西双版纳龙脑香热带雨林乔木物种多样性随空间尺度和空间位置的变化

Spatial variations of species diversity across scales in a tropical rain forest of China，southwest China

兰国玉 胡跃华 曹敏 朱华 王洪 何有才 孙义方 何芳良

中国科学院西双版纳热带植物园

Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences

浙江 杭州

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Introduction

- It has been well recognized that different sampling size (or spatial scale) can lead to different estimation of diversity and diversity patterns (Colwell and Coddington 1994; Palmer and White1994; He and Legendre 1996; Crawley and Harral 2001; He et al. 2002; Willis and Whittaker 2002; Rahbek 2005; Turner and Tjorve 2005) No measure of species diversity is scale invariant. This is because abundance and richness, the two base variables on which other species diversity measures are defined, have different scaling effects. Abundance is additive when aggregated up scales, while richness is nonadditive.

- Another related problem in sampling diversity is spatial locality, i.e., where samples are taken will have substantial effect on the results. This is so because species rarely randomly distribute in space, and random sampling is not necessarily an effective sampling scheme for nonrandom distribution and may not be feasible either in field sampling. It is therefore interesting to compare diversity derived from one part of an area is consistent with those derived from other parts. In particular, we are interested in knowing whether diversity of the entire plot can be effectively predicted from data sampled from different parts of the study area.

Questions:

- (1) How tree abundance and species richness change across scales and at what scales tree abundance and species richness have the largest variations?
- (2) How the Shannon and Simpson diversity indices change with scale?
- (3) How species-area curves vary with localities and can species richness in a larger area be equally predicted from the species-area curves constructed from smaller subareas?

The location

Bubeng, mengla,

Xishuangbanna,

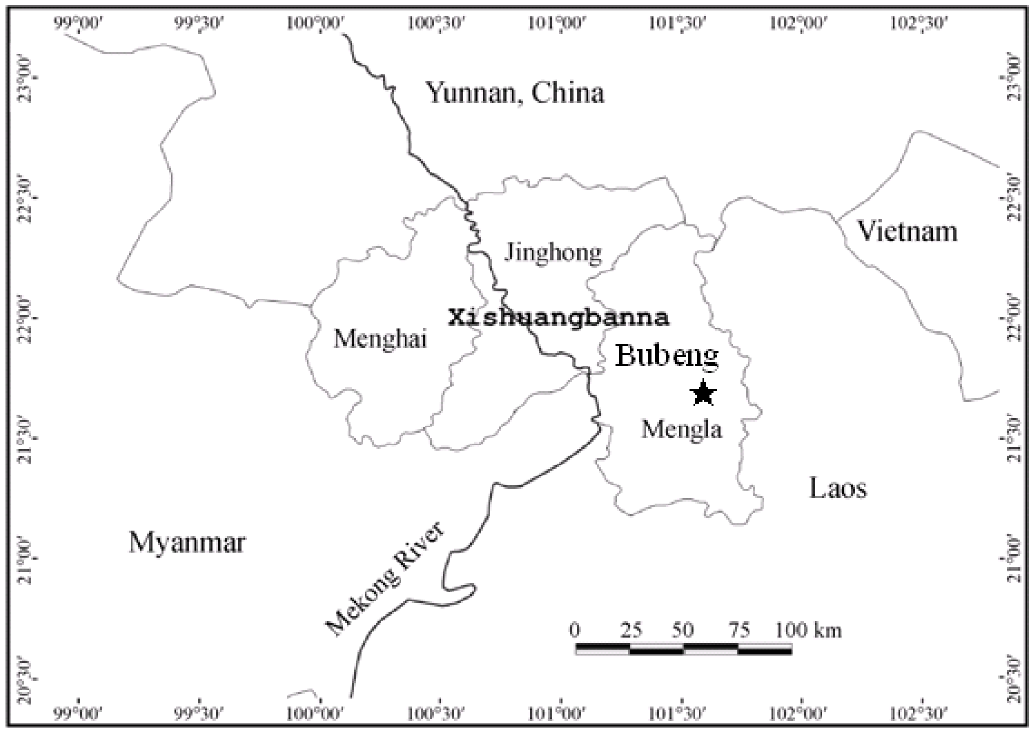
Yunnan province

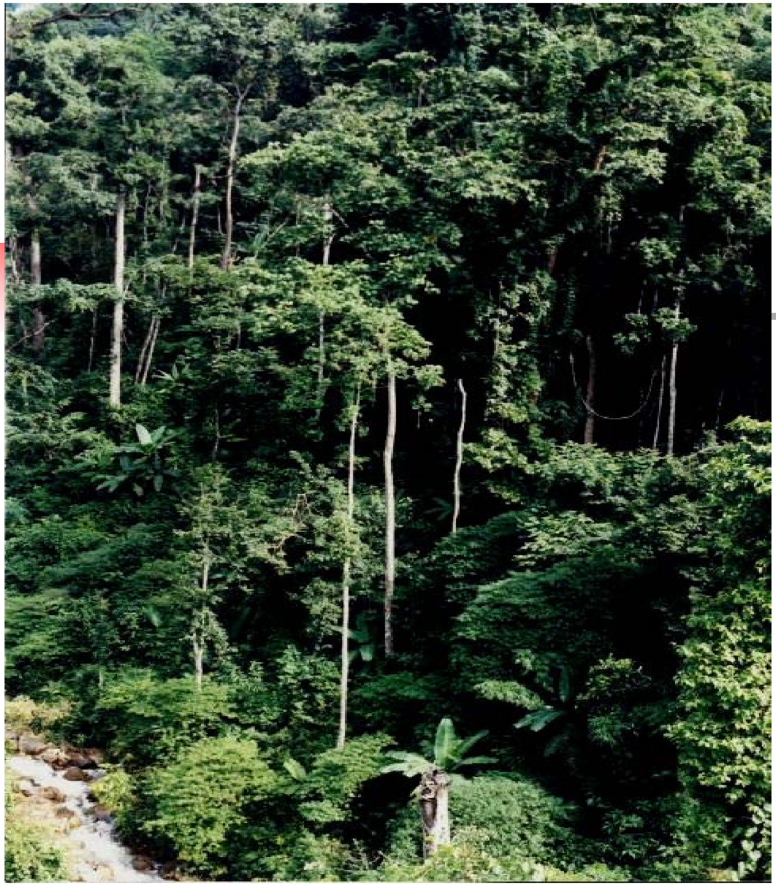
China

Location：

101° 34′ 26 ″ -47″ E，

21° 36′ 42″ -58″ N





Forest type：

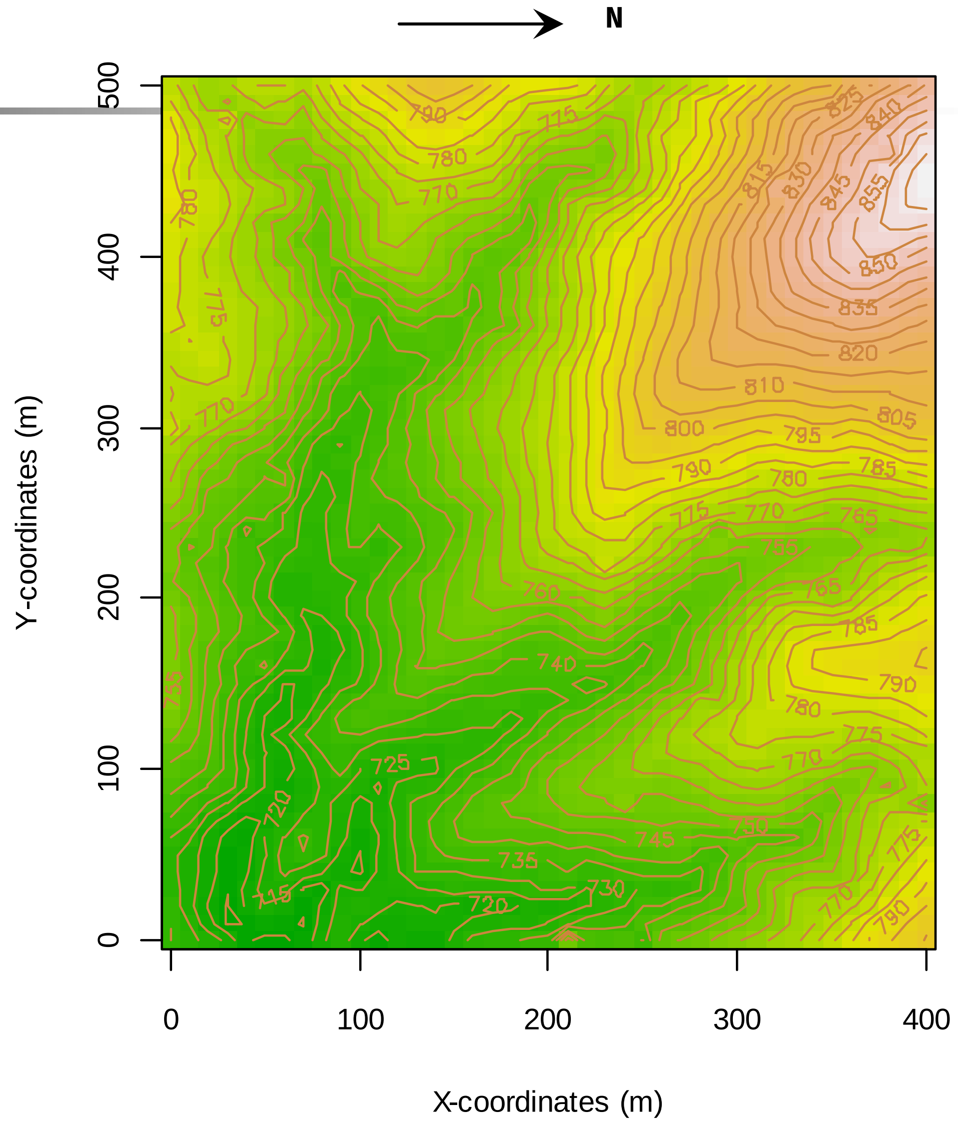
Dipterocarp tropical rain forest

The topography

Area： 20 hm2
（400m×500m）

east-west 500m，
south-north 400m；

Elevation：
709.27m－869.14 m



Methods

- (1) We divided the 20 ha plot into grid systems using seven grain sizes: 5×5 (8,000 cells), 10×10 (2,000), 20×20 (500), 25×25 (320), 50×50 (80), 100×100 (20), 200×250 m (4).

- (2) We counted the total tree abundance and the number of species in each cell for each grain size and produced abundance and richness maps for each grain size.

- (3)Spearman coefficients of correlation were computed to assess the association among the abundance maps of different scales. The coefficients of correlation were also computed for richness maps.

- (4)The scale effects on abundance and richness were further compared to that expected from the random placement model. Under this model, the abundance-area has the form:

Random placement model

- **The abundance-area has the form:**

$$N_a = \frac{N}{A} a$$

- **Where *Na* is the expected number of tree in sampling area *a*, *N* is the total abundance in the 20 ha plot (=95,498 trees), *A* is the size of the plot (=200,000 m2)**

Random placement model

- The spatial variance of *Na* for random placement also follows equation.

$$V(N_a) = \frac{N}{A}a$$

And thus the coefficient of correlation changes with *a* is:

$$CV(N_a) = \sqrt{\frac{A}{Na}}$$

Random placement model

- **The random placement species-area curve is given by Coleman (1981)**

$$S_a = S - \sum_{i=1}^{S} \left(1 - \frac{a}{A}\right)^{n_i}$$

Where *S* is the total number of species and *ni* is the total abundance of species *i* in the entire 20 ha plot.

Random placement model

- **The variance of *Sa* is**

$$V(S_a) = \sum_{i=1}^{S}(1-\frac{a}{A})^{n_i} - \sum_{i=1}^{S}(1-\frac{a}{A})^{2n_i}$$

The coefficient of correlation of *Sa* is

$$CV(S_a) = \frac{\sqrt{V(S_a)}}{S_a}$$

Random placement model

The expected Shannon index is the same as the entire plot.

$$p_i = \frac{(a/A)n_i}{\sum_{i=1}^{S}(a/A)n_i} = \frac{n_i}{N}$$

$$H = -\sum_{i=1}^{S} p_i \ln(p_i)$$

$$V(H) = \frac{\sum_{i=1}^{S} p_i (\ln p_i)^2 - H^2}{N}$$

$$CV(H) = \frac{\sqrt{V(H)}}{H}$$

Random placement model

- **And the Simpson index is** $$D = 1 - \sum_{i=1}^{S} p_i^2$$

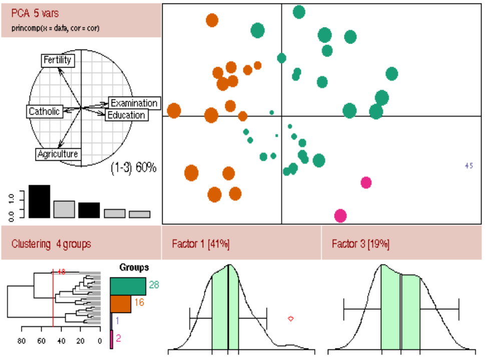
The variance and CV are as follows:

$$V(D) = \frac{4}{N}\left[\sum_{i=1}^{S} p_i^3 - \left(\sum_{i=1}^{S} p_i^2\right)^2\right] \qquad CV(D) = \frac{\sqrt{V(D)}}{D}$$

Data analysis

Software: R software

Package: Spatstat



Abundance cross scales

Figure 1. Maps of tree abundance in the Xishuangbanna tropical rainforest plot at six grain sizes (5×5, 10×10, 20×20, 50×50, 100×100 and 200×250 m).

The northeast part has the highest value at all scales from 5×5 m to 200×250 m.

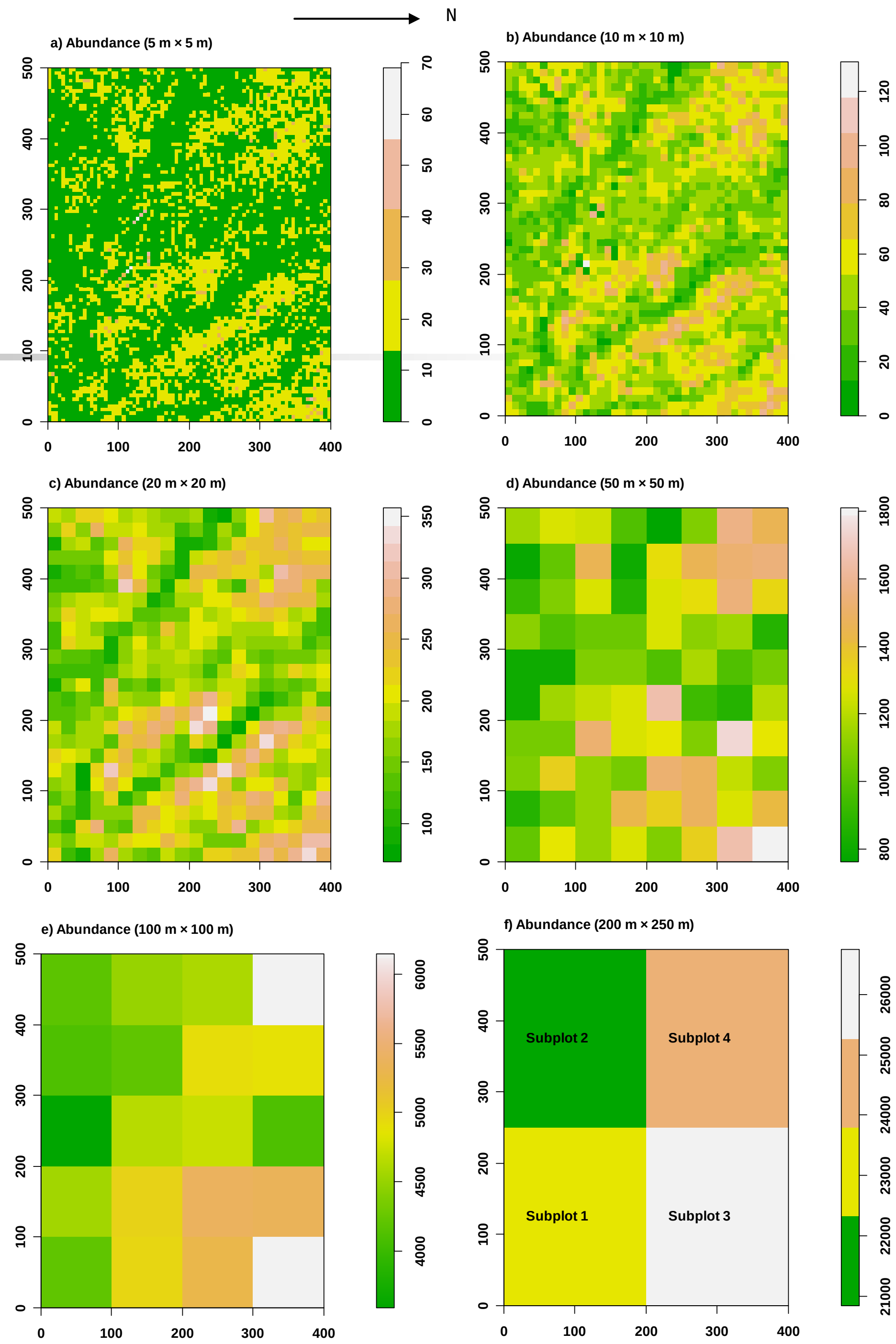


Table 1. Spearman correlation coefficients for abundance maps at different grain sizes

	5×5	10×10	20×20	25×25	50×50	100×100
10×10	**0.053 (8000)**					
20×20	**0.060 (8000)**	**0.102 (2000)**				
25×25	**0.107 (8000)**	**0.108 (8000)**	**0.153 (8000)**			
50×50	**0.110 (8000)**	**0.147 (2000)**	**0.195 (2000)**	**0.187 (320)**		
100×100	**0.142 (8000)**	**0.194 (2000)**	**0.245 (500)**	**0.192 (320)**	**0.279 (80)**	
200×250	**0.093 (8000)**	**0.127 (2000)**	**0.161(2000)**	**0.168 (320)**	**0.225 (80)**	**0.335 (80)**

Richness across scales

- **Figure 2.** Maps of species richness in the Xishuangbanna tropical rainforest plot at six grain sizes

- The northeast reigon has lowest richness value at 200×250m

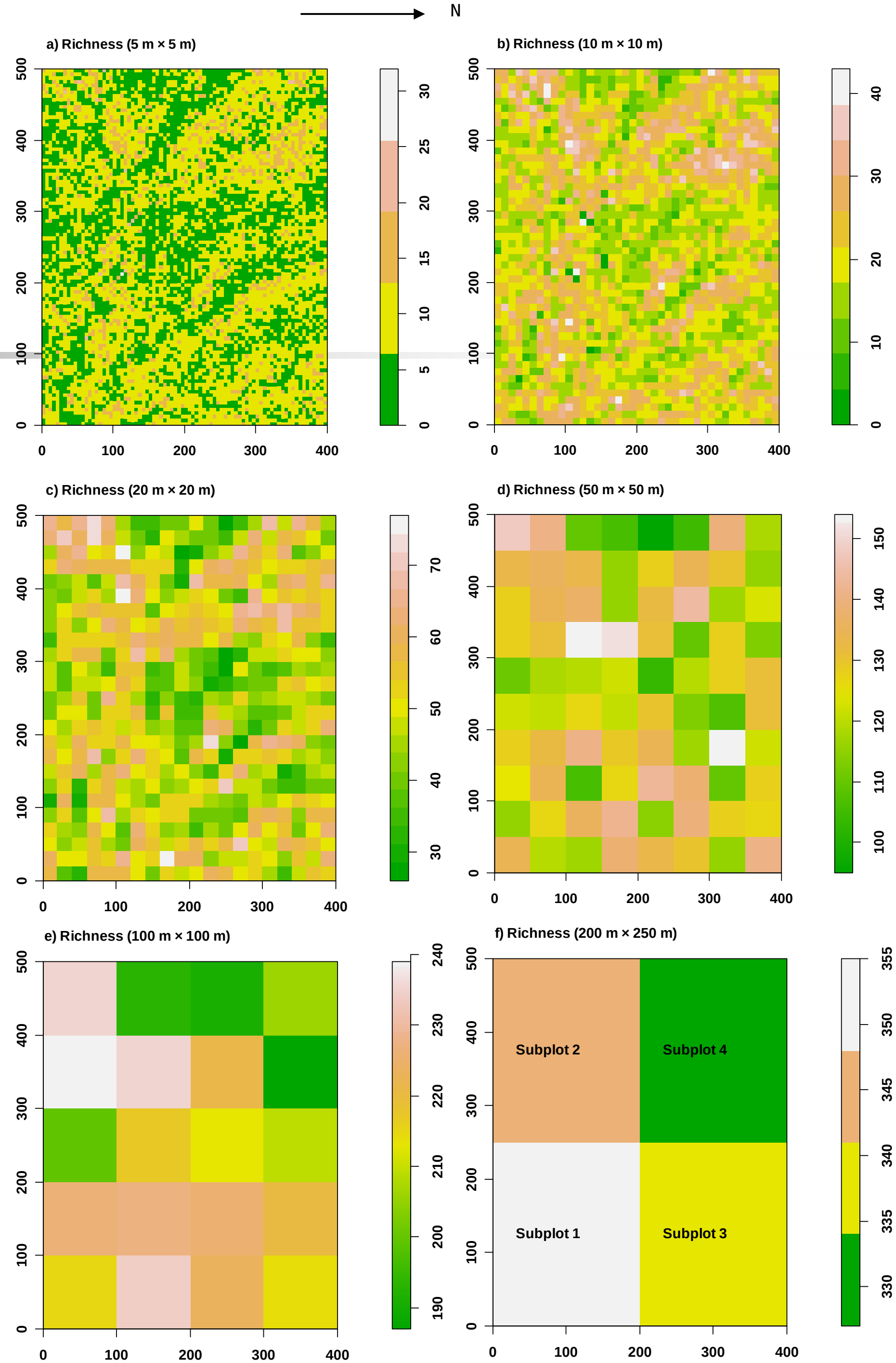


Table 2. Spearman correlation coefficients between richness maps at different grain sizes (as Table 1)

	5×5	10×10	20×20	25×25	50×50	100×100
10×10	0.034 (8000)					
20×20	0.019 NS (8000)	0.080 (2000)				
25×25	0.062 (8000)	0.100 (8000)	0.112 (8000)			
50×50	-0.001 NS (8000)	0.001 (2000)	0.026 NS (2000)	0.141 (320)		
100×100	0.018 NS (8000)	0.064 (2000)	0.113 (500)	0.077 NS (320)	0.057 NS (80)	
200×250	-0.079 (8000)	-0.021 NS (2000)	0.041 NS (2000)	0.057 NS (320)	0.107 NS (80)	0.411 (80)

“NS” indicates not significant at p-value < 0.05.

Table 3. Spearman correlation coefficients between abundance and richness at different grain sizes.

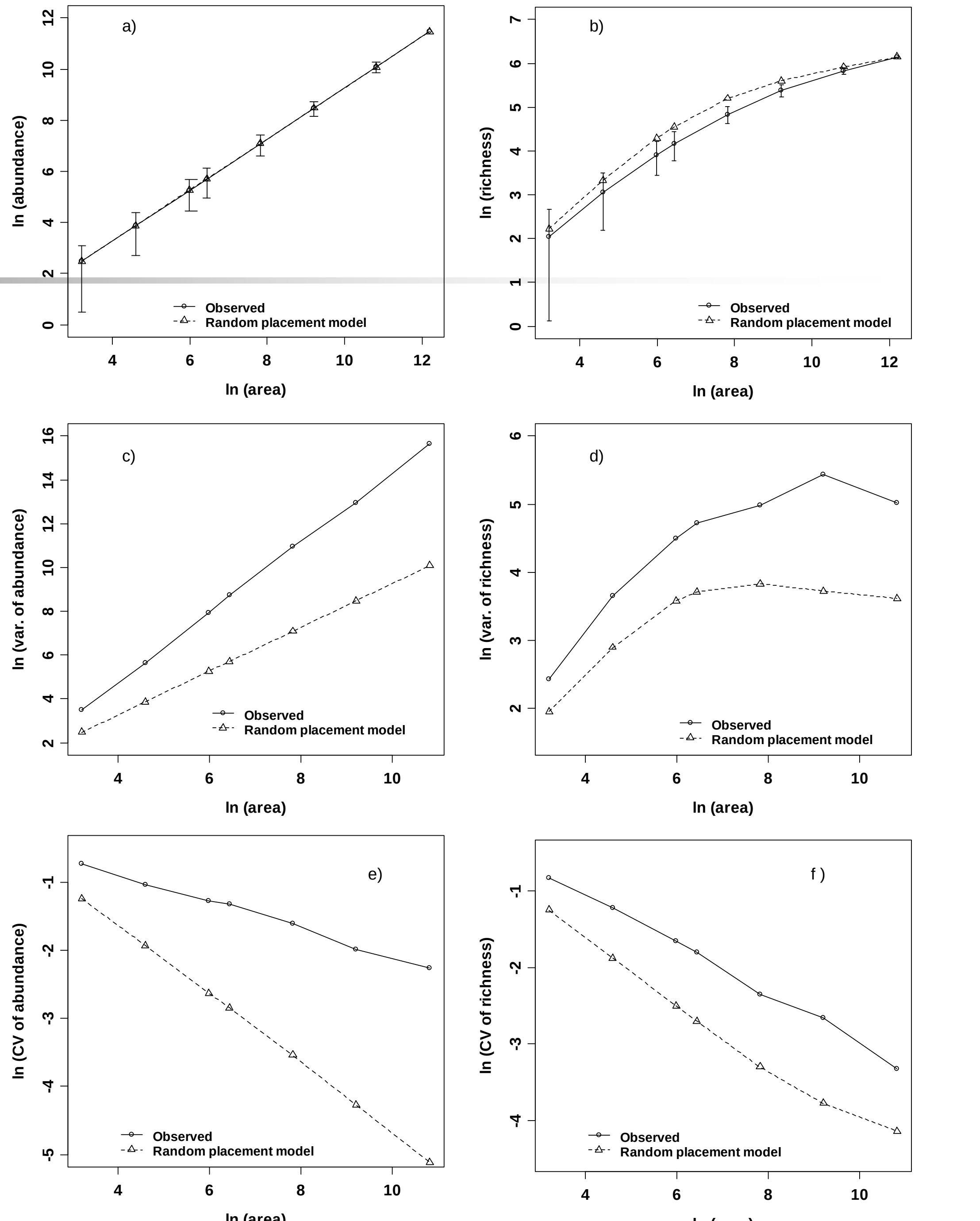
	5×5	**10×10**	**20×20**	**25×25**	**50×50**	**100×100**	**200×250**
Corr. coef.	**0.794**	**0.650**	**0.523**	**0.570**	**0.406**	**-0.035**	**-0.593**
n	**8000**	**2000**	**500**	**320**	**80**	**16**	**4**
***p*-value**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**0.882**	**0.4074**

n is the number of quadrats for each grain size.

- Figure 3. Spatial variances and coefficients of variations of tree abundance and richness in the Xishuangbanna tropical rainforest plot across seven grain sizes (5×5, 10×10, 20×20, 25×25, 50×50, 100×100 and 200×250 m).

- For abundance-area and richness-area curves, the vertical bars are the 95% confidence intervals.

- At large scales, abundance and richness appear to have smaller confidence intervals, which is distortion due to the log-transformation of the confidence. The original variance actually increases with scale as shown in *c* and *d*.



- **Figure 4.** Spatial variances and coefficients of variation of Shannon and Simpson indices in the Xishuangbanna tropical rainforest plot across seven grain sizes (5×5, 10×10, 20×20, 25×25, 50×50, 100×100 and 200×250 m).

- For Shannon-area and Simpson-area curves, the vertical bars indicate the 95% confidence intervals calculated from data.

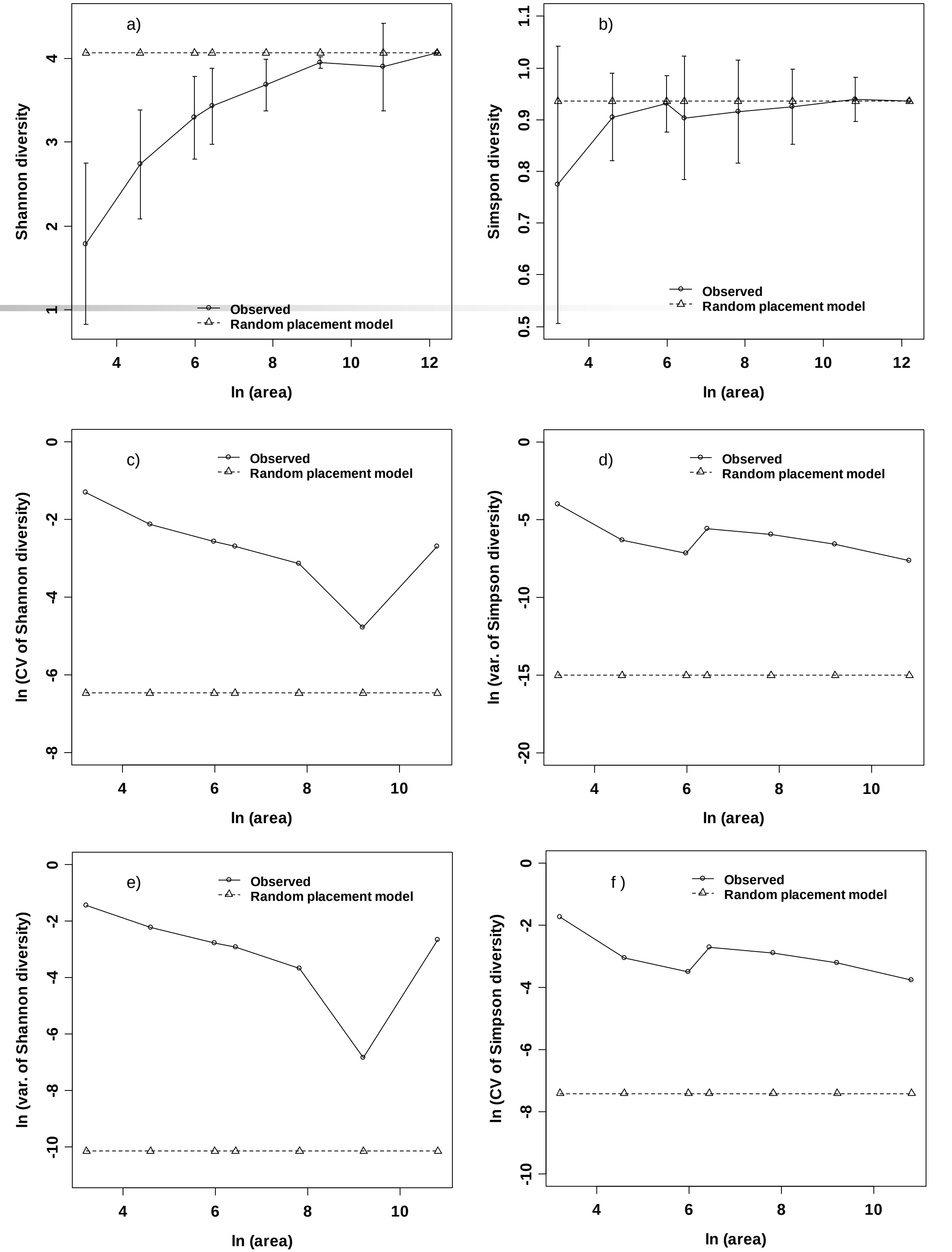


Figure 5. Abundance-area curves (a), species-area curves (b), Shannon diversity-area curves (c) and Simpson diversity-area curves (d) of the four subplots. Mean abundance (richness, Shannon, Simpson diversity) is the average of abundance (richness, Shannon, Simpson diversity) in each cell for each grain size.

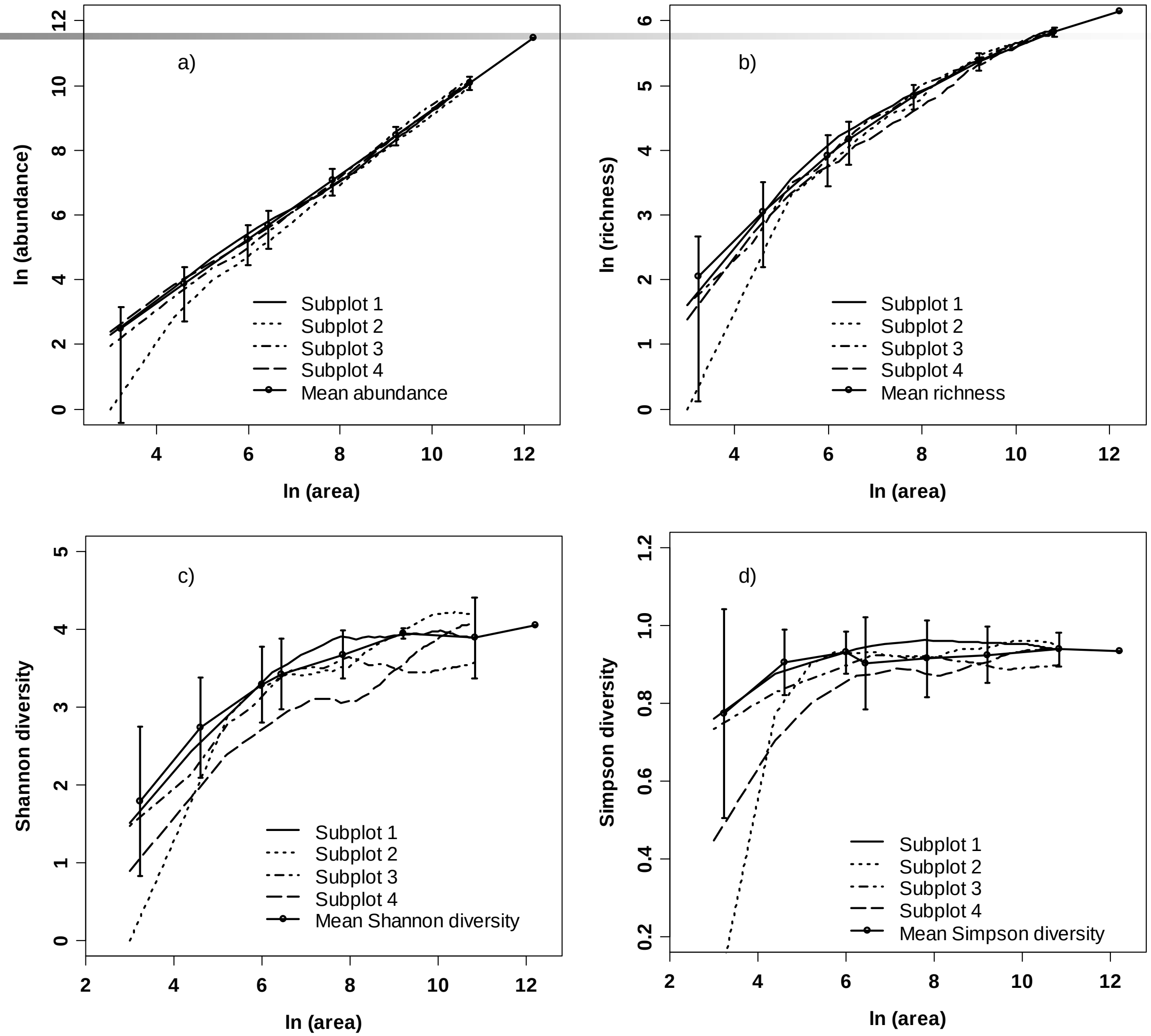


Figure 6. The power model (log-log transformation) species-area curves and their 95% confidence intervals for the four subplots as shown in Fig. 1.

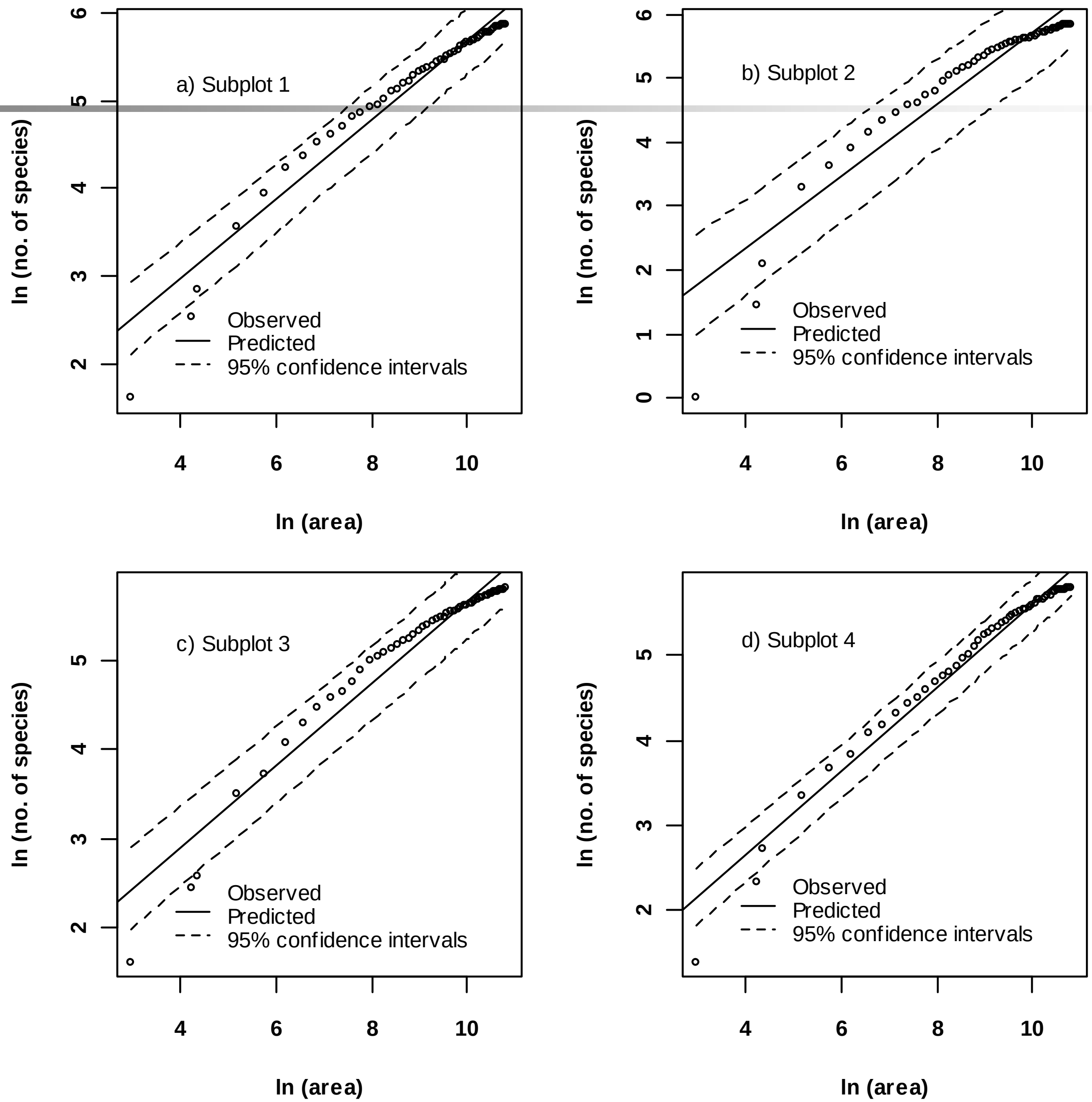


Figure 7. The observed and expected species richness of the entire plot

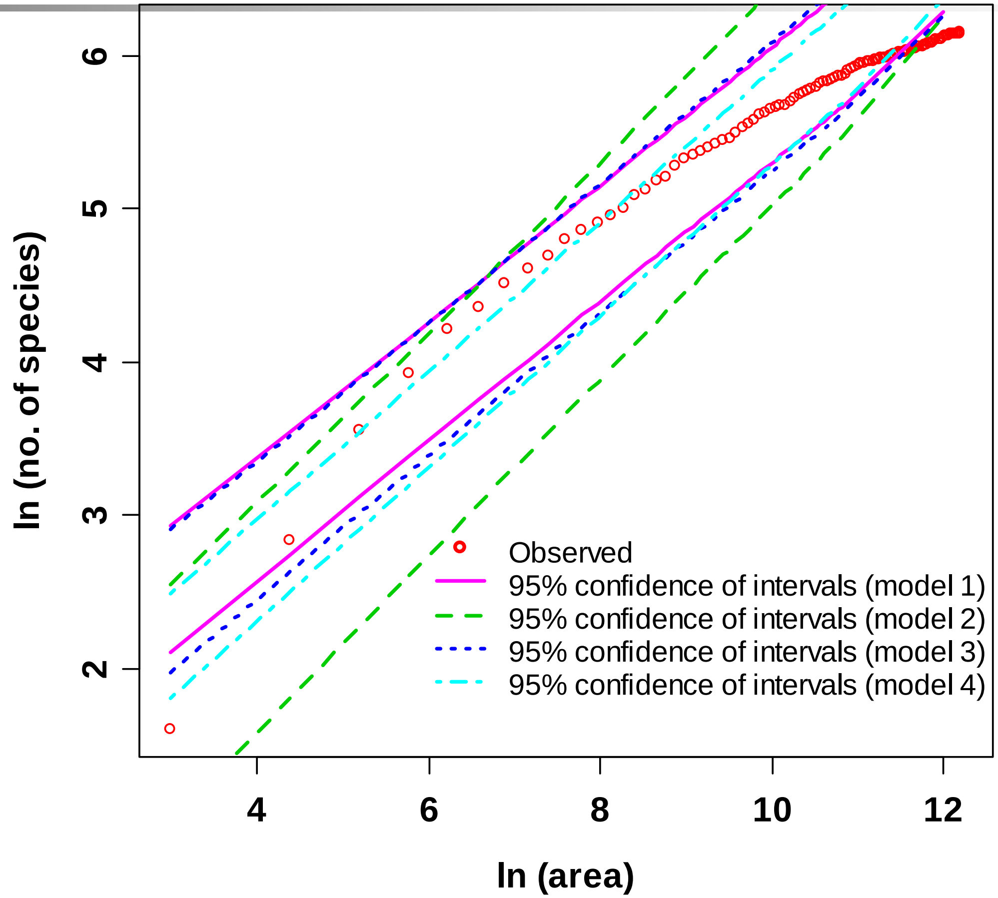


Table 4. Comparison of the species-area curves for the four subplots and the estimated the numbers of species for the entire plot by extrapolating the four log-log power models.

	c	z (slope)	Adjusted R^2	P-value	Predicted S
Model 1	**3.225(1.145)**	**0.451(0.015)**	**0.949**	**<0.001**	**789.10**
Model 2	**1.077(1.288)**	**0.565(0.028)**	**0.894**	**<0.001**	**1064.71**
Model 3	**2.886(1.163)**	**0.461(0.017)**	**0.941**	**<0.001**	**799.72**
Model 4	**1.958(1.116)**	**0.493(0.012)**	**0.971**	**<0.001**	**798.86**

S: number of species, *z*: the slope, *c*: the intercept. Numbers in parentheses are standard errors.

Conclusion

- (1) Tree abundance shows a linear relationship with scale (grain size) due to the additive nature, while richness shows an erratic variation across scale. The nonadditive property of richness makes the identification of biodiversity hotspots problematic as a hotspot at one scale can become a coldspot at another scale.

- (2) The spatial variance of richness has a hat shape across scale with the largest variance occurring at 100×100 m. Shannon's and Simpson's indices generally decrease with scale, with the smallest variance occurring at 100×100 and 20×20 m, respectively. The variances of all the diversity indices are larger than that of the random placement model, reflecting that spatial distribution of species in the study area is more heterogeneous than random distribution.
- (3) Abundance, richness and other diversity indices are not only dependent on spatial scale, but also on spatial locality. Species-area curves constructed from different subplots of the 20 ha plot are very different and can lead to drastically different predictions for the total richness of the 20 ha plot.

- In conclusion, extreme caution should be exercised if one has to use diversity measured at a single scale or one locality for the purposes of diversity management and conservation.

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