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RESEARCH ARTICLE

Where did they come from, where did they go? Niche conservatism in woody and herbaceous plants and implications for plant-based paleoclimatic reconstructions

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Abstract

Premise: The ecological conditions that constrain plants to an environmental niche are assumed to be constant through time. While the fossil record has been used previously to test for niche conservatism of woody flowering plants, additional studies are needed in other plant groups especially since they can provide insight with paleoclimatic reconstructions, high biodiversity in modern terrestrial ecosystems, and significant contributions to agriculture.

Methods: We tested climatic niche conservatism across time by characterizing the climatic niches of living herbaceous ginger plants (Zingiberaceae) and woody dawn redwood (*Metasequoia*) against paleoniches reconstructed based on fossil distribution data and paleoclimatic models.

Results: Despite few fossil Zingiberaceae occurrences in the latitudinal tropics, unlike living Zingiberaceae, extinct Zingiberaceae likely experienced paratropical conditions in the higher latitudes, especially in the Cretaceous and Paleogene. The living and fossil distributions of *Metasequoia* largely remain in the upper latitudes of the northern hemisphere. The Zingiberaceae shifted from an initial subtropical climatic paleoniche in the Cretaceous, toward a temperate regime in the late Cenozoic; *Metasequoia* occupied a more consistent climatic niche over the same time intervals.

Conclusions: Because of the inconsistent climatic niches of Zingiberaceae over geologic time, we are less confident of using them for taxonomic-based paleoclimatic reconstruction methods like nearest living relative, which assume a consistent climatic niche between extant and extinct relatives; we argue that the consistent climatic niche of *Metasequoia* is more appropriate for these reconstructions. Niche conservatism cannot be assumed between extant and extinct plants and should be tested further in groups used for paleoclimatic reconstructions.

KEYWORDS

Cenozoic, climatic niche, Cretaceous, *Metasequoia*, nearest living relative, paleoclimate, Zingiberaceae

Niches are the ecological conditions that constrain a species to a particular habitat and role within it (Wiens and Graham, 2005; Wiens et al., 2010; Jablonski et al., 2013; Pocheville, 2015; Polechová and Storch, 2017), conceptualized by the different sets of conditions needed for a species to persist in an environment. Two predominant concepts are discussed in the literature: Grinellian and Hutchinsonian niches. The Grinellian niche concept encapsulates the environmental and climatic conditions that allow for a species to persevere (Tingley et al., 2009; Soberón and Peterson, 2020), while the Hutchinsonian niche concept focuses on the intersectionality of a species with the living and abiotic forces of an environment (Colwell and Rangel, 2009). Within these niche concepts, there are two types of niches:

fundamental niches that comprise all the conditions in which species could maintain a viable population and realized niches that are the subset of conditions in which a species does live, reduced by factors such as competition and dispersal ability; fundamental niches for a species are accepted to be larger than realized niches (Jackson and Overpeck, 2000; Soberón and Arroyo-Peña, 2017). We can also consider how a niche changes over time, whether it has remained the same (niche conservatism) or evolved by adapting to novel environmental conditions (Colwell and Rangel, 2009).

According to the concept of niche conservatism, species persist within their niche through time, so that living organisms retain the ecological and climatic constraints of their ancestral relatives (Wiens and Graham, 2005). Niche changes are thought to be constrained by an organism's ability to adapt in changing environments and their ability to distribute within preferred climates (Wiens and Graham, 2005; Wiens et al., 2010). Niche conservatism has implications for other ecological fields including biodiversity, ecosystem function, and responses to climatic change (Wiens et al., 2010), which is especially pertinent today as severe ecosystem and organismal shifts are expected due to anthropogenic climatic change (Jones et al., 2009; Grimm et al., 2013; Malhi et al., 2020; McDowell et al., 2020; Weiskopf et al., 2020; Parmesan et al., 2022). The fossil record can be used to test niche conservatism. In invertebrates, niches were found to be conserved over time in many groups (Holland and Zaffos, 2011; Hopkins et al., 2014; Stigall, 2014; Chiu et al., 2020). However, while niche conservatism has been explored in plants, most studies have focused on large, woody flowering plants; temperate woody plants had conserved climatic niches, while (para)tropical woody plants expanded their niches (Ackerly, 2009; Koecke et al., 2013; Zhang et al., 2022). Further research into other plant groups is required. For plants, integration of paleodata is most easily done considering climatic niche, i.e., the climatic conditions that pertain to a species' proper growth and development (Silvertown, 2004), because other niche dimensions (e.g., edaphic factors, community composition) are difficult to reconstruct with certainty at many localities. In terms of the niche concepts introduced earlier, the realized Grinellian niche is the focus of most extinct plant studies and therefore this study.

Plants, climate, and niches over time

Climatic information from plants greatly contributes to paleoclimatix reconstructions and modeling (e.g., Upchurch and Wolfe, 1987; Wilf et al., 1998; Spicer et al., 2009; Boucot et al., 2013; Stults and Axsmith, 2015; Upchurch et al., 2015; Peppe et al., 2018; Macarewich et al., 2022). For example, occurrences of fossil palms (Arecaceae) are frequently used to indicate above-freezing temperature minima for a fossil locality, since these plants cannot survive freezing due to exposed apical meristems (Wing and Greenwood, 1993; Dransfield et al., 2008; Reichgelt et al., 2018). While some plant-based paleoclimatic proxy methods are ataxonomic and rely on physical relationships between morphology and climate (e.g., climate leaf analysis multivariate program [CLAMP; Wolfe, 1993; Herman and Spicer, 1997; Spicer et al., 2009; Yang et al., 2011], leaf margin analysis [LMA; Wilf, 1997], leaf area analysis [Wilf et al., 1998]; digital leaf physiognomy [DiLP; Peppe et al., 2011]), other methods are rooted in using climatic information from living relatives as a proxy for fossil taxon climatic niche by applying the climatic ranges of an extinct plant's closest modern taxon to the fossil locality. These include the coexistence approach and, more recently, bioclimatic analysis. The coexistence approach incorporates the nearest living relative climatic regimes for all fossil taxa in a locality and makes the climatic reconstruction based on the overlap of fossil plant limits (Mosbrugger and Utescher, 1997; Utescher et al., 2014). More statistically rigorous versions of the coexistence approach include cRacle, which implements a likelihood framework (Harbert and Nixon, 2015; Harbert and Baryiames, 2019), and bioclimatic analysis, which includes additional climatic outliers in a data set that would be missed ordinarily (Kershaw and Nix, 1988; Greenwood et al., 2003, 2017; Hyland et al. 2018). These paleoclimatic reconstruction tools assume that the climatic niche of related plants remained constant and did not drastically change over time. If the environmental and climatic stresses for a plant significantly changed over geologic time, then their paleoniche may not be represented within the living niche.

There are three main hypotheses that discuss phylogenetic biogeography of latitudinal diversity gradients and may provide an explanation for how niches evolved or were conserved in plant lineages. The first hypothesis, tropical niche conservatism (TNC), states that tropical plant lineages originated in the tropics, but did not extend out of tropical latitudes because ecological conditions were suitable across time within their original distributions (Wiens and Donoghue, 2004; Wiens and Graham, 2005). The TNC predicts static regional occurrences because these tropical plants did not adapt to colder temperatures and then could not have migrated to higher latitudes, so their climatic niche remained conserved across geologic time (Wiens and Graham, 2005). The second hypothesis, out of the tropics (OTT), focuses on niche evolution from plant dispersal. OTT predicts that because tropically originated plant lineages were able to survive in a greater diversity of environments and climates, they gradually moved to higher latitudes from tropical origins, so their distributions and climatic niche expanded over geologic time while also retaining original tropical occurrences (Jablonski et al., 2013). The third hypothesis, into the tropics (ITT), states that species originated in high latitudinal, temperate environments but had adaptations that could withstand higher temperatures in the tropics, and thus migrated toward the tropics, with descendent lineages gaining new climatic niches (Hinojosa et al., 2016). These niche hypotheses focus on plant distributions and dispersal strategies, but it is important to note that in the geologic past, plants could exist in paratropical conditions (tropical climatic conditions [cold month mean temperature >18°C] that are located outside the geographic tropical latitudes between 23.44°N and 23.44°S; Graham, 1972; Manos and Stanford, 2001; Koecke et al., 2013). As such, plant lineages will have different histories of niche evolution/conservatism, and it is important to consider any fossil evidence for ancient distributions and paleoclimatic niche.

The origin of angiosperms in the late Mesozoic and their rise to dominance in early Cenozoic landscapes

Gymnosperms were once the dominant land plants from their origination in the Permian (298–252 million years ago [Ma]) through most of the Mesozoic (252–66 Ma; Pigg and Trivett, 1994; Kerp, 1996; Peñalver et al., 2012). This changed with the origin of flowering plants (angiosperms) in the Early Cretaceous (~140 Ma), that subsequently diversified across landscapes, became prevalent in most terrestrial ecosystems, and experienced several significant environmental and climatic shifts across the Cenozoic (66 Ma to present; McElwain and Punyasena, 2007; Wang et al., 2009; Friis et al., 2010; Coiffard et al., 2011; Benton et al., 2022). A factor contributing to their abundance, distribution, and diversity is the climatic niche that a taxon occupies (Silvertown, 2004). Plants are able to grow in a great diversity of environments depending on how broad their niche is. For example, some palms (e.g., *Phoenix* sp.) can be found in both deserts and tropical rainforests, likely stemming from similar temperature regimes that the palm can tolerate (Dransfield et al., 2008). To better distinguish between taxon-specific and universal patterns of plant–climate interactions, it is important to examine different plant groups, such as angiosperms and gymnosperms, and how plant fossils contribute to the understanding of climatic niche shifts.

While "physiological uniformitarianism"—that shared morphologies of a group's fossil and living representatives mean they have the same physiological tolerances (Tiffney, 2008)—is typically assumed in plant-based paleoclimatic reconstructions, for most of the Cenozoic now-extinct plants inhabited different latitudes and climates than their living relatives, and physiology is difficult to measure directly from fossils (though some aspects can be done, e.g., photosynthetic physiology via C isotopes: see Sheldon et al., 2020; McElwain et al., 2024). Further, there may be a difference in the degree of conservatism between faster-evolving herbaceous plants and slower-evolving woody plants, both within and across lineages (Smith and Beaulieu, 2009). Fossil woody angiosperms had high diversity at higher latitudes during the Paleogene (66–23 Ma) and early Neogene (23–2.6 Ma for the entire epoch; 23–11 Ma for early Neogene), but their ecological and climatic distributions differed significantly between tropical and temperate taxa (Shiono et al., 2018). Some lineages of woody angiosperms could survive freezing temperatures and thus expanded to higher latitudes and maintained this expanded climatic niche across time ("temperate" taxa; Kerkhoff et al., 2014; Qian and Sandel, 2017). Other lineages of woody angiosperms occupied high latitudes due to warm temperatures in the early Cenozoic, but as their range became constricted by colder temperatures as the Cenozoic progressed, they were extirpated from higher latitudes due to their conserved and narrow climatic niche (Lee et al., 2001; Shiono et al., 2018). Nonwoody angiosperms such as *Carex* demonstrated similar differences in climatic requirements between extinct and extant species to those of woody angiosperms (Benítez-Benítez et al., 2018). However, woody angiosperms have a much slower rate of climatic niche evolution, which would allow for nonwoody angiosperms to disperse and adapt to new environments more quickly (Smith and Beaulieu, 2009).

Here, we used a novel approach to test for shifting climatic niches using two test cases: Zingiberaceae (the ginger family, a primarily tropical, herbaceous plant lineage), and *Metasequoia* (the dawn redwood, Cupressaceae, a woody conifer). These plant groups were chosen because they both have reliable fossil records across the Cenozoic (Tables 1, 2) and living relatives, we are confident in the identifications, and we can directly compare climatic niche change (or lack thereof) between herbaceous and woody plants. In doing so, we mapped fossil occurrences from the literature and estimated ancient climatic thresholds by interpolating paleoclimatic modeling data. The paleoclimatic simulations were given a fixed set of boundary conditions (e.g., paleogeography, vegetation cover, orbital forcing, and paleoCO_2) and were not forced or calibrated by the Zingiberaceae or *Metasequoia* climatic signals (i.e., temperature and precipitation), which thus provided fully independent climatic scenarios from which to derive our ancient climatic niches (Farnsworth et al., 2019; Acosta et al., 2022; Gaskell et al., 2022). Based on the Grinnellian and fundamental niche concepts and nearest living relatives' climatic niches, we hypothesize that the climatic niches of Zingiberaceae and *Metaequoia* were largely conserved across geologic time. We determined whether the paleoclimatic niche of each plant group was significantly different than the present and compared the results of the two taxa to better understand niche evolution and conservatism in woody and nonwoody plants.

MATERIALS AND METHODS

Obtaining and implementing living and fossil plant occurrences

Present-day occurrences of Zingiberaceae were downloaded from the Global Biodiversity Information Facility (GBIF.org, 2020), while living occurrences of *Metasequoia* were obtained from botanical garden records because the wild distribution is largely geographically restricted (Liu et al., 2007). We adopted the following methodology to clean the GBIF Zingiberaceae living occurrence data: (1) All occurrences that lacked descriptive information were removed, and (2) to keep within the native range of Zingiberaceae, we removed horticulturally grown plants and

TABLE 1 Fossil occurrences of Zingiberaceae. They are arranged by geologic age first and then alphabetized by species name; same species are organized chronologically by study. Locality occurrences refer to the number of distinct field sites where fossil Zingiberaceae occur; a number is present if there is more than one occurrence. Both the modern and paleocoordinates are included to help with describing paleobiogeography. Only the Cretaceous, Eocene, and Miocene occurrences are used in the climatic niche analysis, but all time periods are included to describe past biogeography of the family.

Age	Fossil species	Locality or Formation (No. occurrences)	Country/Modern coordinates	Paleocoordinates	Reference
Cretaceous (Cenomanian)	*Spirematospermum chandlerae*	Black Creek Fm.	USA 35.4, −78	30.1, −44.1	Friis et al. (1988)
(Cenomanian)	*S. friedrichii*	Kreide	Poland 48.8, 19.6	40.2, 18	Knobloch and Mai (1986)
(Cenomanian)	*Striatornata sanantoniensis*	Cerro del Pueblo Fm.	Mexico 25.2, −101.2	24.7, −68.4	Rodríguez-de la Rosa and Cevallos-Ferriz (1994)
(Cenomanian)	*Zingiberites alaskensis*	Yukon-Koyukuk Basin	USA 64.2, −158.1	73.7, −111.4	Hollick (1930)
(Cenomanian)	*Z. pulchellus*	Kome Flora	Norway/Svalbard 79, 13.3	64.1, 26.3	Heer (1874)
(Cenomanian)	*Z. pulchellus*	Atane Flora	Denmark/ Greenland 70, −52	57.5, −16.4	Heer (1883)
(Maastrichtian)	*Momordiocarpon cardiospermum*	Deccan Flood Basalt (7)	India 22, 79.2	−26.8, 61.4	Smith et al. (2021)
(Maastrichtian)	*Orthogonospermum patanense*	Deccan Flood Basalt	India 19.6, 79.2	−29, 60.3	Smith et al. (2021)
(Maastrichtian)	*Spirematospermum* sp.	Kössen Flora	Austria 47.7, 12.4	38.1, 12.1	Goth (1986)
(Maastrichtian)	*Zingiberopsis attentuata*	Hell Creek Fm.	USA 46.9, −101.5	52.8, −73.3	Hartman and Johnson (2002)
(Maastrichtian)	*Z. magnifolia*	Fox Hills Fm.	USA 46.5, −100.5	52.3, −72.3	Peppe et al. (2007)
(Maastrichtian)	*Z. magnifolia*	Lance Fm. (2)	USA 43.1, −104.7	49.8, −78.5	Hickey and Peterson (1978)
Paleocene	*Spirematospermum wezleri*	London Clay	UK 50.8, −0.64	44.8, −2.5	Collinson (1983)
	Unnamed fruits, leaves (Zingiberaceae)[a]	Beicegel Creek Flora (2)	USA 47.4, −103.6	52.6, −80.6	Benedict (2012)
	Zingiberaceae	Cerrejón Fm.	Colombia 11, −72.7	8.5, −59	Wing et al. (2009)
	Zingiberites dubius	Denver Fm.	USA 39.8, −105.2	45.4, −85.2	Brown (1962)
	Zingiberopsis sp. (SJ-065)	Ojo Alamo Sandstone (5)	USA 36.3, −108	42, −88.1	Flynn (2020)
	Zingiberopsis sp. (SJ-115)	Ojo Alamo Sandstone (9)	USA 36.2, −107.9	42.3, −88.9	Flynn and Peppe (2019)
	Zingiberopsis attentuata	Paskapoo Fm.	Canada 52.4, −113.8	59, −89.7	Hickey and Peterson (1978)
	Z. isonervosa	Golden Valley Flora	USA 48.2, −109.9	54.4, −87.2	Hickey and Peterson (1978)
	Z. isonervosa	Wasatch Fm.	USA 41.2, −109	47.5, −88.7	Wilf (2000)

TABLE 1 (Continued)

Age	Fossil species	Locality or Formation (No. occurrences)	Country/Modern coordinates	Paleocoordinates	Reference
Eocene	*Spirematospermum headonense*	Hordwell Beds	UK 50.8, −1.6	45.7, −5.2	Hastings (1853)
	S. wetzleri	Bovey Tracey Lignite	UK 50.6, −3.7	45.9, −3.3	Chandler (1925)
	S. wetzleri	Bovey Tracey Lignite	UK 50.6, −3.7	45.9, −3.3	Collinson (1983)
	Zingiberopsis isonervosa	Golden Valley Flora	USA 46, −103.7	50.6, −84.2	Hickey (1977)
	Z. isonervosa	Big Horn Basin (29)	USA 44, −107	47.1, −90.3	Wing (1984)
	Z. isonervosa	Puget Group	USA 47.3, −122	54.2, −104.1	Burnham (1994)
	Z. isonervosa	Wasatch Fm. (19)	USA 41.5, −108.5	47.1, −90.2	Wilf (2000)
Oligocene	*Spirematospermum* sp.	Bobovdol	Bulgaria 42.4, 23	42.3, 20.2	Bozukov et al. (2009)
	Spirematospermum wetzleri	Weißelster Basin	Germany 51, 12.4	50.9, 9.1	Mai and Walther (1978)
	S. wetzleri	London Clay	UK 50.8, −0.64	50.2, −3.6	Chandler (1925)
	S. wetzleri	Turgai Plateau (4)	Kazakhstan 48.9, 63.8	49.5, 61	Dorofeev (1963)
	S. wetzleri	Andornaktálya sandpit	Hungary 47.9, 20.4	47.7, 17.4	Hably (1993)
	S. wetzleri	Saxony Lusatia	Germany 51.1, 14.3	50.9, 11.1	Mai (1997)
	S. wetzleri	Weißelster Basin	Germany 51.1, 12.4	50.7, 9.2	Kunzmann (2012)
	Zingiberoideophyllum liblarense	Weißelster Basin	Germany 51.1, 12.4	50.7, 9.2	Kunzmann (2012)
	Zingiberites petiolaris	Aix en Provence	France 43.3, 5.4	42.9, 2.7	Saporta (1888)
	Zingiberopsis sp.	Bridge Creek	USA 44.9, −120.4	46.2, −114.3	Meyer and Manchester (1997)
Miocene	*Donax kasauliensis*[b]	Kasauli Fm.	India 30.9, 77.1	31.4, 76.2	Antal and Prasad (1995); Srivastava and Guleria (2004)
	Donax ovatus[b]	Kasauli Fm. (2)	India 30.9, 77.1	31.4, 76.2	Srivastava and Guleria (2004)
	Spirematospermum sp.	Bílina Flora	Czech Republic 50.6, 13.7	50.8, 12.4	Kvaček (1998)
	S. wetzleri	Baltic Flora	UK 50.6, −3.7	50.6, −4.8	Heer (1869)
	S. wetzleri	Wetterau	Germany 50.2, 8.6	50.4, 7.3	Kirchheimer (1957)
	S. wetzleri	Dobrzyń nad Wisła	Poland 52.4, 19.2	52.7, 17.9	Kownas (1959)

(Continues)

TABLE 1 (Continued)

Age	Fossil species	Locality or Formation (No. occurrences)	Country/Modern coordinates	Paleocoordinates	Reference
	S. wetzleri	Western Siberia (5)	Russia 61, 69	56.9, 73.6	Dorofeev (1963)
	S. wetzleri	Jutland Flora	Denmark 56.03, 9.05	56.3, 7.6	Friedrich and Koch (1970)
	S. wetzleri	Mastixioid Flora (2)	Czech Republic 49.4, 19.5	49, 15.6	Knobloch and Kvaček (1976)
	S. wetzleri	Upper Palatinate Lignite	Germany 49.3, 12.2	49.5, 10.9	Gregor (1978)
	S. wetzleri	Lower Rhenish Basin	Germany 50.9, 6.3	51, 4.9	Van der Burgh (1987)
	S. wetzleri	Bukkabrany Flora	Hungary 47.9, 20.7	48.2, 19.5	László (1991); Erdei et al. (2011)
	S. wetzleri	Wackersdorf Flora; Myldlovary (2)	Germany, Czech Republic 49.3, 12.2 49.1, 14.4	49.3, 13.1 49.5, 10.9	Kovar-Eder et al. (2001)
	S. wetzleri	Meuro Fm.	Germany 51.7, 12.7	52, 11.4	Mai (2001)
	S. wetzleri	Melnik Flora	Bulgaria 41.5, 23.4	41.9, 22.3	Palamarev et al. (2002)
	S. wetzleri	Mataschen Flora	Austria 46.8, 16	47.1, 14.7	Meller and Hofmann (2004)
	S. wetzleri	Nástup Quarry	Czech Republic 50.4, 13.4	50.7, 12.5	Teodoridis and Kvacek (2006)
	S. wetzleri	Nakamura Fm.	Japan 35.4, 137	35.9, 136	Tsukagoshi and Matsuhashi (2012)
	S. wetzleri	Hannuoba Fm.	China 42.1, 117.8	42.2, 114.5	Li et al. (2018)
	Zingiberites sp.	Konan Flora	Japan 44.3, 142.3	49.1, 132.5	Narita et al. (2020)
	Zingiberoideophyllum liblarense	Steinhein Basin (2)	Germany 48, 9.2	48.3, 7.9	Horst (1992)
	Z liblarense	Rhenish Browncoal	Germany 50.9, 6.5	51.1, 5.2	Kvaček and Wilde (2006)
	Z liblarense	Ponholz Flora	Germany 49.2, 12.1	49.5, 10.9	Fischer et al. (2009)
Pliocene	*Donax lishensis*[b]	Kasauli Fm.	India 30.9, 77.1	30.5, 77.5	Srivastava and Guleria (2004)
	Spirematospermum wetzleri	Ob River Flora	Russia 56.4, 84.1	56.5, 84.1	Nikitin (1948)
	S. wetzleri	Thueringen Flora	Germany 51.5, 10.8	51.7, 10.3	Mai and Walther (1988)

[a] Fossils unpublished, but resemble *Spirematospermum*.

[b] Although labeled as *Donax kasuliensis*, *D. lishensis*, and *D. ovatus* (Marantaceae), we consider these fossils to be Zingiberaceae based on leaf architecture.

occurrences outside of the tropical latitudes (23.44°N to 23.44°S) with the exception of native Zingiberaceae in the Himalayas (~27°N to 35°N; 74.5°E to 95.5°E). This procedure was conducted to limit erroneous reporting from public databases (Maldonado et al., 2015). Next, the cleaned coordinate data of the living occurrences and bioclimatic variables raster data from WorldClim (climatic data 1970–2000; Fick and Hijmans, 2017; WorldClim, 2021)

TABLE 2 Fossil occurrences of *Metasequoia*. They are arranged by geologic age first and then alphabetized by species name. Locality occurrences refer to the number of distinct field sites where fossil *Metasequoia* occur; a number is present if there is more than one occurrence. Both the modern and paleocoordinates are also included to help with describing paleobiogeography. Only the Cretaceous, Eocene, and Miocene occurrences are used in the climatic niche analysis, but all time periods are included to describe past biogeography of the family.

Age	Fossil species	Locality or formation (No. occurrences)	Country and modern coordinates (Lat, Long)	Paleocoordinates	Reference
Cretaceous (Cenomanian)	*Metasequoia* sp.	Arkagala Fm.	Russia 68, 153	51, 128.1	Lebedev (1976)
(Cenomanian)	*Metasequoia* sp.	Arkagala and Dolgin Fms.	Russia 63.1, 147	67.8, 134.4	Samylina (1988)
(Cenomanian)	*Metasequoia* sp.	Amkinskaya Fm.	Russia 59, 140.4	62.7, 132.5	Lebedev (1987)
(Cenomanian)	*Metasequoia* sp.	n/a	USA 64.7, −156.1	77.4, −144.8	Patton and Moll-Stalcup (2000)
(Cenomanian)	*Metasequoia* sp.	n/a	USA 64.5, −158.5	77.6, −140.2	Patton and Moll-Stalcup (2000)
(Cenomanian)	*Metasequoia* sp.	Dunvegan Fm. (5)	Canada 54.6, −121.3	63.9, −91.5	Bell (1963)
(Cenomanian)	*Metasequoia occidentalis*	Lower Agraphenian floristic complex	Russia 63.4, 121	43.1, 130	Sveshnikova (1967)
(Maastrichtian)	*Metasequoia* sp.	Iliysk Depression (2)	Kazakhstan 43.5, 77.1	43.7, 74	Makulbekov (1974)
(Maastrichtian)	*Metasequoia* sp.	Pokurskoi Fm. (2)	Russia 62.6, 87.2	58.7, 72.1	Lebedev (1962)
(Maastrichtian)	*Metasequoia* sp.	Lance Fm.	USA 43.4, −104.3	52.1, −72.9	Dorf (1942)
(Maastrichtian)	*Metasequoia* sp.	Medicine Bow Fm.	USA 40.5, −107.6	50, −77.9	Dorf (1942)
(Maastrichtian)	*Metasequoia* sp.	Vermejo Fm. (9)	USA 37.5, −105	47.9, −82.6	Knowlton (1917b)
(Maastrichtian)	*Metasequoia* sp.	Judith River Fm.	USA 46.7, −108	38.8, −68.6	Knowlton (1905)
(Maastrichtian)	*Metasequoia* sp.	n/a	USA 55.9, −160.8	68.7, −148.1	Patton and Moll-Stalcup (2000)
(Maastrichtian)	*Metasequoia occidentalis*	Lance Fm.	USA 46.4, −100.9	44.2, −80.6	Brown (1935b)
(Maastrichtian)	*Metasequoia occidentalis*	Hell Creek Fm.	USA 46.3, −103.9	44.5, −81	Chaney (1951)
(Maastrichtian)	*Metasequoia occidentalis*	Koryak Fm. (2)	Russia 62.4, 179.3	73.2, 176.7	Herman and Spicer (1997)
(Maastrichtian)	*Metasequoia occidentalis*	Wuyun Fm.	China 49.1, 129.1	62.6, 109.5	Liu et al. (1999)
(Maastrichtian)	*Metasequoia occidentalis*	Wuyun Fm.	China 46.3, 130.1	36.6, 139.5	Zhang et al. (1990)
	Metasequoia sp.	Comox Fm. (2)	Canada 49.6, −125	61.5, −83.4	Bell (1962)
	Metasequoia sp.	Protection Fm.	Canada 49.2, −123.9	53.3, −83.4	Bell (1962)
	Metasequoia sp.	n/a	Canada 53.3, −113.9	53.97, −80.6	Bell (1949)

(Continues)

TABLE 2 (Continued)

Age	Fossil species	Locality or formation (No. occurrences)	Country and modern coordinates (Lat, Long)	Paleocoordinates	Reference
	Metasequoia sp.	Eagle Sandstone	USA 47.6, –111	52.5, –80.8	Bell (1963)
	Metasequoia sp.	Fruitland Fm.	USA 36.3, –108.3	54.5, –78	Knowlton (1917a)
	Metasequoia sp.	Lance Fm.	USA 45.3, –107.7	52.8, –76.2	Knowlton (1911)
	Metasequoia sp.	New Siberia Island	Russia 74.5, 139.4	71.9, 131.3	Baikovskaya (1956)
	Metasequoia sp.	Zhubankari Mountain near Lake Zaisan	Kazakhstan 48.1, 84.1	47.3, 116.8	Shilin and Romanova (1978)
	Metasequoia sp.	Savayama Fm.	Russia 51.1, 142.3	55.8, 140.3	Vakhrameev (1988)
Paleocene	*Metasequoia* sp.	Napanskya Fm.	Russia 57.3, 157.1	56.1, 131	Maslova (2000)
	Metasequoia sp.	Firkanten Fm. (3)	Svalbard 78.6, –12	73, –11.1	Harland et al. (1976)
	Metasequoia sp.	Summit Creek Fm.	Canada 64.6, –125.3	78.2, –81.6	Sweet et al. (1989)
	Metasequoia sp.	Sagavanirktok Fm.	USA 69.2, –148.2	75.5, –135.3	Spicer et al. (1994)
	Metasequoia sp.	Sustut Group (4)	Canada 56.6, –126.6	64.7, –101.6	Bell (1949)
	Metasequoia sp.	Rapid Fm.	Canada 59.1, –128.6	64.7, –102.2	Gabrielse (1963)
	Metasequoia sp.	Turtle Mountain Fm.	Canada 49, –100.3	60.5, –93.4	Wickendan (1945)
	Metasequoia sp.	Edmonton Fm.	Canada 57.3, –112.5	63.4, –85.3	Williams and Dyer (1930)
	Metasequoia sp.	Sentinel Butte Fm.	USA 47.3, –103.9	47.8, –84.5	Hoganson (1997)
	Metasequoia sp.	Asuwa Flora	Japan 36.1, 136.1	39.7, 128.4	Matsuo (1962)
	Metasequoia foxii	Paskapoo Fm. (6)	Canada 53.2, –114.2	56.6, –90.1	Stockey et al. (2001)
	Metasequoia occidentalis	Tsagaya Flora	Russia 49.5, 129.5	50.6, 119.2	Krasilov (1976)
	Metasequoia occidentalis	Malomikhailovka Fm.	Russia 52.3, 140.2	52.3, 120.4	Akhmetiev and Golovneva (1997)
	Metasequoia occidentalis	Atanikerdluk Fm. (6)	Greenland 70, –52.2 69.2, –53.1	62.1, –22 61.4, –23.7	Koch (1964)
	Metasequoia occidentalis	Agatdal Fm. (3)	Greenland 70.5, –53.1	62.5, –22.7	Koch (1963, 1964)
	Metasequoia occidentalis	Volcanic Tuff Flora	Canada 54.2, –118.5	60, –89.9	Christophel (1976)
	Metasequoia occidentalis	Fort Union Fm. (43)	USA 42.6, –105.5	51.6, –81.2	Brown (1962)

TABLE 2 (Continued)

Age	Fossil species	Locality or formation (No. occurrences)	Country and modern coordinates (Lat, Long)	Paleocoordinates	Reference
	Metasequoia occidentalis	Pipestone Fm.	USA 48.2, −120.1	54.6, −81.3	Royse (1965)
	Metasequoia occidentalis	Ravenscrag Fm. (8)	Canada 49.3, −109.2	55.3, −85.9	McIver and Basinger (1993)
	Metasequoia occidentalis	Expedition Fm. (2)	Canada 78.4, −81.6	81.4, −69.3	McIver and Basinger (1999)
	Metasequoia occidentalis	Boshnyakovskayaand Conglomeratovaya Fms. (2)	Russia 49.4, 142.1	48, 120	Krasilov (1979)
	Metasequoia occidentalis	Wuyun Fm.	China 48.4, 130.3	50.5, 118.6	Xiong (1986)
Eocene	*Metasequoia* sp.	Okanagan Flora (8)	USA 54.8, −127.2	60.4, −93.7	Sheldon et al. (2020)
	Metasequoia sp.	Manastash Fm. (3)	USA 47.6, −122	60.08, −92.9	Sheldon et al. (2020)
	Metasequoia sp.	Thomas Ranch	USA 49.4, −120.5	60.7, −92.3	Sheldon et al. (2020)
	Metasequoia sp.	Clarno Fm.	USA 44.5, −119.6	60.7, −92.1	Sheldon et al. (2020)
	Metasequoia sp.	Penjin Bay	Russia 63.5, 168	72.5, 158.8	Kryshtofovich (1958)
	Metasequoia sp.	Naibuchi Fm.	Russia 47.2, 142.5	64.5, 151.8	Kodrul (1999)
	Metasequoia sp.	Liaoning Province	China 41.9, 123.9	41, 119.6	Academic Sinica (1978)
	Metasequoia sp.	Copper Lake Fm.	USA 58.9, −153.3	71.5, −136.2	Detterman et al. (1996)
	Metasequoia sp.	Kamloops Group (6)	Canada 50.1, −120.5	58.5, −96.5	Armentrout (1981)
	Metasequoia sp.	Chu Chua Fm. (2)	Canada 51.5, −120.1	58.6, −96.4	Armentrout (1981)
	Metasequoia sp.	n/a	Canada 57.8, −131.4	57.9, −91.9	Sheldon et al. (2020)
	Metasequoia sp.	Horsefly Riverbeds	Canada 52.3, −121.4	58.2, −91.8	Wilson (1977)
	Metasequoia sp.	Elko Fm.	USA 40.8, −115.8	57.4, −96.3	Wing (1987)
	Metasequoia sp.	Renova Fm. (2)	USA 45.2, −112.2	40.2, −102.7	Call and Dilcher (1997)
	Metasequoia sp.	Yubari Fm.	Japan 43.3, 142.2	52.2, 142.7	Endo (1968)
	Metasequoia sp.	Woodwardia Fm.	Japan 43.2, 142	52.2, 142.6	Endo (1968)
	Metasequoia sp.	Okanagan Flora (8)	USA 54.8, −127.2	60.4, −93.7	Sheldon et al. (2020)
	Metasequoia sp.	Manastash Fm. (3)	USA 47.6, −122	60.1, −92.9	Sheldon et al. (2020)

(Continues)

TABLE 2 (Continued)

Age	Fossil species	Locality or formation (No. occurrences)	Country and modern coordinates (Lat, Long)	Paleocoordinates	Reference
	Metasequoia sp.	Thomas Ranch	USA 49.4, −120.5	60.7, −92.3	Sheldon et al. (2020)
	Metasequoia sp.	Clarno Fm.	USA 44.5, −119.6	60.7, −92.1	Sheldon et al. (2020)
	Metasequoia sp.	Penjin Bay	Russia 63.5, 168	72.5, 158.8	Kryshtofovich (1958)
	Metasequoia sp.	Naibuchi Fm.	Russia 47.2, 142.5	64.5, 151.8	Kodrul (1999)
	Metasequoia occidentalis	Atanikerdluk Fm.	Greenland 70.8, −54.1	53.3, −87	Koch (1963)
	Metasequoia occidentalis	Qeqertarssuatsiaq	Greenland 70.4, −54.9	53.1, −88.5	Koch (1963, 1964)
	Metasequoia occidentalis	Aspelintoppen Fm.	Faroe Island 78.1, −15.6	62, −17.6	Kvaček and Manum (1997)
	Metasequoia occidentalis	Renardodden Fm.	Faroe Island 77.5, −14.5	61.9, −17.8	Kvaček et al. (1994)
	Metasequoia occidentalis	Forlandsundet Fm.	Faroe Island 78.7, −12.5	61.9, −18.1	Kvaček et al. (1994)
	Metasequoia occidentalis	Iceberg Bay Fm.	Canada 81.9, −69.7	61.9, −93.2	McIver and Basinger (1999)
	Metasequoia occidentalis	Margaret Fm.	Canada 77.9, −83.6	65.1, −99.1	McIver and Basinger (1999)
	Metasequoia occidentalis	Buchanan Lake Fm. (2)	Canada 79.9, −89	68.7, −102.7	Basinger (1991)
Oligocene	*Metasequoia* sp.	Snatol Fm.	Russia 58, 158.1	60.1. 155.4	Gladenkov et al. (1991)
	Metasequoia sp.	Kutanbulakskaya Fm. (2)	Russia 47.1, 57.5	45.8, 52.1	Zhilin (1974)
	Metasequoia sp.	Chiliktinskaya Fm.	Russia 47.3, 60.3	46.3, 55.1	Zhilin (1974)
	Metasequoia sp.	Lake Khanka	Russia 45, 132.3	42.2, 118.2	Kryshtofovich (1958)
	Metasequoia sp.	Omoloi River Basin	Russia, 70.5, 133.3	70.8, 130.3	Dorofeev (1972)
	Metasequoia sp.	Lake Zaysan	Russia, 48.1, 84.4	57.5, 80.3	Kryshtofovich (1958)
	Metasequoia sp.	Kasparanskaya Fm.	Russia 56.3, 85.1	55.3, 81	Gorbunov and Shilkina (1972)
	Metasequoia sp.	Polevskoi River	Russia 59.1, 57.3	59.6, 51	Dorofeev (1970)
	Metasequoia sp.	Kovachin Fm. (2)	Russia 58, 158.1	58.5, 152	Gladenkov et al. (1991)
	Metasequoia sp.	Chiliktinskaya Fm.	Russia 47.5, 60.8	46.2, 55.2	Zhilin (1989)
	Metasequoia sp.	Machigarskaya Fm.	Russia 54.1, 142.2	53, 137	Fotyanova (1988)

TABLE 2 (Continued)

Age	Fossil species	Locality or formation (No. occurrences)	Country and modern coordinates (Lat, Long)	Paleocoordinates	Reference
	Metasequoia sp.	Khoindzho Fm.	Russia 51, 142.2	49.8, 137	Fotyanova (1988)
	Metasequoia sp.	Arakaiskaya Fm.	Russia 49.2, 142.1	48.1, 137	Fotyanova (1988)
	Metasequoia sp.	Yangliantun Fm.	China 41.3, 123.3	42.8, 113.8	Jin and Shang (1998)
	Metasequoia sp.	Hemlock Conglomerate	USA 58.2, −154	60.3, −138.2	Detterman et al. (1996)
	Metasequoia sp.	Kootznahoo Fm. (6)	USA 56.4, −134	58.5, −128	Hollick (1936)
	Metasequoia sp.	John Day Fm. (3)	USA 44.4, −119.5	46.8, −100.3	Meyer and Manchester (1997)
	Metasequoia sp.	Weaverville Fm.	USA 40.4, −123.3	42, −101.4	MacGinitie (1937)
	Metasequoia sp.	Iwake Fm.	Japan 37, 140.5	39.1, 127.6	Endo (1963)
	Metasequoia sp.	Kobe Fm.	Japan 34.4, 135.1	36.5, 122.7	Kobayashi et al. (1995)
	Metasequoia sp.	Sakito Fm.	Japan 33.3, 129.3	35.6, 116.2	Matsuo (1970)
	Metasequoia occidentalis	Kiwado Fm.	Japan 34.2, 131.1	36.3, 118	Uemura et al. (1999)
	Metasequoia occidentalis	Kameoka Fm. (2)	Japan 38.2, 140.5	40.2, 127.4	Tanai (1961)
	Metasequoia occidentalis	Shirakawa Fm.	Japan 34.4, 135.1	36.5, 122.8	Tanai (1961)
	Metasequoia occidentalis	Shakubetsu and Yubetsu Fms.	Japan 43.1, 145.1	45.8, 135.4	Matsue and Onoe (1995)
	Metasequoia occidentalis	Clarno Fm.	USA 44.2, −121.1	46.9, −100	Ashwill (1983)
	Metasequoia occidentalis	Little Butte Volcanic Series (2)	USA 44.4, −122.3	46, −100.2	Meyer (1973)
	Metasequoia occidentalis	Poul Creek Fm.	USA 60.1, −140.1	62.4, −124.2	Wolfe (1977)
	Metasequoia occidentalis	Endako Group (2)	Canada 53.2, −122.5	55.2, −103	Tipper (1963)
	Metasequoia occidentalis	Nomomikhailovskaya Fm. (2)	Russia 57.4, 66.1	57.9, 60.4	Sveshnikova (1963)
Miocene	*Metasequoia* sp.	Lower Medvezhkinskaya Fm.	Russia 60.3, 165.9	60.2, 167.6	Chelebaeva (1978)
	Metasequoia sp.	n/a	Russia 45.5 58.5	45.3, 57.7	Zhilin (1974)
	Metasequoia sp.	Gusinskoi Fm.	Russia 63.5, 168	63.6, 169.5	Ablaev (1985)
	Metasequoia sp.	Khasanskaya Fm.	Russia 42.7, 130.8	42.2, 129.7	Pimenov (1990)

(Continues)

TABLE 2 (Continued)

Age	Fossil species	Locality or formation (No. occurrences)	Country and modern coordinates (Lat, Long)	Paleocoordinates	Reference
	Metasequoia sp.	Karaganda Oblast	Russia 48.9, 65.5	49.16, 64.6	Zhilin (1989)
	Metasequoia sp.	Granatovaya Fm.	Russia 45.8, 137.6	44.1, 134.7	Klimova (1981)
	Metasequoia sp.	Botchinskaya Fm.	Russia 45, 132.2	47.6, 131.4	Ablaev et al. (1994)
	Metasequoia sp.	Mammoth Mountain	Russia 63, 133.3	62.5, 134.5	Dorofeev (1969)
	Metasequoia sp.	Khasanskaya Fm.	Russia 44.2, 132.7	44.8, 134.1	Pimenov (1990)
	Metasequoia sp.	Beaufort Fm. (2)	Canada 72, −125.7	69.9, −123.6	Matthews (1987)
	Metasequoia sp.	Plateau Cap gravels	Canada 69.2, −127	72.6, −121.9	Matthews and Ovenden (1990)
	Metasequoia sp.	Shakhterskaya and Verkhneduiskaya Fms. (2)	Russia 49.2, 142.2	49.3, 144	Fotyanova (1988)
	Metasequoia sp.	Tumenzi Fm.	China 43.6, 128.4	40.8, 129.4	Li and Yang (1984)
	Metasequoia sp.	Kenai Fm. (19)	USA 64.2, −142	62.6, −146.6	Foster (1969)
	Metasequoia sp.	Sanctuary Fm. (2)	USA 65.4, −150.1	60.3, −149.4	Leopold and Liu (1994)
	Metasequoia sp.	n/a	USA 45.2, −113.9	47.2, −113.8	LePage et al. (2005)
	Metasequoia sp.	n/a	USA 46.5, −116.7	45.8, −110.9	LePage et al. (2005)
	Metasequoia sp.	n/a	USA 42.2, −122.8	48.5, −114.6	LePage et al. (2005)
	Metasequoia sp.	n/a	USA 47, −116.3	48.4, −113.8	LePage et al. (2005)
	Metasequoia sp.	Keumkwandong Fm.	South Korea 36, 129.6	36.7, 128.7	Chun (1982)
	Metasequoia sp.	Minamitama Fm.	Japan 35.6, 137.8	38.8, 137.2	Ida (1955)
	Metasequoia sp.	Itahana Fm.	Japan 48.9, 65.5	49.2, 64.6	LePage et al. (2005)
	Metasequoia sp.	Kita–Aiki Fm.	Japan 60.1, −139.2	61.4, −150.9	Endo (1963)
	Metasequoia sp.	Dajie Fm.	Japan 62.5, −150.9	63.4, −148.5	Wang et al. (2019)
	Metasequoia occidentalis	Latah Fm. (10)	USA 47.67, −117.4	47.7, −113.3	Brown (1935a)
	Metasequoia occidentalis	Yakataga Fm.	USA 60.1, −139.2	65, −139.2	Wolfe (1977)
	Metasequoia occidentalis	Deadman Fm.	Canada 51.1, −120.9	51.7, −117.8	Campbell and Tipper (1971)

TABLE 2 (Continued)

Age	Fossil species	Locality or formation (No. occurrences)	Country and modern coordinates (Lat, Long)	Paleocoordinates	Reference
	Metasequoia occidentalis	Eagle Creek Fm.	USA 45.6, −122	46.3, −119.3	Krause (1999)
	Metasequoia occidentalis	Calvert Fm.	USA 38.9, −77	39, −73.9	Berry (1909)
	Metasequoia occidentalis	Shihti Fm.	China 25.1, 121.5	25.2, 118.5	Canright (1972)
	Metasequoia occidentalis	Tongcheon Fm. (2)	South Korea 38.7, 128.2	37.9, 130.4	Huzioka (1972)
	Metasequoia occidentalis	Hamjindong Fm.	South Korea 40.9, 129.4	38.2, 132.4	Huzioka (1972)
	Metasequoia occidentalis	Kogeonweon flora (2)	South Korea 42.5, 129.8	38, 132.3	Huzioka (1972)
	Metasequoia occidentalis	Hoengyeong Fm. (2)	South Korea 42.5, 129.8	38, 132.3	Huzioka (1972)
	Metasequoia occidentalis	Yuseon Fm. (2)	South Korea 42.5, 129.8	38, 132.3	Huzioka (1972)
	Metasequoia occidentalis	Yunoki and Fukui Fms.	Japan 61.3, −151.8	62.2, −149.3	Tanai (1961)
	Metasequoia occidentalis	Hachinokubo bed	Japan 62.5, −151	62.3, −149.1	Matsue and Onoe (1995)
	Metasequoia occidentalis	Nakamura Fm. (5)	Japan 45.8, 137.6	45.9, 139.6	Ina (1992)
	Metasequoia occidentalis	Hiramaki Fm.	Japan 72, −125.7	74.8, −119.3	Ina (1992)
	Metasequoia occidentalis	Oidawara Fm.	Japan 49.2, 142.2	48, 141.3	Ina (1992)
	Metasequoia occidentalis	Yagii Fm.	Japan 49, 143; 25.1, 121.5	47.3, 140.2	Ozaki (1991)
	Metasequoia occidentalis	Kanisawa Fm.	Japan 43.6, 128.4	38.3, 127.2	Horiuchi (1996)
	Metasequoia occidentalis	Suki Fm.	Japan 64.2, −142	60.8, −150.4	Hojo (1973)
	Metasequoia occidentalis	Nabeyama Fm.	Japan 65.4, −150.1	60.3, −149.4	Tanai (1961)
	Metasequoia occidentalis	Koura Fm.	Japan 65.2, −152	60.7, −149.4	Matsue and Onoe (1995)
	Metasequoia occidentalis	Oshimojo Fm.	Japan 61.1, 151.2	62.5, 134.5	Ina (1992)
	Metasequoia occidentalis	Seto Fm. (2)	Japan 35.9, 138.6	38.8, 137.1	Ozaki (1991)
	Metasequoia occidentalis	Kosho Fm.	Japan 35.4, 137.1	38.7, 137	Uemura et al. (2001)
	Metasequoia occidentalis	Akeyo Fm. (3)	Japan 36.6, 140.4	39, 136.7	Onoe (1978)
	Metasequoia occidentalis	Kobe flora	Japan 36.6, 140.4	38.7, 136.4	Hori (1987)

(Continues)

TABLE 2 (Continued)

Age	Fossil species	Locality or formation (No. occurrences)	Country and modern coordinates (Lat, Long)	Paleocoordinates	Reference
	Metasequoia occidentalis	Hokutan Fm.	Japan 33.2, 129.7	38.4, 137.4	Onoe (1978)
	Metasequoia occidentalis	Toyooka Group	Japan 24.2, 101.4	23, 98.5	Onoe (1978)
	Metasequoia occidentalis	Seya Fm. (3)	Japan 47.7, −117.4	48.4, −113.8	Onoe (1978)
	Metasequoia occidentalis	Yanagida Fm.	Japan 60.3, 165.9	61.5, 152	Ishida (1970)
	Metasequoia occidentalis	Ningyo-Toge Fm.	Japan 45.5, 58.5	45.3, 57.7	Tokunaga and Onoe (1969)
	Metasequoia occidentalis	Tochiwara Fm.	Japan 63.5, 168	63.6, 169.5	Matsue and Onoe (1995)
	Metasequoia occidentalis	Fuganji Fm.	Japan 42.7, 130.8	38.7, 128.1	Hojo (1973)
	Metasequoia occidentalis	Naidabu Fm. (2)	Japan 43.3, 142	44.2, 138.1	Tanai (1955)
	Metasequoia occidentalis	Sekinai Fm. (2)	Japan 42.3, 139.9	39.5, 138.6	Tanai and Suzuki (1972)
	Metasequoia occidentalis	Fukuyama Fm. (2)	Japan 43, 140.5	39.31, 138.3	Tanai and Suzuki (1963)
	Metasequoia occidentalis	Yoshioka Fm. (2)	Japan 41.4, 140.9	39.5, 138.1	Tanai and Suzuki (1963)
	Metasequoia occidentalis	Kunnui Fm. (4)	Japan 42.3, 139.9	37.5, 137.3	Tanai and Suzuki (1963)
	Metasequoia occidentalis	Soya Fm. (2)	Japan 45.3, 142.3	49.4, 133.9	Tanai (1961)
	Metasequoia occidentalis	Sakipembersu/Nokonan Fm. (2)	Japan 43.5, 142.2	48.06, 132.9	Tanai, 1971
	Metasequoia occidentalis	Asahi Fm. (2)	Japan 43.1, 142	48, 133.9	Tanai (1961)
	Metasequoia occidentalis	Honjin-no-sawa Fm. (2)	Japan 44, 141.7	48.24, 132.7	Tanai (1961)
	Metasequoia occidentalis	Niipaku Fm. (2)	Japan 42.8, 142.8	48.5, 132.9	Tanai (1961)
	Metasequoia occidentalis	Tachikarabetsu Fm. (2)	Japan 44.8, 142.7	48.8, 132.1	Tanai (1961)
	Metasequoia occidentalis	Shanabuchi Fm. (2)	Japan 44.1, 143.5	49.9, 132.6	Tanai (1961)
	Metasequoia occidentalis	Aburato and Iragawa Fms. (2)	Japan 38.7, 139.7	38.4, 137.6	Matsue and Onoe (1995)
	Metasequoia occidentalis	Kamigo Fm. (2)	Japan 38.3, 140.1	38.4, 137.1	Tanai (1961)
	Metasequoia occidentalis	Imaichi and Oguni Fms. (2)	Japan 38.1, 139.8	38.8, 137.2	Onoe (1974)
	Metasequoia occidentalis	Takamine and Tenoko Fms. (2)	Japan 38, 139.8	38.8, 137.1	Uemura (1988)

TABLE 2 (Continued)

Age	Fossil species	Locality or formation (No. occurrences)	Country and modern coordinates (Lat, Long)	Paleocoordinates	Reference
	Metasequoia occidentalis	Shichiku Fm. (2)	Japan 36.8, 140.8	38.7, 137	Huzioka (1964)
	Metasequoia occidentalis	Shirasaka Fm. (2)	Japan 37, 140.81	39, 136.7	Tanai (1961)
	Metasequoia occidentalis	Tennoji Fm. (2)	Japan 37.8, 140.4	38.7, 136.4	Tanai (1961)
	Metasequoia occidentalis	Masuzawa Fm. (2)	Japan 39.7, 141.1	38.6, 136.4	Tanai (1961)
	Metasequoia occidentalis	Hitomaru Fm. (2)	Japan 34.4, 131.1	35.5, 127.4	Huzioka (1974)
	Metasequoia occidentalis	Sauramachi and Ajiri Fms. (2)	Japan 38.3, 141	38.4, 137.4	Tanai (1955)
	Metasequoia occidentalis	Kunimi Fm. (2)	Japan 36.2, 136.2	38.7, 130.9	Tanai (1961)
	Metasequoia occidentalis	Monzen Fm. (2)	Japan 39.9, 139.8	37.3, 133.1	Huzioka (1964)
	Metasequoia occidentalis	Senosawa Fm. (2)	Japan 40.3, 140.3	37.2, 132.9	Huzioka (1964)
	Metasequoia occidentalis	Iwadate Fm. (3)	Japan 40.4, 139.7	38.1, 132.9	Huzioka (1964)
	Metasequoia occidentalis	Yokonetoge Fm. (2)	Japan 39.4, 140.1	38.3, 132.7	Huzioka (1964)
	Metasequoia occidentalis	Aniai Fm. (2)	Japan 40, 140.4	38.1, 132.5	Huzioka (1964)
	Metasequoia occidentalis	Utto Fm. (2)	Japan 40, 140.4	37.9, 132.4	Huzioka, 1963
	Metasequoia occidentalis	Hamjindong Fm.	South Korea 37.8, 139.5	35.9, 127.5	Huzioka (1972)
	Metasequoia occidentalis	Kuroishizawa Fm.	Japan 35.4, 132.7	38, 130.7	Huzioka (1964)
	Metasequoia occidentalis	Yamanokami Fm.	Japan 35.5, 133.1	37.9, 130.4	Huzioka (1964)
	Metasequoia occidentalis	Toki Fm. (2)	Japan 36, 138.6	38.4, 137.4	Tokunaga and Onoe (1969)
	Metasequoia occidentalis	Tokoname Fm.	Japan 35.6, 137.8	38.4, 137.1	Ozaki (1991)
	Metasequoia sp.	Lower Medvezhkinskaya Fm.	Russia 60.3, 165.9	60.2, 167.6	Chelebaeva (1978)
	Metasequoia sp.	n/a	Russia 45.5, 58.5	45.3, 57.7	Zhilin (1974)
	Metasequoia sp.	Gusinskoi Fm.	Russia 63.5, 168	63.6, 169.5	Ablaev (1985)
	Metasequoia sp.	Khasanskaya Fm.	Russia 42.7, 130.8	42.2, 129.7	Pimenov (1990)
	Metasequoia sp.	Karaganda Oblast	Russia 48.9, 65.5	49.2, 64.6	Zhilin (1989)

(Continues)

TABLE 2 (Continued)

Age	Fossil species	Locality or formation (No. occurrences)	Country and modern coordinates (Lat, Long)	Paleocoordinates	Reference
	Metasequoia sp.	Granatovaya Fm.	Russia 45.8, 137.6	44.1, 134.7	Klimova (1981)
	Metasequoia sp.	Botchinskaya Fm.	Russia 45, 132.2	47.6, 131.4	Ablaev et al. (1994)
Pliocene	*Metasequoia* sp.	Ob River	Russia 56.2, 83.6	56, 83.2	Zamer et al. (1963)
	Metasequoia sp.	n/a	Georgia 41.6, 42	41.45, 41.8	Chochieva (1975)
	Metasequoia sp.	Beaufort Fm.	Canada 76, −116	76, −115.8	Matthews et al. (1990)
	Metasequoia sp.	Izumi Fm. (6)	Japan 37.3, 139.4	37, 139.6	Manabe et al. (1970)
	Metasequoia sp.	Shiotsubo Fm.	Japan 37.4, 139.5	37, 139.6	Suzuki (1959)
	Metasequoia sp.	Kuroiwa Fm.	Japan 36.5, 140.3	36.2, 140.4	Suzuki (1959)
	Metasequoia sp.	Aichi Prefecture	Japan 35, 135.6	34.5, 135.7	Miki (1941)
	Metasequoia sp.	Hyogo Prefecture (5)	Japan 34.4, 134.6	34, 134.7	Endo (1955)
	Metasequoia sp.	Osaka Fm. (2)	Japan 34.3, 134.6	34, 134.7	Kobayashi et al. (1995)
	Metasequoia sp.	Fujiwara Fm.	Japan 35.5, 137.3	35, 137.5	Kokawa (1955)
	Metasequoia sp.	Atago and Goshikihama Fms.	Japan 34.1, 134.4	33.6, 134.6	Momohara and Mizuno (1999)
	Metasequoia sp.	Mogi Fm.	Japan 32.4, 129.6	32.1, 129.7	Endo (1963)
	Metasequoia sp.	Hitoyoshi Fm.	Japan 32.2, 130.5	31.7, 130.6	Miki and Kokawa (1962)
	Metasequoia occidentalis	Kenai Fm.	USA 60, −151.4	60.22, −150.65	Wolfe (1966)
	Metasequoia occidentalis	Oriwata Fm.	Japan 38.4, 140.1	38.1, 140.2	Tanai (1961)
	Metasequoia occidentalis	Koriyama and Tabira Fms.	Japan 31.5, 130.3	31.2, 130.4	Matsue and Onoe (1995)
	Metasequoia occidentalis	Kume Fm.	Japan 36.2, 140.3	35.9, 140.5	Takimoto et al. (1998)
	Metasequoia occidentalis	Akima Fm.	Japan 36.2, 139	35.7, 139.2	Horiuchi (1996)

were imported into ArcGIS Pro (ESRI, 2023). To identify the modern-day climatic regime for both plants, the climatic raster data were overlaid with the occurrence data points, then interpolated to extract the climatic data (MAT, MAP, CMMT, WMMT) corresponding to the distribution data. For Zingiberaceae, this process was repeated for each subfamily (Alpinioideae, Siphonochiloideae, Tamijioideae, Zingiberoideae), to test niche variation among extant subfamilies.

Macrofossil occurrences of Zingiberaceae and *Metasequoia* were collected from the literature (Tables 1–2; LePage et al., 2005; Smith et al., 2012, 2015; Li et al., 2018 [no occurrences were excluded for this analysis]). Zingiberales pollen have a reduced exine and are not found fossilized (Kress and Specht, 2006), which is why we focused on macrofossils for both groups. Fossils of Zingiberaceae remain identified only to the family level because direct taxonomic affinities to living genera are uncertain, with no specific morphological diagnostics for determining the species yet published (Fischer et al., 2009; Li et al., 2018), especially for leaves. There are some instances where zingiberoid foliage and seeds co-occur (e.g., Kunzmann, 2012), and the record is complicated by the known taphonomic bias in the northern hemisphere that leaf assemblages are predominant in North America, while carpofloras are more prevalent in Eurasian assemblages (Table 1; Collinson, 1990; Fischer et al., 2009; Benedict, 2012; S. Y. Smith, personal observations). Thus, while not ideal, in the absence of other evidence such as clear genus-level morphological distinctions grounded in studies of living Zingiberaceae, we chose to examine the fossil record—dominated by *Spirematospermum* and zingiberoid foliage—together. *Spirematospermum* is thought to be within the Alpinioideae (Smith et al., 2018). We removed occurrences like fossil "*Alpinia*" (Mai and Walther, 1985, 1991; Mai, 1999) because they are no longer considered affiliated with Zingiberaceae (Smith et al., 2015). The fossil data points were imported into GPlates 2.2 (Müller et al., 2018) and the PALEOMAP package (Scotese, 2016) for reconstructing the fossil global distribution. Tectonic plate identifications were assigned to each occurrence for use within PALEOMAP so that fossil occurrences were tracked to the correct positioning in the past. The fossil occurrences with the new coordinate data for Zingiberaceae were then interpolated through climatic raster data from the paleoclimatic models (see below). Climates were compared between the extinct Zingiberaceae and both living groups of Zingiberaceae (family) and Alpinioideae (subfamily) since extinct Zingiberaceae occurrences are attributed to either group (Smith et al., 2012, 2015). We applied the same approach to *Metasequoia*, but with fossil occurrence data; this group was kept at the genus level to include the extinct species along with the only living species, *M. glyptostroboides* (LePage et al., 2005; Kunzmann and Mai, 2011; Simoneit et al., 2016; Wang et al., 2019). Living distributions of both plant groups were arranged with simplemappr (Shorthouse, 2010) while fossil distributions were arranged with PALEOMAP (Scotese, 2016).

Past and present climatic data

The paleoclimatic simulations used in this study were based on recently published paleoclimatic simulations of the late Mesozoic and Cenozoic (Farnsworth et al., 2019; Acosta et al., 2022; Gaskell et al., 2022). While paleoclimatic proxy data have much value and have been effectively used in other paleoclimate-related studies (e.g., Wolfe, 1979, 1993; Royer, 2001; Sheldon and Tabor, 2009; Fricke et al., 2010; Henderson et al., 2010; Sachse et al., 2012; Hren et al., 2013), both paleoclimatic simulations and proxy data each have their own set of biases and constraints. The use of paleoclimatic simulations in this study was used because (1) the climatic simulations allow for independent means to test the range of climate that plants can exist in a given region, (2) spatial availability of climatic reconstructions spans across each proxy locality, and (3) localized, terrestrial proxy sources for each fossil occurrence do not exist. Although the goals of this study do not include model–proxy intercomparisons, available paleoclimatic proxy data (plant macrofossils, paleosols, and isotopes) for the localities used here were compared with the paleoclimatic simulation data used in this study and found to largely overlap (Appendix S1–S3); Bebout, 1977; Wolfe, 1990; Basinger et al., 1994; Herman and Spicer, 1997; Wolfe et al., 1998; Utescher et al., 2000; Ivanov et al., 2002; Vitali et al., 2002; Erdei et al., 2007; Li et al., 2009; Peppe et al., 2011; Arens and Allen, 2014; Śliwińska et al., 2014; Mishra et al., 2022).

Three paleoclimatic simulations (Cenomanian, early Eocene, and middle Miocene) were run under fully coupled atmosphere–ocean configurations and used the Community Earth System Model version 1.2 (CESM1.2; Meehl et al., 2013; Zhu et al., 2020; Acosta et al., 2022). The simulations were carried out with a grid spacing of 1.9° × 2.5° under the finite volume dynamical core version of the atmosphere model. The ocean and sea ice models have a 1° resolution. Versions of the early Eocene and middle Miocene simulations have been previously used in Deep-Time Model Intercomparison Project (DeepMIP; Burls et al., 2021; Lunt et al., 2021; Acosta et al., 2023; Cranwinckel et al., 2023).

The Cenomanian (~95 Ma) and early Eocene (~55 Ma) simulations were both run with a CO_2 concentration of 1700 ppm (six times preindustrial levels of 280 ppm), while the middle Miocene (~15 Ma) simulation was set to 400 ppm (Acosta et al., 2022) (see Appendix S1). The paleoclimatic simulations (Lunt et al., 2012; Goldner et al., 2014; Tabor et al., 2016; Zhu et al., 2019; Acosta et al., 2022) used the most recent CO_2 reconstructions (Sosdian et al., 2020; Rae et al., 2021) and were able to estimate global mean annual temperature. Miocene simulations with 560 and 850 ppm CO_2 are available to estimate climatic conditions of the middle Miocene Climatic Optimum (Acosta et al., 2022; Gaskell et al., 2022). Because the entirety of the Miocene experienced much lower CO_2 and colder conditions, and none of our fossil specimens were situated during the Miocene climatic optimum, we used the 400 ppm CO_2 simulation. We also provide low CO_2 (280 ppm) paleoclimatic simulations to assess the range of precipitation and temperature distribution without the influence of elevated CO_2 relative to pre-industrial values (see Appendix S2).

Because a majority of the Cretaceous fossil occurrences used here were in the Maastrichtian (72–66 Ma), we used a Maastrichtian run from Farnsworth et al. (2019) instead of the Cenomanian simulation of Acosta et al. (2022) for those fossils in the Cretaceous data set. Farnsworth et al. (2019)

used similar methodologies to the models used here, but notably included model runs for the Early and Late Cretaceous. To verify that this substitution was reasonable (i.e., model assumptions did not differ enough to introduce methodological error in comparing reconstructed paleoniche), we compared the Cenomanian model output of Acosta et al. (2022) with the Cenomanian output of Farnsworth et al. (2019) and found that the temperature and precipitation data for extinct Zingiberaceae did not significantly differ (Student's *t*-tests; $P > 0.1$). Because the two separate models resulted in comparable reconstructions for the same time period, we chose to use the Maastrichtian climate run of Farnsworth et al. (2019) for the Maastrichtian-aged Zingiberaceae fossils to ensure the closest appropriate paleoclimatic output. For simplicity, we treated the Cenomanian and Maastrichtian are treated together as the "Cretaceous" (see below for time binning details and specifics on the Cenomanian paleoclimatic model; the Maastrichtian climatic data is included in Appendix S1). Maastrichtian CO_2 levels range in the literature from 1–6× that of the pre-industrial (Royer, 2006; Hunter et al., 2008; Menezes et al., 2022), so while we used the higher end of Maastrichtian CO_2 in the model run (i.e., 1700 ppm), we also included the climatic variables output from the lower CO_2 run (280 ppm) for the Cretaceous climatic data in Appendix S2.

Previous rigorous global paleoclimatic model-data studies have had moderate success at capturing the mean equilibrium climatic state, especially when compared to terrestrial proxies (Burls et al., 2021; Zhu et al., 2022; Acosta et al., 2023; Cramwinckel et al., 2023). However, climatic extremes such as the Last Glacial Maximum, Miocene Climatic Optimum, and Paleocene–Eocene Thermal Maximum, and various associated climatic feedbacks during such periods (e.g., polar-amplified warming, cloud feedbacks, and equator-to-pole temperature gradient at the sea surface) still remain as outstanding problems for the models (Knutti and Rugenstein, 2015; Sherwood et al., 2015; Lunt et al., 2017; Inglis et al., 2020; Burls and Sagoo, 2022). In addition, reconstruction of boundary conditions such as paleogeography and CO_2 have a critical role in determining regional climatic variability. Thus, the outputs from our simulations are approximations of potential climatic niches and do not characterize exact model-data comparison. Testing the sensitivity of our data-model comparison to such boundary-conditions changes is beyond the scope of this study; thus, a more rigorous examination of a specific time and region, in combination with additional fossil samples, should be further pursued.

The time bins used for investigating changes in plant climatic niches corresponds to the age of each climatic simulation. The Cretaceous time bin (95 Ma) refers to the Cenomanian (101–94 Ma) and Maastrichtian (72–66 Ma) aged fossil occurrences, the Eocene time bin (55 Ma) for any Eocene-aged (56–34 Ma) fossil occurrences, and the Miocene time bin (15 Ma) for fossil occurrences within the Miocene (23–5 Ma) epoch. The proxy paleo-coordinates were reconstructed based on the respective simulations. Within such bins, the climate varied; thus, we also provided both cold and warm climatic scenarios to test the robustness of our analysis and show the other extreme climatic state from the simulation used in the main analysis (Cretaceous and Paleocene, Miocene, respectively).

For this study, we used mean annual temperature (MAT), mean annual precipitation (MAP), warm month mean temperature (WMMT), and coldest mean month temperature (CMMT) because these variables best describe climate–plant relationships across large temporal scales (Yang et al., 2011; Srivastava et al., 2012; Reichgelt et al., 2018). The present-day climatic data were generated from WorldClim (2021; Appendix S4) and, with the paleoclimatic simulations, were used to model the living and paleoclimatic niches for both plant groups (Tables 3, 4). Other bioclimatic variables were not included because they involved seasonal variation (O'Donnell and Ignizio, 2012), which was concluded to require too many assumptions that are, at the present time, difficult to validate with independent proxies in the geologic past (e.g., Gallagher et al., 2019; but see Wolfe, 1993; Spicer et al., 2009; Hyland et al., 2018). Plots of the living and paleoniches of each group were created using the python package Matplotlib (ver. 3.8.1; Hunter, 2007).

Testing for niche similarity

We tested niche similarity by generating separate probability density function plots of the climatic variables for each geologic period and comparing between probability density function pairs through Hellinger's *H* distance and Schoener's *D* statistical tests. These statistical tests determine the niche similarity between each climatic group. Hellinger's *H* test analyzes the distance between niches and assigns a value based on proximity (no separation in niches, $H = 0$; distant niches, $H = 1$), while Schoener's *D* metric determines the overlap in given probability density function plots (no overlap in niche space, $D = 0$; complete overlap in niche space, $D = 1$; Barmi and Simonoff, 2000). We used the kerneval R package (Antell et al., 2021) to calculate *H* and *D* values and to plot the niche dissimilarity comparisons between extinct and extant groups (script available in Appendix S5).

RESULTS

The fossils of Zingiberaceae are largely distributed in the northern hemisphere. In the Late Cretaceous, the Zingiberaceae were distributed within the tropics of India and higher latitudes of North America and Europe (Figure 1). From the Paleocene to Pliocene, Zingiberaceae remained generally within the 60° to 30° N latitudes of North America, Europe, and east Asia, although there were some Paleocene occurrences in South America (Wing et al., 2009). There is a highly concentrated grouping of fossil

TABLE 3 Zingiberaceae and subfamilies and *Metasequoia* climatic data from living taxa, including bioclimatic variable data and elevation from WorldClim (Hijman et al., 2017; WorldClim, 2021). Each set of values is represented by the minimum and maximum value, followed by the average in parentheses.

Group; Climatic variable	Mean annual temperature (MAT, °C)	Cold month mean temperature (CMMT, °C)	Warm month mean temperature (WMMT, °C)	Mean annual precipitation (MAP, mm)
Zingiberaceae	22–26 (24)	−21–29 (22)	2.4–32 (25)	2–6800 (2300)
Alpinioideae	3.6–29 (24)	0.79–29 (23)	4.7–32 (25)	2–6800 (2300)
Siphonochiloideae	14–29 (23)	11–26 (21)	16–32 (25)	150–4200 (1600)
Tamijioideae	18–28 (25)	17–28 (25)	18–28 (25)	1600–4200 (3000)
Zingiberoideae	−5.2–29 (24)	−13–29 (21.3)	2.4–32 (25)	330–5600 (2400)
Metasequoia	1.9–21 (13)	−10–13 (2.8)	9–28 (22)	340–1900 (1100)

TABLE 4 Paleoclimatic modeling data for fossil Zingiberaceae and *Metasequoia*. Each set of values is represented by the minimum and maximum value, followed by the average in parentheses.

Group/Age; Climatic variable	Mean annual temperature (MAT, °C)	Cold month mean temperature (CMMT, °C)	Warm month mean temperature (WMMT, °C)	Mean annual precipitation (MAP, mm)
Zingiberaceae				
Cretaceous	11–36 (23)	−14–33 (14)	27–38 (33)	410–1900 (1000)
Eocene	22–26 (23)	6.9–20 (8.78)	30–51 (39)	698–2771 (1100)
Miocene	2.1–24 (10)	−19–22 (−0.27)	16–32 (21)	500–2000 (960)
Metasequoia				
Cretaceous	−2–24 (14)	−23–23 (0.72)	17–42 (30)	400–3500 (1400)
Eocene	6.3–32 (17)	−13–22 (1.4)	25–51 (36)	480–1900 (1100)
Miocene	−7.2–25 (14)	−33–23 (5.1)	3.5–29 (22)	380–2500 (1600)

occurrences in the Miocene of Europe. Zingiberaceae have a sparse fossil record in the tropical latitudes—the predominant distributional range of living Zingiberaceae—until the modern day. *Metasequoia*'s living and fossil distributions are similar to each other (although some living specimens represent cultivated occurrences), ranging primarily in the mid to upper latitudes of the northern hemisphere (Figure 1B, D).

The main extant Zingiberaceae occupy warm climates with MAT of 24°C (Table 3), although some outliers persist in areas with subfreezing MAT, likely the Himalayan Zingiberaceae (Benedict et al., 2016; Zhao et al., 2016). The subfamilies (Figure 2) follow a similar temperature pattern. Zingiberaceae, Alpinioideae, and Zingiberoideae are found in moist climates with an average of 2400 mm MAP. Siphonochiloideae tend to occupy drier areas (average of 1600 mm), while Tamijioideae are in even wetter areas (average of 3000 mm). All groups persist in areas with CMMT between 21° and 25°C, with Tamijioideae living at higher temperature values since this subfamily is only found in Borneo (Larsen, 2005). All groups also persist in WMMT on average of 25°C, but both Zingiberoideae and Alpinoideae have some occurrences below 10°C. Based on these data, Alpinioideae and Zingiberoideae largely occupy a tropical rainforest and tropical seasonal forest Whittaker biome, respectively (Whittaker and Lieth, 1975), Tamijioideae a tropical rainforest biome, and Siphonochiloideae a tropical seasonal savannah biome.

The climatic niche of *Metasequoia* is both cooler and drier than that of Zingiberaceae (Table 3). *Metasequoia* today is found in environments with an average MAT of 13°C, an average CMMT of 2.8°C, and an average WMMT of 22°C. Similarly, average MAP for *Metasequoia* was 1100 mm, which is much lower than all of the Zingiberalean groups. *Metasequoia* from this data set thus largely occupies a temperate seasonal forest biome (Whittaker and Lieth, 1975).

Based on the paleoclimatic modeling data, extinct Zingiberaceae occupied areas of varying temperature and precipitation (Table 4; Figures 3, 4). In the Cretaceous, extinct Zingiberaceae had average MAT of 23°C, average WMMT of 33°C, cooler average CMMT of 14°C, and average MAP of 1000 mm. Similar patterns were observed in the Eocene,

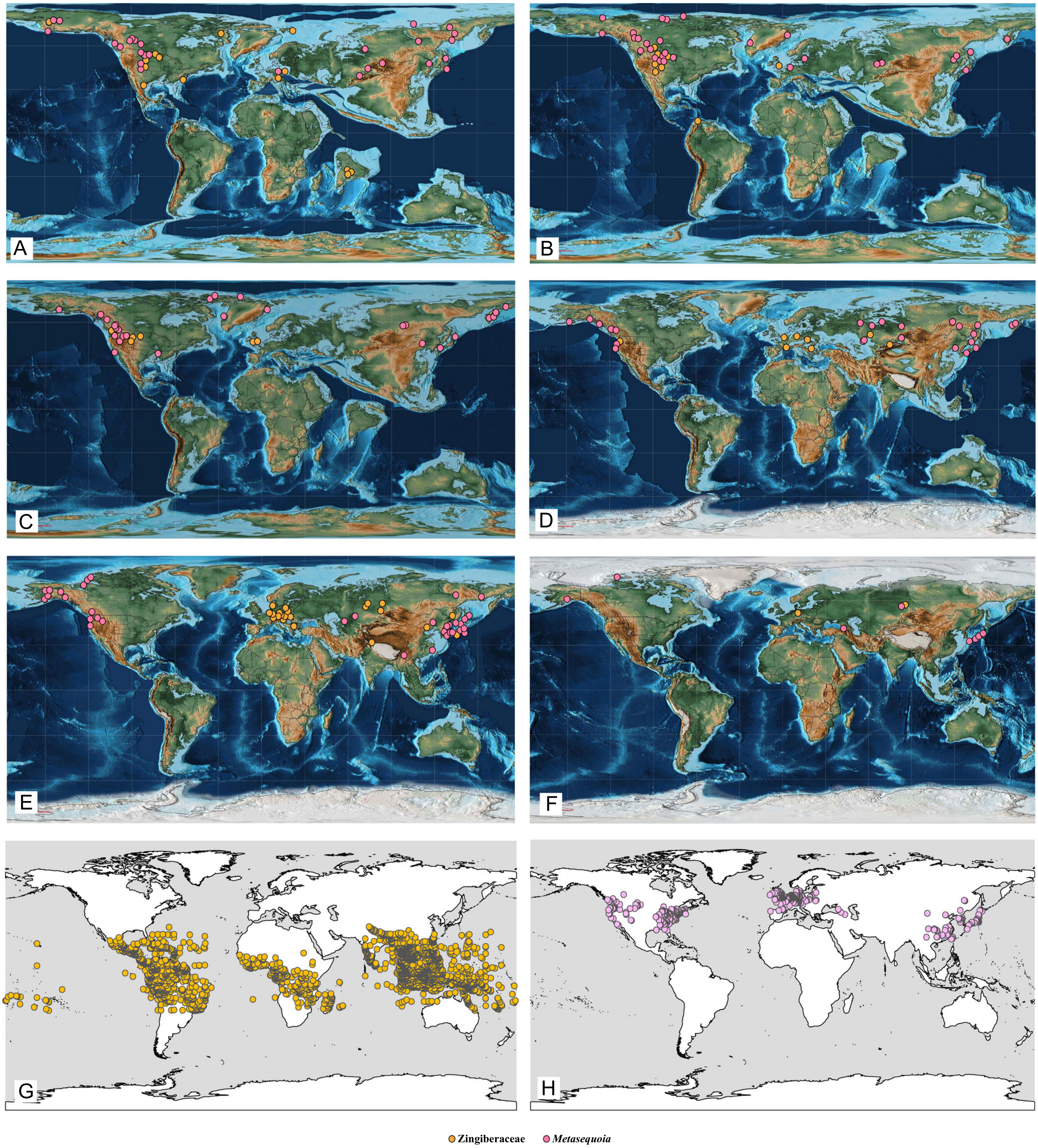

FIGURE 1 Distribution of fossil Zingiberaceae and *Metasequoia* for the (A) Cretaceous, (B) Paleocene, (C) Eocene, (D) Oligocene, (E) Miocene, and (F) Pliocene and of living Zingiberaceae (G) and *Metasequoia* (H).

with high average MAT of 23°C, average WMMT of 39°C, average CMMT of 8.8°C, and average MAP of 1100 mm. However, in the Miocene, we found a shift; extinct Zingiberaceae experienced colder and more arid environments, with average MAT of 10°C, average WMMT of 21°C, average CMMT of −0.27°C, and average MAP of 960 mm. These climatic values differed significantly compared to those for the living Zingiberaceae (Table 3).

Based on paleoclimatic model data, the fossilized *Metasequoia* group experienced relatively consistent climates across

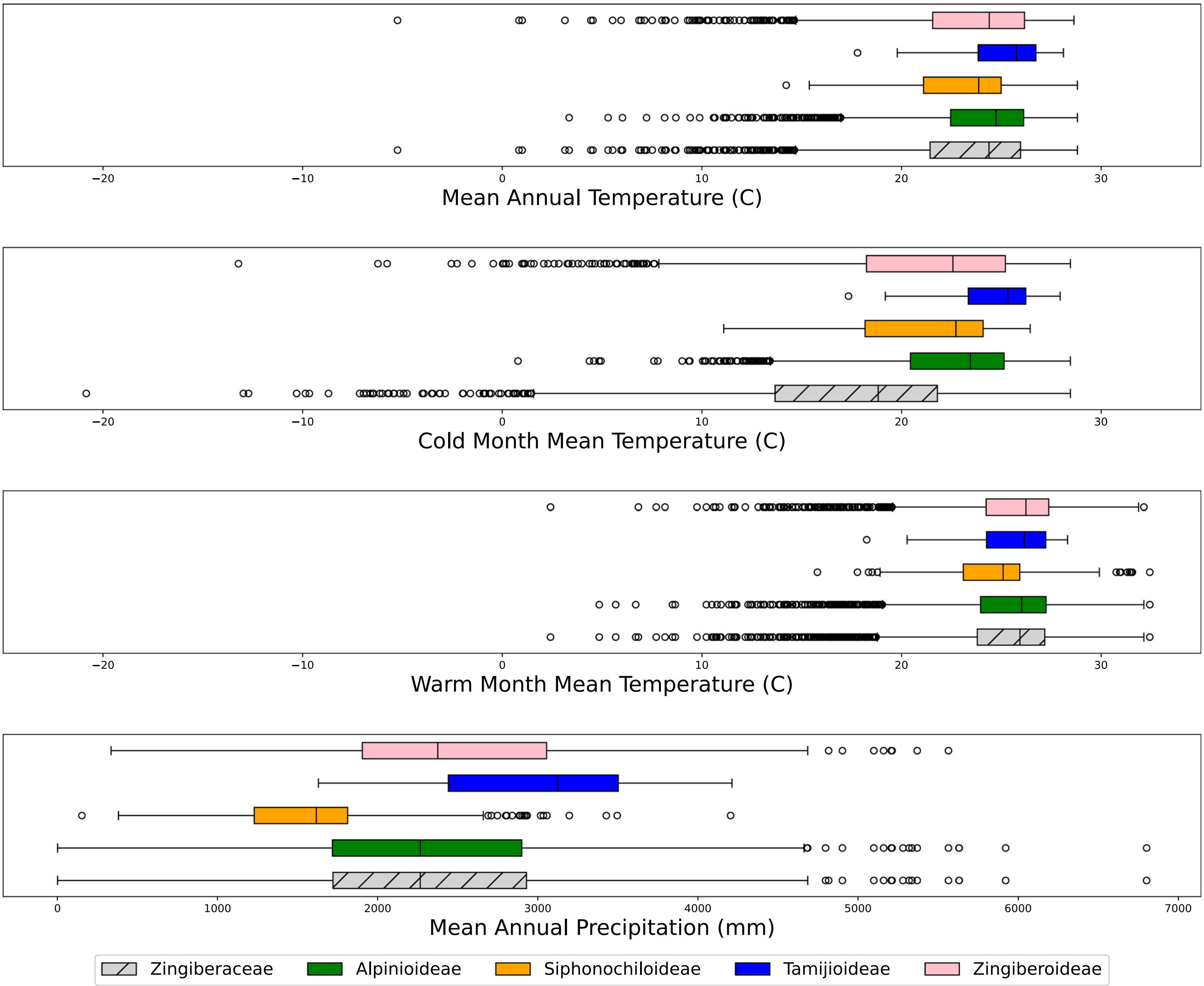

FIGURE 2 Mean annual temperature, mean annual precipitation, warm month mean temperature, and cold month mean temperature ranges for living Zingiberaceae and its subfamilies.

the examined geologic time intervals. Cretaceous members of *Metasequoia* persisted through cool average MAT of 14°C, average CMMT of 0.72°C, average WMMT of 30°C, and average MAP of 1400 mm. *Metasequoia* in the Eocene experienced more variable climates, with higher average MAT and WMMT of 17°C and 36°C, respectively, but lower average CMMT of 1.4°C compared to the Cretaceous; average MAP in the Eocene was also lower (1100 mm). In the Miocene, *Metasequoia* encountered relatively cool average MAT and WMMT of 14°C and 22°C respectively, though had greater values of average CMMT (5.1°C) and MAP (1600 mm) compared to the previous geologic interval. These climatic values fell within the climatic constraints of living plants of the genus (Liu et al., 2007; Table 3, Figure 5).

For both Zingiberaceae and *Metasequoia*, the niche dissimilarity metrics were consistent across the living and fossil representatives. The Hellinger's distance (H) values were mostly greater than 0.5, (and therefore Schoener's D values were mostly <0.5) among the three fossil Zingiberaceae groups, and between the living Zingiberaceae (including Alpinoideae alone) and fossil Zingiberaceae groups (Table 5). For *Metasequoia*, H values were all less than 0.5, while Schoener's D values were mostly >0.5. Therefore, the climatic niches for extinct Zingiberaceae were largely distant and not overlapping in niche space ($H > 0.5$), while those of the fossilized *Metasequoia* were closer and had overlapping niche space ($H < 0.5$).

DISCUSSION

Zingiberaceae underwent shifts in climatic niche

The transition out of the tropical, low latitudes for Zingiberaceae in the Cretaceous and early Cenozoic was likely

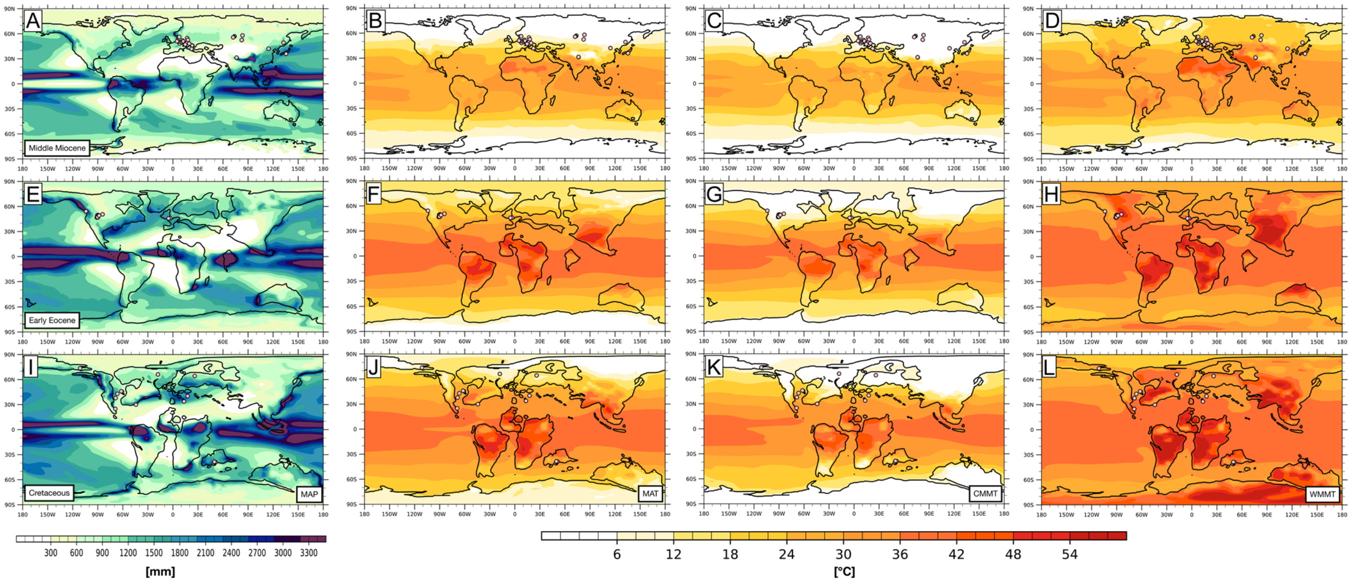

FIGURE 3 Precipitation and surface temperature plots from geologic time periods (A–D) middle Miocene, (E–H) early Eocene, and (I–L) Cretaceous. Climate variables: (A, E, I) mean annual precipitation, (B, F, J) mean annual temperature, (C, G, K) cold month mean temperature, and (D, H, L) warm month mean temperature. Pink points: Zingiberaceae fossil occurrences; *Metasequoia* occurrences are not shown to reduce redundancy.

due to warmer temperatures in the higher latitudes (Manchester, 1999; Tiffney and Manchester, 2001; Tiffney, 2008), especially since these taxa did not deviate from this geographic space for the rest of their fossil record (Figure 1C). The initial movement toward cooler climatic niches was possibly spurred by India's Paleogene collision with Eurasia. This idea is supported by the literature in that a member of Zingiberaceae first appeared in the Miocene of southern Eurasia (Srivastava and Guleria, 2004; Smith et al., 2021; Zhao et al., 2022). Though there are few post-Paleocene fossil occurrences of Zingiberaceae that overlap with the living distribution, it is probable that they were always present in the tropics and that the paucity of low-latitude fossils is due to preservation biases leading to sparse tropical records (Mittelbach et al., 2007). In addition to preservation biases against tropical regions, Zingiberaceae pollen grains were not preserved due to its thin exine, so there is no palynological record (Kress, 1990; Kress and Specht, 2006), and early paleontological collection efforts were focused on the temperate northern hemisphere (Raja et al., 2021). We would expect to find fossilized Zingiberaceae from central African localities based on the living distribution, but none have been discovered yet. This data set also lacks significant representation of southern hemisphere fossils due to preservation bias (i.e., less preservation in Zingiberaceae-growing environments and less plant biomass produced or contributed to potential fossil assemblages; e.g., Smith [2013]) and collection efforts bias, which account for gaps in the fossil record (Locatelli, 2014; Xing et al., 2016). It is more likely that Cenozoic Zingiberaceae expanded their range to include both the tropical and higher latitudes, rather than shifting their range out of the tropics. Although few fossilized Zingiberaceae occur within the tropical distribution of living plants, the climatic data suggest that the higher latitude occurrences of Zingiberaceae are within paratropical climatic conditions, at least for the Cretaceous and Paleogene Zingiberaceae occurrences.

Based on the required range of average MAT and CMMT for environments (Belda et al., 2014; Reichgelt et al., 2018), all living zingiberalean groups have a tropical (CMMT > 18°C) to subtropical (CMMT < 18°C but MAT > 16°C) climatic regime. Zingiberaceae are most diverse and generally distributed in the tropics, although some members can persist in more extreme environments, which is demonstrated by the presence of some Zingiberaceae genera in the Himalayas today (Larsen et al., 1998; Zhao et al., 2016). This ability likely stems from the rhizomatous growth form of Zingiberaceae that allows these plants to withstand harsher conditions (either cold or dry seasons) by dropping their leaves and going into dormancy, remaining solely as rhizomes until favorable conditions return (Larsen et al., 1998).

Based on available data, extinct Zingiberaceae did not experience consistent climatic niches across the Cretaceous and the Cenozoic. Extinct Zingiberaceae occupied a tropical (CMMT > 18°C) to subtropical climatic regime (CMMT < 18°C, but MAT > 16°C) within the Cretaceous, which was sustained through the Eocene but contracted to a temperate climate in the Miocene (MAT < 16°C; Table 4). The Cretaceous and Miocene Zingiberaceae had a much higher MAT and lower CMMT than living Zingiberaceae, while the Eocene Zingiberaceae did overlap with the modern range, albeit at higher latitudes. Low values of MAP outside of the precipitation regime of extant plants may be due to the range of uncertainty within the paleoclimatic models. For example, paleogeography and paleotopography have a

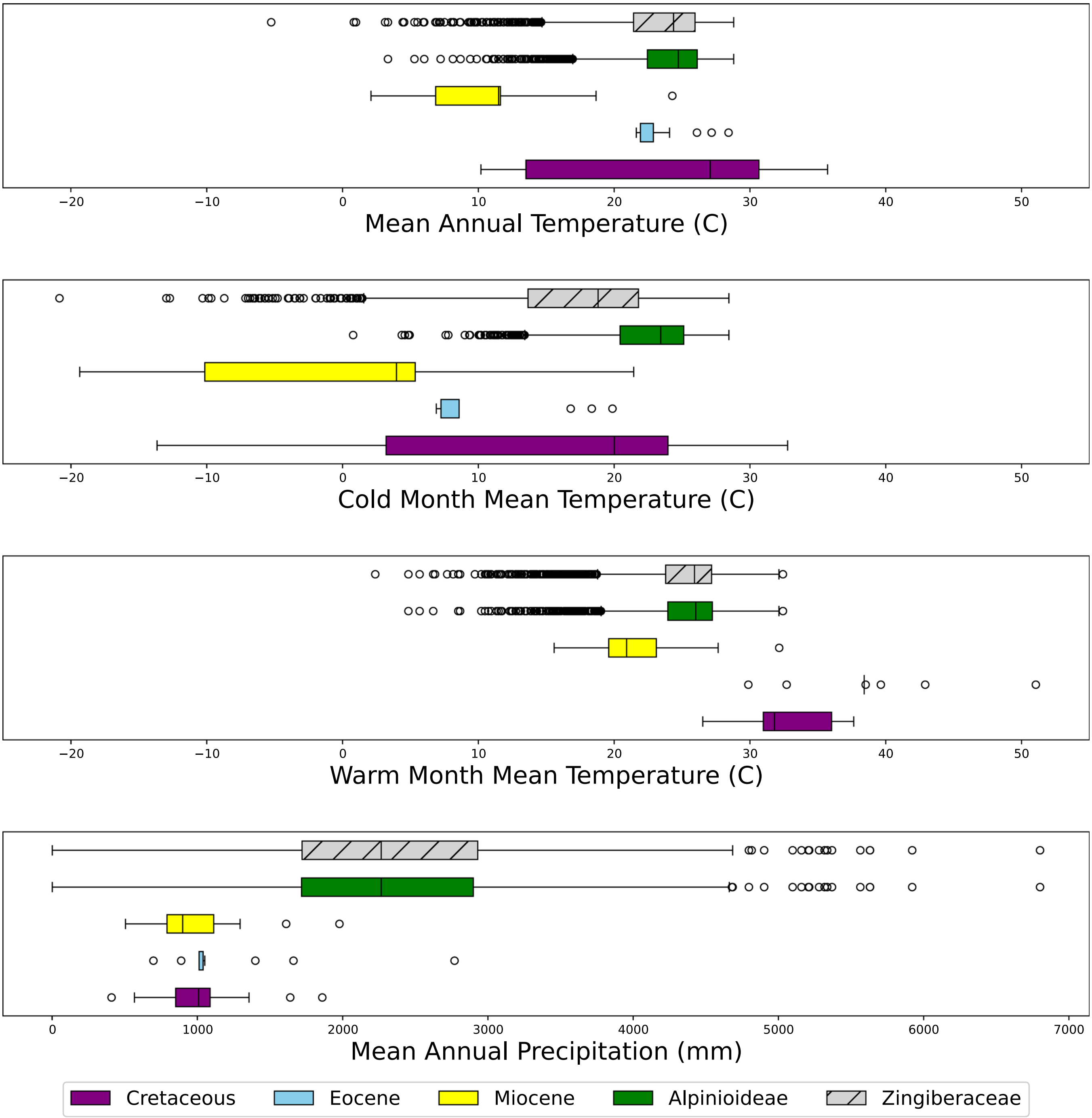

FIGURE 4 Cold month mean temperature (CMMT), warm month mean temperature (WMMT), mean annual temperature (MAT), and mean annual precipitation (MAP) ranges for living and fossil Zingiberaceae and Alpinioideae. Eocene WMMT data is concentrated around 38°C, so there is not a distribution of values for that data set.

substantial impact on MAP and MAT (Lunt et al., 2016; Acosta et al., 2022), and increased MAT of the Cretaceous and Eocene represents an expansion of subtropical dry zone or increased precipitation across the tropics and the high latitudes (West et al., 2015; Acosta et al., 2023; Cramwinckel et al., 2023). Additionally, current climatic models have trouble capturing polar-amplified warming at these higher latitudes, generally have a weaker equator-to-pole temperature gradient than that reconstructed from proxies, and can only provide a certain level of output for higher CO_2 conditions, based on current CO_2 estimates (Burls et al., 2021). Such model-data mismatch also impacts MAP distribution, especially in the subtropics (Acosta et al., 2023; Cramwinckel et al., 2023) and could be the reason why the range of CMMT and MAP for extinct Zingiberaceae do not overlap as much with the range for living Zingiberaceae.

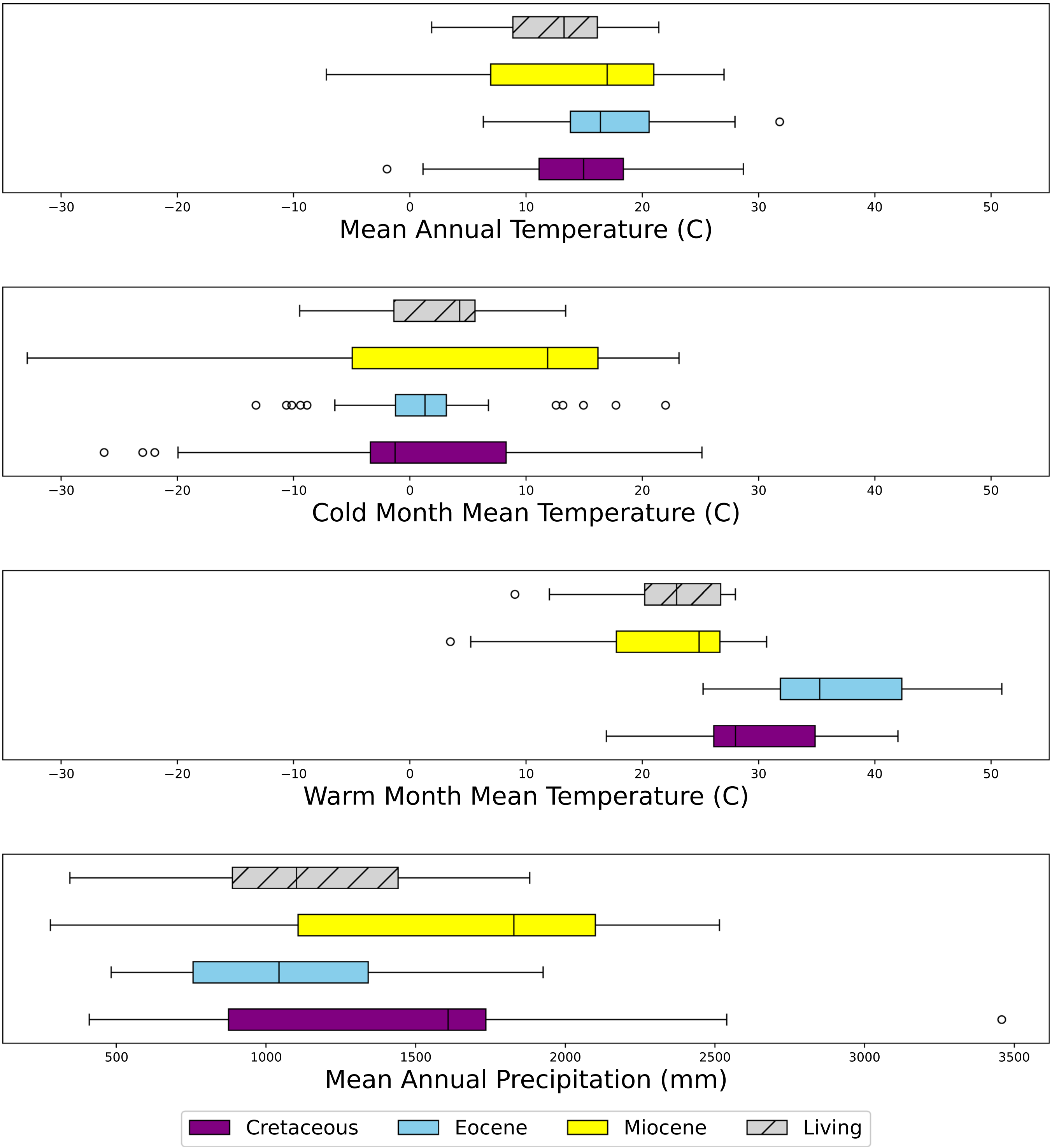

FIGURE 5 Cold month mean temperature (CMMT), warm month mean temperature (WMMT), mean annual temperature (MAT), and mean annual precipitation (MAP) ranges for living and fossil *Metasequoia*; living climatic niche based on occurrences from Liu et al. (2007).

While there is some overlap in the climatic variables between extant and extinct Zingiberaceae, the fossil plants occupied much colder climates than the modern, especially for the Miocene Zingiberaceae (Nikitin, 2007; Fischer et al., 2009). The Miocene Zingiberaceae largely belong to the genus *Spirematospermum*, a morphogroup that existed from the Cretaceous to Pliocene in Eurasia predominantly (Fischer et al., 2009). While probably not the same lineage as modern Himalayan Zingiberaceae (Smith et al., 2018), *Spirematospermum* must have had significant cold tolerance

TABLE 5 Niche dissimilarity metrics, Hellinger's distance *H* and Schoener's *D* between fossil and living occurrences of Zingiberaceae, Alpinioideae and *Metasequoia* for mean annual temperature (MAT), cold month mean temperature (CMMT), warm month mean temperature (WMMT), and mean annual precipitation (MAP). High *H* and low *D* values represent large distance and low overlap between niche spaces, while low *H* and high *D* values represent closer and greater overlapped niche spaces.

Group/Age	MAT *H* (*D*)	CMMT *H* (*D*)	WMMT *H* (*D*)	MAP *H* (*D*)
Zingiberaceae				
Cretaceous-Eocene	0.56 (0.33)	0.66 (0.25)	0.93 (0.03)	0.71 (0.25)
Cretaceous-Miocene	0.45 (0.51)	0.45 (0.49)	0.72 (0.21)	0.25 (0.71)
Eocene-Miocene	0.48 (0.44)	0.72 (0.23)	0.89 (0.05)	0.77 (0.17)
Cretaceous-Living	0.48 (0.47)	0.48 (0.51)	0.63 (0.31)	0.51 (0.38)
Eocene-Living	0.54 (0.36)	0.83 (0.09)	0.9 (0.07)	0.88 (0.08)
Miocene-Living	0.79 (0.13)	0.87 (0.22)	0.5 (0.4)	0.59 (0.33)
Alpinoideae				
Cretaceous-Living	0.51 (0.44)	0.47 (0.22)	0.62 (0.31)	0.51 (0.38)
Eocene-Living	0.56 (0.33)	0.85 (0.08)	0.9 (0.07)	0.88 (0.08)
Miocene-Living	0.81 (0.11)	0.77 (0.15)	0.51 (0.39)	0.6 (0.33)
Metasequoia				
Cretaceous-Eocene	0.18 (0.86)	0.29 (0.66)	0.32 (0.66)	0.23 (0.73)
Cretaceous-Miocene	0.21 (0.75)	0.24 (0.71)	0.37 (0.7)	0.24 (0.74)
Eocene-Miocene	0.23 (0.78)	0.46 (0.45)	0.58 (0.37)	0.38 (0.62)
Cretaceous-Living	0.25 (0.77)	0.26 (0.76)	0.34 (0.65)	0.21 (0.77)
Eocene-Living	0.3 (0.7)	0.32 (0.65)	0.57 (0.4)	0.1 (0.89)
Miocene-Living	0.38 (0.57)	0.44 (0.51)	0.14 (0.85)	0.36 (0.63)

due to their rhizomatous habit (Zhao et al., 2016, 2022). These Miocene plants were not simply representatives of tropical conditions; they were adapting to new climatic conditions in higher latitude areas toward which they had expanded, as shown for woody angiosperms (McElwain, 2018; Shiono et al., 2018), although this lineage is now extinct. This interpretation of Miocene niche suggests that even if distributions of Zingiberaceae were present in lower latitudes of the past, the expansion from only tropical to including temperate occurrences still demonstrates a large shift in range driven by adaptation to new climatic niches. The decrease in global CO_2 (especially in the Neogene) likely stimulated extinct Zingiberaceae to adapt to much colder annual conditions at higher latitudes compared to the general climatic niche of their modern relatives in the tropics.

The niche dissimilarity metrics also suggest that the climatic niche among extinct and extant Zingiberaceae was inconsistent across time. The probability density function plots for MAT, WMMT, and CMMT especially confer this dissimilarity since the niche space among the occurrence groups are far apart from each other and hardly overlap (Figure 6). Distant niche areas (high *H* values) and less overlap (low *D* values) indicate high dissimilarity (Antell et al., 2021) in temperature constraints across geologic time and compared to both living Alpinioideae and Zingiberaceae. The MAP generally follows this same trend, with the exception of the Eocene when there is much higher density proportionally to the other geologic periods perhaps due to topography; the Eocene fossils include a significant number of occurrences in the rainshadow of the Rocky Mountains (which would account for lower MAP in these areas, although we note that the fossils are preserved in lacustrine depositional environments), while the Cretaceous and Miocene fossils occurred in more tropical environments and across Eurasia, respectively (Wing et al., 2005; Currano, 2008; Zhu et al., 2020).

Limitations with fossil Zingiberaceae preservation

Although the results suggest labile climatic niches for Zingiberaceae across geologic time, the family is limited by preservation bias. Most occurrences are recorded from the northern hemisphere, with Europe having a majority of the Miocene occurrences, and the Eocene occurrences are clustered around a couple North American fossil localities

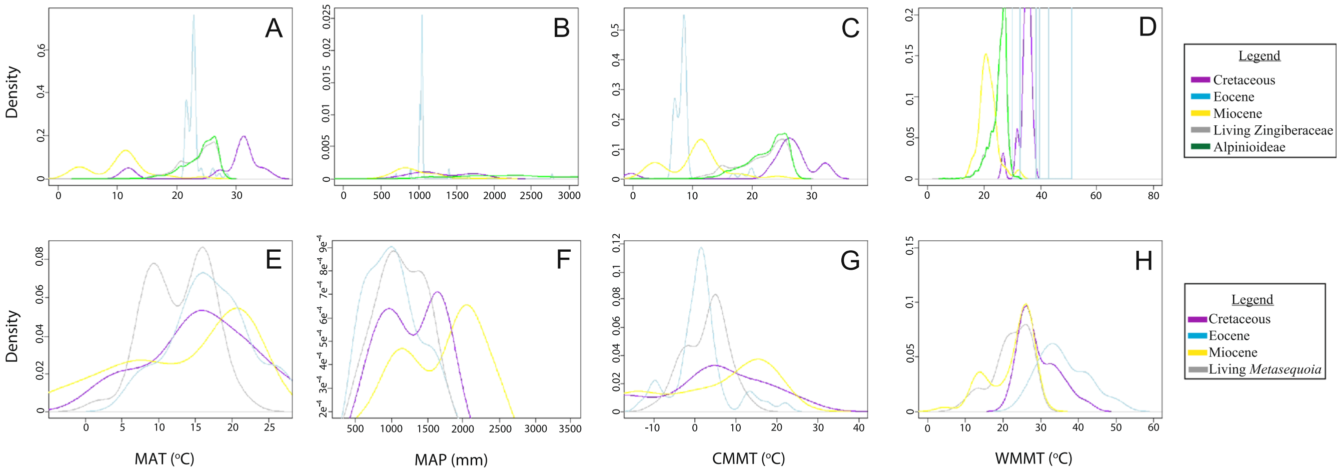

FIGURE 6 Probability density function plots for climatic variables for (A–D) living and fossil Zingiberaceae and (E–H) *Metasequoia*. (A, E) Mean annual temperature (MAT), (B, F) mean annual precipitation (MAP), (C, G) cold month mean temperature (CMMT), (D, H) warm month mean temperature (WMMT).

(Figure 1; Wing, 1984; Wilf, 2000). However, the absence elsewhere may be due to the lack of discovery of other potential fossil sites that could preserve Zingiberaceae. Additionally, the climatic conditions and resulting distributions from the fossils can be argued to reflect that equivalent conditions from the past no longer exist today, especially paratropical conditions at higher latitudes. Much of the tropical climates during the Cretaceous and Paleocene reached exceedingly warm temperatures, and while ancient plants were able to persist and diversify, modern ecosystems are notably constrained by heat stress (Jaramillo et al., 2010; Morley, 2011; Zhang et al., 2019; Klages et al., 2020; Yin et al., 2023). The warmer climates of greenhouse worlds allowed for plants to occur at higher latitudes, outside of their present distributions (Shiono et al., 2018). Even during the global cooling of the Neogene, some areas may have experienced microenvironments to act as climate refugia, providing the needed (sub)tropical conditions for these plants to persist in much higher latitudes (Martinez et al., 2021; Quirk and Hermsen, 2021). Our finding of an expanded niche in the Neogene suggests that these extinct Zingiberaceae could survive cooler climates once they had reached these higher latitudes.

To address this problem of preservation likelihood, niche modeling estimation analysis like Maxent (Phillips and Dudik, 2008) could be used to infer what other Eocene environments might have been suitable for Zingiberaceae and test whether known Eocene fossil localities overlap with these estimations, and if Zingiberaceae are preserved. However, using niche modeling estimation analysis to estimate other potential fossil Eocene occurrences of Zingiberaceae comes with some caveats. First, because the climatic constraints of the Zingiberaceae family are not consistent across time, the living environmental data (e.g., MAT, MAP) may not be the best with which to infer which Eocene environments could have had Zingiberaceae. Second, there is disagreement over what time scales niche models can be applied: Some studies suggest that only living or geologically recent (late Pliocene at oldest) data sets are suitable (Lima-Ribeiro et al., 2015; Eduardo et al., 2018), while others have used older data sets, such as from the Cretaceous (Chiarenza et al., 2019, 2020). Future work could examine predicted occurrences from paleoclimatic modeling of the family and other herbaceous plants, which have lower likelihoods of preservation, which could be used to identify if suitable rock types exist, of the right age, to be prospected for new fossils. While this approach would be less effective for taxa with shifting niche breadth/space, even for them it could help identify localities where they would be expected to be found and help add new occurrences (which could be useful for other kinds of analyses, e.g., disparity analysis) or identify other limiting factors to that taxon's distribution (if not found where expected). As with all modelling, such a model will not be able to predict novel niches, which is why broader prospecting to find new fossil localities is also needed.

It is also difficult to assess the significance of the absence of Zingiberaceae throughout the fossil record. We attempted to identify a plant group that consistently co-occurred with Zingiberaceae in the fossil record using a literature review. While some fossils of Zingiberaceae (i.e., Paleocene *Zingiberopsis* of North America) were documented to be associated with ferns like *Lastria goldiana* (Hickey and Peterson, 1978), other occurrences in the geologic record do not establish similar, repeated co-occurrences with this group (Meyer and Manchester, 1999; Peppe et al., 2007; Benedict, 2012; Table 1). It could be that Zingiberaceae, and other monocots, are isolated occurrences in the fossil record due to low prevalence in past environments (Meyer and Manchester, 1999; Kunzmann, 2011) although they appear to have been locally abundant at some localities (e.g., Fischer et al., 2009; Wing et al., 2012).

The climatic niche of *Metasequoia* underwent less change across time

Fossilized *Metasequoia* shows a much more consistent climatic niche based on the paleoclimatic models. *Metasequoia* had a temperate climatic niche first in the Cretaceous, which was sustained through the Eocene and Miocene and conserved to the modern day. All climatic variables for the fossil taxa align closely with data for the extant taxa. This close alignment is supported by the niche dissimilarity metrics. In each of the climatic variable plots (Figure 5), the climatic distributions of *Metasequoia* from different time periods were highly overlapping, suggesting that the climatic niche for *Metasequoia* was conserved across geologic time. Some, however, like Miocene and living CMMT, were more distant in niche space than the other variables, but we attribute this difference based on living *Metasequoia* having a highly restricted geographic distribution and a portion of the data set contained cultivated plants outside of their limited native range (Liu et al., 2007).

Conflicts over fossil Zingiberaceae taxonomy and comparing results with other studies

We acknowledge that making assertions on extinct Zingiberaceae and climatic niche conservatism (or lack thereof) is less than ideal due to the current inability to taxonomically assign many of the fossils further than the family level. Taxonomy of fossil Zingiberaceae currently reflects temporal, spatial, and organ distinctions in addition to morphological differences (Hickey and Peterson, 1977, 1978; Benedict, 2012; Smith et al., 2018). The oldest Zingiberalean fossils are from North America (Friis, 1988), and Cretaceous through Paleogene Zingiberaceae are predominantly found in North America (as leaves; Hickey and Peterson, 1978; Peppe et al., 2007), while Neogene Zingiberaceae are primarily recovered from Eurasia (as reproductive structures; Fischer et al., 2009; Kunzmann, 2012). Some significant overlap in geographic distributions did exist for Oligocene Zingiberaceae between North America and Eurasia, likely from the North American–Eurasian Land Bridge linking the two continents (Milne, 2006; Denk et al., 2010), though they are mostly restricted to Eurasia (Bozukov et al., 2009; Kunzmann, 2012). Fossil Zingiberaceae are also taxonomically distinguished by plant organ type, specifically leaves (*Zingiberopsis*, *Zingiberoideophyllum*, and *Zingiberites*; Hickey and Petersen, 1978; Wilf et al., 1998; Peppe et al., 2007; Kunzmann, 2012; Flynn and Peppe, 2019; Narita et al., 2020) and fruits/seeds (*Spirematospermum*; Chandler, 1925; Koch and Friedrich, 1971; Mai and Walther, 1985; Van der Burgh, 1987; Friis, 1988; Kvaček, 1998; Fischer et al., 2009). There is speculation that these different morphotaxa together might represent a “natural” (biological, whole-plant) taxon (Fischer et al., 2009; Kunzmann, 2012; S. Y. Smith, personal observations) and would then be more akin to other genera used in paleoclimatic reconstructions. While we chose to treat fossils of Zingiberaceae as a singular morphogroup, we acknowledge that this designation violates many assumptions and principles of taxonomic-based paleoclimatic reconstruction methods (Utescher et al., 2014; Harbert and Nixon, 2015) that are typically constrained to genus- or species-levels. Thus, our interpretation here is, by necessity, more conservative. Extant Zingiberaceae are highly diverse and have a wide range in the modern climate (as we demonstrate above), but the discontinuity of specific formally recognized extinct Zingiberaceae species and ambiguity of what represents a “natural” taxon renders it rather difficult to discern species-specific climatic niches. Future work on the fossil record of this plant family will focus on resolving taxonomic divisions.

Because *Metasequoia* is monotypic today and has few fossil species, this group is more easily comparable to other studies than extinct Zingiberaceae. Our results of a conserved climatic niche for *Metasequoia* largely follows how other woody tree groups fared in the upper latitudes through the Cenozoic, especially as global temperatures decreased in the Neogene (Pennington et al., 2009; Shiono et al., 2018; Vieira et al., 2023). This similarity is also shared with late Quaternary palynological studies, with conifer species generally not experiencing severe climatic niche shifts (Pearman et al., 2008; Cheddadi et al., 2016). While this study does not focus much on the late–recent Cenozoic (i.e., Pliocene-Pleistocene-Holocene), there is a high number of Quaternary *Metasequoia* occurrences in the literature (LePage et al., 2005), and these could prove useful in determining more complete and near-time patterns in plant climatic niches (Chevalier et al., 2020; Kirschner et al., 2022). Based on the results of this study, we hypothesize that even though geographical and taxonomic diversity were severely reduced during this time interval (Jagels and Equiza, 2007), the Pliocene and Quaternary climatic niches for *Metasequioa* would still be temperate (thus conserved through near and deep time). However, our study has shown that having a strongly conserved climatic niche is potentially a drawback under changing conditions. Thus, *Metasequoia* likely was restricted to specific, high-elevation populations from the Quaternary to today due to lack of climatic niche adaptation (and likely along with different plant competitors as ecosystems shifted).

Using Zingiberaceae vs. *Metasequoia* for taxonomic-based and morphological paleoclimatic reconstructions

The results from this study allow us to partially reject our null hypothesis: The climatic niche was not conserved for Zingiberaceae over geologic time, but that of *Metasequoia* was well-conserved. As such, we caution against using fossil Zingiberaceae for taxonomic-based paleoclimatic reconstructions like nearest living relative or the coexistence approach (Mosbrugger and Utescher, 1997; Greenwood et al., 2003, 2017; Utescher et al., 2014; Hyland et al., 2018). First, although we included a significant percentage of fossil occurrences of Zingiberaceae of the Cenozoic, there are still a substantial number of Paleocene and Oligocene fossils (Dorofeev, 1963; Kunzmann, 2012; Flynn and Peppe, 2019; Flynn, 2020) that were not included because of a lack of appropriate paleoclimatic simulation data. Including these occurrences in future studies could refine our understanding of long-term patterns in niche shifts. Second, using only a portion of the living niche removes other habitable areas for these plants to persist. We specifically show that Miocene Zingiberaceae (*Spirematospermum* sp.) grew in colder environments compared to the average Zingiberaceae today and compared to pre-Miocene *Spirematospermum*, but comparable to those of the Himalayan Zingiberaceae (MAT: −5.2 to 25°C, CMMT: −13 to 19°C, WMMT: 2.4–30°C; Benedict et al., 2016; Zhao et al., 2016). Thus, if just the warm (sub)tropical portion of the living niche was used, this colder niche portion would not be represented (Smith et al., 2012, 2015; Li et al., 2018). Due to the wide range of habitable climatic zones Zingiberaceae occupy, we deem Zingiberaceae unfit for this type of paleoclimatix reconstruction. In contrast, *Metasequoia* represents a better candidate for taxonomic paleoclimatic reconstructions due to their more consistent climatic niche (Wang et al., 2019; this study). Leaf water-use efficiency and other leaf traits within the genus show strong correlations with carbon dioxide in the fossil record, which provides useful information on climate–plant relationships for fossil occurrences of *Metasequoia* in the geologic past (LePage et al., 2005; Sheldon et al., 2020). One caveat for using this group as a paleoclimatic proxy is that some individual fossil species, extinct in the modern day, do show a potential shift in preferences (*Metasequoia milleri*, Ng and Smith, 2020, although this species is known only from a single locality). Future testing focused on other plant groups with more species and a broader fossil distribution can better ascertain the consistency of inferred niche conservatism in woody plants.

The observed dissimilarity in Zingiberaceae climatic niche through time compared to the more conserved *Metasequoia* climatic niche is consistent with the idea that plant growth and reproductive strategies may play a larger role in niche evolution and conservatism (Smith and Beaulieu, 2009; Donoghue and Edwards, 2014; Zanne et al., 2014). Compared to woody gymnosperms, the quicker life cycles of herbaceous Zingiberaceae would allow for faster distribution to higher latitude areas (Liu et al., 2007; Xu and Chang, 2017). *Metasequoia* is restricted by their reproductive maturity since they will not successfully produce viable seeds until they are at least 15 m tall, which takes approximately 25 years (Vann, 2005; Tang et al., 2011). A subset of Zingiberaceae plants can enter a dormant rhizome state in unfavorable conditions, an ability that may have granted the extinct members of the group to expand both their latitudinal distributions and climatic niche over time through a higher persistence in more extreme environments (Branney, 2005; Zhao et al., 2016; Wang et al., 2019). Some living Zingiberaceae have retained this trait of tolerating freezing climates: several *Roscoea* species are reported to tolerate a minimum temperature of −20° to −25°C, and some other taxa (e.g., *Hedychium*, *Zingiber*) are close to that also (Branney, 2005). In this case, as climates became colder globally in the late Miocene, and reached a critical threshold of CMMT (−10°C; Wing and Greenwood, 1993; this study), we hypothesize that some Zingiberaceae lineages tracked the (sub)tropical climatic niche, resulting in a constricted geographical distribution, similar to niche changes inferred for woody dicots (Shiono et al., 2018). Other lineages (in both Zingiberoideae and Alpinioideae) were able to adapt to the new cooler temperatures, including *Spirematospermum*, and later descendants either returned to (sub)tropical areas or diversified in temperate areas. For example, *Hedychium* is a cold-tolerant, dormancy-experiencing genus thought to have originated and diversified in the late Miocene, but with one derived clade that lacks dormancy (Ashokan et al., 2022). Refinement of the Zingiberaceae fossil record and combining it with geologic and phylogenetic data will provide future insights into which lineages may have retained vs. newly originated cold tolerance, but our climatic niche modelling here supports that this ability was present in Zingiberaceae since at least the Miocene. While adult plants may be more frost-tolerant, seedlings and young plants might have different needs (Wing and Greenwood, 1993) and thus represent a different barrier to maintaining a steady, genetically diverse population in declining Neogene temperatures.

Hypothetical taxa for future climatic niche studies

Other potential plant taxa could provide additional insight on climatic niche conservatism. Suitable woody plant analogs include *Quercus* sp. (oaks) and *Acer* sp. (maples) since both groups have a widespread spatial living distribution and a long temporal fossil record, similar to *Metasequoia* (Kvaćek and Walther, 1989; Manchester, 1994; Gao et al., 2020). While Arecaceae (palms) are technically non-woody flowering plants, their growth form and reproductive strategies are more similar to *Metasequoia* than to Zingiberaceae. As such, the fossil and living distributions of Arecaceae could bring useful comparisons on climatic niches since these plants are found in both the northern and southern hemispheres (Pan et al., 2006; Hartwich et al., 2010; Thomas and De Franceschi, 2012; Reichgelt et al., 2018; Matsunaga et al., 2019). A drawback to palms, though, is that more taxonomic precision is needed for many fossils before future studies can be done; many are placed in form genera or lack characters diagnostic of a subfamily, tribe, or genus. Finding a suitable analog for Zingiberaceae that has a similar temporal and spatial fossil record is more difficult, especially since macrofossils are rarer than typical occurrences of microfossils (pollen). Living Poaceae (grasses) are found worldwide and have a sufficient spatial and temporal distribution in the fossil record through well-preserved phytoliths, although microfossils (pollen and phytoliths) can be transported much farther from source compared to macroremains, and thus, there can be more uncertainty in determining their exact geographic origin (Prasad et al., 2011; Jiménez-Mejías et al., 2016; Strömberg et al., 2018; Wu et al., 2018; Gallaher et al., 2022). The main issue with using other herbaceous fossil groups for this analysis is that there is an insufficient macrofossil record for individual genera. Manchester et al. (2015) explored the fossil record of Asteridae (asterids), one of the largest groups of extant flowering plants, and found that most of its families and genera had many pollen occurrences and fewer macrofossils (if any). Until we find a fossil record of an herbaceous flowering plant that would fit the requirements laid out in our study, Zingiberaceae appears to have the best macrofloral record for examining geological-scale climatic niche shifts in herbaceous flowering plants.

CONCLUSIONS

The wide spatial, temporal, and climatic fossil distribution of an herbaceous flowering plant family, Zingiberaceae, in combination with paleoclimatic model data, suggests that its paleoclimatic niche has changed through time, and therefore that climatic niches are not necessarily conserved on geological time scales. The paleoclimatic niche of Zingiberaceae shifted over time from strictly subtropical to expanded temperate climates during exceedingly warm climatic periods across the Cretaceous and Cenozoic. In contrast, we inferred a more consistent temperate climatic niche for *Metasequoia*. This discrepancy can be explained at least in part to be due to plant growth form, because we demonstrated that an herbaceous taxon (Zingiberaceae) experienced climatic niche expansion while a woody taxon (*Metasequoia*) experienced niche conservatism. Our evidence for large differences in living and past climatic niches for Zingiberaceae is from the group's largest geographic and temporal distribution and varying climatic zones, which contradicts the living-past plant niche assumptions of niche conservation theory. These aspects are corroborated by extensive paleoclimatic modelling efforts presented in this study. While caveats remain about biases and assumptions regarding geographic fossil occurrence data (i.e., Zingiberaceae) and paleoclimatic model validity, these results demonstrate the potential utility of this combined approach. These hypotheses can be further tested in the future as researchers refine fossil systematics and address model "correctness." The discovery of new fossil occurrences of Zingiberaceae and the inclusion of other plant groups in this type of study will provide a greater framework of how climate has influenced different plants across geologic time.

Consequently, for groups that have life history traits amenable to more rapid evolution, testing for—rather than assuming—niche conservatism is recommended to strengthen estimates of paleoclimates, reconstructions of paleoenvironments, and understanding of plant evolutionary history. This kind of work testing for paleoniche conservatism also demonstrates the latent ability of a plant species to rapidly adapt (or not) to shifting climatic regimes. Ultimately, with more examples of when climatic niches are conserved (or not), we can begin to identify the processes responsible for these patterns, which could help predict how a plant species will react to current anthropogenic climatic changes and inform conservation practices.

AUTHOR CONTRIBUTIONS

Z.J.Q. and S.Y.S. conceptualized the study and collected the fossil occurrences. Z.J.Q. collected and analyzed data and wrote the manuscript with feedback from S.Y.S., R.P.A., and C.J.P. R.P.A., and C.J.P. created and provided the paleoclimatic model results. R.P.A. created Figure 3.

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DATA AVAILABILITY STATEMENT

All data from this study are provided in the manuscript figures, tables, and supplementary materials. Coding script for the niche dissimilarity is also included (Appendix S5). Inquiries can be sent to the corresponding author. Paleoclimatic simulation data sets used in this study are in the University of Michigan, Deep Blue Repositories (Acosta et al., 2022). The data sets are available in NetCDF format.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Paleoclimatic data for Zingiberaceae and *Metasequoia* used in this study; Cretaceous and Eocene models were run at 1700 ppm CO_2, Miocene models at 400 ppm CO_2.

Appendix S2. Paleoclimatic data for Zingiberaceae and *Metasequoia*; model was run at 280 ppm.

Appendix S3. Paleoclimatic model comparison with proxy data from the literature.

Appendix S4. Climatic data (from WorldClim; Hijman et al., 2017; WorldClim, 2021) for living Zingiberaceae and *Metasequoia*.

Appendix S5. Code to calculate Hellinger distance (*H*) and Schoener's *D* for determining niche dissimilarity.

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