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Latitudinal Diversity Gradients and Rapoport Effects in Chinese Endemic Woody Seed Plants

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Abstract: The distribution of plant species diversity has long been a major focus on biogeography. Yet, the universality of the popular Rapoport's rule remains controversial for endemic plants, as previous studies have focused more on broad-ranged species. Here, we collected data for 4418 endemic woody seed plant species across China, including trees, shrubs, and lianas, to explore the latitudinal patterns of species range size and richness, and test the relevant biogeographic law. The species range size distribution was examined for conformity with Rapoport's rule using four methods (i.e., Steven's, Pagel's, the mid-point, and the across-species method). Spatial patterns of species richness along latitudinal gradient were also investigated by parabolic regression. Results showed that species range size increased with latitude for all species as well as by trees, shrubs and lianas, especially assessed by Pagel's method. Species richness was highest at low latitude, where species range size was smallest, and decreased with increasing latitude. The species range size and richness of shrubs were maximum, followed by trees then lianas. These findings prove that Rapoport's rule is strongly supported by latitudinal patterns of species distribution in Chinese endemic woody seed plants.

Keywords: China; endemic woody seed plants; geographic diversity; Rapoport's rule; species range size; species richness

1. Introduction

Understanding biodiversity patterns has long been a key goal in the fields of biogeography and ecology [1–3]. Species range size and richness are two important biodiversity indicators [4–6]. Variation in either species range size or richness along geographical gradients can reflect the ecological adaptability, dispersal capability and evolutionary history of the tested species [7,8]. With the increasing availability of large-scale maps of species distributions, considerable progress has been made in describing continental and global patterns for species including animals, plants and microorganisms with broad geographic ranges [9–11]. However, the spatial patterns described by species with restricted ranges have received relatively little attention. The spatial shifts of plant distribution on latitudinal range caused by global climate change may increase the risk of extinction, especially for species with small ranges [12,13]. Information on the range sizes and richness of species with small ranges can thus provide insights into where to establish protected areas [14,15]. Therefore, more studies on the distributions of small-ranged species not only help to deepen our understanding of large spatial vegetation dynamics, but also contribute to biodiversity conservation [16].

Many researchers have attempted to explore the spatial patterns of species range size [15,17,18]. In a groundbreaking study, Rapoport (1975) [19] concluded that the range size of species was positively correlated with latitude. Stevens (1989) [17] dubbed this pattern as the latitudinal Rapoport's rule, which predicted that species range size increased with latitude. Later, an elevational Rapoport's rule was described, stating that species range size also became larger with increasing elevation [20]. Since the description of Rapoport's rule, many studies have tested Rapoport effects in different taxa for various geographical regions. However, most of these studies focus on animal ecosystems [21,22]. In addition, researches of plants are mostly about the elevational Rapoport's rule instead of latitudinal Rapoport's rule (see Table S1 in Supplementary material). Inconsistent with species range size, the distribution of species richness is negatively correlated to latitude. A biogeographic law is that species richness declines in response to increased latitude [23]. The Rapoport-rescue hypothesis has been advanced to explain this pattern of species richness [17,24]. The Rapoport-rescue hypothesis posits that, at low-latitudes where species ranges are small, sites receive a constant influx of migrants, inflating the number of species in low-latitudinal communities; this creates the latitudinal gradient in species richness.

Up to now, the universality of latitudinal Rapoport's rule is still controversial. There is a high degree of variability in support for the rule. For instance, Rohde (1996) [25] described latitudinal Rapoport's rule as a local phenomenon, occurring only at latitudes from 40–50°, and unable to explain latitudinal gradients in species diversity. However, misleading results may be obtained if the study area is limited and provides only partial coverage of species ranges [26]. Thus, studies at the macro-scale are particularly important for testing the universality of latitudinal Rapoport's rule. In addition, Rapoport effects of widespread species have been discussed in a large number of studies, especially in animal taxa [27,28]. However, there is a lack of verification of endemic plant species. The geographical distribution of endemic plants is very limited. Many endemic plants distribute in narrow ranges such as a specific geographic location, alpine, valley, etc. [29]. If the distribution of endemic plants follows latitudinal Rapoport's rule, it will provide supplementary evidence in small populations.

China extends across five climatic zones (i.e., tropical, subtropical, warm temperate, middle temperate and cold temperate) and has abundant natural resources and floral diversity [30]. These diverse ecosystems play an important role in conserving global biodiversity and make China immensely suitable for analyzing macro-scale patterns of species range size and richness [31]. Flora in China is also highly endemic [32]. Exploring the distributional pattern of these rare and endangered species is urgent for biodiversity protection. So far, no studies have explored Rapoport effects in endemic woody seed plants in China. In this study, we focus on exploring geographical patterns of endemic species range size and richness along the latitudinal gradient. We hypothesize that: (1) the pattern of species range size of Chinese endemic woody seed plants follows the latitudinal Rapoport's rule; and (2) the pattern of species richness of endemic plants conforms to the biogeographic law that species richness is negatively correlated with latitude.

2. Materials and Methods

2.1. Species Range Size and Richness of Chinese Endemic Woody Seed Plants

Distribution data of plant species were extracted from the Chinese Endemic Seed Plants Distribution Database [29]. The database was compiled from vast document resources including monographs, published articles, checklists, inventory reports, atlases of flora of China, as well as a great many specimens (see Appendix SI in Supplementary material for the lists of references and herbaria). The growth forms of species were unequivocally differentiated by the taxonomic standards as outlined in *Flora Reipublicae Popularis Sinicae* and *Flora of China* (http://www.iplant.cn/frps). For some species in question, we contacted the local taxonomist for further confirmation. It should be noted that bamboo species and subspecies were excluded from the species list. In conclusion, there were 4418 species of Chinese endemic woody seed plants, belonging to 131 families and 557 genera and including 1407 trees, 2346 shrubs and 665 lianas in this study.

Given that the location records of species were georeferenced to the spatial unit of county level in the database, we used county as the basic analysis unit. The county is a relative stable administrative unit in the history of China [15]. There are 2377 counties with areas ranging from 22.4 to 208,134 km^2, of which 2215 are less than 10,000 km^2 [33]. Species location was taken as the latitude and longitude of the centroid of relevant county. For all studied species, the latitude ranged from 18° to 52° N. The study area was divided into 35 latitudinal bands; each latitudinal band spanned 1° of latitude. The species range size was estimated as the difference between the maximum and minimum latitude at which that species occurred. The total number of species was tabulated in each latitudinal band to determine species richness. Both species range size and richness were calculated for all species, and separately for the trees, shrubs and lianas.

2.2. Data Analysis

Far too often, just one method is being used in similar biodiversity or macro-ecology papers [21], and the results may be contingent upon the selected method. Therefore, four mainstream algorithms were used to test for the Rapoport effect on species range size, including Steven's method [17], Pagel's method [34], the mid-point method [35] and the across-species method [36].

The first three methods examined the relationship between the mean species range size and the midpoint of each latitudinal band (1° of latitude). The definition of the mean species range size varied across these three methods. Steven's method defined mean species range size as the average of all species that occurred in each latitudinal band. Pagel's method quantified the average species range size of all species whose upper distribution limit fell within a given latitudinal band. The mid-point method calculated the average species range size of all species whose mid-point fell within a given latitudinal band. In the across-species method, scatter plot was made with latitudinal range size and mid-point of each independent species as coordinates. The existence of the Rapoport effect was tested according to the slope of the fitted linear model.

Similar to Stevens (1992) [20] and Bernhard (2006) [27], linear regression was used to examine the relationship between species range size and the midpoint of each latitudinal band. However, our data showed the fitting effect of parabolic regression was a little better than that of linear regression especially in analysis of mid-point method. We subsequently also used parabolic regression to test relationships between species range size and latitude. We assessed the Akaike information criterion (AIC) values from both linear regression and parabolic regression and found that AIC values were lower from parabolic regressions than linear regressions in all cases except when species range size was quantified by Pagel's method, with which parabolic and linear regressions yielded similar AIC values, i.e., the difference in AIC values was smaller than 2. We presented both linear and parabolic regressions.

Species richness for each latitudinal band was plotted against latitude, using parabolic regressions to test their relationships. We fitted parabolic regressions and generalized additive mixed models (GAMM) from the *mgcv* R package [37]. The GAMM provided the best fitting among the alternatives and was chosen for the final presentation. Statistical analyses were performed in R version 3.6.3 [38].

3. Results

Range size of all species of Chinese endemic woody seed plants increased linearly with latitude as determined by Pagel's method (Figure 1). Linear component was also statistically significant for

Steven's method. The scatter plot obtained from the across-species method showed a triangular pattern. The slop of the fitted linear model was above 0.5. Thus, Rapoport's rule was supported by observed latitudinal changes in the species range size of Chinese endemic woody seed plants. However, a unimodal pattern was evidently showed by parabolic regression in result of mid-point method. This may be due to the limitations of the mid-point method.

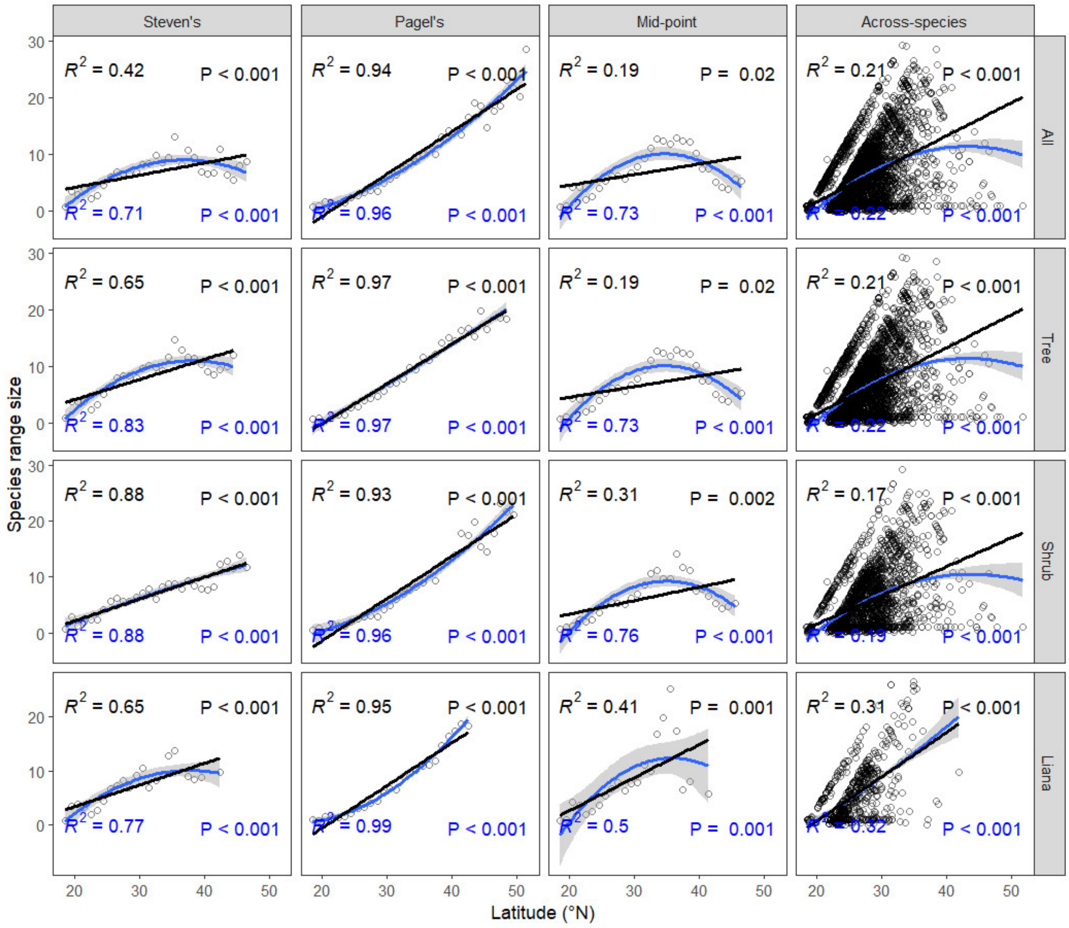

Figure 1. Species range size versus latitude for three growth forms of Chinese endemic woody seed plants, and their tests for Rapoport effects by Steven's method, Pagel's method, mid-point method, and across-species method. Black solid lines represented fitted relationships between species range size and latitude. They were all positive except in mid-point method. Blue lines and shades were fitted by parabolic regressions with 95% confidence intervals. Groups included all species, trees, shrubs, and lianas.

The relationships between species range size of Chinese endemic woody seed plants and latitude were qualitatively similar for the three growth forms including shrubs, trees, and lianas (Figure 1). The response of lianas was a little more sensitive to latitude (R^2 was larger). The latitudes occupied by shrubs ranged nearly from 18–50° N, a greater range than that occupied by trees (18–45° N) and lianas (18–40° N). Together, observed relationships between species range size and latitude of three growth forms were all significantly positive, further indicating that Rapoport effects generally exist in Chinese endemic woody seed plants.

Species richness of Chinese endemic woody seed plants decreased with latitude, rapidly from 18–35° N and then falling slowly thereafter (Figure 2). Only a handful of Chinese endemic woody seed plants occurred at high latitudes (up to 45° N). Among different growth forms, shrubs had the highest species number, particularly at low and mid latitudes, followed by trees and lianas. The response of shrubs was a little more sensitive to latitude (R^2 was larger).

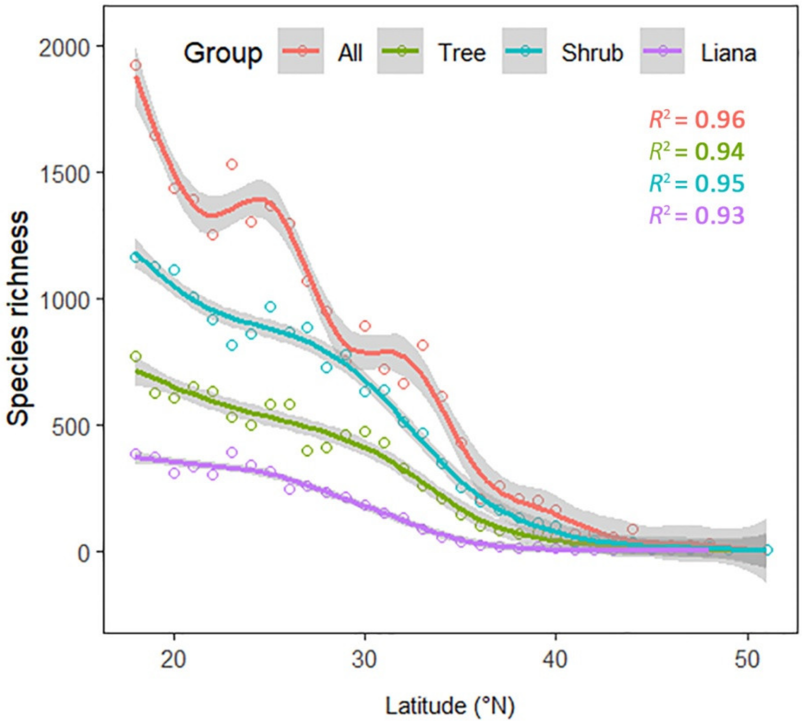

Figure 2. Species richness versus latitude for three growth forms of Chinese endemic woody seed plants. Lines and shades were fitted by parabolic regressions with 95% confidence intervals. All *p*-values < 0.01.

4. Discussion

Our results revealed that Chinese endemic woody seed plants provided support for the Rapoport's rule as species range size increased with latitude, in particular, assessed by Pagel's method. Pagel's method maybe more effective to obtain linear relationship between species range size and latitude. It does not mean that the Rapoport effect is overestimated, which is exactly the advantage of Pagel's method. Similar findings were also reported in other researches [34,39]. Although the results of mid-point method violate Rapoport's rule, it's reliable to conclude the existence of Rapoport effect in Chinese endemic woody seed plants by comprehensively evaluating the results of other three methods.

Many studies show that the latitudinal pattern of species range size generated by mid-point method is unimodal [27,39]. It may be due to the two limitations of mid-point method. One is the statistical non-normality and spatial autocorrelation in mean latitudinal range of species. There will be some statistical deviation caused by "statistical non-normal" when we use the mid-point method [40]. The mean latitudinal ranges of species calculated by mid-point method overlap with each other, which leads to non-independence of space on species range size [41]. This problem is avoided by using the across-species method which takes each species as a separate sample point. The other limitation of the mid-point method is boundary limit, i.e., mid-domain effect [39]. In the geographical area with obvious boundary, the closer to the south or north boundary, the mean latitudinal range of species is smaller. This constraint of distribution boundary on the species range size will result in the pseudo species distribution from non-ecological causes. The latitudinal range calculated by the mid-point method of endemic plants may be also affected by the mid-domain effect particularly due to their localized distribution, and then shows a unimodal pattern.

What causes the Rapoport effect in species range size? The climatic variability hypothesis has often been invoked to explain this effect in species distribution, because difference of species range size is a reflection of difference among species in climatic tolerance [28]. The tendency for climatic variability to increased latitude favors the evolution of broader climatic tolerances of species at high latitude. According to WorldClim Database (https://www.worldclim.org/), the variations in mean annual temperature and annual precipitation are larger in more northern as opposed to more southern counties in China. Thus, high-latitudinal endemic woody seed plants in China may be more tolerant and have larger range sizes than low-latitudinal species. Climatic changes in the Pleistocene may have acted to limit species range size at low latitudes. Several studies show that Rapoport effects may be explained as after-effects of Pleistocene glaciation [27,42]. The glacier expansion pushes many plant seeds out of high-latitudinal regions, expanding the latitudinal range of plant species [43]. In addition, according to the speciation-pressure hypothesis [42], speciation rates can also affect the distribution of species range sizes. If speciation is frequently allopatric and speciation rates are lower at high latitude, high-latitudinal species will have more living space and broader latitudinal range. Furthermore, the differential extinction of endemic species with restricted occurrences may have contributed to Rapoport effects, but extinction alone is not sufficient to explain observed patterns. Much remains to be learned about this topic.

Results showed that shrubs (18–50° N) tended to have larger latitudinal ranges than trees (18–45° N) and lianas (18–40° N), suggesting that shrubs may have broader environmental tolerances [28]. However, the linear fitting of lianas range size to latitude was stronger than shrubs and trees. It may be because lianas are woody climbers that rely on other plants for their survival, then the spatial distribution of lianas is largely dependent on the distribution of shrubs and trees [44]. Thus, the spatial niches of lianas are relatively narrower and more variable. In addition, lianas are very different from shrubs and trees in physiological traits, such as thin stems, wide vessels, deep root systems, and a relatively high leaf-area: basal-area ratio. It also leads to particular differences in survival needs of lianas in different environments compared to shrubs and trees [45]. Hence lianas have more sensitive spatial variation in response to latitude.

Given the current extent of biodiversity loss, prioritizing high-diversity regions is now more important for biodiversity conservation than ever [46,47]. Our results showed that the species richness of Chinese endemic woody seed plants was highest in the tropics and decreased gradually with increased latitude. This pattern conforms to the general biogeographic law [23]. We also found that species richness of endemic woody plants was higher and rapidly changing below 35° N, where should be taken seriously in study of biodiversity conservation. It is consistent with the finding that the 19 biodiversity conservation hotspots of Chinese endemic seed plants all locate to the south of 35° N in China [29]. The Rapoport-rescue hypothesis could explain the descending pattern in species richness along the latitudinal gradient. The increase of species richness towards the equator is often paralleled by a decrease in the mean latitudinal range of species [17,20]. As species at low-latitude have narrower ranges than high-latitudinal species, more small-ranged species, such as endemic plants, exist in low-latitudinal areas [15,29]. Furthermore, according to the Rapoport-rescue hypothesis, more individuals can disperse into surrounding unfavorable areas at low latitude, leading to higher species richness.

The species richness of shrubs was more than that of trees and lianas, further indicating that shrubs have better environmental adaptability. Therefore, shrubs are able to maintain stable populations better [48]. Additionally, the species richness of shrubs was very sensitive to changes in latitude. It suggests that environmental differentiation with latitude may be most conducive to the speciation of shrubs. This result is also confirmed by Xu et al., 2018, who found that the importance of climate change with latitude was greater for shrubs than trees and lianas [15]. We note that the Rapoport-rescue hypothesis alone is insufficient in explaining latitudinal gradients in species richness, because patterns of species richness are produced by a combination of historical and contemporary factors, including environmental heterogeneity and stochasticity [49]. Therefore, we suggest that more species from multiple taxa (e.g., herbs and ferns) and impact factors should be considered to evaluate the extinction risk of species in the future, notably in exploring relationships between plant species and climate change.

5. Conclusions

Using the distribution data of 4418 endemic woody seed plant species across China, we found support for Rapoport's rule from the latitudinal pattern of endemic species range sizes. Among different growth forms, shrubs of Chinese endemic woody seed plants had the broadest species range size and highest species richness, followed by trees and lianas. The relationship between species richness and latitude was negative. The reliability of this study is that we test the Rapoport effect in endemic plants by combining the results of four common methods. The main purpose of this study is to explore the distribution patterns of species range size and richness along latitudinal gradient. The specific formation mechanism of these patterns in endemic plants is still unknown. We have tried our best to discuss it. However, besides some theories mentioned above, there may be more possible reasons, e.g., human disturbance [50]. During the early period of New China, natural forests with more than 10 billion forest volumes were cut for society and economic construction. The natural forest area is account for only 7.59% of country's forest area. Therefore, we consider that disturbance may have an important role in the distribution of endemic plants in China. More works need to be done. We will further explore the clear causes of variations in species distribution on Chinese endemic plants in the future.

Supplementary Materials: The following are available online at www.mdpi.com/1999-4907/11/10/1029/s1. Table S1: The important researches about Rapoport's rule. Appendix SI: References and herbarium consulted to establish Chinese endemic seed plants species inventory and collect their distribution information.

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