GEOSCIENCES

Is the East Asian flora ancient or not?

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ABSTRACT

The East Asian flora (EAF) is a key biodiversity hotspot for understanding the origin and evolution of Northern Hemisphere floras, but there is an ongoing debate on whether it is a museum or a cradle for seed plants. Within the EAF, two main floras, the Sino-Himalayan Flora (mainly the *Rhododendron* Flora) and the Sino-Japanese Flora (mainly the *Metasequoia* Flora), have been recognized. Previous studies suggested that the EAF is ancient and the *Metasequoia* Flora is older than the *Rhododendron* Flora. To test this hypothesis, we synthesized molecular as well as fossil data on seed plants, focusing on the biogeographical origins and historical evolution of the EAF. We compared the ages of its two constituent floras, and examined the impact of the Asian monsoon and other environmental changes on the development of EAF through meta-analysis. Our results suggest that the EAF might be relatively young, with most of its clades originating since the Miocene. The *Rhododendron* Flora and the *Metasequoia* Flora are probably of a similar age. The formation and development of the Asian monsoon might have been the main factors that have driven the evolution of EAF. In the *Rhododendron* Flora, the north-south mountain chains increased the concentration of species and reduced extinction, and the barriers between the east and west have resulted in species differentiation, which triggered it to become a diversity center. The EAF appears to have multiple biogeographical origins, having closely affiliated not only with other floras in the Northern Hemisphere, but also with Gondwanan floras.

Keywords: Asian monsoon, East Asian Flora, *Metasequoia* Flora, *Rhododendron* Flora, temporal and spatial evolution

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INTRODUCTION

The assembly of the temperate forest floras of the Northern Hemisphere over time have attracted much attention from botanists and biogeographers [1,2]. These forests are thought to represent Cenozoic relict floras, derived from plant communities once widely distributed across a large part of the Northern Hemisphere during the Cenozoic, which have now developed in the warm and humid areas of North America, Europe and East Asia (EA) due to historical climatic and geological changes [3,4]. Because the greatest plant species diversity and many Cenozoic relict seed plants occur in EA, including *Tetracentron*, *Cercidiphyllum*, *Davidia*, *Trochodendron*, *Euptelea*, *Ginkgo*, *Cathaya* and *Metasequoia*, many botanists consider EA to be a key area if we are to understand the origin and evolution of the Northern Hemisphere temperate forest floras [5–8]. There are more than 600 endemic genera and 31 endemic families in EA and, as a result, Wu and

Wu (1996) proposed the former 'Eastern Asiatic region' to be an independent floristic kingdom, the 'East Asiatic floristic kingdom'. This can be subdivided into two main subkingdoms: the Sino-Japanese forest subkingdom including part of North China, subtropical China (Central/South/East), the Korean Peninsula and the Japanese Archipelago, but excluding the tropical parts of South China; and the Sino-Himalayan forest subkingdom mainly including the Yunnan Plateau, East Himalayas and Hengduan Mountains [7,9]. This floristic kingdom covers a large part of EA and exhibits quite complex topographical and climatic characters. Profoundly impacted by the seasonal Asian monsoon climate [7,10], this region contains large mountain systems (Himalayas, Hengduan Mountains), high plateaus (Qinghai-Tibet Plateau, Yunnan-Guizhou Plateau), deep river gorges (Yangtze-Salween-Mekong—the 'three river gorges') in the west, and extensive plains and relatively small

mountains (such as Wuling Mountains, Qinling Mountains, Daba Mountains, Dabie Mountains) in the east, with the altitude ranging from approximately 20 to 5000 m and the latitude roughly from 22N° to 45N° [11].

EA harbors most families of gymnosperms of the world and a large number of angiosperm families, including phylogenetically primitive and advanced ones [8]. According to the most recent classification system, 75% of families of extant gymnosperms [12] and more than 60% of angiosperm families (258 of 416) of the Angiosperm Phylogeny Group (APG) can be found in EA [13]. Furthermore, the East Asian flora (EAF) has higher species diversity (more than 3000 genera) than other regions of the Northern Hemisphere, e.g. North America [14,15]. In addition, it has high plant endemism, including paleoendemic and neoendemic genera, most of which are monotypic or oligotypic [7,11]. However, plant diversity is not evenly distributed across the EAF: there is high species diversity in the east warm-to-cold temperate mountains and low-plain areas, low species diversity in the high west cold-dry and snowy regions of the Qinghai-Tibet Plateau (QTP) and the greatest plant diversity in the 'intermediate belt' of Southwest China, which comprises a mosaic of plateaus, mountains, basins and river valleys [7,9,10]. According to previous studies, the Sino-Himalayan subkingdom is considered to have been an important diversification and distribution center for the temperate flora in EA and even the Northern Hemisphere, with most neoendemic taxa of the EAF and many of the largest north temperate genera such as *Rhododendron*, *Primula*, *Pedicularis*, *Corydalis*, *Saxifraga*, *Gentiana* and *Saussurea* concentrated in this region [16,17]. According to our database, the Sino-Himalayan region is the diversification and distribution center for more than 80% of the large genera of China (i.e. those containing more than 100 species; see details in Appendix 1). However, the Sino-Japanese subkingdom is generally considered to be a relic or survival center for seed plants in the Northern Hemisphere, with most paleoendemic lineages or living fossil taxa such as *Metasequoia*, *Cathaya*, *Ginkgo*, *Pseudolarix*, *Trochodendron*, *Eucommia*, *Davidia* and *Cercidiphyllum* located in this area [11].

Here we use the term '*Metasequoia* Flora' to represent the core area of the Sino-Japanese flora [18,19], since the living fossil plant *Metasequoia glyptostroboides* is one representative of the relics or living fossil lineages that are found in this area. Similarly, we also propose the term '*Rhododendron* Flora' to better represent the core region of the

Sino-Himalayan flora, as *Rhododendron* is the largest genus with a significant center of diversity in this region, plus it is representative of the flora in this area (Fig. 1).

The key to understanding a floristic region clearly is to investigate where it originated and how it assembled over time. The accumulation of molecular phylogenetic data over the past decades has provided detailed evidence of phylogenetic relationships, ages and the biogeographical origins of floras [20,21]. Recently, many studies have focused on the assembly of floristic regions or specific biomes, such as the Australian flora [22–24], the African flora [25,26], the Amazonian forest flora [27], the flora of Madagascar [28], the Andes island forest flora [29] and the Californian flora [21]. This has been achieved by integrating molecular phylogenetic data (molecular dating, biogeography) and Palaeo-environmental evidence at different spatial and temporal scales.

As a natural floristic region, it has been proposed that the evolution of the flora of EA was greatly affected by historical climatic and geological changes during the Cenozoic (the last 65 Ma) [4]. Global climate fluctuations, including warming, cooling, aridification and Quaternary glaciation [4,30,31], as well as geographical changes such as the disappearance of the Bering and North Atlantic Land bridges, the closure of the Turgai Strait, the retreat of the Tethys Sea, the collision of the Indian subcontinent with the Asian continent and the uplift of the QTP [3,4,32–34] have changed this flora profoundly. Although many climatic and geographic factors have been proposed to correlate with the formation of the EAF, some questions still needed to be discussed. As many living fossil plants (Cenozoic plant relics) only occur in EA today, many researchers have suggested that the EAF is an ancient flora [35–39] and that it is the cradle of North American, European floras and even the modern Paleo-tropical flora [11,40]. In addition, EA has also been considered to be the center of origin and/or diversification of angiosperms [11,38,39]. However, the absence of old fossils of these living fossil plants in EA [41] may challenge this hypothesis, and many botanists, especially Chinese botanists, have mistakenly considered Southwest China as the center of origin of these paleoendemic or relic genera, since they are currently still being distributed across these regions [42]. In addition, as most paleoendemic taxa of the EAF occur in the *Metasequoia* Flora and neoendemic taxa are concentrated in the *Rhododendron* Flora, previous studies have suggested that the *Metasequoia* Flora is older than the *Rhododendron* Flora [7,43]. However, this suggestion is only based on the distribution of endemic taxa, which are difficult to
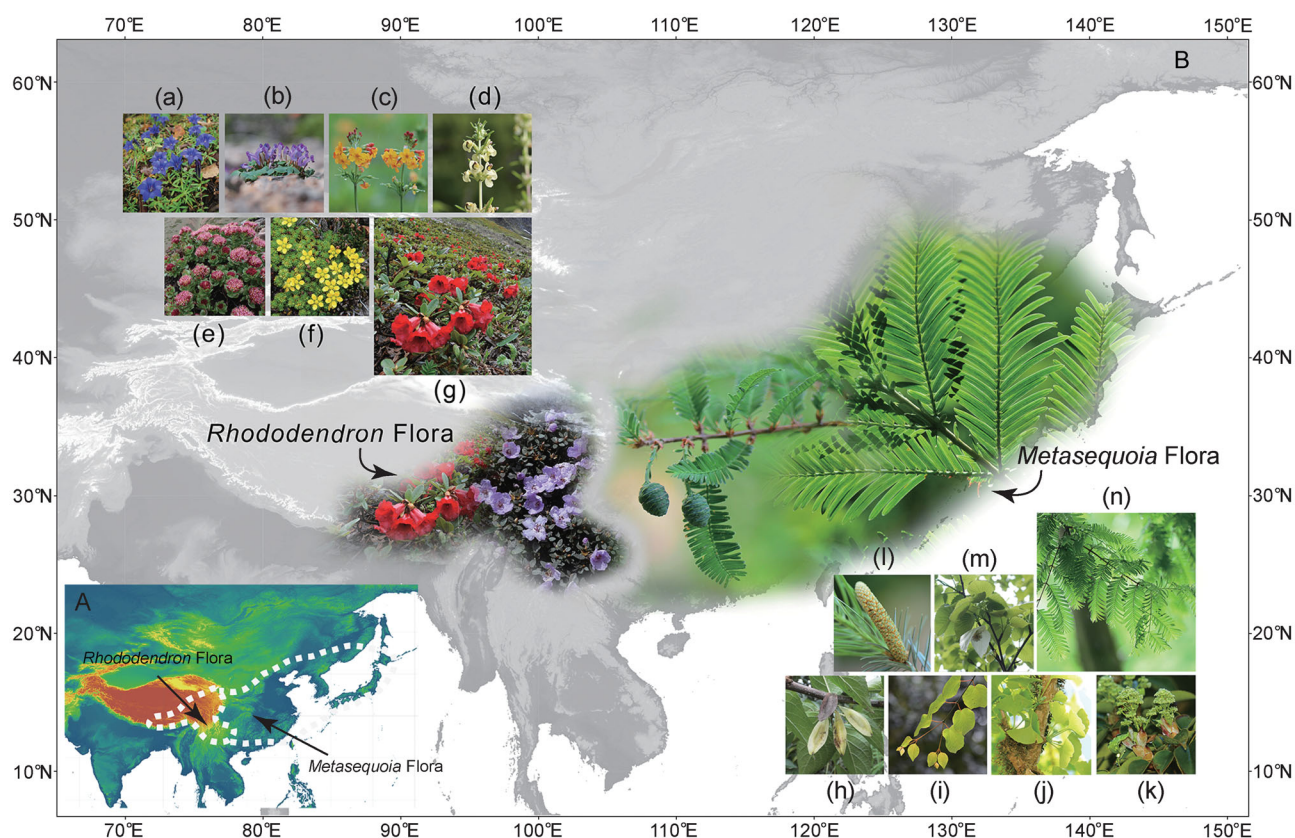
Figure 1. Floristic regions of the Eastern Asiatic Floristic Kingdom and its two subkingdoms [(A) and (B)] based on Wu and Wu (1996) [7]. White dashed lines (A) demarcate boundaries of the two floristic subkingdoms. Photos of representative living plants (B) for each subkingdom: (a) *Gentiana*, (b) *Corydalis*, (c) *Primula*, (d) *Pedicularis*, (e) *Rhodiola*, (f) *Saxifraga*, (g) *Rhododendron*, (h) *Eucommia*, (i) *Cercidiphyllum*, (j) *Ginkgo*, (k) *Trochodendron*, (l) *Cathaya*, (m) *Davidia*, (n) *Metasequoia*.

evaluate because they lack closely related sister taxa in other regions that could be analysed for molecular divergence estimates. Furthermore, many botanists insist that the *Rhododendron* Flora is a diversity center for many large genera of the Northern temperate zone and that it supports much greater species diversity than the *Metasequoia* Flora [16,43]. However, the formation mechanism that may explain this is limited.

In this study, we first synthesized published molecular phylogenetic data as well as fossil information on seed plants, focusing on the biogeographical origins and historical evolution of the EAF. Our aims were: (i) to test whether the EAF is as old as previously thought; (ii) to compare clade ages within the *Metasequoia* Flora to those within the *Rhododendron* Flora, from which we can trace the evolutionary history of the EAF spatially and temporally by integrating these datasets with paleoenvironmental studies that are related to this area; (iii) to explain the unequal distribution of plant diversity in these two floras; and (iv) to determine the biogeographical origins of the EAF.

RESULTS FROM BIOGEOGRAPHIC SCENARIOS

Data acquisition

To obtain datasets pertinent to the ages and biogeographical origins of the EAF, we collected data from published molecular phylogenetic and biogeographical studies as well as from our own studies (including research on *Adenocaulon*). The following criteria were applied: representatives from the EAF should be included, and the ages and the ancestral areas of these representatives should be available. In total, 213 clades of seed plants (species, genera or family level) were then used in our study (see details in Appendix 2), representing 203 genera and 81 families of seed plants, with two families of gymnosperms. The angiosperm families in this study were evenly distributed throughout the APG phylogenetic tree, with almost every major clade sampled, covering 36 of the 64 orders [13].

To confirm the origin time of the EAF from a different perspective, we also collected fossil data by focusing on the first appearance time of East Asian

endemic genera in the EAF according to previous studies [19,41] (see details in Appendix 3).

Clade coding and area definitions

The 213 clades were assigned to different floristic elements according to the distribution of most species from each clade, using a clade-based approach at the level of family, genus or species. For example, we treated *Cyananthus* as one of the floristic elements of the *Rhododendron* Flora, since most species of this genus are found in this area, and we considered Stachyuraceae as a constituent of the whole EAF due to its broad distribution over the whole of EA. We classified the 213 clades into three elements: the *Rhododendron* floristic element (45 clades), the *Metasequoia* floristic element (50 clades) and the East Asian element (both regions; 118 clades) (see details in Appendix 2).

The biogeographical origins inferred for each clade were attributed to specific geographical areas, determined by consulting original studies and floristic region definitions, but with some adjustment. We split these origin areas into two categories: Laurasian and Gondwanan. The Laurasian category include five sources: Arctic/Boreal origin, North American origin, East Asian origin, Tethyan origin, tropical Asian origin and Northern Hemisphere unknown origin (ancestral area ambiguous or the range is beyond the geographical scope of the floristic region above). Similarly, the Gondwanan origin could be classified into four sources: African origin, Australian origin, South American origin and Southern Hemisphere unknown origin (see details in Appendix 2).

Divergence time

The origin time (stem ages) of the clades of the EAF, *Rhododendron* Flora and *Metasequoia* Flora was obtained from the original literature. The most common time used here is the time of the split between an East Asian taxon and its close relatives; this was used when available. When this time was not available, we employed a proximate time to represent the origin time of a clade. For example, we used the diversification time (crown time) of a large clade (including taxa from EA and other places) as the origin time of the East Asian clade (See details in Appendix 2).

Meta-analysis

We calculated the mean and median values of origin times for all the lineages of the EAF, lineages of the *Rhododendron* Flora and lineages of the *Metasequoia*

Flora. To compare the ages of the *Rhododendron* Flora and *Metasequoia* Flora, the difference in origin time between the two lineages was also tested using an independent sample *t*-test (SPSS ver. 21). The median ages of the EAF and other floras of the world such as the South African flora (56 clades) [25], the Andes flora (30 clades) [29], the Amazonian flora (23 clades) [27], the Californian flora (97 clades) [21] and the Australian flora (57 clades) [23] were also compared, using the data provided in these studies.

When attempting to understand a flora's evolutionary history, it is important to trace its biogeographical origins. Using the criteria for the area definition mentioned above, we grouped the ancestral areas of the EAF into two large categories: Gondwanan origins and Laurasian origins, including a total of 10 sub-categories. We also calculated the proportion of members of each sub-category.

Origin time of EAF

The mean and median ages of the whole EAF were estimated at 16.66 Ma (standard error = 0.86) and 13.60 Ma, respectively, with the oldest lineage dated to 68.25 Ma (*Stachyuraceae*) and the youngest to 0.97 Ma (*Thermopsis*). Compared with other floras of the world, the EAF has an older median age than the Andes flora (6.40) the Amazonian flora (8.30) and the Californian flora (10.60); however, it is younger than the Australian flora (18.80) and the South African flora (18.70) (Fig. 2). The distribution of ages for the EAF shows a predominance of clades less than 22.23 Ma (Early Miocene), although some lineages are much older (Fig. 3). On average, the *Metasequoia* and *Rhododendron* lineages had very similar mean and median ages—13.29 ± 1.42 Ma (median age = 10.07) and 13.05 ± 1.29Ma (median age = 10.31) (Fig. 4)—and they were not significantly different ($t = 0.127$, $df = 93$, $P = 0.427$). The available fossil data show that the first appearances of the East Asian endemic genera in the EAF range from the Late Jurassic to the Pleistocene, with most clades occurring since the Miocene. Among these fossil records, the gymnosperm fossils seem to be much older than the angiosperm fossils. The first appearance time of gymnosperm fossils that are members of the EAF can be dated to the Late Cretaceous, for example *Cathaya*, *Pseudolarix*, *Metasequoia* or even to the Late Jurassic (*Ginkgo*). Among the angiosperm fossils, the only genera that could be dated to the Eocene were *Eucommia* and *Sinomenium*.
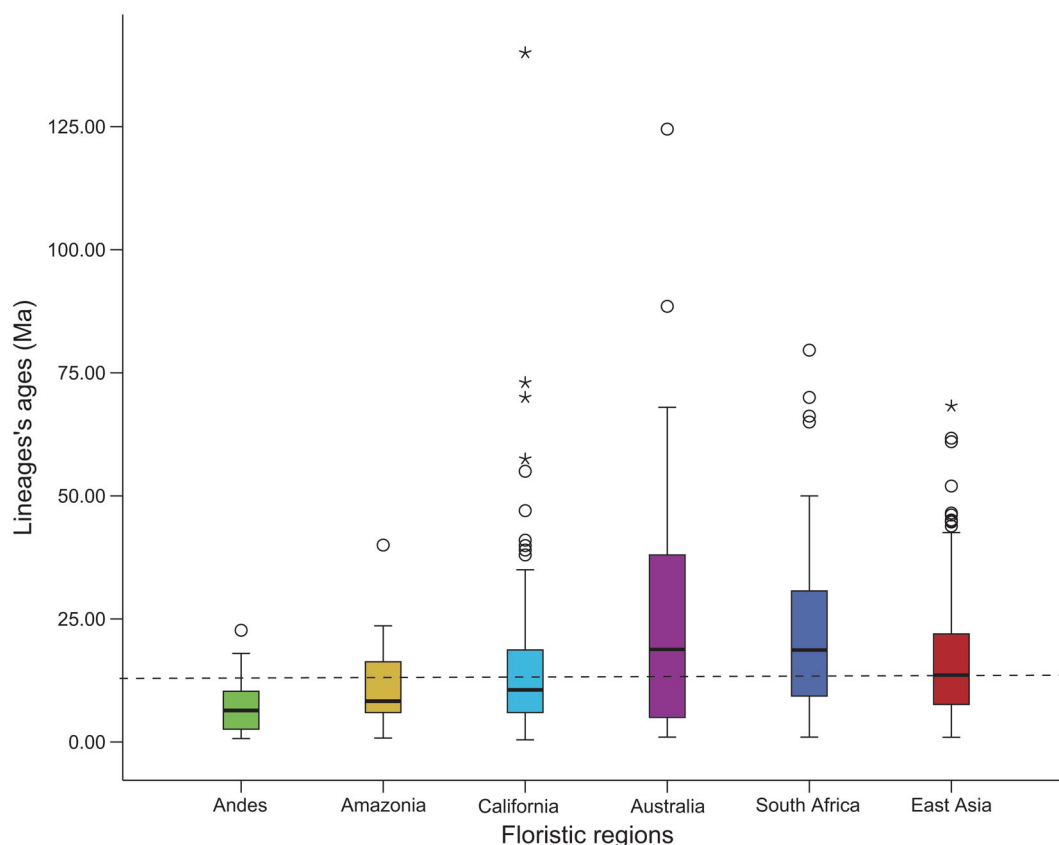
Figure 2. Lineage ages of different floristic regions in the world: South African flora (56 clades), the Andes flora (30 clades), the Amazonian flora (23 clades), the Californian flora, the Australian flora (57 clades) and the East Asian flora (213 clades). The boxes show the median and the 25th and 75th percentiles, whereas the error bars show the 2.5th and 97.5th percentiles.

Geographical origins

Although the geographical origins of the EAF were multiple, the EAF seems to have a closer relationship with other Laurasian floras [including North America (11%), Arctic/Boreal (1%), Tethyan areas (10%), Tropical Asia (9%) except those taxa which originated *in situ* (48%) and unknown place of Northern Hemisphere (13%)] than with the Gondwanan floras [including Africa (4%), Australia (2%), South America (1%) and unknown place of Southern Hemisphere (1%)] (Fig. 5).

DISCUSSION AND PERSPECTIVES
The timing of the formation of the EAF

Previous studies have suggested that the EAF is relatively ancient among the Northern Hemisphere floras [35,37–39,44] and that EA may have been the cradle for the modern Northern Hemisphere temperate floras, and even the modern Palaeotropical floras [11,44]. In addition, since many ancient lineages of angiosperm in this area, many botanists have argued that EA may have been the

center of origin and/or diversification of the angiosperms [5,7,11,37,38,45,46]. However, before the Neogene, there was a vast arid zone from Southeast to Northwest China [47] and the main EAF was completely different from the modern flora [5,45,48–52]. This suggests the age of modern EAF could not be earlier than the Miocene.

The evolution of floras through the Northern Hemisphere was greatly affected by geological and climatic changes during the Cenozoic [3,4], since this period represented the major time of diversification for modern angiosperms. The EAF also experienced complex evolutionary processes from the Paleogene to the Neogene. According to previous Paleo-vegetation zone reconstruction, China (as the main area hosting the EAF) was covered by a xerophytic flora due to the existence of a vast arid zone, controlled by the zonal planetary wind system, during the Paleogene [48–50,52,53]. This flora was characterized by the presence of *Palibina* and *Ephedra* accompanied by a few temperate and tropical elements [51,52], with regional occurrences of warm temperate forest vegetation in humid and warm parts of the northeast and

southernmost as well as the southwest edge of China [6,45,49,50,54,55].

However, the flora has changed greatly since the Early Miocene, with climatic and geological changes from the Paleogene, including the Indian-Eurasian collision, the uplift of the QTP [6,56], global cooling, warming, aridification and Quaternary glaciation [9,14,31,48,51]. By the Neogene, the vegetation of EA was rapidly modernized, the plants of EAF were closer to modern taxa and the flora was more complex in composition, with the development of extensive humid forest [48]. This shift seems well-reflected by the fossil history of Fagaceae, which is one of the characteristic elements of East Asian forests today [57]. Previous studies show some Fagaceae fossils in EA can be dated to the Paleogene such as *Cyclobalanopsis* [57,58] and *Quercus* [59]; however, it was not until the Neogene that these taxa became common and became the dominant elements of the East Asian fossil flora (especially in the Metasequoia Flora) [57,58,60]. There was also a growing trend for steppe and deciduous vegetation in North China, mainly related to the cooling and drying of this area as caused by the development of a monsoon climate and the move towards global cooling [31,53,61,62].

Our molecular data indicates that the median age of the EAF is 13.60 Ma (Middle Miocene), with most sample clades appearing since 22.23 Ma (the Early Miocene) (Fig. 3), although a few lineages could be dated to the Oligocene, Eocene or an even older geological times. This implies that the formation of the EAF may have been greatly affected by the environmental variations during the Neogene. During that period, the topography of EA became closer to that of the present [48,63], the main mountain system and drainage systems were formed [64] and the most important environmental change in EA occurred: the formation and development of the Asian monsoon [65]. Although there is some debate about the formation time of the Asian monsoon [66–69], the commonly accepted view is that it was established during the Neogene [47,70]. The establishment of the Asian monsoon led to parts of China that had been arid becoming much more humid and the geographical location of the arid region in North China began to resemble that which we see today [65]. Since the EAF is found in those areas that were greatly influenced by the monsoon climate, it is reasonable to argue that the

formation and development of the Asian monsoon may have affected the formation of the EAF. The formation of the monsoon [53] probably prompted the shift in the EAF from the original xerophytic flora in the Palaeogene to the much more humid forest flora seen today, especially in areas such as Central and Southeast China [48]. At present, these regions are the core areas of the EAF [7]. With the onset of global cooling and aridification in the Neogene, floras across the Northern Hemisphere underwent many changes [4]. However, for the EAF, this change is only reflected in North China, whereas the vegetation of South China exhibited no noticeable change [61,62].

Our fossil data from East Asian endemic genera also supports the formation time of the EAF as being later than the Miocene. According to Appendix 3, most extant East Asian endemic genera that have a fossil record first occurred in EA after the Miocene, although some gymnosperms with a fossil record can be dated to even older geological times in EA. The majority of older fossils of these genera formerly occurred in Europe and/or North America (see details in Appendix 3), indicating that they are post-Miocene relictual survivors in EA rather than originating there [19,41,71]. *Metasequoia* represents a good example of such relictualism. The fossil record of *Metasequoia* suggests that this genus may have originated in high latitudes of the Northern Hemisphere in the Late Cretaceous and had a broad distribution in Laurasia during the Paleogene. However, it became a relictual element of the flora of Central China during the Pleistocene as geological and climatic changes drove populations extinct elsewhere [72]. All evidence tends to support the suggestion that EA simply provided refugia for those ancient lineages which are immigrants from other places of Northern Hemisphere, and the final formation of the EAF may have been much more recent.

Furthermore, compared to other floristic regions of the world, the EAF is not an ancient flora according to our data (Fig. 2). Indeed, the Australian and South African floras have older median ages, although the Andes, Amazonian and Californian floras have younger median ages. Like the EAF, the formation and evolution of these floras were closely linked to local or global environmental changes. The formation and development of the tropical Andes island forest flora were closely linked to Andean uplift and the resulting isolation [29]. Similarly, the

Figure 3. (a) Plot of the tempo of origin of the 213 clades in EAF for which divergence time estimates are available. For each clade, point and error estimations were taken directly from the literature (see Appendix 2). Estimates of climatic oscillations through time are based on Zachos *et al.* (2001) [31] and major abiotic events. (b) Age distribution of the East Asian flora lineages. The mean age ± standard error, median and quartile values are indicated.
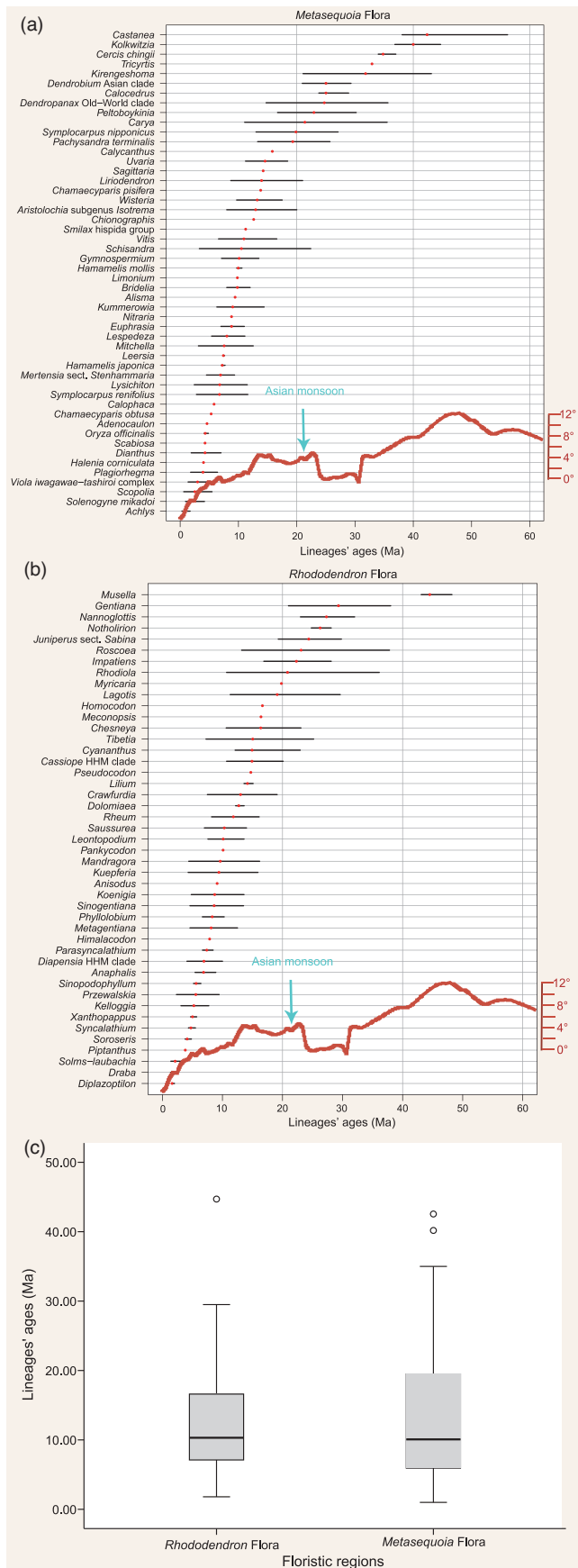
evolution of the Amazonian forest flora was associated with the uplift of the Andes. Changes in regional climate, landscape and the drainage patterns associated with the Pre-Quaternary Andean uplift were the main drivers of the evolution of the Amazonian ecosystems [27]. The evolution of the Californian flora was closely related to the development of a Mediterranean climate in the region [21]. For the evolution of the Australian and the South African flora, climate changes, especially aridification, also played a significant role [23,25].

Based on the above discussion, we propose that the EAF is relatively young: it formed gradually since the middle Miocene along with the development of the Asian monsoon, progressive global cooling and drying, and local geological changes during that time. It is noted that the young age (Miocene and younger) of the modern EAF does not mean that no ancient (Pre-Neogene) elements exist in this flora now. In fact, as we have shown above, several ancient elements (e.g. relict taxa) survived in the EAF.

Is the *Metasequoia* Flora older than the *Rhododendron* Flora?

Previous studies have suggested that the *Metasequoia* Flora is older than the *Rhododendron* Flora [7,43], since there are many ancient lineages, including living fossils and Cenozoic relic plants, concentrated in the *Metasequoia* Flora. Also it is noted that a recent study suggests that some parts of the *Rhododendron* Flora (e.g. the Hengduan Mountain flora) are much younger than its Eastern counterpart (i.e. the *Metasequoia* Flora) [73]. However, our data suggest that the *Metasequoia* Flora and the *Rhododendron* Flora have very similar median and mean ages, with no significant differences between the two ($P = 0.427$) (Fig. 4). Nevertheless, the existence of ancient lineages in a floristic region does not mean the flora

Figure 4. Plot of the tempo of origin of the 50 clades of the *Metasequoia* Flora (a) and the 45 clades of the *Rhododendron* Flora (b) for which divergence time estimates are available. For each clade, point and error estimations were taken directly from the literature (see Appendix 2). Estimates of climatic oscillations through time are displayed based on Zachos *et al.* (2001) [31] and major abiotic events. (c) Lineage ages of the *Rhododendron* Flora and the *Metasequoia* flora. The boxes show the median and the 25th and 75th percentiles, whereas the error bars show the 2.5th and 97.5th percentiles. The open circle above the error bar is an outlier.
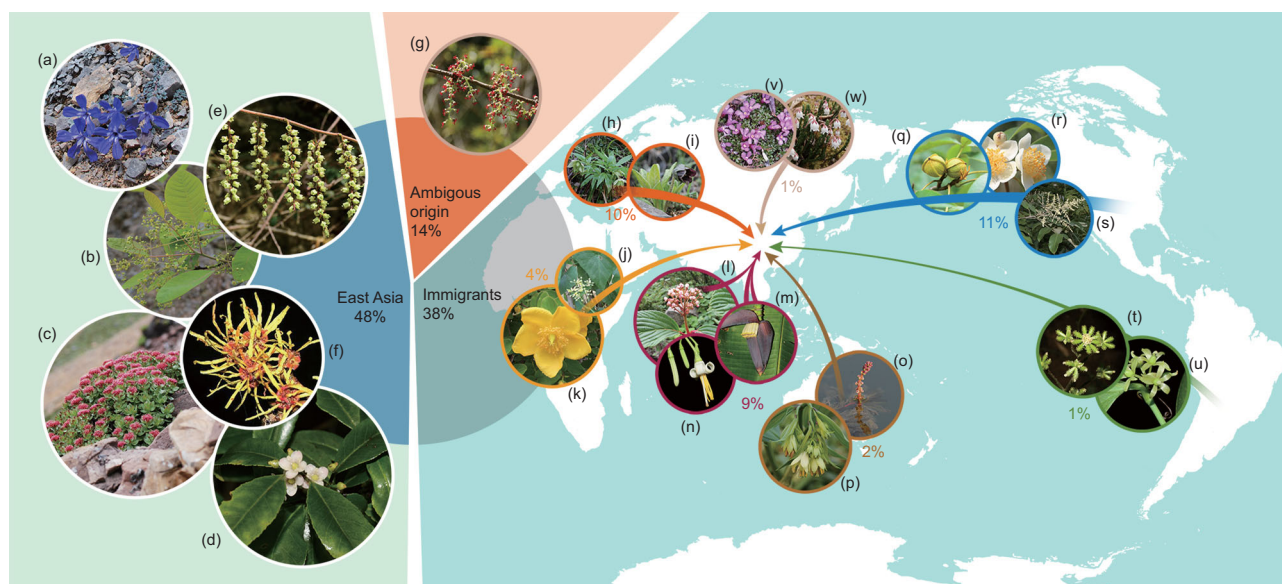
Figure 5. Geographical origins of the East Asian flora. The pie chart illustrates the percent of taxa that originated *in situ,* that have ambiguous origins and that represent immigrants from other floras. Arrows indicate the biogeographical origin of East Asian elements from other regions. Photos of representative living plants that have different geographical origins: (a) *Cyananthus,* (b) *Cotinus,* (c) *Rhodiola,* (d) *Ilex,* (e) *Stachyuraceae,* (f) *Hamamelis,* (g) *Coriaria,* (h) *Helleborus,* (i) *Mandragora,* (j) *Cissus,* (k) *Hypericum,* (l) *Viburnum,* (m) *Musa,* (n) *Alangium,* (o) *Myriophyllum,* (p) *Disporum,* (q) *Carya,* (r) *Schima,* (s) *Rhus,* (t) *Adenocaulon,* (u) *Smilax,* (v) *Diapensia,* (w) *Cassiope.*

of that region is an old flora. In fact, the *Metasequoia* floristic region may simply be a center in which many relict taxa survived to more recent times [19,71,74]. Global cooling, especially the Quaternary glaciations and the Plum rain caused by the development of the Asian monsoon may have driven extirpation of these taxa in other regions, whereas they survived as a paleoendemic element in this area [74]. As both the *Metasequoia* Flora and the *Rhododendron* Flora experienced a simultaneous change from an arid to a wet environment [52], we argue that the establishment of the *Metasequoia* Flora and *Rhododendron* Flora might have occurred at a similar time, namely after the formation of the Asian monsoon.

Why are there many genera with a center of diversity in the *Rhododendron* Flora?

There is consensus that the *Rhododendron* Flora represents a center of distribution and diversification for the temperate flora, with many important and large north temperate genera found in this area. According to our database, more than 80% of large genera containing more than 100 Chinese species, such as *Rhododendron, Primula, Pedicularis, Gentiana, Saxifraga, Saussurea, Rhodiola, Corydalis, Aconitum, Salix* and *Berberis,* are concentrated in the *Rhododendron* Flora (Appendix 1). Previous studies suggested that this may be due to the diverse and heterogeneous topography and climate (e.g. seasonal

uniformity in temperature) of this region, caused by the uplift of the QTP [16,75,76], since this uplift created high mountains, deep valleys and changes in the original drainage systems [77,78]. These new habitats, along with habitat fragmentation across a wide elevational range, may have prompted the emergence of new lineages and triggered rapid diversification in this area [75]. For example, *Rhododendron, Saussurea, Aconitum* and *Gentiana* [79] are thought to have experienced rapid radiations within the *Rhododendron* floristic region with the uplift of the QTP and Himalayas and global cooling. However, the topography of the *Metasequoia* floristic region has been stable since the Neogene and lacked strong influences from Quaternary glaciations, making this region a survival center for relict plants [11].

Besides, the north-south mountains in the *Rhododendron* Flora provide corridors for floristic exchange between the north and south, but represent barriers to migration between the east and west. Conversely, the east-west-oriented mountains in the *Metasequoia* Flora provide corridors for floristic exchange between the west and east, but are a barrier to migration between the north and south. Although all mountains in the *Rhododendron* Flora and *Metasequoia* Flora could have served as locations for both survival and speciation [71], the east-west-oriented ranges may have increased extinction rates by blocking southward migration during cooling [4]. Furthermore, the north-south mountains and valleys in

the *Rhododendron* Flora could have acted as migration corridors or centers of distribution for different latitudes, while the meridional isolation of plants may have been the main driver of plant speciation and diversification in this area [75]. A lack of plant exchange between different latitudes along with horizontal isolation may be the reason for the reduced plant diversity in the *Metasequoia* Flora.

The biogeographical origins of the EAF

Our results suggest multiple biogeographical origins of the EAF (Fig. 5). However, the EAF does exhibit a close relationship with Laurasian floras including those of Arctic/Boreal (1%), North America (11%), the Tethyan area (10%) and tropical Asia (9%), if we exclude those taxa that originated *in situ* (48%) and whose origin in the Northern Hemisphere is unknown (13%), rather than the Gondwanan floras. This pattern may be explained by the appearance and disappearance of barriers and corridors associated with floristic exchanges between or within continents [34].

Biogeographical analysis revealed that only 8% of East Asian clades originated from the continents derived from Gondwana. This may reflect the stable separation between the Gondwanan and Laurasian floras by the Tethys [80]. However, this separation was not absolute and long-lasting. Floristic exchanges between EA and Gondwanan fragments could have been facilitated by links provided by island chains or peninsulas (such as Southeast Asia between EA and Australia) [34], the drifting of India [81], geological movement between Africa and EA due to the (Africa-) Arabia-Eurasia collision [82], land bridges (e.g. between EA and South America via the North America and Bering or North Atlantic land bridges) [83,84] as well as long-distance dispersal [85]. For example, the ancestor of East Asian *Myriophyllum* could have migrated to EA from Australia due to the emergence of the Malay Archipelago [86]; dispersal from Africa to EA by the ancestors of the Ascyreia group of *Hypericum* may have been facilitated by the collision of the Arabian plate with Eurasia [87]; and the ancestor of the East Asian species of the *Smilax hispida* group and some taxa of Malpighiaceae may have colonized EA from South America to North America via the Bering or North Atlantic land bridges [83,84]. Aside from these specific examples, floristic exchanges between EA and the fragments of Gondwana may have been the result of long-distance dispersal, as for example *Solenogyne mikadoi* [88], species of *Cissus* [89] and species of *Disporum* [85].

Other barriers to floristic exchange between EA and other regions of the Northern Hemisphere include the Pacific and Atlantic Oceans (during most of the Cenozoic) and the Turgai Strait (from the Paleocene to the late Oligocene), which reduced floristic exchange between EA and North America as well as the Tethyan area [3,4]. However, the Bering and North Atlantic land bridges did function as significant corridors for floristic exchanges between different regions [90–92]. Furthermore, the retreat of the Turgai Strait also provided the opportunity for biotic exchange between EA and the Tethyan area and other parts of Eurasia [3,4]. The close relationship between the EAF and North American floras has attracted the attention of botanists and biogeographers for decades [93]. Recently, it has been suggested that many East Asian taxa first originated in North America and then migrated to EA via either the Bering or the North Atlantic land bridges at different times. Examples of such taxa include *Carya* [94] and some genera of Theaceae [95]. In addition, climatic cooling led to the southward migration of Arctic/Boreal species such as *Diapensia* [96] and *Cassiope* [97] to EA as well. Floristic exchanges between the EAF and Tethyan floras were also quite frequent, especially for those herbaceous species that migrated into the EAF from the Tethyan flora due to the seasonal continental climate present through central Asia and the formation of the Eurasian steppe. Such genera include *Scabiosa* [98], *Dontostemon* [99] and *Tragopogon* [100] after the disappearance of the Turgai Strait. Aside from these, the EAF shows a close relationship with the tropical Asian flora (9%), perhaps due to the close proximity of the two regions. It has been proposed that taxa such as *Viburnum* [101], Alangiaceae [102], some taxa of Euporbiaceae [103] and *Paederia* [104] originated in the tropical Asian flora and then dispersed to EA and other regions [105].

CONCLUSION

In this study, we have synthesized numerous studies in an attempt to trace the evolution of the EAF. Our results have revealed that the EAF is not as old as previously thought and that its two subkingdoms may have originated at a similar time, which also differs from suggestions in previous studies. The formation of the EAF and its two subkingdoms may have been related to the development of the Asian monsoon. These suggestions are quite different from previous views. However, our sampling remains constrained by studies that have already been conducted and many more studies are needed to make more robust conclusions. Besides this, our studies failed to

suggest a single clear mechanism that explains the divergence between the two subkingdoms; this issue requires further study.

SUPPLEMENTARY DATA

Supplementary data are available at *NSR* online.

Conflict of interest statement. None declared.

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