



Climatic niche divergence explains angiosperm diversification across clades in China

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Keywords:	angiosperms, diversification rate, climatic niche width, climatic niche divergence, geographic extent, climatic niche position
Abstract:	<p>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.</p>

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10 4 Short running title: Climate width and diversification in Chinese plants
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17 27 **Abstract**
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19 28 Diversification rates are critically important for understanding patterns of
20 29 species richness among clades. However, the effects of climatic niche width
21 30 on plant diversification rates remain to be elucidated. Based on the
22 31 phylogenetic, climatic, and distributional information of angiosperms in
23 32 China, a total of 26,906 species from 182 families were included in this
24 33 study. We aimed to test relationships between diversification rate and
25 34 climatic niche width and climatic niche width related variables (including
26 35 climatic niche divergence, climatic niche position, and geographic extent,
27 36 climatic niche evolutionary rate) using phylogenetic methods. We found
28 37 that climatic niche divergence had the largest unique contribution to the
29 38 diversification rate, while the unique effects of climatic niche width, climatic
30 39 niche position, geographic extent, and climatic niche evolutionary rate on
31 40 the diversification rate were negligible. We also observed that the
32 41 relationship between diversification rate and climatic niche divergence was
33 42 significantly stronger than the null assumption (Artefactual relationship
34 43 between diversification and clade-level climatic niche width via sampling
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4 44 more species). Our study supports the hypothesis that wider family climatic
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7 45 niche widths explain faster diversification rates through a higher climatic
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9 46 niche divergence rather than via higher geographic extent, higher climatic
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12 47 niche evolutionary rate or separated climatic niche position. Hence, the
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15 48 results provide a potential explanation for large-scale diversity patterns
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17 49 within families of plants.
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22 51 **Keywords:** Angiosperms, diversification rate, climatic niche width, climatic
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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

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4 76 niche width might also lead to higher rates of speciation because it would
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7 77 increase the likelihood of encountering ecological or geographical barriers
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9 78 (Darwin, 1859; Rosenzweig, 1995; Gaston, 2003). The second hypothesis is
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11
12 79 the niche conservatism hypothesis. In contrast to the divergence
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15 80 hypothesis, niche conservatism suggests that narrower climatic niches are
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18 81 associated with a higher diversification rate via allopatric speciation (Kozak
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20 82 & Wiens, 2007). For example, Baselga et al. (2011) indicated that species
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22 83 with overlapped climatic niches tend to have a higher diversification rate,
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25 84 potentially supporting the climatic niche conservatism mechanism.

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27 85 Despite the aforementioned hypotheses, very few studies have directly
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30 86 explored the effect of climatic niche width on the diversification rate at a
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33 87 large scale. Among the few previous studies, the results have not been
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36 88 consistent across different biological groups. For example, Gómez-
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38 89 Rodríguez et al. (2015) and Castro-Insua et al. (2018) found a positive
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41 90 relationship between climatic niche width and diversification rate in both
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44 91 amphibian and mammalian families. In contrast, Rolland and Salamin (2016)
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47 92 found that species with narrower climatic niche widths tended to have
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50 93 higher diversification rates among amphibians, mammals, and birds.
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53 94 However, to our knowledge, no studies have tested how climatic niche
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56 95 width affects the diversification rate among clades in plants at a large scale.
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59 96 Liu et al. (2020) estimated the climatic niche width for both plants and
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97 animals, however, they did not explore the effects of climatic niche width

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4 98 on the diversification rate.
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6 99 There may also be more indirect relationships between climatic niche
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9 100 width and diversification rates of clades. For example, a wider climatic niche
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12 101 might be accompanied by larger geographic ranges, which can lead to a
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14 102 higher diversification rate. Moreover, a higher evolutionary rate of climatic
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17 103 variables might expand the climatic niche width, then accelerate the
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20 104 diversification rate (Kozak and Wiens, 2010, Castro-Insua et al., 2018).
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22 105 Alternatively, species in different niche positions may have different
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25 106 climatic niche widths, leading to different diversification rates. For example,
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28 107 some previous studies indicated that species in tropical regions have a
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31 108 lower diversification rate than in temperate zones (Harvey et al., 2020; Igea
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33 109 et al., 2020; Tietje et al., 2022). Generally, the niche width for temperature-
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36 110 related climatic variables may be narrower in the tropical zone than that in
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39 111 the temperate zone (Janzen, 1967; Ghalambor et al., 2016), whereas the
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42 112 niche width for precipitation-related climatic variables can be wider in the
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45 113 tropical zone (Quintero & Wiens, 2013).

46 114 Here, we used a nearly complete dataset of Chinese angiosperms to
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49 115 test whether climatic niche divergence or climatic niche conservatism
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52 116 better explains species diversification among plant clades. Using these
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55 117 (and similar) resources, several studies have assessed the patterns of
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58 118 phylogenetic structure in Chinese plant assemblages at the regional scale
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60 119 (Qian et al., 2019; Gheyret et al., 2020). In addition, Su et al. (2020) reported

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4 120 that different climatic niche position predicts species richness patterns for
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7 121 tropical and temperate families. However, the mechanism by which
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9 122 climatic niche width affects the diversification rate and subsequently leads
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12 123 to species richness unevenness among plant clades remains unclear.

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14 124 In this study, we estimated the climatic niche width among the 182
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17 125 families and 26,906 species of angiosperms in China. We defined climatic
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20 126 niche divergence as the residuals of the relationship between family
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23 127 climatic niche width and mean species climatic niche width as described by
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25 128 Gómez-Rodríguez et al. (2015). We also estimated the climatic niche
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28 129 evolution rate, geographic extent (area), and diversification rate of the
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31 130 families to test the relationship between these variables across families
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34 131 using phylogenetic methods. Specifically, we aimed to address the
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37 132 following seven hypotheses (Table 1), with one hypothesis related to niche
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40 133 conservatism (H1) and five hypotheses related to niche divergence (H2–
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43 134 H6), as follows: a narrower climatic niche width predicts the diversification
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46 135 rate (H1); a wider climatic niche width explains the diversification rate via
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49 136 increasing climatic niche divergence (H2), increasing the climatic niche
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52 137 evolution rate (H3), decreasing the extinction rate (H4), increasing the
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55 138 geographic extent (H5), and changing climatic niche position (the
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58 139 separated geographic effects) (H6). Because clades with more species tend
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140 to have wider climatic niche widths, this may lead to a higher diversification
141 rate. We also tested a null hypothesis, that is, (H0) an artifactual relationship

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4 142 between diversification rate and clade-level climatic niche width occurs via
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6 143 sampling more species.
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11 145 **2 Materials and methods**

13 146 **2.1 Phylogenetic tree and climatic data**

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17 147 The phylogenetic tree in our study was based on Lu et al. (2018). The tree
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19 148 was constructed using the sequences of five genes (*atpB*, *matK*, *ndhF*, *rbcl*,
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21 and *matR*). They first generated a dated phylogeny including 5,864 species
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23 149 native to China, representing 2,665 genera and 273 families. With this tree
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25 150 as the backbone, a species-level tree including 28,076 Chinese angiosperm
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27 151 species was generated by inserting species that were not sampled in our
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29 152 generic tree within the genera to which they belong, using the package
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31 153 “S.PhyloMaker” (Qian & Jin, 2016) in R software. After matching the
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33 154 phylogenetic tree with distribution information, there were 26,977 species
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35 155 with 235 families, including 96 % and 86 % of the angiosperm species and
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37 156 families, respectively, in China (Lu et al., 2018). At least three species in each
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39 157 family were needed to run the Ornstein–Uhlenbeck (OU) model in the
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41 158 following analysis. Finally, 182 families and 26,906 species were used for
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43 159 the analysis in our study, encompassing approximately 10 % of the plant
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45 160 species worldwide.
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48 162 We performed most of the analyses on a consensus of these 1,000 trees.

49 163 We used a maximum-clade credibility tree based on the mean heights of
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4 164 these trees using TREEANNOTATOR version 1.10 (Bouckaert et al., 2014).
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6 165 The tree was fully resolved (no polytomies). All of the 182 families were
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9 166 monophyletic.
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12 167 Distributional and climatic data were generated in Lu et al. (2018). They
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14 168 divided the study area in China into 100 × 100 km (i.e., 10,000 km²) grid
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16 169 cells. The area of the grid cells on the border with less than 5,000 km² were
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18 170 excluded. The species distribution information in each grid cell were
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20 171 collected from all published national and provincial floras as well as some
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22 172 local flora, checklists, and herbarium records. There were more than
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24 173 1,400,000 records of distribution information in total. Only the mean
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26 174 annual temperature (BIO1) and mean annual precipitation (BIO12) were
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28 175 included in their dataset. We also needed the maximum temperature of the
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30 176 warmest month (BIO5), minimum temperature of the coldest month (BIO6),
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32 177 precipitation of the wettest quarter (BIO16), and precipitation of the driest
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34 178 quarter (BIO17) to estimate the climatic niche width and for the other
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36 179 analyses. Therefore, we extracted the climate data from maps of WorldClim
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38 180 version 1.4 (<http://www.worldclim.org/>), with a spatial resolution of 10 min
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40 181 (approximately 340 km²). To match the distribution information, we
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42 182 estimated these climatic variables in each grid cell (10 000 km²) using
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44 183 ArcGIS 10.1 (<http://www.esri.com/>) based on these maps. In summary, the
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46 184 species richness and niche position (BIO1, BIO5, BIO6, BIO12, BIO16, and
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48 185 BIO17) in each grid cell were included. The geographic extent (area) of each
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4 186 family was also estimated based on the distribution information. We used
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7 187 these data in our study.
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11 189 2.2 Climatic niche widths

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14 190 We estimated the family climatic niche width and the mean species climatic
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17 191 niche width in our study according to the approaches of Gómez-Rodríguez
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20 192 et al. (2015). For family climatic niche width, all species in the family were
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23 193 merged to form a single distribution area. The range of climatic data of
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25 194 each family was estimated as $Rg = \max(\text{var}) - \min(\text{var})$. Then, the climatic
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27 195 niche width for a given family i in a dataset with j families was estimated as:
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30 196 $StRg_i = [Rg_i - \min(Rg_1:Rg_j)] / [\max(Rg_1:Rg_j) - \min(Rg_1:Rg_j)]$. This yields a value
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33 197 between 0 and 1. The temperature and precipitation niche width were
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35 198 based on BIO1, BIO5, BIO6, BIO12, BIO16, and BIO17, respectively. Species
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38 199 climatic niche width was estimated based on the same protocol as the
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41 200 family climatic niche width. The mean species climatic niche width was then
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43 201 the average climatic niche width of all species within the family. Climatic
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46 202 niche divergence is the residuals of the relationship between family climatic
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49 203 niche width and mean species climatic niche width as described by Gómez-
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51 204 Rodríguez et al. (2015), which reflects a non-overlap of climatic niches
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54 205 within families (Fig. S1). The overall climatic niche width was the
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56 206 temperature niche width multiplied by the precipitation niche width. The
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59 207 niche position was described in terms of BIO1, BIO5, BIO6, BIO12, BIO16,
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4 208 and BIO17 across the geographic range of the family. All niche parameters
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6 209 are explained in Table 2. Using the abovementioned approaches, we also
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9 210 determined correlations between diversification rate, climatic niche width,
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12 211 and niche divergence across 49 orders.
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17 213 **2.3 Diversification rate and niche evolutionary rate**

19 214 The diversification rate of each family was estimated using a method
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22 215 of moment estimator (Magallón & Sanderson, 2001). The species richness
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25 216 of China and the stem age of each family were used. Stem ages were used
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28 217 because crown ages would require more extensive sampling of the species
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31 218 in each family, and monotypic families could not be incorporated (Meyer
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33 219 & Wiens, 2018). To make our results more robust, we selected three relative
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36 220 extinction rates (ϵ): two extremes ($\epsilon = 0, 0.9$) and one median ($\epsilon = 0.5$). In an
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39 221 alternative analysis, we also used the total species richness of each family
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42 222 to estimate the diversification rate. We used the R package
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45 223 "TAXONLOOKUP" version 1.1.5 (Pennell et al., 2016) to obtain the total
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48 224 species richness in each family. The data source used for this package was
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51 225 based on Plant List version 1.1 (2013). Some endemic Chinese species were
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54 226 included in the Flora of China (Wu et al., 2013), but, at the time of the study,
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57 227 have not been accepted by The Plant List. Therefore, we also included
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60 228 "unresolved" species (i.e., not yet assigned a status of "Accepted" or
229 "Synonym). We used both accepted and unresolved species to represent

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4 230 the global species richness of each family. The species richness, stem age
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7 231 and diversification rate were in Supplementary Data 1.
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9 232 Many other approaches are available to study diversification. However,
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11 233 most other methods would be impractical here because they need detailed
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14 234 species-level phylogenies within each clade. This level of detail is lacking
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17 235 for many species in our study, as described above. Furthermore, we aimed
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20 236 to explain differences in richness and diversification rates among families,
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22 237 not shifts in diversification rates over time. Therefore, the method of
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25 238 moment estimator with stem age is the most appropriate approach for our
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28 239 study.

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30 240 The evolutionary rates of the BIO1 and BIO12 were estimated to
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32 241 represent the climatic niche evolution rate. We focused on these two
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35 242 variables because they should reflect the most important aspects of the
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38 243 climatic distribution of the species (e.g., BIO1: tropical vs. temperate; BIO12:
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41 244 arid vs. mesic), and more so than short-term, extreme values (BIO5, BIO6,
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43 245 BIO16, BIO17). We first used the fitContinuous function in the package
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45 246 "geiger" version 2.0.7 (Harmon et al., 2008; Pennell et al., 2014) to fit four
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48 247 evolutionary models, namely, the Brownian motion (BM), Ornstein--
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51 248 Uhlenbeck (OU), lambda (LA), and white noise (WN). Then, the best-fitting
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53 249 model was selected based on the lowest Akaike information criterion (AIC).
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56 250 The variance (σ^2) in the best model was used as the evolutionary rate of the
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59 251 variables for each family.
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6 253 **2.4 Statistical analysis**

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9 254 The best-fit model for the diversification rate of each family was the LA
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11 255 model (Table S1). Therefore, phylogenetic generalized least-squares
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13 256 regression (PGLS) (Martins & Hansen, 1997) in the R package "caper"
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15 257 version 1.0.1 (Orme, 2013) was used to analyze the relationship between
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17 258 diversification rate and niche climatic variables. Following standard
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19 259 practice, lambda values (phylogenetic signal) were estimated by maximum
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21 260 likelihood to transform the branch lengths, with kappa and delta values
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23 261 both set to 1 (Pagel, 1999; Orme, 2013). The contribution of individual and
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25 262 combined variables (niche width, niche divergence, niche position, and
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27 263 geographic extent) was estimated using the function varpart in R package
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29 264 "vegan" version 2.5-6 (Oksanen et al., 2019). Given that the niche position
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31 265 consists of six variables, we used a stepwise procedure to select the niche
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33 266 position variables. We found that the diversification rate ~
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35 267 BIO5+BIO12+BIO16 was the best model in the stepwise analysis; then, we
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37 268 selected these three climatic variables to represent the niche position in the
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39 269 analysis.

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41 270 To account for the effect of species richness on the relationship
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43 271 between the diversification rate and climatic niche width, we created the
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45 272 same species richness for each of the families by randomly sampling from
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47 273 the whole species pool. Null niche width was estimated from a randomly
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4 274 sampled species pool of richness equivalent to real families. We randomly
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7 275 sampled 1,000 times from the 182 null families and compared the
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9 276 distribution of the coefficient of determination (r^2) of the aforementioned
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11 277 PGLS with the observed r^2 in the original families. We used the function
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14 278 "quantile" in the R base package to estimate the values of 1000 r^2 at a 95
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17 279 % confidence interval. If the observed r^2 was in the 95 % confidence interval
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19 280 of the 1,000 r^2 values, we assumed the relationship found between the
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22 281 diversification rate and niche variables was because families with more
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25 282 species span more climatic conditions. Otherwise, we assumed that the
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27 283 niche variables contributed to the diversification rate. The same
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30 284 approaches were also used for species at the order level.
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286 3 Results

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38 287 We found a strong and positive relationship between the diversification
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40 288 rate and family climatic niche width for precipitation ($r^2 = 0.389\text{--}0.437$, $P <$
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42 289 0.001), temperature ($r^2 = 0.360\text{--}0.374$, $P < 0.001$), and the overall of both
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44 290 ($r^2 = 0.413\text{--}0.468$, $P < 0.001$). While a negatively weak or non-significant
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46 291 relationship was observed between the diversification rate and mean
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48 292 species climatic niche width for precipitation ($r^2 \leq 0.001$, $P = 0.609\text{--}0.794$),
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50 293 temperature ($r^2 = 0.031\text{--}0.045$, $P < 0.004\text{--}0.018$), and the overall ($r^2 = 0.004\text{--}$
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52 294 0.011 , $P = 0.160\text{--}0.420$). This provided a stronger relationship between the
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58 295 diversification rate and climatic niche divergence (residuals of family
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4 296 climatic niche width versus mean species climatic niche width) for
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7 297 precipitation ($r^2 = 0.512\text{--}0.576$, $P < 0.001$), temperature ($r^2 = 0.482\text{--}0.503$,
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9 298 $P < 0.001$), and the overall ($r^2 = 0.480\text{--}0.558$, $P < 0.001$) (Fig. 1, Table S2).

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12 299 Therefore, the diversification rate was mainly explained by climatic niche
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14 300 divergence (H2) rather than climatic niche conservatism (H1). Neither the
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17 301 evolutionary rate of mean annual temperature nor precipitation showed a
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20 302 significant relationship with diversification rate, family climatic niche width,
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22 303 and mean species climatic niche width (Fig. S2), rejecting the hypothesis
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25 304 that the diversification rate was explained by climatic niche divergence via
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27 305 increased climatic niche evolution rate (H3). The weak or negative
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30 306 relationships between diversification rate and mean species climatic niche
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33 307 width as found in our study suggested that, wider climatic niches
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35 308 increasing diversification via reduced extinction rates (H4) was rejected,
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38 309 because the validity of this hypothesis depends on a strong relationship
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41 310 between diversification rate and mean species niche width (Table 1). Similar
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44 311 results were obtained when we divided the species into 49 orders (Fig. S3).

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46 312 To evaluate whether the effects of climatic niche width on
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48 313 diversification rate are via the geographic extent (H5) or niche position (H6),
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51 314 we first built PGLS models for the two hypotheses. A significant positive
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54 315 relationship was observed between the diversification rate and geographic
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56 316 extent ($r^2 = 0.393\text{--}0.471$, $P < 0.001$) (Fig. 2, Table S2). The relationship
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59 317 between the diversification rate and climatic niche position varied. We
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4 318 found a significantly positive relationship between the diversification rate
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6 319 and BIO5 ($r^2 = 0.272-0.320$, $P < 0.001$) and BIO16 ($r^2 = 0.009-0.110$, $P <$
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8 0.001), while a significantly negative relationship was observed between
9 320
10 0.001), while a significantly negative relationship was observed between
11 321 the diversification rate and BIO1 ($r^2 = 0.251-0.310$, $P < 0.001$), BIO6 ($r^2 =$
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13 0.271-0.292, $P < 0.001$), BIO12 ($r^2 = 0.272-0.324$, $P < 0.001$), and BIO17 (r^2
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15 = 0.219-0.231, $P < 0.001$) (Fig. 3, Table S2). The climatic niche position,
16 323
17 family climatic niche width, climatic niche divergence, and geographic
18 324
19 extent showed an important partition in explaining the diversification rates
20 325
21 (Table S2, S3). These variables were then used to determine their unique
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23 contribution to diversification rates. The explanation from climatic niche
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25 position (0.3 %), geographic extent (1 %), and climatic niche width (0.5 %)
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27 were negligible. Climatic niche divergence was the variable with the largest
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29 unique contribution (11.0 %). Most of the variances were shared among
30 330
31 climatic niche divergence, climatic niche width, geographic extent, and
32 331
33 climatic niche position (38.2 %) (Fig. 4). Therefore, the unique effects of
34 332
35 climatic niche width on the diversification rate via geographic extent (H5)
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37 or climatic niche position (H6) were limited.
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335 In the null models, we found that the observed relationship between
336 336 diversification rate and family climatic niche width, as well as the mean
337 337 species climatic width of precipitation, was generally stronger than that of
338 338 the null model (Fig. S4B, E). However, the relationship between
339 339 diversification rate and family climatic niche width, as well as the mean
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4 340 species climatic width of temperature (Fig. S4A, D) and overall climatic
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6 341 niche width (Fig. S4C, F) were not significantly different from that of the null
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9 342 model. For the climatic niche divergence, the relationship between
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11 343 diversification rate and the climatic niche divergence of temperature and
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13 344 precipitation and the overall climatic niche divergence were all more robust
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15 345 than that of the null model (Fig. S4G, I, H). Overall, the precipitation niche
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17 346 width (including family niche width and mean species niche width) was
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19 347 important for accelerating the diversification rate, while climatic niche
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21 348 divergence of both temperature and precipitation were important in
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23 349 accelerating the diversification rate for angiosperms of China. Therefore,
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25 350 the hypothesis that an artifactual relationship between diversification and
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27 351 clade-level climatic niche width would occur via sampling more species (H0)
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29 352 was rejected. We also found that the null model hypothesis (H0) was
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31 353 rejected at the order level (Fig. S5).
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355 **4 Discussion**

356 Few studies have investigated the relationship between climatic niche
357 width and species diversification rates, except for several studies in animals
358 (Gómez-Rodríguez et al., 2015; Rolland & Salamin, 2016; Castro-Insua et al.,
359 2018). Here, we explored the relationship between the climatic niche width
360 and the diversification rate of plants in China at a large scale (including
361 26,906 species and 182 families) for the first time. Our results suggest that

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4 362 climatic niche divergence (H2) rather than climatic niche conservatism (H1)
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7 363 explains the diversification rate in angiosperm clades of China. Moreover,
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9 364 we suggest that a wider family climatic niche width explains a faster
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11 365 diversification rate through higher climatic niche divergence (H2), rather
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14 366 than increasing the climatic niche evolution rate (H3), decreasing the
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17 367 extinction rate (H4), increasing the geographic extent (H5), or a separated
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20 368 climatic niche position (H6). The relationship between the diversification
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22 369 rate and family niche width for precipitation and niche divergence for
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25 370 temperature was significantly higher than that of the null assumptions,
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27 371 demonstrating that our findings were supported, rather than an artifactual
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30 372 relationship between diversification and clade-level niche width occurring
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33 373 as a result of sampling of more species (H0).

374 **4.1 Niche divergence and niche conservatism mechanisms explain** 375 **species diversification**

376 Our results have two important implications. First, we found that wider
377 climatic niche width predicts a higher diversification rate via climatic niche
378 divergence, potentially leading to species unevenness among families of
379 Chinese angiosperms (Table S4). Moreover, our results were consistent
380 with amphibian (Gómez-Rodríguez et al., 2015) and large-scale mammal
381 (Castro-Insua et al., 2018) studies. Therefore, the results suggest that plant
382 diversification may exhibit trends similar to animals. This consistency
383 suggests why animals and plants follow similar richness patterns,

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4 384 biogeographic regions, biomes, and biodiversity hotspots on a global scale
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7 385 (Liu et al., 2020). There are two potential explanations as to why climatic
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9 386 niche divergence predicts the diversification rate of angiosperms in China.
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11 387 On the one hand, a higher climatic niche divergence would decrease the
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13 388 overlap of species climatic niches, thereby reducing competition within
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15 389 families and creating additional opportunities for speciation (Kozak &
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17 390 Wiens, 2010a). Furthermore, a higher climatic niche divergence would
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19 391 cause higher spatial isolation and thus decrease the connectivity between
20
21 392 these species, reduce gene flow (Birand et al., 2010; Wiens et al., 2012) and
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23 393 lead to the emergence of reproductive barriers, and consequently
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25 394 accelerate the diversification rate.
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33 395 The niche conservatism hypothesis states that species with shared
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35 396 evolutionary history (i.e., species in an evolutionary clade) tend to tolerate
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37 397 similar environmental conditions and thus exhibit similar geographic or
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39 398 climatic distributions (Latham & Ricklefs, 1993; Wiens & Donoghue, 2004).
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41 399 This hypothesis was supported by previous studies that explain the species
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43 400 assemblages in China (Qian et al., 2019), Eastern Asia (Su et al., 2020), and
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45 401 the tropical and subtropical regions on a global scale (Cerezer et al., 2020).
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47 402 However, these studies tend to explain species unevenness at the regional
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49 403 scale rather than among clades in our study. Notably, the niche
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51 404 conservatism hypothesis postulated in previous studies generally found
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53 405 that in tropical and subtropical regions, species originated earlier and more
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4 406 abundantly, although they have low diversification rates (Harvey et al.,
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6 407 2020; Igea et al. 2020; Tietje et al. 2022). Similarly, we also showed that a
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9 408 low diversification rate was associated with high species richness patterns
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12 409 at a regional scale (Fig. S6). However, our study emphasized that the
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14 410 diversification rate was explained by climatic niche divergence, potentially
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17 411 leading to variable species unevenness among clades (Table S4). Several
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19
20 412 previous studies in animals also indicated that species richness generally
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23 413 accumulated through climatic niche conservatism at the regional level,
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25 414 while the diversification rate among clades was more commonly explained
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28 415 by climatic niche divergence (Kozak & Wiens, 2010a, b; Wiens et al., 2011;
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30 416 Kozak & Wiens, 2012).

31 32 417 **4.2 Effect of climatic niche evolution rate on diversification rate via** 33 34 35 418 **change niche divergence**

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38 419 Our results do not support hypothesis H3 that the niche evolution rate
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41 420 increases climatic niche width and climatic niche divergence. In general, a
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44 421 rapid change in the climatic niche rate would allow species to be
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47 422 distributed into new environments (increase climatic niche width), and thus
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50 423 decrease the climatic niche overlap (increase climatic niche divergence)
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53 424 among species and lead to an increase in the diversification rate (Kozak and
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56 425 Wiens, 2010, Liu et al. 2020). The discrepancy between our results and
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59 426 previous studies was probably because species with higher climatic niche
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427 evolution rates can explore new niches, while some species might be

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4 428 extinct in their original habitats. This would not increase the climatic niche
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7 429 width and climatic niche divergence of the families and, therefore, would
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9 430 not increase the diversification rate of the families. This concept needs to
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12 431 be tested in future studies.

13 14 432 **4.3 Effect of climatic niche width on diversification rate via change** 15 16 17 433 **climatic niche evolution rate**

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19 434 Our results reject the hypothesis that a wider mean species climatic
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22 435 niche width is associated with the diversification rate by decreasing the
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25 436 extinction rate (H4), which is consistent with the findings of Gómez-
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28 437 Rodríguez et al. (2015) and Castro-Insua et al. (2018). In contrast, Rolland
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31 438 and Salamin (2016) found lower extinction rates in birds, mammals, and
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34 439 amphibians with narrower climatic niches. Another study found that
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37 440 specialist species grown in narrower climatic niche ranges have a higher
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40 441 risk of extinction rates (Harris & Pimm, 2008). This discrepancy may be
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43 442 caused by human-related factors (such as excessive deforestation) and
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46 443 anthropogenic climate change, implying that the extinction of some
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49 444 groups may not have been related to their natural evolutionary history.

50 51 445 **4.4 Effect of geographic extent and niche position on diversification rate**

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54 446 The unique contribution of the geographic extent and niche position
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57 447 was negligible. Thus, the hypothesis that wider climatic niches facilitate
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60 448 faster diversification by allowing greater range expansion (H5) or changing
449 the niche position (H6) was also limited. These results are consistent with

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4 450 those of Gómez-Rodríguez et al. (2015) and Castro-Insua et al. (2018).
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7 451 However, we observed a significant negative relationship between the
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9 452 diversification rate and BIO1 (annual mean temperature) and BIO12
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11 453 (annual precipitation). This was not observed in the animals studied by
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14 454 Gómez-Rodríguez et al. (2015) and Castro-Insua et al. (2018). However,
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17 455 Igea and Tanentzap (2020a) and Jetz et al. (2012) found that the
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19 456 diversification rate slows down for angiosperms and birds in tropical and
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21 457 subtropical regions, respectively. Early studies have hypothesized
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23 458 “density-dependent” effects on diversification, where the rates of
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25 459 species accumulation within a clade would slow down over time due to
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27 460 increasing species density (Phillimore & Price, 2008; Rabosky & Lovette,
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29 461 2008; Rabosky, 2009). This hypothesis could potentially explain the
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31 462 diversification patterns in China as regions with high precipitation and
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33 463 temperature in China tend to have more species. These species originated
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35 464 earlier than those distributed in cold and dry regions (Lu et al., 2018), which
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37 465 would slow down the diversification rate in warm and wet regions because
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39 466 of their high species density. A positive relationship between diversification
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41 467 rate and BIO5, and a negative relationship between diversification rate and
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43 468 BIO6 and BIO17 were found, indicating that tolerance to extreme climatic
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45 469 habitats (such as hot, cold, and dry environments) facilitates the
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47 470 diversification of plants. The positive relationship between the
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49 471 diversification rate and BIO16 was unexpected, probably because regions
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4 472 with high temperatures usually tend to have high precipitation in China.
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6 473 **4.5 Potential sources of error**

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9 474 We acknowledge that some important sources of error may have
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12 475 impacted our results. First, our analyses were based primarily on species
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15 476 occurring in China, whereas most families and genera are more broadly
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18 477 distributed. Actually, we also estimated the diversification rate in each
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21 478 family using species found across the world. We found niche variables
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24 479 (estimated using distribution information of China) had a weaker
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27 480 relationship with a diversification rate estimated using global species
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30 481 richness (Table S3) than that of using Chinese species richness (Table S2).
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33 482 Therefore, it is reasonable to use the climatic niches of China to explain
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36 483 species diversification among clades in this region. However, this currently
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39 484 cannot be generalized to the rest of the world. Indeed, it remains to be seen
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42 485 whether the patterns reported here hold true when global sampling is used.

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45 486 Second, because of the relatively low resolution, climatic
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48 487 heterogeneity within cells was high, especially in the mountainous regions.
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51 488 While it is well known that local finer-scale niches can affect the
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54 489 diversification of lineages (Hutter et al. 2013), we did not consider the
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57 490 micro-environment of each species. It is likely that doing so would result in
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60 491 deviations in niche width. Future studies should test the same set of
492 hypotheses at smaller spatial scales (e.g. 1-km grid cells).

493 **Conclusion**

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4 494 In summary, we found climatic niche divergence explains the
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7 495 diversification rate among angiosperm families in China. These results are
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10 496 important for explaining large-scale patterns of species unevenness
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12 497 among clades in plants. Since our results for plants are consistent with that
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14 498 of animals observed in previous studies (such as birds, mammals, and
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16 499 amphibians; Gómez-Rodríguez et al., 2015; Castro-Insua et al., 2018), they
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19 500 could also explain why animals and plants follow similar richness patterns,
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22 501 biogeographic regions, biomes, and biodiversity hotspots.
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27 503 **Compliance and ethics** The authors declare that they have no known
28
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47 512 Sciences (ISEE2020YB01).
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667 **Figure legends**

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

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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

<p>niche width could facilitate diversification rate via decreased extinction rate.</p>	<p>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.</p>
<p>H5: Wider climatic niche width could facilitate diversification rate via geographic extent.</p>	<p>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.</p>
<p>H6: Wider climatic niche widths could facilitate diversification rate via separated geographic effects (niche position).</p>	<p>Strong and positive relationship between diversification rate and climatic niche position. This relationship was stronger than relationship between diversification rate and climatic niche width.</p>
<p>H0: Relationship between diversification rate and clad-level climatic niche width via sampling more species.</p>	<p>(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 (r^2) in (3) were stronger than results of randomly selected species in each family.</p>

674 **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

675

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

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684 **Fig. 2** Relationship between family climatic niche width and mean species

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4 685 climatic niche width (A, B, C). A significant relationship between
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6 686 diversification rate and geographic extent (D). Darker colors indicate
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9 687 greater overlap of data points. Diversification rates were estimated based
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11 688 on stem-group ages of families with $\epsilon=0.5$, including only species in China.
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13 689 Use of alternative values of ϵ (0, 0.9) and global richness of families yields
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15 690 similar results (Table S2, S3). Geographic extent was the distribution area
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17 691 of each family.
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25 693 **Fig. 3** Relationship between diversification rate and climatic niche position.
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27 694 BIO1, BIO5, BIO6 and BIO12, BIO16, BIO17 represent annual mean
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29 695 temperature, maximum temperature of the warmest month, minimum
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31 696 temperature of the coldest month, annual precipitation, precipitation of
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33 697 the wettest quarter and precipitation of the driest quarter respectively.
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35 698 Darker colors indicate greater overlap of data points. Diversification rates
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37 699 were estimated based on stem-group ages of families with $\epsilon=0.5$, including
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39 700 only species in China. Use of alternative values of ϵ (0, 0.9) and global
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41 701 richness of families yields similar results (Table S2, S3).
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50 702
51 703 **Fig. 4** Venn diagram showing the results of variance partitioning on a full
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53 704 model of diversification rate with climatic niche position (NP), climatic
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55 705 niche width (NW), climatic niche divergence (ND), geographic extent (GE)
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57 706 as explanatory variables. Results are shown as percentage of explained
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9 709 **Fig. S1** Relationship between family climatic niche width, mean species
10 climatic niche width and climatic niche divergence. Different color of the
11 curves represent species niche, R1, R2 and R3 are niche divergence.
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19 713 **Fig. S2** Relationship between climatic niche evolution rate and
20 diversification rate (A, B), family climatic niche width (C, D), mean species
21 climatic niche width (E, F), climatic niche divergence (G, H) for both
22 temperature and precipitation. Darker colors indicate greater overlap of
23 data points.
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32 718 **Fig. S3** Relationship between diversification rate and order climatic niche
33 width (A, B), mean species climatic niche width (C, D) and climatic niche
34 divergence (E, F) for MAP, MAT respectively. Darker colors indicate greater
35 overlap of data points. Diversification rates were estimated based on stem-
36 group ages of order with $\varepsilon=0.5$, including only species in China. Darker
37 colors indicate greater overlap of data points.
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50 725 **Fig. S4** Results from the null model at family level. The observed r^2 is
51 indicated with a vertical gray line. The black curves represent the
52 distribution of r^2 values from PGLS across the 1000 null datasets. The range
53 of dashed lines were 95% confidence intervals of r^2 across the 1000 random
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4 729 samples. Diversification rate vs family climatic niche width were shown in
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6 730 A, B, C; Diversification rate vs mean specie climatic niche width were shown
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9 731 in D, E, F; Diversification rate vs climatic niche divergence were shown in G,
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11 732 H, I. Temperature niche width were showed in A, D, E, precipitation niche
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13 733 width were showed in B, E, H, overall niche width (temperature niche width
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15 734 x precipitation niche width) were showed in C, F, I.
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22 736 **Fig. S5** Results from the null model at order level. The observed r^2 is
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24 737 indicated with a vertical gray line. The black curves represent the
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26 738 distribution of r^2 values from PGLS across the 1000 null datasets. The range
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28 739 of dashed lines were 95% confidence intervals of r^2 across the 1000 random
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30 740 samples. Diversification rate vs order climatic niche width were shown in A,
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32 741 B; Diversification rate vs mean specie climatic niche width were shown in C,
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34 742 D; Diversification rate vs climatic niche divergence were shown in E, F.
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36 743 Temperature niche width were showed in A, C, E, precipitation niche width
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38 744 were showed in B, D, F.
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48 746 **Fig. S6** Diversification rate and species richness patterns of Chinese
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50 747 angiosperms. Diversification rates were determined based on stem-group
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52 748 ages of families with $\epsilon=0.5$.
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58 750 **Table S1** Best model of all traits were estimated in our study. The lowest
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4 751 AIC was marked in bold. WN, BM, OU, LA were models of white noise,
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6 752 Brownian motion, Ornstein-Uhlenbeck and lambda respectively.
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11 754 **Table S2** Relationship between diversification rate and climatic niche
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14 755 position, family climatic niche width, mean species climatic niche width,
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17 756 climatic niche divergence, climatic niche evolution rate and geographic
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20 757 extent. Results were estimated from univariate phylogenetic generalized
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22 758 least-squares (PGLS) regression models. The diversification rates were
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25 759 estimated base on species richness of China for each family, three
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27 760 alternative extinction rate ($\epsilon=0, 0.5$ and 0.9) were selected. Significant
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30 761 relationship were shown in bold.
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35 763 **Table S3** Relationship between diversification rate and climatic niche
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38 764 position, climatic family niche width, mean climatic niche width, climatic
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41 765 niche divergence, climatic niche evolution rate and geographic extent.
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43 766 Results were estimated from univariate phylogenetic generalized least-
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46 767 squares (PGLS) regression models. The diversification rates were estimated
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48 768 base on global species richness for each family, three alternative extinction
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51 769 rate ($\epsilon=0, 0.5$ and 0.9) were selected. Significant relationship were shown in
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53 770 bold.
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58 772 **Table S4** Relationship between species richness (including Chinese species
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4 773 and total species at global) and diversification rate, stem age. Results were
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7 774 estimated from univariate phylogenetic generalized least-squares (PGLS)
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9 775 regression models. The diversification rates were estimated base on global
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12 776 species richness for each family, three alternative extinction rate ($\epsilon=0, 0.5$
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14 777 and 0.9) were selected. Significant relationships are shown in bold.

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781 **Supporting Information**

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

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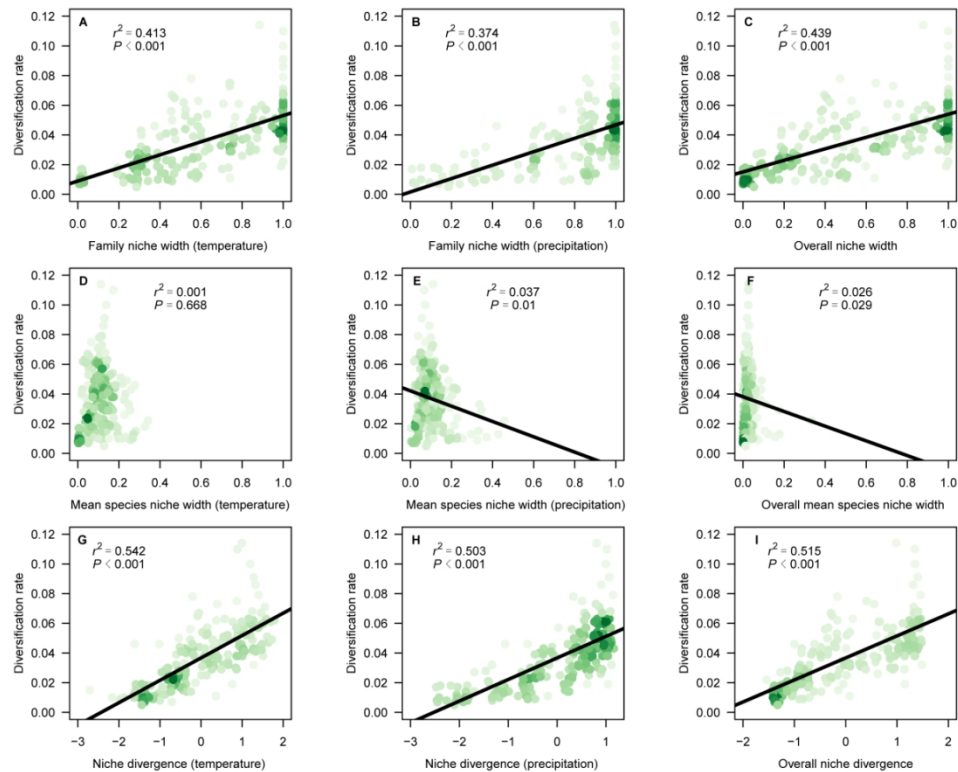


Fig. 1 Relationship between diversification rate and family climatic niche width (A, B, C), mean species climatic niche width (D, E, F) and climatic niche divergence (G, H, I) for MAP, MAT and overall respectively. Darker colors indicate greater overlap of data points. Diversification rates were estimated based on stem-group ages of family with $\epsilon=0.5$, 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).

147x114mm (220 x 220 DPI)

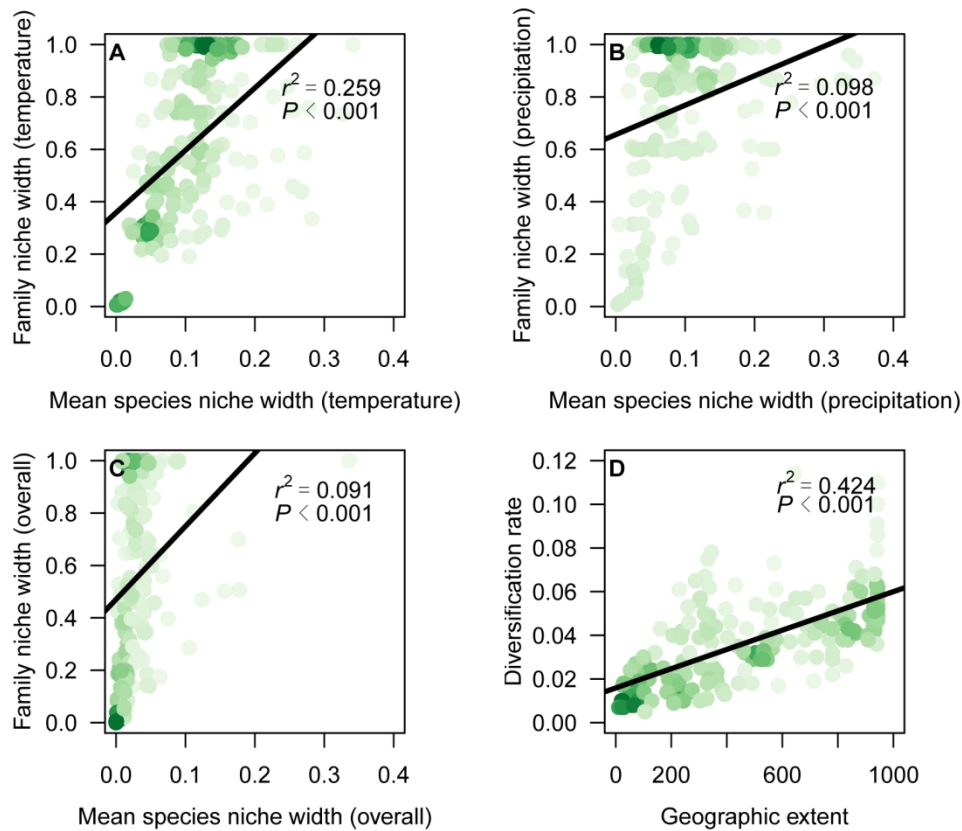


Fig. 2 Relationship between family climatic niche width and mean species climatic niche width (A, B, C). A significant relationship between diversification rate and geographic extent (D). Darker colors indicate greater overlap of data points. Diversification rates were estimated based on stem-group ages of families with $\epsilon=0.5$, 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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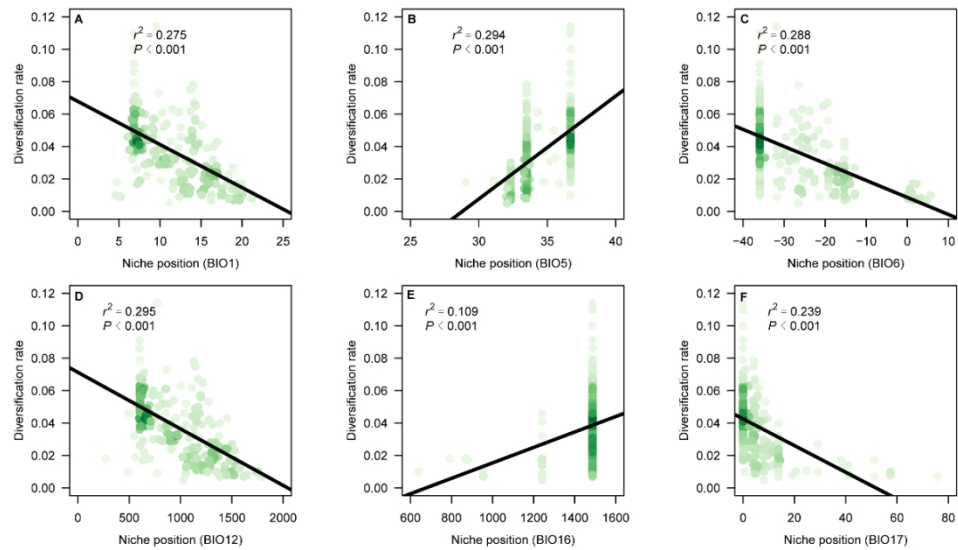


Fig. 3 Relationship between diversification rate and climatic niche position. BIO1, BIO5, BIO6 and BIO12, BIO16, BIO17 represent annual mean temperature, maximum temperature of the warmest month, minimum temperature of the coldest month, annual precipitation, precipitation of the wettest quarter and 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 $\epsilon=0.5$, 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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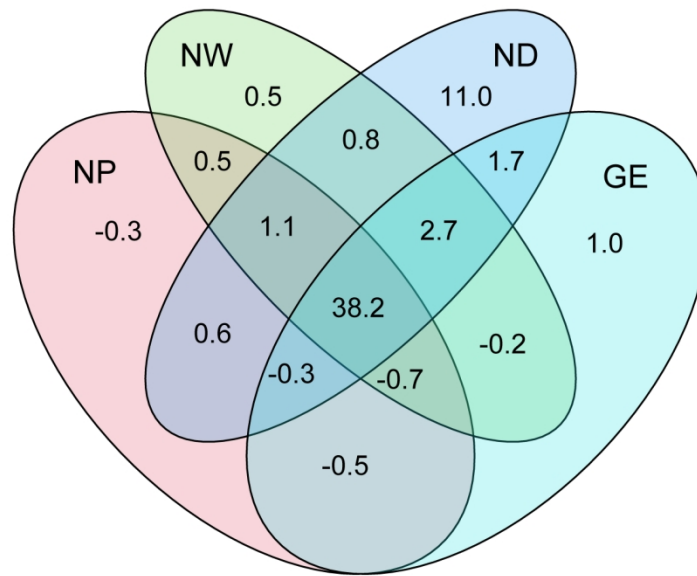


Fig. 4 Venn diagram showing the results of variance partitioning on a full model of diversification rate with climatic niche position (NP), climatic niche width (NW), climatic niche divergence (ND), geographic extent (GE) as explanatory variables. Results are shown as percentage of explained variance.

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16
17 27 **Abstract**
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19 28 Diversification rates are critically important for understanding patterns of
20 29 species richness among clades. However, the effects of climatic niche width
21 30 on plant diversification rates remain to be elucidated. Based on the
22 31 phylogenetic, climatic, and distributional information of angiosperms in
23 32 China, a total of 26,906 species from 182 families were included in this
24 33 study. We aimed to test relationships between diversification rate and
25 34 climatic niche width and climatic niche width related variables (including
26 35 climatic niche divergence, climatic niche position, and geographic extent,
27 36 climatic niche evolutionary rate) using phylogenetic methods. We found
28 37 that climatic niche divergence had the largest unique contribution to the
29 38 diversification rate, while the unique effects of climatic niche width, climatic
30 39 niche position, geographic extent, and climatic niche evolutionary rate on
31 40 the diversification rate were negligible. We also observed that the
32 41 relationship between diversification rate and climatic niche divergence was
33 42 significantly stronger than the null assumption (Artefactual relationship
34 43 between diversification and clade-level climatic niche width via sampling
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4 44 more species). Our study supports the hypothesis that wider family climatic
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7 45 niche widths explain faster diversification rates through a higher climatic
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9 46 niche divergence rather than via higher geographic extent, higher climatic
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12 47 niche evolutionary rate or separated climatic niche position. Hence, the
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15 48 results provide a potential explanation for large-scale diversity patterns
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17 49 within families of plants.
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22 51 **Keywords:** Angiosperms, diversification rate, climatic niche width, climatic
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25 52 niche divergence, geographic extent, climatic niche position
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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

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4 76 niche width might also lead to higher rates of speciation because it would
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7 77 increase the likelihood of encountering ecological or geographical barriers
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9 78 (Darwin, 1859; Rosenzweig, 1995; Gaston, 2003). The second hypothesis is
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11
12 79 the niche conservatism hypothesis. In contrast to the divergence
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15 80 hypothesis, niche conservatism suggests that narrower climatic niches are
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18 81 associated with a higher diversification rate via allopatric speciation (Kozak
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20 82 & Wiens, 2007). For example, Baselga et al. (2011) indicated that species
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22 83 with overlapped climatic niches tend to have a higher diversification rate,
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25 84 potentially supporting the climatic niche conservatism mechanism.

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27 85 Despite the aforementioned hypotheses, very few studies have directly
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30 86 explored the effect of climatic niche width on the diversification rate at a
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33 87 large scale. Among the few previous studies, the results have not been
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36 88 consistent across different biological groups. For example, Gómez-
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38 89 Rodríguez et al. (2015) and Castro-Insua et al. (2018) found a positive
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41 90 relationship between climatic niche width and diversification rate in both
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44 91 amphibian and mammalian families. In contrast, Rolland and Salamin (2016)
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47 92 found that species with narrower climatic niche widths tended to have
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50 93 higher diversification rates among amphibians, mammals, and birds.
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53 94 However, to our knowledge, no studies have tested how climatic niche
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56 95 width affects the diversification rate among clades in plants at a large scale.
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59 96 Liu et al. (2020) estimated the climatic niche width for both plants and
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97 animals, however, they did not explore the effects of climatic niche width

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6 99 There may also be more indirect relationships between climatic niche
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9 100 width and diversification rates of clades. For example, a wider climatic niche
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12 101 might be accompanied by larger geographic ranges, which can lead to a
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14 102 higher diversification rate. Moreover, a higher evolutionary rate of climatic
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17 103 variables might expand the climatic niche width, then accelerate the
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20 104 diversification rate (Kozak and Wiens, 2010, Castro-Insua et al., 2018).
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22 105 Alternatively, species in different niche positions may have different
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25 106 climatic niche widths, leading to different diversification rates. For example,
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28 107 some previous studies indicated that species in tropical regions have a
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31 108 lower diversification rate than in temperate zones (Harvey et al., 2020; Igea
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33 109 et al., 2020; Tietje et al., 2022). Generally, the niche width for temperature-
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36 110 related climatic variables may be narrower in the tropical zone than that in
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39 111 the temperate zone (Janzen, 1967; Ghalambor et al., 2016), whereas the
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42 112 niche width for precipitation-related climatic variables can be wider in the
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45 113 tropical zone (Quintero & Wiens, 2013).

46 114 Here, we used a nearly complete dataset of Chinese angiosperms to
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49 115 test whether climatic niche divergence or climatic niche conservatism
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52 116 better explains species diversification among plant clades. Using these
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55 117 (and similar) resources, several studies have assessed the patterns of
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58 118 phylogenetic structure in Chinese plant assemblages at the regional scale
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60 119 (Qian et al., 2019; Gheyret et al., 2020). In addition, Su et al. (2020) reported

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4 120 that different climatic niche position predicts species richness patterns for
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7 121 tropical and temperate families. However, the mechanism by which
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9 122 climatic niche width affects the diversification rate and subsequently leads
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12 123 to species richness unevenness among plant clades remains unclear.

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14 124 In this study, we estimated the climatic niche width among the 182
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17 125 families and 26,906 species of angiosperms in China. We defined climatic
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20 126 niche divergence as the residuals of the relationship between family
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23 127 climatic niche width and mean species climatic niche width as described by
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25 128 Gómez-Rodríguez et al. (2015). We also estimated the climatic niche
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28 129 evolution rate, geographic extent (area), and diversification rate of the
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31 130 families to test the relationship between these variables across families
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34 131 using phylogenetic methods. Specifically, we aimed to address the
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37 132 following seven hypotheses (Table 1), with one hypothesis related to niche
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40 133 conservatism (H1) and five hypotheses related to niche divergence (H2–
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43 134 H6), as follows: a narrower climatic niche width predicts the diversification
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46 135 rate (H1); a wider climatic niche width explains the diversification rate via
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49 136 increasing climatic niche divergence (H2), increasing the climatic niche
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52 137 evolution rate (H3), decreasing the extinction rate (H4), increasing the
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55 138 geographic extent (H5), and changing climatic niche position (the
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58 139 separated geographic effects) (H6). Because clades with more species tend
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60 140 to have wider climatic niche widths, this may lead to a higher diversification
141 rate. We also tested a null hypothesis, that is, (H0) an artifactual relationship

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4 142 between diversification rate and clade-level climatic niche width occurs via
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11 145 **2 Materials and methods**

13 146 **2.1 Phylogenetic tree and climatic data**

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17 147 The phylogenetic tree in our study was based on Lu et al. (2018). The tree
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20 148 was constructed using the sequences of five genes (*atpB*, *matK*, *ndhF*, *rbcl*,
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22 149 and *matR*). They first generated a dated phylogeny including 5,864 species
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25 150 native to China, representing 2,665 genera and 273 families. With this tree
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28 151 as the backbone, a species-level tree including 28,076 Chinese angiosperm
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30 152 species was generated by inserting species that were not sampled in our
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33 153 generic tree within the genera to which they belong, using the package
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35 154 “S.PhyloMaker” (Qian & Jin, 2016) in R software. After matching the
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38 155 phylogenetic tree with distribution information, there were 26,977 species
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41 156 with 235 families, including 96 % and 86 % of the angiosperm species and
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43 157 families, respectively, in China (Lu et al., 2018). At least three species in each
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46 158 family were needed to run the Ornstein–Uhlenbeck (OU) model in the
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49 159 following analysis. Finally, 182 families and 26,906 species were used for
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51 160 the analysis in our study, encompassing approximately 10 % of the plant
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54 161 species worldwide.

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56 162 We performed most of the analyses on a consensus of these 1,000 trees.

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58
59 163 We used a maximum-clade credibility tree based on the mean heights of
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4 164 these trees using TREEANNOTATOR version 1.10 (Bouckaert et al., 2014).
5
6 165 The tree was fully resolved (no polytomies). All of the 182 families were
7
8
9 166 monophyletic.
10

11
12 167 Distributional and climatic data were generated in Lu et al. (2018). They
13
14 168 divided the study area in China into 100 × 100 km (i.e., 10,000 km²) grid
15
16 169 cells. The area of the grid cells on the border with less than 5,000 km² were
17
18 170 excluded. The species distribution information in each grid cell were
19
20 171 collected from all published national and provincial floras as well as some
21
22 172 local flora, checklists, and herbarium records. There were more than
23
24 173 1,400,000 records of distribution information in total. Only the mean
25
26 174 annual temperature (BIO1) and mean annual precipitation (BIO12) were
27
28 175 included in their dataset. We also needed the maximum temperature of the
29
30 176 warmest month (BIO5), minimum temperature of the coldest month (BIO6),
31
32 177 precipitation of the wettest quarter (BIO16), and precipitation of the driest
33
34 178 quarter (BIO17) to estimate the climatic niche width and for the other
35
36 179 analyses. Therefore, we extracted the climate data from maps of WorldClim
37
38 180 version 1.4 (<http://www.worldclim.org/>), with a spatial resolution of 10 min
39
40 181 (approximately 340 km²). To match the distribution information, we
41
42 182 estimated these climatic variables in each grid cell (10 000 km²) using
43
44 183 ArcGIS 10.1 (<http://www.esri.com/>) based on these maps. In summary, the
45
46 184 species richness and niche position (BIO1, BIO5, BIO6, BIO12, BIO16, and
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48 185 BIO17) in each grid cell were included. The geographic extent (area) of each
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4 186 family was also estimated based on the distribution information. We used
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6
7 187 these data in our study.
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11 189 2.2 Climatic niche widths

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14 190 We estimated the family climatic niche width and the mean species climatic
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16
17 191 niche width in our study according to the approaches of Gómez-Rodríguez
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19
20 192 et al. (2015). For family climatic niche width, all species in the family were
21
22
23 193 merged to form a single distribution area. The range of climatic data of
24
25 194 each family was estimated as $Rg = \max(\text{var}) - \min(\text{var})$. Then, the climatic
26
27 195 niche width for a given family i in a dataset with j families was estimated as:
28
29
30 196 $StRg_i = [Rg_i - \min(Rg_1:Rg_j)] / [\max(Rg_1:Rg_j) - \min(Rg_1:Rg_j)]$. This yields a value
31
32
33 197 between 0 and 1. The temperature and precipitation niche width were
34
35 198 based on BIO1, BIO5, BIO6, BIO12, BIO16, and BIO17, respectively. Species
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37
38 199 climatic niche width was estimated based on the same protocol as the
39
40
41 200 family climatic niche width. The mean species climatic niche width was then
42
43 201 the average climatic niche width of all species within the family. Climatic
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45
46 202 niche divergence is the residuals of the relationship between family climatic
47
48
49 203 niche width and mean species climatic niche width as described by Gómez-
50
51 204 Rodríguez et al. (2015), which reflects a non-overlap of climatic niches
52
53
54 205 within families (Fig. S1). The overall climatic niche width was the
55
56 206 temperature niche width multiplied by the precipitation niche width. The
57
58
59 207 niche position was described in terms of BIO1, BIO5, BIO6, BIO12, BIO16,
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4 208 and BIO17 across the geographic range of the family. All niche parameters
5
6 209 are explained in [Table 2](#). Using the abovementioned approaches, we also
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8
9 210 determined correlations between diversification rate, climatic niche width,
10
11
12 211 and niche divergence across 49 orders.
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15 212

17 213 **2.3 Diversification rate and niche evolutionary rate**

19 214 The diversification rate of each family was estimated using a method
20
21
22 215 of moment estimator (Magallón & Sanderson, 2001). The species richness
23
24
25 216 of China and the stem age of each family were used. Stem ages were used
26
27
28 217 because crown ages would require more extensive sampling of the species
29
30
31 218 in each family, and monotypic families could not be incorporated (Meyer
32
33 219 & Wiens, 2018). To make our results more robust, we selected three relative
34
35
36 220 extinction rates (ϵ): two extremes ($\epsilon = 0, 0.9$) and one median ($\epsilon = 0.5$). In an
37
38
39 221 alternative analysis, we also used the total species richness of each family
40
41
42 222 to estimate the diversification rate. We used the R package
43
44
45 223 "TAXONLOOKUP" version 1.1.5 (Pennell et al., 2016) to obtain the total
46
47
48 224 species richness in each family. The data source used for this package was
49
50
51 225 based on Plant List version 1.1 (2013). Some endemic Chinese species were
52
53
54 226 included in the Flora of China (Wu et al., 2013), but, at the time of the study,
55
56
57 227 have not been accepted by The Plant List. Therefore, we also included
58
59
60 228 "unresolved" species (i.e., not yet assigned a status of "Accepted" or
229 "Synonym). We used both accepted and unresolved species to represent

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4 230 the global species richness of each family. The species richness, stem age
5
6
7 231 and diversification rate were in Supplementary Data 1.
8

9 232 Many other approaches are available to study diversification. However,
10
11 233 most other methods would be impractical here because they need detailed
12
13
14 234 species-level phylogenies within each clade. This level of detail is lacking
15
16
17 235 for many species in our study, as described above. Furthermore, we aimed
18
19
20 236 to explain differences in richness and diversification rates among families,
21
22 237 not shifts in diversification rates over time. Therefore, the method of
23
24
25 238 moment estimator with stem age is the most appropriate approach for our
26
27
28 239 study.
29

30 240 The evolutionary rates of the BIO1 and BIO12 were estimated to
31
32 241 represent the climatic niche evolution rate. We focused on these two
33
34
35 242 variables because they should reflect the most important aspects of the
36
37
38 243 climatic distribution of the species (e.g., BIO1: tropical vs. temperate; BIO12:
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40
41 244 arid vs. mesic), and more so than short-term, extreme values (BIO5, BIO6,
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43 245 BIO16, BIO17). We first used the fitContinuous function in the package
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45
46 246 "geiger" version 2.0.7 (Harmon et al., 2008; Pennell et al., 2014) to fit four
47
48 247 evolutionary models, namely, the Brownian motion (BM), Ornstein--
49
50
51 248 Uhlenbeck (OU), lambda (LA), and white noise (WN). Then, the best-fitting
52
53
54 249 model was selected based on the lowest Akaike information criterion (AIC).
55
56 250 The variance (σ^2) in the best model was used as the evolutionary rate of the
57
58
59 251 variables for each family.
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6 253 **2.4 Statistical analysis**

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8
9 254 The best-fit model for the diversification rate of each family was the LA
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11 255 model (Table S1). Therefore, phylogenetic generalized least-squares
12
13
14 256 regression (PGLS) (Martins & Hansen, 1997) in the R package "caper"
15
16
17 257 version 1.0.1 (Orme, 2013) was used to analyze the relationship between
18
19 258 diversification rate and niche climatic variables. Following standard
20
21
22 259 practice, lambda values (phylogenetic signal) were estimated by maximum
23
24
25 260 likelihood to transform the branch lengths, with kappa and delta values
26
27
28 261 both set to 1 (Pagel, 1999; Orme, 2013). The contribution of individual and
29
30
31 262 combined variables (niche width, niche divergence, niche position, and
32
33
34 263 geographic extent) was estimated using the function varpart in R package
35
36
37 264 "vegan" version 2.5-6 (Oksanen et al., 2019). Given that the niche position
38
39
40 265 consists of six variables, we used a stepwise procedure to select the niche
41
42
43 266 position variables. We found that the diversification rate ~
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46 267 BIO5+BIO12+BIO16 was the best model in the stepwise analysis; then, we
47
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49 268 selected these three climatic variables to represent the niche position in the
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51
52 269 analysis.

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54
55 270 To account for the effect of species richness on the relationship
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58 271 between the diversification rate and climatic niche width, we created the
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61 272 same species richness for each of the families by randomly sampling from
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63
64 273 the whole species pool. Null niche width was estimated from a randomly

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4 274 sampled species pool of richness equivalent to real families. We randomly
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6
7 275 sampled 1,000 times from the 182 null families and compared the
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9 276 distribution of the coefficient of determination (r^2) of the aforementioned
10
11 277 PGLS with the observed r^2 in the original families. We used the function
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13
14 278 "quantile" in the R base package to estimate the values of 1000 r^2 at a 95
15
16
17 279 % confidence interval. If the observed r^2 was in the 95 % confidence interval
18
19 280 of the 1,000 r^2 values, we assumed the relationship found between the
20
21
22 281 diversification rate and niche variables was because families with more
23
24
25 282 species span more climatic conditions. Otherwise, we assumed that the
26
27
28 283 niche variables contributed to the diversification rate. The same
29
30 284 approaches were also used for species at the order level.
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285

286 3 Results

37
38 287 We found a strong and positive relationship between the diversification
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40 288 rate and family climatic niche width for precipitation ($r^2 = 0.389\text{--}0.437$, $P <$
41
42 289 0.001), temperature ($r^2 = 0.360\text{--}0.374$, $P < 0.001$), and the overall of both
43
44 290 ($r^2 = 0.413\text{--}0.468$, $P < 0.001$). While a negatively weak or non-significant
45
46 291 relationship was observed between the diversification rate and mean
47
48 292 species climatic niche width for precipitation ($r^2 \leq 0.001$, $P = 0.609\text{--}0.794$),
49
50 293 temperature ($r^2 = 0.031\text{--}0.045$, $P < 0.004\text{--}0.018$), and the overall ($r^2 = 0.004\text{--}$
51
52 294 0.011 , $P = 0.160\text{--}0.420$). This provided a stronger relationship between the
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58 295 diversification rate and climatic niche divergence (residuals of family
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4 296 climatic niche width versus mean species climatic niche width) for
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6 297 precipitation ($r^2 = 0.512\text{--}0.576$, $P < 0.001$), temperature ($r^2 = 0.482\text{--}0.503$,
7
8
9 298 $P < 0.001$), and the overall ($r^2 = 0.480\text{--}0.558$, $P < 0.001$) (Fig. 1, Table S2).
10
11 299 Therefore, the diversification rate was mainly explained by climatic niche
12
13 300 divergence (H2) rather than climatic niche conservatism (H1). Neither the
14
15 301 evolutionary rate of mean annual temperature nor precipitation showed a
16
17 302 significant relationship with diversification rate, family climatic niche width,
18
19 303 and mean species climatic niche width (Fig. S2), rejecting the hypothesis
20
21 304 that the diversification rate was explained by climatic niche divergence via
22
23 305 increased climatic niche evolution rate (H3). The weak or negative
24
25 306 relationships between diversification rate and mean species climatic niche
26
27 307 width as found in our study suggested that, wider climatic niches
28
29 308 increasing diversification via reduced extinction rates (H4) was rejected,
30
31 309 because the validity of this hypothesis depends on a strong relationship
32
33 310 between diversification rate and mean species niche width (Table 1). Similar
34
35 311 results were obtained when we divided the species into 49 orders (Fig. S3).

312 To evaluate whether the effects of climatic niche width on
313 diversification rate are via the geographic extent (H5) or niche position (H6),
314 we first built PGLS models for the two hypotheses. A significant positive
315 relationship was observed between the diversification rate and geographic
316 extent ($r^2 = 0.393\text{--}0.471$, $P < 0.001$) (Fig. 2, Table S2). The relationship
317 between the diversification rate and climatic niche position varied. We
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4 318 found a significantly positive relationship between the diversification rate
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6 319 and BIO5 ($r^2 = 0.272-0.320$, $P < 0.001$) and BIO16 ($r^2 = 0.009-0.110$, $P <$
7
8 0.001), while a significantly negative relationship was observed between
9 320
10 0.001), while a significantly negative relationship was observed between
11 321 the diversification rate and BIO1 ($r^2 = 0.251-0.310$, $P < 0.001$), BIO6 ($r^2 =$
12
13 0.271-0.292, $P < 0.001$), BIO12 ($r^2 = 0.272-0.324$, $P < 0.001$), and BIO17 (r^2
14 322
15 = 0.219-0.231, $P < 0.001$) (Fig. 3, Table S2). The climatic niche position,
16 323
17 family climatic niche width, climatic niche divergence, and geographic
18 324
19 extent showed an important partition in explaining the diversification rates
20 325
21 (Table S2, S3). These variables were then used to determine their unique
22 326
23 contribution to diversification rates. The explanation from climatic niche
24 327
25 position (0.3 %), geographic extent (1 %), and climatic niche width (0.5 %)
26 328
27 were negligible. Climatic niche divergence was the variable with the largest
28 329
29 unique contribution (11.0 %). Most of the variances were shared among
30 330
31 climatic niche divergence, climatic niche width, geographic extent, and
32 331
33 climatic niche position (38.2 %) (Fig. 4). Therefore, the unique effects of
34 332
35 climatic niche width on the diversification rate via geographic extent (H5)
36 333
37 or climatic niche position (H6) were limited.
38 334

335 In the null models, we found that the observed relationship between
336 336 diversification rate and family climatic niche width, as well as the mean
337 337 species climatic width of precipitation, was generally stronger than that of
338 338 the null model (Fig. S4B, E). However, the relationship between
339 339 diversification rate and family climatic niche width, as well as the mean
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4 340 species climatic width of temperature (Fig. S4A, D) and overall climatic
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6
7 341 niche width (Fig. S4C, F) were not significantly different from that of the null
8
9 342 model. For the climatic niche divergence, the relationship between
10
11 343 diversification rate and the climatic niche divergence of temperature and
12
13 344 precipitation and the overall climatic niche divergence were all more robust
14
15 345 than that of the null model (Fig. S4G, I, H). Overall, the precipitation niche
16
17 346 width (including family niche width and mean species niche width) was
18
19 347 important for accelerating the diversification rate, while climatic niche
20
21 348 divergence of both temperature and precipitation were important in
22
23 349 accelerating the diversification rate for angiosperms of China. Therefore,
24
25 350 the hypothesis that an artifactual relationship between diversification and
26
27 351 clade-level climatic niche width would occur via sampling more species (H0)
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29 352 was rejected. We also found that the null model hypothesis (H0) was
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31 353 rejected at the order level (Fig. S5).
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355 **4 Discussion**

356 Few studies have investigated the relationship between climatic niche
357 width and species diversification rates, except for several studies in animals
358 (Gómez-Rodríguez et al., 2015; Rolland & Salamin, 2016; Castro-Insua et al.,
359 2018). Here, we explored the relationship between the climatic niche width
360 and the diversification rate of plants in China at a large scale (including
361 26,906 species and 182 families) for the first time. Our results suggest that
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4 362 climatic niche divergence (H2) rather than climatic niche conservatism (H1)
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7 363 explains the diversification rate in angiosperm clades of China. Moreover,
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9 364 we suggest that a wider family climatic niche width explains a faster
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11 365 diversification rate through higher climatic niche divergence (H2), rather
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13
14 366 than increasing the climatic niche evolution rate (H3), decreasing the
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16
17 367 extinction rate (H4), increasing the geographic extent (H5), or a separated
18
19
20 368 climatic niche position (H6). The relationship between the diversification
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22 369 rate and family niche width for precipitation and niche divergence for
23
24
25 370 temperature was significantly higher than that of the null assumptions,
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27 371 demonstrating that our findings were supported, rather than an artifactual
28
29
30 372 relationship between diversification and clade-level niche width occurring
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32
33 373 as a result of sampling of more species (H0).

374 **4.1 Niche divergence and niche conservatism mechanisms explain** 375 **species diversification**

376 Our results have two important implications. First, we found that wider
377 climatic niche width predicts a higher diversification rate via climatic niche
378 divergence, potentially leading to species unevenness among families of
379 Chinese angiosperms (Table S4). Moreover, our results were consistent
380 with amphibian (Gómez-Rodríguez et al., 2015) and large-scale mammal
381 (Castro-Insua et al., 2018) studies. Therefore, the results suggest that plant
382 diversification may exhibit trends similar to animals. This consistency
383 suggests why animals and plants follow similar richness patterns,

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4 384 biogeographic regions, biomes, and biodiversity hotspots on a global scale
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7 385 (Liu et al., 2020). There are two potential explanations as to why climatic
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9 386 niche divergence predicts the diversification rate of angiosperms in China.
10
11 387 On the one hand, a higher climatic niche divergence would decrease the
12
13 388 overlap of species climatic niches, thereby reducing competition within
14
15 389 families and creating additional opportunities for speciation (Kozak &
16
17 390 Wiens, 2010a). Furthermore, a higher climatic niche divergence would
18
19 391 cause higher spatial isolation and thus decrease the connectivity between
20
21 392 these species, reduce gene flow (Birand et al., 2010; Wiens et al., 2012) and
22
23 393 lead to the emergence of reproductive barriers, and consequently
24
25 394 accelerate the diversification rate.
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32
33 395 The niche conservatism hypothesis states that species with shared
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35 396 evolutionary history (i.e., species in an evolutionary clade) tend to tolerate
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37 397 similar environmental conditions and thus exhibit similar geographic or
38
39 398 climatic distributions (Latham & Ricklefs, 1993; Wiens & Donoghue, 2004).
40
41 399 This hypothesis was supported by previous studies that explain the species
42
43 400 assemblages in China (Qian et al., 2019), Eastern Asia (Su et al., 2020), and
44
45 401 the tropical and subtropical regions on a global scale (Cerezer et al., 2020).
46
47 402 However, these studies tend to explain species unevenness at the regional
48
49 403 scale rather than among clades in our study. Notably, the niche
50
51 404 conservatism hypothesis postulated in previous studies generally found
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53 405 that in tropical and subtropical regions, species originated earlier and more
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4 406 abundantly, although they have low diversification rates (Harvey et al.,
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6 407 2020; Igea et al. 2020; Tietje et al. 2022). Similarly, we also showed that a
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8
9 408 low diversification rate was associated with high species richness patterns
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12 409 at a regional scale (Fig. S6). However, our study emphasized that the
13
14 410 diversification rate was explained by climatic niche divergence, potentially
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16
17 411 leading to variable species unevenness among clades (Table S4). Several
18
19
20 412 previous studies in animals also indicated that species richness generally
21
22 413 accumulated through climatic niche conservatism at the regional level,
23
24 414 while the diversification rate among clades was more commonly explained
25
26
27 415 by climatic niche divergence (Kozak & Wiens, 2010a, b; Wiens et al., 2011;
28
29
30 416 Kozak & Wiens, 2012).

31 32 417 **4.2 Effect of climatic niche evolution rate on diversification rate via** 33 34 35 418 **change niche divergence**

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37
38 419 Our results do not support hypothesis H3 that the niche evolution rate
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40 420 increases climatic niche width and climatic niche divergence. In general, a
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43 421 rapid change in the climatic niche rate would allow species to be
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45
46 422 distributed into new environments (increase climatic niche width), and thus
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48 423 decrease the climatic niche overlap (increase climatic niche divergence)
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51 424 among species and lead to an increase in the diversification rate (Kozak and
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53 425 Wiens, 2010, Liu et al. 2020). The discrepancy between our results and
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56 426 previous studies was probably because species with higher climatic niche
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59 427 evolution rates can explore new niches, while some species might be
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4 428 extinct in their original habitats. This would not increase the climatic niche
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7 429 width and climatic niche divergence of the families and, therefore, would
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9 430 not increase the diversification rate of the families. This concept needs to
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12 431 be tested in future studies.

13 14 432 **4.3 Effect of climatic niche width on diversification rate via change** 15 16 17 433 **climatic niche evolution rate**

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19 434 Our results reject the hypothesis that a wider mean species climatic
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21
22 435 niche width is associated with the diversification rate by decreasing the
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24
25 436 extinction rate (H4), which is consistent with the findings of Gómez-
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27
28 437 Rodríguez et al. (2015) and Castro-Insua et al. (2018). In contrast, Rolland
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30
31 438 and Salamin (2016) found lower extinction rates in birds, mammals, and
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33
34 439 amphibians with narrower climatic niches. Another study found that
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37 440 specialist species grown in narrower climatic niche ranges have a higher
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39
40 441 risk of extinction rates (Harris & Pimm, 2008). This discrepancy may be
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43 442 caused by human-related factors (such as excessive deforestation) and
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46 443 anthropogenic climate change, implying that the extinction of some
47
48
49 444 groups may not have been related to their natural evolutionary history.

50 51 445 **4.4 Effect of geographic extent and niche position on diversification rate**

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53
54 446 The unique contribution of the geographic extent and niche position
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56
57 447 was negligible. Thus, the hypothesis that wider climatic niches facilitate
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59
60 448 faster diversification by allowing greater range expansion (H5) or changing
449 the niche position (H6) was also limited. These results are consistent with

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4 450 those of Gómez-Rodríguez et al. (2015) and Castro-Insua et al. (2018).
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6
7 451 However, we observed a significant negative relationship between the
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9 452 diversification rate and BIO1 (annual mean temperature) and BIO12
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11 453 (annual precipitation). This was not observed in the animals studied by
12
13
14 454 Gómez-Rodríguez et al. (2015) and Castro-Insua et al. (2018). However,
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17 455 Igea and Tanentzap (2020a) and Jetz et al. (2012) found that the
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19 456 diversification rate slows down for angiosperms and birds in tropical and
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21
22 457 subtropical regions, respectively. Early studies have hypothesized
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25 458 “density-dependent” effects on diversification, where the rates of
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27
28 459 species accumulation within a clade would slow down over time due to
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30
31 460 increasing species density (Phillimore & Price, 2008; Rabosky & Lovette,
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33
34 461 2008; Rabosky, 2009). This hypothesis could potentially explain the
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37 462 diversification patterns in China as regions with high precipitation and
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39
40 463 temperature in China tend to have more species. These species originated
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42
43 464 earlier than those distributed in cold and dry regions (Lu et al., 2018), which
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45
46 465 would slow down the diversification rate in warm and wet regions because
47
48
49 466 of their high species density. A positive relationship between diversification
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51
52 467 rate and BIO5, and a negative relationship between diversification rate and
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54
55 468 BIO6 and BIO17 were found, indicating that tolerance to extreme climatic
56
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58 469 habitats (such as hot, cold, and dry environments) facilitates the
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61 470 diversification of plants. The positive relationship between the
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64 471 diversification rate and BIO16 was unexpected, probably because regions

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4 472 with high temperatures usually tend to have high precipitation in China.
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6 473 **4.5 Potential sources of error**

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9 474 We acknowledge that some important sources of error may have
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12 475 impacted our results. First, our analyses were based primarily on species
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14 476 occurring in China, whereas most families and genera are more broadly
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17 477 distributed. Actually, we also estimated the diversification rate in each
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20 478 family using species found across the world. We found niche variables
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22 479 (estimated using distribution information of China) had a weaker
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25 480 relationship with a diversification rate estimated using global species
26
27 481 richness (Table S3) than that of using Chinese species richness (Table S2).
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29
30 482 Therefore, it is reasonable to use the climatic niches of China to explain
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33 483 species diversification among clades in this region. However, this currently
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35
36 484 cannot be generalized to the rest of the world. Indeed, it remains to be seen
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38 485 whether the patterns reported here hold true when global sampling is used.
39

40 486 Second, because of the relatively low resolution, climatic
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43 487 heterogeneity within cells was high, especially in the mountainous regions.
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46 488 While it is well known that local finer-scale niches can affect the
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48 489 diversification of lineages (Hutter et al. 2013), we did not consider the
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51 490 micro-environment of each species. It is likely that doing so would result in
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54 491 deviations in niche width. Future studies should test the same set of
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56 492 hypotheses at smaller spatial scales (e.g. 1-km grid cells).
57

58 493 **Conclusion**

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4 494 In summary, we found climatic niche divergence explains the
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7 495 diversification rate among angiosperm families in China. These results are
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10 496 important for explaining large-scale patterns of species unevenness
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12 497 among clades in plants. Since our results for plants are consistent with that
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14 498 of animals observed in previous studies (such as birds, mammals, and
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16 499 amphibians; Gómez-Rodríguez et al., 2015; Castro-Insua et al., 2018), they
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18 500 could also explain why animals and plants follow similar richness patterns,
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22 501 biogeographic regions, biomes, and biodiversity hotspots.
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667 **Figure legends**

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

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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

<p>niche width could facilitate diversification rate via decreased extinction rate.</p>	<p>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.</p>
<p>H5: Wider climatic niche width could facilitate diversification rate via geographic extent.</p>	<p>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.</p>
<p>H6: Wider climatic niche widths could facilitate diversification rate via separated geographic effects (niche position).</p>	<p>Strong and positive relationship between diversification rate and climatic niche position. This relationship was stronger than relationship between diversification rate and climatic niche width.</p>
<p>H0: Relationship between diversification rate and clad-level climatic niche width via sampling more species.</p>	<p>(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 (r^2) in (3) were stronger than results of randomly selected species in each family.</p>

674 **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

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

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684 **Fig. 2** Relationship between family climatic niche width and mean species

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4 685 climatic niche width (A, B, C). A significant relationship between
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6 686 diversification rate and geographic extent (D). Darker colors indicate
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9 687 greater overlap of data points. Diversification rates were estimated based
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12 688 on stem-group ages of families with $\epsilon=0.5$, including only species in China.
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14 689 Use of alternative values of ϵ (0, 0.9) and global richness of families yields
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17 690 similar results (Table S2, S3). Geographic extent was the distribution area
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20 691 of each family.

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25 693 **Fig. 3** Relationship between diversification rate and climatic niche position.
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27 694 BIO1, BIO5, BIO6 and BIO12, BIO16, BIO17 represent annual mean
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30 695 temperature, maximum temperature of the warmest month, minimum
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33 696 temperature of the coldest month, annual precipitation, precipitation of
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36 697 the wettest quarter and precipitation of the driest quarter respectively.
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38 698 Darker colors indicate greater overlap of data points. Diversification rates
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41 699 were estimated based on stem-group ages of families with $\epsilon=0.5$, including
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44 700 only species in China. Use of alternative values of ϵ (0, 0.9) and global
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47 701 richness of families yields similar results (Table S2, S3).

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51 703 **Fig. 4** Venn diagram showing the results of variance partitioning on a full
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54 704 model of diversification rate with climatic niche position (NP), climatic
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57 705 niche width (NW), climatic niche divergence (ND), geographic extent (GE)
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60 706 as explanatory variables. Results are shown as percentage of explained

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9 709 **Fig. S1** Relationship between family climatic niche width, mean species
10 climatic niche width and climatic niche divergence. Different color of the
11 curves represent species niche, R1, R2 and R3 are niche divergence.
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19 713 **Fig. S2** Relationship between climatic niche evolution rate and
20 diversification rate (A, B), family climatic niche width (C, D), mean species
21 climatic niche width (E, F), climatic niche divergence (G, H) for both
22 temperature and precipitation. Darker colors indicate greater overlap of
23 data points.
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32 718 **Fig. S3** Relationship between diversification rate and order climatic niche
33 width (A, B), mean species climatic niche width (C, D) and climatic niche
34 divergence (E, F) for MAP, MAT respectively. Darker colors indicate greater
35 overlap of data points. Diversification rates were estimated based on stem-
36 group ages of order with $\varepsilon=0.5$, including only species in China. Darker
37 colors indicate greater overlap of data points.
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50 725 **Fig. S4** Results from the null model at family level. The observed r^2 is
51 indicated with a vertical gray line. The black curves represent the
52 distribution of r^2 values from PGLS across the 1000 null datasets. The range
53 of dashed lines were 95% confidence intervals of r^2 across the 1000 random
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4 729 samples. Diversification rate vs family climatic niche width were shown in
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6 730 A, B, C; Diversification rate vs mean specie climatic niche width were shown
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9 731 in D, E, F; Diversification rate vs climatic niche divergence were shown in G,
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11 732 H, I. Temperature niche width were showed in A, D, E, precipitation niche
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13 733 width were showed in B, E, H, overall niche width (temperature niche width
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15 734 x precipitation niche width) were showed in C, F, I.
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22 736 **Fig. S5** Results from the null model at order level. The observed r^2 is
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24 737 indicated with a vertical gray line. The black curves represent the
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26 738 distribution of r^2 values from PGLS across the 1000 null datasets. The range
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28 739 of dashed lines were 95% confidence intervals of r^2 across the 1000 random
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30 740 samples. Diversification rate vs order climatic niche width were shown in A,
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32 741 B; Diversification rate vs mean specie climatic niche width were shown in C,
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34 742 D; Diversification rate vs climatic niche divergence were shown in E, F.
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36 743 Temperature niche width were showed in A, C, E, precipitation niche width
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38 744 were showed in B, D, F.
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48 746 **Fig. S6** Diversification rate and species richness patterns of Chinese
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50 747 angiosperms. Diversification rates were determined based on stem-group
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52 748 ages of families with $\epsilon=0.5$.
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58 750 **Table S1** Best model of all traits were estimated in our study. The lowest
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4 751 AIC was marked in bold. WN, BM, OU, LA were models of white noise,
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6 752 Brownian motion, Ornstein-Uhlenbeck and lambda respectively.
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11 754 **Table S2** Relationship between diversification rate and climatic niche
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14 755 position, family climatic niche width, mean species climatic niche width,
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17 756 climatic niche divergence, climatic niche evolution rate and geographic
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20 757 extent. Results were estimated from univariate phylogenetic generalized
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22 758 least-squares (PGLS) regression models. The diversification rates were
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25 759 estimated base on species richness of China for each family, three
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27 760 alternative extinction rate ($\epsilon=0, 0.5$ and 0.9) were selected. Significant
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30 761 relationship were shown in bold.
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35 763 **Table S3** Relationship between diversification rate and climatic niche
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38 764 position, climatic family niche width, mean climatic niche width, climatic
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41 765 niche divergence, climatic niche evolution rate and geographic extent.
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43 766 Results were estimated from univariate phylogenetic generalized least-
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45 767 squares (PGLS) regression models. The diversification rates were estimated
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48 768 base on global species richness for each family, three alternative extinction
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51 769 rate ($\epsilon=0, 0.5$ and 0.9) were selected. Significant relationship were shown in
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53 770 bold.
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58 772 **Table S4** Relationship between species richness (including Chinese species
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4 773 and total species at global) and diversification rate, stem age. Results were
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7 774 estimated from univariate phylogenetic generalized least-squares (PGLS)
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9 775 regression models. The diversification rates were estimated base on global
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12 776 species richness for each family, three alternative extinction rate ($\epsilon=0, 0.5$
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14 777 and 0.9) were selected. Significant relationships are shown in bold.

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781 **Supporting Information**

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

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