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Global biogeography and macroevolutionary patterns of angiosperm inflorescence types

Yunyun Wang¹, Ao Luo², Dimitar Dimitrov³, Robert P Freckleton⁴, Zhanqing Hao¹, Zhiheng Wang^{2*}

¹ Shaanxi Key Laboratory of Qinling Ecological Intelligent Monitoring and Protection, School of Ecology and Environment, Northwestern Polytechnical University, Xi'an 710000, China

² Institute of Ecology and Key Laboratory for Earth Surface Processes of the Ministry of Education, College of Urban and Environmental Sciences, Peking University, Beijing 100871, China

³ Department of Natural History, University Museum of Bergen, University of Bergen, P.O. Box 7800, 5020 Bergen, Norway

⁴ School of Biosciences, University of Sheffield, Sheffield S10 2TN, UK

Author for correspondence: Zhiheng Wang. *Email*: zhiheng.wang@pku.edu.cn

ORCID

Yunyun Wang, <https://orcid.org/0000-0002-2019-8996>

Dimitar Dimitrov: <https://orcid.org/0000-0001-5830-5702>

Ao Luo: <https://orcid.org/0000-0003-1270-6353>

Robert P. Freckleton: <https://orcid.org/0000-0002-8338-864X>

Zhanqing Hao: <https://orcid.org/0000-0003-2875-6419>

Zhiheng Wang: <https://orcid.org/0000-0003-0808-7780>

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Summary

- The huge variety of inflorescences plays an important role in the reproductive success and diversification of flowering plants. However, the influence of climate on inflorescence diversity at macroecological and macroevolutionary scales remains poorly understood.
- In this study we map the global spatio-temporal pattern of inflorescence types and investigate the influence of climate on the spatiotemporal patterns of angiosperm inflorescence diversity.

- Our results reveal a clear latitudinal trend in inflorescence types, with indeterminate inflorescence frequency increasing away from the equator. Pollination mode composition and temperature variables are strong correlates of the geographic variation in inflorescence type frequency. We further reveal that lineages with determinate inflorescence have significantly higher net diversification rate than those with indeterminate inflorescence. The frequency of evolutionary transitions from indeterminate to determinate inflorescences consistently decreased during the Cenozoic. Significantly, the evolutionary dynamics of inflorescence types during the Cenozoic show clear latitudinal differences: the proportion of indeterminate inflorescence at high latitudes increased with time and with the decline of paleotemperature, while that at middle to low latitudes decreased.
- These results indicate strong climatic forcing on floral dynamics via influencing inflorescence types and their coevolution with animal pollination over large biogeographical and macroevolutionary scales.

Key words: inflorescence type; determinate; indeterminate; macro evo-devo; evolutionary transition; climate change; angiosperm diversification

Introduction

The inflorescence (i.e. the arrangement of flowers in the floral axis on flowering plants) plays a key role in reproductive success of flowering plants and the evolution of plant diversity because of its effect on pollination mechanisms (i.e. the dynamics of pollen availability and pollen transfer) and pollinator behavior (Stebbins, 1973; Wyatt, 1982; Jordan & Harder, 2006; Hake, 2008; Kirchoff & Claßen-Bockhoff, 2013). Inflorescences have been widely classified into two major types, namely determinate and indeterminate (Bull-Hereñu & Claßen-Bockhoff, 2011; Claßen-Bockhoff & Bull-Hereñu, 2013). The apical meristem can either remain active and continue to produce new flowers over an extended period (indeterminate), or it can be completely used up after producing a certain number of flowers (determinate). Indeterminate inflorescences have the theoretical capacity to continue elongating and producing new flowers, whereas determinate inflorescences cannot. These differences between indeterminate and determinate inflorescences may lead to differential capacities in population establishment and success in certain ecological and geographical settings (Prusinkiewicz *et al.*, 2007). Unravelling the dynamics of inflorescence types at large spatial and taxonomic scales can provide insight into the functional responses of angiosperms to climate change (Kirchoff & Claßen-Bockhoff, 2013; Endress, 2010). However, the biogeography of inflorescence types has received little attention, although the evolution of flowers has been of considerable interest (Endress, 2010).

Theoretical and empirical work has demonstrated the association between variations in the frequency of different inflorescence types and climate (Stebbins, 1973; Prusinkiewicz *et al.*, 2007). The length of the growing season (i.e., the period of time between the last spring frost and the first fall frost) has been found to impose strong selective pressure on inflorescence type frequency (Stebbins, 1973; Prusinkiewicz *et al.*,

2007). Indeterminate inflorescences can continuously grow and produce flowers throughout the growing season in response to changing environmental cues (Stebbins, 1973). In high-latitude regions, where the growing season is typically short, pollinators may be less abundant or active for shorter periods, and extreme climate conditions such as late frosts are common. In these regions, the extended/flexible flowering period of indeterminate inflorescences could be more resource-efficient, increasing the chances of successful pollination (Barrett *et al.*, 1994; Karron *et al.*, 2004; Boff *et al.*, 2021). Additionally, the ability to produce flowers continuously enhances the likelihood of cross-pollination (Barrett *et al.*, 1994; Karron *et al.*, 2004), which contributes to greater genetic diversity—a competitive advantage for species with indeterminate inflorescences in high-latitude regions (Stebbins, 1974). These advantages may make species with indeterminate inflorescence better suited to the post-LGM recolonization of high (northern) latitudes that have experienced severe climate change since the Last Glacial Maximum (Prentice *et al.*, 1991; Nolan *et al.*, 2018).

By contrast, determinate inflorescences tend to display multiple flowers intensively in a short period which may reduce reproductive success if the blooming time coincides with unfavorable/extreme climate (e.g. seasonal variations of extreme events), especially at high latitudes where unfavorable climate is more common. Moreover, a strategy which “puts all eggs in one basket” is also likely to lead to a higher risks of among-flower self-pollination (Barrett *et al.*, 1994; Karron *et al.*, 2004) and an associated reduction in pollen export (Harder and Barrett, 1995; Karron and Mitchel, 2012) and, ultimately, higher incidence of inbreeding depression for embryos and offspring (Stebbins, 1973). On the other hand, determinate inflorescences with more synchronous flowering events can optimize pollination success by increasing attractiveness and competitiveness to pollinators in warm low-latitude regions. They also reduce the risk of repeated herbivory on flowers or flower buds and minimize excessive water use for elongation (Ferguson *et al.* 2019), increasing plant survival during droughts that are common in tropical and subtropical regions (Zhu *et al.* 2024). Therefore, determinate inflorescences were expected to be more favored in warm low-altitude areas that are associated with high temperatures, high herbivory rates and seasonal droughts.

Previous research on the evolutionary transitions between inflorescence types has been controversial (Endress, 2010). Some researchers assumed that determinate inflorescence (e.g. single flower or monotelic inflorescence) is the ancestral state in angiosperms (Stebbins, 1973; Rudall & Bateman, 2010), and that once indeterminate inflorescence evolved it remained stable (Coen & Nugent, 1994). In contrast, other studies found that monotelic inflorescence are completely absent in the early branching angiosperms (ANITA grade) and single terminal flowers are quite rare and only present in a few genera (e.g. *Austrobaileya*, *Schisandra*, and *Illicium*) (Endress, 1980; Endress & Sampson, 1983; Weberling, 1988; Posluszny & Tomlinson, 2003;

Rudall *et al.*, 2007; The Angiosperm Phylogeny Group, 2009; Endress & Doyle, 2009). These findings suggest that the macroevolutionary direction of inflorescence types is probably from indeterminate to determinate, such as in Hamamelidaceae (Endress, 2003). Nevertheless, the fact that most plant families contain species with distinct inflorescence types suggests that they evolved from one another multiple times independently (Watson & Dallwitz, 2023). However, there is a lack of empirical evaluation at broad taxonomic and temporal scale to determine the general macroevolutionary dynamics of inflorescence types, and studies focusing on fine-scale changes in inflorescence types in small taxonomic groups only begin to appear (Bröderbauer *et al.*, 2013; Landrein & Prenner, 2013).

Paleoclimate may have profoundly influenced the evolution of indeterminate inflorescences from determinate ones through a two-step process involving ‘reduction followed by amplification’ (Stebbins, 1973). Specifically, shortening of the growing season may reduce the length of the plant reproductive cycles and then more favorable environments may lead to increased seed production (Stebbins, 1973). Global cooling through the Cenozoic, especially in the last 50 Ma (Zachos *et al.*, 2008), led to great reduction in growing season length, particularly in (northern) high latitudes (Tiffney & Manchester, 2001; Donoghue, 2008; Tierney *et al.*, 2020). We thus expect that this long-term global cooling trend may favor the evolution of indeterminate inflorescences, especially in northern high latitudes, given the advantages of indeterminate inflorescence (i.e., sequential flower display and subdivision of reproduction) in response to environmental fluctuations (Stebbins, 1973; Harder *et al.*, 2004).

Moreover, the decline in global paleo-temperature during the Cenozoic has led to the expansion of grasslands (e.g. temperate grasslands and open tropical savannas) and tundra (Retallack, 2001) and the evolution of wind pollination in high latitudes (Culley *et al.*, 2002), which may have also contributed to the evolution of indeterminate inflorescence. This is likely because wind-pollinated species are predominantly associated with highly condensed inflorescences or inflorescence sub-units (e.g. grass spikelets, Weller *et al.*, 1998). Because high latitudes have experienced a more pronounced decline in temperature than low latitudes since the Cenozoic (Zhang *et al.* 2019), we expect that high-latitude taxa will show greater evolutionary dynamics than low-latitude ones. However, the influence of paleoclimate on the long-term evolutionary transitions among angiosperm inflorescence types at macroevolutionary time scales remains poorly understood.

At present, the global biogeography and macroevolutionary dynamics of angiosperm inflorescence types remain largely unknown due to the lack of the necessary combination of information on functional traits, geographical distributions and phylogenetic relationships across sufficiently large spatio-temporal and taxonomic scales. Here, we describe the global spatio-temporal macroevolutionary dynamics of angiosperm

inflorescence types since the Cenozoic by incorporating the distributions and inflorescence type records of 194476 angiosperm species and a large-scale dated species-level angiosperm phylogeny. Specifically, we aim to test the following three hypotheses: 1) indeterminate inflorescence frequency increases with latitude and historical climate fluctuations but decreases with the increase in growing season length and (mean annual) temperature; 2) high- and low-latitudes taxa differ in their macroevolutionary dynamics of inflorescence types along paleotemperature change gradients over the Cenozoic, with high-latitude taxa displaying greater phenotypic shifts; 3) paleotemperature decline throughout the Cenozoic had contributed to the evolutionary transitions from determinate to indeterminate inflorescences.

Materials and methods

Angiosperm inflorescence types and pollination mode

We collected the most extensive global dataset of angiosperm inflorescence types and pollination modes using series of published floras and trait databases (Wang *et al.*, 2023), including *The Families and Genera of Vascular Plants* (*The Families and Genera of Vascular Plants | Book series home (springer.com)*), *efloras* (<http://efloras.org/>), *Flora of China* (http://www.efloras.org/flora_page.aspx?flora_id=2, accessed in April 2018), plantNET (*National Herbarium of New South Wales (nsw.gov.au)*), *World Flora Online* (<https://www.worldfloraonline.org/>), *Flora of Zambia* (zambiaflora.com), *Flora of Zimbabwe* (zimbabweflora.co.zw), *Flora of Caprivi* (capriviflora.com), *Flora Malesiana* (<https://floramalesiana.org/new/>), and a series of publications (Supporting Data S1). Species names from multiple data sources were standardized following the Catalogue of Life (<http://www.catalogueoflife.org/>).

Angiosperm inflorescence types were classified according to whether flowering units can continue apical growth (indeterminate) or not (determinate) (Claßen-Bockhoff & Bull-Hereñu 2013; Balanzà *et al.* 2019). Specifically, indeterminate inflorescence refers to those where the apical meristem of a flowering shoot remains undifferentiated and produces continuously new flowers until the end of the reproductive phase. Determinate inflorescences are those where the shoot apical meristem differentiates directly, or after the production of a certain number of flowers. Indeterminate inflorescence has diverse types including (compound) raceme, spike, catkin (or aments), spadix, and other indeterminate types (i.e. thyrses, monopodial and polytelic). Determinate inflorescence includes cyme(s), dichasium, monochasium (i.e., scorpioid cyme, helicoid cyme), pleiochasium (i.e., fascicle) and other determinate inflorescences (botryoids, thyrsoid(s), sympodial and monotelic). Species with solitary flowers, pairs of flowers, or those with unclear/inexact or entirely absent descriptions of inflorescence types were excluded. Pollination modes were divided into two types: animal pollination and wind pollination following previous studies (Tong *et al.*,

2023), and species with other pollination strategies, such as water or ambophily, were excluded from this analysis due to their extremely low frequency in our dataset. Finally, 194 476 angiosperm species with inflorescence type spanning 61 orders, 348 families, 9 046 genera and 179 263 species with pollination mode were included in the following analyses (Table S1; Supporting Data S2).

Geographical and climatic data

Species-specific geographic distribution information on worldwide angiosperms was based on occurrence data available through over 1100 data sources (see Luo *et al.* (2023)). Specifically, the distribution data sources comprise published national-level as well as regional floras, checklists, and series of online databases (see Wang *et al.*, (2023) and Luo *et al.*, (2023) for a list of the data sources). The *Catalogue of Life* (<http://www.catalogueoflife.org/>, accessed in May 2018) was used to standardize and unify the nomenclature across different sources. Records referring to cultivated and introduced species were removed. In sum, our dataset consisted of 1,064,282 occurrence records for 194476 angiosperm species.

The geographic units used for data collection of species distributions were generated according to the *Global Administrative Areas Database* (<http://www.gadm.org/>), with a spatial resolution of *ca.* 4 longitude \times 4 latitude (see Wang *et al.*, 2021; Wang *et al.*, 2023; Luo *et al.*, 2023 for details). By incorporating the species-level inflorescence type information and geographic distributions, we calculated the inflorescence type frequency within each geographic unit (that is, the number of species with determinate or indeterminate inflorescence out of the total number of angiosperms with inflorescence type information in each geographic unit). We only presented the geographic variation in indeterminate inflorescence frequencies in the subsequent analyses, considering that the proportions of determinate and indeterminate inflorescences within each geographic unit sum to one.

To assess the effects of contemporary and historical climate conditions on geographic variation in inflorescence type frequencies, we extracted several climate variables including temperature variables (contemporary mean annual temperature [MAT], temperature seasonality [TSN, the standard deviation of monthly mean temperature]), precipitation variables (mean annual precipitation [MAP], and precipitation seasonality [PSN, the coefficient of variation of mean monthly precipitation]), wind speed, historical temperature/precipitation change since the Last Glacial Maximum (LGM, ~22000 years ago) [$MAT_{ano} = MAT_{present} - MAT_{LGM}$, $MAP_{ano} = MAP_{present} - MAP_{LGM}$]. All these bioclimatic attributes were derived from the *WorldClim* website (<http://www.worldclim.org/>) at a spatial resolution of 30 arc-seconds. The value of each bioclimatic variable per geographic unit was calculated as the average values for all 30 arc-second grid cells within that unit (see Xu *et al.* 2013).

Long-term climate change since the Cenozoic may have contributed to the evolutionary dynamics between determinate and indeterminate inflorescences. We also extracted the $\delta^{18}\text{O}$ -based time series of global paleo-temperature from drilling cores (i.e., the mean paleo-temperature in each 1 Mya time interval since the 65 Ma) at both high (above 50° N/S) and middle-low latitudes (0–40° N/S) according to recent work (see Auderset *et al.*, 2022) for more details).

Angiosperm phylogenies

To enable large-scale comparative analyses, we estimated the macroevolutionary transitions between the two inflorescence types based on two dated phylogenies reported by Smith and Brown (Smith & Brown, 2018), both of which have been widely used in previous work on macroecology and macroevolution. One phylogeny (the GBOTB in Smith & Brown, (2018) is the largest species level mega-tree for vascular plants that was generated based on molecular data for 79881 seed plant species from GenBank. The other phylogeny (the ALLOTB tree incorporated the Open Tree of Life taxa (Smith & Brown, 2018) includes 353,185 terminal taxa, most of which were added as polytomies in their corresponding families in the GBOTB phylogeny. After aligning the inflorescence type data of species with the phylogenies, a total of 39774 and 166053 taxa were identified and included for subsequent analyses according to the GBOTB and the ALLOTB phylogenies, respectively. Please see Supporting Data S2 for the species list that were matched onto the phylogenies. For another comparison, we also re-estimated the global geographic pattern of inflorescence type frequency using the taxa that was matched with the GBOTB phylogeny and found highly consistent spatial patterns of inflorescence type with that based on all taxa (Fig. S1a).

The large number of polytomies in the ALLOTB is problematic for comparative phylogenetic analyses which often require fully resolved binary trees. Thus, we resolved the ALLOTB polytomies using a strategy based on the Yule process following previous studies (Kuhn *et al.*, 2011; Roquet *et al.*, 2013). Including species without character data to a backbone phylogeny and resolving polytomies allows to improve estimates of diversification rates and their variation among clades. However, the process of polytomy resolution is not perfect and may introduce unwanted biases. To evaluate whether polytomy resolution had influenced our analyses, we conducted the ancestral state reconstruction using both the 100 randomly resolved phylogenies separately and only the GBOTB phylogeny as comparison (see the following section for further details). We estimated the evolutionary dynamics in angiosperm inflorescence type in each 1 Myr time interval across the 100 phylogenies, and the 5th and 95th quantiles to show the 95% confidence intervals.

Statistical and comparative phylogenetic analyses

First, we used univariate beta regressions to explore the relationships between inflorescence type frequency per geographic unit and pollination mode frequency (i.e. proportion of animal pollination per geographical unit) and bioclimatic explanatory variables (i.e., wind speed, MAT, TSN, MATano, MAP, PSN, MAPano). The model performance of these regressions was indicated by pseudo- R^2 and the significance of each predictor was evaluated using the modified t -test that could account for the impact of spatial autocorrelation on significance levels (Dutilleul *et al.*, 1993). To examine the relative importance of these predictors, we applied hierarchical partitioning to decompose the variance of inflorescence type frequency to the contributions of each bioclimate variable using the “” function in R package “hier.part” (Grömping, 2007).

To assess the reliability of the estimates given the large number of missing taxa of known angiosperm species, genera, and families, we randomly generated 100 subsamples with the same proportion (i.e. 2/3~3/4) of the species in our full dataset but balanced the proportion of inflorescence type according to the full data (i.e. 50.4-52.2% for indeterminate inflorescence). Then, we ran the analysis of global variation for each of the 100 subsamples and calculated the median results, and found the estimates generated by randomly sampling species from our full dataset 100 times were highly consistent with estimates obtained from our full dataset (Fig. S1b).

To assess whether unequal sampling effort across regions introduced biases in estimating the proportions of indeterminate inflorescence per geographical unit, we first calculated the sampling proportion as the ratio of species richness with certain inflorescence type data to the total species richness within each geographical unit. We then used beta regression to investigate the relationship between the proportion of species with indeterminate inflorescence and the sampling proportion per geographical unit. A modified t -test showed no significant correlation between these two variables (Fig. S2), suggesting that uneven sampling effort across regions did not influence the estimated geographical patterns of inflorescence type frequency. Similarly, we also found that the growth form composition (i.e. the proportion of woody species per geographical unit) didn't affect the estimated geographic patterns in proportions of inflorescence types.

Considering the potential effect of climate heterogeneity within geographical units (induced by the large spatial resolution of our species distribution data) on the indeterminate inflorescence frequency, we also examined the relationships between the standard deviation of MAT and the standard deviation of MAP and the indeterminate inflorescence frequency within each geographical unit. We found that climate heterogeneity within geographical units did not significantly bias our findings (Fig. S3).

Hidden State Speciation and Extinction (HiSSE) models were used to reconstruct the ancestral states of angiosperm inflorescence types (Wang *et al.*, 2023). We choose HiSSE models because they allow for a

“null” model where diversification process may be unrelated to the focal trait (inflorescence type here), and can effectively model the possibility that some other unobserved trait may have large impact on the diversification process. For example, other traits (e.g., floral symmetry) associated with inflorescence but not included in the current study can also have effect on diversification processes. In addition, HiSSE models reduce the risk of type I errors (a true null hypothesis is incorrectly rejected), which is known to be a recurring problem with standard BiSSE models (Rabosky & Goldberg, 2015). We used the RevBayes (Höhna *et al.*, 2016) language to run HiSSE models with two and three hidden states and stochastic character mapping.

Models were built allowing for different rate changes between observable states while transition rates between hidden states and observable states were assumed to be equal. For all transition rates we used priors with exponential distributions (see Wang *et al.*, (2021) for more details about the setup of these models). Two independent runs (with two and three hidden states) were initiated for each analysis. Independent runs for both two and three hidden states HiSSE models converged, and results were combined after discarding suboptimal samples as burn-in (10%). All parameters showed good effective sampling size with ESS values above 200. Convergence of independent runs, effective sampling size of estimates and processing and visualization of results was carried out using the R package RevGadgets v1.1.1 (Tribble *et al.*, 2022) and racer v1.7.1 (Rambaut *et al.*, 2018).

To evaluate whether resolving the polytomies in the ALLOTB phylogeny may bias estimates of evolutionary dynamics of inflorescence types, we compared the temporal trends in the indeterminate-to-determinate transition rates based on the HiSSE analyses using the ALLOTB phylogeny with resolved polytomies and the fully-resolved molecular phylogeny (i.e., the GBOTB phylogeny) (Wang *et al.*, 2023). These results are highly consistent, which suggests that polytomy resolution did not significantly bias our conclusions (Fig. S4-S6).

Based on our ancestral state reconstructions, we evaluated the proportion of branches reconstructed as indeterminate inflorescence in each one-million-year time interval and described the temporal changes of inflorescence type frequency (Wang *et al.*, 2023). We also estimated the temporal patterns of the rate of evolutionary transitions from indeterminate to determinate inflorescence for all species, species currently living at high (above 50° N/S) and middle-low latitudes (0–40° N/S), and species currently living within every 10° latitudinal belt along latitudinal gradient. Each species was assigned to a latitudinal belt according to its current distributions. Because there may be 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.* (Donoghue, 2008), 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 (Wang *et al.*, 2023). Consequently, our estimates of transitions through time do not use a simplification based only on tip and root (or internal nodes) states.

Finally, we used beta regressions to explore the impact of paleo-temperature on the temporal trends in the frequency of indeterminate inflorescence and the indeterminate-to-determinate inflorescence transition rate over the Cenozoic. To evaluate the potential impacts of temporal autocorrelation on our results, we further used the ‘*acf*’ and ‘*pacf*’ functions to test the temporal autocorrelation and found that the largest lag involved in the autoregressive (AR) process is lag = 1 (Fig. S7). We then examined the relationships between temporal change of inflorescence type frequency/the relative transition rate of IND→D and paleotemperature with different time lags (i.e. ranging from lag=0 to lag=8) using beta regression. The results indicated that temporal autocorrelation had little impacts on our findings (Table S2).

All analyses were conducted in R 4.2.2 (The R Core Team, 2020), unless otherwise indicated.

Results

Global geographical patterns in inflorescence type frequency

Approximately 54.9% of the species in our dataset possess indeterminate inflorescences. The global distribution of inflorescence type frequency shows a strong latitudinal gradient, with the proportion of species with indeterminate inflorescence increasing away from the equator ($R^2 = 45\%$, Fig. 1 & 2 & S1). Species with indeterminate inflorescence are most prevalent at high latitudes (>66%) in both hemispheres, followed by northern Africa and west Asia (~50%) characterized by its arid and/or dry Mediterranean climates. In contrast, species with determinate inflorescence are most prevalent in tropical and subtropical areas at low latitudes (~40%).

Drivers of global patterns in inflorescence type frequencies

Worldwide, pollination mode frequency showed the strongest association with inflorescence type frequency ($R^2 = 50\%$, $P < 0.001$, Fig. 2). Inflorescence type frequency is also strongly associated with climate (Fig. 2). Specifically, present-day mean annual temperature (MAT) and temperature seasonality (TSN) were the strongest predictors of the spatial pattern in inflorescence types frequency, followed by historical temperature change since the Last Glacial Maximum (MATano). The proportion of species with indeterminate inflorescence was positively correlated with TSN and MATano ($R^2 = 25\% \sim 36\%$, $P < 0.001$), and was negatively correlated with MAT ($R^2 = 41\%$, $P < 0.001$). Precipitation variables showed relatively weak effects on the geographic variation in inflorescence type frequency (all $P > 0.05$). Wind speed had also

a moderately positive effect on the proportion of species with indeterminate inflorescence ($R^2 = 10\%$, $P < 0.01$).

Macroevolutionary dynamics in angiosperm inflorescence types

By reconstructing ancestral states of angiosperm inflorescence types, we found that determinate and indeterminate inflorescence types have similar probabilities of being the ancestral inflorescence state for basal angiosperms (Fig. S8). Overall, the proportion of indeterminate inflorescence was generally higher than 50% during the Cenozoic, suggesting that indeterminate inflorescence was consistently the dominant inflorescence type in angiosperms. Interestingly, the frequency of indeterminate inflorescences decreased over the Cenozoic in low latitudes, but the temporal changes in the fraction of indeterminate inflorescences gradually changed from a decreasing trend to an increasing trend from low latitudes to high latitudes (Fig. 3A & S4A & S5A & S6A & S9A). The proportion of indeterminate inflorescences significantly decreased with paleo-temperature at high latitudes ($R^2 = 0.47$, $P < 0.001$, Fig. 3C & S5C & S6C), but not at low to middle latitudes.

The relative evolutionary transition rates from indeterminate to determinate inflorescences (IND→D) consistently decreased with time (Fig. 3B & S4B & S5B & S6B & S9B), and this temporal trend was consistent across all latitudes. The relative transition rate from indeterminate to determinate inflorescences significantly increased with the increase in paleo-temperature during the Cenozoic ($R^2 = 0.17-0.49$, $P < 0.001$; Fig. 3D & S4D & S5D). Moreover, our results showed that lineages with determinate inflorescence had significantly higher speciation rates than indeterminate lineages, while the extinction rates of the two inflorescence types were similar (Fig. 4).

Discussion

Based on an extensive spatial distribution dataset coupled with phylogenetic and inflorescence type information for 194476 angiosperm species, we have shown that indeterminate inflorescence is more common in high-latitude regions, while determinate inflorescence is more common in low-latitude tropical regions. We have also demonstrated clear latitudinal differences in the temporal changes of inflorescence type frequency during the Cenozoic, with high-latitude ($> 50^\circ$ N/S) taxa displaying increased proportion of indeterminate inflorescence and middle/low-latitude taxa displaying a decreasing trend. Our results demonstrate that climate, particularly temperature, may have greatly contributed to the worldwide distribution and macroevolutionary dynamics of angiosperm inflorescence types. These results advance our

understanding on the spatiotemporal patterns of angiosperm inflorescence types and their ecological and evolutionary responses to climate change at multiple scales.

Global patterns of inflorescence type frequencies

Consistent with our hypothesis, the frequency of indeterminate inflorescence increased with latitude, while that of determinate inflorescence decreased. These results partially support and expand early findings based on analyses with limited taxonomic scope that indeterminate racemes, spike, umbel, head, capitulum are more frequent in areas with short growing seasons (Stebbins, 1973). A recent work based on a “transient model” also found that the frequency of indeterminate racemes was higher in temperate than in tropical climates (Prusinkiewicz *et al.* 2007). However, our results contrast with their family-level finding that determinate cymes are more frequent in temperate climates. Considering the distinct inflorescence types among species in most plant families and the huge difference in species richness across families (Watson & Dallwitz, 2023), family-level surrogates for inflorescence types may have been too coarse to assess the geographic patterns of angiosperm inflorescence types.

Determinants of geographic variation in inflorescence types

Our results demonstrate that pollination mode frequency is the strongest predictor of the geographic variation in inflorescence types. Previous work has shown that inflorescence architecture could evolve to regulate pollinator behaviors and enhance reproductive success in diverse plant lineages (Iwata *et al.*, 2011; Akter *et al.*, 2017). High-latitude areas with relatively lower pollinator availability and higher wind speed (Kumar *et al.* 2015) tend to favor indeterminate inflorescence characterized by simple and condensed structure because the structure typically does not attract a wide variety of pollinators and can also facilitate pollen export and deposition by wind (Culley *et al.*, 2002; Weller *et al.*, 1998). In contrast, the reproductive success of species with determinate inflorescences is intricately tied to stable plant-pollinator relationships and, by extension, to stable climatic conditions. Because these species typically have a more limited window for reproduction, making them particularly vulnerable to climate fluctuations. Even minor climatic disturbances can disrupt the delicate timing necessary for pollination and seed development, thereby constraining their long-term survival and adaptability.

Climate, especially temperature, strongly influences geographic variation in the frequency of inflorescence types. Our results support our hypothesis that indeterminate inflorescence frequency decreases with the increase in growing season length, but increases with historical climate fluctuations and wind speed. The highly desirable season-long flowering of indeterminate inflorescences could increase chances of

outcrossing success and genetic diversity (Harder *et al.*, 2004; Liao & Harder, 2014), which could not only potentially improve the chances of species survival in these challenging high-latitude environments (Stebbins, 1974) but also offer significant benefits for high-latitude species that are often small and more isolated and hence often have limited gene flow (Cisternas-Fuentes & Koski, 2023). Moreover, a continuing apical meristem of a vertical axis in indeterminate inflorescence is one of the most effective mechanisms for restricting pollen removal by individual pollinators (Harder *et al.*, 2004). Such pollen packaging could enhance total pollen export when the proportion of pollen reaching the stigmas through individual pollinators decreases while the amount of pollen removed increases (Harder & Thomson, 1989).

Macroevolution of inflorescence types and its association with paleo-temperature

Our results reveal that the frequency of indeterminate inflorescence in species currently living in high latitudes has increased since the Cenozoic, whereas it has decreased in species currently living in middle/low-latitudes. This may be partially attributed to the latitudinal differences in paleotemperature decline since the Cenozoic. A recent study based on $\delta^{18}\text{O}$ from drilling cores demonstrated that the paleotemperature changes in low/middle latitudes was relatively mild, but was much more severe at high latitudes (Auderset *et al.*, 2022). Therefore, our finding of an increase in indeterminate inflorescence frequency in high-latitude species likely suggests a directional selection induced by the almost continuous intensification of coldness since the early Cenozoic occurring at northern high latitudes. This finding is also consistent with our results about the relationship between geographic variation in indeterminate inflorescence frequency and contemporary climate: across space, colder environments favor higher frequency of indeterminate inflorescence. It's noteworthy that this finding reflects the evolutionary changes of inflorescence type frequency that has occurred in the floras currently living at high latitudes, but not local evolutionary dynamics in each latitudinal belt as for many species distributions have changed during the glacier-interglacier cycles.

In contrast with high latitudes, low/middle latitudes with relatively stable and warm paleotemperature may have favored the evolution of determinate inflorescence, which is consistent with our hypothesis and the spatial results that determinate inflorescence is currently more common in low-latitude tropical areas. Nevertheless, indeterminate inflorescence frequency increased with increasing paleotemperature in low/middle latitudes. This may suggest that the positive effect of low temperature on the frequency of indeterminate inflorescence becomes relatively weak when environmental temperature and growing season length exceed a certain threshold. The difference in speciation and net diversification rate between the two inflorescence types at low latitudes may also have played a role in the temporal trends of the frequency of

indeterminate inflorescence. Indeed, we find that lineages with determinate inflorescence have significantly higher speciation rate and net diversification rate than lineages with indeterminate inflorescence, whereas the extinction rate of the two inflorescence types is similar.

The transition rate from indeterminate to determinate inflorescences had continuously decreased over the entire Cenozoic, which provides further evidence for previous findings that indeterminate inflorescence is the ancestor state for some early branching angiosperms (Stebbins, 1973). Specifically, at the beginning of the Cenozoic when tropical and subtropical climate was widespread across the globe, the relative transition rate from determinate to indeterminate inflorescences ($D \rightarrow IND$) was generally low, but it continuously increased with the decrease in global paleo-temperature. The evolutionary transition from determinate to indeterminate inflorescences can enhance plants' reproductive success due to the better adaptation of indeterminate inflorescence to the shortened growing seasons caused by declining global temperatures, especially for species living at (northern) high latitudes. In other words, this adaptation enhanced their relative fitness and survival in increasingly colder and unstable environments due to the continuous decline in global temperature.

Further, the fossil pollen record suggests that the stepwise cooling after the Palaeocene–Eocene Thermal Maximum (ca. 55 Ma, Auderset *et al.*, 2022) triggered a series of changes in global vegetation patterns including the retreat of “closed ecosystems” (forests) in tropical and subtropical environments and the expansion of “open ecosystems” (e.g., tundra, temperate grasslands, tropical savannas, Graham, 2011), which might have allowed more herbaceous species with indeterminate inflorescence to diversify. Wind pollination is particularly well represented in these open ecosystems due to the expansion of wind-pollinated lineages. The shift to wind pollination may have also contributed to the evolutionary transition from determinate to indeterminate inflorescences, considering the association between the evolution of pollination modes and the evolution of inflorescence types (Hu *et al.*, 2008).

Inflorescence type has been considered a key floral trait that has evolved to control pollinator behaviors under pollinator-mediated selection (Iwata *et al.*, 2012). Since the early Eocene, as some wind-pollinated lineages with indeterminate inflorescence including *Salicaceae*, *Fagaceae*, *Poaceae*, and *Cyperaceae* colonized temperate and polar zones, the advantages of wind pollination had gradually expanded in response to the global trend of climatic cooling and drying. The improvement of air mobility and the enhancement of pollen dispersal ability of wind pollination in these open ecosystems may have promoted the evolution of indeterminate inflorescence for mating success via manipulating the inter- and intra-plant movements of pollen vectors (Harder *et al.*, 2004; Harder & Johnson, 2009).

Conclusions

Spatiotemporal variations in inflorescence type frequencies among flowering plant floras is striking. However, no global description of these variations has been available so far. Using the database of inflorescence types and distributions of angiosperms assembled here, together with a dated phylogeny, we examined and expanded the prominent hypotheses regarding the drivers of the geographic and macroevolutionary patterns of angiosperm inflorescence types. Our results demonstrate that pollination mode and (paleo)temperature significantly contributes to the spatiotemporal dynamics of inflorescence types. With the decline in (paleo)temperature and frequency of animal pollination, the fraction of indeterminate inflorescence increases, especially at high latitudes. We further reveal that lineages with determinate inflorescence have significantly higher net diversification rate than those with indeterminate inflorescence. The emergent view on the spatiotemporal dynamics of inflorescence types and their relationships with animal pollinators and (paleo)temperature highlights evolutionary investment in floral display that may underlie plant adaptation to fluctuated environments. These findings suggest that floral display (i.e., inflorescence type here) can play significant roles in the ecological and evolutionary response of angiosperms to spatiotemporal climate changes.

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Author contributions

YW and ZHW conceived the idea. YW, AL and ZW collected the data. YW performed the analyses with contributions from DD and AL. YW led the writing, and ZW, DD, RF and ZH revised the manuscript throughout. All authors have given final approval to publish this manuscript and agree to be responsible for the work that they conducted.

Competing interests

None declared.

Data availability

All inflorescence type data are available in Dryad. <https://doi.org/10.5061/dryad.73n5tb35w>.

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Figure legends in the main context

Figure 1. The global distribution of indeterminate inflorescence frequency of flowering plants. Within each geographic unit, the frequency of species with indeterminate inflorescence was calculated as the proportion of species with indeterminate inflorescence to all species within that geographic unit. The proportions of the determinate and indeterminate species within each geographic unit sum to one.

Figure 2. The (relative) contribution of different predictors on the variance in indeterminate inflorescence frequency across the globe. (A) The independent (I, lighter blue) and joint (J, the conjoint contribution with all other variables, darker blue) contributions of different variables on proportions of species with indeterminate inflorescence per geographic unit. Hierarchical partitioning analysis was conducted to identify variables' independent and joint effects. (B-I) beta regression results for different predictors (x axes) associated with indeterminate inflorescence frequency per geographical unit (y axes). The environmental variables include pollination mode frequency, wind speed, mean annual temperature [MAT], temperature seasonality [LgTSN], the anomaly of mean annual temperature since the Last Glacial Maximum (LGM) [MATano], mean annual precipitation [MAP], log-transformed precipitation seasonality [LgPSN] and the anomaly of mean annual precipitation since the Last Glacial Maximum (LGM) [MAPano]. Regression lines were drawn when the relationships were significant ($P < 0.05$, see Methods for more details about the significance test). The R^2 value associated with each predictor is displayed on the top left corner of each panel.

Figure 3. Macroevolutionary dynamics of inflorescence types based on the hidden state speciation and extinction (HiSSE) model with two hidden states and their responses to Cenozoic climate change at high (orange dots and lines) and middle-low latitudes (blue dots and lines). (A) The temporal change of the proportion of species with indeterminate inflorescence and (B) the relative evolutionary transition rate from indeterminate to determinate inflorescence (estimated as the ratio of transitions from indeterminate to determinate inflorescence to the total number of transitions) (65 – 0 Mya). (C) Changes in the proportion of angiosperm species with indeterminate inflorescences and (D) the relative transition rate from indeterminate to determinate inflorescence during the Cenozoic as functions of paleo-temperature. The relationships between the response variables and paleo-temperature were evaluated using bivariate beta regressions. D = determinate inflorescence, IND = indeterminate inflorescence.

Figure 4. The effects of inflorescence type (determinate vs. indeterminate) on the speciation and extinction rates of angiosperms estimated using the hidden state speciation and extinction (HiSSE) model and the ALLOTB phylogeny with resolved polytomies. The diversification rates of lineages with different inflorescence types were estimated by the HiSSE model with two (a and b) or three hidden traits (c and d). H1, H2 and H3 denote the hidden traits (blue color is associated with determinate and orange color is associated with indeterminate phenotypes) included in the HiSSE model. The figure summarizes the results of two independent runs for each model (two and three hidden states) which converged and were combined, and suboptimal posterior samples were discarded (10% burn-in was used after examining the traces files). Please see Methods for more details.

Figure legends to Supporting Information

Fig. S1 The global distribution of indeterminate inflorescence frequency of flowering plants.

Fig. S2 Relationships between the per-grid proportion of inflorescence type and the proportion of species sampled and the proportion of growth form composition.

Fig. S3 The effects of climate heterogeneity (standard deviation of temperature and precipitation) within grid cells on the spatial distribution of indeterminate inflorescence frequency.

Fig. S4 Macroevolutionary dynamics of inflorescence types based on the hidden state speciation and extinction (HiSSE) model with three hidden states and their responses to Cenozoic climate change at high (orange dots and lines) and middle-low latitudes (blue dots and lines).

Fig. S5 Macroevolutionary dynamics of inflorescence types based on the hidden state speciation and extinction (HiSSE) model using molecular tree (i.e., the GBOTB phylogeny) and their responses to Cenozoic climate change at high and middle-low latitudes.

Fig. S6 Macroevolutionary dynamics of angiosperm inflorescence type at both high and middle-low latitudes since 138 mya.

Fig. S7 Autoregressive [AR(1)] model partial autocorrelation graph.

Fig. S8 Ancestral states reconstructed using the hidden state speciation and extinction (HiSSE) model shown on the fully-resolved molecular phylogeny (i.e., the GBOTB phylogeny).

Fig. S9 Latitudinal changes in the evolutionary dynamics of inflorescence types since the Cenozoic estimated using HiSSE analyses.

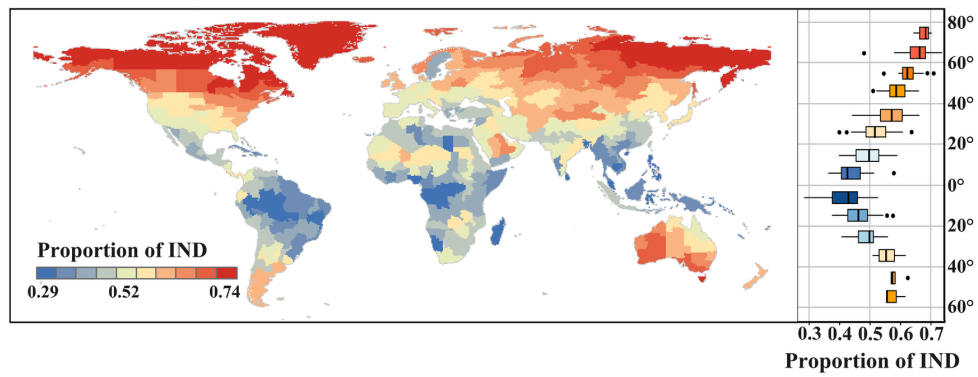


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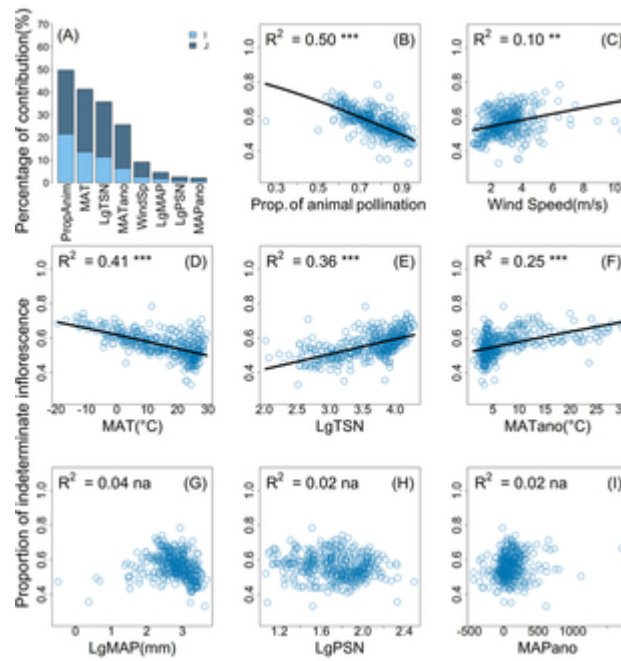


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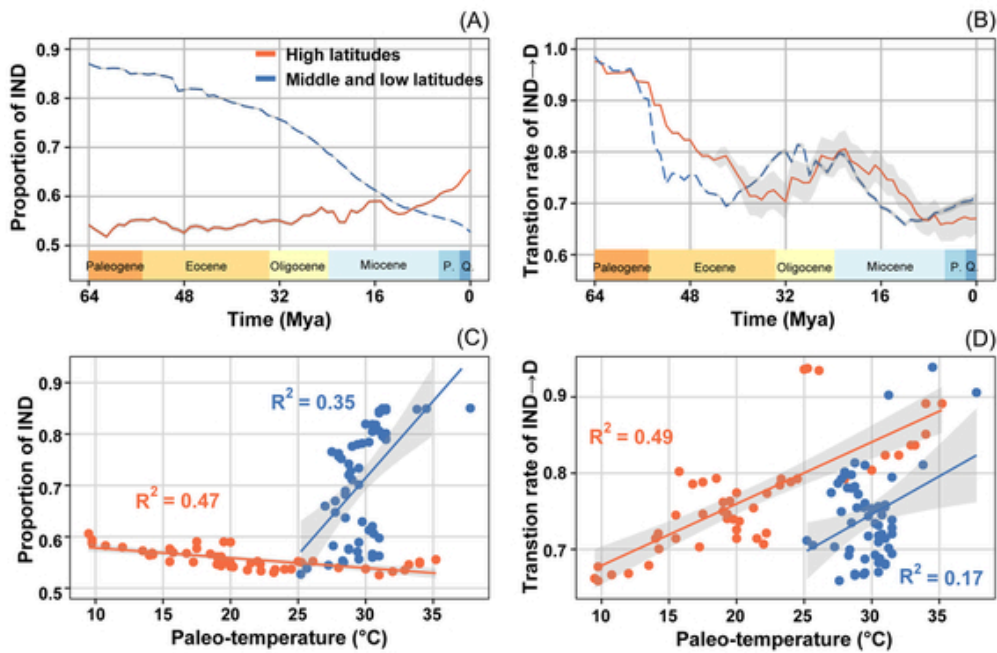


Fig. 3. Macroevo-lutionary dynamics of inflorescence types based on the hidden state speciation and extinction (HISSE) model with two hidden states and their responses to Cenozoic climate change at high (orange dots and lines, above 50° N/S) and middle low latitudes (blue dots and lines, 0–40° N/S). (A) The temporal change of the proportion of species with indeterminate inflorescence and (B) the relative evolutionary transition rate from indeterminate to determinate inflorescence (estimated as the ratio of transitions from indeterminate to determinate inflorescence to the total number of transitions) (65 – 0 Mya). (C) Changes in the proportion of angiosperm species with indeterminate inflorescences and (D) the relative transition rate from indeterminate to determinate inflorescence during the Cenozoic as functions of paleo-temperature. The relationships between the response variables and paleo-temperature were evaluated using bivariate beta regressions. D = determinate inflorescence, IND = indeterminate inflorescence. The shaded light gray area in A and B represents the 95% confidence interval across the 100 randomly resolved phylogenies (see the Materials and Methods for details). And the regression lines in C and D are based on simple linear regression model and 95% confidence interval.

200x132mm (72 x 72 DPI)

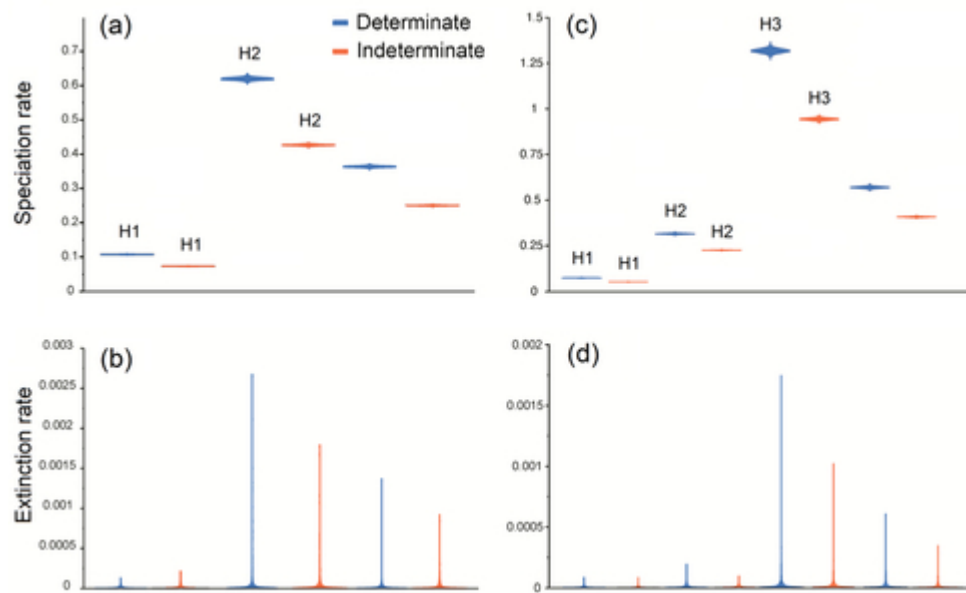


Fig. 3. Macroevo­lutionary dynamics of inflorescence types based on the hidden state speciation and extinction (HiSSE) model with two hidden states and their responses to Cenozoic climate change at high (orange dots and lines, above 50° N/S) and middle low latitudes (blue dots and lines, 0–40° N/S). (A) The temporal change of the proportion of species with indeterminate inflorescence and (B) the relative evolutionary transition rate from indeterminate to determinate inflorescence (estimated as the ratio of transitions from indeterminate to determinate inflorescence to the total number of transitions) (65 – 0 Mya). (C) Changes in the proportion of angiosperm species with indeterminate inflorescences and (D) the relative transition rate from indeterminate to determinate inflorescence during the Cenozoic as functions of paleo-temperature. The relationships between the response variables and paleo-temperature were evaluated using bivariate beta regressions. D = determinate inflorescence, IND = indeterminate inflorescence. The shaded light gray area in A and B represents the 95% confidence interval across the 100 randomly resolved phylogenies (see the Materials and Methods for details). And the regression lines in C and D are based on simple linear regression model and 95% confidence interval.

173x109mm (72 x 72 DPI)