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Rapid assessment and explanation of tree species abundance along the elevation gradient in Gaoligong Mountains, Yunnan, China

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This article presents an analysis of tree species abundance and its association with climatic variables along elevation gradient in the Gaoligong Mountains in west Yunnan, China. Data from scientific papers and books in the Gaoligong Mountains area were collected and extrapolated to elucidate a mechanistic understanding of elevation patterns and the relationship between the elevation range and elevation mid-point of tree species along the gradient by examining climatic variables. Tree species abundance showed a unimodal pattern with a peak at mid-elevation (about 2000 m) and species with a narrow elevation range occurred at higher or lower elevation, while a wider elevation range was found at the middle of the gradient. Tree species abundance was the highest where both temperature and water availability were moderate. The relationship between the climatic variables affecting species appear to be due to both direct and indirect factors, and the effect of these effects varied at different gradients.

tree species abundance, elevation, distribution range, climatic factor, the Gaoligong Mountains

1 Introduction

Identifying the patterns of biodiversity is fundamental to increasing the understanding of ecological and evolutionary processes and informing conservation and management decisions[1,2], and has been considered as the one of the basic researches of ecology and biogeography[3]. This issue is becoming more and more urgent with the decreasing of biodiversity in the whole world[4]. After Brown brought forward the theory of macroecology in 1995, it has become easy to find out and explain the pattern of species abundance, for this method has broken the dimension of the traditional field work, to discover the ecological features on a larger scale[5,6]. Based on this theory, research on species abundance pattern, especially the relationship between species–area relationship and the latitudinal increase of species abundance from the poles towards the equator has obtained substantial progress. The causes for the latitudinal diversity gradient, however, are still debated hotly, but current research focuses mainly on energy availability, evolutionary time, habitat heterogeneity, area and geometric constraints[7−9]. A third environmental gradient, elevation, has often been linked to the latitudinal gradient. It was long believed that a monotonic decrease of species abundance with increasing elevation was the universal pattern and that the elevation pattern therefore reflected the latitudinal pattern[10].

The striking ecological changes that occur along elevation gradients drew the attention of early researchers, such as Darwin[11,12], von Humboldt[13], Wallace[14,15] and Merriam[16]. Numerous hypotheses exist to explain elevational species abundance patterns; however, many are neither mutually exclusive nor independent, and none are consistently supported with empirical evidence[17−19]. Two general patterns have emerged: a monotonic decrease in species abundance and a hump-shaped relation-

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ship with a peak in species abundance at intermediate elevations[19,21,22]. However, the patterns found in different areas are not the same as reported in a variety of literatures, depending on the taxa and elevation range chosen[22,23]. Certain abundance patterns may be a consequence of a particular climatic regime or historical contingency or certain patterns may be represented only by particular taxonomic groups driven by their ecological constraints. If such predictable patterns exist within the taxa and among climates, they will pinpoint driving factors in species abundance [17,19,24].

Biological collections in museums and herbaria can provide important information about the geographical distributions of plant and animal species. Indeed, for some species, collections are the only source of such information. The value of this information is growing with the demand for rapid and inexpensive conservation assessments[25−27]. The aim of this study is to quantify the elevation pattern of species abundance of all tree species in the Gaoligong Mountains and explain the cause of the pattern by climatic variables, based on the data collected and extrapolated from issued literatures. In addition, we want to provide a rapid assessment method of species abundance in a certain region, especially where the biodiversity is threatened by mass constructions. We used trees because their records are more complete and reliable, they may be more influenced by climate than herbaceous species[28], and elevation ranges for trees are more accurate than for smaller plants[29].

2 Location of study area and its vegetation

The Gaoligong Mountains lies in the border area between southwest China and northern Myanmar (24°56′ to 26°09′N and 98°34′ to 98°50′E), being part of the Hengduan Mountain. This region contains extremes in altitude within a very short distance, with the highest point of 4640 m in Gongshan County to the north and the lowest elevation of 650 m along a branch of the Irrawaddy River in Tengchong County to the south. The region forms the northern part of the Burma-Malaya Block of Gondwanaland lying between the Indian and Yangtze landmasses. During the Mesozoic, the block collided with Laurasia and became the southwestern border region of the Eurasian plate. Since the Miocene, the Burma-Malaya Block has moved about 450 km northwards from the equatorial tropical zone and rotated in a clockwise direction. This new tectonic movement led to substantial uplift and was significant in outlining the present geomorphology and subsequent biological diversity of the area[30].

According to the classification principles of China vegetation, the vegetation here is of transit characteristics, for it is located in the transit area from south monsoon evergreen broadleaved forest to middle subtropical evergreen broadleaved forest. And the latter is the zonal vegetation here. There are 8 kinds of vegetation types in the Gaoligong Mountains, namely tropical rainforest, subtropical evergreen broadleaved forest, deciduous broadleaved forest, coniferous forest, shrub, grassland and meadow. Up to 1000 m there is some fragment of tropical rainforest found in the place far from the settlement. Most parts of the area (below 2600 m) are covered by subtropical evergreen broadleaved forest, including three formation groups, monsoon evergreen broadleaved forest, sub-humid evergreen broadleaved forest, and montane wet evergreen broadleaved forest. Warm-temperate coniferous, dominated by *Pinus yunnanensis*, occurs in the north part of the mountain. Cool-temperate mixed forest (2800—3000 m) develops very well in the whole range owing to the warm temperature and plentiful precipitation. Cold-temperate coniferous forest (2900—4000 m) was dominated by *Abies delavayi* and *A. georget* var. *smithii*. The natural shrub and meadow (above 4500 m) are found in the alpine area and on top of the mountain[30,31].

3 Data sources, interpolation and analysis

As one of the richest biodiversity areas in the Hengduan Mountains, there is substantial plant data on the Gaoligong Mountains. This is a broad-scale study covering the whole Gaoligong Mountains elevation gradient. We have used the secondary data source of Flora of the Gaoligong Mountains, which is based on extensive field studies, reviews of published literature, and examinations of herbaria. It provides information on 780 tree species growing from 650 m a.s.l. to the tree line. Those tree species whose distribution range is only crudely mentioned are not included here. To examine the relationship between species abundance and elevation, the total elevation gradient between 650 and 4400 m was divided into 37 elevation intervals (vertical elevation band). The number of tree species present in each band is estimated by the interpolation method. A species was defined as being present in every 100-m interval between its upper and lower elevation limits. For example, *Abies delavyi*, with its elevation limit between 2500 and 4300 m, was assumed to be present in each elevation band of 2500, 2600, and so on up to 4300 m. Another example, *Pinus yunnanensis*, with its elevation limit between 1060 and 3000 m, was taken as 1100 m and 3000 m[19,28]. The term species abundance is defined as the total number of tree species found in each 100 m elevation band, which has been called gamma diversity. The elevation range of each species was estimated as the difference between the maximum and minimum elevations where a species was found within the range of survey sites, rounded off to the nearest 100 m. Species reported from a single site were given an elevation range of 100 and were also included in the analysis. The mid-point of a species at a given site was calculated by averaging the lowest and highest elevation limits of each species present. For example, *Platycladus orientalis*, with its elevation limit between 1330 and 1800 m, was assumed to have a midpoint at 1600 m.

Our analyses used three bioclimatic variables that are expected to have a strong functional relationship with the distribution of tree species in this region: mean annual temperature (T); annul precipitation (P); actual evaporate transpiration (AET). T and P (see Table 1) were selected based on the results of earlier studies[32−40], while AET was calculated using Turc's formula[41], where AET $=P/[0.9 + (P/L)^2]^{1/2}$, with $L= 300 + 25T+ 0.05T^3$.

Table 1 Climatic variables of the Gaoligong Mountains

Elevation (m)	T (℃)	P (mm)
755	22	737
1400	18	1256
1440	16	1763
1648	15	1452
1755	15	1977
1805	15	1204
2000	15	1848
2140	13	2500
2400	12	2392
2520	11	2811
2660	11	2571
2760	10	2681
3210	6	3904

At the beginning, we took elevation as the main factor which constrains the limit of tree species, and we used the same method to examine the relationship between the tree species elevation range and elevation midpoint. Then, linear regression was introduced to analyze the bioclimatic variables change with elevation. At last, in order to analyze the species-area relationship, we chose Generalized Climatic Model[42] to correlate the species elevation range and bioclimatic variables.

4 Results and analysis

A total of 780 tree species (excluding those whose distribution range is poorly described) is reported growing from 650 m up to the timber line in the Gaoligong Mountains (i.e. 4300 m), which comprises about 12% of the total flora of the Gaoligong Mountains. Tree species abundance increases up to 2000 m and decreases afterwards, showing a mid-elevation peak in abundance (see Figure 1). The correlation between elevational mid-point and elevational range showed that the species which occurred at lower and higher elevation have a narrower elevation range, while the species found in the middle elevation have a broader range (see Figure 2). As a

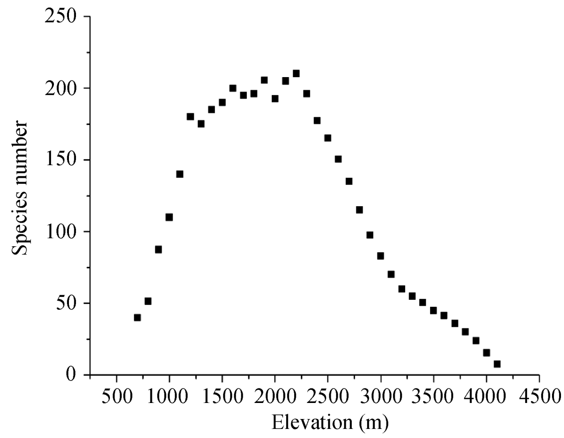

Figure 1 Relationship between tree species abundance and elevation in the Gaoligong Mountains.

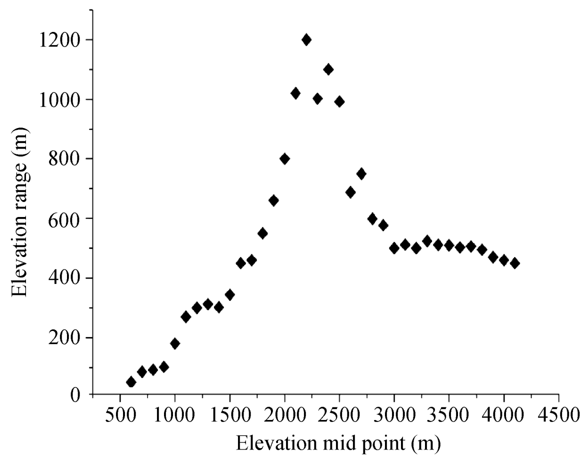

Figure 2 Relationship between the elevation range and elevation mid-point in the Gaoligong Mountains.

whole, most of the species found in the Gaoligong Mountains have a narrow elevation range.

Analysis of bioclimatic variables showed that the annual mean temperature decreased with elevation, being about 6℃ on the top of the mountain (see Figure 3), while at the same time the annual precipitation increased with elevation (see Figure 4), reaching the highest on the top of the mountains. The Gaoligong Mountains have unique precipitation features, with the value up to the highest on the top of the mountains, but actually these mountains are not the highest compared with other mountains in the same region. These unique factors may be due to the fact that the Gaoligong Mountains are near the Bay of Bengal, with warm air rising gradually over the ridge. As a combination of energy and water availability, actual evapotranspiration (AET) showed a hump-shaped relationship with the elevation increase, showing a peak at 1500 to 2000 m (see Figure 5).

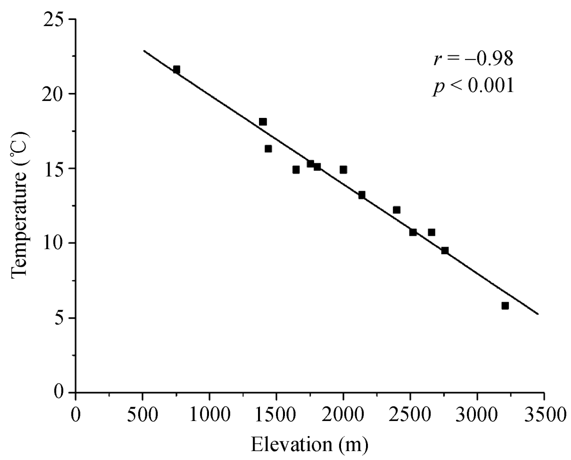

Figure 3 Mean annual temperature.

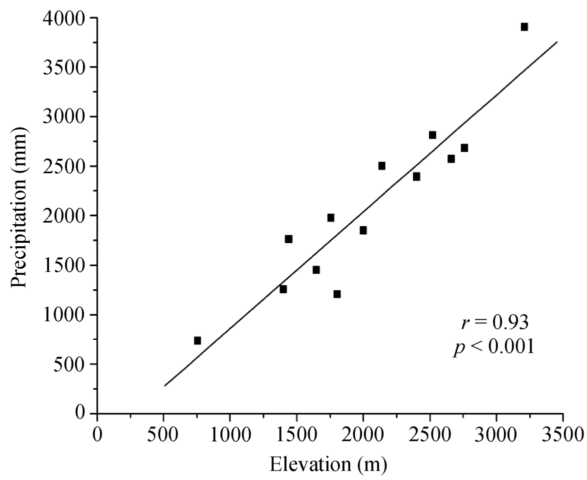

Figure 4 Annual precipitation.

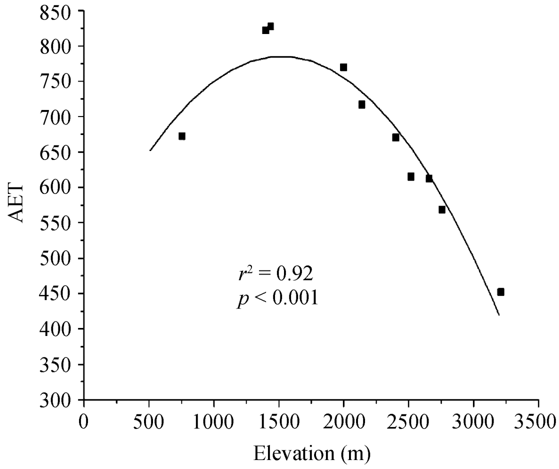

Figure 5 Actual evaporation.

The Generalized Climatic Model demonstrates that tree species abundance appears to be responding to two contrasting gradients (the temperature gradient and precipitation gradient) and one closely correlated gradient (the actual rate of evapo-transpiration) (Figure 6). In the final analysis, temperature and precipitation may not be directly correlated with tree species abundance, but when the species abundance is divided into two parts at the peak point, there is still a clear linear relationship between these factors and tree species abundance. It becomes warmer and wetter from the hot and dry valley up to the middle area of the mountains, which enables many tree species to develop, resulting in further diversification of species. But species abundance decreases when the temperature continues to decline, despite the precipitation increases at upper elevations of the mountains.

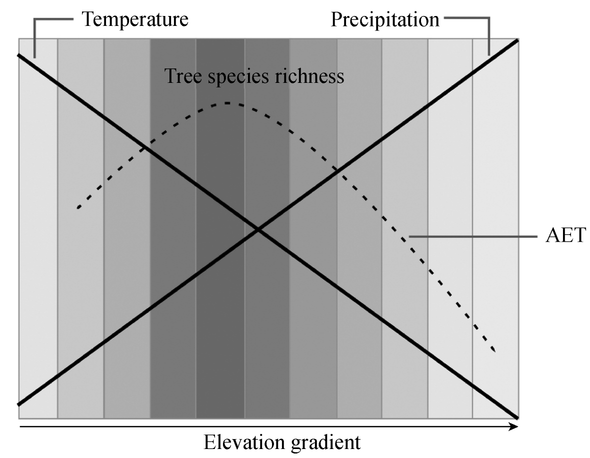

Figure 6 Generalized Climatic Model for elevational gradients in tree species abundance, incorporating a linearly decreasing temperature, a linearly increasing precipitation and a unimodal actual evapotranspiration. Tree species abundance is depicted in grey tones with darker tones indicating more species.

AET is closely correlated with species abundance, for AET is based on combination of energy and water availability, and can clearly reflect these bioclimatic variables.

5 Discussion

In the Gaoligong Mountains, tree species abundance tends to have higher values as elevation increases. This trend is not monotonic but unimodal, with the maximum values appearing in the middle part of the elevation gradient. Wang et al.[43] found the same pattern in the Gaoligong Mountains, and more recently other researchers also found this pattern[44,45]. But this pattern is not the same as that found in the theoretical studies by Steven and Lovett[20,46], in which species abundance exhibits a monotonic trend, decreasing with a rise in elevation. The relationship between tree species midpoint and elevation range demonstrates that the species found at lower or higher elevations have relatively narrow ranges, which is similar to the theoretical result by Colwell and Lee[47] that the species midpoint located in the middle geographical central (middle of the mountains) has a broader elevation range, while the species midpoint found in edges of the geographical range has narrower ranges. However, when compared with other places, for example the Himalaya area, tree species in the Gaoligong Mountains have narrower elevation ranges, probably because of the complexity of the Gaoligong Mountains flora. On account of their geological history, ecology and climatic diversity, the Gaoligong Mountains have been one of the refuges for some ancient floristic elements and experienced a quite strong diversification process. After the Laurasia and Gondwana combined, enabling exchange between East and West, the tropical elements gradually diminished, while temperate elements developed rapidly, all of which made the flora of Laurasia more complex. Furthermore, as the motherland of the Eastern Himalaya Flora, the Gaoligong Mountains are the key area of origin and development of the flora of Eastern Himalayas. The Gaoligong Mountains is also very rich in endemic plant species. 45.04% seeds plants are endemic, 1938 in total.

Climate is an obvious explanation for species distribution and abundance in many areas, especially for vascular plants[48]. Furthermore, climatic and energetic factors have also been suggested as simple widely available correlation with potential productivity for examining large-scale productivity patterns[49−51]. In the Gaoligong Mountains, temperature and precipitation were only weakly correlated with the pattern of species abundance along the whole gradient, but actual evapotranspiration shows a hump-shaped relationship with it. Because actual evapotranspiration is a combination of energy and water availability, the temperature and precipitation do contribute to the observed patterns of tree species in the Gaoligong Mountains. So it is likely that they operate in different ways on different parts of the gradient: linear decrease of temperature along the whole elevational gradient, therefore affecting negatively the increase of species abundance at low gradients, and *vice versa* positively at high elevations. This can be explained as follows: if, on the bottom half of the gradient, high precipitation and its potential benefits to tree species abundance are offset by high humidity and periodic dry times, whereas on the top half of the gradient tree species abundance will be limited by low temperature, especially frost events. That is why the Mediterranean Maquis and savanna vegetation[52] occurrs in the hot-dry valley zone. Taken together, temperature and precipitation may thus limit species abundance at both extremes of the gradient, but in different ways: at the lower end by a reduction of humidity through high temperature, and at the upper end by low temperature. As the combination of temperature and precipitation, AET can correlated well with the change in species abundance. We can conclude that it is the comprehensive effect of bioclimatic variables that decides patterns of species and their abundance, and that is why favorable climate conditions lead to the maximum productive energy available in the ecosystem.

Area is a crucial parameter determining biodiversity patterns[19,21,53] and can have both a direct and an indirect effect on species abundance. For example, it is possible that the variables of area and temperature can act in concert to decrease species abundance [54]. And some research did not find a significant linear species-area relationship for the total species number along the elevational gradient[55]. It was argued that the two-dimensional representation of area is not a good estimate of the actual available surface, which is better to estimated as volumes[22] or fractal dimensions[56]. Consequently, the factor of area was not employed in the analysis in this work.

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