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RESEARCH ARTICLE

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Comparison of fractal characteristics of species richness patterns among different plant taxonomic groups along an altitudinal gradient

Abstract This study was done using the non brown fractal model to quantify and compare the variations in the species richness of trees, shrubs, herbs and all plants along an altitudinal gradient and to characterize the dominating ecological processes that determine the variations.

Two transects were sampled far away from any anthropogenic disturbances along the shady slopes of the Dongling mountains in Beijing, China. Both transects were continuous and 2 m wide, and every individual tree and shrub was recorded in each of them. Discrete quadrats of 1 m × 1 m were located along the transects A and B for estimation of the herb species richness along the altitudinal gradients. The level interval between the quadrats was 10 m and 25 m respectively. In this study, transects A and B were combined into one transect AB, and 40 m was selected as the optimal quadrat length along the altitudinal gradients for measuring the plant species richness patterns. Species richness in each quadrat was calculated using a program written in Matlab 6.0.

Direct gradient analysis was used to describe the overall trends in the species richness of trees, shrubs, herbs and other plants with change in altitude, while the non-brown fractal model was used to detect more accurately their variations at various scales along the gradient. The model assumed that each class of ecological processes affecting the distribution of a variable could be represented by an independent spatial random function. Generally, ecological phenomena are determined not by a single ecological process but by multiple ones. These processes act on ecological patterns within their own spatial scales. In the non-brown fractal model, the spatial random functions are nested within a larger range of spatial scales. The relative contribution of the spatial random functions to the spatial variation of a variable is indicated by a weighting parameter that has to be greater than or equal to zero.

In this paper, we reached the following results and conclusions. Firstly, the direct gradient method describes the general trends of trees, shrubs, herbs and all plants along the altitudinal gradient but is unable to provide further details on the altitudinal variations in the species richness. The non-brown fractal model brought out the altitudinal variations in the species richness of trees, shrubs and herbs at various scales and related them to the ecological processes. The sharp changes in the double-log variograms suggest that the non-brown fractal model is suitable for characterizing the altitudinal patterns in the species richness of trees, shrubs and herbs at various scales but is not appropriate for explaining the variations in the plant species richness, since no significant changes were found in the double-log variograms in this case. Secondly, for the trees, the double-log variogram was divided into two scale ranges (0–245 m and 245–570 m), with a fractal dimension of 1.83 and 1.10, respectively, implying that changes in the tree species richness were random at small scales (0–245 m) and almost linear at large scales (245–570 m) along the altitudinal gradients. This suggests that altitudinal variations in the tree species richness are dominated by short-range processes at small scales and by long-range processes at large scales. Thirdly, for shrubs and herbs, the double-log variograms exhibited three ranges (0–101 m, 125–298 m and 325–570 m), and the fractal dimensions were 1.78 and 1.97, 1.56 and 1.43, and 1.08 and 1.25, respectively. The results indicate that, as in the case of trees, species richness of shrubs and herbs are distributed randomly at small scales and change in a linear manner at large scales although variations in the herb species richness is less heterogeneous than shrub species richness at large scales. Theses results also indicate that species richness of shrubs and herbs change approximately like brown movement at middle scales. The results also suggest that altitudinal variations in the specie

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richness of shrubs and herbs are dominated by three ecological processes, short-range ecological processes at small scales, long-range ecological processes at large scales, and brown fractal processes at middle scales. Interestingly, comparisons of the variations in the species richness of shrubs and herbs reveal that shrubs and herbs present the same scale range in spatial variation in species richness but display different trends in species richness along the altitudinal gradient, i.e. the shrub species richness decreased with increasing elevation whereas the herb species richness peaked at the mid-high elevation. These patterns suggest that although the scales at which the main processes affect patterns in species richness are the same, the processes are completely different, or the processes are similar but the responses of the shrubs and herbs to the ecological processes are different. Finally, the plant species richness did not show any obvious pattern along the altitude gradient and maintained a constant fractal dimension across all scales, this is perhaps because the processes defining the patterns of plant species richness had similar weights and acted over closely related scales.

Keywords altitudinal pattern, biodiversity, ecological processes, fractal dimension, scale, species richness

1 Introduction

Today, our world faces a severe ecological and environmental crisis and species on the Earth are becoming extinct at an unprecedented rate (Pimm et al., 2001). Thus, biodiversity has attracted scientists, governments as well as the public, becoming a hot topic in modern ecology (Chen, 1996; Dong and Li, 1996). In the past decades, research was often focused on large-scale patterns in biodiversity, such as latitudinal gradients and regional patterns (Lyons and Willig, 1999; Gaston, 2000). In recent years, due to the growing importance of mountains in the development of ecology, biogeography and evolutionary biology, and the similarities between altitudinal and latitudinal gradients, there has been a resurgence of researches on the biodiversity of mountains (Lomolino, 2001). Körner (2000), in the hope that probably the mountain biodiversity would provide answers to the global patterns in biodiversity and the mechanisms responsible for their generation.

So far, many types of patterns in biodiversity have been found along altitudinal gradients and there are also several hypotheses to interpret them. But, no general biodiversity theory exists yet (Rahbek, 1995; Rahbek and Graves, 2001; Willg et al., 2003), mainly because of the spatio-temporal scale mismatches in biodiversity researches (Whittaker et al., 2001). Essentially, the scale is inherent in the ecological phenomenon, the ecological patterns and the processes, the key being that ecology is closely related with the scales (Meentemeyer, 1989; Levin, 1992; Legendre, 1993). The patterns that we observe depend on the scale used, and the ecological processes match the patterns only at the corresponding scale (Marceau and Hay, 1999; Nelson, 2001). Consequently, it is fundamental to correctly discover the scale-dependence of patterns in biodiversity for the description and interpretation of the patterns (Lyons and Willig, 1999).

Traditionally, statistical methods, based on random distribution of variables, do not take into account the scale-dependence of spatial variables, therefore, conclusions reached from spatial data analysis are often incorrect (Legendre and Fortin, 1989). Recently, many spatial statistical tools powerful in analyzing complicated natural phenomena were introduced (Marceau and Hay, 1999). Most of these methods however are used just to describe the variation range of spatial patterns, and not for detecting the variation intensity at corresponding scales. Towards the end of the 1970's, Mandelbrot proposed the fractal theory which broke the limit of the traditional Euclidean dimension and allowed the dimension to be a real number. Using this fractional dimension, we can measure the complexity of the system directly (Wang and Cao, 1995; Li and Wang, 1997). Random fractal process is a statistical model to analyze the spatio-temporal characteristics of the natural phenomena. It was firstly used in the hydrology to describe and simulate the noise with fractal characteristics (Burrough, 1981; Li and Wang, 1997). Burrough (1981, 1983a) introduced this model into pedology and landscape science to describe characteristics of spatial distribution of soil and landscape. Recently ecologists are paying more attention to the fractal theory because of its capability to describe complex spatio-temporal patterns (Ma et al., 1997; Palmer, 1988; Zu et al., 1997). Stochastic processes that are ergodic assume that variations occur over all scales. In fact, this is an idealized abstraction. Usually, the variations in time and space are controlled by multiple processes at certain scales. No variation can be observed to be continuous over all scales (Marceau and Hay, 1999). In order to reveal the complexity of the phenomena, Burrough (1983b) established a "non-brown fractal" model, which took into account the spatial variations in soil characteristics at multiple scales. Similarly, spatial distribution of the plant community is also closely related to scales, and apparently are fractal (Levin, 1992; Ma et al., 1997; Zu et al., 1997; Palmer, 1998). Thus the aim of the present study is to quantify and compare the variations of species richness of trees, shrubs, herbs and all plants along the altitudinal gradients and characterize the dominating ecological processes that determine the patterns by using the "non brown fractal" model.

2 Study site

The study site is located on the Dongling Mountains, west of Beijing (40°00′–40°03′ N, 115°26′–115°30′ E), adjacent to the Hebei Province. In this area, the maximal elevation is 2,303 m above sea level, annual mean temperatures are 5–11°C, and the annual precipitation of 600 mm mainly occurs from June to August. The site belongs to a warm temperate semi-humid monsoon climate. Here, the brown soil is developed and the vegetation is classified as a warm temperate deciduous broad-leaved forest, their distributions both show apparently a vertical band spectrum. The flora of this area is abundant with a total of 127 families, 476 genera and 997 species (including varieties and infraspecies), mainly derived from descendants of tertiary flora and dominated by a temperate ingredient (Ma et al., 1997).

3 Data and methods

3.1 Data collection and processes

In the present study, two transects A and B, perpendicular to the contour, were set up on the slopes of the Dongling Mountains, where there is less of anthropogenic disturbance and which is a complicated topography, e.g. away from cliffs and with a large area of outcrop, so that the effects of the altitude on variations in biodiversity did not get confounded by anthropogenic and topographic disturbances. The information about the transects follows in Table 1.

Table 1 Characteristics of two transects along altitudinal gradient

Code of transects	Elevation /m	Width /m	Slope aspect
A	1,800–1,280	2	North-west
B	2,300–1,940	2	North

Data was gathered according to the plant groups of trees, shrubs and herbs, respectively. Trees and shrubs were sampled in continuous transects, each individual of them was mapped, and the specie names were recorded. Also, the elevation and the slope were measured every 50 and 20 m (bevel distance) along transects A and B, respectively. For herbs, discrete quadrats of 1 m × 1 m were sampled along the transects, separated by a bevel distance of 25 m and 10 m in transects A and B, respectively. We also recorded the position of the quadrat in the transect and the herb species in the quadrat. Both transects A and B were north or north-east facing. Although both the transects were not connected end to end, the gap was relatively small (Table 1). In order to detect the altitudinal variations in species richness, we combined transects A and B into one transect AB. The bevel locations of the woody individuals and the quadrats were transformed to their vertical and horizontal positions through horizontal and vertical projections. The data transformation was done using MATLAB 6.0.

We came to the conclusion that in the Dongling Mountains the optimal length of the quadrat side was 40 m along the transect (horizontal distance) when a 2-m width of transect or quadrat was used, to investigate the altitudinal patterns in the tree species richness in the shady slopes (Ren et al., submit). As a result, for trees the transects were divided into consecutive quadrats of 40 m length each. In order to compare the altitudinal variations in the species richness of trees, shrubs, herbs and plants, the same quadrat was employed for shrubs and herbs. However, the transects were not continuous for herbs, thus there could be some differences in the species richness results between the samples from the 2 m × 40 m quadrats and the 1 m × 1 m quadrats involved, but since the sampling was of high density for herbs the differences can be ignored. Species richness was calculated using MATLAB 6.0.

3.2 Methods

Firstly, the variations in species richness were described using the direct gradient method; then the "non-brown fractal" model was used to measure the variations in the species richness along the altitudinal gradient for trees, shrubs, herbs and plants.

The non-brown fractal model assumes that the spatial variations of a variable are determined by multiple processes. Each can be denoted by an independent spatial random function (RF_q) having its own scale (r_q) and weight. Burrough (1983b) pointed out that if the spatial variable was controlled by only one random process function, once the value of a given realization of the random function is determined, the value remains constant for the whole of its own spatial range. Actually, the values of a variable are unlikely to be constant over the spatial range, but change at smaller scales. The change can be described by a second random function nested within the larger scale. Consequently, the actual variations of variables in space reflect the balance between random processes at the various scales (Burrough, 1983b). At a certain scale, the importance of a process can be determined by a weighting parameter. The model was formulated as below.

$$Z(x) = \beta_0 RF_0 + \beta_1 RF_1 + \ldots + \beta_q RF_q$$

where $Z(x)$ is the value of variable Z at x in space, RF_q and β_q are the random function and the weighting parameter of RF_q to $Z(x)$ respectively, $q\sim [0, 1, 2, \ldots, n]$; from RF_0 to RF_q, the random functions RFs are arranged so that the range of each is nested within the range of the next.

We created the standard semi-variance function of variable Z, and calculated the spatial fractal dimension D of variable Z according to its double-log semi-variograms (Burrough, 1983b).

$$\mathrm{D} = (4 - m)/2$$

where m was the slope of fitted linear of the double-log semi-variograms.

Similar to the brown fractal model, when D = 2, the variations in spatial variables were considered to be homogeneous or random; smaller the value of D, stronger was the spatial heterogeneity; if D = 1, the variations in space showed a monotonic or linear gradient (Zu et al., 1997; Palmer, 1988). However, compared to the brown fractal model, the "non-brown fractal model" has the following important properties (Burrough, 1983b):

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First, partial correlations exist in spatial variables over all scales within the range of the random process that operates over the longest distance. Second, the contribution of each random function *RF* to the semi-variance relies on its weight and the ratio of the sampling interval and the autocorrelation range of the random function. Third, this model need not satisfy the rigid stationary assumption. Fourth, the semi-variance increases as new large autocorrelation-range, random functions are introduced. Changes in the value of an important process result in sharp changes in the variograms or the double-log variograms. The sharp changes can be taken as a pattern scale.

Because of these characteristics of the "non-brown fractal model", in the present study, the double-log variograms were linearly fitted in subsections separated by sharp changes. The fractal dimensions were calculated by the slopes of fitted lines. Based on that, we compared the fractal characteristics of the species richness of trees, shrubs, herbs and all plants along the altitudinal gradients. The standard semi-variance was calculated by WinGslib 1.3 (demonstration version).

4 Results

The aim of this paper is to primarily describe and compare the fractal characteristics of the species richness of trees, shrubs, herbs and all plants along the altitudinal gradients. The results show that the species richness of plants does not appear in the gradient (Fig. 1a), but exhibits self-similarity over the whole scale ($R^2 = 0.826\ 4$), with fractal dimension D = 1.7 and no sharp changes on the double-log variograms (Fig. 1b).

Generally, the species richness of trees decreased with increase in elevation and no further information could be gathered (Fig. 2a). The double-log variograms of the species richness of trees were divided into two scale ranges, 0–245 m and 270–570 m, with fractal dimensions of 1.83 and 1.10 respectively (Fig. 2b).

As for shrubs, the species richness decreased with increase in elevation (Fig. 3a). The double-log variograms of the species richness were divided into three scale ranges, 0–101 m, 125–298 m and 325–570 m. The fractal dimensions were 1.78, 1.56 and 1.08 respectively (Fig. 3b).

For herbs, the species richness at higher elevations was apparently greater than at lower elevations, the maximum value occurring in the upper-middle elevation (Fig. 4a); Just like for shrubs, the double-log variograms of the species richness of herbs were divided into three scale ranges, 0–101 m, 125–298 m and 325–570 m. The fractal dimensions were 1.97, 1.43 and 1.25 respectively (Fig. 4b).

5 Discussion and conclusions

Scale is an important concept in ecology. It is closely related to ecological patterns and processes, thus it is essential to describe the patterns and find the ecological processes controlling the patterns (Levin, 1992; Marceau and Hay, 1999; O'Neill et al., 1996). The concept of scale involves the size of

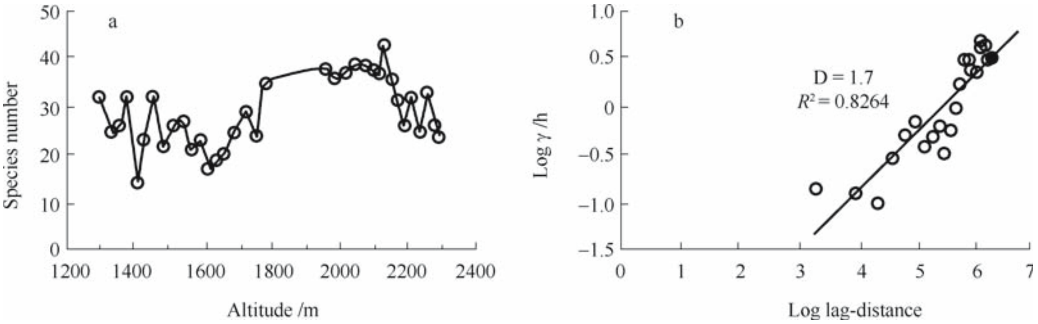

Fig. 1 a. Patterns of plant species richness along altitudinal gradient, b. Double-log variogram for plant species richness along altitudinal gradient

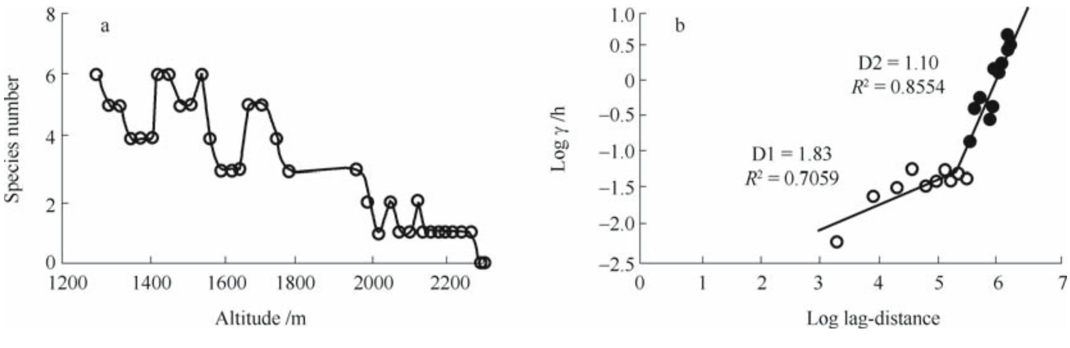

Fig. 2 a. Patterns of tree species richness along altitudinal gradient, b. Double-log variogram for tree species richness along altitudinal gradient

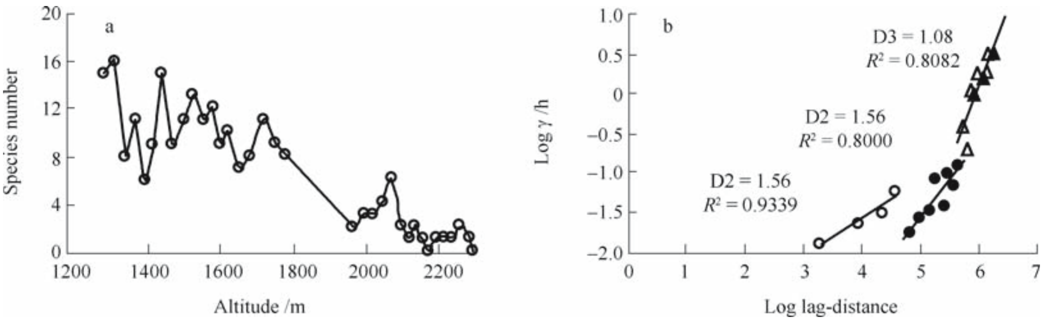

Fig. 3 a. Patterns of shrub species richness along altitudinal gradient, b. Double-log variogram for shrub species richness along altitudinal gradient

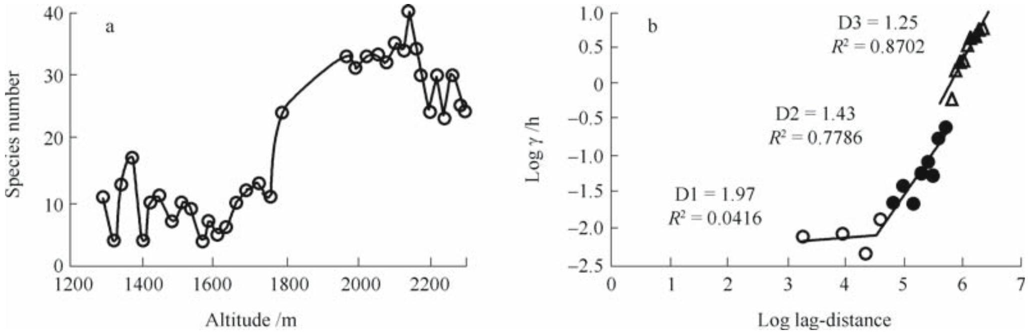

Fig. 4 a. Patterns of herb species richness along altitudinal gradient, b. Double-log variogram for herb species richness along altitudinal gradient

the sampling unit, the sampling interval and the extent of the study area and so on (Perry et al., 2002; Nelson, 2001; Jelinski and Wu, 1996). In plant ecology, the sampling unit is traditionally 20 m × 20 m for a warm-temperate forest community. In the present study, the transect of the trees was 2 m wide and the length of the quadrat side along the transect was 40 m; thus, the quadrat size was much smaller. However, some studies show that the optimal size of the sampling unit, used in evaluating the variation in the species richness along the altitudinal gradients, is determined by the anisotropy of the specie turnover in space. The minimum size of the sampling unit obtained from this method is much smaller than that obtained from the species-area relationship method. Further, it has been suggested that the quadrat of 2 m × 40 m (with the long side perpendicular to the contour) is sufficient to correctly describe the variations in the tree species richness along the altitudinal gradient in the Dongling Mountains. In order to easily compare the pattern of the species richness of trees, shrubs, herbs and all plants, the same sampling unit as that for trees was used for shrubs and herbs in this study, although the herb transect was not continuous.

Essentially, natural phenomena are structured hierarchically in space, and such a hierarchy is closely correlated to the observed scales (O'Neill et al., 1996; Jelinski and Wu, 1996). Consequently, spatial increments of a variable often do not follow a normal distribution. Sometimes, the spatial variation is gradual but often it is abrupt. Thus only the non-brown fractal mode is suitable for describing such patterns (Burrough, 1983b). In the present study, the abrupt changes appeared in all the double-log variograms of the species richness of trees, shrubs and herbs. The results demonstrate that the species richness along the altitudinal gradient is nested or hierarchically structured for trees, shrubs and herbs, and hence the "non-brown fractal model" is recommended for characterizing the spatial variations for such species richness. As for plants, no threshold was discerned on the double-log variograms. There could be two reasons for the same. One, the species richness of all plants did not show a hierarchical structure and if the extent of the study were to be enlarged a hierarchical structure could emerged; the second is that the variation in species richness of all plants along the altitudinal gradients is determined by a series of processes that operate over closely related scales and have a similar contribution to the variations in the species richness of all plants.

Presently, there is no general theory on biodiversity yet. This is mainly because the relationships between patterns and processes at different scales are not clear, that is, patterns are not correctly connected at corresponding scales to the relative ecological processes (Whittaker et al., 2001). Neither the direct gradient method nor the classic regression analysis, widely used in studies on the vertical patterns of biodiversity, reveals the variations in biodiversity at different scales. With the emergence and widespread application of spatial statistical techniques, we are gaining insights into the scale-dependence of ecological variables, furthering our knowledge of ecology (Dale et al., 2002). However, many of these techniques are sensitive to the trends of variables at larger scales and do not reveal the intensity of variation at different scales. In this study, the "non-brown fractal model" was applied to detect the spatial variation in species richness at different scales. The results show that the direct gradient method describes the general trends of species richness along the altitudinal gradients, for trees, shrubs, herbs and plants, but is unable to provide more details on the altitudinal variations of species richness (Fig. 1a, Fig. 2a, Fig. 3a, Fig. 4a). For trees, there was a sharp change at a scale of 245 m in the double-log variograms of species richness, and the fractal dimension was equal to 1.83 over smaller scales of 0–245 m, while it was equal to 1.10 on larger scales (Fig. 2b). This result implies that changes in tree species richness are random at small scales and almost linear at large scales along the altitudinal gradients. For shrubs and herbs, the double-log variograms exhibit three sections (0–101 m, 125–298 m and 325–570 m), and the fractal dimensions are 1.78 and 1.97, 1.56 and 1.43, and 1.08 and 1.25, respectively (Fig. 3, Fig. 4). The results indicate that, like for trees, the species richness of shrubs and herbs are distributed randomly at small scales (0–101 m). However, at middle scales (125–298 m), the fractal dimension is about 1.5, suggesting that on this scale the increment in species richness of shrubs and herbs is a random distribution along the altitudinal gradient and does not show a long-distance correlation, that is, the previous increment in species richness does not influence the next one along the altitudinal gradient. At large scales (325–570 m), the fractal dimension is about 1, indicating that the species richness changes dramatically along the altitudinal gradient, almost linearly, especially for shrubs.

When comparing the fractal characteristics of the variations in species richness of trees, shrubs, herbs and plants along the altitudinal gradients, there is only one critical point on the double-log variograms of the species richness for trees, whereas there are two such points for shrubs and herbs. Moreover, the scale at which the first critical point occurs is larger for trees on the double-log variograms of the species richness than for shrubs and herbs (Fig. 2b, Fig. 3b, Fig. 4b). The results suggest that in the Dongling Mountains two types of ecological processes control the variations in the tree species richness along the altitudinal gradients, one is random in nature and works over small scales, and the other is long-distance correlated in nature and acts on larger scales. Long-distance correlation refers to the relationship between the previous and the next increments in the species richness along the altitudinal gradients. The ecological processes with long-distance correlation are not independent in space and thus also influence the variations in species richness at other scales in space. The results also indicate that the altitudinal variations in species richness of shrubs and herbs are dominated by three kinds of ecological processes: random ecological processes over small scales, approximate brown fractal processes on middle scales, and processes with long-distance correlation on large scales. The present study shows that on large scales the fractal dimensions for trees and shrubs are similar, but are less than that for herbs, suggesting that the variations in the species richness of trees and shrubs are larger than that of herbs. (Fig. 2b, Fig. 3b, Fig. 4b). Although for shrubs and herbs the scales over which the double-log variograms changed were similar, the gradients in the species richness were greatly different along the altitude (Fig. 3b, Fig. 4b). Generally speaking, species richness of shrubs decreased at higher elevations, whereas that of herbs peaked at mid-high elevations (Fig. 3a, Fig. 4a). Consequently, although the scales over which the ecological processes dominate the variations in the species richness of shrubs and herbs along the altitudinal gradient are closely correlated, (probably the processes are completely different, or similar but with different ways to act on the variations in the species richness of both plant groups) the response and the adaptation to environmental stress are different for shrubs and herbs. The variations in the species richness are similar for trees and for shrubs along the altitudinal gradient and the fractal properties for both groups are similar over small and large scales but different on middle scales. The result suggests that an ecological process that acts on middle scales has an important effect on the distribution of the shrub species richness but little effect on that of the tree species richness. Unlike for other groups, for plants no sharp changes appears on the double-log variograms of the plant species richness and the fractal dimension is 1.7 over the entire range of scales, suggesting that the species richness of plants is not hierarchically structured along the altitudinal gradient and apparently shows self-similarity (Fig. 1b). This might be because the ecological processes that determine the altitudinal variations in the species richness of trees, shrubs and herbs operate over closely related scales (Burrough, 1983b). In this context, biodiversity researches based on different plant groups according to life forms would probably be able to improve our understanding of the biodiversity changes in space.

From the above analyses and discussions, we reached the following conclusions:

Firstly, the “non-brown fractal model” takes into account the abrupt changes of the biological variable in space and assumes that the spatial variations are determined by a series of ecological processes that act over various scales. The present study suggests that the non-brown fractal model is suitable for characterizing the altitudinal patterns in the species richness of trees, shrubs and herbs at various scales but not for detecting the variations in the plant species richness. There are probably two reasons for the inadvisability. One is the limitations of the elevation in the study extent, if the extent were to be expanded enough, the plant species richness might show an hierarchical structure. The other is that the variations of the plant species richness are determined by some ecological processes that operate over closely related scales.

Secondly, the variations in species richness of trees along the altitudinal gradient are mainly controlled by two kinds of ecological processes: the stochastic processes over small scales and the processes with long-distance correlation on large scales.

Thirdly, the altitudinal variations in the species richness of shrubs and herbs are dominated by three kinds of ecological processes. On small and large scales, like for the species richness of trees, the processes were independently random;

however, on middle scales the brown fractal processes control the altitudinal variations in the species richness. Although the scales at which the processes determining the variations in the species richness act are similar, shrubs and herbs respond differently to the effects of these processes. This is probably because the processes themselves are completely different

Overall, this study not only provides the basis for sampling in the investigation of vertical patterns of biodiversity in the Dongling Mountains or in any other warm temperate zone, but has also deepened our understanding of the vertical changes of biodiversity and the mechanisms of forming them. Also we have concluded that the variations in the species richness along the altitudinal gradient are a result of the interaction of a series of independent and random processes at various scales. The "Non-brown fractal model" is able to quantify the weight for the variations in the species richness of every process at relative scales (Burrough, 1983b), but the paper did not discuss this problem as further researches are needed. Only transects in shady slopes were sampled in this study, more researches are required to integrate our knowledge.

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