Climatic niche divergence explains angiosperm diversification across clades in China

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Climatic niche divergence explains angiosperm diversification across clades in China

Short running title: Climate width and diversification in Chinese plants

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Abstract

Diversification rates are critically important for understanding patterns of species richness among clades. However, the effects of climatic niche width on plant diversification rates remain to be elucidated. Based on the phylogenetic, climatic, and distributional information of angiosperms in China, a total of 26,906 species from 182 families were included in this study. We aimed to test relationships between diversification rate and climatic niche width and climatic niche width related variables (including climatic niche divergence, climatic niche position, and geographic extent, climatic niche evolutionary rate) using phylogenetic methods. We found that climatic niche divergence had the largest unique contribution to the diversification rate, while the unique effects of climatic niche width, climatic niche position, geographic extent, and climatic niche evolutionary rate on the diversification rate were negligible. We also observed that the relationship between diversification rate and climatic niche divergence was significantly stronger than the null assumption (Artefactual relationship between diversification and clade-level climatic niche width via sampling more species). Our study supports the hypothesis that wider family climatic niche widths explain faster diversification rates through a higher climatic niche divergence rather than via higher geographic extent, higher climatic niche evolutionary rate or separated climatic niche position. Hence, the results provide a potential explanation for large-scale diversity patterns within families of plants.

Keywords: Angiosperms, diversification rate, climatic niche width, climatic niche divergence, geographic extent, climatic niche position

1 Introduction

A fundamental goal in evolutionary biology is to explain why some clades have higher species richness than others. In general, species richness among clades can be explained either by time (i.e., greater species richness accumulates over time) or diversification rate (i.e., higher diversification rate leads to higher species richness). The diversification rate is the rate of speciation minus the extinction rate (Ricklefs, 2007; Givnish, 2010). Previous studies have indicated that species richness unevenness among clades (i.e., families, phyla) was largely explained by diversification rates (Scholl & Wiens, 2016; Hernandez-Hernandez & Wiens, 2020). Therefore, it is essential to uncover the ecological and evolutionary processes that determine differences in diversification rates among clades to understand their richness patterns.

The climatic niche width is the set of climatic conditions where a species is able to maintain viable populations. It reflects the physiological tolerance of a species to climatic environments (Soberon, 2007; Anacker & Strauss, 2014). The relationship between climatic niche width and diversification rate has been studied based on two hypotheses that could potentially explain it. One is the niche divergence hypothesis, which suggests that a wider climatic niche width explains diversification by reducing the extinction rate (e.g., survival from climate change, Wiens, 2016), thus increasing the diversification rate of clades. A wider climatic niche width might also lead to higher rates of speciation because it would increase the likelihood of encountering ecological or geographical barriers (Darwin, 1859; Rosenzweig, 1995; Gaston, 2003). The second hypothesis is the niche conservatism hypothesis. In contrast to the divergence hypothesis, niche conservatism suggests that narrower climatic niches are associated with a higher diversification rate via allopatric speciation (Kozak & Wiens, 2007). For example, Baselga et al. (2011) indicated that species with overlapped climatic niches tend to have a higher diversification rate, potentially supporting the climatic niche conservatism mechanism.

Despite the aforementioned hypotheses, very few studies have directly explored the effect of climatic niche width on the diversification rate at a large scale. Among the few previous studies, the results have not been consistent across different biological groups. For example, Gómez-Rodríguez et al. (2015) and Castro-Insua et al. (2018) found a positive relationship between climatic niche width and diversification rate in both amphibian and mammalian families. In contrast, Rolland and Salamin (2016) found that species with narrower climatic niche widths tended to have higher diversification rates among amphibians, mammals, and birds. However, to our knowledge, no studies have tested how climatic niche width affects the diversification rate among clades in plants at a large scale. Liu et al. (2020) estimated the climatic niche width for both plants and animals, however, they did not explore the effects of climatic niche width on the diversification rate.

There may also be more indirect relationships between climatic niche width and diversification rates of clades. For example, a wider climatic niche might be accompanied by larger geographic ranges, which can lead to a higher diversification rate. Moreover, a higher evolutionary rate of climatic variables might expand the climatic niche width, then accelerate the diversification rate (Kozak and Wiens, 2010, Castro-Insua et al., 2018). Alternatively, species in different niche positions may have different climatic niche widths, leading to different diversification rates. For example, some previous studies indicated that species in tropical regions have a lower diversification rate than in temperate zones (Harvey et al., 2020; Igea et al., 2020; Tietje et al., 2022). Generally, the niche width for temperature-related climatic variables may be narrower in the tropical zone than that in the temperate zone (Janzen, 1967; Ghalambor et al., 2016), whereas the niche width for precipitation-related climatic variables can be wider in the tropical zone (Quintero & Wiens, 2013).

Here, we used a nearly complete dataset of Chinese angiosperms to test whether climatic niche divergence or climatic niche conservatism better explains species diversification among plant clades. Using these (and similar) resources, several studies have assessed the patterns of phylogenetic structure in Chinese plant assemblages at the regional scale (Qian et al., 2019; Gheyret et al., 2020). In addition, Su et al. (2020) reported that different climatic niche position predicts species richness patterns for tropical and temperate families. However, the mechanism by which climatic niche width affects the diversification rate and subsequently leads to species richness unevenness among plant clades remains unclear.

In this study, we estimated the climatic niche width among the 182 families and 26,906 species of angiosperms in China. We defined climatic niche divergence as the residuals of the relationship between family climatic niche width and mean species climatic niche width as described by Gómez-Rodríguez et al. (2015). We also estimated the climatic niche evolution rate, geographic extent (area), and diversification rate of the families to test the relationship between these variables across families using phylogenetic methods. Specifically, we aimed to address the following seven hypotheses (Table 1), with one hypothesis related to niche conservatism (H1) and five hypotheses related to niche divergence (H2–H6), as follows: a narrower climatic niche width predicts the diversification rate (H1); a wider climatic niche width explains the diversification rate via increasing climatic niche divergence (H2), increasing the climatic niche evolution rate (H3), decreasing the extinction rate (H4), increasing the geographic extent (H5), and changing climatic niche position (the separated geographic effects) (H6). Because clades with more species tend to have wider climatic niche widths, this may lead to a higher diversification rate. We also tested a null hypothesis, that is, (H0) an artifactual relationship between diversification rate and clade-level climatic niche width occurs via sampling more species.

2 Materials and methods

2.1 Phylogenetic tree and climatic data

The phylogenetic tree in our study was based on Lu et al. (2018). The tree was constructed using the sequences of five genes (*atpB*, *matK*, *ndhF*, *rbcL*, and *matR*). They first generated a dated phylogeny including 5,864 species native to China, representing 2,665 genera and 273 families. With this tree as the backbone, a species-level tree including 28,076 Chinese angiosperm species was generated by inserting species that were not sampled in our generic tree within the genera to which they belong, using the package "S.PhyloMaker" (Qian & Jin, 2016) in R software. After matching the phylogenetic tree with distribution information, there were 26,977 species with 235 families, including 96 % and 86 % of the angiosperm species and families, respectively, in China (Lu et al., 2018). At least three species in each family were needed to run the Ornstein–Uhlenbeck (OU) model in the following analysis. Finally, 182 families and 26,906 species were used for the analysis in our study, encompassing approximately 10 % of the plant species worldwide.

We performed most of the analyses on a consensus of these 1,000 trees. We used a maximum-clade credibility tree based on the mean heights of these trees using TREEANNOTATOR version 1.10 (Bouckaert et al., 2014). The tree was fully resolved (no polytomies). All of the 182 families were monophyletic.

Distributional and climatic data were generated in Lu et al. (2018). They divided the study area in China into 100 × 100 km (i.e., 10,000 km^2) grid cells. The area of the grid cells on the border with less than 5,000 km^2 were excluded. The species distribution information in each grid cell were collected from all published national and provincial floras as well as some local flora, checklists, and herbarium records. There were more than 1,400,000 records of distribution information in total. Only the mean annual temperature (BIO1) and mean annual precipitation (BIO12) were included in their dataset. We also needed the maximum temperature of the warmest month (BIO5), minimum temperature of the coldest month (BIO6), precipitation of the wettest quarter (BIO16), and precipitation of the driest quarter (BIO17) to estimate the climatic niche width and for the other analyses. Therefore, we extracted the climate data from maps of WorldClim version 1.4 (http://www.worldclim.org/), with a spatial resolution of 10 min (approximately 340 km^2). To match the distribution information, we estimated these climatic variables in each grid cell (10 000 km^2) using ArcGIS 10.1 (http://www.esri.com/) based on these maps. In summary, the species richness and niche position (BIO1, BIO5, BIO6, BIO12, BIO16, and BIO17) in each grid cell were included. The geographic extent (area) of each family was also estimated based on the distribution information. We used these data in our study.

2.2 Climatic niche widths

We estimated the family climatic niche width and the mean species climatic niche width in our study according to the approaches of Gómez-Rodríguez et al. (2015). For family climatic niche width, all species in the family were merged to form a single distribution area. The range of climatic data of each family was estimated as Rg = max (var)–min (var). Then, the climatic niche width for a given family i in a dataset with j families was estimated as: $StRg_i = [Rg_i - \min(Rg_1:Rg_j)]/[\max(Rg_1:Rg_j) - \min(Rg_1:Rg_j)]$. This yields a value between 0 and 1. The temperature and precipitation niche width were based on BIO1, BIO5, BIO6, BIO12, BIO16, and BIO17, respectively. Species climatic niche width was estimated based on the same protocol as the family climatic niche width. The mean species climatic niche width was then the average climatic niche width of all species within the family. Climatic niche divergence is the residuals of the relationship between family climatic niche width and mean species climatic niche width as described by Gómez-Rodríguez et al. (2015), which reflects a non-overlap of climatic niches within families (Fig. S1). The overall climatic niche width was the temperature niche width multiplied by the precipitation niche width. The niche position was described in terms of BIO1, BIO5, BIO6, BIO12, BIO16, and BIO17 across the geographic range of the family. All niche parameters are explained in Table 2. Using the abovementioned approaches, we also determined correlations between diversification rate, climatic niche width, and niche divergence across 49 orders.

2.3 Diversification rate and niche evolutionary rate

The diversification rate of each family was estimated using a method of moment estimator (Magallón & Sanderson, 2001). The species richness of China and the stem age of each family were used. Stem ages were used because crown ages would require more extensive sampling of the species in each family, and monotypic families could not be incorporated (Meyer & Wiens, 2018). To make our results more robust, we selected three relative extinction rates (ε): two extremes (ε = 0, 0.9) and one median (ε = 0.5). In an alternative analysis, we also used the total species richness of each family to estimate the diversification rate. We used the R package "TAXONLOOKUP" version 1.1.5 (Pennell et al., 2016) to obtain the total species richness in each family. The data source used for this package was based on Plant List version 1.1 (2013). Some endemic Chinese species were included in the Flora of China (Wu et al., 2013), but, at the time of the study, have not been accepted by The Plant List. Therefore, we also included "unresolved" species (i.e., not yet assigned a status of "Accepted" or "Synonym). We used both accepted and unresolved species to represent the global species richness of each family. The species richness, stem age and diversification rate were in Supplementary Data 1.

Many other approaches are available to study diversification. However, most other methods would be impractical here because they need detailed species-level phylogenies within each clade. This level of detail is lacking for many species in our study, as described above. Furthermore, we aimed to explain differences in richness and diversification rates among families, not shifts in diversification rates over time. Therefore, the method of moment estimator with stem age is the most appropriate approach for our study.

The evolutionary rates of the BIO1 and BIO12 were estimated to represent the climatic niche evolution rate. We focused on these two variables because they should reflect the most important aspects of the climatic distribution of the species (e.g., BIO1: tropical vs. temperate; BIO12: arid vs. mesic), and more so than short-term, extreme values (BIO5, BIO6, BIO16, BIO17). We first used the fitContinuous function in the package "geiger" version 2.0.7 (Harmon et al., 2008; Pennell et al., 2014) to fit four evolutionary models, namely, the Brownian motion (BM), Ornstein-–Uhlenbeck (OU), lambda (LA), and white noise (WN). Then, the best-fitting model was selected based on the lowest Akaike information criterion (AIC). The variance (σ^2) in the best model was used as the evolutionary rate of the variables for each family.

2.4 Statistical analysis

The best-fit model for the diversification rate of each family was the LA model (Table S1). Therefore, phylogenetic generalized least-squares regression (PGLS) (Martins & Hansen, 1997) in the R package "caper" version 1.0.1 (Orme, 2013) was used to analyze the relationship between diversification rate and niche climatic variables. Following standard practice, lambda values (phylogenetic signal) were estimated by maximum likelihood to transform the branch lengths, with kappa and delta values both set to 1 (Pagel, 1999; Orme, 2013). The contribution of individual and combined variables (niche width, niche divergence, niche position, and geographic extent) was estimated using the function varpart in R package "vegan" version 2.5-6 (Oksanen et al., 2019). Given that the niche position consists of six variables, we used a stepwise procedure to select the niche position variables. We found that the diversification rate ~ BIO5+BIO12+BIO16 was the best model in the stepwise analysis; then, we selected these three climatic variables to represent the niche position in the analysis.

To account for the effect of species richness on the relationship between the diversification rate and climatic niche width, we created the same species richness for each of the families by randomly sampling from the whole species pool. Null niche width was estimated from a randomly sampled species pool of richness equivalent to real families. We randomly sampled 1,000 times from the 182 null families and compared the distribution of the coefficient of determination (r^2) of the aforementioned PGLS with the observed r^2 in the original families. We used the function "quantile" in the R base package to estimate the values of 1000 r^2 at a 95 % confidence interval. If the observed r^2 was in the 95 % confidence interval of the 1,000 r^2 values, we assumed the relationship found between the diversification rate and niche variables was because families with more species span more climatic conditions. Otherwise, we assumed that the niche variables contributed to the diversification rate. The same approaches were also used for species at the order level.

3 Results

We found a strong and positive relationship between the diversification rate and family climatic niche width for precipitation (r^2 = 0.389–0.437, $P < 0.001$), temperature (r^2 = 0.360–0.374, $P < 0.001$), and the overall of both (r^2 = 0.413–0.468, $P < 0.001$). While a negatively weak or non-significant relationship was observed between the diversification rate and mean species climatic niche width for precipitation ($r^2 \leq 0.001$, P = 0.609–0.794), temperature (r^2 = 0.031–0.045, P< 0.004–0.018), and the overall (r^2 = 0.004–0.011, P = 0.160–0.420). This provided a stronger relationship between the diversification rate and climatic niche divergence (residuals of family climatic niche width versus mean species climatic niche width) for precipitation (r^2 = 0.512–0.576, P < 0.001), temperature (r^2 = 0.482–0.503, P < 0.001), and the overall (r^2 = 0.480–0.558, P < 0.001) (Fig. 1, Table S2). Therefore, the diversification rate was mainly explained by climatic niche divergence (H2) rather than climatic niche conservatism (H1). Neither the evolutionary rate of mean annual temperature nor precipitation showed a significant relationship with diversification rate, family climatic niche width, and mean species climatic niche width (Fig. S2), rejecting the hypothesis that the diversification rate was explained by climatic niche divergence via increased climatic niche evolution rate (H3). The weak or negative relationships between diversification rate and mean species climatic niche width as found in our study suggested that, wider climatic niches increasing diversification via reduced extinction rates (H4) was rejected, because the validity of this hypothesis depends on a strong relationship between diversification rate and mean species niche width (Table 1). Similar results were obtained when we divided the species into 49 orders (Fig. S3).

To evaluate whether the effects of climatic niche width on diversification rate are via the geographic extent (H5) or niche position (H6), we first built PGLS models for the two hypotheses. A significant positive relationship was observed between the diversification rate and geographic extent (r^2 = 0.393–0.471, P < 0.001) (Fig. 2, Table S2). The relationship between the diversification rate and climatic niche position varied. We found a significantly positive relationship between the diversification rate and BIO5 (r^2 = 0.272–0.320, $P < 0.001$) and BIO16 (r^2 = 0.009–0.110, $P < 0.001$), while a significantly negative relationship was observed between the diversification rate and BIO1 (r^2 = 0.251–0.310, $P < 0.001$), BIO6 (r^2 = 0.271–0.292, $P < 0.001$), BIO12 (r^2 = 0.272–0.324, $P < 0.001$), and BIO17 (r^2 = 0.219–0.231, $P < 0.001$) (Fig. 3, Table S2). The climatic niche position, family climatic niche width, climatic niche divergence, and geographic extent showed an important partition in explaining the diversification rates (Table S2, S3). These variables were then used to determine their unique contribution to diversification rates. The explanation from climatic niche position (0.3 %), geographic extent (1 %), and climatic niche width (0.5 %) were negligible. Climatic niche divergence was the variable with the largest unique contribution (11.0 %). Most of the variances were shared among climatic niche divergence, climatic niche width, geographic extent, and climatic niche position (38.2 %) (Fig. 4). Therefore, the unique effects of climatic niche width on the diversification rate via geographic extent (H5) or climatic niche position (H6) were limited.

In the null models, we found that the observed relationship between diversification rate and family climatic niche width, as well as the mean species climatic width of precipitation, was generally stronger than that of the null model (Fig. S4B, E). However, the relationship between diversification rate and family climatic niche width, as well as the mean species climatic width of temperature (Fig. S4A, D) and overall climatic niche width (Fig. S4C, F) were not significantly different from that of the null model. For the climatic niche divergence, the relationship between diversification rate and the climatic niche divergence of temperature and precipitation and the overall climatic niche divergence were all more robust than that of the null model (Fig. S4G, I, H). Overall, the precipitation niche width (including family niche width and mean species niche width) was important for accelerating the diversification rate, while climatic niche divergence of both temperature and precipitation were important in accelerating the diversification rate for angiosperms of China. Therefore, the hypothesis that an artifactual relationship between diversification and clade-level climatic niche width would occur via sampling more species (H0) was rejected. We also found that the null model hypothesis (H0) was rejected at the order level (Fig. S5).

4 Discussion

Few studies have investigated the relationship between climatic niche width and species diversification rates, except for several studies in animals (Gómez-Rodríguez et al., 2015; Rolland & Salamin, 2016; Castro-Insua et al., 2018). Here, we explored the relationship between the climatic niche width and the diversification rate of plants in China at a large scale (including 26,906 species and 182 families) for the first time. Our results suggest that climatic niche divergence (H2) rather than climatic niche conservatism (H1) explains the diversification rate in angiosperm clades of China. Moreover, we suggest that a wider family climatic niche width explains a faster diversification rate through higher climatic niche divergence (H2), rather than increasing the climatic niche evolution rate (H3), decreasing the extinction rate (H4), increasing the geographic extent (H5), or a separated climatic niche position (H6). The relationship between the diversification rate and family niche width for precipitation and niche divergence for temperature was significantly higher than that of the null assumptions, demonstrating that our findings were supported, rather than an artifactual relationship between diversification and clade-level niche width occurring as a result of sampling of more species (H0).

4.1 Niche divergence and niche conservatism mechanisms explain species diversification

Our results have two important implications. First, we found that wider climatic niche width predicts a higher diversification rate via climatic niche divergence, potentially leading to species unevenness among families of Chinese angiosperms (Table S4). Moreover, our results were consistent with amphibian (Gómez-Rodríguez et al., 2015) and large-scale mammal (Castro-Insua et al., 2018) studies. Therefore, the results suggest that plant diversification may exhibit trends similar to animals. This consistency suggests why animals and plants follow similar richness patterns, biogeographic regions, biomes, and biodiversity hotspots on a global scale (Liu et al., 2020). There are two potential explanations as to why climatic niche divergence predicts the diversification rate of angiosperms in China. On the one hand, a higher climatic niche divergence would decrease the overlap of species climatic niches, thereby reducing competition within families and creating additional opportunities for speciation (Kozak & Wiens, 2010a). Furthermore, a higher climatic niche divergence would cause higher spatial isolation and thus decrease the connectivity between these species, reduce gene flow (Birand et al., 2010; Wiens et al., 2012) and lead to the emergence of reproductive barriers, and consequently accelerate the diversification rate.

The niche conservatism hypothesis states that species with shared evolutionary history (i.e., species in an evolutionary clade) tend to tolerate similar environmental conditions and thus exhibit similar geographic or climatic distributions (Latham & Ricklefs, 1993; Wiens & Donoghue, 2004). This hypothesis was supported by previous studies that explain the species assemblages in China (Qian et al., 2019), Eastern Asia (Su et al., 2020), and the tropical and subtropical regions on a global scale (Cerezer et al., 2020). However, these studies tend to explain species unevenness at the regional scale rather than among clades in our study. Notably, the niche conservatism hypothesis postulated in previous studies generally found that in tropical and subtropical regions, species originated earlier and more abundantly, although they have low diversification rates (Harvey et al., 2020; Igea et al. 2020; Tietje et al. 2022). Similarly, we also showed that a low diversification rate was associated with high species richness patterns at a regional scale (Fig. S6). However, our study emphasized that the diversification rate was explained by climatic niche divergence, potentially leading to variable species unevenness among clades (Table S4). Several previous studies in animals also indicated that species richness generally accumulated through climatic niche conservatism at the regional level, while the diversification rate among clades was more commonly explained by climatic niche divergence (Kozak & Wiens, 2010a, b; Wiens et al., 2011; Kozak & Wiens, 2012).

4.2 Effect of climatic niche evolution rate on diversification rate via change niche divergence

Our results do not support hypothesis H3 that the niche evolution rate increases climatic niche width and climatic niche divergence. In general, a rapid change in the climatic niche rate would allow species to be distributed into new environments (increase climatic niche width), and thus decrease the climatic niche overlap (increase climatic niche divergence) among species and lead to an increase in the diversification rate (Kozak and Wiens, 2010, Liu et al. 2020). The discrepancy between our results and previous studies was probably because species with higher climatic niche evolution rates can explore new niches, while some species might be extinct in their original habitats. This would not increase the climatic niche width and climatic niche divergence of the families and, therefore, would not increase the diversification rate of the families. This concept needs to be tested in future studies.

4.3 Effect of climatic niche width on diversification rate via change climatic niche evolution rate

Our results reject the hypothesis that a wider mean species climatic niche width is associated with the diversification rate by decreasing the extinction rate (H4), which is consistent with the findings of Gómez-Rodríguez et al. (2015) and Castro-Insua et al. (2018). In contrast, Rolland and Salamin (2016) found lower extinction rates in birds, mammals, and amphibians with narrower climatic niches. Another study found that specialist species grown in narrower climatic niche ranges have a higher risk of extinction rates (Harris & Pimm, 2008). This discrepancy may be caused by human-related factors (such as excessive deforestation) and anthropogenic climate change, implying that the extinction of some groups may not have been related to their natural evolutionary history.

4.4 Effect of geographic extent and niche position on diversification rate

The unique contribution of the geographic extent and niche position was negligible. Thus, the hypothesis that wider climatic niches facilitate faster diversification by allowing greater range expansion (H5) or changing the niche position (H6) was also limited. These results are consistent with those of Gómez-Rodríguez et al. (2015) and Castro-Insua et al. (2018). However, we observed a significant negative relationship between the diversification rate and BIO1 (annual mean temperature) and BIO12 (annual precipitation). This was not observed in the animals studied by Gómez-Rodríguez et al. (2015) and Castro-Insua et al. (2018). However, Igea and Tanentzap (2020a) and Jetz et al. (2012) found that the diversification rate slows down for angiosperms and birds in tropical and subtropical regions, respectively. Early studies have hypothesized "density-dependent" effects on diversification, where the rates of species accumulation within a clade would slow down over time due to increasing species density (Phillimore & Price, 2008; Rabosky & Lovette, 2008; Rabosky, 2009). This hypothesis could potentially explain the diversification patterns in China as regions with high precipitation and temperature in China tend to have more species. These species originated earlier than those distributed in cold and dry regions (Lu et al., 2018), which would slow down the diversification rate in warm and wet regions because of their high species density. A positive relationship between diversification rate and BIO5, and a negative relationship between diversification rate and BIO6 and BIO17 were found, indicating that tolerance to extreme climatic habitats (such as hot, cold, and dry environments) facilitates the diversification of plants. The positive relationship between the diversification rate and BIO16 was unexpected, probably because regions with high temperatures usually tend to have high precipitation in China.

4.5 Potential sources of error

We acknowledge that some important sources of error may have impacted our results. First, our analyses were based primarily on species occurring in China, whereas most families and genera are more broadly distributed. Actually, we also estimated the diversification rate in each family using species found across the world. We found niche variables (estimated using distribution information of China) had a weaker relationship with a diversification rate estimated using global species richness (Table S3) than that of using Chinese species richness (Table S2). Therefore, it is reasonable to use the climatic niches of China to explain species diversification among clades in this region. However, this currently cannot be generalized to the rest of the world. Indeed, it remains to be seen whether the patterns reported here hold true when global sampling is used.

Second, because of the relatively low resolution, climatic heterogeneity within cells was high, especially in the mountainous regions. While it is well known that local finer-scale niches can affect the diversification of lineages (Hutter et al. 2013), we did not consider the micro-environment of each species. It is likely that doing so would result in deviations in niche width. Future studies should test the same set of hypotheses at smaller spatial scales (e.g. 1-km grid cells).

Conclusion

In summary, we found climatic niche divergence explains the diversification rate among angiosperm families in China. These results are important for explaining large-scale patterns of species unevenness among clades in plants. Since our results for plants are consistent with that of animals observed in previous studies (such as birds, mammals, and amphibians; Gómez-Rodríguez et al., 2015; Castro-Insua et al., 2018), they could also explain why animals and plants follow similar richness patterns, biogeographic regions, biomes, and biodiversity hotspots.

Compliance and ethics The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Figure legends

Table 1 Potential hypothesis to explain diversification rate and climatic niche width based on Gómez-Rodríguez et al. (2015).

Hypothesis	Predictions
H1: Narrower niches facilitate diversification rate via niche conservatism.	(1) Strong and positive relationship between family climatic niche width and mean species climatic niche width; (2) Negative relationship between diversification rate and family climatic niche width; (3) Negative relationship between diversification rate and mean species climatic niche width.
H2: Wider climatic niche widths facilitate diversification rate via climatic niche divergence.	(1) No or weak relationship between family climatic niche width and mean species climatic niche width; (2) No relationship between diversification rate and mean species climatic niche width; (3) Strong and positive relationship between diversification rate and climatic niche divergence (residuals of relationship between family climatic niche width and mean species climatic niche width).
H3: Wider climatic niche widths facilitate diversification rate via increased climatic niche evolution rate.	(1) Strong and positive relationship between diversification rate and climatic niche evolution rate; (2) Positive relationship between climatic niche width and climatic niche evolution rate; (3) Positive relationship between climatic niche divergence and climatic niche evolution rate.
H4: Wider climatic	(1) Positive relationship between family and

niche width could facilitate diversification rate via decreased extinction rate.	mean species climatic niche width; (2) Strong and positive relationship between diversification rate and mean species climatic niche width and family climatic niche width; (3) No relationship between diversification rate and climatic niche divergence.
H5: Wider climatic niche width could facilitate diversification rate via geographic extent.	Strong and positive relationship between the diversification rate and geographic area of clade. This relationship was stronger than the relationship between diversification rate and climatic niche width.
H6: Wider climatic niche widths could facilitate diversification rate via separated geographic effects (niche position).	Strong and positive relationship between diversification rate and climatic niche position. This relationship was stronger than relationship between diversification rate and climatic niche width.
H0: Relationship between diversification rate and clad-level climatic niche width via sampling more species.	(1) Strong and positive relationship between diversification rate and species richness among families; (2) Positive relationship between family and mean species climatic niche width; (3) Positive relationship between diversification rate and family and mean species climatic niche width; (4) The relationship (r2) in (3) were stronger than results of randomly selected species in each family.

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Table 2 Overview of the niche parameters in our study.

Niche variables	Explanation of the niche variables
Family climatic niche width	Climatic niche width of the family
Mean species climatic niche width	Mean value of climatic niche width for all the species within the family
Climatic niche divergence	Residuals of family climatic niche width versus mean species climatic niche width
Climatic niche position	Climate variables (including BIO1, BIO5, BIO6, BIO12, BIO16, BIO17)
Climatic niche evolution rate	Evolutionary rate of BIO1 and BIO12
Geographic extent	Area of species distribution of the family

Fig. 1 Relationship between diversification rate and family climatic niche width (A, B, C), mean species climatic niche width (D, E, F) and climatic niche divergence (G, H, I) for MAP, MAT and overall respectively. Darker colors indicate greater overlap of data points. Diversification rates were estimated based on stem-group ages of family with ε=0.5, including only species in China. Use of alternative values of ε (0, 0.9) and global richness of families yields similar results (Table S2, S3).

Fig. 2 Relationship between family climatic niche width and mean species climatic niche width (A, B, C). A significant relationship between diversification rate and geographic extent (D). Darker colors indicate greater overlap of data points. Diversification rates were estimated based on stem-group ages of families with ε=0.5, including only species in China. Use of alternative values of ε (0, 0.9) and global richness of families yields similar results (Table S2, S3). Geographic extent was the distribution area of each family.

Fig. 3 Relationship between diversification rate and climatic niche position. BIO1, BIO5, BIO6 and BIO12, BIO16, BIO17 represent annual mean temperature, maximum temperature of the warmest month, minimum temperature of the coldest month, annual precipitation, precipitation of the wettest quarter and precipitation of the driest quarter respectively. Darker colors indicate greater overlap of data points. Diversification rates were estimated based on stem-group ages of families with ε=0.5, including only species in China. Use of alternative values of ε (0, 0.9) and global richness of families yields similar results (Table S2, S3).

Fig. 4 Venn diagram showing the results of variance partitioning on a full model of diversification rate with climatic niche position (NP), climatic niche width (NW), climatic niche divergence (ND), geographic extent (GE) as explanatory variables. Results are shown as percentage of explained variance.

Fig. S1 Relationship between family climatic niche width, mean species climatic niche width and climatic niche divergence. Different color of the curves represent species niche, R1, R2 and R3 are niche divergence.

Fig. S2 Relationship between climatic niche evolution rate and diversification rate (A, B), family climatic niche width (C, D), mean species climatic niche width (E, F), climatic niche divergence (G, H) for both temperature and precipitation. Darker colors indicate greater overlap of data points.

Fig. S3 Relationship between diversification rate and order climatic niche width (A, B), mean species climatic niche width (C, D) and climatic niche divergence (E, F) for MAP, MAT respectively. Darker colors indicate greater overlap of data points. Diversification rates were estimated based on stem-group ages of order with ε=0.5, including only species in China. Darker colors indicate greater overlap of data points.

Fig. S4 Results from the null model at family level. The observed r^2 is indicated with a vertical gray line. The black curves represent the distribution of r^2 values from PGLS across the 1000 null datasets. The range of dashed lines were 95% confidence intervals of r^2 across the 1000 random samples. Diversification rate vs family climatic niche width were shown in A, B, C; Diversification rate vs mean specie climatic niche width were shown in D, E, F; Diversification rate vs climatic niche divergence were shown in G, H, I. Temperature niche width were showed in A, D, E, precipitation niche width were showed in B, E, H, overall niche width (temperature niche width x precipitation niche width) were showed in C, F, I.

Fig. S5 Results from the null model at order level. The observed r^2 is indicated with a vertical gray line. The black curves represent the distribution of r^2 values from PGLS across the 1000 null datasets. The range of dashed lines were 95% confidence intervals of r^2 across the 1000 random samples. Diversification rate vs order climatic niche width were shown in A, B; Diversification rate vs mean specie climatic niche width were shown in C, D; Diversification rate vs climatic niche divergence were shown in E, F. Temperature niche width were showed in A, C, E, precipitation niche width were showed in B, D, F.

Fig. S6 Diversification rate and species richness patterns of Chinese angiosperms. Diversification rates were determined based on stem-group ages of families with ε=0.5.

Table S1 Best model of all traits were estimated in our study. The lowest

AIC was marked in bold. WN, BM, OU, LA were models of white noise, Brownian motion, Ornstein-Uhlenbeck and lambda respectively.

Table S2 Relationship between diversification rate and climatic niche position, family climatic niche width, mean species climatic niche width, climatic niche divergence, climatic niche evolution rate and geographic extent. Results were estimated from univariate phylogenetic generalized least-squares (PGLS) regression models. The diversification rates were estimated base on species richness of China for each family, three alternative extinction rate (ε=0, 0.5 and 0.9) were selected. Significant relationship were shown in bold.

Table S3 Relationship between diversification rate and climatic niche position, climatic family niche width, mean climatic niche width, climatic niche divergence, climatic niche evolution rate and geographic extent. Results were estimated from univariate phylogenetic generalized least-squares (PGLS) regression models. The diversification rates were estimated base on global species richness for each family, three alternative extinction rate (ε=0, 0.5 and 0.9) were selected. Significant relationship were shown in bold.

Table S4 Relationship between species richness (including Chinese species and total species at global) and diversification rate, stem age. Results were estimated from univariate phylogenetic generalized least-squares (PGLS) regression models. The diversification rates were estimated base on global species richness for each family, three alternative extinction rate (ε=0, 0.5 and 0.9) were selected. Significant relationships are shown in bold.

Supporting Information

Additional supporting information may be found online in the Supporting Information for this article.

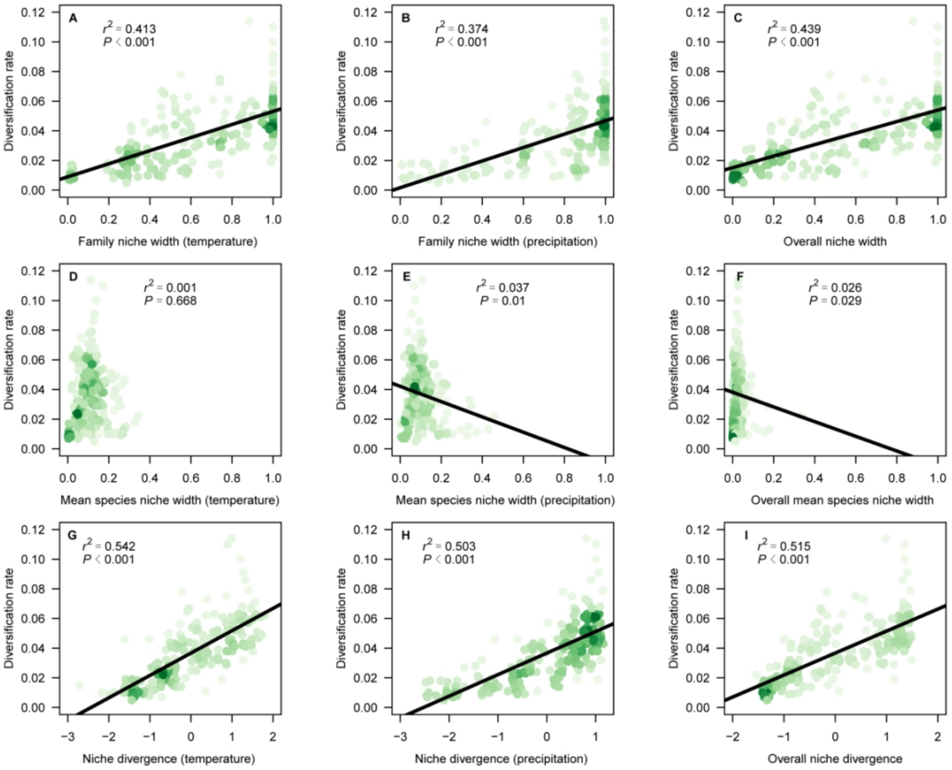

Fig. 1 Relationship between diversification rate and family climatic niche width (A, B, C), mean species climatic niche width (D, E, F) and climatic niche divergence (G, H, I) for MAP, MAT and overall respectively. Darker colors indicate greater overlap of data points. Diversification rates were estimated based on stem-group ages of family with ε=0.5, including only species in China. Use of alternative values of ε (0, 0.9) and global richness of families yields similar results (Table S3, S4).

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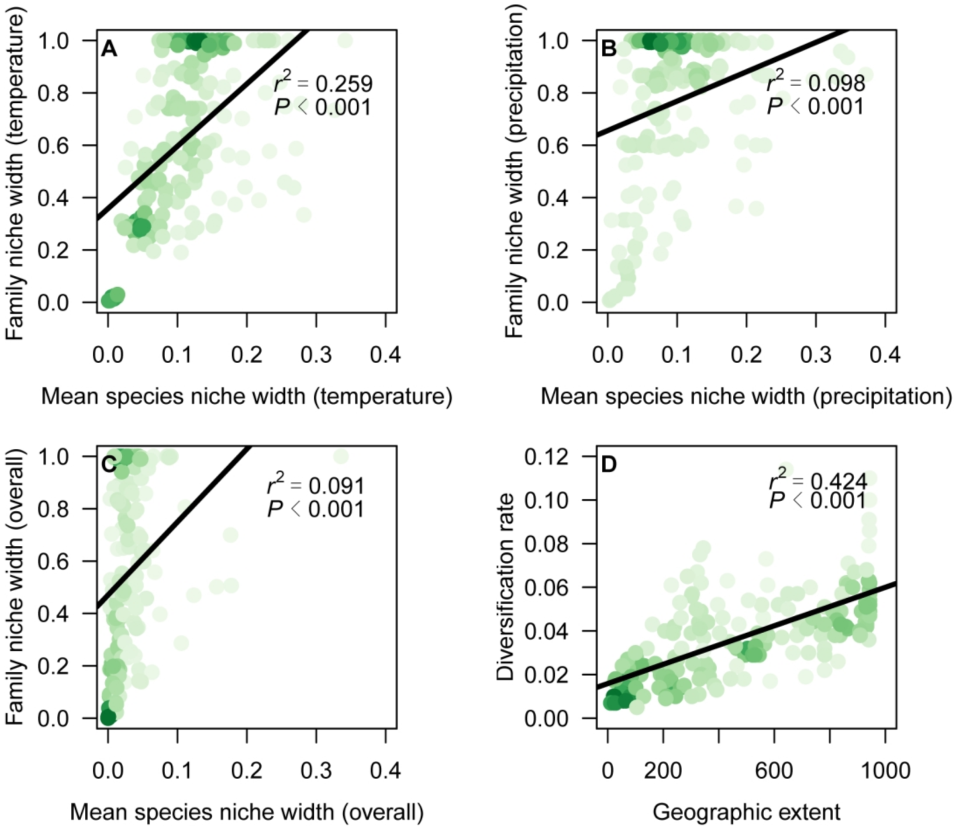

Fig. 2 Relationship between family climatic niche width and mean species climatic niche width (A, B, C). A significant relationship between diversification rate and geographic extent (D). Darker colors indicate greater overlap of data points. Diversification rates were estimated based on stem-group ages of families with ε=0.5, including only species in China. Use of alternative values of ε (0, 0.9) and global richness of families yields similar results (Table S3, S4). Geographic extent was the distribution area of each family.

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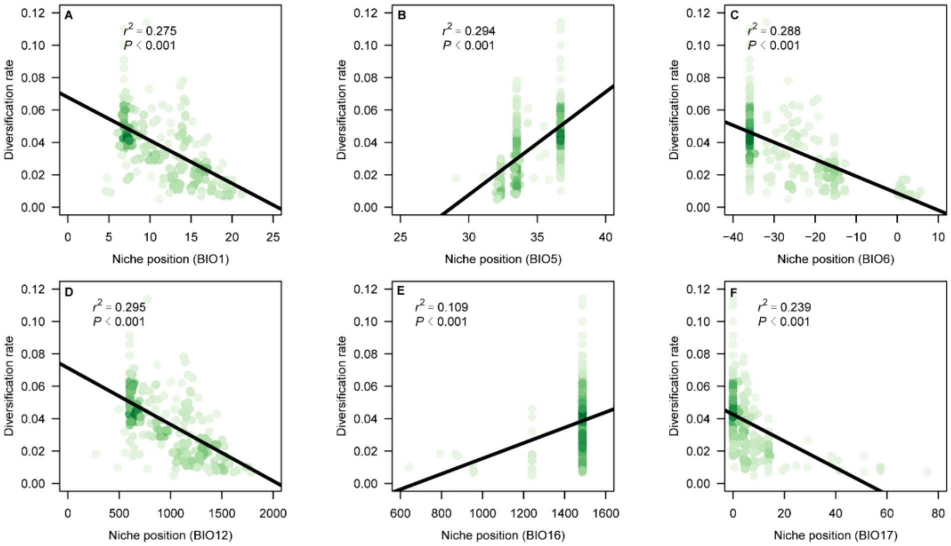

Fig. 3 Relationship between diversification rate and climatic niche position. BIO1, BIO5, BIO6 and BIO12, BIO16, BIO17 represent annual mean temperature, maximum temperature of the warmest month, minimum temperature of the coldest month, annual precipitation, precipitation of the wettest quarter and precipitation of the driest quarter respectively. Darker colors indicate greater overlap of data points. Diversification rates were estimated based on stem-group ages of families with ε=0.5, including only species in China. Use of alternative values of ε (0, 0.9) and global richness of families yields similar results (Table S3, S4).

146x81mm (220 x 220 DPI)

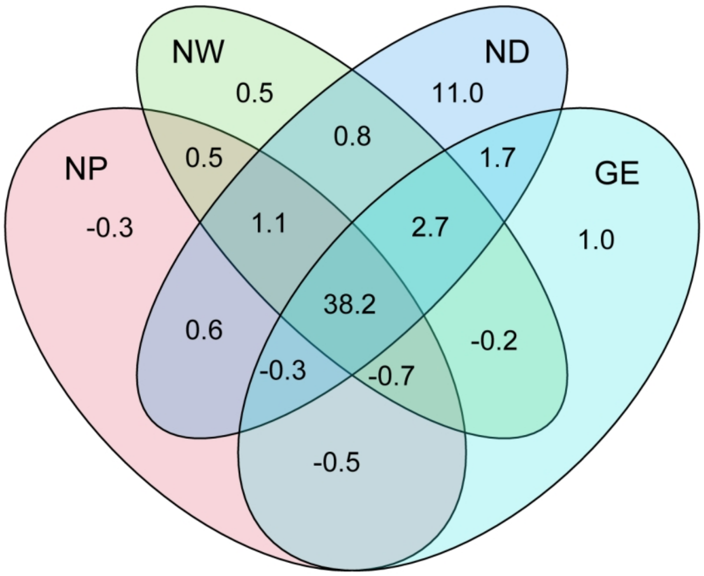

Fig. 4 Venn diagram showing the results of variance partitioning on a full model of diversification rate with climatic niche position (NP), climatic niche width (NW), climatic niche divergence (ND), geographic extent (GE) as explanatory variables. Results are shown as percentage of explained variance.

114x184mm (300 x 300 DPI)

Climatic niche divergence explains angiosperm diversification across clades in China

Short running title: Climate width and diversification in Chinese plants

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Abstract

Diversification rates are critically important for understanding patterns of species richness among clades. However, the effects of climatic niche width on plant diversification rates remain to be elucidated. Based on the phylogenetic, climatic, and distributional information of angiosperms in China, a total of 26,906 species from 182 families were included in this study. We aimed to test relationships between diversification rate and climatic niche width and climatic niche width related variables (including climatic niche divergence, climatic niche position, and geographic extent, climatic niche evolutionary rate) using phylogenetic methods. We found that climatic niche divergence had the largest unique contribution to the diversification rate, while the unique effects of climatic niche width, climatic niche position, geographic extent, and climatic niche evolutionary rate on the diversification rate were negligible. We also observed that the relationship between diversification rate and climatic niche divergence was significantly stronger than the null assumption (Artefactual relationship between diversification and clade-level climatic niche width via sampling more species). Our study supports the hypothesis that wider family climatic niche widths explain faster diversification rates through a higher climatic niche divergence rather than via higher geographic extent, higher climatic niche evolutionary rate or separated climatic niche position. Hence, the results provide a potential explanation for large-scale diversity patterns within families of plants.

Keywords: Angiosperms, diversification rate, climatic niche width, climatic niche divergence, geographic extent, climatic niche position

1 Introduction

A fundamental goal in evolutionary biology is to explain why some clades have higher species richness than others. In general, species richness among clades can be explained either by time (i.e., greater species richness accumulates over time) or diversification rate (i.e., higher diversification rate leads to higher species richness). The diversification rate is the rate of speciation minus the extinction rate (Ricklefs, 2007; Givnish, 2010). Previous studies have indicated that species richness unevenness among clades (i.e., families, phyla) was largely explained by diversification rates (Scholl & Wiens, 2016; Hernandez-Hernandez & Wiens, 2020). Therefore, it is essential to uncover the ecological and evolutionary processes that determine differences in diversification rates among clades to understand their richness patterns.

The climatic niche width is the set of climatic conditions where a species is able to maintain viable populations. It reflects the physiological tolerance of a species to climatic environments (Soberon, 2007; Anacker & Strauss, 2014). The relationship between climatic niche width and diversification rate has been studied based on two hypotheses that could potentially explain it. One is the niche divergence hypothesis, which suggests that a wider climatic niche width explains diversification by reducing the extinction rate (e.g., survival from climate change, Wiens, 2016), thus increasing the diversification rate of clades. A wider climatic niche width might also lead to higher rates of speciation because it would increase the likelihood of encountering ecological or geographical barriers (Darwin, 1859; Rosenzweig, 1995; Gaston, 2003). The second hypothesis is the niche conservatism hypothesis. In contrast to the divergence hypothesis, niche conservatism suggests that narrower climatic niches are associated with a higher diversification rate via allopatric speciation (Kozak & Wiens, 2007). For example, Baselga et al. (2011) indicated that species with overlapped climatic niches tend to have a higher diversification rate, potentially supporting the climatic niche conservatism mechanism.

Despite the aforementioned hypotheses, very few studies have directly explored the effect of climatic niche width on the diversification rate at a large scale. Among the few previous studies, the results have not been consistent across different biological groups. For example, Gómez-Rodríguez et al. (2015) and Castro-Insua et al. (2018) found a positive relationship between climatic niche width and diversification rate in both amphibian and mammalian families. In contrast, Rolland and Salamin (2016) found that species with narrower climatic niche widths tended to have higher diversification rates among amphibians, mammals, and birds. However, to our knowledge, no studies have tested how climatic niche width affects the diversification rate among clades in plants at a large scale. Liu et al. (2020) estimated the climatic niche width for both plants and animals, however, they did not explore the effects of climatic niche width on the diversification rate.

There may also be more indirect relationships between climatic niche width and diversification rates of clades. For example, a wider climatic niche might be accompanied by larger geographic ranges, which can lead to a higher diversification rate. Moreover, a higher evolutionary rate of climatic variables might expand the climatic niche width, then accelerate the diversification rate (Kozak and Wiens, 2010, Castro-Insua et al., 2018). Alternatively, species in different niche positions may have different climatic niche widths, leading to different diversification rates. For example, some previous studies indicated that species in tropical regions have a lower diversification rate than in temperate zones (Harvey et al., 2020; Igea et al., 2020; Tietje et al., 2022). Generally, the niche width for temperature-related climatic variables may be narrower in the tropical zone than that in the temperate zone (Janzen, 1967; Ghalambor et al., 2016), whereas the niche width for precipitation-related climatic variables can be wider in the tropical zone (Quintero & Wiens, 2013).

Here, we used a nearly complete dataset of Chinese angiosperms to test whether climatic niche divergence or climatic niche conservatism better explains species diversification among plant clades. Using these (and similar) resources, several studies have assessed the patterns of phylogenetic structure in Chinese plant assemblages at the regional scale (Qian et al., 2019; Gheyret et al., 2020). In addition, Su et al. (2020) reported that different climatic niche position predicts species richness patterns for tropical and temperate families. However, the mechanism by which climatic niche width affects the diversification rate and subsequently leads to species richness unevenness among plant clades remains unclear.

In this study, we estimated the climatic niche width among the 182 families and 26,906 species of angiosperms in China. We defined climatic niche divergence as the residuals of the relationship between family climatic niche width and mean species climatic niche width as described by Gómez-Rodríguez et al. (2015). We also estimated the climatic niche evolution rate, geographic extent (area), and diversification rate of the families to test the relationship between these variables across families using phylogenetic methods. Specifically, we aimed to address the following seven hypotheses (Table 1), with one hypothesis related to niche conservatism (H1) and five hypotheses related to niche divergence (H2–H6), as follows: a narrower climatic niche width predicts the diversification rate (H1); a wider climatic niche width explains the diversification rate via increasing climatic niche divergence (H2), increasing the climatic niche evolution rate (H3), decreasing the extinction rate (H4), increasing the geographic extent (H5), and changing climatic niche position (the separated geographic effects) (H6). Because clades with more species tend to have wider climatic niche widths, this may lead to a higher diversification rate. We also tested a null hypothesis, that is, (H0) an artifactual relationship between diversification rate and clade-level climatic niche width occurs via sampling more species.

2 Materials and methods

2.1 Phylogenetic tree and climatic data

The phylogenetic tree in our study was based on Lu et al. (2018). The tree was constructed using the sequences of five genes (*atpB*, *matK*, *ndhF*, *rbcL*, and *matR*). They first generated a dated phylogeny including 5,864 species native to China, representing 2,665 genera and 273 families. With this tree as the backbone, a species-level tree including 28,076 Chinese angiosperm species was generated by inserting species that were not sampled in our generic tree within the genera to which they belong, using the package "S.PhyloMaker" (Qian & Jin, 2016) in R software. After matching the phylogenetic tree with distribution information, there were 26,977 species with 235 families, including 96 % and 86 % of the angiosperm species and families, respectively, in China (Lu et al., 2018). At least three species in each family were needed to run the Ornstein–Uhlenbeck (OU) model in the following analysis. Finally, 182 families and 26,906 species were used for the analysis in our study, encompassing approximately 10 % of the plant species worldwide.

We performed most of the analyses on a consensus of these 1,000 trees. We used a maximum-clade credibility tree based on the mean heights of these trees using TREEANNOTATOR version 1.10 (Bouckaert et al., 2014). The tree was fully resolved (no polytomies). All of the 182 families were monophyletic.

Distributional and climatic data were generated in Lu et al. (2018). They divided the study area in China into 100 × 100 km (i.e., 10,000 km^2) grid cells. The area of the grid cells on the border with less than 5,000 km^2 were excluded. The species distribution information in each grid cell were collected from all published national and provincial floras as well as some local flora, checklists, and herbarium records. There were more than 1,400,000 records of distribution information in total. Only the mean annual temperature (BIO1) and mean annual precipitation (BIO12) were included in their dataset. We also needed the maximum temperature of the warmest month (BIO5), minimum temperature of the coldest month (BIO6), precipitation of the wettest quarter (BIO16), and precipitation of the driest quarter (BIO17) to estimate the climatic niche width and for the other analyses. Therefore, we extracted the climate data from maps of WorldClim version 1.4 (http://www.worldclim.org/), with a spatial resolution of 10 min (approximately 340 km^2). To match the distribution information, we estimated these climatic variables in each grid cell (10 000 km^2) using ArcGIS 10.1 (http://www.esri.com/) based on these maps. In summary, the species richness and niche position (BIO1, BIO5, BIO6, BIO12, BIO16, and BIO17) in each grid cell were included. The geographic extent (area) of each family was also estimated based on the distribution information. We used these data in our study.

2.2 Climatic niche widths

We estimated the family climatic niche width and the mean species climatic niche width in our study according to the approaches of Gómez-Rodríguez et al. (2015). For family climatic niche width, all species in the family were merged to form a single distribution area. The range of climatic data of each family was estimated as Rg = max (var)–min (var). Then, the climatic niche width for a given family i in a dataset with j families was estimated as: $StRg_i = [Rg_i - min(Rg_1:Rg_j)]/[max(Rg_1:Rg_j) - min(Rg_1:Rg_j)]$. This yields a value between 0 and 1. The temperature and precipitation niche width were based on BIO1, BIO5, BIO6, BIO12, BIO16, and BIO17, respectively. Species climatic niche width was estimated based on the same protocol as the family climatic niche width. The mean species climatic niche width was then the average climatic niche width of all species within the family. Climatic niche divergence is the residuals of the relationship between family climatic niche width and mean species climatic niche width as described by Gómez-Rodríguez et al. (2015), which reflects a non-overlap of climatic niches within families (Fig. S1). The overall climatic niche width was the temperature niche width multiplied by the precipitation niche width. The niche position was described in terms of BIO1, BIO5, BIO6, BIO12, BIO16, and BIO17 across the geographic range of the family. All niche parameters are explained in Table 2. Using the abovementioned approaches, we also determined correlations between diversification rate, climatic niche width, and niche divergence across 49 orders.

2.3 Diversification rate and niche evolutionary rate

The diversification rate of each family was estimated using a method of moment estimator (Magallón & Sanderson, 2001). The species richness of China and the stem age of each family were used. Stem ages were used because crown ages would require more extensive sampling of the species in each family, and monotypic families could not be incorporated (Meyer & Wiens, 2018). To make our results more robust, we selected three relative extinction rates (ε): two extremes (ε = 0, 0.9) and one median (ε = 0.5). In an alternative analysis, we also used the total species richness of each family to estimate the diversification rate. We used the R package "TAXONLOOKUP" version 1.1.5 (Pennell et al., 2016) to obtain the total species richness in each family. The data source used for this package was based on Plant List version 1.1 (2013). Some endemic Chinese species were included in the Flora of China (Wu et al., 2013), but, at the time of the study, have not been accepted by The Plant List. Therefore, we also included "unresolved" species (i.e., not yet assigned a status of "Accepted" or "Synonym). We used both accepted and unresolved species to represent the global species richness of each family. The species richness, stem age and diversification rate were in Supplementary Data 1.

Many other approaches are available to study diversification. However, most other methods would be impractical here because they need detailed species-level phylogenies within each clade. This level of detail is lacking for many species in our study, as described above. Furthermore, we aimed to explain differences in richness and diversification rates among families, not shifts in diversification rates over time. Therefore, the method of moment estimator with stem age is the most appropriate approach for our study.

The evolutionary rates of the BIO1 and BIO12 were estimated to represent the climatic niche evolution rate. We focused on these two variables because they should reflect the most important aspects of the climatic distribution of the species (e.g., BIO1: tropical vs. temperate; BIO12: arid vs. mesic), and more so than short-term, extreme values (BIO5, BIO6, BIO16, BIO17). We first used the fitContinuous function in the package "geiger" version 2.0.7 (Harmon et al., 2008; Pennell et al., 2014) to fit four evolutionary models, namely, the Brownian motion (BM), Ornstein-–Uhlenbeck (OU), lambda (LA), and white noise (WN). Then, the best-fitting model was selected based on the lowest Akaike information criterion (AIC). The variance (σ^2) in the best model was used as the evolutionary rate of the variables for each family.

2.4 Statistical analysis

The best-fit model for the diversification rate of each family was the LA model (Table S1). Therefore, phylogenetic generalized least-squares regression (PGLS) (Martins & Hansen, 1997) in the R package "caper" version 1.0.1 (Orme, 2013) was used to analyze the relationship between diversification rate and niche climatic variables. Following standard practice, lambda values (phylogenetic signal) were estimated by maximum likelihood to transform the branch lengths, with kappa and delta values both set to 1 (Pagel, 1999; Orme, 2013). The contribution of individual and combined variables (niche width, niche divergence, niche position, and geographic extent) was estimated using the function varpart in R package "vegan" version 2.5-6 (Oksanen et al., 2019). Given that the niche position consists of six variables, we used a stepwise procedure to select the niche position variables. We found that the diversification rate ~ BIO5+BIO12+BIO16 was the best model in the stepwise analysis; then, we selected these three climatic variables to represent the niche position in the analysis.

To account for the effect of species richness on the relationship between the diversification rate and climatic niche width, we created the same species richness for each of the families by randomly sampling from the whole species pool. Null niche width was estimated from a randomly sampled species pool of richness equivalent to real families. We randomly sampled 1,000 times from the 182 null families and compared the distribution of the coefficient of determination (r^2) of the aforementioned PGLS with the observed r^2 in the original families. We used the function "quantile" in the R base package to estimate the values of 1000 r^2 at a 95 % confidence interval. If the observed r^2 was in the 95 % confidence interval of the 1,000 r^2 values, we assumed the relationship found between the diversification rate and niche variables was because families with more species span more climatic conditions. Otherwise, we assumed that the niche variables contributed to the diversification rate. The same approaches were also used for species at the order level.

3 Results

We found a strong and positive relationship between the diversification rate and family climatic niche width for precipitation (r^2 = 0.389–0.437, $P <$ 0.001), temperature (r^2 = 0.360–0.374, $P < 0.001$), and the overall of both (r^2 = 0.413–0.468, $P < 0.001$). While a negatively weak or non-significant relationship was observed between the diversification rate and mean species climatic niche width for precipitation ($r^2 \leq 0.001$, P = 0.609–0.794), temperature (r^2 = 0.031–0.045, $P <$ 0.004–0.018), and the overall (r^2 = 0.004–0.011, P = 0.160–0.420). This provided a stronger relationship between the diversification rate and climatic niche divergence (residuals of family climatic niche width versus mean species climatic niche width) for precipitation (r^2 = 0.512–0.576, P < 0.001), temperature (r^2 = 0.482–0.503, P < 0.001), and the overall (r^2 = 0.480–0.558, P < 0.001) (Fig. 1, Table S2). Therefore, the diversification rate was mainly explained by climatic niche divergence (H2) rather than climatic niche conservatism (H1). Neither the evolutionary rate of mean annual temperature nor precipitation showed a significant relationship with diversification rate, family climatic niche width, and mean species climatic niche width (Fig. S2), rejecting the hypothesis that the diversification rate was explained by climatic niche divergence via increased climatic niche evolution rate (H3). The weak or negative relationships between diversification rate and mean species climatic niche width as found in our study suggested that, wider climatic niches increasing diversification via reduced extinction rates (H4) was rejected, because the validity of this hypothesis depends on a strong relationship between diversification rate and mean species niche width (Table 1). Similar results were obtained when we divided the species into 49 orders (Fig. S3).

To evaluate whether the effects of climatic niche width on diversification rate are via the geographic extent (H5) or niche position (H6), we first built PGLS models for the two hypotheses. A significant positive relationship was observed between the diversification rate and geographic extent (r^2 = 0.393–0.471, P < 0.001) (Fig. 2, Table S2). The relationship between the diversification rate and climatic niche position varied. We found a significantly positive relationship between the diversification rate and BIO5 (r^2 = 0.272–0.320, $P < 0.001$) and BIO16 (r^2 = 0.009–0.110, $P < 0.001$), while a significantly negative relationship was observed between the diversification rate and BIO1 (r^2 = 0.251–0.310, $P < 0.001$), BIO6 (r^2 = 0.271–0.292, $P < 0.001$), BIO12 (r^2 = 0.272–0.324, $P < 0.001$), and BIO17 (r^2 = 0.219–0.231, $P < 0.001$) (Fig. 3, Table S2). The climatic niche position, family climatic niche width, climatic niche divergence, and geographic extent showed an important partition in explaining the diversification rates (Table S2, S3). These variables were then used to determine their unique contribution to diversification rates. The explanation from climatic niche position (0.3 %), geographic extent (1 %), and climatic niche width (0.5 %) were negligible. Climatic niche divergence was the variable with the largest unique contribution (11.0 %). Most of the variances were shared among climatic niche divergence, climatic niche width, geographic extent, and climatic niche position (38.2 %) (Fig. 4). Therefore, the unique effects of climatic niche width on the diversification rate via geographic extent (H5) or climatic niche position (H6) were limited.

In the null models, we found that the observed relationship between diversification rate and family climatic niche width, as well as the mean species climatic width of precipitation, was generally stronger than that of the null model (Fig. S4B, E). However, the relationship between diversification rate and family climatic niche width, as well as the mean species climatic width of temperature (Fig. S4A, D) and overall climatic niche width (Fig. S4C, F) were not significantly different from that of the null model. For the climatic niche divergence, the relationship between diversification rate and the climatic niche divergence of temperature and precipitation and the overall climatic niche divergence were all more robust than that of the null model (Fig. S4G, I, H). Overall, the precipitation niche width (including family niche width and mean species niche width) was important for accelerating the diversification rate, while climatic niche divergence of both temperature and precipitation were important in accelerating the diversification rate for angiosperms of China. Therefore, the hypothesis that an artifactual relationship between diversification and clade-level climatic niche width would occur via sampling more species (H0) was rejected. We also found that the null model hypothesis (H0) was rejected at the order level (Fig. S5).

4 Discussion

Few studies have investigated the relationship between climatic niche width and species diversification rates, except for several studies in animals (Gómez-Rodríguez et al., 2015; Rolland & Salamin, 2016; Castro-Insua et al., 2018). Here, we explored the relationship between the climatic niche width and the diversification rate of plants in China at a large scale (including 26,906 species and 182 families) for the first time. Our results suggest that climatic niche divergence (H2) rather than climatic niche conservatism (H1) explains the diversification rate in angiosperm clades of China. Moreover, we suggest that a wider family climatic niche width explains a faster diversification rate through higher climatic niche divergence (H2), rather than increasing the climatic niche evolution rate (H3), decreasing the extinction rate (H4), increasing the geographic extent (H5), or a separated climatic niche position (H6). The relationship between the diversification rate and family niche width for precipitation and niche divergence for temperature was significantly higher than that of the null assumptions, demonstrating that our findings were supported, rather than an artifactual relationship between diversification and clade-level niche width occurring as a result of sampling of more species (H0).

4.1 Niche divergence and niche conservatism mechanisms explain species diversification

Our results have two important implications. First, we found that wider climatic niche width predicts a higher diversification rate via climatic niche divergence, potentially leading to species unevenness among families of Chinese angiosperms (Table S4). Moreover, our results were consistent with amphibian (Gómez-Rodríguez et al., 2015) and large-scale mammal (Castro-Insua et al., 2018) studies. Therefore, the results suggest that plant diversification may exhibit trends similar to animals. This consistency suggests why animals and plants follow similar richness patterns, biogeographic regions, biomes, and biodiversity hotspots on a global scale (Liu et al., 2020). There are two potential explanations as to why climatic niche divergence predicts the diversification rate of angiosperms in China. On the one hand, a higher climatic niche divergence would decrease the overlap of species climatic niches, thereby reducing competition within families and creating additional opportunities for speciation (Kozak & Wiens, 2010a). Furthermore, a higher climatic niche divergence would cause higher spatial isolation and thus decrease the connectivity between these species, reduce gene flow (Birand et al., 2010; Wiens et al., 2012) and lead to the emergence of reproductive barriers, and consequently accelerate the diversification rate.

The niche conservatism hypothesis states that species with shared evolutionary history (i.e., species in an evolutionary clade) tend to tolerate similar environmental conditions and thus exhibit similar geographic or climatic distributions (Latham & Ricklefs, 1993; Wiens & Donoghue, 2004). This hypothesis was supported by previous studies that explain the species assemblages in China (Qian et al., 2019), Eastern Asia (Su et al., 2020), and the tropical and subtropical regions on a global scale (Cerezer et al., 2020). However, these studies tend to explain species unevenness at the regional scale rather than among clades in our study. Notably, the niche conservatism hypothesis postulated in previous studies generally found that in tropical and subtropical regions, species originated earlier and more abundantly, although they have low diversification rates (Harvey et al., 2020; Igea et al. 2020; Tietje et al. 2022). Similarly, we also showed that a low diversification rate was associated with high species richness patterns at a regional scale (Fig. S6). However, our study emphasized that the diversification rate was explained by climatic niche divergence, potentially leading to variable species unevenness among clades (Table S4). Several previous studies in animals also indicated that species richness generally accumulated through climatic niche conservatism at the regional level, while the diversification rate among clades was more commonly explained by climatic niche divergence (Kozak & Wiens, 2010a, b; Wiens et al., 2011; Kozak & Wiens, 2012).

4.2 Effect of climatic niche evolution rate on diversification rate via change niche divergence

Our results do not support hypothesis H3 that the niche evolution rate increases climatic niche width and climatic niche divergence. In general, a rapid change in the climatic niche rate would allow species to be distributed into new environments (increase climatic niche width), and thus decrease the climatic niche overlap (increase climatic niche divergence) among species and lead to an increase in the diversification rate (Kozak and Wiens, 2010, Liu et al. 2020). The discrepancy between our results and previous studies was probably because species with higher climatic niche evolution rates can explore new niches, while some species might be extinct in their original habitats. This would not increase the climatic niche width and climatic niche divergence of the families and, therefore, would not increase the diversification rate of the families. This concept needs to be tested in future studies.

4.3 Effect of climatic niche width on diversification rate via change climatic niche evolution rate

Our results reject the hypothesis that a wider mean species climatic niche width is associated with the diversification rate by decreasing the extinction rate (H4), which is consistent with the findings of Gómez-Rodríguez et al. (2015) and Castro-Insua et al. (2018). In contrast, Rolland and Salamin (2016) found lower extinction rates in birds, mammals, and amphibians with narrower climatic niches. Another study found that specialist species grown in narrower climatic niche ranges have a higher risk of extinction rates (Harris & Pimm, 2008). This discrepancy may be caused by human-related factors (such as excessive deforestation) and anthropogenic climate change, implying that the extinction of some groups may not have been related to their natural evolutionary history.

4.4 Effect of geographic extent and niche position on diversification rate

The unique contribution of the geographic extent and niche position was negligible. Thus, the hypothesis that wider climatic niches facilitate faster diversification by allowing greater range expansion (H5) or changing the niche position (H6) was also limited. These results are consistent with those of Gómez-Rodríguez et al. (2015) and Castro-Insua et al. (2018). However, we observed a significant negative relationship between the diversification rate and BIO1 (annual mean temperature) and BIO12 (annual precipitation). This was not observed in the animals studied by Gómez-Rodríguez et al. (2015) and Castro-Insua et al. (2018). However, Igea and Tanentzap (2020a) and Jetz et al. (2012) found that the diversification rate slows down for angiosperms and birds in tropical and subtropical regions, respectively. Early studies have hypothesized "density-dependent" effects on diversification, where the rates of species accumulation within a clade would slow down over time due to increasing species density (Phillimore & Price, 2008; Rabosky & Lovette, 2008; Rabosky, 2009). This hypothesis could potentially explain the diversification patterns in China as regions with high precipitation and temperature in China tend to have more species. These species originated earlier than those distributed in cold and dry regions (Lu et al., 2018), which would slow down the diversification rate in warm and wet regions because of their high species density. A positive relationship between diversification rate and BIO5, and a negative relationship between diversification rate and BIO6 and BIO17 were found, indicating that tolerance to extreme climatic habitats (such as hot, cold, and dry environments) facilitates the diversification of plants. The positive relationship between the diversification rate and BIO16 was unexpected, probably because regions with high temperatures usually tend to have high precipitation in China.

4.5 Potential sources of error

We acknowledge that some important sources of error may have impacted our results. First, our analyses were based primarily on species occurring in China, whereas most families and genera are more broadly distributed. Actually, we also estimated the diversification rate in each family using species found across the world. We found niche variables (estimated using distribution information of China) had a weaker relationship with a diversification rate estimated using global species richness (Table S3) than that of using Chinese species richness (Table S2). Therefore, it is reasonable to use the climatic niches of China to explain species diversification among clades in this region. However, this currently cannot be generalized to the rest of the world. Indeed, it remains to be seen whether the patterns reported here hold true when global sampling is used.

Second, because of the relatively low resolution, climatic heterogeneity within cells was high, especially in the mountainous regions. While it is well known that local finer-scale niches can affect the diversification of lineages (Hutter et al. 2013), we did not consider the micro-environment of each species. It is likely that doing so would result in deviations in niche width. Future studies should test the same set of hypotheses at smaller spatial scales (e.g. 1-km grid cells).

Conclusion

In summary, we found climatic niche divergence explains the diversification rate among angiosperm families in China. These results are important for explaining large-scale patterns of species unevenness among clades in plants. Since our results for plants are consistent with that of animals observed in previous studies (such as birds, mammals, and amphibians; Gómez-Rodríguez et al., 2015; Castro-Insua et al., 2018), they could also explain why animals and plants follow similar richness patterns, biogeographic regions, biomes, and biodiversity hotspots.

Compliance and ethics The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Figure legends

Table 1 Potential hypothesis to explain diversification rate and climatic niche width based on Gómez-Rodríguez et al. (2015).

Hypothesis	Predictions
H1: Narrower niches facilitate diversification rate via niche conservatism.	(1) Strong and positive relationship between family climatic niche width and mean species climatic niche width; (2) Negative relationship between diversification rate and family climatic niche width; (3) Negative relationship between diversification rate and mean species climatic niche width.
H2: Wider climatic niche widths facilitate diversification rate via climatic niche divergence.	(1) No or weak relationship between family climatic niche width and mean species climatic niche width; (2) No relationship between diversification rate and mean species climatic niche width; (3) Strong and positive relationship between diversification rate and climatic niche divergence (residuals of relationship between family climatic niche width and mean species climatic niche width).
H3: Wider climatic niche widths facilitate diversification rate via increased climatic niche evolution rate.	(1) Strong and positive relationship between diversification rate and climatic niche evolution rate; (2) Positive relationship between climatic niche width and climatic niche evolution rate; (3) Positive relationship between climatic niche divergence and climatic niche evolution rate.
H4: Wider climatic	(1) Positive relationship between family and

niche width could facilitate diversification rate via decreased extinction rate.	mean species climatic niche width; (2) Strong and positive relationship between diversification rate and mean species climatic niche width and family climatic niche width; (3) No relationship between diversification rate and climatic niche divergence.
H5: Wider climatic niche width could facilitate diversification rate via geographic extent.	Strong and positive relationship between the diversification rate and geographic area of clade. This relationship was stronger than the relationship between diversification rate and climatic niche width.
H6: Wider climatic niche widths could facilitate diversification rate via separated geographic effects (niche position).	Strong and positive relationship between diversification rate and climatic niche position. This relationship was stronger than relationship between diversification rate and climatic niche width.
H0: Relationship between diversification rate and clad-level climatic niche width via sampling more species.	(1) Strong and positive relationship between diversification rate and species richness among families; (2) Positive relationship between family and mean species climatic niche width; (3) Positive relationship between diversification rate and family and mean species climatic niche width; (4) The relationship (r2) in (3) were stronger than results of randomly selected species in each family.

Table 2 Overview of the niche parameters in our study.

Niche variables	Explanation of the niche variables
Family climatic niche width	Climatic niche width of the family
Mean species climatic niche width	Mean value of climatic niche width for all the species within the family
Climatic niche divergence	Residuals of family climatic niche width versus mean species climatic niche width
Climatic niche position	Climate variables (including BIO1, BIO5, BIO6, BIO12, BIO16, BIO17)
Climatic niche evolution rate	Evolutionary rate of BIO1 and BIO12
Geographic extent	Area of species distribution of the family

Fig. 1 Relationship between diversification rate and family climatic niche width (A, B, C), mean species climatic niche width (D, E, F) and climatic niche divergence (G, H, I) for MAP, MAT and overall respectively. Darker colors indicate greater overlap of data points. Diversification rates were estimated based on stem-group ages of family with ε=0.5, including only species in China. Use of alternative values of ε (0, 0.9) and global richness of families yields similar results (Table S2, S3).

Fig. 2 Relationship between family climatic niche width and mean species climatic niche width (A, B, C). A significant relationship between diversification rate and geographic extent (D). Darker colors indicate greater overlap of data points. Diversification rates were estimated based on stem-group ages of families with ε=0.5, including only species in China. Use of alternative values of ε (0, 0.9) and global richness of families yields similar results (Table S2, S3). Geographic extent was the distribution area of each family.

Fig. 3 Relationship between diversification rate and climatic niche position. BIO1, BIO5, BIO6 and BIO12, BIO16, BIO17 represent annual mean temperature, maximum temperature of the warmest month, minimum temperature of the coldest month, annual precipitation, precipitation of the wettest quarter and precipitation of the driest quarter respectively. Darker colors indicate greater overlap of data points. Diversification rates were estimated based on stem-group ages of families with ε=0.5, including only species in China. Use of alternative values of ε (0, 0.9) and global richness of families yields similar results (Table S2, S3).

Fig. 4 Venn diagram showing the results of variance partitioning on a full model of diversification rate with climatic niche position (NP), climatic niche width (NW), climatic niche divergence (ND), geographic extent (GE) as explanatory variables. Results are shown as percentage of explained variance.

Fig. S1 Relationship between family climatic niche width, mean species climatic niche width and climatic niche divergence. Different color of the curves represent species niche, R1, R2 and R3 are niche divergence.

Fig. S2 Relationship between climatic niche evolution rate and diversification rate (A, B), family climatic niche width (C, D), mean species climatic niche width (E, F), climatic niche divergence (G, H) for both temperature and precipitation. Darker colors indicate greater overlap of data points.

Fig. S3 Relationship between diversification rate and order climatic niche width (A, B), mean species climatic niche width (C, D) and climatic niche divergence (E, F) for MAP, MAT respectively. Darker colors indicate greater overlap of data points. Diversification rates were estimated based on stem-group ages of order with ε=0.5, including only species in China. Darker colors indicate greater overlap of data points.

Fig. S4 Results from the null model at family level. The observed r^2 is indicated with a vertical gray line. The black curves represent the distribution of r^2 values from PGLS across the 1000 null datasets. The range of dashed lines were 95% confidence intervals of r^2 across the 1000 random samples. Diversification rate vs family climatic niche width were shown in A, B, C; Diversification rate vs mean specie climatic niche width were shown in D, E, F; Diversification rate vs climatic niche divergence were shown in G, H, I. Temperature niche width were showed in A, D, E, precipitation niche width were showed in B, E, H, overall niche width (temperature niche width x precipitation niche width) were showed in C, F, I.

Fig. S5 Results from the null model at order level. The observed r^2 is indicated with a vertical gray line. The black curves represent the distribution of r^2 values from PGLS across the 1000 null datasets. The range of dashed lines were 95% confidence intervals of r^2 across the 1000 random samples. Diversification rate vs order climatic niche width were shown in A, B; Diversification rate vs mean specie climatic niche width were shown in C, D; Diversification rate vs climatic niche divergence were shown in E, F. Temperature niche width were showed in A, C, E, precipitation niche width were showed in B, D, F.

Fig. S6 Diversification rate and species richness patterns of Chinese angiosperms. Diversification rates were determined based on stem-group ages of families with $\varepsilon=0.5$.

Table S1 Best model of all traits were estimated in our study. The lowest

AIC was marked in bold. WN, BM, OU, LA were models of white noise, Brownian motion, Ornstein-Uhlenbeck and lambda respectively.

Table S2 Relationship between diversification rate and climatic niche position, family climatic niche width, mean species climatic niche width, climatic niche divergence, climatic niche evolution rate and geographic extent. Results were estimated from univariate phylogenetic generalized least-squares (PGLS) regression models. The diversification rates were estimated base on species richness of China for each family, three alternative extinction rate (ε=0, 0.5 and 0.9) were selected. Significant relationship were shown in bold.

Table S3 Relationship between diversification rate and climatic niche position, climatic family niche width, mean climatic niche width, climatic niche divergence, climatic niche evolution rate and geographic extent. Results were estimated from univariate phylogenetic generalized least-squares (PGLS) regression models. The diversification rates were estimated base on global species richness for each family, three alternative extinction rate (ε=0, 0.5 and 0.9) were selected. Significant relationship were shown in bold.

Table S4 Relationship between species richness (including Chinese species and total species at global) and diversification rate, stem age. Results were estimated from univariate phylogenetic generalized least-squares (PGLS) regression models. The diversification rates were estimated base on global species richness for each family, three alternative extinction rate (ε=0, 0.5 and 0.9) were selected. Significant relationships are shown in bold.

Supporting Information

Additional supporting information may be found online in the Supporting Information for this article.