

# Historical and contemporary climate jointly determines seed plant diversity patterns in eastern Eurasia

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August 21, 2023

## Abstract

Large-scale spatial patterns of species richness are one of the central issues in ecology. Although hypotheses based on effects of contemporary climate, evolutionary history and historical climate change have been employed to explain the mechanisms underlying species richness patterns, variation in relative contribution of different hypothesis remains a major challenge. Here, using newly-compiled distribution data with a spatial resolution of 100 \* 100 km<sup>2</sup> for 43,023 seed plant species in eastern Eurasia, we mapped species richness patterns for plants with different growth forms (i.e., woody vs. herbaceous) and range sizes (i.e., wide-ranged vs. narrow-ranged species), and compared the contribution of four hypotheses on these patterns, i.e., freezing tolerance hypothesis, historical climate change hypothesis, Janzen hypothesis and diversification rate hypothesis. We found that species richness of all seed plants presented a clear latitudinal gradient and was the highest in southwestern China and Central Asian mountains. Notably, species richness patterns and their dominant hypotheses differed between species groups. Historical climate change dominated richness patterns of overall, herbaceous and wide-ranged herbaceous species. The freezing tolerance hypothesis dominated those for all woody and wide-ranged woody species, while the Janzen hypothesis dominated narrow-ranged woody and herbaceous species. Our study suggests that different hypotheses contribute to large-scale species richness patterns via their dominant effects in different species groups. Interestingly, our study did not support the diversification rate hypothesis, but demonstrated high contribution of historical climate change to plant diversity, providing new perspectives on the mechanisms of plant diversity patterns in eastern Eurasia.

## INTRODUCTION

Global biodiversity is facing a rapid loss due to anthropogenic threats, and effective conservation of biodiversity has become a global challenge. Revealing large-scale patterns of species richness and the underlying mechanisms provides data and scientific support for the spatial prioritization of biodiversity conservation, and hence has increasingly intrigued ecologists over the past decades (Wang et al., 2011; Pimm et al., 2014; Mccauley et al., 2015). Previous studies had widely investigated global and regional patterns in species richness of terrestrial vertebrates, especially amphibians (Buckley & Jetz, 2007; Jenkins et al., 2013), birds (Davies et al., 2007; Hawkins et al., 2007; Jetz et al., 2012) and mammals (Schipper et al., 2008; Karanth et al., 2009; Buckley et al., 2010). However, despite the important role in terrestrial ecosystems, the patterns of species richness of seed plants remain much less studied due to the scarcity of high-resolution distribution data across large spatial scales compared to terrestrial vertebrates (Kreft & Jetz, 2007; Jenkins et al., 2013).

In order to comprehend the mechanisms that drive the spatial patterns of species richness, several theoretical hypotheses based on the effects of contemporary environment, diversification rates and historical climate

change have been proposed and widely discussed (Jetz & Rahbek, 2002; Willig et al., 2003; Currie et al., 2004; Ricklefs, 2006; Svenning & Skov, 2007; Wang et al., 2012). Many studies have identified contemporary climate as a crucial driver of patterns in species richness. One of the contemporary climate hypotheses, i.e. the freezing tolerance hypothesis, has been recognized as a key mechanism for explaining the effect of contemporary climate on latitudinal gradients in plant species richness across northern temperate regions (Lathern & Ricklefs, 1993; Wang et al., 2011; Xu et al., 2016; Su et al., 2020). The prerequisite assumption under this hypothesis is evolutionary niche conservatism (Latham & Ricklefs, 1993; Zanne et al., 2014). This hypothesis suggests that most clades originated in tropical climates, and could hardly adapt to and survive the cold climate at high latitudes due to evolutionary niche conservatism, which will lead to the decrease in species richness from the tropics to temperate regions. Based on this hypothesis, winter coldness is suggested to be the dominant factor for the geographic patterns in species richness. This hypothesis has been employed to explain woody species richness in eastern Eurasia (Wang et al., 2011; Su et al., 2020). For example, mean temperature of the coldest quarter was found to be the most influential factor for patterns of woody plants richness in China and of woody families with the tropical affinity in eastern Eurasia (Wang et al. 2011; Su et al., 2020).

Another widely-discussed hypothesis concerning the influence of contemporary climate on patterns of species richness is the Janzen hypothesis (Ghalambor et al., 2006; Gill et al., 2016; Liu et al., 2017; Lyu et al., 2018; Smith, 2018). Janzen (1976) found that tropical mountains have very low temperature seasonality, while temperate mountains have large temperature seasonality. The large temperature seasonality in temperate mountains requires that temperate organisms have to evolve broad ranges of temperature tolerances to adapt to large climate seasonal changes. In contrast, tropical organisms could evolve narrow temperature tolerances due to the less seasonal nature of the tropical climate. Therefore, Janzen (1967) postulated that tropical mountain passes pose a more formidable obstacle to species dispersal than temperate mountain passes with the same elevations, which leads to higher speciation rate and species richness in tropical than in temperate mountains. Several recent studies provided support for the predictions of the Janzen hypothesis. For instance, Polato et al. (2018) revealed that tropical insect species have narrower temperature tolerance, larger genetic differences and higher speciation rate than temperate ones. The Janzen hypothesis also explains well the Rhododendron species richness pattern in China (Shrestha et al. 2018).

In addition to the effects of contemporary environment, recent studies suggest that evolutionary history also exerts a crucial role in shaping geographical species richness patterns (Stevens, 2006, 2011). Specifically, the diversification rate hypothesis argues that high species richness in certain regions is a result of high diversification rate (Mittelbach et al., 2007; Svenning et al., 2008; Tietje et al., 2022). Previous studies have offered evidential support for the diversification rate hypothesis. For example, researches have shown that diversification rate serves as the most influential predictor of the latitudinal gradient of species richness for amphibians (Pyron and Wiens 2013), mammals (Moritz et al., 2014), and flowering plants (Jansson and Davies, 2008).

Recent studies have found that modern species richness may have also been influenced by historical climate change. Since the Last Glacial Maximum (LGM, ca. 21 000 – 18 000 years ago), high latitudes of the northern Hemisphere were covered by massive glaciers. The presence of glaciers had dramatic impacts on plant distributions (Svenning and Skov, 2005; Davies et al., 2009; Sandel et al., 2011), resulting in the migration of a large number of plant species to the south or extinction during the LGM. After the glaciers retreated, species re-colonized the northern latitudes. However, many species didn't spread northward to areas where climate is suitable due to dispersal constraints (Svenning & Skov, 2005; Normand et al., 2011). For example, recent studies showed that climate change since the LGM was the dominant factor of species richness for trees, amphibians, reptiles and dung beetles in Europe (Svenning & Skov, 2005; Araújo et al. 2008; Hortal et al. 2011; Feng et al., 2019), for woody plants in Central Asia (Liu et al., 2019) and trees in the northern Hemisphere (Feng et al. 2019), and played an important role in shaping mammals, birds, and amphibians richness patterns in Africa (Pinkert et al. 2020).

Although these hypotheses have been supported in different studies, their relative contributions on species

richness patterns remains highly controversial, which has hindered the development of general theories on mechanisms of species richness patterns. Moreover, previous studies suggested that eastern Eurasia has been much less affected by climate change since the LGM than Europe and North America (Qian, 2002; Qian & Ricklefs, 2004). Whether climate change since the LGM is a weaker predictor of plant richness patterns in eastern Eurasia than contemporary climate and diversification rates remains to be tested.

Woody and herbaceous growth forms have different responses to climate changes owing to their different life history strategies (Steinberg et al., 1990; Pretzsch, 2002; Massad, 2013; Luo et al., 2022). Moreover, species with different range sizes (i.e., narrow-ranged vs. wide-ranged species) may also respond differently to climate changes (Svenning & Skov, 2007). Previous studies suggest that narrow-ranged species tend to possess constrained dispersal abilities and cannot spread to all suitable habitats, hence their species richness patterns are more susceptible to local evolutionary processes (Dynesius & Jansson, 2000; Jansson, 2003; Liu et al., 2017). On the contrary, wide-ranged species are more able to cope with climate variations, and their richness patterns tend to be more strongly associated with environmental factors (Cauwer et al., 2016). Therefore, understanding variations in drivers behind species richness patterns among woody and herbaceous growth forms, as well as among species with different range sizes would improve our capability to predict the impacts of global changes on communities dominated by different species (Zanne et al., 2018; Luo et al., 2022). Previous studies on plant richness patterns have been strongly biased to woody plants, while species richness patterns of herbaceous plants are much less studied due to lack of data. Freezing tolerance has been frequently considered to be an important factor influencing woody plant richness patterns (Oommen & Shanker, 2005; Wang et al., 2011; Su et al., 2020). Compared with woody species, herbaceous species are less sensitive to freezing due to their shorter lifespan, higher rate of niche evolution, and weaker niche conservatism (Smith & Beaulieu, 2009; Zanne et al., 2018). However, whether woody and herbaceous species richness is similarly dominated by the freezing tolerance hypotheses remains to be tested.

Eastern Eurasia has high plant species richness and preserves high proportions of endemic and relict plant taxa, especially in the mountains in Southwest China and Central Asia. In addition, eastern Eurasia contains several global biodiversity hotspots (i.e., Central Asian mountains, Himalayas, Southwest China mountains) (Myers et al., 2000). Previous studies indicated that plant species richness in eastern Eurasia is significantly greater than that observed at equivalent latitudes in Europe and North America due to evolutionary and ecological mechanisms (Milne & Abbott 2002; Qian et al., 2003; Ding et al., 2020). Therefore, understanding species richness patterns in this region is important not only for gaining insights into the evolutionary development of floras in the Northern Hemisphere (Xu et al., 2013; Chen et al., 2018), but also biodiversity conservation planning. However, the paucity of data on plant distributions in eastern Eurasia compared to Europe and North America severely limits our understanding of plant richness patterns and their genesis in this region. In earlier investigations, Wang et al. (2011) and Su et al. (2020) established a database on the distribution of woody plants across China and eastern Eurasia, providing a foundational resource for exploring plant richness in the region. However, data on the distribution of herbaceous plants in this region are still very scarce. Here, we compiled the first more comprehensive database of seed plant distributions in eastern Eurasia and mapped the species richness patterns for all species, different species groups (i.e. woody, herbaceous, wide-ranged and narrow-ranged species). Then we explored the determinants of species richness patterns for different species groups. Our objective is to examine the validity of the following three hypotheses . 1) Climate change since the LGM has lower effect on patterns of species richness in eastern Eurasia than contemporary climate and diversification rate. 2) The dominant hypothesis for species richness patterns differs between different growth forms and different range size. Specifically, we expect that woody and herbaceous species richness is dominated by the cold tolerance hypothesis and climate change since the LGM respectively. Wide-ranged woody and herbaceous richness is dominated by the contemporary climate, while narrow-ranged woody and herbaceous richness is dominated by climate change since the LGM .

## MATERIAL AND METHODS

### Species distribution data

The Database of Seed Plant Distribution in Eastern Eurasia was newly-compiled, containing geographic

distributions with a spatial resolution of  $100 \times 100$  km<sup>2</sup> for 43,023 seed plant species (from 4,479 genera and 316 families). The species distributions were compiled from a great number of published regional and local floras and checklists for China, Central Asia (Kazakhstan, Kyrgyzstan, Tajikistan, Turkmenistan, Uzbekistan), Mongolia and Russia. Occurrence data for these countries were also obtained from online databases, including the ‘National specimen information infrastructure’ (NSII, < [www.nsii.org.cn](http://www.nsii.org.cn) >, accessed in May 2019), ‘the global biodiversity information facility’ (GBIF, <<http://www.gbif.org/>>), and the ‘Virtual guide to the flora of Mongolia’ (<<http://greif.uni-greifswald.de/floragreif/>>).

The raw species distribution data in the data sources were normally recorded in the following formats: 1) spatial polygons (e.g., species distribution ranges), 2) spatial points (e.g., occurrences of specimen collections), and 3) administrative (e.g., villages, towns, counties) and geographic units (e.g., mountains and nature reserves) where species occurrences were recorded. The distribution data in the first two formats from published floras and checklists were manually digitized using ArcGIS 10. In contrast, distribution data in the third format were georeferenced using the following databases, including GeoNames (containing over 25 million geographical names, <http://www.geonames.org> ), Global Administrative Areas Database (<https://gadm.org/> ) and World Geographical Scheme for Recording Plant Distributions (<https://www.tdwg.org/standards/wgsrpd/> ). To enhance the precision of species distributions, we only kept the records of administrative/geographic units at the level of or smaller than counties so that the records can be precisely transformed into 1-2 grid cells. Specially, the coordinates of specimen occurrences available in the online databases were downloaded.

Then the raw distribution data were transformed into gridded distributions using a grid of  $100 \times 100$  km<sup>2</sup>. Specifically, a grid cell was considered as presence for a species when it contained at least one point of specimen locations, or more than 50% of its area was covered the species’ distribution range comprised of polygons and administrative/geographic units. The nomenclature of species names from different sources were merged following the ‘Catalogue of Life’ (<[www.catalogueoflife.org](http://www.catalogueoflife.org) >). After finishing the general database, we carefully examined the species distribution data manually to enhance the quality of the database. The records of cultivated species and exotic species were removed and intraspecific units (i.e., subspecies and varieties) were merged to species. It’s noteworthy that the completeness of our database varies across different regions. Compared to China and Russia, the sampling effort in Mongolia and Central Asian countries may be less sufficient. However, our database has collected all available data that could be obtained, and it is currently one of the most comprehensive plant species distribution databases for East Asia to date.

## Environmental data

To assess the impact of the freezing tolerance hypothesis on species richness patterns, mean temperature of coldest quarter (MTCQ, degC. The coldest quarter is defined as period from December through January to February) was used following prior researches (Wang et al., 2011; Liu et al., 2017; Su et al., 2020). We selected temperature seasonality (TSN, standard deviation of monthly mean temperature within one year) and elevational range within a grid cell (TOPO\_RANGE) to represent Janzen hypothesis. MTCQ and TSN were obtained from the WorldClim database (<http://www.worldclim.org>, Ver. 2) with a spatial resolution of 30 arc seconds ( 1 km at the equator). Then, we calculated the average of MTCQ and TSN in each grid cell ( $100 * 100$  km<sup>2</sup>). TOPO\_RANGE with each grid cell was determined by calculating the difference between the maximum and minimum elevations, using GTOPO data at a spatial resolution of  $1 \times 1$  km (<https://www.usgs.gov/>).

Temperature and precipitation changes since the LGM (MAT anomaly LGM and MAP anomaly LGM) were computed as the absolute differences between the LGM and contemporary temperature and precipitation values and were used to assess the impacts of historical climate change on species richness patterns. The temperature and precipitation data in the LGM were reconstructed by MPI-ESM-P model (Watanabe et al. 2011) and were also retrieved from the WorldClim website, with a spatial resolution of 1 arc minute.

## Diversification rate

Net diversification rate (DR) was used to evaluate the effect of diversification rate hypothesis. DR was

estimated following Jetz et al. (2012). This method treated the inverse of species' mean equal splits measure as the species-level lineage diversification rate for each individual species. Here, we used the dated phylogeny containing 353,185 seed plant species generated by Smith and Brown (2018) (i.e., ALLOTB), which has gained substantial traction in macroecological and biogeographical studies (Sandel et al., 2019; Weigelt et al., 2019; Luo et al., 2023). This phylogeny was constructed by placing the molecular phylogenies (containing 79,855 species in total) for major clades (i.e., orders) in the backbone of the Open Tree of Life, and inserting species without molecular data as polytomies in their families. To generate a fully-resolved phylogeny, we conducted a polytomy resolving analysis using a birth-death (Yule) bifurcation process (see Lu et al., 2018). To evaluate whether polytomy resolving process may influence our results, we generated 100 resolved phylogenies by repeating this process 100 times, and repeated our analysis using all these 100 phylogenies.

## Statistical Analyses

Species richness was quantified as the cumulative count of species within each grid cell. We draw species richness patterns in the whole study area using ArcGIS 10. To explore the differences in species richness patterns between growth forms, we divided all species into woody and herbaceous growth forms. Woody species were defined following Zanne et al. (2014) and included trees, shrubs and lianas (Luo et al., 2023). Among all species, 15207 recorded as woody. Then, we also divided all species into wide-ranged and narrow-ranged species. We ranked the species in descending order of range size, and then categorized the upper 25% species as wide-ranged species and the lower 50% as narrow-ranged species following Araujo et al. (2008).

To compare the impacts of different hypotheses on species richness, we first conducted univariate generalized linear models (GLMs) with quasi-Poisson residuals between species richness and different environmental variables, and the slopes and the explanatory power of each variable (i.e., model pseudo- $R^2$ ) were extracted. We also draw scatter plots between species richness and each variable. Second, hierarchical partitioning analysis was applied to estimate the independent and joint contributions of each hypothesis. We drew Venn diagrams of the relative percentage contribution of each hypothesis. Due to the significant negative correlation between species richness and DR, which is in contrast to the prediction of the diversification rate hypothesis, we did not include DR in the hierarchical partitioning analysis. Positive spatial autocorrelations in model residuals can inflate type-I errors when testing statistical hypothesis and lead to an excess of significant results in model tests due to the inter-dependency of residuals. Therefore, in all analyses,  $R^2$  instead of p values were used to compare the performance of models.

All analyses were conducted in R 4.0.3 with ggplot2, picante and ape packages (<http://www.Rproject.org>).

## RESULTS

### Species richness patterns in eastern Eurasia

The overall species richness and species richness of the two growth forms (i.e., woody and herbaceous species) and different range size groups (i.e., wide-ranged and narrow-ranged) in eastern Eurasia decreased with latitude (Figs 1,2). Species richness centers differ between growth forms (Fig. 2a, b) and between wide-ranged and narrow ranged species (Fig. 2c, d, e, f). Specifically, woody species peak in the Southern China (e.g. Yunnan-Guizhou Plateau) (Fig. 2a), while herbaceous species peak in the mountains of central Asia and Hengduan Mountains (Fig. 2b). Most of narrow ranged woody and herbaceous species concentrate in the Southwestern China (Fig. 2d), while wide-ranged woody species peak in the Southern China (e.g. the border of Guangxi and Guizhou, Qinba Mountain) and wide-ranged herbaceous species also peak in the mountains of central Asia (Fig. 2c, e). The overall species richness is similar to the wide-ranged species (Figs. 1,2c).

### Determinants of species richness patterns

Univariate GLMs showed that richness patterns of overall species were positively corrected with MTCQ and TOPO\_RANGE, but negatively corrected with LGM anomaly MAT, LGM anomaly MAP, TSN and DR (Tab. 1; Fig. 3). In other words, regions with high MTCQ and TOPO\_RANGE and low LGM anomaly MAT, LGM anomaly MAP and TSN have high species richness. These results are consistent with the freezing tolerance

hypothesis, the hypothesis of climate change since the LGM and Janzen hypothesis. Species richness was significantly negatively correlated with DR, suggesting that regions with high diversification rate do not have high species richness. This result contradicts the prediction of diversification rate hypothesis.

Hierarchical partitioning analyses showed consistent results with those of univariate GLMs. The relative contributions of different hypotheses (the freezing tolerance hypothesis, climate change since the LGM and Janzen hypothesis) on species richness patterns differ between growth forms and range size groups. For overall, herbaceous, and wide-ranged herbaceous species, the climate change since the LGM had the highest independent contribution on species richness patterns (Figs. 4,5). In contrast, the freezing tolerance hypothesis and Janzen hypothesis had the highest joint and independent effects on woody and narrow-ranged species richness respectively (Fig. 5).

## Discussion

The patterns of species richness for all species and different species groups in eastern Eurasia presented clear latitudinal gradients (Fig.1,2), which was similar to the widely validated latitudinal gradients in species richness of other groups and in other regions (Hawkins et al., 2007; Buckley et al., 2010). However, there are still differences in the spatial patterns in species richness between different species groups, which is mainly due to differences in the responses to the environment, evolution histories and life history strategies among different species groups (Svenning & Skov, 2007; Normand et al., 2011; Zanne et al., 2018). Indeed, our results revealed that the species richness patterns of different groups had different responses to environmental factors. These differences suggest that species richness patterns of different species groups are likely dominated by different hypotheses.

### Climate change since the LGM dominated the patterns of seed plant richness in eastern Eurasia

Early studies generally suggested that eastern Eurasia had been less affected by climate change since the LGM, especially compared to Europe and North America (Qian, 2002; Qian & Ricklefs, 2004). Therefore, there is a general tendency to assume that the species richness patterns in eastern Eurasia are only weakly influenced by climate change since the LGM in comparison with the effects of contemporary climate and long-term diversification rate. However, our results did not support this traditional view. Our findings indicate that climate change since the LGM dominated all plant species richness patterns in eastern Eurasia (Fig. 3). Specifically, the richness of all species combined was significantly negatively correlated with the climate change since the LGM. In other words, species richness of plants was lower at sites with stronger temperature and precipitation changes since the LGM but was higher in regions with more stable climate. The impact of climate change since the LGM on species richness patterns has also been demonstrated in other taxa and other continents. For example, studies on species richness of trees (Svenning and Skov 2007), reptiles and amphibians in Europe (Araujo et al. 2008), consistently highlighted climate change during the LGM as a significant driver shaping species richness patterns.

Previous studies suggest that climate change since the LGM may influence contemporary species richness patterns via its effects on species dispersal. The strong temperature and precipitation changes since the LGM may have significantly affected the northern regions, causing a large number of species to migrate south and to mountainous regions. After the LGM, many species did not spread north and colonize all the areas with suitable climates (Sandel et al., 2011; Wang et al., 2012; Liu et al., 2017). The Central Asian mountains and southern China had experienced relatively weak climate change since the LGM and hence had become refuges for species (Mittermeier et al., 2005; Lopez-Pujol et al., 2011a, b; Sandel et al., 2011; Tang et al., 2018). Their topographic diversity provided sufficient ecological stability to buffer the effects of extreme climatic fluctuations (Sandel et al., 2011).

### The influence of diversification rate hypothesis on species richness patterns

Notably, our results revealed that species richness patterns were negatively correlated with the geographic pattern of average diversification rate, which does not support the diversification rate hypothesis (Mittelbach et al., 2007; Svenning et al., 2008; Tietje et al., 2022). In recent studies, the contribution of net diversification

rate to large-scale species richness patterns remains debated. Previous studies on the species richness of some flower plant groups, such as palms (Arecaceae) (Svenning et al., 2008), Zygophyllaceae (Wang et al., 2018) and Rhododendrons (Shrestha et al., 2018), indicated that net diversification rate was strongly positively correlated with species richness patterns, and hence supported the diversification rate hypothesis. In contrast, Jansson and Davies (2008) and Igea & Tanentzap (2020) found that higher species richness of angiosperms in the tropics cannot be explained by higher diversification rates, which is consistent to our findings. One explanation for the debate on diversification rate as the dominant factor of species richness patterns is that temperate lineages have fewer species and their unoccupied ecological niche space may be large, thus increasing the chances of species divergence (Simpson, 1953; Schluter, 2016). In addition, species richness may also be influenced by the accumulation time of speciation (Mittelbach et al., 2007; Etienne et al., 2019). Compared with the accumulation time of temperate taxa in temperate regions, taxa with tropical origin have occupied tropical regions for a much longer time, and had a longer time to diversify there (Stephens and Wiens, 2003; Li and Wiens 2019).

### **Difference in patterns and determinants of woody and herbaceous species richness**

Our results indicated that the dominant hypothesis for geographic patterns of species richness significant differed between woody and herbaceous growth forms. Specifically, the geographic pattern in species richness of woody plants is dominated by the freezing tolerance hypothesis, while that of herbaceous plants is dominated by the hypothesis related to climate change since the LGM. These findings provide more evidence supporting the importance of the freezing tolerance hypothesis for diversity patterns in different groups and different regions (Francis & Currie, 1998; Wang et al., 2011; Zhao et al. 2020). In China, mean temperature of the coldest quarter has been found to be the dominant factor driving the pattern of woody plant richness (Wang et al., 2011; Su et al., 2020), mainly because China's woody flora contains more tropical and subtropical floristic components (Fang & Yoda, 1989), and most of these tropical species are very sensitive to low temperature in winter and cannot widely spread to the north (Wang et al., 2011). This finding on Chinese woody plants, together with our results at a larger spatial scale, suggested that freezing tolerance hypothesis dominates the species richness patterns of woody plants in the entire eastern Eurasia.

Interestingly, our results indicated much weaker effects of the freezing tolerance hypothesis on herbaceous species richness than on woody species richness. That might be related to difference in functional traits and divergent evolution histories between the two growth forms (Hawkins et al., 2011; Engemann et al., 2016; Zanne et al., 2014, 2018). Above-ground parts of herbaceous plants can die in winter with shoots located above or below ground to avoid cold stress, while woody plants with shoots and branches above ground cannot (Engemann et al., 2016; Zanne et al., 2014, 2018). Woody species typically grow their stems and renewed shoots taller than herbaceous species, exposing them to lower temperatures. Moreover, herbaceous species tend to have shorter generation time, higher evolutionary rates and weaker niche conservatism (Smith & Donoghue, 2008; Qi et al., 2014; Liu et al., 2018), and consequently tend to be less sensitive to freezing than woody species (Smith & Beaulieu, 2009).

Climate change since the LGM has had a weaker impact on woody plant species richness than it had on herbaceous species richness. Compared with woody species, herbaceous species tend to have higher evolutionary rates (Smith & Donoghue, 2008; Qi et al., 2014), which may speed up microevolutionary adaptation of herbaceous plants during environmental changes (Hof et al., 2011; Liu et al., 2018). Therefore, herbaceous species are likely able to track climate change more quickly than woody plant as they could better adapt to environmental changes since the LGM (Albuquerque et al., 2011; Liu et al., 2018). In addition, the distribution of herbaceous plants is also higher in temperate regions, which experienced greater climate change during LGM compared to the southern mountainous regions. These findings may explain why the geographic pattern of herbaceous species richness is more sensitive to climate change during LGM.

### **Difference in patterns and determinants of wide-ranged and narrow-ranged species richness**

Studies had shown that wide-ranged species are important contributors to the overall geographic pattern of species richness because the larger amount of distribution records of wide-ranged species have a higher

contribution to the species richness counts (Lenmon et al., 2003; Liu et al., 2017). Our results found that the richness pattern of wide-ranged woody and herbaceous species showed similar pattern to that of all woody and herbaceous species in eastern Eurasia (Fig. 2a,c; b,e). Moreover, the dominant hypotheses explaining the geographic patterns in wide-ranged woody and herbaceous species were also consistent with those for all woody and herbaceous species respectively. Specifically, the richness pattern of wide-ranged woody species was dominated by the freezing tolerance hypothesis, while that of wide-ranged herbaceous species was dominated by climate change since the LGM (see the previous section).

However, the dominant hypothesis of the richness patterns of narrow-ranged woody and herbaceous species differed from those for all woody and herbaceous species. Compared with other hypotheses, the Janzen hypothesis had the highest explanatory power for the richness pattern of narrow-ranged woody and herbaceous species (Table 1, Fig.5). The dominant impact of Janzen hypothesis on species richness patterns has also been demonstrated in several taxa such as Gesneriaceae and gymnosperms (Liu et al., 2017; Lyu et al., 2018). These studies consistently suggested that areas with low temperature seasonality and high topographic heterogeneity have higher narrow-ranged species diversity. Climate stability preserves more genotypes adapting to specific environments, and these genotypes often have low dispersal ability and propensity, and hence are more likely to have small distributions (Dynesius & Jansson, 2000; Jansson, 2003; Liu et al., 2017). In addition, regions with high topographic heterogeneity can provide a richer variety of habitat types and more biologically available resources, thus providing more ecological niches for more organisms to survive (Currie, 1991). High topographic heterogeneity can also provide a refuge for organisms during environmental changes, thus preserving more organisms (Cun & Wang, 2010; Fjeldsa et al, 2012). Since the mid-Cenozoic, due to diverse habitats and climatic stability, the mountains of southern China have been a refuge for narrow-ranged species, preserving a large number of narrow-ranged species of plants and vertebrates (Lopez-Pujol et al, 2011a; Sandel et al, 2011; Xing & Ree, 2017). However, the mountainous areas in southern China have undergone rapid climate warming, surpassing the rate observed in lowland regions (Pepin et al., 2015). Furthermore, future air temperatures are anticipated to be even higher than current levels (Nogues-Bravo et al., 2007, Rebetz and Reinhard, 2007). Strong climatic changes may have aggravated the extinction risk of the narrow-ranged plant diversity in these mountains (Moritz et al., 2008; Menendez et al., 2014; Rowe et al., 2015).

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Table 1 Relationship between All, different growth forms (Woody, Herb) and range size (Wide-ranged, Narrow-ranged) species richness and environment factors in eastern Eurasia. + indicates a positive correlation, - indicates a negative correlation.

R2	MTCQ	LGM_MATanomaly	LGM_MAPanomaly	TSN	TOPO_RANGE	DR
All	0.53	0.59	0.12	0.54	0.20	0.56
Woody	0.71	0.66	0.14	0.70	0.14	0.39
Herbaceous	0.35	0.48	0.08	0.39	0.21	0.56
Wide-ranged Woody	0.65	0.62	0.13	0.58	0.11	0.37
Narrow-ranged Woody	0.64	0.53	0.03	0.77	0.17	0.54
Wide-ranged Herbaceous	0.27	0.38	0.07	0.25	0.12	0.54
Narrow-ranged Herbaceous	0.32	0.35	0.01	0.50	0.29	0.32

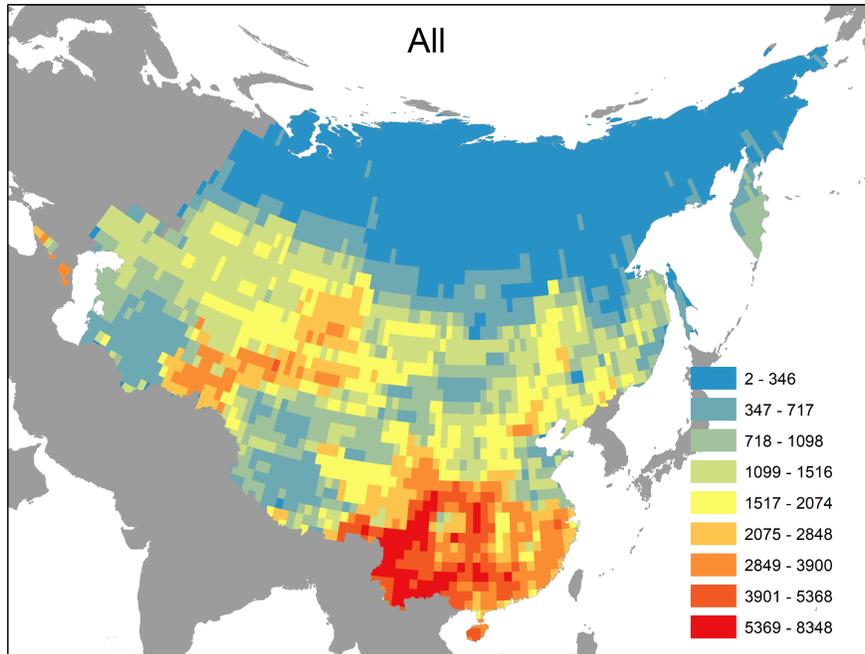


Fig 1 Patterns of all species richness in eastern Eurasia.

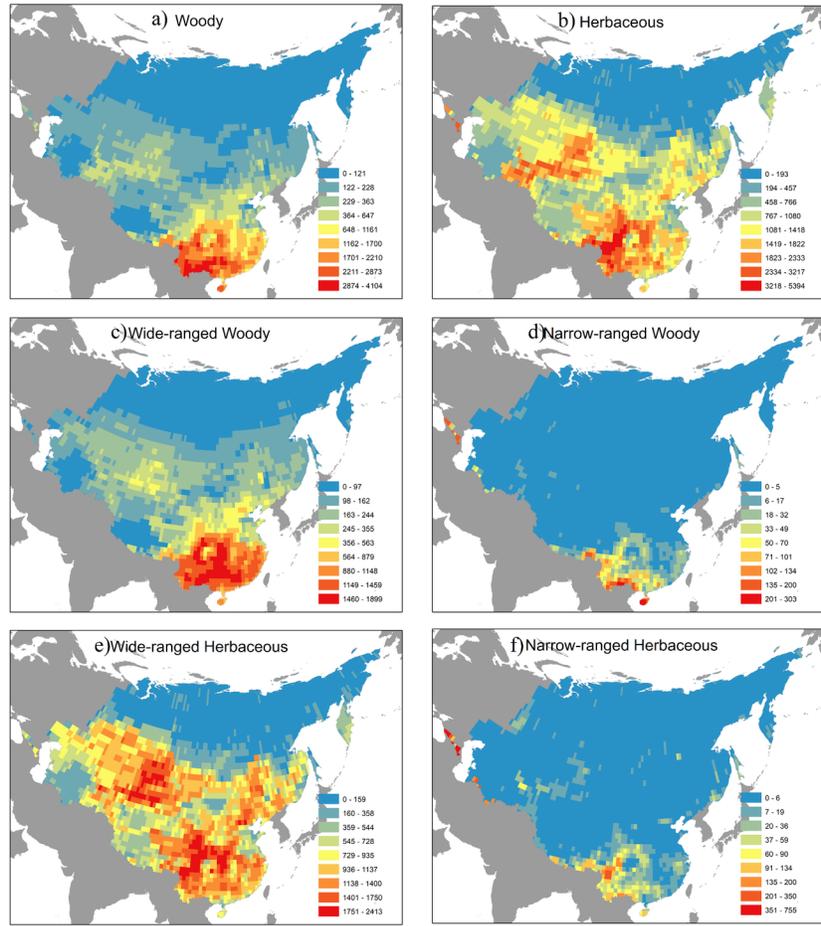


Fig 2 Patterns of woody (a), herb (b), wide-ranged (c) and narrow-ranged species (d) richness in eastern Eurasia.

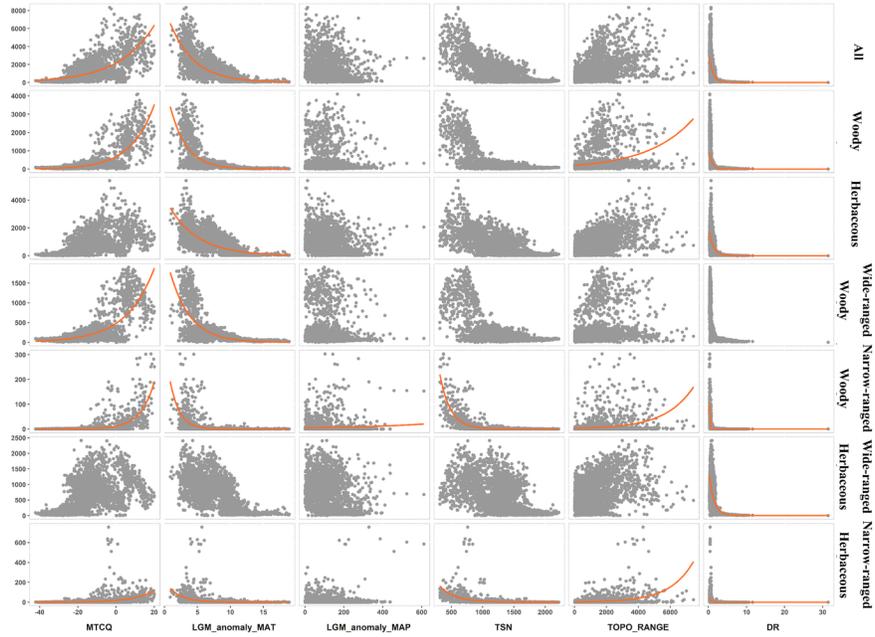


Fig 3 Scatterplot of species richness of all, woody, herb, wide-ranged and narrow-ranged species in eastern Eurasia in relation to impact factors.

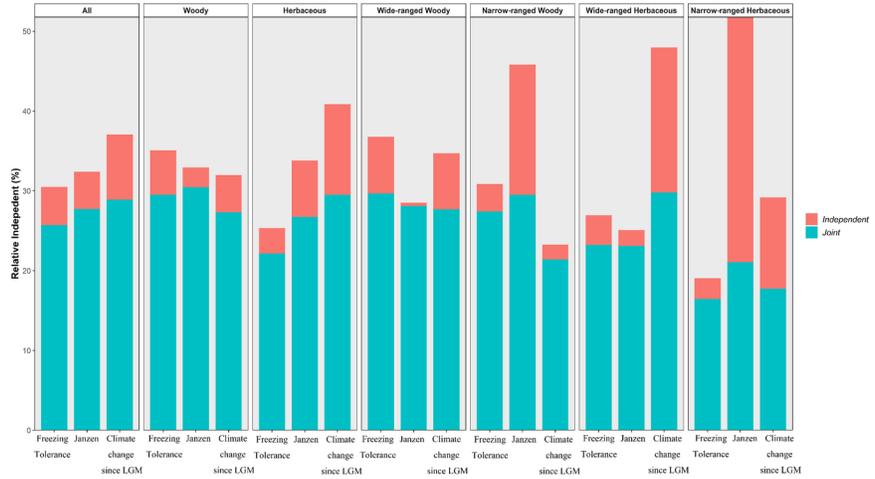


Fig 4 Relative contributions of different hypotheses (percentage) to the woody (a), herb (b), wide-ranged (c) and narrow-ranged (d) species richness pattern. Blue represents the freezing tolerance hypothesis, Red represents the climate change since LGM, Green represents the Janzen hypothesis.