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Review

On the Origin of Evergreen Broad-Leaved Forest in Eastern Asia from the Evidence of Floristic Elements

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Abstract: The arguments on the origin and evolution of the evergreen broad-leaved forest in eastern Asia, especially in the evolutionary process, exist generally, even contrary in some cases. The origin and evolution of the flora of eastern Asia, the formation time of Asian monsoon, and the implications from phylogenetic and molecular biogeographic studies in some important taxa, as well as in palaeobotanical evidences, are debatable. Most researches from different disciplines suggested that the monsoon in Miocene is a key to diversification of eastern Asian flora and its evergreen broad-leaved forest. The common view is that the evergreen broad-leaved forest of East Asia is closely related to the monsoon intensity and developments, which are caused by the uplift of Himalaya-Tibet, during or after the mid-Miocene. The analysis on the floristic elements show that the present subtropical evergreen broad-leaved forest in eastern Asia could have an early or ancient tropical origin and a tropical Asian affinity, but their species are dominated by the Chinese endemic or eastern Asian distribution, many of which are the tropical sister ones. The time of Himalayan uplift and intensity of monsoon climate is believed the key for the formation of the evergreen broad-leaved forest in eastern Asia. Combined existing palaeobotanical findings, the uplift of Himalayas and the formation of monsoon climate, as well as floristic elements of the subtropical evergreen broad-leaved forest, we believe that it was evolved from a Asian tropical rain forest after mid-Miocene in southeastern region of eastern Asia, while the ancient subtropical evergreen broad-leaved forests in southwestern region continuously evolved into the present subtropical ones.

Keywords: Floristic elements; origin and evolution; subtropical evergreen broad-leaved forest; East Asia

1. Debates in the Origin and Evolution of the Flora in East Asia

Wu analyzed Chinese seed plant flora at generic level, giving the conclusion that the Chinese flora had a tropical floristic affinity [1]. In this way, the evergreen broad-leaved forest, as a core evergreen forest in eastern Asia, consequently has a tropical floristic affinity beyond question. In floristic regionalization of the world [2], the area of eastern Asian subtropical evergreen broad-leaved forest was delineated in the Eastern Asiatic floristic region. Later, Wu and Wu raised this floristic region to a kingdom level, the Eastern Asiatic Kingdom, considering its uniqueness with more than 30 endemic families and an exceptionally large number of endemic genera [3]. The Eastern Asiatic Kingdom was further divided into Sino-Himalayan (with 144 endemic genera) and Sino-Japanese (with 104 endemic genera) subkingdoms [3]. The Eastern Asiatic Kingdom was supposed to be one of the major centers for the evolution of higher seed plants, as the floristic kingdom is especially rich in gymnosperms and primitive angiosperms [3]. However, arguments on the origin of the evergreen broad-leaved forest in eastern Asia, and on the floristic subdivision of the Eastern Asiatic Kingdom, referring to their floristic origin, have been existed for a long time.

Generally, East Asia was considered to be home to high biodiversity and endemism [4]. Based on the findings in paleoendemic taxa, eastern Asian region has also been considered to be a floristic museum [3, 5]. It was suggested that direct competition with angiosperms increased the extinction of conifers [6]. In eastern Asia, same should be happen. The angiosperms increased with failing of conifers.

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Mountains of southern China were considered to be both "Plant Museums" and "Plant Cradles" [5]. In Chinese southern mountains, "refugia" and main endemism really existed. It was clarified that young endemics are more in the mountain ranges of the eastern fringe of the Tibetan Plateau ("plant cradles"), but old endemics tend to occur in the mountains of central, south central, and southeastern China ("plant museums"), which were believed to be related to the different geological history of the mountain ranges [5]. The eastern fringe of the Tibetan Plateau mostly formed by the uplift of Himalaya in the late Neogene [7, 8], while central and southern China during most of the Tertiary was tectonic stability. This support Wu & Wu's idea that the Sino-Japanese floristic region was older than the Sino-Himalayan region in floristic origin in East Asia [3]. However, recent palaeobotanical researches revealed that the Qinghai-Tibet Plateau should rise earlier, and would be in Paleogene [9, 10, 11, 12], which challenged the previous ideas.

Studies on evolutionary history of the angiosperm flora of China found that 66% of the angiosperm genera in China did not originate until early in the Miocene epoch (23 million years ago (Mya))[13]. The flora of eastern China bears a syndrome of older divergence (divergence times of 22.04–25.39 Mya), phylogenetic overdispersion (spatial co-occurrence of distant relatives) and higher phylogenetic diversity, while in western China, the flora shows more recent divergence (divergence times of 15.29–18.86 Mya), pronounced phylogenetic clustering (co-occurrence of close relatives) and lower phylogenetic diversity [13]. Eastern China represents a floristic museum, while western China an evolutionary cradle, especially for herbaceous genera; but for woody genera, eastern China has served as both a museum and a cradle [13]. Chen et al. asked a question: is that the East Asian flora ancient or not[14]? They synthesized molecular, fossil data on seed plants, focusing on the biogeographical origins and historical evolution of the East Asia flora. Their results suggest that the East Asia flora might be relatively young, with most of its clades originating since the Miocene. East Asia was a refuge of many ancient relict plants, but not their origin area[14]. The former Sino-Himalayan Flora was renamed as the *Rhododendron* Flora, and the Sino-Japanese Flora as the *Metasequoia* Flora in East Asia Flora, and considered the *Rhododendron* Flora and the *Metasequoia* Flora both were probably of a similar age [14]. It was also suggested that the formation and development of the Asian monsoon might have been the main factors that have driven the evolution of East Asia flora [14].

The current fossil history of five endemic families (Cercidiphyllaceae, Eucommiaceae, Ginkgoaceae, Sargentodoxaceae and Treochodendraceae) and 20 endemic genera was studied [15]. It was found that these endemic plants have three souces: one from Arctic-Tertiary, one boreotropic and one East Asia. The East flora has a complex origin and the modern East Asia plant kingdom would be formed in the late Pliocene or early Quaternary [15].

2. Debates in the Formation Time of Asian Monsoon

The Asian monsoon is believed to be a key factor to the origin of the evergreen broad-leaved forests in eastern Asia. However, the timing of the Asian monsoon formation and intensification is debatable.

Based on the simulation of late Oligocene paleogeographic data, it was suggested that the uplift of the northern Qinghai-Tibet Plateau from the Paleogene enhanced the East Asian monsoon climate system and drove the formation of humid and semi-humid vegetation types dominated by evergreen broad-leaved forests in East Asia [16]. This idea implicated that the evergreen broad-leaved forests in East Asia could be formed in Paleogene. Uplift of the Himalayan and Tibetan Plateau and its linkage with the evolution of the Asian monsoon was discussed [17]. It was suggested that the uplift of the southern and central Tibetan Plateau should have intensified the Indian summer monsoon at 40–35 Mya, and should have intensified the desertification of inland Asia at 25–20 Mya; while the uplift of the northeastern and eastern Tibetan Plateau should have further intensified the East Asian summer monsoon and East Asian winter monsoon at 15–10 Mya [17], which implicated that the evergreen broad-leaved forests in eastern Asia would be formed in Neogene. Although there is much debatable about the timing of the monsoon climate in East Asia, the mainstream view in the past is that in the late Eocene, about 45–50 Mya ago, the Indian plate and the Eurasian plate collided

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and integrated, and the Himalayan-Tibetan Plateau did not strongly rise, but experienced a long process of uplift and deplanation, long at a low altitude (1000-2000 m), as well as the Himalaya was not so high until the Quaternary before 3.4 Mya or 2.5 Mya[7, 8]. It was recently proposed that the Qinghai-Tibet Plateau should rise earlier based on their palaeobotanical researches[9, 10]. It was also believed that the part of Himalayan-Tibetan Plateau had reached 4,600 meters in 35 Mya [18].

The impacts of major geological events on Chinese flora were reviewed [19]. It was stated that the main families of the evergreen broad-leaved forest of East Asia, i.e., Fagaceae, Lauraceae, Magnoliaceae, Fabaceae, Hamamelidaceae have been presented in China since Paleogene, and the floristic composition of fossils in southern China have been similar to the ones of the present evergreen broad-leaved forests at that time. They also pointed out that the monsoon intensity and developments are correlated with the height of the Qinghai-Tibetan plateau, which are the main factor for appearance of the evergreen broad-leaved forest of East Asia [19].

It is common view that the evergreen broad-leaved forest of East Asia is closely related to the monsoon intensity and developments, which are caused by the uplift of Himalaya-Tibet. The question is when the Himalaya-Tibet uplifted to enough height to create the monsoon. This is back again to the controversial issue, such as that the Himalaya-Tibet already uplifted significant height to formation of monsoon before the Miocene [20], or that the Himalaya-Tibet has a slowly uplift to the present height in later Pliocene [21], or the Himalaya was not so high until the Quaternary before 3.4 Mya or 2.5 Mya [7, 8].

During the Cretaceous period, China was high in the east and low in the west, and was in a subtropical high drought zone [22]. The north-south range has expanded from north latitude 18 degrees to about north latitude 38 degrees, and the climate is hot and dry [22]. During that time, there was not a tropical or subtropical evergreen broad-leaved forest in China. Since the late Oligocene-early Miocene (about 26–22 Mya), the Himalayas began to rise strongly, and the Yunnan-Guizhou Plateau was basically formed, as well as the Asian monsoon has significantly increased and the subtropical arid zone of central and eastern China has disappeared, replaced by a warm and humid Asian monsoon climate[22]. A sporopollen assemblages recorded in late Eocene strata of the Jianchuan Basin in southwest China was studied, which implicated that the climate was relatively dry and hot, and the vegetation was a tropical to subtropical sparse forest at that period [23], and later during the period 40.6–37.5 Mya, there was a prominent decrease in xerophilous plants in the fossil assemblages, which implicated that a climate with increased humidity, and the vegetation could be an evergreen deciduous broad-leaved trees mixed with coniferous forest under a subtropical–temperate climate [23]. It was also concluded that the humid monsoon climate may have reached the position of the modern monsoon front by the early late Oligocene[23]. Using a general circulation model and geological data, the drivers controlling the evolution of the monsoon system over the past 150 Mya were explored [24]. It was suggested that, apart from a dry period in the middle Cretaceous, a monsoon system had existed in East Asia since at least the Early Cretaceous[24].

Until now, the timing of the monsoon climate in East Asia, which leads to the formation of the evergreen broad-leaved forest in eastern Asia, is still uncertainty. Undoubtedly, the formation of the Himalayas greatly drives the strength of the southwest monsoon [12].

3. Phylogenetic and Molecular Biogeographic Implications from Important Taxa

Recent years, many phylogenetic and molecular biogeography researches on genera and species with eastern Asia distribution were published, helping to clarify the origin of eastern Asia flora. Several examples are selected as the following:

A group of white pines was studied [25]. It was found that two main clades of subtropical East Asian white pines first diverged in the early Miocene, and by the late Miocene all species appeared[25]. It was suggested that the monsoon-driven assembly of evergreen broad-leaved forests might have significantly affected the diversification of subtropical East Asian white pines [25]. It was also indicated that subtropical East Asia is not only a floristic museum, but also a diversification center for gymnosperms [25]. Evolutionary radiation of the genus *Oreocharis* (Gesneriaceae) has diversified extensively throughout East Asia, especially within the Hengduan Mountains. This genus

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contains 28 species, of which 27 species in China, a fewer in northern Vietnam [26]. The diversification dynamic of *Oreocharis* was believed most likely positively associated with temperature-dependent speciation and dependency on the Asian monsoons [26]. The warm and humid climate of the mid-Miocene, together with the East Asian monsoons and global temperature change may have functioned synchronously as the primary drivers of diversification in *Oreocharis* [26]. The studies on white pines and the *Oreocharis* suggested that the monsoon in Miocene was a key to diversification of eastern Asian flora and its evergreen broad-leaved forest.

The tea family (Theaceae), a characteristic component of the subtropical evergreen broad-leaved forests, integrating data from other characteristic components of subtropical forests, including Fagaceae, Lauraceae and Magnoliaceae, was used to discuss the assembly of Asian evergreen broad-leaved forests [27]. It was found that most of the essential elements of the subtropical evergreen broad-leaved forests appeared to have originated around the Oligocene–Miocene (O–M) boundary, but small woody lineages from Theaceae were dated to the late Miocene [27]. Their results suggested that two independent intensifications of the East Asian summer monsoon around the O–M boundary and the late Miocene may have facilitated the historical assembly of the subtropical evergreen broad-leaved forest in East Asia.

Quercus section *Cyclobalanopsis*, a dominant lineage in East Asian evergreen broad-leaved forests, was studied [28]. The earliest divergences in section *Cyclobalanopsis* correspond to the phased uplift of the Himalayas and lateral extrusion of Indochina at the transition of the Oligocene and Miocene, while the highest rate of diversification occurred in the late Miocene [28]. It was believed that the dispersal of *Cyclobalanopsis* from Sino-Himalaya and the Palaeotropics to Sino-Japan in the Miocene was facilitated by the increased intensity of East Asian summer monsoons and by the Middle Miocene Climatic Optimum [28]. It was implicated that the eastern Asian evergreen broad-leaved forests could begin in Sino-Himalaya, and dispersed into the region of Sino-Japan in the Miocene [28]**.** *Quercus* section *Ilex* was believed to have widespread along the East Tethys sea way from the middle Eocene onward, and the species of the group characterized the sclerophyllous evergreen broad-leaved forest in eastern Asia as a particular Tethys affiliated remnant vegetation [29]. Studied on the origins of the species *Quercus* section *Ilex* (holly oaks) revealed that that the section *Ilex* originated in East Asia and dispersed to Europe through a warm, humid evergreen forest corridor in Tibet-Himalaya during the Oligocene[30].

The biogeographical diversification of mainland Asian *Dendrobium* (Orchidaceae) implicated that the evergreen broad-leaved forests have been established in mainland Asia at least since the Oligocene [31]. The time for evergreen broad-leaved forests established in eastern Asia was suggested earlier [31] than most other researches.

East Asia-North America disjunct distribution genera are an important floristic element in the subtropical evergreen broad-leaved forest in eastern Asia. Tsuga (hemlock) is such a genus of Pinaceae with a typical intercontinental disjunct distribution in East Asia and eastern and western North America. It often occurs on the mountains above the subtropical evergreen broad-leaved forest. Phylogenetic analysis revealed that *Tsuga* very likely originated from North America in the late Oligocene and dispersed from America to East Asia via the Bering Land Bridge during the middle Miocene, and complex reticulate evolutionary pattern among the East Asian hemlock species has happened [32]. The clade Benthamidia in genus Cornus is also *a floristic element in the subtropical evergreen broad-leaved forest in eastern Asia.* It is an *East Asia-North America disjunct distribution taxa [33]. Based on* construction of molecular phylotree and reconstruction of ancestral regions of the clade Benthamidia, it was found that the Benthamidia contains two distinct clades: East Asia and North America, and also found that the ancestors of Benthamidia diverged in the southern part of East Asia, producing the present-day East Asian clade in the middle Oligocene *[33].* These two molecular phylogenetic studies above indicated that the *subtropical evergreen broad-leaved forest in eastern Asia has floristic affinities with northern America in* a certain extent.

Long-term cooling had a disproportionate effect on non-tropical diversification rates, leading to dynamic young communities outside the tropics, while relative stability in tropical climes led to

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older, slower-evolving but still species-rich communities [34], which implicated that the present subtropical communities in eastern Asia could be young.

Although molecular biogeographical researches on different taxa above revealed different occurring time and dispersion roads of the eastern Asian evergreen broad-leaved forest, most researches suggested that the evergreen broad-leaved forest appeared in the Miocene driving by eastern Asian monsoon.

4. Palaeobotanical Evidences

Palaeobotanical studies offer well clues to the origin and evolution of East Asia flora. The fossil history of seed plant genera that are now endemic to eastern Asia, was reviewed [35]. It was found that the majority of now "eastern Asian endemic" genera had fossil records from Europe and/or North America, indicating that eastern Asia served as a late Tertiary or Quaternary refugium for them, although many of these genera may have originated in other parts of the Northern Hemisphere [35]. However, these genera with fossils that are now endemic to eastern Asia, contribute only a small part of the floristic composition of the evergreen broad-leaved forest of eastern Asia.

Based on the Chinese Neogene data including 71 palaeobotanical sites from early Early Miocene to Pliocene, the Neogene vegetation of southern China was reconstructed [36]. It was found that the broad-leaved evergreen component was greater in the more southern areas, and had a further rise of the broad-leaved evergreen component in the southern areas, indicating an increasingly warm and moist climate. The more western areas were drier than the eastern ones in the Early Miocene but this variation vanished in the Late Miocene, and again aridification of the western regions occurred in the Pliocene [36].

The evergreen broad-leaved forest in southwestern China was suggested to start in the later Miocene [37, 38, 39]. However, in late Oligocene, except Trigonobalanus, all genera of Fagaceae had records in China, and dominated in the Neogene fossils, suggesting that the evergreen broad-leaved forest of eastern Asia could be presented since the Neogene [19].

Based on palaeobotanical and molecular phylogeny studies on the psychrophytes in Hengduan Mts, the psychrophytes has built up since early Oligocene [11]. Some present genera and species, such as *Quercus, Alnus, Betula, Carpinus, Carya, Pterocarya*e etc., appeared in Luhe basin in southwestern China (central Yunnan) in early Oligocene (3300-3200 Ma) [40]. The subtropical forests were supposed to exist in the central Qinghai-Tibetan Plateau in 4700 Ma [41]. The occurrence of fossil fruits of the strictly tropical Southeast Asian rain forest family Dipterocarpaceae in the middle Miocene in Fujian, southeast China [38, 42] suggested that southern Fujian had a tropical rain forest vegetation of Southeast Asia at that time [43]. However, fossil sites offer occasionally contradictory implication. For example, a present temperate to subtropical deciduous tree *Parrotia* (Hamamelidaceae) was found in the dipterocarp fossil assemble in the middle Miocene in Fujian, which coexisted with plants of Dipterocarpaceae (*Dipterocarpus, Hopea, Parashorea, Shorea*) [44], but the dipterocarp fossils in the assemble indicated that the fossil assemble represented a tropical SE Asian rain forest. This temperate deciduous tree *Parrotia* found in the tropical fossil assemble complicate the situation.

The paleobotanical evidences reveal that the southwestern and southeastern China could have different vegetation in the Miocene. Obviously, the evergreen broad-leaved forest was suggested already existent in southwestern China in Miocene, but tropical rain forest vegetation of Southeast Asia existed at that time in southern Fujian from palaeobotanical evidences. These entangle the origin of eastern Asia flora including the evergreen broad-leaved forests.

5. The Floristic Elements of the Subtropical Evergreen Broad-Leaved Forest in East Asia

The vegetation characteristics and species composition of the subtropical evergreen broad-leaved forests using eight dynamics plots in evergreen broad-leaved forests in eastern China was studied[45]. These eight dynamics plots are Tiantong (29°48′ N, 121°47′ E, 304–603 m altitude), Gutianshan (29°15′ N, 118°07′ E, 446.3–714.9 m altitude), Baishanzu (27°45′ N, 119°13′ E, 1,470–1,593 m altitude), Badagongshan (29°46' N, 110°25' E, 1,355–1,456 m altitude), Heishiding (23°31′ N, 111°52′

E, 435–698 m altitude), Dinghushan (23°10′ N, 112°31′ E, 230–470 m altitude), Fushan (24°45′ N, 121°33′ E, 650–700 m altitude) and Lianhuachi (23°54′ N, 120°52′ E, 667–845 m altitude). They cover main subtropical evergreen broad-leaved forest types in eastern Asia. Based on the species list of the eight dynamics plots [45], we made an analysis of the floristic elements.

Firstly, at family level, we find that the tropical families contribute 52.69% of the total families, of them the pantropic families make up 37.63%, which is the highest element; while the temperate families contribute 29.04% (Table 1). This indicates that the subtropical evergreen broad-leaved forest could have an early or ancient tropical origin.

Secondly, at generic level, the tropical genera contribute 62.41% of the total genera, of them the tropical Asian genera make up 19.50%, which is the highest ratio; while the temperate genera, including the ones of east Asia and endemic to China, contribute 36.52% (Table 2). This reveals that the subtropical evergreen broad-leaved forest has evidently a tropical affinity at genera, especially affected by tropical Asian element (floristic elements at generic level have been recognized to reflect the floristic affinity in biogeography).

Thirdly, at specific level, the tropical species contribute 25.90% of the total species, of them, the tropical Asian species, including mainland southeast Asian distribution, make up 23.78%; while endemic species to China or east Asia elements contribute 66.63%, which make up the highest ratio (Table 3). This illustrate that the subtropical evergreen broad-leaved forest is dominated by the eastern Asian floristic element at species level, which indicates the present subtropical evergreen broad-leaved forest has evolved into a vegetation almost endemic to east Asia.

Table 1. Biogeographical elements of seed plants at the family level of the subtropical evergreen broad-leaved forest (8 plots) in eastern Asia.

Biogeographical elements at family level	No. of families	Family %*
Cosmopolitan	17	18.28
Pantropic	35	37.63
Tropical Asia & tropical America disjunct	9	9.68
Old World tropic	1	1.08
Tropical Asia to tropical Australia	2	2.15
Tropical Asia	2	2.15
(Tropical in all)	(49)	(52.69)
North temperate	16	17.2
East Asia & North America disjunct	5	5.38
East Asia	5	5.38
Endemic to China	1	1.08
(Temperate in all)	(27)	(29.04)
Total no. of families	93	100

*Percentages are calculated by the number of families in each geographical element divided by the total number of families in all geographical elements, then multiplied by 100%.

Table 2. Biogeographic elements of seed plant taxa at the generic level of the subtropical evergreen broad-leaved forest (8 plots) in eastern Asia.

Biogeographical elements at generic level	No. of genera	Genera %*
Cosmopolitan	3	1.06
Pantropic	50	17.73
Tropical Asia &Tropical America disjunct	15	5.32
Old World tropic	19	6.74
Tropical Asia to tropical Australia	28	9.93
Tropical Asia to tropical Africa	9	3.19
Tropical Asia	55	19.50
(Tropical in all)	(176)	(62.41)
North temperate	32	11.35
East Asia & North America disjunct	25	8.87
Old World temperate	4	1.42
Temperate Asia	1	0.35
Mediterranean, Western Asia to Central Asia	1	0.35
Central Asia	0	0.00
East Asia	31	10.99
15 Endemic to China	9	3.19
(Temperate in all)	(103)	(36.52)
Total no. of genera	282	100.00

*Percentage was calculated by the number of genera in each geographical element divided by the number of genera of all geographical elements, then multiplied by 100%.

Table 3. The distributional patterns of seed plant species in the 8 permanent plots from subtropical evergreen broad-leaved forests in East Asia.

Distributional patterns at specific level	No. of species	Species (%)*
I. Old World Tropic	4	0.50
II. Tropical Asia to Tropical Australia	13	1.62
III. Tropical Asia (India-Malesia) to China or to E Asia	(89)	(11.08)
IIIa. to China	62	7.72
IIIb. To East Asia	27	3.36
IV. Mainland SE Asia to China or to E Asia	(102)	(12.70)
IVa. Mainland SE Asia to China	66	8.22
IVb. Mainland SE Asia to East Asia	36	4.48
V. S Himalayas via Mainland SE Asia to China or E Asia	(58)	(7.22)
Va. S Himalayas via Mainland SE Asia to China or E Asia	46	5.73

Vb. S Himalayas to China or E Asia	12	1.49
VI. Endemic to China or East Asia	(535)	(66.63)
VIa. Endemic to China	410	51.06
VIb. Endemic to East Asia (Northeast to Japan and or Korea)	125	15.57
VII. SW Asia, the Mediterranean to China	2	0.25
总计（All）	803	100.00

*Percentage was calculated by the number of species in each geographical element divided by the number of species of all geographical elements, then multiplied by 100%.

6. Origin and Evolution of the Subtropical Evergreen Broad-Leaved Forest in Eastern Asia

Qian & Ricklefs analyzed the temperate zone genera of eastern Asia and eastern North America and found that eastern Asia has twice species diversity to North America although both of them shared genera in mostly sister pairs and share a common history of adaptaion and ecological relationship before disjunction [4]. It was proposed that the anomality in diversity between eastern Asia and eastern North America was the extreme physiographical heterogeneity of temperate eastern Asia [4]. Therefore, the origin of the eastern Asian flora, including the one of the evergreen broad-leaved forest, should have a more complicated history.

The geological and climatic histories of a region directly affect the formation and evolution of its flora and vegetation [46, 47]. The findings of paleobotanical research not only provide a basis for exploring the time of Himalayan uplift and monsoon climate formation, but also a key factor to solve the evolutionary history of regional flora and vegetation. The time of Himalayan uplift and intensity of monsoon climate is the key for the evergreen broad-leaved forest in eastern Asia.

It was revealed that the Sino-Himalayan flora developed from lowland biomes predominantly characterized by tropical floristic elements before the collision between the Indian subcontinent and Eurasia during the Early Cenozoic [48]. The present Sino-Himalayan flora is relatively young, and influenced by the uplifts of the Himalaya and Hengduan Mountains and the onset and intensification of the Asian monsoon system [48]. This supported our floristic suggestions that the subtropical evergreen broad-leaved forest could have an early or ancient tropical origin, in both the Sino-Japanese region and the Sino-Himalayan region.

Jacques et al. suggested that the more western areas were drier than the eastern ones in the Early Miocene; but this vanished in the Late Miocene with all areas having a balanced supply of moisture, again aridification of the western regions occurred in the Pliocene [36]. The earliest dipterocarp fossils in eastern Asia, which indicated a tropical rain forest vegetation, were found in Maoming Basin in southern China (21 ° 70 ′ N, 110 ° 89 ′ E) in the Late Eocene [49]. In the middle Miocene, dipterocarp fossils were found in southern Fujian (24°12′N, 117°53′E) of southeastern China, which indicated a tropical rain forest vegetation [38, 42, 43]. It is revealed that the tropical rain forest of Southeast Asia appeared in the southern China in the Late Eocene, and later in southeastern China in the middle Miocene. Based on the paleobotanical findings above, we hypothesize that the vegetation in the southeast and southwest of China may have different evolution from the Miocene to the Pliocene. Evergreen broad-leaved forests in eastern China may appear later than those in western China. Evergreen broad-leaved forests in eastern China could be evolved from tropical rain forest after the middle Miocene.

During the hottest period of the Miocene period, the tropical rain forests of SE Asia moved north into southeast China, even to southern Japan [50, 51]. This gives us an idea: the modern subtropical evergreen broad-leaved forest developed in southeastern China with the tropical rain forest retreating to the south after the middle Miocene. On the other hand, in SW China, such as Yunnan, Guizhou and Sichuan, even Xizang (Tibet), there were not fossil records of the typical tropical rain forest components (for example, dipterocarp fossils) during the Neocene, but a lot fossils of the subtropical evergreen broad-leaved forest components found. This could match Jacques et al.'s conclusion that the more western Chinese areas were drier than the eastern ones in the Early Miocene and aridification of the western regions occurred in the Pliocene [36]. We believe that the typical tropical rain forest could not be appeared in SW China during the Miocene to the late Pliocene. As we supposed, the tropical rain forest vegetation could occur late in Yunnan in southwestern China, not earlier than before 5–3Mya [46, 52, 53].

Southern Fujian in southeastern China has a typical subtropical evergreen broad-leaved forest, but a tropical rain forest vegetation of Southeast Asia existed in the middle Miocene [38, 42, 43]; while in the almost same time, the paleobotanical information in southwest China had a subtropical evergreen broad-leaved forest, similar to the present vegetation [37], meaning that the southwestern and southeastern China should have different climatic and vegetation at least in the middle Miocene.

Many tropical Asian taxa are more widespread in subtropical area of eastern Asia, and some are represented in the subtropical evergreen broad-leaved forest, or are locally endemic tropical sister species, for example, these tropical sister species belonging to the tropical or tropical Asian genera such as *Schima*, *Altingia, Exbucklandia*, *Rhodoleia*, *Nyssa, Lithocarpus, Castanopsis*, *Sloanea*, *Symplocos, Daphniphyllum, Meliosma, Illicium, Bischofia* and *Adinandra*. These woody tropical families and genera have evolved subtropical and temperate sister taxa in eastern Asia. Understory of the subtropical evergreen broad-leaved forest in eastern Asia, tropical herbaceous families Gesneriaceae, *Begoniaceae*, and *Elatostema* of Urticaceae have evolved a lot of eastern Asian or Chinese species [54].

An example is the so-call tropical rain forest in Jinggangshan of Jiangxi Province (at 26.57°N) [55], where is in the zone of typical subtropical evergreen broad-leaved forest [56]. From the investigation on the forest in Jinggangshan [55], it has some characteristics, such as big woody lianas, big tree with buttress, which is similar to a tropical rain forest. The tree species with high phytosociological importance are *Distylium myricoides, Castanopsis lamontii, Exbucklandia tonkinensis, Alniphyllum fortune,* which are mostly endemic to China or eastern Asia, but they are tropical sister species because their genera are mainly tropical SE Asia distribution.

Lasianthus is a large genus of Rubiaceae, predominantly in the Old World tropics. The greatest species diversity was found in tropical Asia [57]. The species of the genus occur almost exclusively in the understory of primary forests, especially the tropical rain forest. In this genus, only one species, i.e., *Lasianthus japonicas*, has a typical East Asia distribution. *It* includes two subspecies. Subsp. *japonicus* occurs in southeastern China to Japan below 1000 m alt., and basically in the Sino-Japanese floristic region delineated by Wu & Wu [3]. Subsp. *longicaudus* occurs on montanes over 1000 m alt. of southwestern China to Himalayan region, i.e., Sino-Himalayan floristic region [58, 59, 60]. Formation of the vicarious distribution patterns of the Sino-Himalayan and Sino-Japanese regions is supposed to be related to the uplift of Himalayas in the Tertiary. *Lasianthus japonicus* subsp. *longicaudus* could have differentiated as an altitudinal vicariant of *L. japonicas* with the uplift of Himalayas [58, 59, 60]. As an understory shrub of tropical rain forest, the genus *Lasianthus* and many other shrub and herbaceous plants of tropical genera, although they are presently East Asian endemic species and exist commonly understory of the subtropical evergreen broad-leaved forest [54], they are evidently the sister species of the ones in the tropical rain forest flora in SE Asia. These tropical sister species have been evolved driving by the geological history of East Asia.

From the analysis on the floristic elements of the subtropical evergreen broad-leaved forest above, especially in Sino-Japanese region of East Asia, it is obvious that the present subtropical evergreen broad-leaved forest could have an early or ancient tropical origin at family level, and has a tropical Asian affinity at generic level. The subtropical evergreen broad-leaved forest is dominated by the Chinese endemic or eastern Asian distribution species, but the tropical sister ones. In fact, large number of tropical shrub and herbaceous plants are present understory of the subtropical evergreen broad-leaved forests in eastern Asia, and a lot of the tropical sister tree species in the canopy of the forests, which demonstrate the tropical affinity of the subtropical evergreen broad-leaved forests in eastern Asia.

Combined palaeobotanical findings, the uplift of Himalayas and the formation of monsoon climate, we believe that the subtropical evergreen broad-leaved forest in Sino-Japanese region of east Asia, was evolved from a tropical Asian rain forest after mid-Miocene.

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7. Discussions and Conclusions

The origin and evolution of the eastern Asian evergreen broad-leaved forest are closely related the origin and evolution of the eastern Asian flora. The debates on their origin and evolution, especially in the evolutionary process, are existed generally, even contrary in some cases.

East Asian flora, due to its high biodiversity and abundant paleoendemic taxa, was considered to be a floristic museum. However, the mountainous topography and abundant young endemic taxa in the western and the southwestern China, the flora is also considered to be both floristic museums and cradles, specifically eastern China representing a floristic museum, and western China an evolutionary cradle. The East Asian flora and its evergreen broad-leaved forest, both are almost consistently believed to be strongly affected by geological history and the formation of monsoon climate, especially the event of the uplift of Himalaya and the consequent monsoon formation. Arguments focused on the timing of the uplift of Himalaya and the consequent monsoon formation, which were during the Paleocene or the Neocene. Different theories on geological histories and monsoon formations, incomplete palaeobotanical findings, and the evolutionary history of the angiosperm flora of China, as well as the researches on the phylogenetic and molecular biogeography of important taxa with eastern Asia distribution, give not consistent suggestions and implications to the origin and evolution of the east Asian flora and its evergreen broad-leaved forest. Even the eastern Asian flora was suggested as a refuge of many ancient relict plants, but not their origin area. Whether or not to the debates, the most researches from different disciplines suggested that the monsoon in Miocene is a key to diversification of eastern Asian flora and the origin and evolution of its evergreen broad-leaved forest.

The subtropical forests similar to the present ones in eastern Asia were supposed to exist in southwestern China, especially in Yunnan, since Oligocene. The occurrence of fossil fruits of the strictly tropical Southeast Asian rain forest family Dipterocarpaceae in the middle Miocene in Fujian in southwestern China, suggested that a tropical rain forest vegetation of Southeast Asia existed there at that time. The paleobotanical evidences revealed that the southwestern China could have had the subtropical evergreen broad-leaved forest in the Miocene, but tropical rain forest vegetation of Southeast Asia in southern Fujian of southeastern China at that time. We suggest that southwestern China and southeastern China could have different vegetations in the middle Miocene: the subtropical evergreen broad-leaved forest existed in southwestern China, but tropical lowland rain forest in southeastern China.

From geological history, we agree with Guo et al.'s suggestion that during the Cretaceous period, China was high in the east and low in the west, and was in a subtropical high drought zone [22]. There was not a tropical or subtropical evergreen broad-leaved forests at that time. Since the late Oligocene-early Miocene (about 26-22 million years ago), the Himalayas began to rise strongly, and the Asian monsoon has significantly increased, as well as the subtropical arid zone of central and eastern China has disappeared, replaced by a warm and humid Asian monsoon climate [22]. Such some floristic elements of the subtropical evergreen broad-leaved forests appeared in Oligocene, and the subtropical evergreen broad-leaved forests similar to present ones formed during the Miocene in southwestern China [61], but a tropical rain forest similar to the ones in the present SE Asia appeared in south and southern China during the hottest period of the Miocene period [46]. After the Miocene, the modern subtropical evergreen broad-leaved forest could evolve with the tropical rain forest retreated to the south margin of southeastern China; while the ancient subtropical evergreen broad-leaved forests continuously evolved into the present ones in southwestern China [62, 63]. We also suggested that the typical tropical rain forest could not be appeared in southwestern China from the Miocene to the late Pliocene. As we supposed, the tropical rain forest vegetation in Yunnan occurred later, not earlier than before 5–3Mya.

The analysis on the floristic elements of the subtropical evergreen broad-leaved forest in east Asia, especially in Sino-Japanese region, show that it has a tropical affinity at genera, especially affected by tropical Asian element. The present subtropical evergreen broad-leaved forest is dominated by the eastern Asian and Chinese endemic species. Many species, including almost all life forms in the subtropical evergreen broad-leaved forest are Chinese endemic but tropical Asian sister species. We suggest that the subtropical evergreen broad-leaved forest in Sino-Japanese region of East Asia, could evolve from a tropical Asian rain forest after mid-Miocene.

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