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Scale-dependent spatial patterns of species diversity in the tropical montane rain forest in Jianfengling, Hainan Island, China

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Abstract: ***Aims*** Spatial distribution patterns and formation mechanisms of species diversity are fundamental issues in community ecology. The objectives of this study are to assess the species diversity patterns at the different spatial scales in Jianfengling, Hainan Island, China. ***Methods*** Based on the dataset from the 60 hm^2 plot in the tropical montane rain forest in Jianfengling, Hainan Island, the spatial distribution patterns of species richness, species abundance, Shannon-Wiener, Simpson and Pielou's evenness indices were analyzed at six spatial scales, including 5 m × 5 m, 10 m × 10 m, 20 m × 20 m, 40 m × 40 m, 100 m × 100 m, and 200 m × 200 m, respectively. ***Important findings*** Results showed that spatial distribution patterns of species richness, species abundance and Shannon-Wiener index were much more obviously changed with the spatial scales than Simpson and Pielou's evenness indices. Change of variance of the species richness with the increase of spatial scales was unimodal, which had the maximum value at the 20 m × 20 m scale. Variance of the species abundance showed a linear relationship with the increase of spatial scales. The positive relationship between species richness and abundance gradually decreased and even disappeared with the increase of sampling scales, which may be correlated with the increase of habitat heterogeneity. The effects of spatial scales on Shannon-Wiener, Simpson, and Pielou's evenness indices may be also correlated with the composition of rare species in the plot.

Keywords: Hainan; Jianfengling; tropical montane rain forest; species diversity; sampling scale; spatial distribution patterns

Significant scale effects exist in ecological models and processes (Crawley and Harral, 2001; He et al., 2002; Rahbek, 2005; Wang et al., 2008). A single scale cannot satisfy the study of all the scientific problems (Ray and Hastings, 1996). A good illustration is that small local scale is suitable for competition study of adjacent individuals, whereas large regional scale is required for the effect of climate on species diversity. Recently, the effect of scale on biodiversity is studied from five aspects: (1) selection of the optimum sampling size, shape and range in different study areas (Mouillot and Leprêtre, 1999); (2) study of biodiversity hotspot (Bartha et al., 1998; Fortin et al., 1999; Hurlbert and Jetz, 2007); (3) evaluation of biodiversity and diversity patterns at different spatial scales (He andLegendre, 1996; Wilson et al., 1999; Harte et al., 2009; Colwell et al., 2012; Xu et al., 2012); (4) formation mechanism of biodiversity distribution pattern and the corresponding ecological processes at different scales (Cheng et al., 2011); (5) the relationships among spatial scale effects on species, ecosystem and landscape diversities (Peng et al., 2015). The study of these problems has important significance on the formation and maintenance mechanisms of species diversity, and provides a scientific basis for conservation and effective management of biodiversity (Willis and Whittaker, 2002; Rahbek, 2005; Storch et al., 2007; Giladi et al., 2011).

For the spatial patterns of species diversity at different scales, many studies have been conducted in tropical rain forest (He et al., 2002; Kallimanis et al., 2008), temperate coniferous and broad-leaved mixed forest (Wang et al., 2008), mid-subtropical karst forest (Zhang et al., 2012), and subtropical evergreen broad-leaved forest in southern China (Wang et al., 2008). However, the studies on spatial distribution patterns of species diversity and their correlations with scales in tropical rain forests in China are rare. Hainan Island is at the north edge of tropical area in Asia. The abundant species composition in rain forest enables Hainan Island to be a hotspot for global biodiversity research. In this study, based on the data from the 60 hm^2 dynamic

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monitoring plot of tropical montane rain forest in Jianfengling National Nature Reserve, Hainan Island, we discussed spatial distribution patterns of different species diversity indices in different scales so as to provide a scientific basis for revealing the formation and maintenance mechanisms of species diversity in Jianfengling, Hainan.

1 Materials and methods

1.1 Study area

Jianfengling is located at the boundary of Ledong Li Autonomous County and Dongfang City in southwestern Hainan (18.33°–18.95°N, 108.68°–109.20°E), with the total area of 640 km^2. Jianfengling presents low-latitude tropical island monsoon climate, and has clear dry and rainy seasons. The rainy season is from May to October, and the dry season is from November to the next April (Li et al., 2012). The mean annual precipitation here is 2,449 mm, and the mean annual temperature is 19.8 ℃. The temperatures in the coldest and warmest months are 10.8 ℃ and 27.5 ℃, respectively (Jiang and Lu, 1991). The tropical montane rain forests are distributed in hills with altitudes of 600–1,200 m. The main soil type is brick yellow soil-yellow soil. The tropical montane rain forest is the most widely distributed vegetation type (Jiang and Lu, 1991; Li et al., 2002).

1.2 Sample plot setting and inventory

A 60 hm^2 dynamic monitoring plot for forest diversity was completed in 2012. The plot is located in the primary tropical montane rain forest of Jianfengling, Hannan. The plot was constructed by following the inventory guidelines of Center for Tropical Forest Science (CTFS) of Smithsonian Institution in the US (Condit, 1998). The length of the plot from east to west is 1,000 m, and the width from south to north is 600 m (Fig. 1). A total of 1,500 quadrats in size of 20 m × 20 m were set in this plot. The coordinate locations of all the four corners in each quadrat were determined by an electronic total station and marked by cement piles. The inventory was conducted with each quadrat as a unit area. Every woody plant with a *DBH* (diameter at breast height) ≥ 1.0 cm was measured for *DBH* and coordination in the plot, and the species name was also recorded. The plot was inventoried every five years. The first inventory showed 439,676 live trees or shrubs (*DBH* ≥ 1.0 cm) in the plot, including 391,686 independent plants, 29,103 sprouted shoots and 18,887 branches. Among them, except 61 plants without specific species names, all the other plants belongs to 290 species, 155 genera of 62 families (Xu et al., 2015).

1.3 Data processing and analyses

In this study, we analyzed species richness, species abundance, species diversity indices (Shannon-Wiener index, Simpson index) and Pielou's evenness index to explore the scale effect on spatial distribution patterns of species diversity in the tropical montane rain forest in Jianfengling, Hainan Island, China.

The plot was divided at six spatial scales, including 5 m × 5 m (24,000 quadrats), 10 m × 10 m (6,000 quadrats), 20 m × 20 m (1,500 quadrats), 40m × 40 m (375 quadrats), 100 m × 100 m (60 quadrats), and 200 m × 200 m (15 quadrats), respectively. The five diversity indices were calculated at different spatial scales.

Based on the calculation results, the spatial distribution maps of the five indices were drawn to analyze the spatial distribution and spatial variation of species diversity at different scales. The Spearman correlation coefficients between species richness and abundance at different scales were used to discuss the variation of spatial patterns of species richness and abundance at different scales. Variance and coefficient of variation were usually used to determine inflection points or peak values. Some studies indicated that these inflection points or peak values were important for determining potential physical or ecological processes and even characteristic region of a community at a certain scale (Juhász-Nagy and Podani, 1983; Horne andSchneider, 1995). In addition, the natural logarithm values of variances and coefficients of variation of the five diversity indices were plotted with the natural logarithm values of spatial sampling scales (sampling areas), to explore the scale effect on spatial distribution patterns of species diversity.

The species diversity indices (Hill, 1973) and their variances and coefficients of variation were calculated according to the following formulas.

Shannon-Wiener index: $H = -\sum_{i=1}^{S} (P_i \ln P_i)$

Simpson index: $D = 1 - \sum_{i=1}^{S} P_i^2$

Pielou's evenness index: $E = H / \ln(S)$

Variance: $\delta^2 = (\sum_{j=1}^{n} (X_j - \mu)^2) / (n - 1)$

Coefficient of variation: $CV = (sd / \mu) \times 100\%$

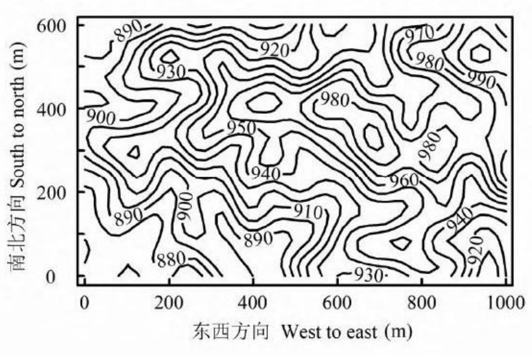

Fig. 1 Topography of the 60 hm^2 Jianfengling Forest Dynamics Plot on Hainan Island

Where, P_i is the ratio of abundance of species *i* at a single plot to the sum of abundance of all species, S is number of species in a single quadrat, n is number of quadrats, X_j is species diversity index of quadrat j, μ is mean value, and sd is standard deviation.

The data were analyzed by R 2.15.3 (https://cran.usthb.dz/).

2 Results

2.1 Spatial distribution patterns of species richness and abundance

With the increase of sampling scale, the species richness and abundance increased (Fig. 2). At small scales (< 20 m × 20 m), the spatial distribution patterns of these two indices were similar, i.e. the high values of both indices appeared at hill ridges or nearby locations (Figs. 1 and 2). At medium scale (40 m × 40 m), this similarity became insignificant. At large scales (> 100 m × 100 m), the inconsistency of the two indices was more obvious in the gray-scale map. For example, at 200 m × 200 m scale, the quadrat with the highest species richness had low species abundance. Moreover, the Spearman rank correlation analysis between species richness and abundance indicated that these two indices had extremely significant positive correlation (p < 0.001) at scales smaller than 40 m × 40 m, and the correlation coefficient significantly decreased once the scale was larger than 20 m × 20 m. When the scale exceeded 40 m × 40 m, there was no significant correlation (Table 1).

2.2 Spatial distribution patterns of Shannon-Wiener, Simpson and Pielou's evenness indices

At different sampling scales, Shannon-Wiener index had high spatial heterogeneity. At scales lower than 10 m × 10 m, the quadrats with high Shannon-Wiener index were usually at hill ridges and nearby locations. With the increase of scale, this phenomenon became insignificant (Figs. 1 and 3). The spatial distribution patterns of Simpson index and Pielou's evenness index were similar (Figs. 3 and 4). At small scales (< 10 m × 10 m), all the quadrats had high and similar Simpson index and Pielou's evenness index, and it was hard to find quadrats with higher values from the gray-scale map.

2.3 Spatial Variation of species richness and abundance at different scales

With the increase of sampling scale, the variances of species richness and abundance had significant different trends (Fig. 5). Species richness had a unimodal pattern with the increase of scale, and showed the peak value at 20 m × 20 m scale. Species abundance had a linear correlation with sampling scale, i.e. it increased along with the increase of sampling scale. Coefficients of variation of species richness and abundance both decreased along with the increase of scale. The coefficient of variation of species richness decreased linearly along with the increase of scale. The coefficient of variation of species abundance decreased slowly and linearly when the scale was smaller than 40 m × 40 m, and decreased drastically once the scale was larger than 40 m × 40 m.

2.4 Spatial variation of species diversity and evenness indices at different scales

Variances and coefficients of variation of Shannon-Wiener index, Simpson index and Pielou's evenness index displayed decreasing trends along with the increase of sampling scale (Fig. 6). However, in comparison to that of Shannon-Wiener index, the variances of Simpson index and Pielou's evenness index were much smaller. Coefficients of variation had no significant difference among the three indices.

3 Discussion

3.1 Spatial distribution patterns of species richness and abundance at different scales

Spatial distribution patterns of species richness and abundance are based on spatial scales. At small scales, they had similar spatial distribution. That is, the quadrats with high values appeared at hill ridges and nearby locations. With the increase of scale, this similarity became insignificant and even disappeared. The Spearman rank correlation analysis indicated that the species richness and abundance had extremely significant positive correlations (p < 0.001) at scales smaller than 40 m × 40 m. The correlation coefficient significantly decreased once the scale was larger than 20 m × 20 m. When the scale was larger than 40 m × 40 m, the correlation between these two indices was insignificant. This suggested that the mechanism to determine biodiversity changed when the scale increased. At small scales, species richness was mainly affected by the number of woody plant individuals in the quadrat (Preston, 1962). With the increase of spatial scale, habitat heterogeneity increased, and species richness also increased due to the appearance of new habitat (Turner and Tjørve, 2005). Thus, the correlation between species richness and abundance became insignificant. Previous studies showed that in the 60 hm^2 dynamic monitoring plot for tropical montane rain forest in Jianfengling, the changing ranges of spatial autocorrelations of thirteen soil chemical properties (total nitrogen, total phosphorus, total potassium, available nitrogen, available phosphorus, available potassium, etc.) and eight soil physical properties (bulk density, water content, porosity, etc.) in different soil layers were around 20–40 m (Shi, 2012). This indicated the ranges of spatial autocorrelation of soil properties. When the scale was small and within the changing range, the spatial variation among quadrats was small, the habitat types were in a relatively stable level, and the species richness and abundance had extremely significant positive correlation. When the scale was larger than the changing range, the spatial distributions of soil properties were usually random, and the correlation between species richness and abundance weakened and even disappeared.

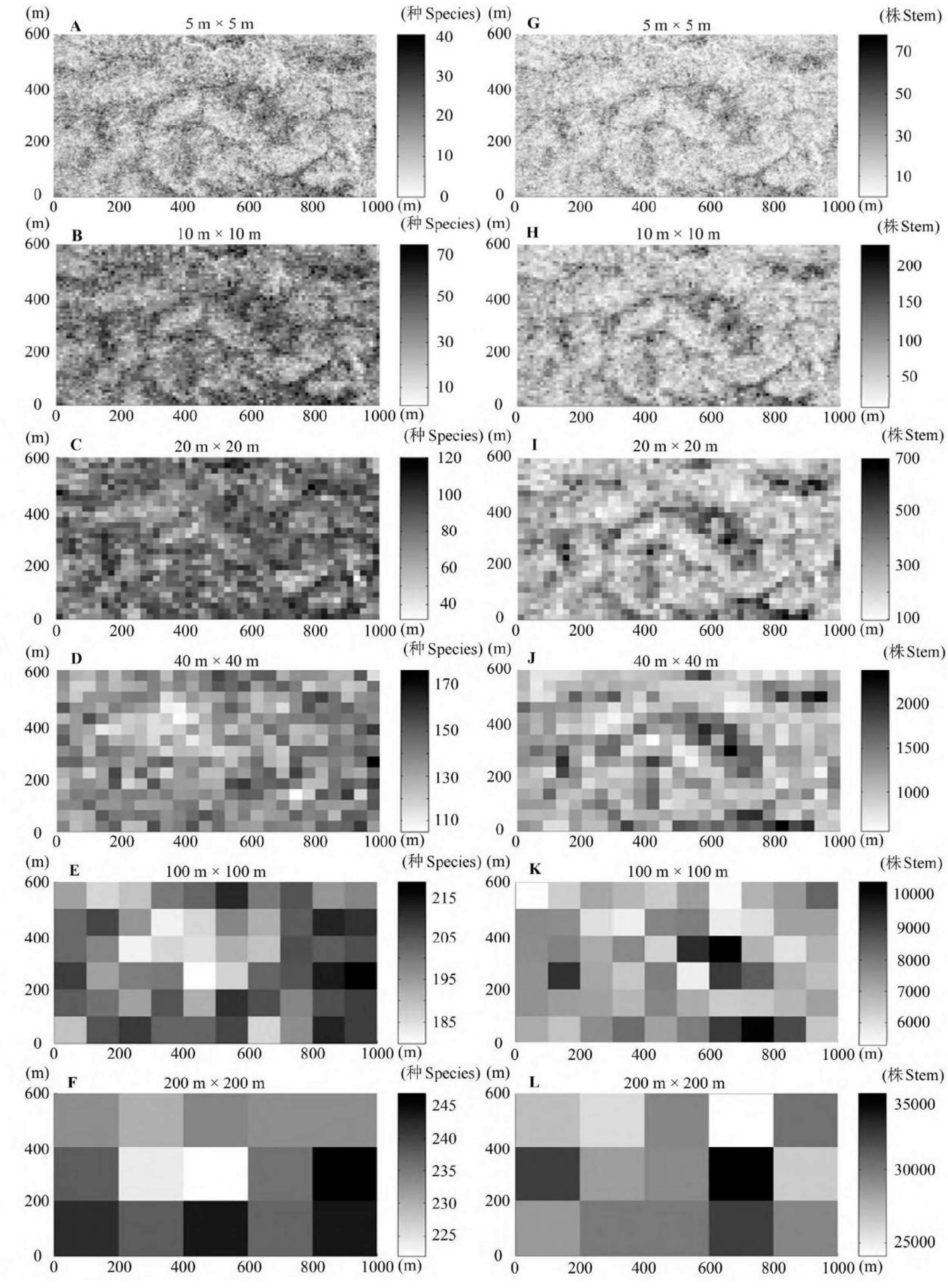

Fig. 2 Spatial distribution patterns of species richness (A–F) and abundance (G–L) at different scales

The sidebars represented the values of species richness or abundance at different quadrats, respectively.

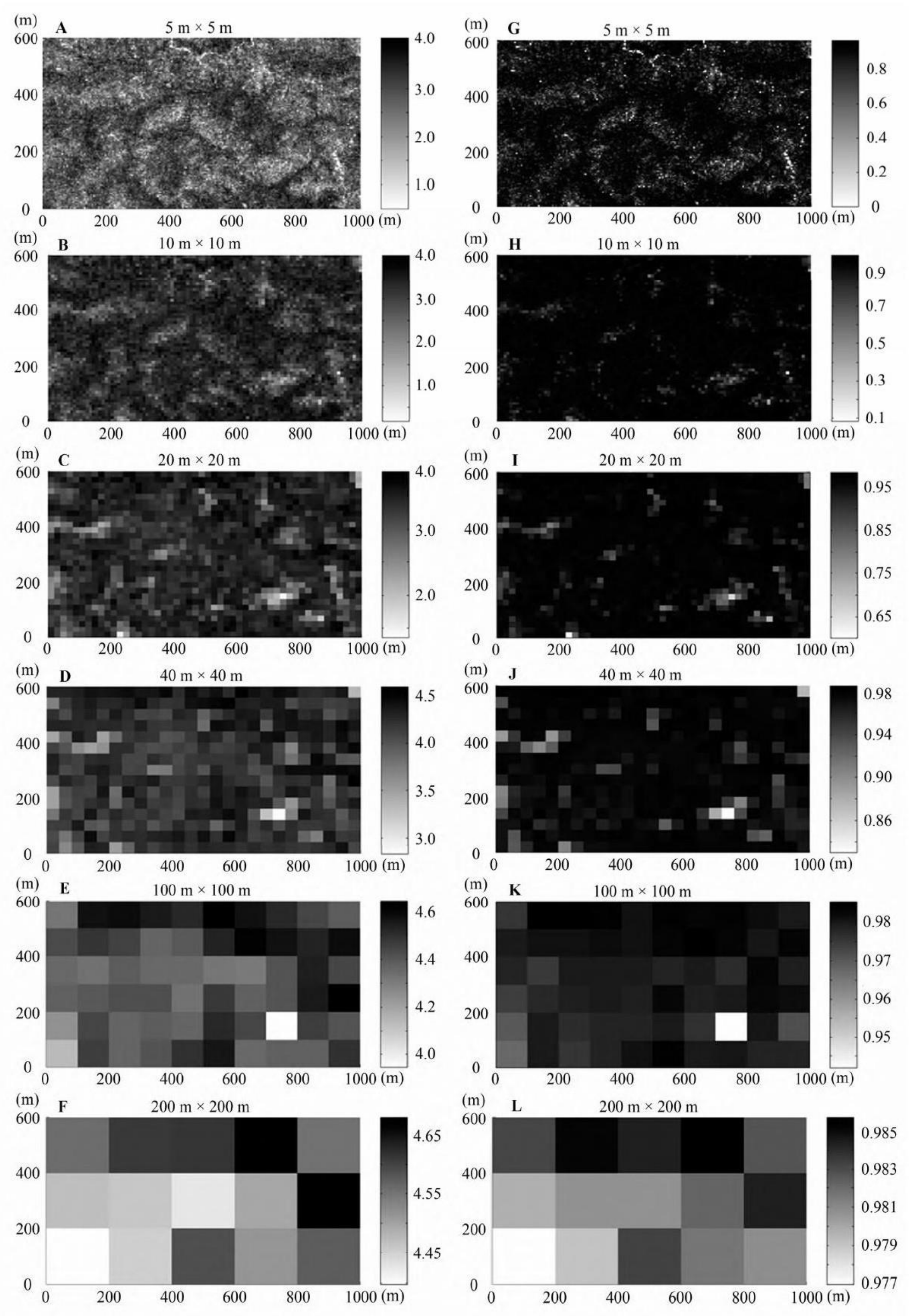

Fig. 3 Spatial distribution patterns of Shannon-Wiener (A–F) and Simpson indices (G–L) at different scales

The sidebars represented the values of Shannon-Wiener or Simpson indices at different plots, respectively.

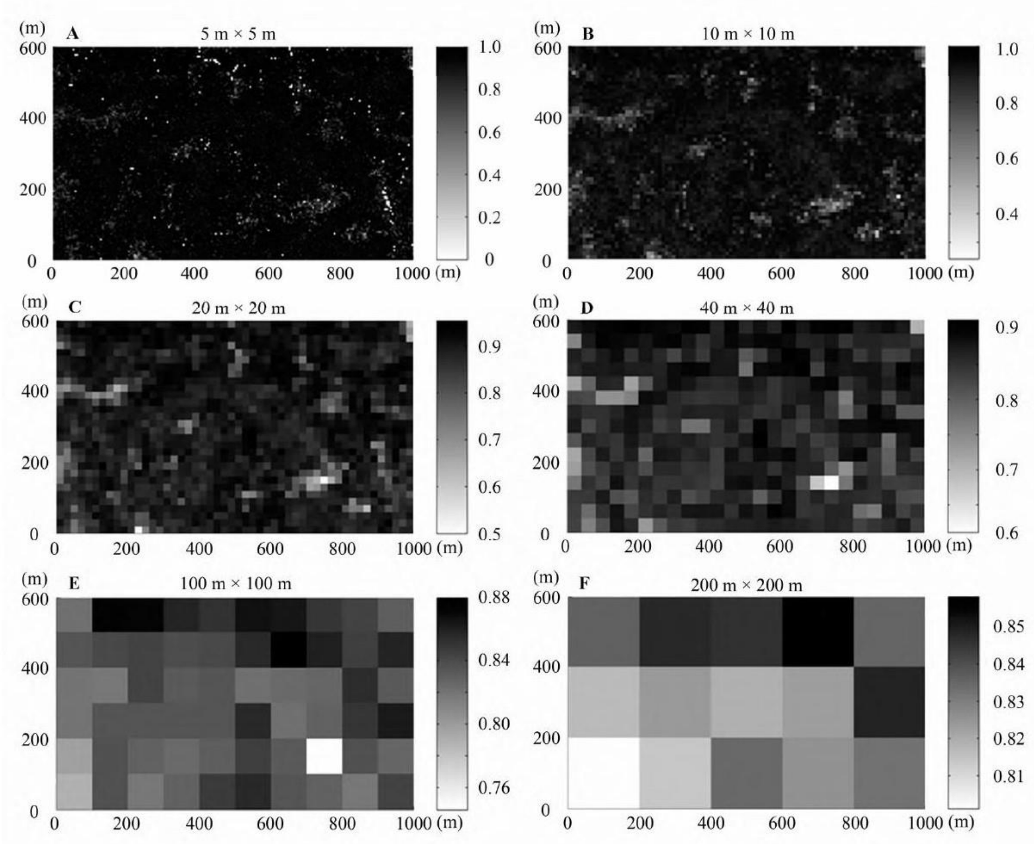

Fig. 4 Spatial distribution patterns of Pielou's evenness index at different scales

The sidebars represented the values of Pielou's evenness index at different quadrats.

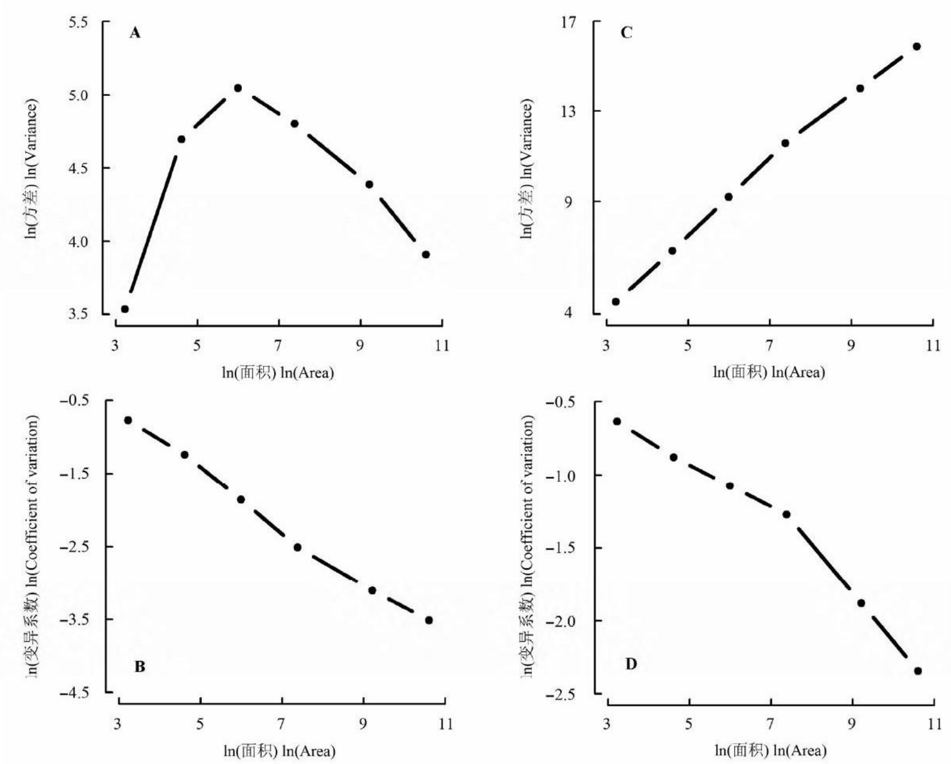

Fig. 5 Spatial variation of species richness (A, B) and abundance (C, D) at different scales

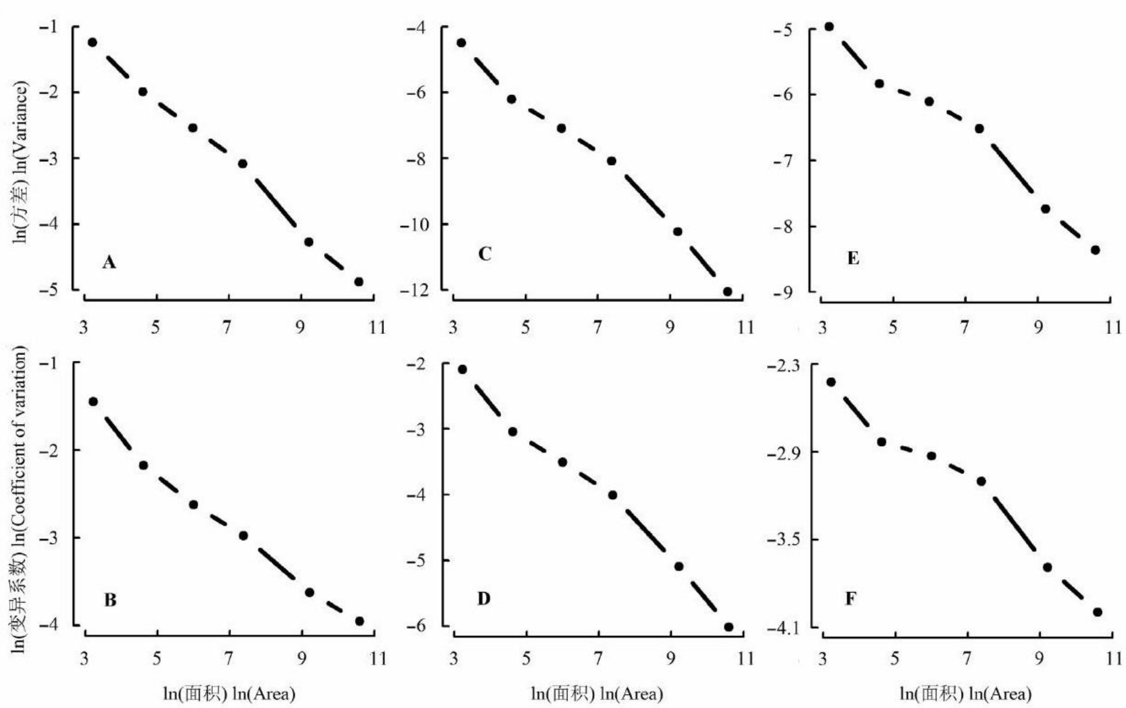

Fig. 6 Spatial variation of Shannon-Wiener (A, B), Simpson (C, D) and Pielou's evenness indices (E, F) at different scales

Table 1 Spearman rank correlation coefficients between species richness and abundance at different spatial scales

取样尺度 Sampling scales	5 m × 5 m	10 m × 10 m	20 m × 20 m	40 m × 40 m	100 m × 100 m	200 m × 200 m
相关系数 Correlation coefficients	0.917	0.873	0.735	0.319	–0.024	0.300
样方数 Number of quadrats	24 000	6 000	1 500	375	60	15
p	0.000	0.000	0.000	0.000	0.856	0.277

3.2 Comparison of variance and coefficient of variation between species richness and abundance

In the 60 hm^2 dynamic monitoring plot for tropical montane rain forest in Jianfengling, the variances of species richness and abundance had different trends along the spatial scale. The variance of species richness displayed a unimodal pattern along with the increase of scale, and peaked at 20 m × 20 m scale. This scale was the same as the scale where distribution patterns of species richness and abundance were differentiated. This result proofed the rationality of determining potential ecological processes at certain scale by inflection points in analysis of variance. The similar patterns were also found in other tropical forest (He et al., 2002), temperate forest (Wang et al., 2008) and mid-subtropical karst forest (Zhang et al., 2012). The variance of species abundance linearly increased along with the increase of sampling scale. This meant, at different scales, the ecological processes affecting species abundance did not change obviously. Different from variance, the coefficients of variation of species richness and abundance decreased along with the increase of sampling scale. This is because that variance reflects the absolute variations of diversity indices, and the coefficient of variation reflects the relative variations of diversity indices. These results indicate that the absolute variations of diversity indices are more reliable in analyzing the effect of ecological process on the spatial distribution pattern of biodiversity.

3.3 Spatial distribution patterns of Shannon-Wiener, Simpson, and Pielou's evenness indices at different scales

Shannon-Wiener index, Simpson index and Pielou's evenness index experienced scale effect. This scale effect was different in different study areas, but similar in the same area. In this study, with the increase of sampling scale, the variances and coefficients of variation of all the three indices had decreasing trends. However, in the 20 hm^2 evergreen broad-leaved forests in Dinghushan in the tropical area of southern China, the variances of the three indices displayed unimodal patterns with the increase of sampling scale (Wang et al., 2008). This may because of different composition of rare species between the two plots. The total number of rare species in Jianfengling plot was 60, accounting for 20.7% of the total number of species (Xu et al., 2015). In Dinghushan plot, the number of rare species was 110, accounting for 52.4% of the total number of species (Ye et al., 2008). In the 50 hm^2 Pasoh rain forest in Malaysia, there were 301 rare species, accounting for 36.5% of the total species. He et al.(1994) studied this area and reported that, in comparison to those at small and large scales, the influence of rare species on scale effect of Shannon-Wiener index was only significant at scales of 10 m × 10 m and 30 m × 30 m. The numbers of rare species in Dinghushan plot and Pasoh plot were much larger than that in Jianfengling plot. This can be one explanation for the difference of spatial distribution patterns. Moreover, at different sampling scales in this study, Shannon-Wiener index exhibited lage spatial variation, whereas Simpson index and Pielou's evenness index exhibited smaller variations. This was because of the characteristics of Shannon-Wiener index and Simpson index. Shannon-Wiener index was closely related to species richness, and Simpson index was sensitive to evenness (Ma et al., 1995; Xu et al., 2011).

In this study, we discussed spatial distribution patterns of species diversity at spatial scales. However, the internal mechanism of this variation still needs further study. For example, how and what degree does habitat heterogeneity affect the spatial distribution of species. The Jianfengling plot has a very complex terrain. In this plot, altitude and slope are in the ranges of 866.3–1,016.7 m and 1.7°–49.3° at 20 m × 20 m scale, respectively. Xu et al. (2015) reported that the spatial distributions of some species were significantly affected by terrain. For example, *Pinanga baviensis* and *Blastus cochichinensis* usually clustered in the valley area. However, the distributions of some species may relate to soil nutrients, such as *Ormosia balansae* (Leguminosae). Some species, such as *Altingia obovata*, may be affected by other factors such as microorganisms. The species preference of habitat directly affects the spatial distribution pattern of species diversity. The study of these species in the future will be helpful in exploring the formation and maintenance mechanisms of species diversity in Jianfengling.

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