0.038)
25 × 25	0.671 (0.121)	0.267 (0.026)
50 × 50	0.671 (0.100)	0.129 (0.008)
100 × 100	0.671 (0.085)	0.049 (0.001)
250 × 250	0.671 (0.048)	0.011 (0.0004)
500 × 500	0.671 (0.041)	0.003 (< 0.001)
500 × 1000	0.671	0.0016

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