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Review

Evolution of East Asian subtropical evergreen broad-leaved forests: When and how?

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Abstract Understanding how East Asian subtropical evergreen broad-leaved forests (EBLFs) have evolved over time is not only vital for biodiversity conservation but also facilitates predictive modeling of ecosystem services under global change scenarios. During recent decades, numerous studies have been devoted to investigating the evolution of EBLFs. However, there are often contradictory interpretations of the different taxa associated with different geological events and environmental backgrounds. Here, we synthesize several key aspects of the spatiotemporal evolution of EBLFs. First, the EBLFs emerged concomitantly with the development of Asian monsoon systems, occurring no earlier than the Eocene. While the southernmost region was inhabited by tropical elements, EBLFs are not the direct relic of boreotropical flora because of the presence of a broad arid belt at that time. Rather, they represent a unique assemblage including boreotropical relics, tropical floras and deciduous broad-leaved forests. Second, the evolution of EBLFs should not be contextualized within an enclave, the adjacent vegetation systems to elucidate the potential connections between EBLFs and other biomes should be considered to avoid an isolated phenomenon. Third, the adaptive response of EBLFs to environmental changes caused by anthropogenic disturbance in subtropical regions remains understudied. Such a knowledge gap must be addressed to develop effective conservation strategies to sustain the ecosystem amid the dual pressure of climate change and human activity in the future. Finally, current research has predominantly focused on the dominant tree species in EBLFs, whereas comprehensive understanding requires expanding the investigation of associated flora, including understory trees and herbaceous plants. This review not only consolidates contemporary perspectives on the evolution of EBLFs but also proposes a framework to navigate the Anthropocene challenges. By bridging historical patterns with future projections, we aim to catalyze transformative research on EBLFs' resilience and sustainable management, fostering further research and development regarding the resurgence.

Key words: biodiversity conservation, Cenozoic, East Asian monsoon, evergreen broad-leaved forests, evolution, geographic distribution.

1 Introduction

The current biome represents a phylogenetic and ecological continuum of the past biome, reflecting the Earth's evolution across geological timescales. The origination and evolutionary dynamics of a biome are intrinsically coupled with environmental drivers, including climatic fluctuations, geological processes, topographic evolution, and anthropogenic disturbance over time.

During the Cenozoic Era, the Indian–Eurasian continental collision constituted the most consequential tectonic event in Asia, triggering several transformative environmental shifts. For instance, the retreat of the Paratethys Sea (Meijer et al., 2019; Wu et al., 2025), the onset of the Asian monsoon (Tardif et al., 2020), and orogenic uplift of the Qinghai–Tibetan Plateau (QTP) (Spicer, 2017; Su et al., 2019; Wu et al., 2022; Lai et al., 2025). These collision-derived phenomena have exerted hierarchical impacts on East Asian biota, particularly on the evolution of East Asian evergreen broad-leaved forests (EBLFs; the abbreviation of EBLFs in this review is specific to the EBLFs in East Asia, not globally).

As a geographically unique biome of East Asia, EBLFs exhibit exceptional biodiversity and high endemism. In addition, EBLFs serve as both cradles of angiosperms (Takhtajan, 1969) and museums of relict taxa from the Cenozoic (Wu & Wu, 1996; Qiu et al., 2011). As the significant ecosystems that are direct descendants of the Cenozoic flora, EBLFs are important for ecosystem services that benefit human beings (Song, 1999, 2013; Fang, 2001; Song & Da, 2016), which play a critical role in maintaining ecosystem functionality and species diversity *in situ* (Fang et al., 2002). Furthermore, EBLFs constitute a zonal biome in China's vegetation system (Song, 1999), which is dominated by four woody families that are Fagaceae, Lauraceae, Theaceae, and Magnoliaceae (e.g., Fang & Yoda, 1989; Tang, 2015a, 2015b; Yu et al., 2017; Zhao et al., 2022). These four families are collectively referred to as the "Big Four" of EBLFs. Beyond these dominant taxa, numerous associated species from other families contribute to the community structure, reflecting the complex assembly history and ecological dynamics of EBLFs, which have been thoroughly explored (Kou et al., 2016; Xiang et al., 2016; Tian et al., 2018; Chen et al., 2020; Song et al., 2020; Wang et al., 2020; Zhang et al., 2020; Meng et al., 2022a, 2022b; Han et al., 2023; Geng et al., 2024; Huang et al., 2024; Ji et al., 2024; Sun et al., 2024).

Concerning geographical distribution, several studies have identified the ranges of EBLFs in China as *ca*. 23° to 34° N and *ca*. 97° to 123° E (Wang et al., 2007; Meng et al., 2022a; Zhu & Tan, 2024). However, the subtropical distributions are just parts of EBLFs, and do not represent the full extent of EBLFs in East Asia. Phytogeographic studies have indicated that typical *Castanopsis*-dominated EBLFs extend as far north as *ca*. 39° N in Japan, with longitudinal coverage spanning from Nepal to Japan (Ohsawa, 1993; Tang et al., 2022). This broader distribution has been adopted in many studies (e.g., Hai et al., 2022; Zhang et al., 2024). That is, EBLFs primarily occur in subtropical China (including the northern part of Taiwan province), although there are fragmented distributions in the montane areas of Japan, South Korea; even in Myanmar, India, and Nepal (Ohsawa, 1973, 1993; Hämet-Ahti et al., 1974; Kira, 1991; Tagawa, 1995; Fang et al., 1996; Tang & Ohsawa, 2009; Song, 2013; Tang et al., 2013; Tang, 2015a). In Asia, there are other subtropical evergreen broad-leaved forests, even the alpine traits at high elevations that are distributed in the Indochina Peninsula as well as the typical evergreen broad-leaved forests distributed along the intermediate-altitude canyons and reviers from east to west Nepal (the field investigations by the 1st author, Hong-Hu Meng). However, we exclude the two regions due to Indochina Peninsula belongs to Southeast Asia; and Nepal belongs to South Asia. Thus, the northernmost EBLFs span the Japanese Archipelago to the southern Korean Peninsula. In subtropical China, the northern boundary follows (Fig. 1): Eastern sector (northern Hangzhou Bay); the western sector (southern slope of the Dabie Mountains, to the southern Qingling Mountains, to the west Sichuan Basin, to the Hengduan Mountains); as well as the western region encompasses the valley of southern Xizang or the Himalayas, which is next to the northernmost tropical rainforests in Medog (Xizang); Westernmost limit (southern Himalayan valleys of Xizang, e.g., Zangnan, is adjacent to Medog's tropical rainforest). The southern boundary constitutes the tropical–subtropical ecotone, representing the biogeographical northern limit of tropical Asia (Wu, 1980; Zhu, 2017, 2018), which was omitted in ancestral area reconstruction, and biogeographic analyses incorporated the Ailaoshan–Honghe fault zone (Tapponnier et al., 1990; Fig. 1) from geological events (e.g., Ballarin & Li, 2018; Meng et al., 2022a).

Why do the South Korean and Japanese distributions of EBLFs reach higher latitudes than in China? This is determined by the milder winter temperatures. Climatically, the 0°C coldness index defined the northern limit, whereas the 22°C warmth index defines the southern margin (Song & Da, 2016). Regional climatic zonation has identified monsoonal temperature seasonality as the primary driver of these distribution patterns (Wolfe, 1979; Ohsawa, 1990, 1993; Kira, 1991; Box, 1995).

EBLFs from distinct biomes are intrinsically linked to the evolution of the Asian monsoon system (Song & Da, 2016). This represents a fundamental focus in biogeography, ecology, and evolution. Extensive phylogenetic and population genetic investigations have been conducted on the most representative EBLF taxa, shedding light on their diversification (Xu et al., 2015; Kou et al., 2016; Xiang et al., 2016; Yu et al., 2017; Meng et al., 2022a), with Asian monsoon system. Molecular dating (Fig. 2A) revealed that dominant species diversification occurred at *ca*. 8 Ma, coinciding with the development of the East Asian Summer Monsoon (EASM) during the late Miocene (Ye & Li, 2022). However the potential origins extended to the early Oligocene or the Oligocene–Miocene boundary (Yu et al., 2017; Zhang et al., 2024). The EASM, which generates humid conditions with pronounced seasonal precipitation, has facilitated the emergence and diversification of dominant lineages of EBLFs. This relationship is well documented across biological and geological disciplines (e.g., Xiang et al., 2016; Yu et al., 2017; Deng et al., 2018; Ye et al., 2019, 2022; Chen et al., 2020; Li et al., 2021; Meng et al., 2022a; Ye & Li, 2022; Qin et al., 2023a). Notably, the Miocene establishment of monsoon was significantly influenced by the QTP uplift (*ca*. 26 Ma, Fig. 2B; Zhu et al., 2019; Tardif et al., 2020), with these climatic

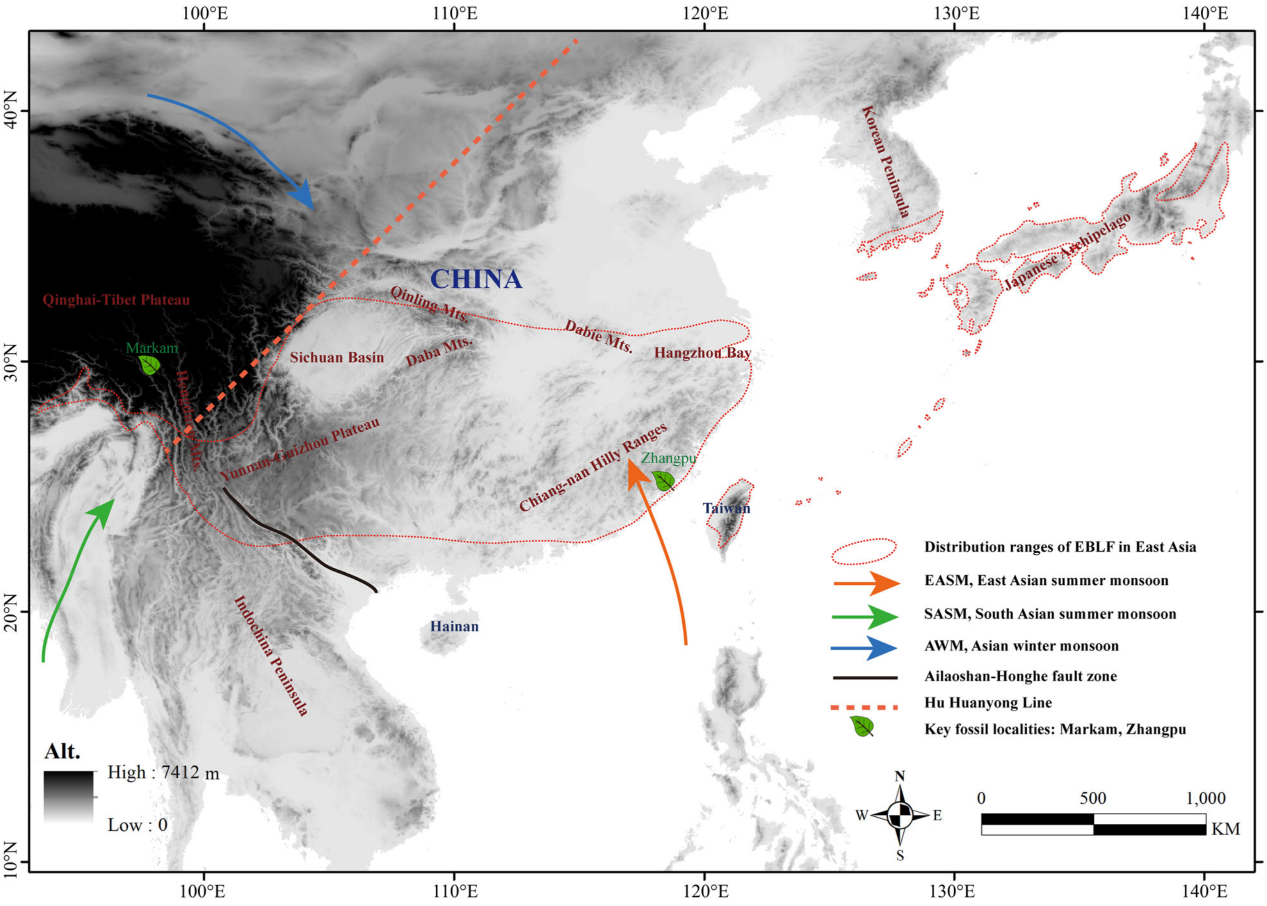

Fig. 1. The distribution ranges of evergreen broad-leaved forests (EBLFs) in East Asia (from Hai et al., 2022; Zhang et al., 2024), the related monsoon system (from Wu et al., 2022), key mountain ranges, fossil localities (from Xu et al., 2016; Wang et al., 2021), Hu Huanyong line (from Hu et al., 2016), and Ailaoshan–Honghe fault zone (from Tapponnier et al., 1990).

transitions generally dated to *ca.* 23–5.33 Ma (Quade et al., 1989; Guo et al., 2002; Sun & Wang, 2005; Zachos et al., 2008; Hansen et al., 2013).

The evolution of EBLFs remains an ongoing process that is now significantly impacted by global change, the past and the future. In particular, the Anthropocene has brought unprecedented challenges owing to climate and human activity (Meng et al., 2021). Additionally, the vegetation structure, climatic and evolutionary drivers are likely the dominant extinction drivers in China based on the proportion of growth forms, but for the EBLFs in Southern China, the climatic driver is the major factor (Zhao et al., 2024). Furthermore, most distributions of EBLFs coincide with densely populated regions that have experienced intensive land use for millennia (Meng et al., 2022a; Zhou et al., 2023; Qin et al., 2023b). As known, EBLFs predominantly occur east of the "Hu Huanyong Line" (Fig. 1), where rapid economic development and population growth are accelerating habitat fragmentation (Hu et al., 2016; Meng et al., 2022a). Despite covering extensive areas of East Asia, EBLFs face significant conservation challenges. This remarkable plant diversity results from complex eco-evolutionary mechanisms that require integrated ecological and evolutionary perspectives for full understanding (Meng & Song, 2023a). Therefore, the evolution of EBLFs must be examined in terms of both past evolutionary processes throughout geological history and the responses to climate change and human activity in the Anthropocene.

While substantial attention and summary have addressed the origin and environmental responses of EBLFs (e.g., Xu et al., 2015; Yu et al., 2017; Meng et al., 2022a; Qin et al., 2023b; Zhang et al., 2024), a synthetic framework linking climate change, geological events, and evolution of EBLFs need a comprehensive review. Therefore, this enabled us to: (i) synthesize the viewpoints of recent advances in the assembly history of EBLFs; (ii) elucidate their environmental responses during the evolutionary process; and (iii) identify critical research directions for the EBLFs in East Asia.

2 When did the EBLFs originate?

2.1 Asian monsoon and the reconstruction of EBLFs

East Asian Monsoons (EAM) has been recognized to play a fundamental role in shaping the emergence and evolution of EBLFs. Monsoon systems are characterized by distinct seasonal precipitation patterns and wind inversions. There is a strong biogeographic connection between monsoon

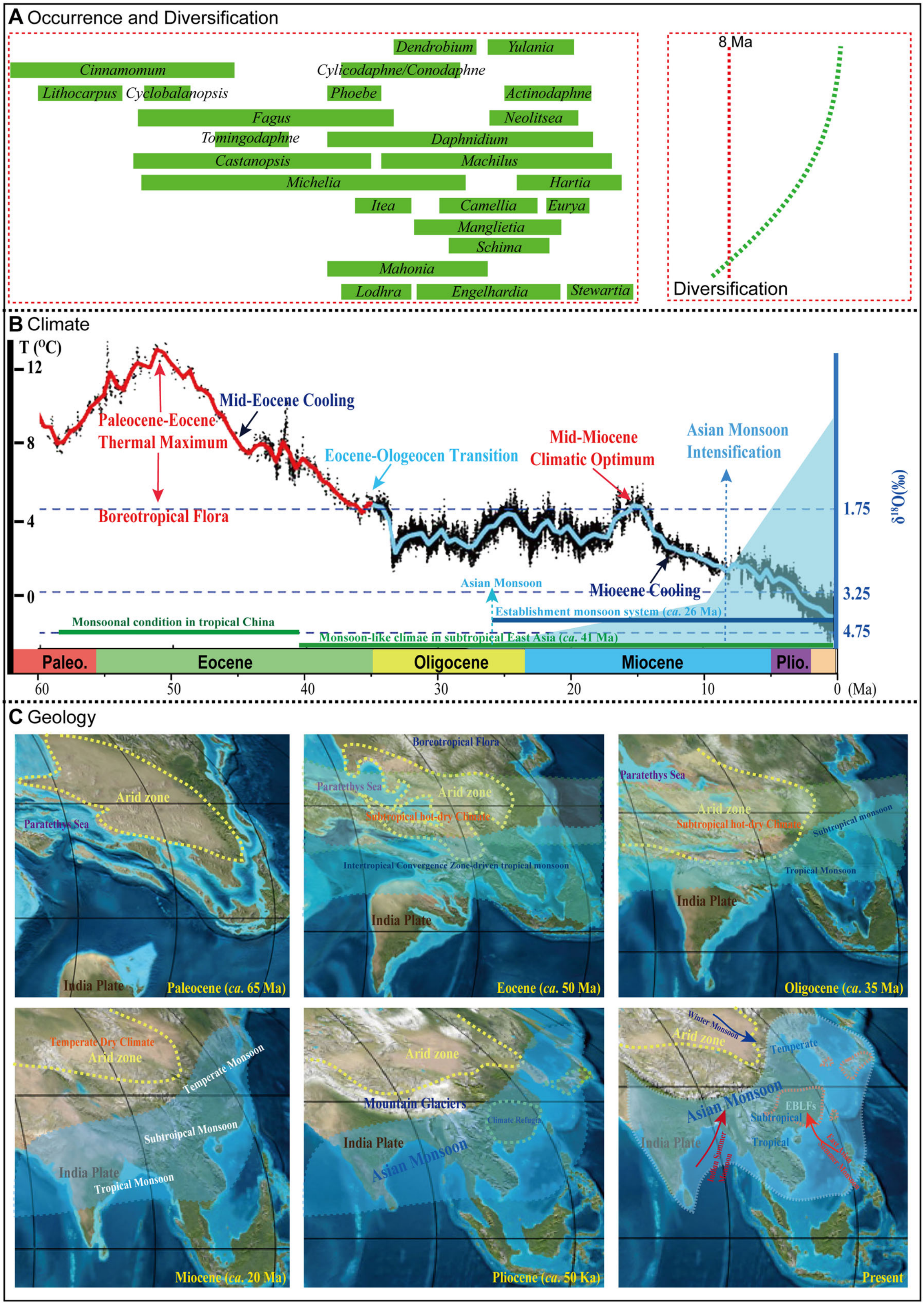

Fig. 2. Continued

systems and the diversification of EBLFs (Wan et al., 2023). The EAM produces a pronounced wet season during summer monsoons and a dry season during winter monsoons (Wang & Ding, 2008), spanning tropical to cool temperate regions across South and East Asia (Figs. 1, 2C). In particular, EASM, a key component of global climate, delivers intensive summer rainfall that sustains EBLFs. Precipitation peaks first in southeastern China (July) before advancing northeastward (July), whereas the Siberian High creates cold and dry winters (Tardif et al., 2020). Many studies have illuminated that the EASM has driven the origin of evergreen habits in dominant lineages of EBLFs, accelerating speciation rates and ecological diversification through increased humidity and seasonal precipitation (e.g., Xiang et al., 2016; Yu et al., 2017; Ye et al., 2019, 2022; Chen et al., 2020; Meng et al., 2022a; Ye & Li, 2022; Qin et al., 2023a). The intensified precipitation associated with the monsoon system since the Early Miocene has played a significant role in shaping the EBLFs (Jin et al., 2024). Therefore, a comprehensive understanding of both the intricate processes of EAM and the spatial distribution patterns of EBLFs is essential.

The exact onset of the Asian monsoon system remains debated within the proposed timings ranging from the latest Oligocene (e.g., Sun & Wang, 2005) to the Early Miocene (e.g., Guo et al., 2002; Wu et al., 2022). The modern EAM system was established concurrently with topographic recognition in the northern QTP and adjacent regions. Traditional hypotheses have attributed monsoon intensification primarily to the Miocene QTP uplift (An et al., 2001; Tardif et al., 2020; Wu et al., 2022), which enhanced the Asian winter monsoon, promoting arid-adapted vegetation in eastern Asia (Qin et al., 2023a). Conversely, the uplift of the Songpan-Ganzi and Qiangtang terranes weakened the winter monsoon, allowing southeasterly moisture penetration and precipitation (Tardif et al., 2020), which is a key driver of EBLFs expansion in southeastern Asia (Li et al., 2021). This period also showed the development of a robust Siberian High during the winter, coupled with global cooling and aridification of the Asian interior (Spicer, 2017). Notably, Wu et al. (2022) argued for an earlier inception during the Middle to Late Eocene, linking it to the uplift of central QTP at *ca*. 41 Ma (Fig. 2B). Additionally, due to the influence of proto-Paratethys Sea and global cooling caused by the QTP uplift, the monsoon expanded northward into temperate regions during that time (Wu et al., 2022). In the late Eocene, Yunnan, Guangxi, and Guangdong, situated at approximately 26° N, experienced expansion of the humid zone that persisted into the Oligocene, maintaining their humid characteristics. The present-day Asian monsoon boundary lies between 30° N and 36° N, while tropical China experienced monsoon conditions driven by the intertropical convergence zone during the late Eocene (Sun & Wang, 2005; Fang et al., 2021; Wu et al., 2022). However, it is important to note that tropical China's geographic extent was relatively small at that time (Fig. 2C).

The initiation and intensification of Asian monsoon are intrinsically linked to the formation of EBLFs. We propose that large regions of EBLFs could not have originated before the Eocene in most regions, except present-day Yunnan, Guangxi, and Guangdong, which were arid and thus unfavorable for EBLF expansion (Fig. 2C). Critically, the EASM intensified at the Oligocene–Miocene boundary, with further strengthening during the late Miocene–Pliocene, coinciding with the rise of the core of EBLFs taxa (Fig. 2A; e.g., Theaceae; Yu et al., 2017), and hemiparasitic lineages like *Brandisia* (Chen et al., 2023). Furthermore, fossil assemblages confirmed that EBLFs appeared in tropical China by the Middle Eocene; spread to southwestern China by the Late Eocene/Early Oligocene, and reached central-eastern China in the Late Oligocene/Early Miocene (Su et al., 2019; Deng et al., 2020; Zhao et al., 2025).

2.2 Is EBLFs the relict of boreotropical flora?

Boreotropical flora, a warm-adapted plant assemblage comprising numerous extant and fossil species, formed a vast biome across the Northern Hemisphere during the Eocene, driven by global warming (particularly the Paleocene–Eocene Thermal Maximum [PETM]; Fig. 2B; Zachos et al., 2001; Mosbrugger et al., 2005). This northward expansion of flora was facilitated by PETM-induced warming, enabling transcontinental dispersal between Eurasia and North America. Subsequent cooling caused a decline in thermophilic taxa, fragmenting their ranges and leading to pantropical disjunction (Meng et al., 2014, 2015a, 2015b). Notably, the Eocene–Oligocene cooling may have coincided with a substantial decline in thermophilic taxa of the Northern Hemisphere (Fig. 2B). Consequently, the PETM facilitated the migration of boreotropical elements toward higher latitudes, occurring between the North American and Eurasian continents. This migration led to the segregation of ancestral lineages of modern tropical plants (van der Hammen & Cleef, 1983; Azuma et al., 2001; Tiffney & Manchester, 2001). We propose that southward migration via long-distance dispersal resulted in boreotropical relics adapting to subtropical

Fig. 2. The evolution of main species in evergreen broad-leaved forests (EBLFs) and the related climatic and geological events. **A,** Main diversification of the typical and company species in East Asia EBLFs, the range of green bars indicates the upper and lower diversification intervals that correspond to the following related geological time scale in part **B,** and the diversification of EBLFs indicated most of the dominant species (*ca*. 76.1%) diversified after the late Miocene, *ca*. 8 Ma (from Ye & Li, 2022). **B,** The related climatic sequence of events including a global average $\delta^{18}O$ curve (right-hand axis) derived from benthic foraminifera which mirrors the major global temperature trends from the Paleocene to Pleistocene (from Zachos et al., 2008; Hansen et al., 2013); monsoon conditions in tropical China, the monsoon-like climate in subtropical East Asia since *ca*. 41 Ma and the fully established of Asian Monsoon since *ca*. 26 Ma (from Wu et al., 2022). **C,** The geological sequence of events related to the evolution of the Asian monsoon system, EBLFs and the uplift of the representation of the extent of the geographic change through time (from Sun & Wang, 2005; Wu et al., 2022).

zones. Thus, EBLFs likely represent descendants of this ancient biome, filtered by post-PETM climatic shifts.

Many plants have evolved beyond their boreotropical origins, as evidenced by molecular and palaeobotanical studies. For instance, Zhang et al. (2022a) demonstrated that the evolutionary trajectory of Juglandaceae was shaped by Cenozoic climate change, driving local extinction and adaptation. Fossil records from the Eocene confirm their widespread distribution across the Northern Hemisphere (Manchester, 1987). As the climate cooled, lineages such as *Palaeocarya* (represented today by Asian *Engelhardia* and American *Oreomunnea* and *Alfaroa*) migrated southward, establishing refugia in Central America and Asia (Meng et al., 2015b). While these forests are distinct from the tropical ecosystem of the Eocene, they may retain remnants or descendants of boreotropical flora, although this is not as direct evidence.

As known, EBLFs comprise diverse taxa, including Lauraceae and Magnoliaceae, with key genera such as *Castanopsis*, *Lithocarpus*, *Cyclobalanopsis*, *Schima*, *Machilus*, *Lindera*, *Cinnamomum*, *Neolitsea*, and *Michelia*. Increasing evidence has suggested that many of these lineages originated from boreotropical ancestors (e.g., Li et al., 2011; Zhang et al., 2022a). Similarly, Juglandaceae, although not dominant in EBLFs, exemplifies a boreotropical legacy, in which the tropical Engelhardioideae and temperate Juglandoideae diverged due to late Eocene cooling, as seen in their fossil distributions (Manchester, 1987; Meng et al., 2015b; Hermsen & Gandolfo, 2016). Other studies have highlighted the role of monsoons in shaping East Asian flora. For example, *Magnolia* sect. *Michelia* (Magnoliaceae) shows dispersal patterns tied to monsoon development (Zhao et al., 2022), whereas Coryphoid palms diversified in boreotropical regions of the Northern Hemisphere before spreading globally (Kumar et al., 2023). Collectively, these findings likely suggest that EBLFs are relictual, albeit modified, successors of boreotropical flora.

However, EBLFs did not arise directly from the Eocene ecosystem due to the lack of the humidity required for thermophilic/hygrophilic plants that are now endemic to EBLFs (Fig. 2B, 2C). Monsoon-driven precipitation only became significant in the Miocene (Li et al., 2021), enabling the expansion of subtropical EBLFs, as seen in *Quercus* sect. *Cyclobalanopsis* (Jin et al., 2024). Thus, while Eocene tropical elements likely persisted along the margins of arid zones, modern EBLFs reflect later adaptations to cooling and monsoon intensification.

Overall, the boreotropical flora was widely distributed across the Northern Hemisphere during the Eocene. However, most distributions of EBLFs during the Palaeogene which were in arid zones, were unsuitable for the growth of subtropical plants. Consequently, EBLFs cannot be regarded as direct relicts of the boreotropical flora, despite occupying areas that once harbored tropical elements during the Eocene. These tropical lineages likely persisted in refugia along the southern margins of the extensive arid belt and later transitioned to subtropical forms. The expansion of EBLFs occurred only after the Miocene, facilitated by global cooling and the intensification of EAM, which created the humid conditions necessary for their development.

2.3 The transformation to subtropical elements

The evolution of EBLFs has undergone significant transformations throughout the extensive process of geological evolution (Fig. 2C), emerging as a vital biogeographic transition zone that connects temperate regions in the north with tropical regions in the south (Fig. 1). EBLFs are consistently recognized as the critical ecological link between tropical and temperate flora in Asia, with current distribution patterns strongly influenced by the onset and intensification of the Asian monsoon system. Meng et al. (2019a) demonstrated that species ranges repeatedly expanded and contracted in response to past climatic fluctuations, particularly through monsoon-driven changes in precipitation and temperature regimes. Additionally, the transformations of EBLFs were observed both prior to monsoon establishment, in which the vast arid belt supported xerophytic vegetation rather than the subtropical forests. The diversification of central Asia's arid-adapted flora, including Northwest China′s dryland plants, was shaped by multiple factors such as the Paratethys Sea retreat, QTP uplift, global cooling, and aridification (Gao et al., 2014; Meng et al., 2015a, 2015b). These conditions persisted until monsoon intensification created suitable humid environments for the evolution of EBLFs.

The transition from tropical-to-subtropical biomes is well documented in palaeobotanical and molecular studies (Wang et al., 2021; Meng et al., 2022a). The Miocene epoch, which lasted from *ca.* 23.03 to 5.33 Ma, was characterized by global warmth. In contrast to current climate conditions, particularly during the Middle Miocene, especially the Mid-Miocene Climatic Optimum (MMCO), played a pivotal role in modern biome formation characterized by elevated CO_2 levels, global warmth, and reduced temperature gradient across latitudes (Zachos et al., 2001; Mosbrugger et al., 2005; Kasbohm & Schoene, 2018; Steinthorsdottir et al., 2021). For instance, the Middle Miocene (*ca.* 14.7 Ma) Zhangpu biota in Fujian, China (Fig. 1), with evidence of a megathermal rainforest that was subsequently replaced by subtropical EBLFs (Wang et al., 2021). Molecular evidence of *Engelhardia* species further corroborates this tropical-to-subtropical transition during the mid-Miocene (Meng et al., 2022a). The Late Eocene to Middle Miocene, with drying and cooling trends, significantly influenced the evolution of EBLFs, promoting deciduous habits in the ancestral lineages (Qin et al., 2023a). Thus, the transition from deciduous broad-leaved forests to EBLFs should be regarded as an alternative evolutionary strategy.

The origin of EBLFs is complex and multifaceted, however, the elaboration of the evolutionary process can be included from the published literature: (i) tropical ancestry, in which some components descended from Miocene tropical elements; (ii) boreotropical relics, in which others represent relictual lineages from the boreotropical forests; and (iii) deciduous adaptation, in which many taxa evolved from deciduous broad-leaved forests. Notably, EBLFs are not only considered relict or remnant of boreotropical flora because the arid belt existed in most regions of current EBLFs. However, they have also evolved from tropical elements and deciduous broad-leaved forests.

2.4 Geographic patterns at high-latitude zones

The high-latitude zones of EBLFs (Fig. 1), encompass most of the Japanese Archipelago and the southernmost region of the Korean Peninsula. These regions are located within the "Sino-Japanese floral region" (Wu & Wu, 1996; Qian & Ricklefs, 2000), which biodiversity has been shaped by a combination of climate influences, complex geo-climate histories, diverse geography, and sea level fluctuations (Ye et al., 2017). However, the geographic patterns of EBLFs in high-latitude zones remain poorly understood despite the presence of many EBLFs with numerous plants in these regions. Regarding the distribution patterns observed in high-latitude zones, we propose that these patterns originate from the mainland and are subsequently dispersed via land bridges. Several widespread plant species have provided key insights into these distribution patterns. For instance, *Quercus glauca* exhibits a broad range (from 97° E to 121° E, and from 23° N to 33° N; distribution range extending from the southern slopes of the Himalayas to Japan), with lineage diversification dating to the late Miocene to Pliocene (Xu et al., 2015). *Quercus gilva* suggests it likely migrated from east-southwest China to South Korea and Japan (Song et al., 2023). *Ophiorrhiza japonica* populations in the Ryukyu archipelago derive from Pleistocene overseas dispersal originating in Taiwan, China (Nakamura et al., 2010). Furthermore, the evolutionary history of *Spiraea japonica* diversified in Japan during the Early Miocene, potentially facilitated by land bridge connection (Luo et al., 2023). It is also important to note that the existence of land bridges during the Pleistocene glacial period, which connected the Chinese Taiwan Islands to the South China Mainland, played a crucial role in facilitating the dispersal of species from the mainland to the islands (Jiang et al., 2019). The flora of these zones consistently reflects mainland affinities, underscoring the pivotal role of land bridges in facilitating species exchanges. Whereas recent studies have specifically investigated the geographic patterns in the southernmost region of the Korean Peninsula and/or the majority of the Japanese Archipelago (Nakamura et al., 2010; Han et al., 2023; Song et al., 2023), significant gaps exist in understanding the distribution of EBLFs in these high-latitude regions. Further research, particularly in the northern EBLFs margins where oceanic climates and monsoon systems create unique ecological gradients, will yield critical insights into the evolutionary assembly of these forests.

3 How do and will EBLFs respond to the anthropogenic changes?

The Anthropocene epoch is marked by the profound transformation of Earth's ecosystems due to human activity and climate change (Meng et al., 2021). As EBLFs predominantly occur in densely populated areas of East Asia (Fig. 1), they face exceptional pressure from human activity as well as climate change. Understanding the responses of EBLFs to anthropogenic changes brought about by human activity and climate change is therefore critical for conservation management.

3.1 Human activity

Human activity has driven forest ecosystem degradation in East Asia throughout the Holocene, from the last 11 000 years (Qin et al., 2023b) to the past 5000 years (Zhou et al., 2023). Obviously, the current distribution of EBLFs (Fig. 1) largely coincides with areas of intensive human settlement, resulting in the widespread conversion of primary forests to secondary growth or plantations (Wu, 1980; Song et al., 2005; Wang et al., 2007; Shang et al., 2014; Zhang et al., 2019). Since the early Holocene, the agriculture civilization, particularly rice domestication, has triggered large-scale transformations of forests (Lu, 2017; Roberts et al., 2017; Zuo et al., 2017; Gutaker et al., 2020; Dong et al., 2021; Zheng et al., 2021), leading to progressive loss of native EBLFs (Song & Chen, 2007; Qin et al., 2023b).

In China, EBLFs are concentrated east of the Hu Huanyong Line, with high-latitude ranges in the southernmost Korean Peninsula, and the southern Japanese Archipelago (Fig. 1). The distribution of EBLFs is closely linked to human activity. Consequently, the impact of human activity on EBLFs has become an increasingly prominent area in ecology, biogeography, and conservation. Unfortunately, there has been a significant decline in biodiversity throughout human history, leading to the imminent onset of the sixth mass extinction in Earth's history (Isbel et al., 2017; Johnson et al., 2017). The remarkable biodiversity of EBLFs is inevitably affected by human activity, particularly due to the rapid economic growth and large population densities in these regions. Historical records have indicated that natural forests in southern China were primarily attributed to the limited human influence during the Qin and Han dynasties (Luo & Jin, 2017). However, the subsequent millennia of extensive land use in EBLF regions were coupled with population growth. As the population has increased, these circumstances have undergone significant changes, and the phenomenon known as the "Great Acceleration" has gained considerable attention and has been documented since around 1950 (Steffen et al., 2015), fundamentally transforming these ecosystems (Meng et al., 2021) and disrupting the biodiversity and community structure of forests (Bruelheide et al., 2011; Feng et al., 2014; Tang, 2015b; Liu et al., 2016). On the one hand, species composition and diversity have changed dramatically, leading to shifts in community functional diversity during succession that follows disturbances (Aiba et al., 2001; Biswas & Mallik, 2010; Hu et al., 2014; Huang & Xia, 2019). On the other hand, the biomass and characteristics of forests consistently shift throughout the process of succession following disturbance (Pregitzer & Euskirchen, 2004; Ali et al., 2016). The habitats of EBLFs have undergone conversions for various alternative purposes. Currently, afforestation is experiencing significant growth, as it not only aids in poverty alleviation through economic development but is also recognized as a highly effective strategy for mitigating climate change (Meng et al., 2019b; Zhang et al., 2023a). For instance, *ca.* 15% of total biodiversity loss is attributed to the transmission networks of electrical power systems, which have significantly contributed to biodiversity loss in China (Jin et al., 2022). The expansion of afforestation has resulted in a notable deficiency in plant collections and has even altered biodiversity patterns (Zhang et al., 2022b, 2023a). Specifically, habitat modification in EBLFs has led to the fragmentation of natural ecosystems, posing urgent threats to biodiversity. Consequently, human disturbances have altered various characteristics of EBLFs, and their recovery processes have been asymmetrical. Therefore, conservation plans aimed at restoring biodiversity and ecosystem functionality in EBLFs should adopt multifaceted strategies (Zhang et al., 2019). It is essential to conduct further investigations to assess the risks associated with habitat fragmentation in EBLFs owing to large-scale human activity.

3.2 Climate changes

EBLFs have undergone significant climate transition throughout their evolutionary history, progressing from arid belts through tropical phases to their current subtropical configuration (Sun & Wang, 2005; Song et al., 2019; Meng et al., 2022b; Wu et al., 2024). The response of climate change to the evolution of EBLFs is influenced by several factors. While modeling the distribution shifts from past to present, and even into the future, does not provide direct evidence of the authentic changes in EBLFs to climate change, it is essential to use these models as supplementary tools in demographic history. Additionally, a diverse array of analytical methods must be employed to investigate the connections between environmental changes and the evolutionary processes of organisms that are also affected by climate change.

Extensive research has examined climate influences on EBLFs using multiple approaches, such as palaeoclimatic reconstructions using proxy evidence and climate modeling simulations (e.g., Xu et al., 2016; Meng et al., 2022a; Lin et al., 2023; Fu & Wen, 2023). Climate change has been identified as the primary factor influencing the survival of EBLFs throughout their extensive evolutionary history. The key findings were as follows: (i) EBLFs demonstrated exceptional climatic stability compared to other biome (Huang & Xia, 2019). (ii) A persistent arid belt and the shifts historically constrained the evolution of EBLFs during the Cenozoic Era (Sun & Wang, 2005). (iii) The Middle Miocene Zhangpu biota (tropical rainforest biome) served as an evolutionary reservoir for subtropical biodiversity in the current distribution of EBLFs (Wang et al., 2021). (iv) *Engelhardia*'s tropical-to-subtropical transition coincided with the onset of the EASM and the cooling of the Miocene at the Oligocene–Miocene boundary (Meng et al., 2022a). (v) Paleo-biome reconstructions (LGM) indicate that EBLFs contracted to a narrow belt south of 24° N (Qian & Ricklefs, 2000; Harrison et al., 2001; Ni et al., 2010). In summary, contemporary EBLFs have undergone arid-tropical succession prior to the establishment of the current subtropical elements.

Recent advances in ecological models have enabled projections of demographic trajectories and climatic responses for the taxa of EBLFs (Meng et al., 2022a; Lin et al., 2023; Jin et al., 2024). These predictions vary depending on the model parameterization and the ecological preferences of different taxa. A growing body of research has revealed diverse range dynamics, including expansion, contraction, and stability (e.g., Shi et al., 2014; Ramírez-Preciado et al., 2019; Fan et al., 2022; Meng et al., 2022a; Tang & Zhao, 2022; Lin et al., 2023). For instance, *Castanopsis*, *Quercus* section *Cyclobalanopsis* and *Cinnamomum camphora* demonstrated a general expansion of their northern range northward (Cheuk & Fischer, 2021; Tang et al., 2022; Fan et al., 2022; Li et al., 2023; Lin et al., 2023). Climate-driven warming and drying in tropical and subtropical regions have reduced the availability of suitable habitats for some species (Shi et al., 2014; Deb et al., 2018; Tang & Zhao, 2022). Despite these shifts, EBLFs remained stable distribution (Meng et al., 2022a). EBLF species demonstrate divergent responses to climate change, manifesting as range expansions, contractions, and distributional stability.

The Pliocene–Quaternary climate oscillations created numerous refugia that continue to shape contemporary distribution patterns of plant species, plant diversity, and endemism in subtropical China. These areas demand prioritized inclusion in sustainable forest management and conservation planning (Wang et al., 2009). EBLFs represent exceptional centers of floristic richness and evolutionary innovation, where complex climatic and topographic heterogeneity has fostered continuous diversification (Wu, 1965; Ying, 2001). Notably, these regions have been identified as global Pleistocene refugia for EBLFs lineages that evolved prior to the Neogene and Quaternary glaciations (Axelrod et al., 1996; Wang et al., 2009). Under current warming trends, EBLFs are expected to act as the principal distribution centers for climate-responsive vegetation (Meng et al., 2022a). The response of EBLFs to climate warming will undoubtedly become increasingly significant and urgent in the context of global warming.

The impact of Earth's organisms on climate change is now well documented (Dillon et al., 2010). Climate warming is driving profound ecological shifts, for example, species range modifications, population decline, terrestrial biosphere degradation, biodiversity loss, altered community dynamics, and extinction risk (Meng et al., 2021). In particular, the mountains of southwestern and southern Yunnan in China serve as long-term stable refugia for seven to nine *Castanopsis* species, making them a conservation priority to mitigate extinction threats (Tang et al., 2022). Given these challenges, leveraging past climatic events to predict future refugia, especially in the Anthropocene, is critical. Tropical and subtropical regions, where biodiversity is highly sensitive to warming, are of particular concern. Notably, mid-Pliocene warm-climate zones may mirror contemporary diversity hotspots in subtropical EBLFs (Meng et al., 2022a). While the warming climate could benefit thermophilic species (Meng et al., 2021), the accelerated pace of current climate change demands urgent action. Just as historical refugia (such as the LGM refugia) preserved species during cooling periods, future refugia will be essential for biodiversity persistence under anthropogenic warming. Identifying and protecting both future and existing refugia within EBLFs is essential for conducting and enhancing our understanding of the evolution of EBLFs; especially how the EBLFs respond to the past and future climate.

4 Perspectives for the future studies

4.1 EBLFs should not be considered isolated enclaves

EBLFs represent a unique biome that serves as an ecological bridge between tropical Asia (the southern part of the Indochina Peninsula), northern deciduous broad-leaved forests, and west alpine regions (Fig. 1). While research has focused on the assembly history of common taxa in EBLFs, little is known about the relationship between EBLFs and the adjacent biome. This knowledge gap highlights the need to study EBLFs as integrative components of broader biogeographic systems, rather than as the isolated enclave. We will discuss EBLFs and their neighboring regions in the following sections.

The QTP uplift, a defining Cenozoic geological event, has significantly shaped the topography of Asia and contributed to global cooling (Raymo & Ruddiman, 1992; Rowley, 1996). Major geological events have profoundly influenced the historical distribution and composition of EBLFs. For instance, the presence of *Quercus* subgenus *Cyclobalanopsis* is a characteristic feature of the EBLFs, and fossilized leaves discovered in the late Eocene–Oligocene boundary deposits of eastern Xizang (Markam; Fig. 1) where are distributed the typical alpine flora. These findings were consistent with those reported by Xu et al. (2015), Zhou et al. (2019), and Su et al. (2020), indicating a humid subtropical ecosystem existed at *ca.* 47 Ma from the palaeobotanical data. The connection between EBLFs and the northwestern part of the QTP suggests that EBLFs should not be considered an isolated enclave.

The transitional zone between subtropical EBLFs and the tropical Indochina Peninsula is a critical biogeographic ecotone that merits systematic investigation. The tropical Indochina Peninsula bioregion, situated near the subtropical EBLFs, is geographically distinct from the Thai-Malay Peninsula bioregion due to the separation at the Isthmus of Kra (Wallace, 1876; Woodruff, 2010; Meng & Song, 2023b). However, studies addressing EBLFs and their extension to the tropical Indochina Peninsula are limited. The flora of Southeast Asia and Australia has highlighted the importance of understanding the relationships between plant species in these adjacent regions (Zhang et al., 2023b). Biogeographical patterns in tropical and subtropical areas have been elucidated by examining the typical distributions of *Engelhardia fenzelii*, *E. roxburghiana*; and *Magnolia* Sect. *Michelia* (Meng et al., 2022a; Zhao et al., 2022). Although there are limitations associated with these specific plant species, their distribution patterns from tropical to subtropical regions could serve as ideal models. Examination of additional taxa will enhance the evaluation of evolutionary processes in subtropical EBLFs and the tropical Indochina Peninsula.

The interface between EBLFs and deciduous broad-leaved forests represents a critical ecotone for East Asian vegetation, which has been known as the mixed forests of evergreen and deciduous broad-leaved species, which are delineated by the Qinling–Huaihe line (Song, 1999). Understanding the geographic distribution patterns across this ecotone is important to understand the development of leaf functional traits that are closely linked to the adaptation of plants to changes in their habitats, such as variations in temperature and precipitation. However, the evolutionary processes of EBLFs and deciduous broad-leaved forests are currently understood within a complex hierarchical structure that encompasses their organization and interconnections between EBLFs and deciduous broad-leaved forests, and vice versa. A significant shift in dominant lineages toward deciduous habits occurred in response to the cooling and drying climate during the Middle to Late Eocene. Additionally, the prevalence of EAM led to an increase in extreme seasonal precipitation in the Early Miocene, accelerating the emergence of evergreen habits in the dominant lineages of EBLFs (Qin et al., 2023a).

In summary, the evolution of EBLFs has been fundamentally shaped by historical environmental changes, both within their core ranges and across adjacent ecotone. Future issues of EBLFs should adopt an integrated biome-scale perspective that incorporates their transitional relationships with adjacent flora or biome. It is essential to focus more attention to not only explore the ecological and evolutionary processes, but also improve our understanding of the origin and demographic history of *in situ* plants associated with EBLFs.

4.2 Conservation of EBLFs will be an urgent issue

Understanding how biodiversity in EBLFs responds to environmental changes, including climate variations and human activity, will provide significant insights into conservation policies and ecological management. Such knowledge enables more accurate predictions about how these changes may affect EBLF ecosystem services. Woodruff (2010) demonstrated that conservation and biogeography are fundamentally linked through their shared dependence on geological history, primary productivity, habitat characteristics, and species richness patterns. Notably, conservation biology and biogeography are intricately interconnected, and evolutionary and ecological research can contribute to the establishment of sustainable conservation objectives that inform current biodiversity patterns and processes (Meng et al., 2022a). In the Anthropocene, when climate change and human activity exerted unprecedented pressure on ecosystems (Meng et al., 2021), this interdisciplinary approach became essential. The integration of conservation, biogeography, and other subfields of biology should be considered during the development of scientific guidelines for biodiversity conservation. Despite the early recognition of this connection (Dasmann, 1972; Diamond, 1975) biogeographic principles remain underutilized in conservation planning, policy-making, and management (Whittaker et al., 2005). Therefore, integrating biogeographic perspectives, particularly regarding species distribution, historical contingencies, and ecological thresholds, is a priority for biodiversity conservation practice.

While the ice sheets devastated high-latitude regions of Europe and North America, East Asia experienced comparatively limited glaciation, with significant ice coverage restricted primarily to high-altitude mountain systems (Ehlers & Gibbard, 2007; Fig. 2C). Consequently, assessing fluctuations in plant biodiversity and their long-term sustainability over extended periods of biogeography can aid in identifying contemporary refugia. This identification emphasizes the importance of biodiversity conservation and the resilience of refugia in the face of regional climate change (Meng et al., 2022a). Therefore, an increasing number of studies have examined the responses of plant taxa in EBLFs to past and future climate shifts, focusing on refugia that have played, and will continue to play crucial roles in preserving the diversity of EBLF plants in potential climate-suitable zones (Qiu et al., 2011; Shi et al., 2014; Sun et al., 2014; Kou et al., 2016; Meng et al., 2019a; Wang, 2024).

Global warming is driving a significant range shift in species distribution, which in turn leads to changes in their genetics, seasonal community interactions, phenology, and extinction rate, which have diverse and significant impacts on organisms (Dillon et al., 2010). Given the escalating phenomenon of climate warming, plant communities experience substantial changes that often delay their response to these shifts (Alexander et al., 2018; Wang et al., 2023). The distribution ranges of EBLFs are primarily concentrated in densely populated areas (Fig. 1), particularly in central and southern Japan, the southernmost regions of Korea, and various parts of China. However, the distribution ranges of EBLFs are complex: EBLFs primarily persist at higher elevations in China, however, these forests occur predominantly at lower elevations (<700 m asl) in Japan and southern Korea. This elevational divergence suggests that highland areas in China may serve as important climate refugia, potentially offering more favorable conditions under ongoing warming.

Furthermore, the rapid population growth and associated resource demands are exerting unprecedented pressure on these ecosystems. If the distribution ranges of species do not keep pace with the rate of climate warming and human disturbance, the potential displacement of EBLFs into new ecological niches may have serious implications for survival. The current distribution of EBLFs indicates the presence of favorable conditions and potentially suitable ranges for future climate change (Meng et al., 2022b). In this scenario, it is imperative to evaluate the response of EBLFs to human activity to determine the necessity of establishing potential buffer zones for EBLFs. Conservation communities and organizations are emphasizing the urgent need to address biodiversity loss in the face of ongoing human activity and climate change. Currently, many researchers are engaged in efforts to identify potential climate refugia, highlighting the need for increased attention to both climate change and human activity (Shoo et al., 2011; Groves et al., 2012; Olson et al., 2012; Meng et al., 2021). Therefore, understanding how EBLFs respond to environmental changes is crucial for ensuring their long-term persistence and survival throughout their evolution. The identification and establishment of targeted conservation areas within the distribution ranges of EBLFs are effective strategies for addressing the challenges posed by the rapid global change.

5 Conclusions and suggestions

Initially, the origin and evolution of EBLFs have been profoundly shaped by monsoon systems intensification, as evidenced by both molecular and palaeobotanical data. Fossil taxa can provide a comprehensive understanding of evolution, as numerous organisms that have inhabited the Earth throughout its history are no longer extant (Meng et al., 2014). Therefore, it is undeniable that fossil records offer valuable insights into the evolution of EBLFs from palaeobotanical evidence. However, the evolution of EBLFs indicated by fossil records may predate molecular dating in biogeography (e.g., Xu et al., 2008; Hoke et al., 2014; Gourbet et al., 2017; Linnemann et al., 2018; Tian et al., 2021). Previous studies have not effectively integrated analyses and concerns related to the reconstruction of palaeoenvironments or molecular dating, as they primarily rely on either the molecular dating of modern plants or the geological ages of fossil records to reconstruct the spatiotemporal evolution of EBLFs. Only a limited number of biogeographic and diversification rate analyses, molecular dating, palaeoenvironmental reconstruction, and geological events have been conducted to provide a comprehensive set of complementary analyses supporting the evolution of EBLFs. We acknowledge that fossil records are consistently scarce and fragmented, resulting in intermittent documentation of geological events. However, fossil records and the availability of open data in databases over time to understand the distribution patterns of EBLFs as well as the integration of molecular evidence into paleontological studies, and vice versa, should be prioritized.

Second, the various patterns of flora distributed around or interspersed within the EBLFs (i.e., the deciduous broad-leaved forests, tropical rainforests, and alpine forests) and the different types of taxa should take into account the evolutionary and ecological aspects of relevant taxa from adjacent regions, rather than solely focusing on the plant taxa of the EBLFs. Therefore, it is of utmost importance to conduct a comprehensive survey of plant species that are representative of each bioregion surrounding the EBLFs, including deciduous broad-leaved forests, tropical rainforests, and alpine forests. Future studies concerning the evolution of EBLFs should not exclusively concentrate on the *in situ* taxa, as EBLFs are not confined to a specific enclave. To determine the extent to which colonization by neighboring plant species versus *in situ* speciation contributes to the diversity of taxa, it is essential to investigate a range of widely distributed taxa across various biomes within a defined geographic framework of the EBLFs. Currently, the evolution of typical taxa, such as the "Big Four" (i.e., Fagaceae, Lauraceae, Magnoliaceae, and Theaceae), has been extensively documented to enhance our understanding of the evolution of EBLFs. However, investigations on the evolutionary patterns of various highly diverse groups, particularly herbaceous plants, remain limited. This is primarily due to the predominant focus on studying common tree species in EBLFs, which do not represent the entirety of the EBLF ecosystem.

In conclusion, this review highlights the critical need to integrate evolution and ecology into the conservation strategies of EBLFs. As we enter the Anthropocene, the combined pressures of climate change and human activity have been closely associated with the evolution of EBLFs, threatening and accelerating biodiversity loss in these ecosystems, particularly for rare plant species that are characterized by limited geographical distribution. For these groups, it is essential to implement effective conservation management strategies and initiate preliminary efforts to mitigate the impact of human activity on the distribution of subtropical EBLFs.

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Author Contributions

Hong-Hu Meng, Yi-Gang Song, Guo-Xiong Hu, Wei Wang, Zhe-Kun Zhou, and Jie Li designed this study. Hong-Hu Meng completed the original draft and revision, writing, and visualization. Hong-Hu Meng, Yi-Gang Song, Guo-Xiong Hu, Xiao-Guo Xiang, Wei Wang, and Zke-Kun Zhou improved the manuscript draft and revision; all authors (Hong-Hu Meng, Yi-Gang Song, Guo-Xiong Hu, Pei-Han Huang, Min Li, Ou-Yan Fang, Ren-Ping Su, Guan-Long Cao, Xiang Cai, Shi-Shun Zhou, Yun-Hong Tan, Xiao-Guo Xiang, Wei Wang, Zhe-Kun Zhou, Jie Li) contributed to the final revision of the manuscript.

Conflicts of Interest

All authors declare that they have no conflict of interest.

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