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Global Patterns of Climatic Niche Evolution in Angiosperms

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ABSTRACT

Aim: A species' rate of climatic niche evolution may reflect its ability to survive changing climates. Yet large-scale studies of these rates remain limited. Here, we assessed global patterns in climatic niche rates among angiosperms and explored the potential drivers shaping these patterns.

Location: Global.

Time Period: Current.

Major Taxa Studied: Angiosperms.

Methods: We estimated broad-scale climatic niches for 231,567 angiosperm species based on distributional data from over 1100 sources. By integrating a published phylogeny of angiosperms, we estimated rates of climatic niche change for each extant species as the difference between its current and ancestral niche divided by the species' age. Global patterns were analysed by averaging rates for all the species found in each geographic unit. We used multiple statistical models to explore the relative contributions of niche width and climatic seasonality to shaping these geographic patterns of niche evolution. We analysed patterns of niche evolution and their underlying drivers separately for temperature-related and precipitation-related niches and for different directions of niche evolution (i.e., increases and decreases in species' temperature and precipitation niche values when compared to their most recent ancestors).

Results: Rates for temperature variables increased with latitude, whereas rates for precipitation variables decreased with latitude. These opposing patterns in temperature and precipitation rates were related to opposing latitudinal patterns in climatic seasonality and species' niche widths for temperature and precipitation. Rates also differed for different directions of niche evolution, with different patterns associated with changes to warmer vs. cooler climates and wetter vs. drier climates.

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Main Conclusions: Our results revealed large-scale geographic patterns in rates of climatic niche change for temperature and precipitation for the largest clade of angiosperms and their underlying drivers. These findings may have important implications for species' abilities to respond to recent climate change.

1 | Introduction

The ecological niche represents the set of environmental conditions in which a species can maintain viable populations, as formalised in the famous 'Concluding Remarks' article of Hutchinson (1957). Macroclimatic conditions are the major constraint on large-scale distributions of plant species (Woodward and Woodward 1987). The evolution of a species' climatic niche may strongly impact the species' survival under environmental changes (Holt 1990; Ackerly 2003, 2009) and can be a crucial process underlying species diversification (Moritz et al. 2000; Kozak and Wiens 2010). Understanding broad-scale patterns in rates of climatic niche evolution (climatic niche evolution rate, CNER hereafter) and their underlying drivers is important for addressing key ecological and evolutionary questions, including the latitudinal gradient in species richness (Rangel et al. 2007; Smith et al. 2012), speciation (Moritz et al. 2000; Graham et al. 2004; Kozak and Wiens 2007; Hua and Wiens 2013; Jezkova and Wiens 2018) and the threat of climate change to species survival (Holt 1990; Quintero and Wiens 2013b; Román-Palacios and Wiens 2020). The realised climatic niche of a species can be measured based on the climatic conditions where that species occurs, and this measure of the niche has been widely used in previous large-scale studies of niche evolution (Smith and Beaulieu 2009; Quintero and Wiens 2013b; Liu et al. 2020). One commonly used measure of the absolute rate of climatic niche evolution is the difference between the contemporary and ancestral climatic niches of a given species divided by its evolutionary age (Quintero and Wiens 2013b; Cang et al. 2016; Jezkova and Wiens 2016; Liu et al. 2020). The recent accumulation of large-scale phylogenetic and distributional data for angiosperms can now allow us to address patterns of niche evolution at large taxonomic and spatial scales.

Previous studies have explored niche evolution in plants and animals at different spatiotemporal scales, ranging from the dynamics at the range edges of populations (Angert 2009) to macroevolutionary patterns among species (Hadly et al. 2009; Vieites et al. 2009). However, few studies have explicitly explored geographic patterns in rates of niche change among species (Lawson and Weir 2014; Jezkova and Wiens 2016; Liu et al. 2020). Whether niche rates demonstrate significant geographical patterns remains controversial. Some studies suggested that temperature-related rates may increase with latitude (Lawson and Weir 2014; Jezkova and Wiens 2016) and precipitation-related rates decrease with latitude (Jezkova and Wiens 2016), whereas others found no latitudinal patterns (Liu et al. 2020). These different findings may reflect sampling biases due to a limited number of clades studied or a restricted geographical scope. The generality of geographical patterns in niche rates might only be captured at the global scale, using well-sampled large clades (such as angiosperms).

The tropical niche conservatism hypothesis has been widely employed to explain the mechanisms underlying the latitudinal gradient in species richness (Wiens and Donoghue 2004; Donoghue 2008). According to this hypothesis, the ancestors of most contemporary species originated in tropical environments, and these ancestors had difficulty colonising temperate regions with low temperatures due to climatic niche conservatism (Wiens and Donoghue 2004; Wiens et al. 2006; Donoghue 2008). The explanatory power of this hypothesis for large-scale species richness patterns has been frequently confirmed (Wiens et al. 2006; Hawkins and DeVries 2009; Romdal et al. 2013; Yang et al. 2022). Based on this hypothesis, we can predict that most species from tropical clades may have stronger niche conservatism for temperature-related variables than species from temperate clades (Wiens and Donoghue 2004; Donoghue 2008). In other words, this hypothesis suggests that species niche rates should increase with latitude and tend to be lower in tropical than in temperate regions. However, this specific aspect of the hypothesis remains to be tested. Furthermore, whether geographic patterns of niche evolution are consistent among different dimensions of climatic niche (e.g., temperature and precipitation; Bennett and Lenski 1993; Silvertown et al. 2015) remains unclear. Jezkova and Wiens (2016) found faster rates of niche evolution at higher latitudes in temperate-related variables and slower rates at higher latitudes in precipitation-related variables, whereas Liu et al. (2020) found no latitudinal trends in rates.

Additionally, previous studies of both plants and animals indicated that adaptation of species to colder and wetter environments may be faster than their adaptation to hotter and drier environments (Araújo et al. 2013; Liu et al. 2020). These findings indicate that rates might be different for different directions of niche evolution (i.e., increasing vs. decreasing temperature and precipitation values). However, to our knowledge, previous studies have not investigated this question.

Latitudinal variation in climatic seasonality may also contribute to geographic patterns in niche evolution. First, high climatic seasonality could drive divergent selection and accelerate the evolution of climate-sensitive traits, which may lead to higher rates (Lawson and Weir 2014). Thus, higher temperature seasonality at high latitudes may lead to faster rates of evolution in temperature variables at high latitudes. In contrast, high precipitation seasonality at lower latitudes might lead to higher rates in precipitation variables at lower latitudes. Yet, neither prediction was supported by Liu et al. (2020) for plants or animals (but see Jezkova and Wiens 2016). Second, climatic seasonality may influence niche rates by impacting the niche width of a species (i.e., the range of climatic conditions that a species experiences over space and time; Janzen 1967; Quintero and Wiens 2013a). High climatic seasonality may allow species to attain broad niche widths and large range sizes (Janzen 1967) as shown in previous studies (Addo-Bediako et al. 2000; Quintero and Wiens 2013a; Saupe et al. 2019).

However, it is unclear whether larger range sizes or broader niche widths should lead to faster rates of niche evolution (Liu et al. 2020). Species with broad niche widths may have

abundant genetic and phenotypic variation associated with climatic adaptation, including seasonal timing (Bradshaw and Holzapfel 2008) and resistance to stressful climatic conditions (Hoffmann et al. 2003; Jump et al. 2008). These factors might contribute to higher niche rates. Furthermore, species with narrow niche widths might have slower rates because of phenotypic trade-offs associated with adaptation to a narrow range of environmental conditions (Futuyma and Moreno 1988). These factors would predict positive relationships between niche rates and the climatic niche widths of species. However, previous studies that tested the relationship between niche rates and species' niche widths found conflicting results. For example, a study of five angiosperm clades (Smith and Beaulieu 2009) found that woody plants have lower niche rates and smaller climatic niche space than herbaceous plants, suggesting a positive relationship between niche rates and climatic niche width. In contrast, Liu et al. (2020) did not find significant relationships between climatic niche width and niche rates using data from dozens of plant and vertebrate clades. Large-scale analyses across angiosperms are lacking, but such studies are necessary to make strong generalisations about the contributions of climatic variability and climatic niche width to niche rates in plants.

Here, we analysed geographic patterns in climatic niche rates for angiosperms. We integrated a newly compiled data set containing the broad-scale global distributions of 231,567 angiosperm species with a time-calibrated phylogeny that included all of these species (Smith and Brown 2018). We estimated geographic patterns in both temperature and precipitation niche rates by averaging rates of all species in the same geographic unit. Then we estimated the effects of climatic variability and niche width on niche rates using both ordinary least squares (OLS) regressions and structural equation models (SEM). We hypothesise that: (1) temperature niche rates increase with latitude and precipitation niche rates decrease with latitude, as predicted given latitudinal patterns in niche width and the potential impact of niche widths on niche rates; and (2) climatic seasonality predicts the latitudinal gradient in niche rates through its positive impact on species niche width.

2 | Methods

2.1 | Distribution Data

The world was divided into 487 geographic standard units (GSUs) with a spatial resolution of ca. 4° longitude ×4° latitude (mean area per GSU: $366,179.4\pm20,245.85$ km²). The boundaries of these geographic units were defined following Liu et al. (2023). These boundaries have been widely used in other studies for compiling species distribution data at the continental scale (Shrestha et al. 2018; Luo et al. 2023). Small islands (<25,000 km²) and Antarctica were removed from the analysis due to limited data on species distributions.

Distribution records of angiosperm species in these GSUs were obtained from the latest published database of global angio-sperm distributions (available at https://en.geodata.pku.edu.cn/index.php?c=content&a=list&catid=198). This database contains 1,815,925 records for 330,690 vascular plant species, which were compiled from over 1100 data sources including published

regional and local floras, floristic investigations, specimen records and online databases. During data compilation, information on the status of species (i.e., native, cultivated, introduced, invasive and hybrid) was also collected. Hybrid species were excluded from the database, as were records of species outside their native ranges. After data compilation, the distribution maps were further checked. Records of cultivated species were removed following the Plants of the World Online (POWO, Accessed: May, 2019. https://powo.science.kew.org/) and efloras (http://www.efloras.org/, Accessed May, 2019). See Liu et al. (2023) for a detailed description of the methods, including the confidence levels associated with distributional data across the globe, integration of data from different data sources, and further quality controls on the distribution map of each species.

Misspelled taxonomic names were corrected using the *Taxonomic Name Resolution Service* 4.0 (TNRS: https://tnrs. biendata.org/). Species names and their taxonomic status in different data sources were standardised following the *Catalogue of Life* (COL, Accessed January 6, 2021. https://www.catalogueo flife.org/), *The Plant List* (TPL, Accessed: January 3, 2015. http://www.theplantlist.org/) and *Plants of the World Online* (POWO, Accessed January 6, 2021. https://powo.science.kew. org/). Taxonomic names that were identified as 'unresolved' in both the COL and POWO were removed.

2.2 | Phylogeny

The angiosperm phylogeny used was extracted from a dated species-level phylogeny of seed plants (i.e., ALLOTB; Smith and Brown 2018). This phylogeny was constructed by placing the molecular phylogenies constructed for major clades (i.e., orders) in a backbone provided by Magallón et al. (2015). We only included species in our niche-rate analyses that were included in this tree (231,567 species included). However, many species in that tree were not represented by sequence data (only 79,881 species had sequence data). Other species were randomly added to the sequence-based tree based on taxonomy, leading to many polytomies. Given that polytomies may influence the reconstruction of ancestral niches, we used 100 randomly resolved phylogenies based on the ALLOTB, which were obtained from Luo et al. (2023). Specifically, Luo et al. (2023) first identified each clade with polytomies and then randomly resolved the polytomies within each clade using the Yule bifurcation process following the method described in Kuhn et al. (2011). They generated 100 fully resolved trees by repeating this process 100 times. The rate estimation in this study was carried out using all 100 fully resolved trees from their study. This method is also applied in the latest studies using meta phylogenies (Wang et al. 2021; Luo et al. 2023). We addressed the impact of using randomly resolved phylogenies by also using a reduced, fully resolved tree that only contained species with sequence data (see below).

2.3 | Estimating Rates of Climatic Niche Evolution and Species' Niche Widths

We analysed six climatic niche variables, including three temperature variables and three precipitation variables. The temperature variables were mean annual temperature (MAT; Bio1), maximum temperature of the warmest month (MTWM; Bio5) and minimum temperature of the coldest month (MTQM; Bio6). The precipitation variables were mean annual precipitation (MAP; Bio12), mean precipitation of the wettest quarter (MPWQ; Bio16) and mean precipitation of the driest quarter (MPDQ; Bio17). These variables are widely used in studies of climatic niche evolution (Graham et al. 2004; Liu et al. 2020).

Climate data were obtained from WorldClim version 2.1 (Fick and Hijmans 2017) at the spatial resolution of 30 arc sec (~1 km). For each climatic variable, the value for each GSU was estimated as the average value of all grid cells within that geographic unit. We also obtained data on climate seasonality for each grid cell based on data from WorldClim, including temperature seasonality (BIO4) and precipitation seasonality (BIO15). For each climatic variable for each species, we used the mean values across all GSUs and the maximum and minimum values (estimated 0.975 quartile and 0.025 quartile, respectively).

One commonly used measure of the rate of niche evolution is the absolute difference between contemporary and ancestral climatic niches of a species divided by its age. This approach has been used in numerous studies in both plants and animals (Quintero and Wiens 2013b; Jezkova and Wiens 2016; Liu et al. 2020). We estimated the niche rate for each variable in each species using these three steps: (1) we reconstructed the ancestral value at the most recent ancestral node of that species, (2) we calculated the difference between the value in that ancestor and the current value of that species (absolute values), and (3) we divided this difference by the age of the most recent ancestral node (in millions of years, Myr) of the species.

Prior to conducting ancestral reconstructions, we used the 'fitContinuous' function in the R package geiger version 2.0.9 (Pennell et al. 2014) to determine the best-fitting model of niche evolution for each climatic variable. Specifically, we compared five models: (1) Brownian motion (BM; Felsenstein 1973); (2) Ornstein-Uhlenbeck model (OU), which assumes niche evolution follows a random walk with a central tendency and an attraction strength proportional to the parameter alpha (Butler and King 2004); (3) estimated lambda (LA), in which lambda reflects estimated phylogenetic signal. Values of lambda close to 0 cause the phylogeny to become more star-like (with no phylogenetic structure, as in the white noise model), whereas a lambda of 1 is equivalent to the BM model (Pagel 1999); (4) earlyburst (EB) model, which assumes the rate of niche evolution increases or decreases exponentially through time (Harmon et al. 2010); and (5) white noise (WN), which assumes that the current niche position of the species comes from a single normal distribution with no phylogenetic structure among species. The Akaike information criterion (AIC) was used to compare model performance (see Table A1 for the AIC of each model). For each climatic variable, the best-fitting model (lowest AIC) was LA (for MAT, Lambda=0.91; for MTWM, Lambda=0.89; for MTCM, Lambda=0.92; for MAP, Lambda=0.92; for MPWQ, Lambda = 0.92; for MPDQ, Lambda = 0.92).

Next, we transformed the trees based on the estimated lambda from the LA model using the 'rescale' function in *geiger* and then conducted ancestral niche reconstructions on the transformed tree. We reconstructed the ancestral values for the mean niche and the maximum and minimum niche limits of the most recent ancestor of each extant species, using the 'asr_squared_change_ parsimony' function in the R package castor version 1.7.2 (Louca and Doebeli 2018). We used this function because it yields the same reconstructions as the maximum likelihood estimates, as implemented by the R package Rphylopars version 0.2.10 (Goolsby et al. 2017), but is more efficient for very large phylogenies. Niche-rate estimates based on these three measures (mean, maximum, minimum) were strongly correlated with each other (Figure A1). Therefore, we only analysed niche rates based on mean niche values. For comparison, we also performed analyses in which the tree was transformed based on the BM model, which uses the original branch lengths of the phylogeny (Kozak and Wiens 2010). The niche-rate patterns based on the BM model (Figure A7) were the same as those generated from the LA model (Figures 1 and A2), presumably because the lambda values in the LA model were close to 1, leading to only limited transformation of the branch lengths in the LA model relative to the BM model.

We reconstructed the values of each variable at the most recent ancestral node of each species using the 100 fully resolved trees and estimated the mean value across the 100 trees. We then categorised the species into four groups based on their direction of niche evolution. These included species whose present-day MAT and MAP values were higher than their ancestors, indicating increasing values (δT_+ and δP_+), vs. species whose present-day MAT and MAP values were lower than their ancestors ($\delta T_$ and δP_-). Among the total 231,567 species, the sample sizes of each group are: δT_+ : 126,835 species; δT_- : 104,732 species; δP_+ : 104,419 species; δP_- : 127,148 species.

Note that throughout the paper we describe rates of 'climatic niche evolution'. We do so because we are analysing these rates with evolutionary methods. However, we acknowledge that some changes among species may not be genetically based (i.e., based on genetically determined physiological tolerances) and that instead some may be related to (for example) incomplete sampling or nonclimatic barriers to dispersal that prevent species' realised climatic niches for a given variable from matching their fundamental niches. Thus, referring to these rates as rates of 'climatic niche change' might be more accurate instead.

Following previous studies (Quintero and Wiens 2013a; Liu et al. 2020), we defined the temperature niche width of a species as the difference between the maximum MTWM and the minimum MTCM across the species' geographic range. Similarly, we defined the precipitation niche width of a species as the difference between the maximum MPWQ and the minimum MPDQ across the species' geographic range. We defined the temperature niche position and precipitation niche position of a species as the mean of MAT (or MAP) across all GSUs in the species' geographic range.

2.4 | Evaluating Geographic Patterns in Rates and Their Underlying Drivers

Unless stated otherwise, the sampling unit in all analyses was the GSU. The mean niche rate and niche width of each GSU



FIGURE 1 | Geographic patterns in rates of climatic niche evolution in angiosperms. (a) mean annual temperature (MAT, °C Myr⁻¹); (b) mean annual precipitation (MAP, mm Myr⁻¹). The niche evolutionary rate in a given geographic unit is calculated as the mean value of the rates of species distributed in that unit. The rate of niche evolution for a given climatic variable in a given species is the absolute difference between the contemporary and ancestral climatic niches of the species divided by its age. The scatterplot to the right of each map illustrates the latitudinal gradients in niche evolutionary rate, where each point represents the mean evolutionary rate (among species) of a geographic unit (n = 487).

were calculated by averaging the values of all species occurring in that GSU. Geographic variation in niche rates and niche width was illustrated by mapping the GSU-averaged values of each variable across the globe. We also mapped the standard error of niche rates within each GSU. To assess the effect of species ages and of spatial variation in ambient climate on the niche patterns, we first mapped the average species age within each GSU. We also calculated the niche rate of MAT using the average species age across all angiosperm species (instead of the actual age of each species) and then calculated the average niche rate within each GSU. Then we compared the latitudinal gradients between the niche rate of MAT measured based on the average species age and that based on the observed actual species age.

We generated a scatterpoint plot along with the GSU map, showing the mean values of rates among latitudes. Furthermore, to quantitatively examine geographic variation in niche rates, we tested for a relationship between the averaged niche rates within each GSU with the absolute latitude of each GSU, using univariate ordinary least squares (OLS) regression. We conducted separate analyses for each climatic variable (MAT, MAP, etc.). Niche rate was the response variable in the OLS models, and latitude was the independent variable. The significance of R^2 in OLS models was tested using a modified *t*-test (Dutilleul et al. 1993) to account for spatial autocorrelation. The modified *t*-test corrects the degrees of freedom based on the amount of autocorrelation in the data, with autocorrelation represented by *Moran's I*. The corrected degrees of freedom were then used to test the significance of the correlation. The test was conducted using the modified t test (Clifford et al. 1989; Dutilleul et al. 1993).

We explored the effects of climatic seasonality and niche width on niche rates using OLS regression. Niche rate was the response variable, and seasonality and niche width were the independent variables. To quantify the independent effects of these two factors on niche rates, structural equation modelling (SEM) was conducted as follows, using the 'sem' function in the R package *lavaan* version 0.6-15 (Rosseel 2012):

Niche Rate \sim Seasonality + Niche Width (1)

Niche Width ~ Seasonality
$$(2)$$

Standardised correlation coefficients (SCC) were used to represent the effects of different predictors. Climatic seasonality was represented by temperature seasonality (BIO4) and precipitation seasonality (BIO15). Niche rates were natural log transformed prior to OLS and SEM to increase the normality of the niche rate data.

2.5 | Sensitivity Analyses

1. Sampling bias. This study involved 231,567 angiosperm species, representing the most complete analysis on

climatic niche evolution in flowering plants conducted to date. Nevertheless, not all known angiosperm species were included (angiosperms currently include ~350,000 known species; https://www.catalogueoflife.org/; 22 March 2025), and the missing species might affect the estimation of niche rates. To test for sampling bias, we repeated the niche-rate estimation using the molecular phylogeny from Smith and Brown (2018), which contained only the 79,881 species with sequence data (GBOTB tree). Then we mapped the GSU-averaged values of niche rates across the globe and compared the resulting patterns to those based on all species. Importantly, this comparison also helped address the question of how geographic patterns were impacted by polytomies, since most polytomies in the full tree were related to adding species to the tree without sequence data.

2. Spatial resolution. The size of GSUs used in this study was relatively large (~4 arc degrees), which may lead to high variation in climate within each GSU. To test for bias in niche position (i.e., the mean values of temperature or precipitation of the occupied GSU of a species) and niche rates caused by the coarse spatial resolution, we conducted three analyses. (i) We compared the niche positions and niche rates between our study and a previous study that used more fine-scaled climatic data (Liu et al. 2020). Liu et al. (2020) analysed 808 angiosperm species from 17 clades, with a fully resolved phylogeny for each species and climatic data at ~1-km² resolution. For species that were included in both studies, we compared the values of MAT and MAP niche between the two studies and estimated their relationships using phylogenetic generalised least-squares regression (PGLS; Martins and Hansen 1997). PGLS was conducted using the function 'pgls' in the R package caper version 1.01 (Orme et al. 2013). The dependent variables were niche rates from Liu et al. (2020), and the independent variables were the corresponding rates in this study. We also estimated niche rates of these species based on Liu et al. (2020) and the phylogeny used in this study, and then obtained the values of each GSU by averaging the niche rates of all species occurring in each GSU. Then we compared the GSU-averaged niche rates based on Liu et al. (2020) with those estimated in this study, using Pearson correlation indexes. (ii) We evaluated the effects of variation within each GSU on the relationship between niche rates and the predictor variables. First, we conducted multiple linear regression models in which the dependent variable was niche rates, and the independent variables were climate seasonality and niche width within each GSU. We then extracted the residuals of the multiple linear regression models and explored the relationships between the model residuals and within-GSU climate variation. We found no significant relationships between the model residuals and the range of climate conditions within GSUs estimated with different variables (Figure A10), indicating that the associations between niche rates and the examined predictors are not biased by within-GSU climate variation. (iii) We compared the relationship between latitude and niche rates using the two data sources (i.e., niche rates measured based on data of this study and data of Liu et al. (2020)). We measured the Pearson correlation indexes between latitude (absolute values) and the mean values of niche rates within each GSU.

3 | Results

3.1 | Patterns in Niche Rates

Rates for mean annual temperature (MAT) and mean annual precipitation (MAP) showed opposite latitudinal patterns (Figure 1). Rates for MAT were the highest in arctic regions and the lowest in the tropics (Figure 1a), and the variation in rates across regions was higher in regions with high rates than in regions with low rates (Figure A13). The absolute latitude of GSUs was strongly correlated with their mean niche rates for MAT (slope = 0.03, R^2 = 0.742, p < 0.001). The geographic pattern in rates for MAT was opposite to the pattern in mean species age, that is, species age in the regions with high niche rates tends to be low (Figure A11). However, the latitudinal gradient was weaker than observed if the rates for MAT were estimated using a constant species age for all species (Figure A12, slope = 0.01, R^2 = 0.672, p < 0.001).

In contrast, rates for MAP were the highest in the tropics and in some subtropical regions, including Southeast Asia and New Guinea, India, northern Australia, southern Arabia, western Africa and Panama. These rates were lowest in temperate regions including Europe, North America, southwestern Australia and the Cape region in southern Africa (Figure 1b). Absolute latitude was negatively correlated with rates for MAP (R^2 =0.058, p<0.002), but the R^2 was much lower than for MAT. The geographic patterns in rates estimated using MAT and MAP were largely consistent with those estimated using other climatic variables for temperature and precipitation (Figure A2), including maximum temperature of the warmest month (MTWM), minimum temperature of the coldest month (MTCM) and the precipitation of the driest quarter (MPDQ) and wettest quarter (MPWQ).

The estimated niche rates and their geographic patterns were robust to sample biases and in the coarse spatial resolution of this study. First, the geographic patterns in niche evolution rates were robust after removing species without molecular (DNA sequence) data (which made up 65.5% of the species; Figure A6). Second, we compared the niche variables with a previous study (Liu et al. 2020), in which mean climatic niches of 808 angiosperm species from 17 clades were estimated from climatic data with 1-km² resolution. We found that the estimated climatic niches were strongly correlated between these two studies (Figure A8). Furthermore, the residuals from the model comparing values of niche variables from our study and Liu et al. (2020) suggest no biases in our estimation of species' climatic niches based on relatively coarse distribution data (Figure A8). The correlations between MAT niche rates and latitude (Figure A9) were also similar between the two studies (our study, r = 0.44; Liu et al. (2020), r = 0.41). We found stronger correlations between precipitation niche rates and latitude in our study (our study, r = -0.33; Liu et al. (2020), r = -0.02). However, data from both studies consistently showed significant negative relationships



FIGURE 2 | Patterns of climatic niche evolution in different directions in angiosperms. (a) Temperature niches of δT_+ species, that is, species that exhibited higher temperature niches than their ancestors. (b) Precipitation niches of δP_+ species, those species that exhibited higher precipitation niche values than their ancestors. (c) Temperature niches of δT_- species, those species that exhibited lower temperature niche values than their ancestors. (d) Precipitation niches of δP_- species, those species that exhibited lower temperature niche values than their ancestors. (d) Precipitation niches of δP_- species, those species that exhibited lower precipitation niche values than their ancestors. The niche evolutionary rate in a given geographic unit is calculated as the mean value of the rates of species distributed in that unit. The scatterplot to the right of each map illustrates the latitudinal gradients of niche evolutionary rates, where each point represents the mean niche evolutionary rate (among species) within a geographic unit (*n*=487). Among the total 231,567 species, the sample sizes of each group are: δT_+ : 126,835 species; δT_- : 104,732 species; δP_+ : 104,419 species; δP_- : 127,148 species.

between MAP rates and latitude. We further conducted multiple linear regressions, with niche rate as the dependent variable and mean climatic seasonality and climatic niche width as the independent variables. We found no significant relationships between the model residuals and the within-GSU variation in climate (Figure A10), which suggests that the associations of niche evolution rate with climatic seasonality and climatic niche width (see below) were not biased by within-GSU variation.

The geographic patterns in rates differed between species whose contemporary climatic niches were higher or lower than those of their ancestors. Specifically, species having higher contemporary temperature values than their ancestors (i.e., species with temperature values increasing, δT_{+} species) had the highest rates for MAT in the drylands ranging from North Africa to West Asia, and in the arctic regions of North America (Figure 2a). Therefore, the rates of δT_{\perp} species did not show significant relationships with latitude ($R^2 = 0.002$, p = 0.183). In contrast, species having lower temperature values than their ancestors (i.e., species with temperature values decreasing, δT_{-} species) showed similar patterns in rates to the overall pattern (Figure 2c), which showed a significant positive relationship with absolute latitude ($R^2 = 0.798$, p < 0.001). Species having higher MAP values than their ancestors (hereafter, δP_{\perp} species) had the highest rates in tropical regions such as in Southeast Asia, New Guinea, India and Central America (Figure 2b), with rates that were significantly positively correlated with absolute latitude ($R^2 = 0.432$, p < 0.001). Species having lower contemporary precipitation values than their ancestors (hereafter,

 δP_{-} species) had the highest rates in the subtropical regions including Mexico, the northern Andes, the grassland of the southern Sahara, eastern and southern Africa (except the Cape region), India, Indochina and northern Australia (Figure 2d). Therefore, these species did not show a significant relationship between rates and latitude ($R^2 = 0.004$, p = 0.094). High-latitude regions had a higher proportion of $\delta T_+/\delta P_+$ species than low-latitude regions (Figure A14).

3.2 | The Relative Effects of Climate Seasonality and Niche Width on Niche Rates

Ordinary least squares (OLS) regressions and structural equation models (SEM) showed that rates based on both MAT and MAP were positively correlated with mean climatic seasonality and mean climatic niche width per geographic unit (Figure 3). Notably, rates based on MAT were strongly related to temperature seasonality ($R^2 = 0.845$, p < 0.001) and mean temperature niche width per geographic unit ($R^2 = 0.908$, p < 0.001). These relationships were stronger than those between MAP rates and precipitation seasonality ($R^2 = 0.164$, p < 0.001) and precipitation niche width ($R^2 = 0.161$, p < 0.001). Relationships between rates and seasonality and niche widths were consistent between species with different directions of niche evolution (i.e., δT_+ vs. δT_- species; δP_+ vs. δP_- species; Figure A3a,b) and when rates were estimated using other temperature and precipitation variables (i.e., MTCM, MTWM, MPDQ, and MPWQ; Figure A3c,d).



FIGURE 3 | Effects of niche width and seasonality on rates of climatic niche evolution. (a) Relationships between climatic niche rates (for MAT and MAP) and either seasonality or niche width, evaluated by the R^2 from univariate OLS models. Each point represents a geographic unit (GSU; n = 487). The significance of each relationship is tested by a modified *t*-test that accounts for spatial autocorrelation. Triple asterisks (***) indicate p < 0.001. (b) The effects of seasonality on niche and its indirect effect via niche width, evaluated by the standardised correlation coefficients (SCC) from structural equation modelling (SEM). Only statistically significant (p < 0.01) SCC values are shown above the arrows connecting variables. The width of the arrows is proportional to SCC values. The units of analysis were geographic units (n = 487). PSN, precipitation seasonality; TSN, temperature seasonality. The values of niche rates were natural log transformed prior to analysis.

Consistent with the OLS results, SEM showed positive correlations between niche rates and climate seasonality and niche width (Figure 3). For MAT rates, temperature seasonality had a stronger indirect effect on rates via niche width than on a direct effect. For MAP rates, the direct and indirect effects of precipitation seasonality were similar.

4 | Discussion

4.1 | Geographic Patterns in Niche Rates Differ Between Temperature and Precipitation

Rates based on temperature niche generally increased with latitude (Figure 1), which suggests that tropical lineages have stronger conservatism in their temperature niches than temperate lineages. This finding is in line with the expectation of the tropical niche conservatism hypothesis (Wiens and Donoghue 2004; Wiens et al. 2006; Donoghue 2008) and hence provides indirect support for this hypothesis.

In contrast to rates for temperature variables, rates based on precipitation variables peaked at lower latitudes, including the Indo-Malayan region and New Guinea, resulting in negative but weaker latitudinal gradients in contrast with temperature rates (Figures 1 and 2). The higher precipitation rates for the Indo-Malayan region may have been caused by the dynamic changes in precipitation shaped by the Himalayan orogeny and the formation of the Asian monsoon system (Ding et al. 2020). Previous phylogenetic studies on taxa in this region (e.g., Hedychium (Zingiberaceae; Ashokan et al. 2022), Ceropegieae (Apocynaceae; Surveswaran et al. 2021) and Piper (Piperaceae; Sen et al. 2019)) have shown that with the uplift of the Himalayas (beginning in the Oligocene), monsoon intensification accelerated diversification and shaped species' adaptation to aridification and seasonal drought (Klaus et al. 2016; Ding et al. 2020). The high rates for MAP in New Guinea

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could reflect the extreme variation in precipitation across New Guinea from 970 mm to 7500 mm per year, providing many opportunities for niche partitioning (Hoover et al. 2017) in water use (Read et al. 2010). The findings on the contrasting patterns in temperature vs. precipitation rates indicated that the tropical niche conservatism hypothesis mainly reflects the effect of temperature rather than precipitation conditions in shaping climatic niches of species.

The climatic niches discussed here refer to the realised climatic niches of species, which represent the climatic conditions that a species experiences within its geographic range (Hutchinson 1957; Lawson and Weir 2014). We do not address the evolution of physiological tolerances directly because the realised climatic niches may not be equivalent to the fundamental niches of species. The realised climatic niches of a species may represent only a subset of a wider fundamental niche because of dispersal limitation and biotic interactions (Guisan et al. 2014) and other abiotic but nonclimatic constraints on species ranges (e.g., soil conditions; Silvertown 2004). Our study was based on > 230,000 species, whereas data on physiological tolerances have been reported for relatively few species. Furthermore, the fundamental niche of a species often remains unclear due to uncertainties in quantifying resource use requirements and physiological limits in a species (Cooper et al. 2010). The measuring of physiological limits can be biased by many factors such as differences in physiological requirements across the life history (Grubb 1977) or Allee effects (Sexton et al. 2009).

Although realised and fundamental climatic niches can differ, studies have also demonstrated that positive relationships do exist between the large-scale climate variation across the geographic range of a species and its climate tolerance (Kearney 2012). For example, a study assessed the fundamental and realised niches of a marine crustacean species (*Calanus finmarchicus*) and found a close relationship between the two niches, and that the relationship remained constant over space and time (Helaouët

and Beaugrand 2009). A study on multiple anuran species found that heritable physiological tolerances conform closely to the position of the niche in climatic hyperspace and that upper thermal limits may be loosely described by the realised limits of species' distributions (Gouveia et al. 2014). A subsequent study on 105 reptile and amphibian species found that their realised thermal niches were generally parallel to their fundamental niches, especially for their cold tolerances (Soberón and Arroyo-Peña 2017). A study on North American mangroves found that their laboratory physiological tolerances closely matched their realised thermal niches (Bardou et al. 2021). Although realised and fundamental climatic niches can differ, it is important to note that these differences do not mean that the realised climatic niches are wrong and the fundamental climatic niches are right. After all, if our goal is to understand the evolution of species climatic distributions, then only considering physiological tolerances may be misleading if other factors are involved in shaping these distributions.

4.2 | Different Directions of Niche Evolution

We found that rates among species with decreasing temperature values (δT_{-} species) showed a more pronounced latitudinal gradient than among δT_{+} species (Figure 2). We also found that δT_{-} species were more dominant and had higher rates in high-latitude regions than δT_{+} species (Figures 2 and A14). Thus, the pattern of higher rates for MAT at higher latitudes may be mainly related to species with recently decreasing temperature values (δT_{-} species). These species had fast evolutionary changes in their temperature niches in response to colder temperatures. Moreover, the rates of δT_{-} species based on MAT were strongly correlated with rates based on MTCM (Pearson r=0.98); Similarly, the rates of δT_{+} species based on MAT were strongly correlated with rates based on MTWM (Pearson r=0.58).

For the precipitation niche, the rates of δP_{\perp} species showed a clear latitudinal gradient, with the highest rates in the tropics (Figure 2). The high rates of MAP in Southeast Asia and New Guinea were mainly due to δP_{\perp} species (Figure A14). In contrast, the rates among δP species did not show a clear latitudinal gradient ($R^2 = 0.004$, p = 0.09). The difference in rates for different directions of precipitation niche evolution may reflect the idea that it is easier for species to evolve to tolerate conditions at the wetter end of the precipitation gradient than towards the drier end. Specifically, there can be extensive variation in precipitation values in some regions with very high rainfall (mostly tropical rainforests), but these differences may be inconsequential relative to surviving in much drier environments (i.e., adapting to an even wetter rainforest is trivial relative to adapting to a desert; Bonetti and Wiens 2014). In support of this idea, the patterns of niche rates among δP species, which may reflect niche evolution in response to drier climates, did not show higher rates in temperate regions (Adams et al. 2017; Liu et al. 2020).

Overall, our results demonstrate that species with higher or lower climatic niche values than their ancestors can have different geographic patterns of niche rates. These findings may have important implications for species' responses to current and future climate change.

4.3 | Climatic Seasonality Affects Niche Rates Both Directly and Indirectly via Niche Width

The relationships of seasonality and niche width with niche rates (Figure 3) suggested that climatic seasonality played a significant role in shaping the geographic patterns in niche rates. High climatic seasonality led to both wider climatic niche width and higher rates across space and species, and wider niche width also led to higher rates. On one hand, high climatic seasonality could accelerate evolution in climate-sensitive traits, which could lead to high rates of niche evolution (Lawson and Weir 2014). On the other hand, species in regions with high climatic seasonality tend to have wider tolerance to climate and consequently tend to have wider climatic niche width, as predicted by Janzen's hypothesis (Janzen 1967) and Rapoport's rule (Stevens 1989). Wider climatic niches allow species to tolerate larger climatic fluctuations (Deutsch et al. 2008; Sunday et al. 2011; Grinder and Wiens 2023), and promote evolutionary rates in the temperature niche (Lawson and Weir 2014). Furthermore, we found that climate seasonality had a stronger effect on geographic variation in niche width than on geographic variation in niche rates, and this finding was consistent for both temperature and precipitation niche rates (Figure 3). These findings suggest that seasonality may have a stronger indirect effect via niche width than the direct effect on rates. Meanwhile, we found the niche rate patterns for both temperature and precipitation were inconsistent with each other but consistent with patterns of climatic seasonality and climatic niche width. Thus, these contrasting latitudinal patterns in niche rates are likely explained by the contrasting latitudinal patterns of temperature and precipitation seasonality. Both temperature seasonality and temperature niche width increase latitudinally (Figures A4 and A5), which is consistent with the latitudinal pattern in temperature niche rates (Figure 1). Both precipitation seasonality and precipitation niche width are the highest in the subtropical regions of Asia and Africa, northeastern Asia, northern Australia, Mexico and the northern Andes (Figures A4 and A5) and are the lowest in high-latitude regions including Europe, eastern North America, Patagonia, southern Australia and New Zealand. One exception was the Indonesian Archipelago, where precipitation niche rates were high but both precipitation niche width and precipitation seasonality were relatively low. This anomalous geographic pattern may help explain why the relationships among niche rates, seasonality and niche widths were much weaker for precipitation variables than for temperature variables (Figure 3).

Our findings suggest that species living at different latitudes may have different abilities to respond to climate changes via climatic niche evolution, depending on the climatic variable. Species living in the tropics may have a lower ability to respond to climate warming via temperature niche evolution than species living in temperate regions, since tropical species have a lower rate of evolution in their temperature niche. Indeed, recent studies on terrestrial insects (Deutsch et al. 2008), woody plants (Peng et al. 2021), land plants (Lancaster and Humphreys 2020), plants and animals (Wiens 2016; Grinder and Wiens 2023) and model-simulated organisms (Bonebrake and Mastrandrea 2010) have demonstrated that species at low latitudes tend to be more sensitive to climate warming due to low tolerance to temperature variation, consistent with our findings. In contrast, species living in regions with more seasonally stable precipitation conditions (e.g., Europe and tropical Africa) may have a limited ability to respond to precipitation-related events (such as extreme fluctuations in precipitation) via precipitation niche evolution. Importantly, previous findings on geographic patterns in the impact of temperature changes on local plant diversity may not be applicable to the impacts of precipitation changes.

4.4 | Potential Caveats

We acknowledge that our study has several limitations, which may influence our estimates of climatic niches and their evolutionary rates. Nevertheless, these limitations should not change our overall conclusions. Firstly, the coarse spatial resolution of species distribution data may affect the estimation of niche values of species. Currently, fine-scale distributional data for most angiosperm species are not available. Thus, we compared our broad-scale estimates of climatic niches based on MAT and MAP with those of Liu et al. (2020), in which mean climatic niches of 808 angiosperm species from 17 clades were estimated from climatic data with 1-km² resolution. We found that the climatic niches and their relationships with latitude estimated here are largely consistent with Liu et al. (2020) (Figures A8 and A9). We found little effect of climate variation within geographic standard units (GSU) on the relationship between niche rates and the predictors (i.e., climatic seasonality and climatic niche width, Figure A10). Together, these results suggest that the estimation of climatic niche and niche evolution rate, and their associations with climatic seasonality and climatic niche width, are not strongly biased by the spatial resolution used in our study.

Secondly, the phylogenetic trees used here do not contain all extant angiosperm species, which may impact the estimation of evolutionary rates. However, the geographic patterns in niche evolution rates were robust after removing species without molecular (DNA sequence) data (which made up ca. 65.5% of the species, Figure A6). Therefore, it seems very unlikely that including more species would dramatically change our conclusions.

Thirdly, uncertainty exists in our interpretation of the underlying drivers of niche rate patterns. Niche shifts may only occur in species that were exposed to new conditions relative to their ancestral species. Tropical species may simply exhibit conservatism in their thermal niches inherited from their ancestors; they have not reached colder regions, limiting the opportunity for adaptation. Additionally, it is noteworthy that temperature seasonality is highly correlated with MTCM (Pearson r = -0.96), and thus the higher niche rates in high latitudes may be the combined effects of adaptation to cold and to more pronounced seasonality. Further experiments on selected tropical species and controlled experiments on temperature and its seasonality may be able to address the extreme tolerance for these species and further help us understand how commonly the above-mentioned circumstances occur across angiosperms.

Fourth, the units of analysis in our study were large-scale geographic units. These units can contain large numbers of species, and many species are shared between units. There is no phylogenetic correction for traits that are shared among species due to common ancestry, nor is there a correction for species that are shared among units (although we did use a correction for spatial autocorrelation). Overall, this approach may not be as conservative as analysing species as units with phylogenetic comparative methods.

4.5 | Implications

We mapped geographic patterns in rates of climatic niche evolution for more than 231,000 angiosperm species at a global scale. Interestingly, we found that geographic patterns in rates differed substantially between temperature and precipitation niches (higher temperature rates at higher latitudes, higher precipitation rates at lower latitudes). These different patterns of rates likely reflect the combined effects of geographic variation in climatic seasonality and climatic niche width on rates, with greater seasonality and wider niche widths leading to faster rates. These results also suggest that species in different regions may be sensitive to different climate change factors, with tropical species potentially being more sensitive to warming and temperate species more sensitive to drought.

Author Contributions

Zhiheng Wang, John J. Wiens and Yunpeng Liu conceived the idea. Zhiheng Wang, Ao Luo, Xiaoting Xu, Xiangyan Su, Yichao Li, Tong Lyu and Yunpeng Liu constructed the distribution data set. Zhiheng Wang and Dimitar Dimitrov conducted the phylogeny. Yunpeng Liu led the analysis and writing, and all authors contributed to the writing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data and code used in this paper are available through Dryad at https:// doi.org/10.5061/dryad.fn2z34v59 once published and at http://datad ryad.org/stash/share/PiFc1oJSPqQNyO5rH9SP8Nqgz6t2ryD01TX WkX0B0q8 during peer review.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.