ECOLOGY

Global distribution and evolutionary transitions of floral symmetry in angiosperms

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Floral symmetry plays an important role in plant-pollinator interactions and may have remarkable impacts on angiosperm diversification. However, spatiotemporal patterns in floral symmetry and drivers of these patterns remain unknown. Here, using newly compiled floral symmetry (actinomorphy versus zygomorphy) data of 279,877 angiosperm species and their distributions and phylogenies, we estimated global geographic patterns and macroevolutionary dynamics of floral symmetry. We found that frequency of actinomorphic species increased with latitude, while that of zygomorphic species decreased. Solar radiation, present-day temperature, and Quaternary temperature change correlated with geographic variation in floral symmetry frequency. Evolutionary transitions from actinomorphy to zygomorphy dominated floral symmetry evolution, although the transition rate decreased with decreasing paleotemperature throughout the Cenozoic. Notably, we found that zygomorphy may not favor diversification of angiosperms as previously observed in some clades. Our study demonstrates the influence of (paleo)climate on spatiotemporal patterns in floral symmetry and challenges previous views about role of flower symmetry in angiosperm diversification.

INTRODUCTION

Floral symmetry is a key feature that has substantial impacts on a suite of evolutionary and ecological outcomes in flowering plants (i.e., angiosperms) (1–4). Previous studies suggest that changes in floral symmetry types during evolutionary history could be an important driver influencing the diversification of angiosperms (5). Moreover, floral symmetry is one of the key components of plant pollination syndromes and plays an important role in plant-pollinator interactions (3). Coevolutionary dynamics between floral traits of plants and their pollinators driven by environmental changes may lead to spatiotemporal dynamics of floral symmetry (6, 7). Both evolutionary lability (where sister clades evolved different types of floral symmetry) and developmental lability (unstable or differing floral symmetry types within a species in response to environments) together lead to a geographic mosaic of floral symmetry which may reflect responses of plants to different ecological and evolutionary settings (8).

Given the potential association of flower symmetry with major transitions in angiosperm diversification and evolutionary dynamics of plant-pollinator interactions, unraveling spatiotemporal patterns of floral symmetry will help advance our understanding of the macroevolution of global angiosperm diversity. However, global spatiotemporal patterns of angiosperm floral symmetry remain unexplored due to the lack of distribution and floral symmetry data at sufficiently large spatial and taxonomic scales. Previous work has focused mostly on the molecular evolutionary mechanisms leading to transitions between radial and bilateral symmetry (9, 10) or has investigated the evolutionary dynamics of floral symmetry using small fractions of angiosperm species (11, 12). Historical trends in the evolutionary transitions between radial symmetry (actinomorphy) and bilateral symmetry (zygomorphy) and their global patterns for all angiosperms remain less clear.

Climate may influence the frequency of plants with different floral symmetry types in plant communities via its effects on the corresponding pollinator assemblages and the interactions between plant species and their pollinators across space (8). Studies in North America found that zygomorphic flowers with higher pollination specialization [i.e., plant species associated with a few potential pollinator species; see (13) for more details] are favored in regions that have high diversity of pollinator species (14). This has been attributed to the finding that zygomorphic flowers are more frequently associated with polarized floral morphology and visual distinctiveness and are therefore more recognizable to pollinators among superficially similar flowers (3, 15). Compared with zygomorphic flowers, actinomorphic flowers tend to have larger nectar tubes and simpler structures (16) and are often associated with a wider array of pollinator species (13) or are wind-pollinated (e.g., Cyperaceae). These findings suggest that actinomorphic flowers that lack obvious morphological features for specialized pollination should be more favored in open habitats at high latitudes with higher seasonality and unpredictable or few pollinators (17).

Abiotic factors can also influence the geographic variation in floral symmetry through direct or indirect selection of floral morphological traits that are associated with floral symmetry, specifically floral orientation and floral pigmentation (18, 19). Floral symmetry together with these associated floral morphological traits can jointly affect the absorption and retention of heat, which will subsequently influence the thermal conditions within flowers for pollen germination, anther and stigma exertion, ovule

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performance, and hence pollinator attraction (*20*). A recent study based on 42 species suggested that the enclosed morphology of some zygomorphic flowers may cause a "microgreenhouse" effect, making zygomorphic flowers more sensitive to temperature changes than actinomorphic flowers with exposed morphology (*21*). This is likely because high-temperature stress induced by this microgreenhouse effect could damage pollen and ovule functions (*20*, *21*) and subsequently influence the reproductive success of zygomorphic species. By contrast, actinomorphic flowers with exposed morphology tend to increase their pigmentation when experiencing increases in temperature (*21*). Because of differences in the heat absorption and retention between zygomorphic and actinomorphic flowers, past climate warming has decreased pigmentation in zygomorphic flowers with enclosed anthers, but increased pigmentation in actinomorphic flowers with exposed anthers [see figure 4 in (*21*)]. These findings suggest that long-term warming, especially the dramatic temperature increase at high latitudes of the northern hemisphere since the Last Glacial Maximum (LGM), might reduce the fitness of species with zygomorphic flowers in temperate regions, but tended to favor species with actinomorphic flowers that could absorb more radiative heat (*21*) and depend on a wide range of pollinators (*13*). Differential responses to long-term climate warming between actinomorphic species and zygomorphic species may thus alter their relative performance in colonizing new habitats and adapting to changing environments.

Previous studies suggest that the northward postglacial recolonization of plant species has strongly contributed to the composition of the modern vegetation at high northern latitudes (*22*). Actinomorphic species, associated with self-pollination (*23*) and more generalized pollination (*13*, *24*), tended to have an advantage in colonizing high latitudes after the LGM. On the basis of these findings, we expect that zygomorphic species should be more favored at low latitudes where temperature increase was low and plant-pollinator interactions remained relatively stable since the LGM, while actinomorphic species should be more frequent at high latitudes with larger temperature increases since the LGM.

Evolutionary transitions between actinomorphy and zygomorphy in angiosperms are relatively frequent (*11*, *25*, *26*). Traditionally, the transition from actinomorphy, the likely ancestral state for angiosperms (*12*, *27*), to zygomorphy has been thought to be common (*9*, *11*, *28*). Compared with actinomorphy, zygomorphy has been found to increase pollination specialization, and its evolution is largely driven by the selection exerted by specialized pollinators (*3*, *25*, *26*). In contrast, the reverse transitions from zygomorphy to actinomorphy have been thought to be far less common (*11*, *29*, *30*).

However, some researchers have suggested that this traditional view of the transition between zygomorphy and actinomorphy may not be fully justified. Molecular studies have indicated that "peloric" mutations are common in different clades, while mutations leading to zygomorphic flowers have been rarely reported (*31*). These findings suggest that the evolutionary transition from actinomorphy to zygomorphy may not be as common as traditionally expected, while the reversals might be more common than expected (*31*, *32*). Evolutionary transitions from zygomorphy to actinomorphy have been reported in several clades such as Lamiales (*32*–*34*) (e.g., Lamiaceae, Plantaginaceae, and Gesneriaceae), Malpighiineae (*11*) (e.g., Malpighiaceae), Tubiflorae (*32*) (e.g., Scrophulariaceae), and others (*34*–*36*). Consequently, evidence from further comparative studies is needed to further clarify the evolutionary patterns in the transitions between actinomorphy and zygomorphy.

Because, as outlined above, the evolution of floral symmetry has been widely found to be associated with plant-pollinator interactions, pollinator-mediated selection has been considered a key driver for the evolutionary transition between actinomorphy and zygomorphy (*25*, *26*). Paleoclimatic changes, however, may break up the mutualistic interactions between plants and their pollinators during different geological periods (*37*, *38*). Thus, zygomorphic species experiencing strong stabilizing selection because of more specialized pollination (*24*–*26*) should be more sensitive to paleoclimate change than actinomorphic species that tend to rely more frequently on generalized pollination or wind pollination.

During the Cenozoic, global climate shifted from the Paleocene-Eocene Thermal Maximum, when tropical ecosystems colonized high paleo-latitudes, to a trend of global cooling and aridification during the late Miocene epoch when tropical ecosystems shrank and open vegetation (e.g., deserts, grasslands, and tundra) greatly expanded (*39*). The dramatic temperature decline and corresponding vegetation changes over the Cenozoic would have led to widespread collapse in pollination systems, especially in high latitudes (*40*). Many plant species that strongly depend on specialized pollination interactions [e.g., plant species with zygomorphic flowers (*13*, *35*, *41*)] would have been highly susceptible to such disruption of plant-pollinator mutualisms and may thus inevitably undergo rapid extinctions (*42*–*44*). At the same time, increasing pollination limitation could lead to the evolution of self-pollination (*45*), wind pollination, and generalized pollination (*46*), which are predominantly associated with actinomorphic flowers (*13*, *24*, *38*, *47*). We thus hypothesize that the transition from actinomorphy to zygomorphy would decrease in association with decreasing temperature through the Cenozoic.

Here, using the global distributions and floral symmetry records of 279,877 angiosperm species and a dated species-level phylogeny, we explored the global biogeography and evolution of angiosperm floral symmetry. Specifically, we analyzed contemporary global patterns in the prevalence of different floral symmetry types, as well as the evolutionary transitions between floral symmetry types since the Cenozoic. We aim to test the following three hypotheses: (i) Actinomorphic species are more frequent in high latitudes with low temperatures, low pollinator diversity, and strong historical climate fluctuations, while zygomorphic species are more strongly associated with specialized pollination interactions are more frequent in tropical regions with more stable climate and high pollinator diversity (*48*); (ii) evolutionary transitions from actinomorphy to zygomorphy are more common than the reverse, but the frequency of actinomorphy-to-zygomorphy transitions would decrease throughout the Cenozoic; (iii) the evolutionary transition rate from actinomorphy to zygomorphy is positively correlated with the paleotemperature decline during the Cenozoic.

RESULTS

Global pattern of actinomorphic floral symmetry and its determinants

We found considerable spatial variation in the global distribution of floral symmetry. The proportion of actinomorphic species increased significantly with latitude ($R^2 = 0.286$, $P < 0.001$), and the slope of the latitudinal gradient was not significantly different

between the Southern and Northern Hemispheres ($P > 0.05$; table S1). Specifically, the proportion of actinomorphic species was highest at high latitudes, in western Europe and the Mediterranean region, but lowest in tropical regions (Fig. 1 and fig. S1). Actinomorphic species in high latitudes were mainly from lineages that often have nonspecialized pollination interactions (e.g., Asteraceae, Brassicaceae, Ranunculaceae, Apiaceae, Caryophyllaceae, Boraginaceae, Polygonaceae, Rubiaceae, and Amaryllidaceae; 50.6, 53.4, and 42.9% at 50°N, 60°N and 40°S, respectively) or are wind-pollinated (e.g., Cyperaceae and Amaranthaceae; 10.1, 14.2, and 12.6% at 50°N, 60°N and 40°S, respectively) (table S2 to S4).

Among the climate variables examined here, solar radiation and mean annual temperature (MAT) were the strongest predictors of the contemporary geographic pattern in the frequency of actinomorphy, followed by historical temperature variability (MAT anomaly since the LGM; MATano) (Fig. 2). However, the effects of MATano contrasted with those of solar radiation and MAT (Fig. 2). The frequency of actinomorphy was negatively correlated with solar radiation and MAT ($R^2 = 25.7$ to 27.7%, $P < 0.001$) but was positively correlated with MATano ($R^2 = 16.5\%$, $P < 0.01$). Among the precipitation variables, only precipitation seasonality (PSN) had a moderately negative effect in explaining the proportion of actinomorphy ($R^2 = 13.6\%$, $P < 0.01$). The frequency of actinomorphy was positively yet weakly correlated with wind speed ($R^2 = 9.0\%$, $P < 0.01$).

Temporal dynamics in floral symmetry frequency and evolutionary transitions

The ancestral reconstruction based on the hidden state speciation and extinction (HiSSE) model showed that actinomorphy is likely the ancestral state for angiosperms (fig. S2), which is consistent with previous evidence (*12, 27*). Overall, the frequency of actinomorphic species increased weakly during the Cenozoic (Fig. 3A). Both the absolute and relative transition rates from actinomorphy to zygomorphy continuously decreased with time during the Cenozoic

(Fig. 3A and figs. S3A and S4). Specifically, actinomorphy-to-zygomorphy transitions accounted for nearly 100% of all transitions between floral symmetry types during the early Cenozoic (Fig. 3A and figs. S3A and S4). It is noteworthy that the relative transition rate from actinomorphy to zygomorphy was generally higher than 50% throughout the Cenozoic (Fig. 3A and fig. S3A), indicating that the actinomorphy-to-zygomorphy transitions were more common than the opposite. The HiSSE analysis indicated that speciation, extinction, and net diversification rates of angiosperms were not significantly influenced by floral symmetry types but are likely driven by some other unobserved (hidden) factor(s) (e.g., pollination mode and inflorescence type) that make angiosperm diversification dynamics heterogeneous across lineages with different floral symmetries (Fig. 4).

Relationship between floral symmetry transitions and paleotemperature

The proportion of actinomorphic species weakly but significantly decreased with the increase in paleotemperature during the Cenozoic ($R^2 = 0.18$, $P < 0.01$; Fig. 3B and fig. S3B). The transition rate from actinomorphy to zygomorphy significantly increased with paleotemperature ($R^2 = 0.27$, $P < 0.001$; Fig. 3B and fig. S3B), and this increase was the most rapid when paleotemperature was around 0°C.

DISCUSSION

Deciphering the spatiotemporal dynamics of floral symmetry and their relationship with the environment (especially climate) contributes to our understanding of the spatiotemporal dynamics of plant diversity and the vulnerability of plant-pollinator interactions under scenarios of global change. On the basis of global distributions and floral symmetry data of angiosperm species, our analyses showed that the geographic variation in the frequency of actinomorphic species is negatively correlated with solar radiation and MAT
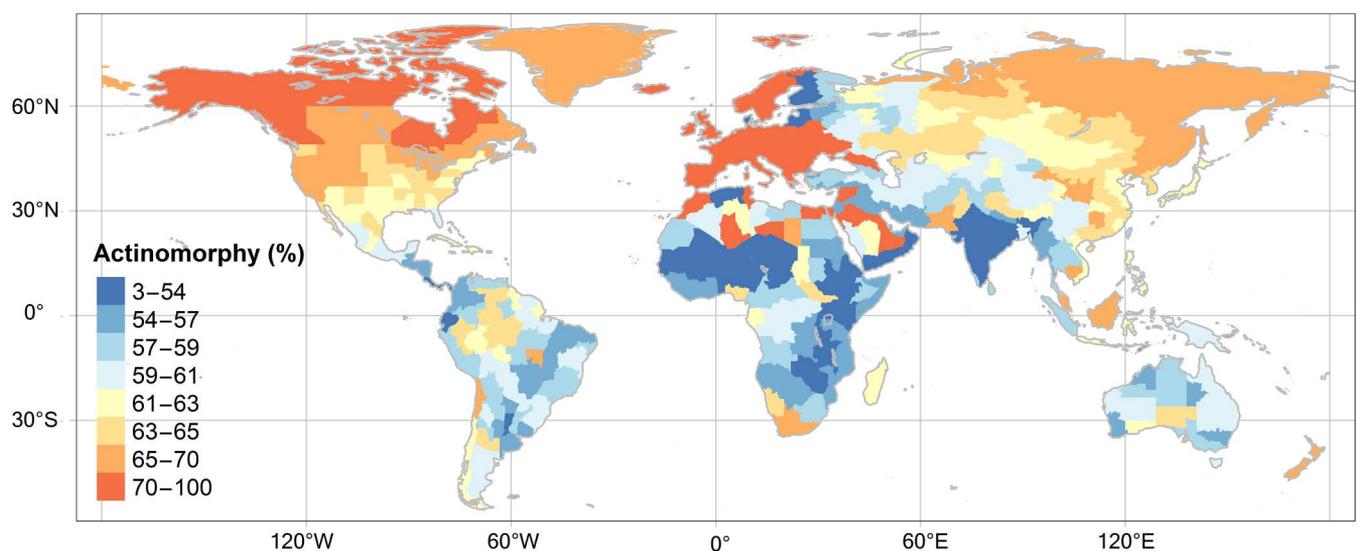

Fig. 1. Global geographic pattern of the prevalence of angiosperm species with actinomorphic flowers. Within each geographic unit, the prevalence of species with actinomorphic flowers was estimated as the proportion of species with actinomorphic flowers to all species within that geographic unit. The proportions of the actinomorphic and zygomorphic species within each geographic unit sum to one.

Fig. 2. The (relative) importance of each environmental predictor on the variance in floral symmetry frequency across the globe. (**A**) The independent (I; lighter colors) and joint (J; the conjoint contribution with all other variables, darker colors) contributions of different variables on proportions of actinomorphic species per geographic unit. Hierarchical partitioning analysis was conducted to identify the variables' independent and joint effects. (**B** to **G**) Relationships between the proportions of angiosperm species with actinomorphic flowers per geographical unit (*y* axis) and environment variables (*x* axis). The environmental variables include latitude, log-transformed solar radiation (LgRAD), mean annual temperature (MAT), the anomaly of MAT since the LGM (MATano), wind speed, and log-transformed precipitation seasonality (LgPSN). Univariate beta regressions were used to evaluate the explanatory power of each variable. Regression lines were drawn when the relationships were significant ($P < 0.05$; see Materials and Methods for more details about the significance test). R^2 values of these regression models are given at the top left corner of each panel.
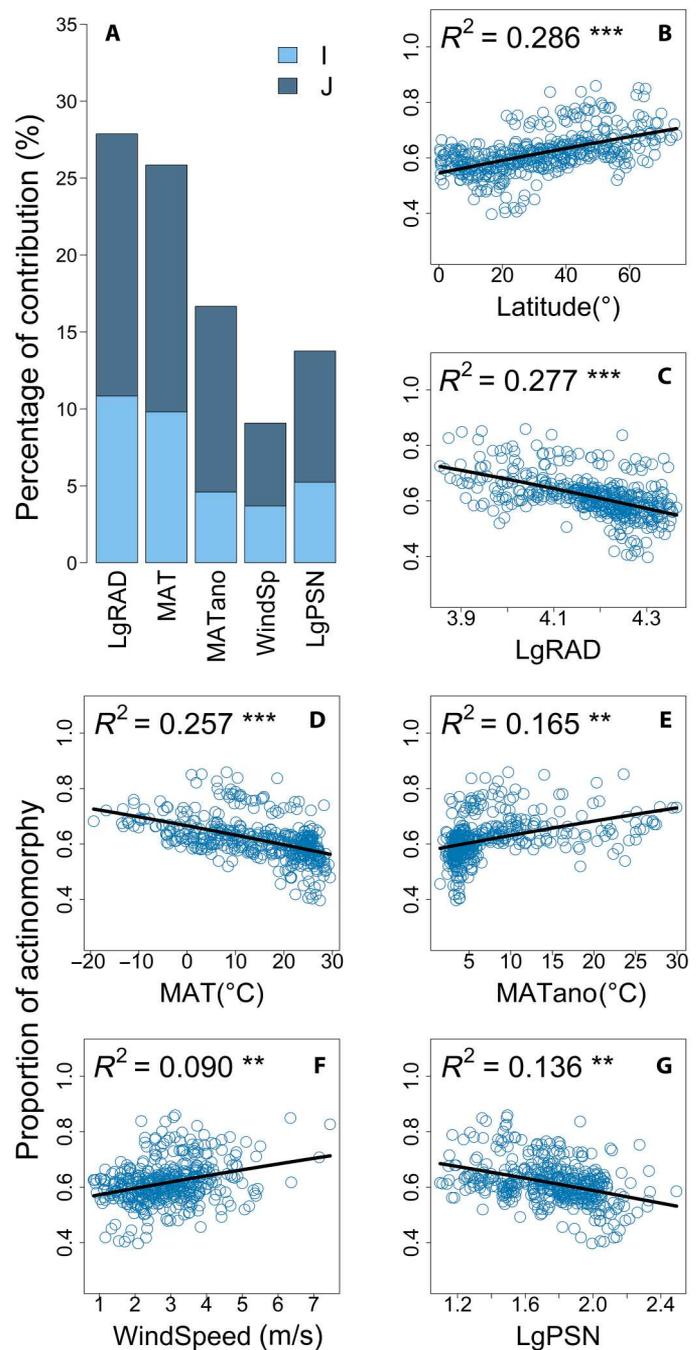
but is positively correlated with temperature change since the LGM. These results are consistent with our hypothesis that species with actinomorphic flowers tend to be favored in regions with low temperatures and strong historical climatic fluctuations. Although the floral symmetry of angiosperms generally evolved from actinomorphy to zygomorphy, the proportion of evolutionary transitions from actinomorphy to zygomorphy decreased through the Cenozoic, which is likely due to the general temperature decline over this period. Together, our findings suggest that climate change, especially temperature change, could mediate spatiotemporal patterns in the floral symmetry of angiosperms, and future climate change

may differentially influence the diversity and distributions of species with different floral symmetry types.

Global patterns in floral symmetry

Geographically, the frequency of actinomorphic species in local floras increased with latitude, and this latitudinal gradient is consistent in the Northern and Southern Hemispheres (see Figs. 1 and 2 and table S1). This finding supports our hypothesis that actinomorphic species tend to be more common at high latitudes that have relatively low plant and pollinator diversity. Previous studies suggest that actinomorphic species are more likely to be self-
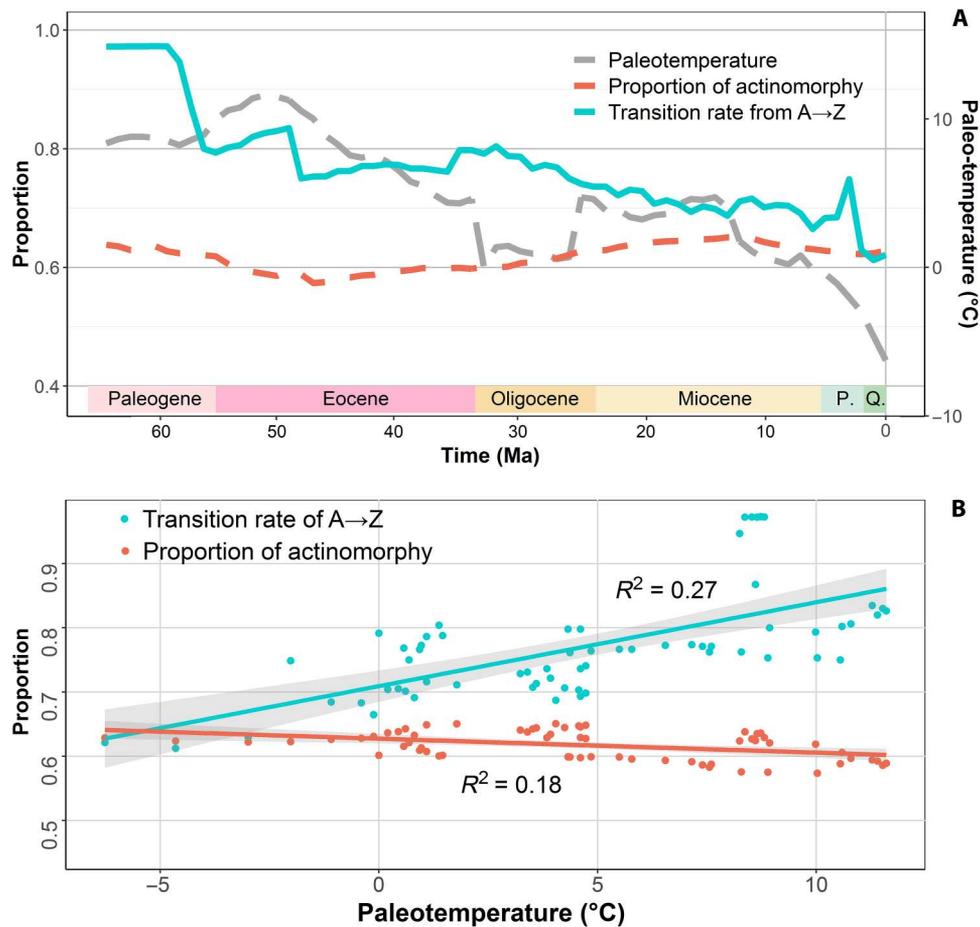
Fig. 3. Macroevolutionary dynamics of floral symmetry in response to Cenozoic climate change. (**A**) The temporal pattern of the proportion of species with actinomorphic flowers and the transition rate from actinomorphic symmetry to zygomorphic symmetry (estimated as the ratio of transition from actinomorphic symmetry to zygomorphic symmetry to the total number of transitions) (65 Ma to 0 Ma ago). (**B**) Changes in the proportion of angiosperm species with actinomorphic flowers and the transition rate from actinomorphic symmetry to zygomorphic symmetry during the Cenozoic as functions of paleotemperature. The evolutionary transition rate here was estimated using the ancestral state reconstruction based on the HiSSE model (see Materials and Methods for more details). The relationships between the response variables and paleotemperature were evaluated using bivariate beta regressions. A, actinomorphic symmetry; Z, zygomorphic symmetry.
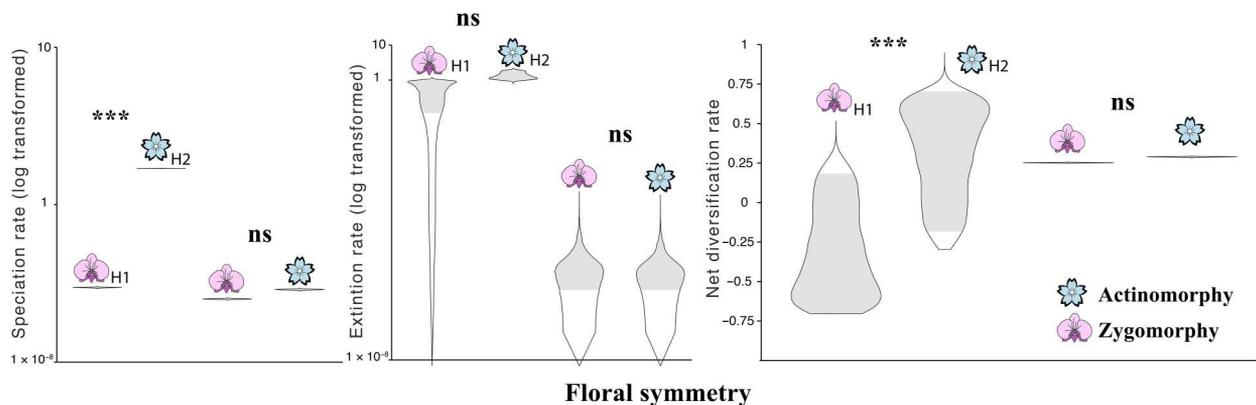

Fig. 4. The effects of floral symmetry (zygomorphy versus actinomorphy) and one hidden trait with two states (H1 versus H2) on the rates of speciation, extinction, and net diversification of angiosperms. Rates of speciation and extinction of zygomorphic and actinomorphic lineages were estimated by the HiSSE model. H1 and H2 denote the states of the hidden trait (H1 is associated with zygomorphy and H2 is associated with actinomorphy) included in the HiSSE model. The results show that the state of a hidden trait associated with actinomorphy (H2) has the strongest effect on angiosperm diversification rate. ***$P < 0.001$; ns, not significant.

fertilized and are more self-compatible than zygomorphic species (*23*). Therefore, our finding on the positive relationship between the frequency of actinomorphic species in local floras and latitude supports Baker's law which predicts that selfers with reproductive assurance are more successful than outcrossers in colonizing new habitats where outcrossing is generally restricted (*49*, *50*). In contrast, zygomorphic species are likely to experience strong selective pressure during colonization due to their dependence on cross-pollination (*3*, *13*) (e.g., due to spatiotemporal mismatch between zygomorphic flowers and their pollinators). Differences in the adaptation of actinomorphic and zygomorphic species to environmental variations, especially those linked to temperature increase since the LGM and geographic variation in pollinator assemblages, may explain the different geographic patterns in the frequency of floral symmetry types.

Drivers of the geographic patterns of floral symmetry

Our results suggest that solar radiation, MAT, and temperature anomaly since the LGM are strong predictors of the geographic pattern in the frequency of angiosperm floral symmetry. The frequency of actinomorphy decreased with the increase in solar radiation and temperature but increased with the increase in temperature anomaly since the LGM along the latitudinal gradient. These findings are consistent with our hypothesis that species with actinomorphic flowers tend to be favored in temperate areas with low temperatures and strong historical climate fluctuations. In contrast, species with zygomorphic flowers are more frequent in regions with relatively stable climates (e.g., relatively stable temperatures) and high pollinator diversity (*14*).

Solar radiation and temperature could influence the geographic distribution of floral symmetry frequency possibly by influencing a suite of floral and vegetative traits of plants and plant-pollinator interactions. Previous studies demonstrated that, compared with zygomorphic taxa, the vast majority of actinomorphic species typically have simpler floral morphology (*3*) and are more widely associated with generalized pollination or wind pollination (*13*, *46*, *47*). These characteristics of actinomorphic species have been found to be associated with large variations in their phenotypes (e.g., flower size variation) and strong adaptation to unstable environments (e.g., unstable pollination environment) (*24*). For example, wind-pollinated species with actinomorphic flowers (e. g., Cyperaceae and some Juncaceae) may be more frequent in temperate regions or at high latitudes of the Northern Hemisphere (*46*), which may also partially contribute to the latitudinal gradient of angiosperm floral symmetry frequency. We found that wind speed showed a relatively weak yet significant effect on the geographic pattern of actinomorphy frequency (see Fig. 2). Thus, actinomorphic species may be more flexible in adapting to environmental changes and have adaptive advantage to extend their ranges faster at higher latitudes which have high climatic seasonality and unpredictable or unavailable pollinators for plants and have experienced severe fluctuations in temperature due to glacial-interglacial cycles (*51*).

Moreover, climatic instability or locally highly variable conditions may have further regulated this general spatial pattern of floral symmetry frequency through their impact on plant-pollinator networks. Previous studies indicate that stronger climatic fluctuations in high latitudes may have led to fluctuations in pollinator availabilities, which would have hindered the survival of zygomorphic species with more specialized pollination interactions than actinomorphic species (*11*). Such processes may also, to some extent, explain the notable regional patterns at relatively smaller spatial scales such as the Ural Mountains (see fig. S5).

Compared with temperate regions, tropical areas normally have higher solar radiation and MAT, higher plant species richness, and more food sources and thus tend to maintain higher pollinator species richness, higher specialization level in pollination networks, and higher visitation frequency by pollinators (*52*, *53*). This is especially beneficial for zygomorphic flowers because compared with actinomorphic flowers, zygomorphic flowers often depend more strongly on specialized pollination and bear more showy shapes (*3*) and restricted nectaries to help attract more selective pollinator species (*53*, *54*).

Temporal trends in evolutionary transition from actinomorphy to zygomorphy

Our results suggest that evolutionary transitions between the two floral symmetry types proceeded more frequently in the actinomorphy-to-zygomorphy direction. This result agrees with previous findings based on fossil records which suggest that zygomorphy is a derived state appearing relatively late [ca. 70 million years (Ma)] in angiosperm evolutionary history compared with actinomorphy (*3*). However, we also find that the transition rate from actinomorphy to zygomorphy has gradually decreased since the early Cenozoic (see Fig. 3), although it has been generally higher than the rate of the reverse transitions during the entire Cenozoic. The transition from actinomorphy to zygomorphy could increase pollination efficiency (*55*, *56*) but also comes with a cost: Species with zygomorphic flowers depend more strongly on specific pollinators, leading to more specialized pollination interactions and hence may have a higher risk of extinction if these pollinators become scarce either episodically or permanently (*11*).

Previous studies found that some zygomorphic clades had higher species diversity than their actinomorphic sister clades and suggested that zygomorphy might have enhanced the speciation of angiosperms (*5*). Our HiSSE analyses across all major clades of angiosperms suggest that actinomorphic species tend to have higher speciation and net diversification rates than zygomorphic species, but the difference in these evolutionary rates may not be caused by floral symmetry types (see Fig. 4). Our results suggest that some other traits associated with floral symmetry but not considered here (i.e., hidden trait) may have influenced speciation and net diversification rates of actinomorphic and zygomorphic species, leading to higher speciation and net diversification rates in some actinomorphic taxa (see Fig. 4). For example, Lázaro and Totland (*57*) have revealed that the pollinator-mediated stabilizing selection for zygomorphic species can also be regulated by population-dependent factors, such as the degree of ecological generalization and dependence on pollinators. This may explain that, despite the overall decline in the rate of evolutionary transitions in the actinomorphy-to-zygomorphy direction, transitions to zygomorphy could still possibly have a positive effect on the diversification of some clades as shown by previous sister-clade comparisons (*5*).

There are some uncertainties surrounding our results given the potential effects of inaccurate phylogenetic relationships between species. Specifically, to fulfill the requirement of the HiSSE models, which require fully resolved phylogenies (i.e., phylogenies without polytomies), the polytomies in the complete angiosperm

phylogeny (*58*) used in our analysis were randomly resolved using a Yule bifurcation process following previous studies (*59*, *60*). This polytomy resolution may lead to inaccurate species relationships and hence introduces uncertainties in the ancestral reconstruction (*61*). It is noteworthy that our results based on the complete phylogeny with polytomies randomly resolved and those based on the molecular phylogeny containing no polytomies showed a consistent temporal trend in the transition rate between actinomorphy and zygomorphy, which suggests that our analysis was not substantially affected by the polytomy resolution (fig. S3). Nevertheless, more complete phylogenies based on molecular data are needed for understanding the macroevolution of the functional and morphological traits of angiosperms.

Relationship between transition rate from actinomorphy to zygomorphy and paleotemperature

Consistent with our hypothesis, the rate of transition from actinomorphy to zygomorphy continuously decreased in association with the decrease of paleotemperature since the early Cenozoic. This result suggests that changes in the abiotic environment could have played a role in the evolution of floral symmetry (*62*). On the one hand, the global paleotemperature decreases since the early Cenozoic and the extreme temperature fluctuations during the Quaternary due to glacial-interglacial cycles may have influenced the spatiotemporal turnover in the diversity of both plants and pollinators over geological timescales (*37*, *38*, *63*, *64*). Such instabilities of plant and pollinator diversity could have negative impacts on plant-pollinator interactions and may have strongly influenced the pollination specificity and even the maintenance of zygomorphic species with more specialized pollination interactions (*3*, *25*, *26*). Therefore, paleotemperature decrease since the early Cenozoic and Quaternary temperature fluctuations might have compromised the evolutionary transition toward zygomorphic species. On the other hand, continuous decreases in paleotemperature and a global trend of aridification during the Cenozoic may have led to much wider open ecosystems at the global scale favoring plant species associated with more generalized pollination or wind pollination, both of which could provide a selective advantage to the evolutionary transition from zygomorphy to actinomorphy. In contrast to the suppressive effects of temperature decline, warm environments may contribute to the evolution of zygomorphy by regulating floral orientation (*62*, *65*). Recent studies suggest that a shift to vertical floral orientation is likely the first evolutionary step toward the evolution of zygomorphy (*56*).

Overall, our results indicate that the spatiotemporal dynamics of species with zygomorphic flowers are likely to be associated with warm climates, which exemplifies how climate change may influence the macroevolutionary and ecological processes of species with different floral symmetry types and how floral symmetry as a key reproductive trait can be used to understand complex community dynamics in response to global warming.

MATERIALS AND METHODS
Floral symmetry of angiosperms
We compiled a global dataset of angiosperm floral symmetry based on published floras and trait databases, including eFloras (http://efloras.org/), The Families and Genera of Vascular Plants [The Families and Genera of Vascular Plants | Book series home

(springer.com)], Flora of China (http://www.efloras.org/flora_page.aspx?flora_id=2, accessed April 2018), Flora of Zimbabwe (zimbabweflora.co.zw), Flora of Zambia (zambiaflora.com), Flora of Mozambique (mozambiqueflora.com), Flora of Botswana (botswanaflora.com), Flora of Caprivi (capriviflora.com), Flora of Malawi (malawiflora.com), Flora of Sri Lanka, Plant Trait Database (TRY) (*66*), Botanical Information and Ecology Network (BIEN) (*67*), Flora Republicae Popularis Sinicae (126 issues of 80 volumes), and Go Botany (Native Plant Trust, https://gobotany.nativeplanttrust.org), as well a large number of publications on regional and local floras (text S1). Species with conflicting records of floral symmetry in different sources were double-checked. In total, 279,877 angiosperm species with floral symmetry information belonging to 12,657 genera, 407 families, and 64 orders were included in our final dataset (table S5).

All species were classified into two categories based on their floral symmetry following previous studies (*8*, *25*, *26*): zygomorphy (i.e., flowers with just one axial plane dividing the flowers into two symmetrical halves) and actinomorphy (i.e., flowers with two or more axial planes, each of which divides the flowers into two symmetrical halves). Zygomorphic species included those with flowers recorded as monosymmetry, (some) irregular, and bilateral symmetry. Actinomorphic species included species with flowers recorded as polysymmetry, regular, and radial symmetry. Last, although asymmetrical flowers do occur across angiosperms, we did not include them in our study due to their extremely low frequencies following previous studies (*26*). In the final dataset, 60.8% of all species were recorded as actinomorphic, which is consistent with a previous estimation [see figure S1 in (*68*)].

In particular, the flower symmetry of species from several families (i.e., Asteraceae, Poaceae, Apiaceae, and Brassicaceae) might be controversial. We therefore provided the specific assessment criteria of zygomorphy versus actinomorphy symmetry types for these families (see text S1 and data file S2 for more details). Moreover, as a comparison, we re-estimated the global geographic pattern of floral symmetry frequency after excluding the species with controversial symmetry from two large families Asteraceae and Poaceae and found that the result was highly consistent with that when all species were included (fig. S1A).

Global angiosperm distributions and geographic patterns in the frequency of floral symmetry
The global distributions of angiosperm species were compiled from more than 1100 data sources, including published national-level and regional floras and checklists, peer-reviewed papers, and online databases (see data file S1 for a list of the data sources). The nomenclature of different sources was standardized following the Catalogue of Life (www.catalogueoflife.org/, accessed May 2018). The geographic units used for the compilation of species distribution data were generated from the Global Administrative Areas Database (www.gadm.org/) and have a spatial resolution of ca. 4 longitude × 4 latitude [for details, see text S2; (*69*)]. This layer of geographic units has been used for the compilation of species distributions in several previous studies (*69*–*71*). By integrating the data of floral symmetry and geographic distributions, we estimated the proportions of actinomorphic and zygomorphic species within each geographic unit. As the proportions of the two floral symmetry types within each geographic unit sum to one, we focused on the

geographic pattern in the proportion of actinomorphic species in the following analyses.

Current and historical climate

To evaluate the effects of contemporary climate on geographic variations in floral symmetry composition, we selected several climate variables including contemporary MAT (MAT), temperature seasonality (TSN; the SD of monthly mean temperature), wind speed, mean annual precipitation (MAP), and PSN (the coefficient of variation of mean monthly precipitation). Solar radiation was also used because previous studies indicated that it may contribute to geographic variation in floral traits [e.g., floral color (72)]. Data for these variables with a spatial resolution of 30 arc sec were obtained from the WorldClim website (www.worldclim.org/), which has been widely used in macroecological studies (69, 73).

The MAT and MAP in the LGM reconstructed by the WorldClim website

Previous studies suggest that historical climate change since the LGM [ca. 18,000–22,000 years before the present (BP)] substantially influenced the spatial distribution of plant species (22). Following previous studies, the anomaly of MAT (or MAP) between the LGM and the present ($MATano = MAT_{present} − MAT_{LGM}$, $MAPano = MAP_{present} − MAP_{LGM}$) (69) was used to examine the effects of historical climate change on the geographic pattern of angiosperm floral symmetry frequency (74). The value of each climate variable (MAT, TSN, MAP, PSN, wind speed, solar radiation, MATano, and MAPano) in each geographic unit was estimated as the average of all 30–arc sec grid cells within it [see (75) for more details].

Long-term climate change is one of the drivers influencing the evolutionary dynamics of floral traits (e.g., flower color) (21, 73), which may also contribute to shifts in floral symmetry. To assess the impact of paleotemperature on the evolutionary transition rate between zygomorphy and actinomorphy during the Cenozoic, we used the long-term time series of global mean paleotemperature estimated from sediment oxygen isotope [see (76) for more details]. This dataset has been widely used to present paleotemperature change in previous studies (69). In our analysis, the mean paleotemperature in each 1-Ma time interval since 65 Ma ago was estimated.

Angiosperm phylogenies

To analyze the evolutionary transitions between floral symmetry types, two dated phylogenies generated by Smith and Brown (58) were used: (i) the dated molecular species-level phylogeny of seed plants containing 79,881 tips [i.e., the GBOTB phylogeny in (58)] and (ii) the dated species-level phylogeny of all angiosperms containing 353,185 tips [i.e., the ALLOTB phylogeny in (58)]. Both phylogenies have been widely used in previous studies on macroevolution and macroecology (69). By matching the tips of the two phylogenies (i.e., the GBOTB and the ALLOTB phylogenies) with the species with floral symmetry information, 54,743 and 204,945 species were retained for the following analyses based on the two phylogenies respectively (figs. S3 and S4 and table S5).

It is noteworthy that the ALLOTB phylogeny was constructed by inserting all species without GenBank sequence data into the GBOTB phylogeny as polytomies in their corresponding families (58), which leads to methodological difficulties in the analysis of evolutionary rates and ancestral state reconstructions. To resolve this issue, the polytomies of this phylogeny were resolved using a

Yule bifurcation process following previous studies (59, 60), although resolving polytomies on phylogenetic trees is not trivial, including species that do not have sequence data allows to improve estimates of diversification rates and their variation among clades with different traits (77, 78). To evaluate whether the process of resolving the polytomies in the ALLOTB phylogeny may influence our analysis, we conducted the ancestral state reconstruction using the GBOTB phylogeny that is fully resolved based on molecular data and the resolved ALLOTB phylogeny based on a Yule bifurcation process separately (61) (see the "Statistical analyses" section for details). As another comparison, we also re-estimated the global geographic pattern of floral symmetry frequency using the dataset that was matched with the phylogenies and found highly consistent geographic patterns of floral symmetry with that based on all families (fig. S1B).

Statistical analyses

First, we used univariate beta regression (79) to explore the latitudinal gradient of the proportion of actinomorphic species per geographic unit and to evaluate the effects of each environmental predictor (including solar radiation, MAT, MATano, TSN, wind speed, MAP, PSN, and MAPano) on the geographic pattern of the proportion of actinomorphic species. The residuals of the beta regression models were approximately normally distributed (e.g., fig. S6). A modified t test was used to test the significance of each predictor, which could account for the impact of spatial autocorrelation on significance levels. Furthermore, we used hierarchical partitioning analysis to identify the independent effect of each environmental predictor using the 'hier.part' function in the R package 'hier.part' (80).

Then, to evaluate the consistency of the latitudinal gradient of floral symmetry in the Northern and Southern Hemispheres, we conducted a generalized least squares (GLS) regression with the proportion of actinomorphic species as the response variable, and the absolute latitude, the Hemispheres (as a grouping variable) and their interaction as the predictors (table S1). A correlation structure with a spherical form was used in the GLS model to account for the potential influences of spatial autocorrelation on model significance following previous studies (81). This was conducted using the 'gls' function of the R package 'nlme'.

As floral symmetry may potentially influence the diversification of angiosperms (5), we used state-dependent speciation and extinction models to reconstruct the ancestral states of angiosperm floral symmetry. Because unknown traits in addition to floral symmetry that are not included in the analysis may have impacts on the diversification rates of angiosperms, we used stochastic character mapping and HiSSE models (with two hidden states; see table S6, for the details of the priors) conducted in RevBayes (82) [see (69) for more details about the setup of these models]. The HiSSE models allow for a "null" model where the diversification process may be unrelated to the focal trait (floral symmetry here) in contrast to the original BiSSE implementation where this is not considered (83). Implementing this approach in HiSSE effectively reduces the risk of type I errors (erroneous rejection of the true null hypothesis), which has been recognized as a common issue for the standard BiSSE models (84).

According to the ancestral state reconstruction, we calculated the proportion of branches reconstructed as actinomorphy in each 1-Ma time interval and estimated the temporal changes of floral

symmetry frequency (i.e., the proportion of branched reconstructed as actinomorphy among all branches). We then estimated the temporal patterns of the rate of evolutionary transitions from actinomorphy to zygomorphy. In particular, there are several ways to shift from one state to the other and some of them involve more complex paths over evolutionary time according to Donoghue *et al.* (*32*), so we accounted for this by binning the tree and then calculating the transitions in each time interval relative to the states in the preceding one. Consequently, our estimates of the transitions do not simplify things based only on tip and root states.

To evaluate whether resolving the polytomies in the ALLOTB phylogeny may influence the estimation of the evolutionary transitions between actinomorphy and zygomorphy, we compared the temporal trends in the actinomorphy-to-zygomorphy transition rates based on HiSSE analyses using the ALLOTB phylogeny with resolved polytomies and the fully resolved molecular phylogeny (i.e., the GBOTB phylogeny) (*58*). We found that the temporal trends in the evolutionary transition rates between actinomorphy and zygomorphy were highly consistent between the two phylogenies (fig. S3), which suggests that polytomy resolution did not substantially bias our conclusions. To evaluate whether the uncertainties in the coding of flower symmetry types for the species in two large families Asteraceae and Poaceae may bias our analysis of the transitions between flower symmetry types, we also estimated the temporal trends in the actinomorphy-to-zygomorphy transition rates based on HiSSE analysis using the ALLOTB phylogeny with Asteraceae and Poaceae excluded. We found that the temporal trend of the evolutionary transition rate between actinomorphy and zygomorphy based on this reduced dataset was highly consistent with that based on the full dataset (fig. S7), suggesting that the treatment of floral symmetry of these families may not substantially affect our results. Last, beta regressions were used to assess the effect of paleotemperature on the temporal changes in the actinomorphy frequency and the actinomorphy-to-zygomorphy transition rate. All analyses were conducted in R 3.6.3 and R 4.2.2. (The R Core Team, 2020, 2022).

Supplementary Materials

This PDF file includes:
Figs. S1 to S8
Tables S1 to S6
Texts S1 and S2
Legends for data S1 and S2
References

Other Supplementary Material for this manuscript includes the following:
Data S1 and S2

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