The tropical-subtropical evergreen forest transition in East Asia: An exploration

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ABSTRACT

The transition from tropical to subtropical (warm temperate) evergreen forests is more clearly apparent in East Asia, from Nepal to the western Pacific coast, than elsewhere in the tropics. We review the nature of this transition and hypothesize the physical, ultimately climatic, factors that may maintain it, with a special focus on how the increasing instability and warming of climates will affect these forests. A primary climatic mediator of the transition is proposed, thereby offering a testable hypothesis for the climate–forest transition relationship. What is known of this transition is summarized in context of the primary climatic mediators of elevational zonation of forest formations in equatorial Asia to the tree line, in the Himalaya at the India-Indo-Burma northern tropical margin, and as both elevational and latitudinal zonation in southern China. Consequent secondary edaphic and other physical changes are described for the Himalaya, and hypothesized for southern China. The forest ecotones are seen to be primarily defined by tree floristic change, on which account changes in structure and physiognomy are determined. The montane tropical-subtropical transition in the Himalaya is narrow and observed to correlate with an as yet ill-defined frost line. A distinct tropical-subtropical transition forest is recognized in the southwest China mountains. There is a total change in canopy species at the Himalayan ecotone, but subcanopy tropical species persist along an elevational decline of c. 400 m. The latitudinal transition in South China is analogous, but here the tropical subcanopy component extends north over ten degrees latitude, albeit in decline. The tropical-subtropical transition is uniquely clear in East Asia because here alone a tropical wet summer-dry winter monsoon extends to 35° north latitude, encompassing the subtropical evergreen forest, whereas subtropical evergreen forests elsewhere exist under drier temperate summer climate regimes.

1. Introduction

The northern margin of the Asian tropics where it passes through evergreen forests is unique, directly abutting warm temperate evergreen forests to its north (known in East Asia as subtropical), and running continuously almost 2000 km from 85° East longitude in east-central Nepal to 122° E in Guangxi, Hainan, and southern Guangdong provinces in southern China. Increasing in richness eastwards, the northern margin of the Asian tropics marks the northern border of the Indo-Burmesian tropical and East Asian-Chinese subtropical biogeographic provinces, where it contributes to the greatest of all floristic diversity hotspots: China south of the east-west climatic barrier of the Qinling Mountains (Wu and Wu, 1996; Axelrod et al., 1998; Qian and Ricklefs, 1999; Zhu, 2013 & elsewhere). The northern margin of the Asian tropics is nevertheless held together by a suite of widespread transitional tree species through its greatest extent (elev. 2000 m in the mountains) until descending from SW Yunnan to the coast.

In this review, we compare our combined plot data and expertise from studying tropical forests in different regions of Asia. Zhu has investigated the tropical northern evergreen and montane forests of China (Zhu, 2004, 2016b, 2017 a, b; Zhu et al., 2005), while Ashton has investigated the equatorial and southern continental tropical seasonal forests of Asia (Ashton, 2017, summarized in Ashton, 2014). Our underlying motive is to understand the imminent impact that climate change will have on the placement of...
ecotones between forest formations, especially between adjacent tropical and subtropical forest ecosystems. This review will allow us to draw inferences on the likely consequences of climate change on agricultural and forestry crops and cropping systems.

We review what is known about vegetation gradients in evergreen forest structure and physiognomy in East Asia. These forests range from lowland elevations to the tree line, and in latitude from the humid tropics to the limits of warm temperature evergreen forests (known in East Asia as subtropical forests). Ecophysiologists have claimed that the range of major vegetation formations is determined by multiple correlated factors, expressed by an index (Walter, 1973, Walter and Lieth, 1960). Ohsawa (1990, 1991a, b, c 1995b, 1996) reported that vegetation gradients in the Himalaya and East Asia are correlated with Kira’s Warmth Index (1977), which is defined as the annual sum of all positive differences between monthly means of temperature and −5 °C. Consistent with Ohsawa, Grubb et al. (2013) reported that a latitudinal correlation exists between medium latitude evergreen forests worldwide and climate, notably temperature. These authors together concluded that climatic factors, notably temperature, cause no consistent breaks in continuity. However, equatorial evergreen montane forests had long been recognized globally to comprise elevationally distinct formations, reviewed for Asian including Himalayan forests by Ashton (2014). Ashton (2003, 2014, 2017) hypothesized that specific climatic factors and events, namely the diurnal altitude of the summer monsoon cloud base, seasonal diurnal canopy penetration by cloud, and onset of cold dry season air frost, respectively mediate the ecotones between these formations. Identifying such single limiting factors enables the formulation of hypotheses that can be tested in the field and by experiment. The existence and nature of these ecotones in the evergreen forests of East Asia is a major theme of this review, and the apparent existence and nature of one at the tropical-subtropical evergreen forest interface in East Asia is a principal focus. We nevertheless do recognise that a continuous gradient within each of these broad formations, broadly correlating with an index of climate, does exist.

Research in China has been focused on defining the structure, physiognomy, and floristics of the principal forest formations of tropical and subtropical South China (Wu, 1980, 1987; Zhu, 2017a), and the historical biogeography of their taxa at generic and familial level (Zhu, 2017b). The northern margin of the tropics has thereby been defined biogeographically (Zhu et al., 2007; Zhu, 2017a, 2018) (Fig. 1). Although the floristic differences between forest formations of tropical and subtropical southern China have been described, the physical nature of ecotones between them have not been examined or documented. The limiting physical factors that define ecotones between the tropical montane forest formations in South Asia and the Far East are now quite well understood (Whitmire, 1984; Ashton, 2003, 2014, 2017). We will use these factors as a basis for hypotheses regarding the nature of analogous ecotones in southern China. However, with the notable exception of the work of Kitayama and colleagues on Mount Kinabalu, northern Borneo (6° 03′N) (Kitayama, 1992; Kitayama and Aiba, 2002; Aiba and Kitayama, 1999, 2004), there have been no documented transects across elevations or ecotones, nor transplant or other experimental work with which to test such hypotheses.

Globally, the floristic margin of the lowland tropics roughly follows the Tropics of Cancer and Capricorn, 23° 26′ north and south of the geographical Equator, where the sun reaches its maximum and minimum zenith in summer and winter respectively, and annual winter air frost occasionally comes to reach its lower latitudinal limits in the lowlands. The northern margin of the South Asian tropics is exceptional in this respect, as frost-free climates are drawn further north by protection from the cold dry winter north-east monsoon off the Qinghai-Tibet Plateau, and by the sheltering east-west trending high Himalaya to the north whose south-facing slopes experience nightly winter fog and precipitation as dewfall. Thus, the margin, close to the Tropic of Cancer in the southernmost Middle East, is drawn up to 32° N in the Himalayan foothills in NW India. Summer low pressure over the Qinghai-Tibet Plateau draws the wet south-east trades of the Indian summer monsoon north of the equator to turn south-west owing to the Coriolis Effect; the southern limit of frost protection afforded by the Plateau coincides at this same latitude, in the Himalayan front ranges at c. 2000 m (Ashton, 2014, 2017). The margin ascends eastwards to c. 2000 m and at c. 27° N in Central Nepal, where to the south and at lower elevations, a frost-free winter, tropical lower montane climate is sustained by the moist orographic updrafts. The margin continues eastwards at that elevation and latitude until it crosses the north-south trending Myanmar—China frontier ranges. To their east, the margin returns close to the Tropic of Cancer in the deep-cutting Salween (Nu) and Mekong (Lancang) valleys, before ascending again on the mountains of south-east Yunnan and northern Vietnam. There it interdigitates with the lesser north-west to south-eastward trending Red River (Yuanjiang) and other river valleys. East of the Qinghai-Tibet Plateau in central China, the east-west Qinling Shan/Hua Shan mountain complex (c. 34° N) draws the wet summer monsoon further north, to 30°–34° N, far north of the south-east lowland China winter frost limit, yet not high enough to fully halt the cold winter north-easterlies. Lowland winter frost here therefore descends to the Tropic of Cancer, as elsewhere in the world, following the north-south trending valleys there. Winter weather in the East Asian coastline and off-shore islands north-east to southern Zhejiang is ameliorated by warm diurnal on-shore breezes off the north-flowing Mindanao and Kuroshio currents of the western North Pacific Ocean, marking the northern limit of coastal mangrove. Northern Vietnam also receives moist frost-free winter north-easterlies off the sea. Moist orographic updrafts there also bring moisture from nightly fog and dewfall. In summary, a warm summer-wet, cool but frost-free winter dry climate prevails on south-facing slopes north to the tropical margin at 25°–27° N in NE India, Myanmar, and easternmost Yunnan, but only to c. 23° N in southern China lowlands away from the coast.

Our focus is on trees and forests; specifically, we are examining how trees and forests change at the tropical—temperate interface. We first review the ecology of the elevational gradient in the montane forests of everwet equatorial and seasonally dry northern tropical Asia, and the existence and nature of zonal ecotones. We then discuss the extent that tropical taxa range north of the tropical margin in Chinese subtropical forests, and that temperate taxa range south of this margin, with emphasis on species distributions. We furthermore examine the tropical forest ecosystems of southern China in their regional and global contexts, and evaluate the continuity of elevational and latitudinal gradients in evergreen forests. We focus especially on comparing the nature of the tropical-temperate forest transition, that is, the tropical margin, in China with that in the Himalaya. We will argue that the warm temperate evergreen forests of East Asia differ importantly from warm temperate evergreen forests in other parts of the world. Specifically, warm temperate evergreen forests of East Asia have a unique climate, which justifies calling these forests alone subtropical. We will also discuss numerous unanswered questions.

2. What do we know?

2.1. Equatorial Asia

The existence of elevational zonation of forests on both continuously and seasonally wet mountains of equatorial tropical Asia (lands between 10° north and south latitude) has long been recognized and known to conform with those of other tropical
continents (Burtt Davy, 1938; Grubb et al., 1963; Ashton, 2003, 2014, 2017). Although Ohsawa (1995a, 2006) correlated this zonation, and its change with latitude in the seasonally dry tropics to their north, to changes in Kira’s Warmth Index, one of us has argued that individual limiting climatic factors, which in turn influence soil formation and forest composition and dynamics, are causally correlated with forest zonal ecotones in a way that can be tested (Ashton, 2003, 2014, 2017). Specifically, these evergreen elevational zonal forests differ in stature, structure, and, notably, predominant leaf size. On that account we follow Webb (1959) in dividing Raunkaier’s (1934) mesophyll leaf size class (2025–18,225 mm²) into a larger mesophyll (4500–18,225 mm²) and a smaller noto-phyll (2025–4500 mm²) size class.

These lowland forests give way to a notophyll-dominated lower montane forest in the Far East. However, in South Asia dipterocarp canopy dominance is replaced by Fagaceae, with other characteristic families including Lauraceae, Magnoliaceae, and Theaceae. This ecotone (between 700 and 1200 m) coincides with the wet season cloud base and the transition from tropical ultisol to temperate mull soils. Two higher ecotones occur on equatorial mountains below 8°C/14°C latitude. The lower of these two ecotones extends from tropical lower to upper montane evergreen forest (misleadingly termed southern montane wet temperate forest by Champion, 1936). This equatorial upper montane forest is characterized by short stature and crooked boles, and by Myrtaceae and other southern families, with the continuing presence of lower montane genera. This ecotone, at (850–) 1700–2200 m, coincides with canopy penetration of diurnal fog for at least ten months, with consequent dewfall precipitation leading to soil leaching and podsolization. The upper ecotone, from upper montane forest to evergreen subalpine thicket, is at 2900–3650 m. It is more gradual, and coincides with increasing incidence and strength of air frost. Few of these equatorial mountains are high enough to experience cold dry (winter) season frost, but these include those of New Guinea, and (occasionally) Kinabalu in northern Borneo. The occurrence of occasional air frost on equatorial mountains is associated with the appearance of thickets of small trees and shrubs distinguished by smaller (microphyll and smaller, nanophyll often dominant) leaves that are coriaceous, and often revolute and with retuse or obtuse apices and shiny upper surfaces (Ashton, 2014). This change occurs across an ecotone of varying width, apparently correlated with the onset of frost, at first varying in frequency and intensity, termed by us here as the frost line. However, the precise definition and nature of its correlation with the forest ecotone must await careful and sustained yearly observation.

The most complete account of frost on Asian equatorial mountains is that of van Steenis (1972) who compared the mountains of West and East Java. Air frost occurs in the tropics at the driest time of the year, which is during the winter at higher latitudes, and under two site conditions. The first site condition occurs on upper slopes and peaks. Near the equator these sites occur at c. 3500 m, whereas in the Sri Lankan and Indian mountains at 8°C/12°C these sites occur at c. 2000 m. The second site condition occurs in valleys where the floor is wide or blocked, which causes heavy cold air to descend from above and pool. This occurs down to 1500 m, or even 1000 m in more seasonal sites. Years of relatively mild frost, with onset at higher elevations, are interrupted by single or double years of markedly more intense frost which result in burning of foliage of more sensitive species, and mortality, especially among seedlings and larger young individuals. Slope and summit sites usually manifest an ecotone from low dense and twiggy upper montane forest to subalpine thicket in which the canopy becomes increasingly broken. At valley sites, and on some summits, especially on karst limestone, woody upper montane vegetation is killed and...
replaced by grassland dominated by temperate grass and broad-leaved genera. Frost-sensitive woody species disperse as seed and germinate in these open sites, but above ground parts are killed. If several frost-free years ensue, rootstocks may survive and thicken, while shoots recover until once again cut to ground level. Only where frost-prone grassland is invaded by frost-hardy taller plants, such as dwarf bamboos, do frost-sensitive woody seedlings survive longer within the latent heat stored nocturnally within their canopy. There, eventually, they may emerge to establish their own frost-resistant crowns along an unstable forest-grassland ecotone. On peaks and slopes the frost line declines with latitude. For example, on the northern peaks of the Western Ghats in India (7–12°N to c. 18°N), the frost line has descended below 2000 m, thereby truncating the upper montane forest. South Indian mountains experience a cloud-free dry season exceeding two months. Under these conditions, summits above 2000 m lack sufficiently continuous diurnal fog to support densely mossy upper montane forest. They are interspersed there with fire-prone grasslands which have co-existed there since the Pleistocene (Sukumar et al., 1993). Thus, on these peaks few temperate taxa occur. Most temperate taxa that occur are herbaceous. Very few woody species occur, although these include the locally endemic weakly frost tolerant South Asian sister species of the temperate Rhododendron arboreum, a Berberis and a Gaultheria (Ericaceae).

Above 18°N, in the mountains of Indo-Burma, equatorial upper montane forest is absent, and lower montane forest continues to the frost line, generally still at c. 2000 m. The very few high summits and shallow valleys begin to accumulate temperate herbaceous, and a few woody taxa, whose presence coincides with the presence of occasional winter dry season air frost. Thus, Rhododendron delavayi and Lyonia ovalifolia occur on northern Thai mountains, and a rich temperate flora occurs in the savanna grassland around the summit of Doi Chiangdao (elev. 2175 m) (Smitinand, 1966).

2.2. The eastern Himalaya

The Himalaya, extending from Afghanistan to the Myanmar–China frontier, carries the tropical climatic margin, i.e., the frost line, from NW India to China (Ashton, 2014). The associated forest transition was first described and classified by Champion (1936). In the foothills, the ecotone from lowland wet tropical evergreen and semi-evergreen forest to lower montane tropical rain forest is gradual, beginning at c. 800 m and terminating by 1200 m. Emergent Dipterocarpaceae and often Leguminosae are characteristic of these lowland forests, and the dominant leaf size is mesophyll. This ecotone coincides with the diurnal pre-rain cloud base during the south-west wet monsoon, and is at the same elevation as on the Equator. Importantly, this lower, tropical ecotone also universally coincides with the edaphic tropical margin. Specifically, the tropical ecotone extends from lowland soils in which rates of litter decomposition exceed rates of litterfall to montane soils in which litter and particulate organic matter accumulate. In other words, the tropical ecotone extends from tropical ultisol and latosol soils to temperate humic mull soils. These soils have different characteristics: in tropical ultisol and latosol soils termites and their fungal symbionts are the primary decomposers and visible particulate organic matter is concentrated near the surface; in temperate humic mull soils earthworms are the primary decomposers and carry organic matter down the profile, thereby discoloring it (Ashton, 2014, 2017). It is here, therefore that the tropical–temperate edaphic ecotone occurs in the Himalaya, not at the frost line.

A tropical to warm temperate, i.e., subtropical, forest ecotone is best known in the wetter, central and eastern Himalaya, notably of Nepal and Bhutan (Stainton, 1972; Grierson et al., 1987–2001; Ohsawa, 1983, 1991a, b; Ashton, 2003, 2017). The presence of a distinct tropical-subtropical floristic ecotone and its associated environment is distinguished in the following ways:

- A forest ecotone extends from eastern Nepal to the north–south trending mountain ranges of eastern Myanmar. This tropic-subtropical floristic ecotone occurs on upper slopes and ridges at c. 2000–2100 m down to c. 1500 m in valleys, and is bordered at lower elevations by the truncation of the upper limit of tropical lower montane rain forest (misleadingly called subtropical broadleaf wet hill forest by Champion, 1936), and at higher elevations by montane subtropical evergreen forest (Himalayan montane wet temperate forest of Champion). The ecotone is defined by an almost complete change in canopy species, notably Fagaceae.
- The ecotone is usually quite narrow up the steep slopes of the Himalaya, and typically restricted to c. 100 m change. Above, replacement of tropical subcanopy woody species continues over a further c. 500 m.
- Tree species composition therefore continues to change with increasing elevation, and witnesses an almost complete turnover of species from tropical to warm temperate (subtropical) forest by c. 2300 m, although the dominant speciose families of both tropical lower montane and subtropical evergreen forests, Fagaceae and Lauraceae, remain the same, as do characteristic subordinate families, including Magnoliaceae, Theaceae and Cornaceae.
- The subtropical forest flora shares species with the lowland subtropical flora in South China, including a substantial proportion of the tree species. The shared species composition of these forest formations provides an excellent basis for comparative examination of floras and other characters along the full length of the tropic margin in East Asia. Such comparative analysis is expected to guide further field survey and generate important hypotheses to explain differences between these forest formations.
- The ecotone is exceptionally rich in cryptogetic epiphytes, both vascular and non-vascular.
- Because of the floristic β-diversity that the tropical margin of the Himalaya and northern Burmese mountains generates, this ecotone marks a peak in species, and to a lesser extent in higher taxa. Furthermore, the overall flora of this ecotone represents the meeting point of taxa with contrasting origins and histories.
- The subtropical evergreen forest is structurally and physiognomically similar to the tropical lower montane forest, with straight boles lacking buttresses, but has slightly smaller average canopy leaf sizes in which microphylls may come to dominate (Ashton, 2014).
- These vegetational changes coincide with intense diurnal fogginess during the wet summer monsoon and occasional incidence of air frost during clear moonlit winter nights, which nevertheless varies annually in intensity and elevational occurrence. Therefore, this ecotone coincides with the tropical-temperate frost line.

Ohsawa (1991a, b, 1995a) termed this ecotonal transitional zone upper montane forest. However, although this ecotonal transitional zone shares some understory genera with equatorial upper montane forest, including species of Ardisia, Symplecos, and Meliosma, the continuing predominance of lower montane forest families, especially Fagaceae and Lauraceae, and the broad continuity of structure and physiognomy, excludes such close comparison, as we will discuss.
The ecotone between the floristically less rich and mostly deciduous tropical and temperate forests of the more seasonally dry western Himalayan hills is less clearly defined.

In summary, current knowledge of the prevailing forest formations of equatorial Asia, and tropical and subtropical (warm temperate) Himalaya, and their correlation with physical environmental factors, are described here from variably detailed field accounts; but precise diagnoses from plots and continuous observation remain few.

3. Tropical forests in south China

3.1. Historical biogeography of China's tropical and subtropical tree flora in an East Asian context

3.1.1. Sources of immigration

The northern tropical margin in East Asia hosts one of the great centres of plant species diversity, in large part because it marks the collision of two distinct floras with separate geological and phylogenetic histories. East Asia was formerly mooted as the cradle of Angiosperms (Merrill, 1923; Takhtajan, 1969; Axelrod et al., 1998), but palaeontological and molecular phylogenetic evidence has conclusively shown that cradle is instead West Gondwana, i.e., South America and West Africa (Raven and Axelrod, 1974), and that East and South-East Asia has received its flora by migration. This East Asian immigration has followed several routes (for summary see Morley, 2018):

- The major tropical, and the only perhumid equatorial migration route, has been through immigration into the Indian tectonic plate (‘Noah’s Arc’) as it moved north-northeast across the equator, from the hardly moving East African tropics 60–55 ma. This flora then migrated across the nascent Bay of Bengal from central India into southern Indo-Burma when both were at equatorial latitudes, 50–45 ma; and then later again by a seasonally wet tropical overland corridor across the head of the Bay of Bengal in the late Oligocene to early Miocene eras 30–25 ma, when global temperatures were warm and the Himalaya and Qinghai-Tibet Plateau were beginning their rise. Taxa currently concentrated or confined to perhumid equatorial regions of Asia, such as the Bombacoid Durioineae, likely subjects of that first migration, are hardly or not represented in the flora of tropical China, but several of more seasonal climates had already arrived before the end of the Eocene (Herman et al., 2017).

The fossil record indicates that the exclusively tropical family Dipterocarpaceae arrived early in South China. For example, a fossil fruit that likely belongs to a species in the Anthoshoarea section of Shorea was found in a coal seam at Maoming, Guangdong, 21°50’N, whose rich leaf flora otherwise implies tropical lowland forest (Feng et al., 2013; Herman et al., 2017). In contrast, in nearby mines, seams dated from the upper Eocene to lower Oligocene bear subtropical floras, which, based on the presence of Corylopois, Alnus and Platycarya, were probably at lower montane elevations. Overall, these floras imply conditions, and a tropical margin, remarkably similar to those of the present day, though Dipterocarpaceae fruit have been recorded from lower Miocene beds in subcoastal Fujian at 24°12’N, 117°53’E (Shi and Li, 2010), not far south of the latitude of the current northermost natural limit of coastal mangroves. Furthermore, Artocarpus (Moraceae), Bauhinia (Leguminosae), Boehmeria (Urticaceae), Calophyllum (Calophyllaceae), Flacourtia (Salicaceae), and Macaranga (Euphorbiaceae) were described from the same site with Dipterocarpaceae fruit in the subcoastal Fujian (Jacques et al., 2015).

- Previously, the tropical flora of East Asia was thought to have immigrated during the Palaeocene and Eocene from West Gondwana to North America, then eastward by way of Europe and the Middle east. During this time period the global climate was tropical to high north temperate latitudes. This track would have been within temperate wind systems (Hadley cells), which would have been both temperature- and rainfall-seasonal, albeit humid through most of its length. This model is broadly supported by the European fossil record, although obligately tropical families are poorly confirmed or absent. Currently, little fossil evidence supports the existence of this track eastwards along putative southern Eurasian coastal lowlands, prior to the Indian collision.

- A third, initially and mostly warm temperate, route followed eastwards along a subantarctic Gondwanan track to Australasia, finally entering the tropics of the Malesian Archipelago from the Australasian Plate as it shifted north-east, approaching contact with South-East Asia c. 17 ma. The few taxa occurring in China include Podocarpaceae, Myrtaceae, Pittosporaceae, and Proteaceae. The discovery of fossil Dacrycarpus (Podocarpaceae) from the lower Miocene in the Guiping Basin, Guangxi (Wu et al., 2019) indicates early dispersal into Asia by island hopping. It is remarkable that, even at present, Dacrycarpus has hardly spread north beyond tropical lower montane forest in South China. Very few taxa, notably Monimiaceae subfamily Hortornoideae (Renner et al., 2010) and Heliciopsis (Johnson and Briggs, 1975), directly entered the Indian Plate from the Antarctic >60 ma.

- Fourthly, migration of temperate families followed a northern, warm temperate route eastwards from North America through temperate Laurasia and westwards across the Bering Strait, from both of which tropical Asian taxa diversified, notably Fagaceae. The former route would have closed during the Oligocene as the global climate cooled, the latter c. 15 ma as climate started to cool and the Bering Strait opened (Although important in the flora of China, few of these taxa are present on the South Indian mountain summits, implying that they failed to cross the Ganggetic plain). The history of Fagaceae remains uncertain because the pollen is difficult to discriminate. The likely origin of this family is East Asian tropical-subtropical (e.g., Cannon and Manos, 2003). There is a recent putative record of Castanopsis from the Eocene of Patagonia (Wilf et al., 2019). However, the land between Gondwana Australasia and East Asia was not sufficiently close for poorly dispersed ectomycorrhizal Fagaceae until the Miocene (c. 17 ma). Moreover, apparent Fagaceae are well represented in the Eocene beds of southern China (Herman et al., 2017). The leaves and twigs of the Patagonian fossil illustrated by Wilf et al. (2019) resemble more the current northern temperate deciduous sister genus Castanlea, with its many veins and sharply prominent marginal teeth, than modern Castanopsis species.

The regional historical biogeographical relationships of the current tropical forest flora of China has been documented at the generic and familial level by one of us (Zhu et al., 2003; Zhu, 2008, 2017a; Zhu and Yan, 2009) and will not be further addressed here.

3.1.2. Current species’ ranges within China

The greatest centre of temperate flowering plant diversity in the world is located in China. This plant diversity can be explained by several factors. The geology and topography of China have been especially active since the Tertiary (Qian and Ricklefs, 1999) and southern China has an abundance of karst limestone. China hosts the widest continuous juxtaposition of tropical and warm temperate vegetation and floras (Axelrod et al., 1998), and the
Chinese flora consequently has diverse origins. Importantly, the flora is rich because China is bordered by the western coast of the Pacific Ocean, the world's widest ocean. The coastal and southern regions of China currently support a vast expanse of moist warm seasonal climates, a region which, though varying greatly in area over geological time, has persisted since before the arrival of the angiosperms. Thanks to the continuity of its climate, China's subtropical flora especially harbors an exceptional number of older angiosperm families, and it is the sharing of taxa in basal families which characterizes the similarities of its warm temperate flora with that of eastern North America (Qian and Rickleffs, 1999, 2000; Qian, 2002).

The range in China of species characteristic of tropical forests, but apparently occurring also in some subtropical forest formations, can be ascertained from their descriptions in the Flora of China (Wu et al., 1999–2009). This Flora does not indicate vegetation types or the forest formations in which the species occur in China. Therefore, tree species that the Flora states also occur in cited nations within the Asian tropics were listed by us with tree species which are confined to temperate vegetation in excluded nations (Table 1; Appendix 1.2). The Chinese provinces in which these occur, and their elevational ranges in the Flora where recorded, were listed. The elevational ranges of these species in tropical floras other than the Flora of China, which consistently documents them, were also listed. These floras include Brandis' Indian Trees (1907), which records tree species occurring from modern Pakistan to Myanmar (Burma), the Flora of Bhutan and Sikkim, those families whose treatment has been published for the Flora of Thailand (Smithinand et al., 1978–present), and Field Guide to the Trees of Northern Thailand (Gardner et al., 2000) in which forest types are implied by their preferred elevational range. The elevational range of each species was listed for each of the forest types are implied by their preferred elevational range. The elevation and forest formation of species occurring in the tropical margin in S. China.a

Table 1
The tropical margin in S. China.a

| Province | Number of species | Province | Number of species |
|----------|------------------|----------|------------------|
| Yunnan   | 1271             | Henan    | 89               |
| Guangxi  | 959              | Anhui    | 84               |
| Guangdong| 665              | Qinghai  | 71               |
| Hainan   | 607              | Jiangsu  | 66               |
| Guizhou  | 444              | Shaanxi  | 39               |
| Fujian   | 341              | Jiangxi  | 37               |
| Taiwan   | 330              | Shandong | 12               |
| Xizang   | 284              | Gansu    | 10               |
| Sichuan  | 236              | Hebei    | 7                |
| Hunan    | 228              | Shanxi   | 5                |
| Zhejiang | 151              | Liaoning | 5                |
| Hubei    | 137              |          |                  |

a Tree species in Flora of China confirmed to be tropical by their citation in those tropical Asian floras where elevational ranges are indicated: South Asia and Myanmar (Brandis, 1907), Bhutan and Sikkim (Grierson et al., 1987–2001). Total tree species documented: 1702.

The pantropical tree families Dipterocarpaceae, Myristicaceae, Lecythidaceae, Chrysobalanaceae and Crypteroniaceae, as well as the exclusively tropical Old World Ancistrocladaceae, all of which occur in southern China's tropical forests, are absent from adjacent frost-prone subtropical forests as is the case in other continents. Also confined to frost free, or apparently only weakly frost-prone habitats are the few representatives of families of southern warm temperate Australasian origin — Podocarpaceae, Myrtaceae, Proteaceae — which succeeded in diversifying into east Asian lowland tropical forests but seem not to have successfully restored full frost hardiness in East Asian subtropical latitudes.

The floristic geography of southern China is already known to differ from the eastern Himalayan in the following respects, confirmed by our list:

- Many species, recorded only at tropical lower montane elevations in tropical Asian floras to the south, descend to lowland elevations according to the Flora of China, and therefore by inference to subtropical (warm temperate) climates. But many, endemic to southern Chinese lower montane forests, do not.
- Many tropical taxa are more widespread in subtropical China than anywhere else in the temperate world (Appendix 1.2), and several are represented in China by subtropical or locally endemic tropical sister species, especially on karst limestone. Notable among these are the widespread tropical lower montane Schima wallichii (Theaceae); Altingia excelsa, Exbucklandia populnea, and Rhododendron championii (Hamamelidaceae); Nyssa javanica (Nyssaceae); Sloanea javanica and S. sigun (Elaeocarpaceae); and Phoeonia davidiana and Eriobotrya bengalensis (Rosaceae).

We used evidence from the Asian tropical floras to identify three distribution patterns of tropical species in forest formations in China (Table 1). First, tropical species occur in surprisingly low numbers in SE Tibet (Xizang). This dearth of tropical species is most surely because the tropics of Tibet occupy a small area, which is located along the lowland and slopes of the Brahmaputra (Yarlung Zangbo) river as it approaches the Indian frontier, having descended below 2000 m from the temperate climate of the Qinghai-Tibet Plateau. Similarly, tropical species occur in low numbers in Taiwan, as tropical rain forest is confined to the extreme south-east (Zhu,
and in its coastal mainland provinces where frost-free conditions are increasingly limited northward to protected coastal slopes. Coastal regions are among the most affected by human activity and deforestation. Second, tropical species occur in high numbers in provinces through which the tropical margin passes, notably Yunnan, Guangxi, and Guangdong. Numbers of species recorded in other Asian tropical floras are lower in Hainan than in Guangdong, in part reflecting its smaller area, although the total number of tropical species is greater in Hainan because of the greater role of endemic SE China tropical elements there (Zhu, 2016b). Third, the number of tropical tree species decreases in provinces north of the east–west mountain barrier that includes the Qinling Mountains, i.e., Gansu, Shaanxi, Anhui, and Jiangsu (Appendix 2). This residue is concentrated in the north–east of the eastern, coastal end of the tropical margin, in warm temperate China. Here, with cool dry north–easterlies dominating in winter, and the south–west monsoon interrupted and more variable, evergreen forest is replaced by deciduous forest except in restricted areas. The species persisting here are predominantly those of the evergreen subcanopy, with few pioneers or canopy species. In China, principally tropical families and genera have evolved temperate taxa in warm temperate more often than putative temperate taxa; have evolved taxa in the tropics to their south (Appendices 1, 3). This diversification is overwhelmingly strongest in China, and concentrated in the broadleaved tropical and sub-tropical evergreen notophyll and microphyll forests of the monsoon region south of the central east–west mountain massif. This extension and diversification of tropical woody genera, and accumulation of endemic species within them, has also occurred among herbaceous woodland taxa, especially Gesneriaceae, Begonia, and Elatostema (Urticaceae), thereby amply justifying the term sub-tropical to the warm temperate forests of monsoon Central and South China. This term has been used northwards to the limits of evergreen broadleaved forest in south-western Korea and southernmost Japan to Ibaraki prefecture, Honshu (Ohawa, 1995b, 1996; Grubb et al., 2013). The climatic origins of these genera can be inferred by molecular phylogenetic analysis. Several families, including Rubiaceae and Leguminosae, in the broad sense are globally well represented by woody taxa in both tropical and temperate zones, although more diverse in the tropics. A few tropical taxa are represented in subtropical and tropical Asia alone, notably Symplocos, Daphniphyllum, Meliosma, Illicium, and Clethra (also in North America). Many of these taxa are monotypic in their families, which further complicates our understanding of their climatic origin. Although our survey is restricted to taxa which are also cited in our selected floras of tropical nations to the south, we note that woody species cited in the Flora of China as endemic to tropical regions of China reveal an extraordinary level of local endemicity in the four quite limited regions that comprise the Chinese tropics. Tropical genera that have diversified into subtropical China are also highly endemic. This endemicism in subtropical China increases from cooler and drier climates in the north to warmer and wetter climates towards the south until the tropical margin is seemingly reached. According national floras, south of the tropical margin endemicity declines.

The Flora of China could have identified consistently recorded sites for tropical species, but few specific localities were recorded for more than ten species. Recorded sites include Longzhou (22°24′N) in Guangxi, Medog (Motuo) (29°24′N) in Tibet, and Jinghong (21°56′N), Mengla (21°30′N), Maguan (23°02′N), and Ruili (24°01′N) in southern Yunnan, all south of the tropical margin and assumed by us to be tropical. North of the margin, the richest apparent refuges are in southern Guizhou, notably Libo, 26°25′N, 107°50′E, inland and well north of the Tropic of Cancer. The most frequently cited location in south-west Sichuan is at 25°24′N in a region where many tropical trees important in the rural economy are planted, including the Asian kapok tree Bombax ceiba, Indian mango Mangifera indica, and the rose apples Syzygium jambos and S. samarangense.

It is unclear why other forests nearby are not apparently richer in relict tropical species, even though exceptional apparently subtropical sister species do occur, e.g., Terminalia franchetii in rainshadow valleys in SW Sichuan and northern Yunnan. Many relict tropical species represent associates of karst topography which is exceptionally widespread in subtropical China. Karst provides terrestrial islands too steep and often too rocky for cultivation, which conserves patches, sometimes extensive, where aboriginal vegetation survives. In addition, their extreme topography and elevation may also harbor pockets of climate exceptional for their region. Such refuges may facilitate diversification of isolated populations of tropical species and their radiation into habitat that are only occasionally prone to killing frost. For example, the tropical lower montane S. wallichii diversified into four endemic Schima spp., the widespread tropical lower montane A. excelsa into five Altingia spp., also E. populnea to one Euchlaenidae sister, and the widespread tropical mostly lower montane Bischosia javanica to sister B. polyarpa.

But no forests north of the tropical margin contain any sister representatives of any of the five exclusively tropical families. Asian lower montane tropical forests lack any representatives of several temperate Far Eastern and East Asian tree and shrub families, which in China include several basal dicot families - Calycanthaceae, Eupomatiaceae, Eupteleaceae, Lardizabalaceae, Trochodendraceae, and Tetracentraceae. These families must therefore be regarded as exclusively temperate, especially subtropical (Table 2).

Only two globally distributed largely temperate woody families have diversified into the Asian lowland tropics: Magnoliaceae (Magnolia) and Fagaceae (Lithocarpus, Quercus section Cyclobalanopsis, Trigonobalanus, and Formanodendron) (Appendix 3). Fagaceae are absent from South Asia, while Castanopsis and Lithocarpus alone have migrated east to New Guinea. Quercus and Trigonobalanus are pollinated by wind, while other genera are pollinated by insects. These two are mostly confined to ridges in the wet tropics, where they experience diurnal orographic wind-drifts, and kerangas (‘heath forest’) with its diffuse-foliaged canopy. Of all species sampled, Cyclobalanopsis glauca is exceptional. It has a wide geographical range and ecological amplitude, is found from seasonally wet lower montane and warmest temperate forest in the Central Himalaya to East Asian subtropical forest, and is even hardy in western European Atlantic climates.

The vast pantemperate Astereaceae are represented in tropical Asia by one widespread tropical Asian genus, Vernonia, and two taxa endemic to hot dry rainshadow valleys in SW Sichuan and Yunnan, Leucomeris decora and Nouelavia insignis. Among temperate woody genera, the species-rich Rhododendron subgenus Rhodo- dendron is represented solely by one weakly frost-hardy species group, R. arboreum of the western Himalaya, with sister species in frost-prone South Asian montane grasslands, and R. delavayi on the East Asian higher summits. In contrast, the exclusively wet tropical mountain Rhododendron subgenus Scutiananthus of southern Indo-Burmese and Malesian range is frost sensitive and mostly equato- rial upper montane.

Several species widespread in Asian tropical lower montane forest belong to genera which are otherwise temperate. Of these, Alnus nepalensis (widespread from Nepal to the mountains of Indo-Burma and Yunnan), Aesculus indica, Carpinus vimineus, Betula utilis (restricted to C. and E. Himalayan and E. Asian mountains), Cupressus rostrata (widespread in SE China), and Acer laurinum (widespread through Indo-Burma and the Sunda lands to Sulawesi) have pantemperate conge- ners, while tropical Styrax species and N. javanica have Chinese and
North American congeners as part of the long-recognized East Asian-eastern North American phytogeographic connection (Gray, 1846); A. excelsa, Rhodoleia championii, Distyliopsis dumii, E. populnea (Hamamelidaceae), and Anneslea fragrans (Rosaceae) have one or more subtropical East Asian congeners and are members of unequivocally temperate families. But Podocarpus neriifolius (Podocarpaceae) and S. wallchii (Theaceae), with several apparently subtropical East Asian congeners, are tropical lower montane species in families which in Asia are otherwise exclusively or mostly lowland as well as montane tropical.

In tropical regions to the south and west of China there are only two localities distant from the tropical margin where temperate and tropical tree species co-occur: the summit areas of Victoria Peak (Nat Ma Taung, Khonuamthung), Myanmar (elev. 3053 m; and tropical tree species co-occur: the summit areas of Victoria Peak, which is well above the frost line, harbors Quercus semicarpfolia, a species of seasonally dry lower montane forest of the Central Himalaya (Kingdon-Ward, 1944, 1958). At Doi Chiandao, which has a frost-prone environment, Q. semicarpfolia Quercus floribunda, Quercus kingiana, Acer garrettii, Buddleia macrostichus, Cornus oblonga, Cotoneaster franchetii, L. ovalifolia, and Fraxinus floribunda co-occur in an open forest where a grassy field layer supports several temperate herbaceous genera in a frost prone environment (Smitinand, 1966) (Appendix 2).

3.2. Forest formations and community types

3.2.1. Natural community types

In China, the major forest formations in the south were defined by a monograph by C.W. Wang (1961). Wang recognized two major broadleaved evergreen forest formations in South China:

- (Tropical) Rain Forest, analogous to lowland tropical evergreen and semi-evergreen forests worldwide and in Asia, now termed northern seasonal evergreen dipterocarp forest (Ashton, 2014). These forests are confined below 750–1000 m, and are essentially floristically homogeneous at the familial level, although with regional differentiation of species. Northern seasonal evergreen dipterocarp forests occur in the south of Tibet (Xizang), Yunnan and Guanxi, Hainan, and coastal Guandong and Fujian; also Taiwan where inland tropical forest is confined to the extreme south and south-east, and lacks those five tree families elsewhere confined to the tropics. Taiwan’s present tropical climate zone is geologically recent, perhaps entirely Holocene, and its tropical flora originates through immigration from the Philippine islands to southern Taiwan.

- ‘Evergreen broad-leaved sclerophyllous forest’. Wang includes two separate formations. One formation occurs above 500 m in Taiwan, and above 1000–1200 m in southern Yunnan and Guanxi, although with its lower ecotone at >750 m. This formation also occurs from the lowlands upwards in the north, although it is now much restricted by conversion to agriculture. On the continent, Wang noted Castanopsis tribuloides, C. Indica, S. wallchii, Anneslea fragrans, Reevesia siamensis, and Garcinia, but also Castanopsis hystrix. These taxa are widespread and characteristic of tropical continental Asian lower montane forests from Vietnam to Nepal, and in several cases south to Java and Mount Kinabalu. We conclude that this forest formation is tropical lower montane forest, on both the continent and Taiwan. Wang also described ‘evergreen oak’ forest on a dissected plateau at <1000–2000 and to 2400 m in western Sichuan, at 1000–1500 m in northern Guangxi, and to 3000 m in Yunnan, with ‘bushy growth’ extending to 3500 m. It is unclear whether these more northern forests are truly frost free and tropical, or warm temperate ‘subtropical’. They most appear to represent a subtropical vegetation type within Wu’s ‘sclerophyllous evergreen broadleaved forest’ that occurs on mountains at 2000–3500 m in the low rainfall region of NW Yunnan and SW Sichuan. Species of Quercus are frequently canopy dominants in these regions (Wu, 1980, 1987).

The current nomenclature for forest formations in China is attributable to the works of Z. Y. Wu (1980, 1987). However, researchers today use inconsistent terminology to describe forest formations, especially when referring to forests in montane south-west Yunnan. Wu divided China’s evergreen tropical forests into two principal categories: lowland seasonal evergreen rainforest, which is included by Ashton (2014) in his northern seasonal evergreen dipterocarp forest, and lower montane evergreen rainforest forest. Both are regarded by Wu as mesophyllous. Although the tropical montane evergreen broadleaved forests (called monsoon evergreen broadleaved forests in Wu’s work) share the greatest familial and generic similarities with warm temperate evergreen broadleaved forests to their north (termed subtropical by Chinese researchers), these forests differ physiognomically as well as floristically from the lowland tropical forests. Specifically, the mean leaf size of tropical montane evergreen broadleaved forests is smaller, within the mesophyll (2025–18.225 mm²) size range. Webb (1959) divided the mesophyll leaf size category into two: the larger mesophyll and the smaller notophyll (25–4500 mm²). These importantly distinguish the Chinese predominantly mesophyll lowland rainforest forests from the predominantly notophyll and microphyll tropical lower montane and subtropical evergreen broadleaved forests. Wu further divided China’s tropical-subtropical montane forests into three categories: monsoon evergreen broadleaved forests (tropical lower montane evergreen broadleaved forest in international terminology; see Zhu, 2004; Zhu et al., 2005, 2019); mid-montane wet evergreen broadleaved forest, which is termed upper montane in studies by Zhu (2016b) and Zhu et al. (2019), and which is the formation of the montane foggy transitional tropical-temperate zone which will be further discussed here; and semi-wet evergreen broadleaved forest which shares a similar elevational range as the latter but is in a drier climate (Zhu et al., 2019), and which we will treat as subtropical. Wu also recognized tropical monsoon forest, a semi-evergreen or wholly deciduous formation occurring in lowland regions with a relatively long dry season (Wu, 1980, 1987), and where more evergreen formations have been degraded by human activity and fire. This is analogous to the semi-evergreen and tall deciduous forest formations of the Asian tropics, as defined by Ashton (2014). The latter is not included in vegetation maps, and will not be discussed further here.
Song (2004, 2011) and Song et al. (2017) revised the classification of Wu's evergreen broadleaved forest of China, and changed the names of the three subtropical evergreen broadleaved forests as following: monsoon evergreen broadleaved forest was renamed subtropical seasonal evergreen broadleaved forest of western China and placed under the subtropical seasonal evergreen broadleaved forest vegetation type; semi-wet evergreen broadleaved forest and mid-montane wet evergreen broadleaved forest were included in the vegetation sub-type semi-moist typical evergreen broadleaved forest of western China placed under the typical evergreen broadleaved forest vegetation type. Except the name and rank changes, no essential changes were made in Song's system.

Hou (1983) published the vegetation map of China (with legend in English, which provides brief floristic information on the vegetation types numbered on the map). The map provides an invaluable record of the distribution of the major tropical and adjacent subtropical (partially termed warm temperate) forest formations, as well as agricultural areas that share the same conditions, at the time of publication. This has enabled us to approximate the line of the tropical margin. They are numbered as follows:

3.2.1. Needle-leaved forests

- (5), Needle-leaved evergreen forests of subtropical or tropical zones: 7a, Pinus yunnanensis, b, P. kesiya forests or savannas; respectively occupying subtropical and tropical wet seasonal dry sunny fire-prone slopes at lower montane elevations, their separate but not distinct distributions facilitating location of the tropical margin in southwestern China. (P. massoniana occupies similar lowland subtropical slopes, and has widely supplanted semi-evergreen subtropical forests in southern and southeastern China).

- (6), Needle-leaved evergreen forests on mountains of subtropical and tropical zones. No tropical species are cited, and we conclude these to be cool temperate only.

3.2.1.2. Broadleaved forests. Based on floristic composition, we classify all formations as subtropical, except for the following:

- (14), Broadleaved evergreen lowland and lower montane forests of the transitional tropical zone: 22, Mixed forest containing Castanopsis, Lauraceae and Theaceae, with some belonging to tropical families. This vegetation type is mapped at subtropical latitudes along the central to north-western and -eastern lowlands of Taiwan and within the tropics of southern lowland Hainan. It is extraordinary that such forest of the tropical margin, where it reaches the lowlands in the mainland, has no mapped adjacent lowland wet evergreen lowland oak-laurel forest formation of this type, even along the coast. This may be due to deforestation since ancient times, and the vast reforestation of such areas with Eucalyptus in recent decades.

- (16), Tropical broad-leaved (seasonal) semi-evergreen forests, 24, on limestone soils; 25, on acid ('lateritic') soils.

- (17), Tropical broadleaved evergreen forests: 26, Tropical rain forest.

3.2.1.3. Scrub and coppice lands

- (20), Mixed broadleaved evergreen and deciduous scrub on acid soils of subtropical and tropical zones: 32, Melastoma, Aporosa secondary scrub. This vegetation type is mapped over lowland areas along the southern Chinese frontier, from the lowermost Mekong valley eastwards through Yunnan into Guangxi along the coastal plains to southernmost Fujian. Although apparently frost-free in SE Yunnan, Hevea rubber planted on the Funing-Napo plains of SE Yunnan and SW Guangxi was killed in the severe winter of 1976, and has not been replanted; the Longzhou plains (22°24′N), north of the Longzhou Reserve, frequently experience temperatures down to −3 °C. Whether the tropical species recorded from Nonggang in the Flora were observed on adjacent frost-free slopes is undocumented. The foliage of Melastoma shrubs that occur at and beyond the tropical margin are scorched by light frost but recover, and the ranges of the two widespread tropical Asian species in China (M. duodecandrum, M. malabathricum) extend far into subtropical regions. We conclude that this category includes secondary tropical vegetation near the coast, and warm temperate scrub further inland, and that the tropical margin, that is the transitional ecotone, probably runs within them as a broad ecotone.

3.2.1.4. Steppes and savannas. The ecotone between tropical and subtropical forest formations therefore broadly follows Zhu's tropical biogeographic margin (2017a, 2018), but wanders to the north and south of this margin in response to local topography.

We have re-numbered these vegetation types, which were more fully elaborated in a previous study (Hou et al., 1979, English translation). Elevational ranges of forest types have not been indicated on these maps. The absence of elevational ranges of the forest types on the map hinders comparison with the Himalaya and upper Burma, but it is clear that the steep ascent of the east-west Himalayan chain leads to constriction of zonation, which, in the north-south trending and more seasonal mountains of southern China east of the Mekong Valley (Lancang River Valley), become spread latitudinally north-south by the latitudinal spread of both temperature and rainfall seasonality.

Two of the Needle-leaved Forests of Hou et al., 's 1979 Vegetation Map is (5) 11: a, Pinus yunnanensis, which is subtropical, is distinguished from 11b, Pinus kesiya (syn. khasiya), which is tropical; each respectively equivalent to type 7a, b of the Hou's 1983 map.

In the broad category Broadleaved forest and woodland, Hou et al., 's 1979 vegetation map recognizes two unequivocal tropical forest formations: (18) Tropical broadleaved evergreen forest, subgroup 33 (Hou's 1983 type 26); Tropical (lowland) rain forest, of which there are four regional community types—Hainan, Tibet, Guangxi, and Taiwan; and (17) Tropical broadleaved semi-evergreen forest, in two main subgroups (1983 types 24, 25)—(31) seasonal forest on limestone soil, and (32) seasonal forest on acid latertic soil. Each includes two community types. The species for which these forests are named include deciduous taxa widespread in continental SE Asian tropical semi-evergreen and tall deciduous forests, including the deciduous Kleinhovia hospita, Spondias pinnata, Lagerstroemia intermedia, Chukrasia tabularis, and evergreen Pometia tomentosa. This indicates that these are tropical lowland forests, although other cited species are evergreen or of the tropical understory. The presence of Burrettiodendron hsiennu on limestone soil, a species confined to SE Guangxi and north-east Vietnam, might imply transitional forest. All occupy significant areas on the map. In contrast, whereas subtropical deciduous and evergreen forest on limestone soil (11) is widespread in the lowland ecological karst islands of South China, several subtropical types (12), labeled 24 and 25 on the 1979 vegetation map, occur on yellow-brown soils, and are apparently restricted to the mountains. Is this due to ancient conversion of their lowland range to agriculture?
3.3. Comparative structure of the southern China lowland forest formations

The four large sampled and censused tree demography plots of the CTFS collaboration located between 21°10′N and 29°10′N reveal the changes in forest structure that occur from tropical to increasingly subtropical evergreen formations in China (Tables 5 and 6). The forests in the Dinghushan and Gutianshan plots are unequivocally subtropical: Castanopsis chinensis, which dominates much of the Dinghushan plot canopy at a mere 23°25′N, is unknown from tropical forest but widespread in subtropical Chinese forests between 300 and 1700 m (Wu et al., 1999–2009).

Comparison of the plots showed a massive drop in the number of emergent species from lowland tropical forest to lower montane forest either side of their ecotone within the Xishuangbanna (Mengla) plot, and an increase in the proportion of subcanopy species, trends which increase in the two subtropical forest plots compared here. The number of true pioneers in the tropical Nonggang plot is smaller than that in the Xishuangbanna plot. This difference in pioneer numbers may be explained by the sheltered nature of the Xishuangbanna site. Furthermore, the Nonggang plot faces north and is exposed to north-easterlies. This decline in tree pioneers continues in subtropical forests of increasing latitudes. Yet, surprisingly, temperate deciduous pioneers of the Betulaceae and Salicaceae families are poorly represented and their numbers do not increase with latitude. Indeed, Chinese endemic species in euphorbiaceous pioneer genera in subtropical plots, even Macaranga, appear physiognomically indistinguishable from shade tolerant subcanopy species of other families. In these respects, floristic continuity is only somewhat interrupted between lowland tropical and subtropical forests, with the clearest floristic discontinuity occurring in the canopy. In contrast, the tropical lower montane forest and subtropical forests belong to a structurally-physiognomic continuum.

3.4. Identification of the tropical-temperate (subtropical) ecotone in China

The ranges of canopy species, as recorded in the Flora, indicate a clear distinction in regional distribution between tree species that are exclusively tropical and other tree species. No subtropical climax canopy species extend south of the tropical-subtropical ecotone into tropical forests. With the exception of the northern Vietnam-SW China endemic Canarium album, which reaches the Guangdong subtropics, the only widespread tropical canopy species to extend beyond the tropical margin northwards is the tropical lower montane later successional Engelhardia roxburghiana.

The ranges of the many tropical subcanopy species that extend across the tropical interface into subtropical evergreen forests have gradually declining northern range limits, although the central Chinese east-west barrier at Qinling Mountains does coincide with the northern limits of most (Ashton, 2014). The northern tropical margin in southern China is most clear among the exclusively tropical tree families, and among species of Fagaceae (Ashton, ibid., Table 3.15), but it is also apparent in the limited representation of temperate Chinese species south of the margin (Appendix 3).

Two further apparent forest formations are recognized in both the maps of China’s vegetation (Hou et al., 1979; Hou, 1983), although their climatic status is unclear in the 1983 map: (13) Broadleaved evergreen forest of the subtropical zone, in two categories with, respectively, two and four types in the 1979 key; and (14) Broadleaved evergreen forest of the transitional forest zone. As their names indicate, these forests are dominated by a canopy of Castanopsis species. Widespread Castanopsis species in the tropical

Table 3

| Lower Montane forest in southern Yunnan | (Summary findings of Zhu et al., 2005). |

- ‘Monsoon broadleaved evergreen forest’ (Tropical Lower Montane Forest of international terminology):
  - 3 plots, 5, 25 × 20 m subplots: Mengsong (Xishuangbanna) (1320–1380 m), Nangong mt. (Xishuangbanna) (1170–1200 m), Casyanghe (Simao) (1450–1500 m).
- Physiognomy:
  - Few epiphytes, more lianas & spp. with compound leaves, lower species diversity, than in Asian equatorial lower montane
- Dominant families:
  - Theaceae, Fagaceae, Lauraceae, Euphorbiaceae.
- Species included: Lithocarpus foahensis, L. arisutus, L. truncatus, Castanopsis myrsinaefoliae, C. hystrix, C. echinocarpa, C. ceratocantha, C. calathiformis, C. mokongensis, C. densispinosus (no Quercus).
- Acrochaia pedunculata, Annona fragrans, Betula alnoides, Chaerophyllum auxillaris, Cratoxylon cochinchinense, Engelhardia colebrookiana, E. roxburghiana, E. scipata, Eurya griffithii, E. cerisefolia, Hordeum glabrum, Macaranga indica, M. kurzii, M. denticulata, Michelia floribunda, Myrica esculenta, Pithecellobium clypéaria, Radermachera microideas, Schima wallichii, Symplocos cochinchinensis, S. yuananensis, Syzygium brachythyrsum, S. cuminii, S. leptanthum, Tenstroemia gymnacranthera, ...

Table 4

| Nonggang reserve, Guangxi | (summary of Anon., 1998–1999). |

- Three parcels on the border of Longzhou and Ninming counties, Guangxi autonomous region: 106°22′ – 107°04′E, 22°14′ – 22°33′N.
- Physical Environment:
  - Karst geology, with deep moist valleys carrying yellow-red clay loam and rocky hills and tops with shallow brown rendzina soils.
  - 1150–1500 mm mean annual rainfall, 76% in May–September during SW monsoon; highest sun and lowest rain (6.5%) in cool winter season during NE monsoon, high incidence of winter fog and dew formation, with lowest sunshine in February–March under a stationary South China Front.
  - Frostless over >320 days, but annual cold wave down Zhujiang river valley causes serious plant injury. Hottest (<40°C) in late summer.
- Floristics:
  - Poverty of Dipterocarpaceae, Fagaceae, Myrtaceae reflects high soil calcium, alkalinity.
  - Possible transition forest or temperate (subtropical) components
  - Trees and shrubs:
    - Forest:
      - Camellia caudata, C. longangensis, C. indochinensis
      - Fraxinus retusa
    - Karst summit rocks:
      - Camellia impressinervis, Prunus (3 spp.), Allophanthus guangxianensis, Buxus (3 spp.), Sargentodoxa cuneata, Ulmus tenuifolia, Quercus glauca, Gleditsia sinensis, G. australis, Firmiana calcaria, Euonymus (3 spp.), Celastrus chinensis, Zanthoxylum dimorphophyllyum, Carpinus retipes, Mallotus tenuifolius, Kohlrueberia bipinnata, Pipturus chinensis, P. weinmannifolia, Platycarya grossidentata, Cornus wilsoniana, Schefflera octandra, Buddleia officinalis, Viburnum trilinerve, Sambucus chinensis
and warm temperate (subtropical) elevational zones of the eastern Himalaya and Myanmar provide evidence of the climate in which each type occurs in southern China; those that are tropical provide evidence of their likely elevation. Thus forest types named after the presence of *C. indica* in the 1979 vegetation map are lower montane tropical: (13)27d, (14)28b, c; forests types with endemic *C. chinensis*, *C. glauca*, and endemic *Castanopsis eyrei* are subtropical (13) 26a, (14)28a. In the 1979 list, Chinese forests with *C. hystrix* appear to span both tropical and subtropical forests.

Owing to the contrast in topography between mountainous southwestern and undulating south-eastern China, the tropical lower montane forest (called monsoon evergreen broadleaved forest in Chinese literature) is thought to represent the transition between the tropical seasonal evergreen dipterocarp forest and subtropical (warm temperate) evergreen broadleaved forest in the mountainous southwest, while the southern subtropical evergreen broadleaved forest is thought to represent the transition in the south-eastern lowlands. This implies that the margin in the latter is gradual, representing part of a latitudinal tropical-subtropical continuum. However, although there is little consistent difference between the structure and physiognomy of tropical lower montane and subtropical evergreen broadleaved forest in southern China, the two are at once distinguished by the dramatic change in canopy tree floristics that occurs between them across the putative frost line.

### 3.5. Montane forest formations

The Xishuangbanna plot (elev. 709–869 m) unequivocally represents tropical forest, but includes the lowland-montane montane forest ecotone with both lowland northern seasonal evergreen dipterocarp and lower montane forest represented within the plot (Table 5). The ecotone, generally gradual between c. 750–1200 m elevation elsewhere, is sharp here, differentiating lowland forest with emergent *Parashorea chinensis* from lower montane forest with canopy dominated by non-emergent *Fagaceae* on upper slopes and ridges at c. 750–800 m (see Photo 1). Among the 468 species in the plot that exceed 1 cm in diameter, only 229 occurred in the florals of other Asian tropical regions cited in this study, reflecting a high proportion of China endemism. Of the 352 species represented with >10 individuals, 60% predominated in the lowland forest, 15% in the lower montane forest, which occupies less than one quarter of the plot area, 25% in both. Exclusively tropical families are represented in the lowland forest alone by the lofty emergent dipterocarp *Parashorea chinensis*, and in the subcanopy by *Horsfieldia glabra*, *Horsfieldia kingii*, *H. pandurifolia*,*H. tetrapetala* (Myristicaceae) and *Crypteronia paniculata* (Crypterionaceae). A lowland tropical semi-evergreen forest that had a similar flora but included the deciduous *Garuga floribunda* was documented by Zhu (2004) in a south-facing slope habitat at 22°30'–38°N in Caiyanghe Nature Reserve, S Yunnan; in the same location, lower montane forest also occurs above 1200 m.

Chinese tropical forests have been comprehensively documented by sample plots in lowland tropical seasonal evergreen forest (Zhu, 1997; Zhu, 2004) and lower montane forests based on plot censuses at three sites at 1200–1800 m in southern Yunnan, under the name Tropical Montane Broadleaved Evergreen forest (Zhu et al., 2005) (Photo 2) (Table 3). *C. indica* was not recorded in the tropical lower montane broadleaved evergreen forests of southern Yunnan, probably because it is a successional species frequently dominant in China. However, this forest included many widespread species typical of lower montane forest, including three *Lithocarpus*, six *Castanopsis*, *Cyclolalanopsis myrsinifolius*, three *Engelhardia*, *S. wallchii* (but not warmest subtropical *Schima conferiflora*), *Anneslea fragrans*, two *Symplocos*, and two *Eurya*. Additional species found in the lowlands that were recorded in southern Yunnan tropical lower montane montane broadleaved evergreen forests include three *Macaranga*, *G. glabra*, *Syzygium leptanthum* and *S. cumingii*, *Cratoxylon chinichinense*, *Acronychia pedunculata*, and *Radermachera macrostachys*. *Betula alnoides* and *C. hystrix* were also recorded in these forests, which, according to Himalayan evidence, suggests that at the upper levels sampled occasional frost occurs (Brandis, 1907; Grierson et al., 2001). Evidence that flora changes along a continuous gradient within each elevational forest formation zone has been further provided by research on the Bulong Nature Reserve in the far south-west of Yunnan (22°N), close to the Myanmar frontier (Zhu et al., 2005). Groups of five 0.5-ha. plots were censused here, of trees >5 cm dbh, each in six recognized floristic community types. These were below 1100 m in the lowland–lower montane forest ecotone, at 1100–1600 m within the lower montane forest formation, and above 1600 m in a ‘mid-montane’ forest zone. Lauraceae were rich in species in all zones, but dominance (Importance Value) in the transition zone was among Euphorbiaceae then Sapotaceae; whereas Fagaceae and Lauraceae shared dominance at the higher elevations sampled, which were therefore floristically typical of Asian tropical lower montane forest. All zones were rich in Lauraceae, but in the transition zone Euphorbiaceae, then Sapotaceae, had higher dominance (Importance Value). At the higher elevations, Fagaceae and Lauraceae shared dominance. These dominance patterns are floristically typical both of Asian tropical lower montane and subtropical forest. Cornaceae and Magnoliaceae were more represented at higher elevations. Although *C. hystrix* is restricted to transition forest above 1600 m in the Himalaya, at the Bulong Nature Reserve it was present down to 1100 m. However, the Himalayan transition forest species *Alcimandra cathcartii* and *Syzygium brachythyrsus* were present at Bulong Nature Reserve above 1600 m. The authors note that freezing temperatures may occur (presumably on open

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**Table 5**

| Plot areas, site elevations, floristics and forest types sampled: |
|---|
| Xishuangbanna, S Yunnan, 21°36′N, 20 ha., 709–869 m elev. |
| Fisher’s alpha diversity index: 42, 468 species censused, all tropical, 229 (49%) of which are cited in other tropical Asian floras. |
| Lowland northern seasonal evergreen dipterocarp forest and lower montane f. above c. 750 m on ridges |
| Nonggang, SW Guangxi, 22° 14′–39′N, 15 ha., 194–374 m |
| Fisher’s alpha: 29, 217 species censused, all tropical, of which cited in other tropical Asian floras. |
| Lowland northern seasonal evergreen rain forest on karst |
| Dinghushan, Guangdong, 23°25′N, 20 ha., 230–470 m elev. |
| Fisher’s alpha: 22, 195 species censused, 133 (68%) in tropical Asian floras |
| Southern subtropical broadleaved evergreen forest (Castanopsis chinensis) |
| Gutianshan, Zhejiang, 29°10′N, 25 ha., 446–714 m elev. |
| Fisher’s alpha: 18, 159 species censused, of which 70 (44%) in other tropical floras. |
| Typical subtropical broadleaved evergreen forest (Castanopsis eyrei) |
ground) down to elevations between 900 and 1000 m in this part of the Mekong valley: Is there any other floristic or other evidence of a descent of the tropical-temperate transition there? (Further north up the valley, a drier summer climate is associated with an open semi-evergreen or evergreen woodlands in which the Mediterranean, that is, warm temperate, genera *Olea* and *Pistacia* predominate (Zhu and Cai, 2004)).

The several types within Hou et al., ‘s 1979 vegetation map categories (13) and (14) in which *C. hystrix* is regarded as characteristic are of particular interest. *C. hystrix*, which occurs west to Bhutan, is confined in the Himalaya to elevations between (1800–)2000–2400 m (Grierson et al., 1987–2001; Brandis, 1907), within which light winter frost begins to occur most years. The lower limit of *C. hystrix*, therefore, approaches the upper tropical margin on the map. Another possible explanation for the presence of these tree species in one location is that they indicate the tropical-subtropical ecotone. According to the *Flora of China*, *C. hystrix* occurs to sea level in southern China. That in turn implies that some of these transitional types follow the tropical margin as it descends eastwards to the lowlands of Guangxi, where cold northeasterly winter breezes flow over the descending hills. There, subtropical forest first likely truncates the lower levels of tropical lower montane forest as frost descends to lower elevations, but eventually, in the lowlands or to the north, the ecotone is formed between lowland tropical seasonal evergreen dipterocarp and subtropical evergreen and semi-evergreen forest. Such a lowland tropical-subtropical ecotone has not been documented, nor has evidence of an edaphic frontier from tropical to warm temperate soils across it. Examples may no longer survive.

Based on previous studies and our personal observations of the floras of the Himalaya and China, we conclude that whereas the formations numbered (13)/26 in Hou et al., ‘s 1979 Vegetation Map another possible explanation for the presence of these tree species in one location is that they indicate the tropical-subtropical ecotone. According to the *Flora of China*, *C. hystrix* occurs to sea level in southern China. That in turn implies that some of these transitional types follow the tropical margin as it descends eastwards to the lowlands of Guangxi, where cold northeasterly winter breezes flow over the descending hills. There, subtropical forest first likely truncates the lower levels of tropical lower montane forest as frost descends to lower elevations, but eventually, in the lowlands or to the north, the ecotone is formed between lowland tropical seasonal evergreen dipterocarp and subtropical evergreen and semi-evergreen forest. Such a lowland tropical-subtropical ecotone has not been documented, nor has evidence of an edaphic frontier from tropical to warm temperate soils across it. Examples may no longer survive.

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The elevation of the ecotone between tropical lower montane and subtropical evergreen forests, and by inference the frost line, which is so clear in the Himalaya, seems not to have been recorded in the south Chinese mountains. Xu et al. (2017) analyzed the elevational range of all vascular species in the Honghe region of south-east Yunnan (22°26'–24°45'N), sampling a total of 5947 species in 1488 genera and 225 families, including 43 families, 60 genera and 74 exotic species. They found that species diversity in this region followed a bell-shaped distribution in relation to elevation. Elevations in this region range between the lowlands to 3057 m, while mean annual rainfall varies between 876 and 1926 mm, implying that the seasonal climate varies from dry to wet. This study recognized the following forest zones from low to high elevations, although without indicating elevational ranges: tropical rain forest, montane rain forest, monsoon evergreen broadleaved forest, montane mossy evergreen broadleaved forest, and summit mossy broadleaved evergreen forest. The researchers did not document whether an edaphic frontier extended along this lowland ecotone from tropical to warm temperate soils. The ‘montane rain forest’ is a higher elevational subtype of the tropical rain forest vegetation type in Wu’s classification (Wu, 1987). He classified the tropical rain forest vegetation type into two subtypes: seasonal rain forest at

Photo 1. Lowland northern seasonal evergreen dipterocarp forest. photos taken at 21°36' N, 750 m elev. Xishuangbanna, southern Yunnan (by H. Zhu).
lower sites and montane rain forest at higher sites in southern Yunnan, from which almost all related Chinese references followed. The ‘montane rain forest’ and the ‘monsoon evergreen broadleaved forest’ are in the same elevational zone, but in different habitats: the ‘montane rain forest’ occurs discontinuously in some wet habitats of lower mountain valleys and has some physiognomic and structural features of lowland seasonal rain forest (i.e. tropical rain forest), whereas the ‘monsoon evergreen broadleaved forest’ occurs on drier slopes with monsoonal seasonal drought, and was therefore classified as a different vegetation type from the tropical rain forest. We infer that ‘montane rain forest’ is equivalent to lower montane forest, and forests above it are temperate. The curve in species diversity peaked at 1500 m, which implies that this is explained by inclusion at this elevation of the ecotone between tropical lower montane and subtropical (warm temperate) forest, therefore two distinct formations and floras. This indicates that in the Honghe region the frost line is below 2000 m, which would be consistent with the isolation of Xilong Shan, the mountain included in their analysis, and its proximity to the eastern limits of montane South China.

Recently, though, one of us (Zhu, 2016b) has documented all trees >1 cm dbh in six 1-ha plots set at 2190–2730 m in Central Yunnan in forest named by him Upper Montane Broadleaved Evergreen forest following the terminology of Ohsawa in the Eastern Himalaya (Appendix 4) (Photo 3). Both these forests occur at similar elevations and share a few characteristic species. But equatorial upper montane forest differs from this higher latitude type in important respects (Grubb, 1973; Grubb et al., 1963; Whitmore, 1984, 1998). The equatorial formation is of short stature, with short crooked boles; all species are evergreen;
dominant leaf sizes are microphyll or smaller (<2.025 cm²), lacking drip tips and coriaceous. Species of this Chinese high latitude putative upper montane formation are instead predominantly notophyll (in the sense of Webb, that is, 2.025–4.5 cm²) similar to tropical lower montane and warm temperate evergreen forests (Therefore, all leaf sizes are smaller than Webb’s mesophyll (4.5–8.2 cm²) size class, which dominates tropical lowland evergreen forests). Ohsawa and Nitta (1997) observed that certain genera, notably Symplocos and Ardisia, are particularly well represented in both equatorial and higher latitude upper montane forests, as are vascular cryptogams; but those angiosperms that dominate the latter, notably Fagaceae, are subordinate or absent in the equatorial formation. The equatorial and tropical margin ‘upper montane’ tree floras are otherwise almost entirely different at all taxonomic levels. The ecotone between tropical lower and Ohsawa’s upper montane forest in the eastern Himalaya is marked by high turnover among the dominant Fagaceae canopy species. Whereas high latitude upper montane forest is rich in angiospermous epiphytes, most or all in low population densities, equatorial upper montane forests support dense populations of few vascular epiphyte species. Most notable, the equatorial formation is dense with moss and liverwort tussocks from the ground to the branches, which are thereby enveloped in cryptogamic sleeves. These cryptogamic sleeves are confined to
the equatorial formation, where they serve as a primary diagnostic, and to aseasonal continuously wet climates where cloud penetrates the canopy in a diurnal orographic breeze. The continuous drip resulting from this fog capture leaches the soil, which podzolizes with accumulation of acid raw humus, in contrast to the mesic humic mulls of tropical lower montane and warm temperate (including subtropical) ecosystems. In the Himalaya and southern China, diurnal fogginess is confined to the south-west summer monsoon period, lasting little more than six months. Because the intertropical (wind) convergence zone is overhead during the southern Chinese midsummer, fogginess penetrates the canopy in these regions at precisely the same elevation as in equatorial regions. Fog prevails only at the elevation of the ‘upper montane forest’, that is above c. 1800 m. During the rest of the year though, which includes the winter when dry north-easterly winds prevail and the days are mostly sunny, nocturnal rather than diurnal fog is frequent at this elevation, namely on slopes where forest canopies have been warmed by the sun, and have evaporated water vapor during the day to condense into fog as the nocturnal temperature declines. The predominant precipitation during this time is therefore fog drip, and this may lead to some soil acidification within the lower montane forest which receives it; but we have observed that the soils remain typical humic mulls. Nocturnal fog likely also occurs in this ‘upper montane’ forest during the hot pre-wet monsoon dry season (March through May), but during the coldest months evaporates each morning as the sun rises, leading to occasional air frost during moon-lit nights. Research has yet to determine whether accumulation of acid-reacting surface raw humus and incipient podzolization ever occurs in this transitional climatic as well as floristic zone. Higher up, or further north, montane subtropical broadleaved evergreen forests experience increasingly intermittent diurnal fogginess during the wet monsoon, decline in nocturnal fog drip during the dry season, a mid-winter period of increasingly continuous air frost, and eventually ground frost where the canopy is more deciduous, or shorter; and the soils return to humic mulls. These montane subtropical evergreen broadleaved forests are striking for their clean boles, free of moss, implying seasonally dry conditions.

Notably, in Zhu's (2016b) ‘upper montane’ plots, species that primarily had a subtropical ecological and geographic range were highly represented (49/124) and were mixed with many species primarily from a tropical lower montane range (28/124); a further 29 species shared both distributions. Ten species were limited to the formation alone, including several found that are also found in the Central Himalaya (Appendix 4). Therefore, whereas we have previously regarded the Himalayan formation as an ecotone between tropical lower montane and subtropical forest formations, which is generally narrow there and does not exceed elevations of 500 m (Ashton, 2014, 2017), Zhu's plots demonstrate that in Yunnan the formation can extend over uniform terrain. The formation includes a small but diagnostic tree species element, both endemic to China and extending west into the Himalaya, including A. cathcartii and Michelia doltsopa, and perhaps C. hystrix (though not listed for the plots). The formation is surmounted on wet subtropical mountain slopes by other floristically distinct zones, including cooler temperate conifer and deciduous angiosperm-dominated woodland formations, and does not therefore merit the epithet upper. This formation is unique, however, in including substantial representation of both tropical and temperate arboreal elements. Thus, this formation is the true tropical-temperate transition forest. We hypothesize that this transition forest occurs at the elevations where the summer wet monsoon cloud most enters the forest canopy diurnally, but where nocturnal drip is also received during much of the dry season. However, nocturnal fog may not reach its elevation during periods of full moon, when air temperatures may drop below freezing. These are analogous to conditions in the summit upper montane woodlands of the South Asian mountains. There, natural tropical lower montane species' regeneration continues within the forest canopy although the air above the canopy is apparently below freezing temperature; but young regeneration is killed by frost in adjacent anthropogenic grasslands where temperate herb and grass genera predominate. This provides the opportunity for similar observations in the South Chinese montane monsoon foggy zone. Whereas the tropical species in the transition forest formation may initially regenerate only within its putatively frost-free understory, the subtropical species represented may do so where there are windthrows and other causes of canopy opening and soil exposure.

Zhu et al. (2019) presents a map (see Zhu et al. Fig. 3) in which the current distribution of lower montane and transition forest is indicated. Transition forest fragments are separated to the north-east of the lower montane, except in two instances near the Yunnan-Myanmar, and Yunnan-Laos frontiers. This implies that extensive cultivation, mainly for tea, has eliminated this formation, which probably coincides with the upper elevation of tea cultivation.

A further montane zonal forest formation, whose residual fragments are in turn geographically separated to the north-east of the transition forest’s, is termed by Zhu (loc. cit.) semi-wet evergreen broad-leaved forest, following Wu (1980, 1987). According to Zhu this forest is located between 1500 and 2600 m, therefore overlapping in elevation both the upper limit of tropical lower montane forest and the lower limit of transition forest. The forest is remarkable for its low epiphyte and cryptogam load, which we hypothesise is due to lack of winter nocturnal fog and clear dry winter nights with periodic frost. This forest, in which two 1-ha plots were censused, included nine species which also occur in tropical lower montane forests among the 36 species listed, but all except one, Ficus virens, extend to temperate elevations in the eastern Himalaya. The ranges of the rest extend north to northernmost Yunnan and the provinces bordering the southern slopes of the Qinling Mountains, while one third of these occur to the north beyond, to Shaanxi, or S. Gansu, Shanxi, Henan and Anhui. We infer from these ranges that they are subtropical, that is, warm temperate, species, and that this forest type represents the southern limit of the montane community type of the subtropical evergreen and semi-evergreen forest formation of central and southern China.

Ecotones have not been documented between tropical-temperate transition forest and tropical lower montane, subtropical evergreen, or semi-evergreen broad-leaved forests, respectively. The montane forests along the tropical margin have almost entirely been obscured by cultivation, so we infer that the tropical margin itself, that is this newly recognized transition forest, courses between the north-eastern limits of tropical lower montane forest and the south-western limits of subtropical broad-leaved forest.

Further east, approaching the eastern and southern boundary of Guizhou province, where it meets the south-eastern boundary of Yunnan, the hills decline in elevation below the lowest recorded elevation of the transition forest. The tropical margin, which appears to trend south-east in the mountains east of the Mekong valley, probably from an initial c. 26°N as in the Himalaya, eventually approaches the Tropic of Cancer in the Guangxi lowlands. The floristic changes that occur as the margin descends are as yet undocumented. The survival of individuals of species characteristic of transition forest, such as C. hystrix perhaps, which are otherwise unknown to occur to low elevations, may betray its course where it passes through summer-wet seasonal climates.
3.6. Lowland forest formations in China

We compared the proportion of tropical taxa occurring in lowland forests at four sites on either side of the Tropic of Cancer using data from large tree demography plots of the Chinese Biodiversity Monitoring Network (CForBio), affiliated with the global plot network of the Center for Tropical Forest Science of the Smithsonian Institution (Tables 4 and 5). These plots include the Xishuangbanna (Mengla) plot (20° ha., 21°36′N, elev. 709–869 m), northern seasonal evergreen dipterocarp forest, for which a species list is available (Cao et al., 2008); the Nonggang karst plot in SW Guangxi (15° ha., 22°14′–39′N, elev. 194–374 m), lowland northern seasonal evergreen rain forest on karst, for which leading species are listed (Wang et al., 2014; Guo et al., 2015); Dinghushan plot in Dinghu Shan National Nature Reserve, Guandong (20 ha, 23°25′N, elev. 230–470 m) southern subtropical broadleaved evergreen forest (Ye et al., 2013); and the Guitianshan Nature Reserve plot, (25 ha, 29°10′N, elev. 446–714 m), typical subtropical broadleaved evergreen forest (Ma et al., 2009). In the two tropical forest plots (Xishuangbanna and Nonggang) there is a surprisingly high proportion of endemic species. These are succeeded to the north-east by the southernmost subtropical forest plot, Dinghushan; representatives of the tropical tree species in these subtropical forest plots declines northwards consistent with the provincial figures in Fig. 1, also see Appendix 1.

The lowlands of tropical south-east China are a diverse terrain of rocky karst inselbergs <1500 m, set in a level or undulating plain, with sedimentary hills to the north-east (Hu, 1979). These lowlands are the cradle of ten millennia of irrigated agriculture. What forest remains is reduced to island refuges, particularly on steep karst that has resisted cultivation. Ecotones between lowland and lower montane, and tropical and subtropical forests, seem not to have survived. Two lowland tree demography plots, at Nonggang Reserve, in forest described by its instigators as Karst Seasonal Rain Forest, and at Dinghu Shan National Nature Reserve 600 km to its east, described as Southern Subtropical Forest (Photo 4), lie close to the Tropic of Cancer, the geographical tropical margin; both are below an elevation of 500 m and somewhat over 100 km inland. No ecotonal forest between these two locations is known to us. Comparison of the structural, physiognomic, and floristic characteristics is nevertheless particularly informative (Tables 5 and 6).

Nonggang (or Longgang) forest proves to be a lowland site of exceptional interest (Table 5). Situated virtually on the Tropic of Cancer, the Nonggang Reserve is set in undulating lowlands along the eastern side of the Ninning River. Divided into three fragments, the reserve represents a fragmented range of late Permian and early Devonian karst limestone running from south-east and near the coast, north and north-west towards the Vietnam frontier, with peaks exceeding 600 m but mostly <400 m. Nonggang Reserve has an archipelagic karst landscape and habitat complex unusually well represented in southern and central China, which continues south into Tonkin, Vietnam, and in a separate archipelago in north-western Thailand and adjacent Myanmar; yet karst is absent from South Asia. Six soil types are mapped. They are generally shallow, with exposed rocks towards summits, and of the yellow-red ultisols typical of karst in the humid tropics. Liang and collaborators (Liang, 1988) note that the reserve is south of the Longzhou Basin, which is surrounded by mountains (except to the east, from which winter winds originate) and is therefore subject to frost ponding (see also Deng et al., 2004). Mostly agricultural now, the land surrounding the Nonggang Reserve still bears patches of a seasonally dry forest, which, according to Hou et al., ’s 1979 vegetation map, includes Drypetes confertiflora, Cleistanthus saichikii, and Garcinia paucinervis, southern China endemics of tropical genera which, with Excentrodendron tonkinensis (syn. B. hsienmu), imply cold dry winters that may include occasional air frost. These factors suggest that this forest may represent a transitional community type. To the south-west of this forest, however, the residual natural vegetation appears to either be secondary seasonal wet tropical or transitional, and includes Aporosa chinensis and the Myrtaceous taxa Rhodomyrtus tomentosa, Baeccki frutescens, and Melastoma candidum. Tracking the local distribution of exclusively tropical taxa in this more seasonally dry region might allow identification of a clear tropical-temperate ecotone; but observations in the similar climate in the Siwalik frontal ranges of western Nepal (Stainton, 1972) suggest that transition zones become gradual in this climate.

The Nonggang Report describes periodic winter air frost within Nonggang Reserve valleys. But the proveness of the karst summits to frost is not mentioned, nor is there any reference to the relationship of the forest flora to slope aspect. We hypothesize that lowland tropical rain forest will be richest on sheltered south or south-west facing slopes that experience winter orographic nocturnal dewfall; north-east facing slopes, shaded through much of the day in winter, may experience periodic air frost, and will likely then be drier. This prediction is consistent with the species list, which includes many deciduous canopy species (Table 4). Nevertheless, members of the plot census team and other observers have no record of frost damage among evergreen tree crowns on the reserve slopes.

Forest on the Nonggang karst bears a canopy broken by frequent gaps (Xiang et al., 2019), and its structure reflects variable stability (Zong et al., 2012), which is consistent with a high diversity and abundance of vines (Jiang et al., 2017), also observed by Zhu et al. (2005) in Yunnan lower montane forest. This canopy instability may be accounted for in part by the steep and unstable karst topography, but also and perhaps more by the location within the typhoon belt. Herbaceous climbers were better represented in the valleys.

The structure of the Nonggang plot, as inferred by the maximum diameter achieved by the commoner trees (Table 6c), indicates that the majority of species attain a single upper canopy stratum, although the dipterocarp Parasorea chinensis adds an emergent stratum elsewhere in the reserve. Based on the maximum height and individual characteristics of species, the structure of the Nonggang plot indicates that two emergent pioneer species, Alstonia scholaris and B. ceiba, are present, and that there are apparently equal numbers of subcanopy shade-tolerant and light-demanding pioneer species. The unstratified overall forest structure, combined with the species categories represented, is consistent with its canopy instability.

The Dinghu Shan Nature Reserve lies on undulating hills <1000 m over Tertiary sedimentary rock. Soils are yellow-red ultisols on the slopes below 300 m, grading to paler yellow-brown humic mulls towards the ridges and above 300 m. Occasional frost events <-1 °C occur here annually, usually for only 1–2 days. Based on the maximum height and individual characteristics of species, the structure of the Nonggang plot indicates that two emergent pioneer species, A. scholaris and B. ceiba, are present, and that there are apparently equal numbers of subcanopy shade-tolerant and light-demanding pioneer species. The dominant canopy broadleaved species of the Dinghushan plot is C. chinensis, a species which characterizes the southernmost mainland lowland subtropical forest formation. Two locally endemic tropical Burseraceae are present: the large canopy tree C. album, the only large buttressed tree in a forest formation where species otherwise lack prominent buttresses; and the widespread tropical lower montane late successional Engelhardtia roburghiana, which is a common canopy constituent of the western, lower part of the plot. The
western section of the Dinghushan plot has an abundance of large trees of the subtropical species *Pinus massoniana* and lacks individuals less than 10 cm in diameter. These findings imply that the forest is undergoing succession, likely after clearance or fire, or alternatively, the forest is recovering from a massive windthrow. The predominance of subtropical species in the Dinghushan plot canopy contrasts with its subcanopy flora, where species with both tropical and subtropical ranges prevail. In fact, one-third of those eighty-five species in the Dinghushan plot subcanopy which range south into tropical regions of Asia, occur in tropical lower montane forest.

Leaf characteristics at Nonggang and Dinghushan plots differ (Table 6b). At Nonggang, there are twice as many mesophyll species as notophyll species, which in equatorial Asia is typical for evergreen mixed dipterocarp forest on loam soils. Furthermore, mesophyll and notophyll species comprise a total of 85% of all leaf sizes; microphyll species represent only 10%. However, at Dinghushan, notophyll species exceed mesophyll species, and microphyll species comprise 22% of all species, ratios typical of tropical lower montane forest. The dominant canopy *C. chinensis* is microphyll. Pinnate and deciduous species at Nonggang greatly outnumber those at Dinghushan, partly explicable by the proximity of surrounding drier plains; most of the modest microphyll representation at Nonggang consists of pinnate and deciduous leaflets. The abundance of small-leaved, often coriaceous subcanopy species is an unexpected feature at Dinghushan; but leaves of these species are mostly dull, and never revolute as has been observed in lightly frost-prone equatorial alpine thickets and evergreen subcanopy components of warm temperate deciduous forests (Ashton, 2014, 2017).

Photo 4. Southern subtropical broadleaved evergreen forest, photos taken at 23°25′ N, 230°470 m elev. in Dinghushan plot, Guangdong (by Li Jiong).
Overall, the structure and physiognomy of the Nonggang forest, notably mesophyll dominance, is typical of lowland tropical evergreen rainforest in unstable habitats, whereas that of the Dinghushan forest, with notophyll dominance, most resembles a tropical lower montane forest.

The Nonggang Reserve’s list of both trees and herbs includes unequivocally lowland tropical species but for one putatively subtropical member, *Fraxinus retusa* (Table 4). Two members of exclusively tropical families are represented: *Parashorea chinensis* and *H. kingii* (syn. *hainanensis*), both of which are rare and local, but confirming that lowland tropical seasonal evergreen forest is present. A diverse tropical component appears to prevail through the landscape as a whole, and the site of the 15-ha tree demography plot is on an east-facing example. These slopes bear a rich calcareous flora, and tropical pioneers are well represented. Besides species characteristic of the northern seasonable evergreen dipterocarp forest, deciduous northern semi-evergreen forest components are present at Nonggang with several tropical Bignoniaceae, including *Markhania caudo-felina*, *Oroxylum indicum*, three Radermachera, two *Stereospermum*, *Firmiana calcarca*, *Acrocarpus fraxinifolius*, five *Dalbergia*, and *C. tabularis*.

Exclusively lower montane taxa are absent at Nonggang, but *Camellia* is represented by five taxa, one of which is common. This genus, which is generally absent from tropical seasonal evergreen lowland forest, is absent from the Xishuangbanna plot, and has few tropical lower montane species which are usually local. *Camellia* species are more diverse, widespread, and common in subtropical evergreen forest (Appendix 1). Although there is but a single Fagaceae in the plot, *Lithocarpus areca*, elsewhere in the reserve Fagaceae are represented by eleven taxa. None are dominant. Of these, nine are endemic to southern China, and may be tropical, subtropical, or both. *Quercus* (*Cyclobalanopsis*) *glauca*, a species which extends from seasonally dry northern seasonal semi-evergreen forest west to the north-west Himalaya, is rare and confined to craggy cliffs, as are the locally endemic *Lithocarpus reticulatus*, *Quercus longzhouensis*, and *Quercus sinii*.

The following species characteristic of the warmest region subtropical forests, including on plains subject to occasional frost, in the Nonggang Reserve include *Excentrodendron tonkinense*, *Ulmus tonkinensis*, *Liquidambar formosana*, *Toona sinensis*, nine *Zanthoxylum* species, three *Prunus* and *Ailanthus guanxiensis* (Table 4). A few of these woody species occur in valleys, which periodically experience frost-bearing north-easterly winter down drafts. These valleys do support a rich temperate generic grassland flora, only a few of which, including *Polygonum trichophloph*, *Lysimachia calcarca*, and *Caryopteris incana* also occur on the peaks and cliffs, which are rocky and apparently almost devoid of soils and herbaceous grassland. Two *Cycas* species are supported by cliffs, while subtropical woody elements appear most manifest on the peaks and upper cliffs, which also harbor trees and shrubs in the genera *Gleditsia*, *Euonymus*, *Buxus*, *Zanthoxylum*, *Ulmus*, *Pistacia*, *Viburnum*, and the species *Platycarya grossidentata*, *C. rupestris*, and *Corns tumultiana*, many of which are deciduous. Although the flat Nonggang valley bottoms sometimes pond frosted air, evidenced by the rich temperate perennial flora that borders them, no subtropical woody elements are recorded along the lower slopes, nor have we heard evidence of frost-burning of tree crowns. Although meteorological observations are lacking, a local karst endemic and temperate conifer, *Pseudotsuga brevifolia*, occurs at c.1300 m on some peaks outside the reserve.

One-third of the Nonggang tree flora extends into subtropical southern China (Table 6A). Nearly one-third occurs widely in equatorial Asian forests, mainly in the lowlands, but only 4% are confined to South-east Asia. One-quarter of the Nonggang tree flora is common to the northern Asian tropics, while remarkably, of the nearly one-half that is endemic to China, half of these are restricted to the karst of SE Guangxi and Tonkin.

Similarly, half of the species recorded at Dinghushan are in the tropical Asian floras compared in this study. Of these, one-fifth are confined to the northern seasonal tropics of the Himalaya and Indo-Burma. One-third of the Dinghushan plot flora is endemic to tropical and subtropical China, as well as northernmost Vietnam. Of these species, 14% are restricted to South-East China. Only 12% of the Dinghushan species are exclusive to subtropical East Asia, replacing a proportion of the tropical species of the south-east at Nonggang whose ranges extend to subtropical China. The great majority of the Dinghushan species occurring in the tropics are distributed in the lowlands, very few in the lower montane. Thus, most Dinghushan plot species have tropical distributions. The percentage of Dinghushan species that are endemic to China is similar to that of Nonggang Reserve; furthermore, the Dinghushan endemic species are endemic to south-eastern China. However, a greater proportion of the Dinghushan tropical species are widespread in equatorial Asia. In summary, the geography of the tree flora in the Dinghushan plot is remarkably similar to that of the tree flora at the Nonggang plot but for the incipient presence of exclusively subtropical (that is warm temperate) elements, especially in the canopy, in spite of its markedly different stand structure and physiognomy.

3.7. Coastal forests

The presence of mangroves, whose salt-tolerant transpiration physiology is destroyed by freezing, indicates the northern limits of frost-free coastal climates. Mangroves occur in nature north to Fujian, and in cultivation into Zhejiang. They persist north to Okinawa in the Ryukyus, and a small stand of *Kandelia obovata* occurs in the Bay of Kagoshima in Kyushu, Japan (at 30° N). Tropical tree species, including the light-demanding pioneer *Macaranga tanarius*, extend to the typhoon-prone Okinawan forests, where the tree flora, including all canopy species, is nevertheless subtropical (S.-I. Aiba, pers. Comm.), and a few persist in surviving localities on the mainland north into Zhejiang, likewise dominated by subtropical elements (Ashton, 2014). This flora likely survives in sheltered pockets where air frost is rare or absent, and where tropical survivors are able to successfully compete with a predominant subtropical flora. The existence of these tropical tree species is likely explained by periodic extinction and reimmigration as well as the avoidance of catastrophic weather, rather than a predominant climate defined by a prevailing warmth index. However, evidence for these explanations will be hard to obtain.

In this third part of our paper, we have addressed our central objective: to compare and, where possible, to integrate our understanding of the tropical and subtropical evergreen forest formations of northern tropical and subtropical East Asia, and their correlation with physical factors of climate and soil. Our primary focus has been the ecological and physical nature of the transition, or ecotone, between the tropical and temperate (here subtropical) ecosystems of the region, for which the broad causative physical mediator has been implied.

4. What, then, do we not know?

1. Although we estimate that the tropical margin is probably at c. 2000 m, the precise elevation of the tropical margin as it enters South China from adjacent Myanmar and skirts the Mekong (Lancang) valley eastwards is unknown. This is because the area where the upper limits of tropical lower montane forest meets the Tropical—Subtropical Transition Forest along the tropical margin in south-west Yunnan is now mostly under cultivation. We also do not
know the path of the tropical margin’s descent into the foothills and plains of south-east China.

2. Research has yet to document the ecotone between the indisputable tropical lower montane forest and the Transition (tropical lower montane to subtropical evergreen montane) forest formation that marks the tropical margin; nor has an ecotope been documented between the Transition forest and the subtropical montane evergreen and semi-evergreen broadleaved forests above it and in a lower rainfall climate on the south-west Chinese mountains. Few locations of either the transition forest or its ecotones likely now exist owing to conversion to agriculture, especially tea. This implies that no consistent records exist of the presence and nature of a line, north of which killing air frosts occur, and possibly ground frosts, also in open sites including grassland. Yet the presence of the isolated high peak Xilong Shan (elev. 3057 m) in Honghe district in the upper Red River of south-east Yunnan, close to the Vietnam frontier, indicates that a montane frost line and transition forest must occur here, with an associated ecotope to an island of subtropical montane flora (Xu et al., 2017). The forest formations cited imply that this occurs on Xilong Shan somewhat below 2000 m. This is consistent with documentation of floristic change with elevation on the northern Vietnam high mountains of Hoa Binh, Lao Cai, and Ha Giang (Hou, 1983). Observations recorded in the lower montane forest zone of Fan Si Pan, (elev. 3143 m, 22° 19′ N) (Nguyen, 2007), Leading species recorded at elevational intervals of 500 m indicate the presence of Transition forest tree species, such as Huodendron tibeticum and A. cathcartii, as well as the tropical S. wallisii between 1500 and 2000 m. The presence of both transition and tropical tree species suggests that the tropical margin is below 2000 m, consistent with findings in the Xilong mountains. The summit area of Fan Si Pan is anthropogenic grassland in which hoar frost can occur down to 1000 m.

3. Similarly, research has yet to identify the ecotope between tropical lowland forests, either seasonal evergreen or semi-evergreen, and lowland subtropical forests in the south-eastern Chinese lowlands. Ohsawa (1995b, 2006) inferred that forest with floristic characteristics of lower montane forest descends to low elevation as the tropic of Cancer is approached. In the foothills and lowlands of southernmost Guizhou and Guangxi, and in usually frost-free coastal sites to the north-east, floristic differentiation is made difficult within landscapes by three factors: the widespread presence of karst limestone and its edaphic and topographic influence, the drier winter months with less dew-drop from fog, and the presence of a higher proportion of taxa, many of them successful, that are widespread in the Asian tropics but that may be to some extent adapted to frost. But near-coastal mountains at latitudes near the Tropic of Cancer bear tropical lower montane forest to their summits. These include Yingge Ling on Hainan (elev. 1812 m, c. 19° 10′ N) and Ba Vi (elev. 1228 m, 21° 99′ N) in Vietnam, on which hoar frost in open secondary grassland has been observed down to 400 m. And although frost and ice has been recorded on ship rigging in Hong Kong harbor, tropical taxa occur in secondary vegetation in south-facing coastal sites north-east through Guangdong to Fujian, and to a lesser extent to Zhejiang (Ding et al., 2013), which implies that lowland tropical rain forest was once present in these regions.

4. The breadth of the tropical margin is unknown. In other words, we do not know how broad the ecotope is that marks the transition between tropical and subtropical (i.e., warmest temperate) evergreen forest in China. Observations in the Himalaya suggest that the tropic margin is narrow in these mountains. However, the occurrence of a distinct Tropical-Subtropical Transition Forest (Zhu et al., 2016) on some summits that transgresses the tropical margin in Yunnan implies that this margin may be broader and floristically characteristic of such site conditions. Field surveys of the elevational distribution and range of the species that appear diagnostic of this forest type, including C. hystrix and other associates occurring in Ohsawa’s analogous East Himalayan ‘upper montane forest’, would be particularly informative.

5. To fill gaps in our knowledge, demographic and physiological studies are required for selected predominantly tropical and predominantly subtropical species that co-occur in transition forests, particularly in regard to their response to occasional frosts of varying intensity. Which species are most sensitive to frost as seeds and as seedlings, and which survive to reproductive maturity? What are the conditions in indigenous forests under which this regeneration can occur?

6. The ecotones between the elevational zones of tropical montane forest formations, including that between tropical and subtropical (warm temperate) formations, is governed by floristic change, which is the cause of simultaneous changes in structure and physiognomy. We do not know how these floristic changes are mediated, especially at the tropical forest margin, and how floristic and associated forest change is specifically related to the intensity and frequency of freezing temperatures in atmospherically moist and also seasonally dry conditions. Under what conditions do tree seeds retain dormancy, and how and to what extent do germinant and older individuals resist freezing? In what way do these influences differ between slopes and ridges subject to frosted downwdrifts, and valley bottoms where air ponding sometimes becomes frosted? The only observations known to us are from plantations, including seedling trials, conducted years ago at the Indian Forest Research Institute, Dehra Dun (Nantiyal, 1934; Seth and Jabral, 1957).

7. Most important at this time of climate change, what evidence is there of successful seedling establishment of these species in and beyond the ecotope on either side of these Transition forests?

8. The forest soils of tropical and warm temperate China have not been documented. The agricultural soils of southern China are well known thanks to the research of M.E. Ren and his colleagues (1961, 1963, 1991), but tilling leads to the elimination of the horizons of humic discoloration that so characterize forest soils. Do edaphic and floristic ecotones coincide where the lower northern tropical lowland seasonal evergreen dipterocarp forests of southern China coincide with the tropical lower montane forest formation? If so, where, and under what forest type, is the edaphic ecotope between tropical lowland ultisols and latisols, which are rich in termites and in which organic matter is concentrated in near-surface horizons, and lowland and subtropical (warm temperate) humic mulls, which are rich in earthworms and in which particulate organic matter is dispersed to lower horizons? Hou (1983) describes the soils of China’s seasonal tropical rain forest as ‘laterite’, from which we infer them to be tropical ultudults. True ferricrete (‘laterite’) bearing soils are confined to deciduous forests experiencing wide seasonal variation in soil water content. Hou variously describes Chinese subtropical soils as yellow and red earths, or acid yellow-brown. These would be consistent with ultisolic soils in lowland semi-evergreen or deciduous forest, alternatively earthworm-rich humic loam soils in both lowland subtropical, and lower montane tropical as well as subtropical broadleaved oak-laurel forest formations; but detailed study is urged!

9. What are the respective historical biogeographies of the floras that meet along the tropical margin as it descends in elevation from 2000 m to the lowlands?

10. Do isolated ecological islands of frost-free climate, which support refugia of tropical forests and flora, occur north of the tropical margin in China, especially on isolated karst mountains? Or do these floristic islands survive through evolution of frost tolerance among their constituents?
11. Where do warm Chinese frost-tolerant temperate woody flora, if not forests, occur south of the tropical margin in the Chinese or Indochinese mountains to the south, other than on Vietnam’s Hoang Lien range, and isolated peaks elsewhere in Indo-Burma?

12. The tropical margin likely differs in location and nature in the open secondary and weedy vegetation associated with conversion to agriculture; and its climate and soil conditions may differ in their impact on suitable crops, their reliability and productivity. The climatic limits of tropical crops such as Brazilian rubber, Hevea brasiliensis, may already have been the subject of research, the results of which could be availed of by forest ecologists and silviculturists.

13. Despite this lack of knowledge, it is certain that current climate change is and will continue to bring changes in the nature and location of the climatic conditions that define the tropical forest margin, and these changes will migrate northwards at a rate which will likely overtake the seed dispersal potentials of much of the flora (Ohsawa, 2006).

These omissions, in a rigorous understanding of the physical factor or factors which govern the ecotone between tropical and subtropical forest formations in East Asia, identify future research priorities and their practical significance at this time of changing climate. These will now be discussed.

5. Discussion

The most floristically diverse region of the temperate world is in China. This region is bordered in the north by the low climatic barrier of the east-west Qinling-Hua Shan, which marks the inland limit of the East Asian wet summer monsoon and the rigor of cold dry winter north-easterly winds. In the south this region is bordered by the tropical margin along China’s southern frontier. Because this region is close to the Pacific Ocean, the climate has remained stable, and only the mean temperature has varied over geological time. Consequently, a frost-free tropical climate and lowland rainforest extended to southernmost China at least as early as the Eocene-lower Oligocene global warm period (Herman et al., 2017). Following a cooler, drier Oligocene, warm, wet tropical conditions in the lower Miocene extended again as far north as Fujian, before retreating to their current latitudes. Land continuity from Central China to the Indo-Chinese tropics has combined with diversification of topography and surface geology, from at least the lower Tertiary epoch, when its warm humid temperate climate became increasingly both enhanced and restricted by renewed mountain building. The central Chinese east-west massif arose to moderate elevations, alleviating the winter north-easterlies to only mild frostiness to their south; at the same time, constriction of the Indonesian throughflow led to warming of the South China Sea and consequent intensification of the East Asian wet monsoon. This has created uniquely favorable conditions for flowering plants, especially woody plant diversification. Post-Oligocene enhancement of floristic diversification has continued unabated by major climate change. Within this region, one of the world’s major floristic refuges for archaic taxa has also persisted. A wealth of tropical species has extended to varying distances north into subtropical climates, protected from frost within a frost-hardy evergreen canopy. This has promoted extraordinary levels of endemism arising from the evolution of a unique range of frost-hardy taxa arising out of otherwise tropical families and genera. The karst forests and rocks, especially, support extraordinary diversity and endemism of herbaceous taxa, including Gesneriaceae, Elatostema (Urticaceae), Begonia, Impatiens, and others. Together, these facts explain why the term subtropical has, in China, been justifiably used to categorize the evergreen forests of this warm temperate region.

The region and landscape in which the tropical-temperate transition (‘tropical margin’) is placed marks the hotspot within China’s plant megadiversity region by virtue of the co-occurrence there of the most species diverse tropical and warm temperate plant communities and ecosystems of that region (Xu et al., 2019); but the most diverse individual plant communities among them are the lowland northern seasonal wet dipterocarp forests.

The elevation, location, and course of the tropical-temperate ecotone in south-western and southern Yunnan, from the place at which it arrives from Myanmar, seems not to have been documented, but is likely to enter China well north of the Tropic of Cancer and at first approaching an elevation of 2000 m, as in Myanmar. Following south-eastwards from there, it descends to the lowlands near the Yunnan-Guani border into south-western Guangxi. The eastward decline of the Yunnan mountains is associated with increasingly southerly penetration of cold north-easterly winds into the lowlands. Exposed lands along the elevational descent of the tropical margin seem to be dominated by nightly, winter dry cold north-easterly winds, which move above moist orographic air from the ocean, which is abundant in winter dewfall and which prevails on sheltered sites and slopes. Climate conditions in the forested karst of Nonggang Reserve, for example, in the lowlands close to the tropic of Cancer, appear to partially replicate the two site conditions that characterize the upper montane-subalpine ecotone on Asian equatorial mountains. At Nonggang, the presence of frost-prone valley sites with a temperate herbaceous flora, and the possible but unconfirmed presence of occasional frost on the rocky karst summits, is belied by the absence of a subtropical woody element on the slopes. The structure and physiognomy of the forest is typical for steep slopes over loam soils in a tropical mixed dipterocarp forest. From the karst around Nonggang, to its east and north, occasional winter ground and air frost apparently effects truncation, then elimination of tropical lower montane forest, latitudinal displacement of the tropical margin, and eventual displacement of tropical lowland forest with subtropical evergreen or semi-evergreen forest.

Ohsawa (1990, 1991c, 1995a, b, 1996, 2006) inferred that lowland northern tropical seasonal evergreen dipterocarp forest seamlessly gives way to lowland subtropical evergreen forests at the lowland tropical-subtropical transition. This would imply that the transition is accompanied by gradual changes to the structural, physiognomic and floristic characteristics of these two forest formations. This assumption is not supported by surviving examples, except perhaps by the coastal or near-coastal subtropical Taiwan forest numbered 22 on the vegetation map, i.e. ‘Broad-leaved mixed forest in the transitional zone, containing Castanopsis, and with some taxa belonging to tropical families’, a forest with which we are unfamiliar. The only truly lowland continental example of this category is mapped on the southern coast of Hainan (18°N), therefore, well within the tropics. Although the ‘lower’ southern subtropical broadleaved evergreen forest at Dinghu Shan, which descends to 200 m at 23°25’N, dominated by C. chinensis, and with families and genera similar to lower montane tropical forest including Lauraceae, Magnoliaceae, Theaceae, and exceptional Elaeocarpus diversity, one quarter of its species are exclusively temperate (Table 5). The ancient history of agriculture in southern China may explain the absence of such subtropical or transitional evergreen forests in the plains. Ohsawa (2006) indicates the existence of plots in such evergreen subtropical forest north to beyond 35°N. We infer that he refers to distant sites in the south-east Korean peninsula and Kyushu and south-eastern Honshu, Japan, where such forest does indeed occur down to the coast.

Most of the tropical margin and transition zone will now be under cultivation in China, where it will pass through open herbaceous cropland and pasture, also woody Eucalyptus and...
agricultural plantations that may include frost-prone crops such as *Hevea* rubber as well as certain tea varieties, particularly those hybridized with the tropical Assam form. In agricultural landscapes the survival of individuals of tree species characteristic of the transition forest along the tropical margin might provide critical indications of its former course in Yunnan, Guangxi, and possibly southern Guizhou.

At the beginning of the Holocene, frost-sensitive tropical lower montane elements occurred as far north as Kunming (Walker, 1986); and in the Middle Miocene, lowland tropical elements occurred as far north as inland Fujian (Shi and Li, 2010; Jacques et al., 2015). The widespread persistence of tropical elements on karst mountains throughout warm temperate China, that is south of the Qinling Mountains, such as at Libo in southern Guizhou, implies that at least through the Holocene pockets of tropical climate may have persisted north of the tropical margin through this region. Isolation will also have fostered endemic speciation. Further study of sites that have tropical elements north of the tropical margin would benefit greatly from the establishment of on-site weather stations.

The structural, physiognomic, and floristic characteristics of the Nonggang forest contrast so vividly with those of the warmest subtropical evergreen forests at Dinghushan as to leave no doubt that the tropical margin has been crossed in the plains between them. A frost-free climate has here been exchanged for a frost-prone one, the detailed ecophyleiological consequences of which await investigation; but the dominance of subtropical species in the Dinghushan canopy, beneath which species of tropical range prevail, implies that the canopy traps warm air during frosty nights as has been observed in the upper montane equatorial tropics (Ashton, 2014). The dominance of notophyll and microphyll leaf sizes together in the tree flora at Dinghushan contrasts with that of mesophylls at Nonggang, but microphylls do not dominate the flora as has been observed in warm temperate evergreen forests of other continents (Grubb et al., 2013). In this regard the Dinghushan forest resembles Kyushu subtropical lowland evergreen forests, although in these forests the notophyll *Cyclobalanopsis gilva* commonly dominates, whereas at the Dinghushan plot the dominant *C. chinensis*, dominants *C. eyrei* and *C. carlesii* further north (Deng et al., 2004) and *C. cuspidata* in northern Taiwan (Hsieh et al., 1998), are all microphyll, recalling the dominant microphyll dipterocarp *Shorea gardneri* in Sri Lankan lower montane forests. Overall, our evidence suggests a major discontinuity in structure and physiognomy between the closest evergreen forest formations either side of the lowland frost line, notably a descent of lower montane forest characteristics from c. 800–1300 m to lowland elevations to its north. There are few exclusively subtropical species represented in the large tropical forest plots at Nonggang and Xishuangbanna. In contrast, a high proportion of tropical elements extend into subtropical China, albeit declining in proportion northwards. East Asia, and lowland China in particular, is unique among regions with a tropical margin: We argue that the forest physiognomy, structure, and floristics across a major ecotone of lowland China are correlated with a frost line, contrary to evidence from other regions (Grubb et al., 2013). There is otherwise a continuous northward gradient in these forest characteristics, which appears correlated with a warmth index that includes one or more climatic factors, notably winter temperature and the length of the summer wet monsoon.

In summary, we hypothesize that incidence of one or more days of air temperature below 0 °C is lethal within exposed crowns of tropical species confined south of the tropical margin, and all mature tropical forest canopy species; but that closed mature evergreen canopies of subtropical forests trap frost-free air within which tropical subcanopy species differentially survive, as frost of increasing intensity penetrates the canopy at increasing latitude or distance from marine influences. Fagaceae, and notably the characteristic *Castanopsis* species, dominate the canopy of lower montane and subtropical evergreen forests either side of the tropical margin. Indeed *C. indica* does so in northern seasonal wet evergreen dipterocarp forest, as it does in mixture with the emergent dipterocarp *Parashorea chinensis* in the Mengla plot, Xishuangbanna. *Castanopsis* species change in dominance in the subtropical forests from their southern margin to southern Korea, Kyushu and south-eastern Honshu. *Castanopsis* species, as other Fagaceae and also the red meranti *Shorea* (Diterocarpaceae) of the equatorial mixed dipterocarp forests (Wyatt-Smith, 1963), achieve dominance as light-demanding climax species of late forest succession. We hypothesize specifically that air-frost mortality among these species is most likely to occur in forest canopy gaps, following establishment of their dominance over pioneers and other early succession species, including tropical vines, many of which may themselves be frost-sensitive.

What, then, is the specific climatic cause of the transition from tropical to subtropical (i.e., warm temperate) forest in East Asia? In the mountains, the transition takes place on slopes over an elevation of 1800–2100 m, often representing an elevational distance of no more than 100 m, by which all but very few tropical canopy species have been replaced by temperate species. Within a further 400–500 m tropical subcanopy species have been replaced by temperate. Mean annual temperature will not have changed more than 3 °C. We conclude that the major climate gradient in the lowlands consists of minimum winter temperature events in which air frost frequency and intensity increases with elevation, but only slowly with latitude. In the mountains, a frost gradient is compressed into little more than a kilometer, which in the lowlands of South East China, extends from the Tropic of Cancer to the Qinling Mountains 1800 km to the north, and beyond, as winter deciduous species increasingly dominate the canopy thereby eliminating any frost-free subcanopy. This climate gradient appears consistent with that recorded in the subtropical evergreen forests of southernmost Japan from its coastal tropical margin northward, for which Kohyama notes Kira's Cold Index range of 0–5 (~10). The index is based on mean annual temperatures, and does not take account of the presence or absence of occasional air frost, but winter frost occurs in most, perhaps all of the Indices' Japanese range (Grubb et al., 2013). Kira's Warmth Indices for subtropical forests in other regions of the world exceed zero, implying that these forest experience little frost, a condition which differs greatly from East Asian subtropical evergreen forests. It is unclear whether frost-prone (therefore in our sense truly temperate) evergreen forests exist within or adjacent to these putative subtropical examples in other regions, and whether any frost-correlated tropical margin, in our sense, exists as an ecotone among them, although frost has been recorded at the higher latitudes of the South African and Australian examples.

East Asian subtropical evergreen lowland forests differ from all others in experiencing a tropical climate at warm temperate latitudes; that is, East Asian subtropical evergreen lowland forests experience summers with a wet summer south-west monsoon deluge that alternates with mostly cool dry, mostly sunny but periodically frosted winter nights under the influence of continental north-easterly winds (Walter and Lieth, 1960). Periodic mild air frosts (<–3 °C in mostly frost-free nights extend here from the Tropic of Cancer northwards, to the first east-west mountain chains, which protect them from colder nights and snow: the Qinling Mountains and associated mountains of central China, and the Japanese alpine chain, extending to mild lowlands to their south, and north-east to Ibaraki Prefecture at 36°N. The north-flowing east Asian Kuroshio ocean current also augments,
allowing subcanopy and a few pioneer tropical elements to survive in coastal refugia north to southernmost Japan. Warm temperate evergreen forests in all other continents, deemed subtropical, experience essentially temperate climates, mostly winter-wet and summer dry, though sometimes equable throughout. The distinct climate of the Asian subtropical evergreen forest formations has prompted us to ask whether all so-called subtropical forest examined fall within a single forest formation or whether the term subtropical defies clear definition (Ashton, 2014, p. 235). The distinctness of the East Asian subtropical forest climate is dramatized by the fact that the range of subtropical evergreen forest there coincides with the area which is the global center of China tea cultivation, yet tea cultivation hardly exists in other subtropical forest regions. We therefore follow the custom in Chinese and Japanese botanical literature by using the term subtropical as synonymous with warm temperate, but if the presence of periodic air frost is adopted as criterion (as we have done), then the other forests in Grubb and co-authors paper might rather be considered warm temperate, or even tropical seasonal evergreen if truly frost-free.

In the Himalaya, the canopy dominance of the tropical lower montane C. tribuloides is replaced by C. hystrix in a narrow transition zone, at c.1800–2000 m elevation; but the familial and generic composition remains essentially intact above it, while the lower montane subcanopy woody flora becomes entirely replaced by subtropical species over an increase of c. 500 m in elevation. Soils change little there in the Himalaya, tropical lateritic soils dominated by termites having been replaced by temperate humic mulls dominated by earthworms below 1200m, at the lowland-lower montane forest ecotone. In the lowlands of China, near the Tropic of Cancer, lowland rainforest is replaced north of the transition by a lowland subtropical forest formation that more resembles a lower montane forest in structure, physiognomy, and generic composition. Termite-dominated lowland tropical soils, we infer, are replaced by temperate humic mull mediated by earthworms, although this has yet to be confirmed by widespread field observation. We hypothesize that the descent of forest with a lower montane forest structure, physiognomy, and soils to the lowlands at the lowland tropical-subtropical transition may in part be caused by the onset of periods of maritime winter fog and rain between the clear frosted moonlit periods. Specifically, we hypothesize that the floristic transition in the forest canopy is caused by the incidence of killing air frosts in the crowns of their juveniles during succession.

We hypothesize that the diversification of temperate plant taxa into tropical forests has been limited because of the energetic cost of their genetically imbedded frost hardiness on their competitiveness in a frost-free environment; whereas diversification of tropical taxa northwards has been possible thanks to persistence of relatively frost-free refuges associated in particular by the extreme local climatic diversity presented by archipelagic karst geomorphology and topography. China presents unique opportunities for testing these hypotheses.

6. Conclusion

The extraordinary diversification of many tropical woody taxa into warm temperate China is, with a few exceptions, unmatched by diversification of temperate taxa south into the Asian tropics. This woody flora is unique in its local and regional endemism, which increases in its relative representation in forest community types southwards until the tropical margin is reached. That has resulted in greater plant species diversity in southern China than any other place in the temperate world, though this diversity is more manifest in temperate herbaceous than woody taxa: woodland and saxicolous species diversity among Gesneriaceae, Begonia, Elatostema (Urticaceae), and other taxa has attained extraordinary levels in the diverse environments of warm temperate China south of the Qinling Mountains, far in excess of that in the tropical forests to its south. Nevertheless, diversity of woody taxa in warm temperate China is extraordinary, and substantially due to the opportunities for northward diversification of tropical taxa that has persisted since ancient geological times owing to China's placement at the western margin of the world's widest ocean, and the persistence of the wind systems within associated climatic Hadley Cells irrespective of temperature change over geological time (Morley, 1999). This extraordinary biological diversity has been enhanced in warm temperate China by periodic uplifting of archipelagoes of Devonian-Permian limestone mountains furnished with unique climatic and habitat diversity.

The authors recognize that a gradient in forest structure, physiognomy, and floristics, including declining diversity, exists up the slopes of tropical East Asian mountains, and that this gradient is broadly correlated with a complex climate gradient in which temperature is paramount. However, this gradient is broken by ecozones between the major forest formations, each of which correlate with a single limiting climatic factor. This limiting climatic factor in turn may mediate changes in the soil. Among these As-tones is one which seemingly correlates with the onset of air frost ('the frost line') and represents the tropical-subtropical (warm temperate) forest transition. Forest structure and physiognomy hardly change here, although canopy species change completely - as at all tropical elevational zonal ecotones (such zonation is obscured at temperate latitudes owing to their wide seasonal range of temperature and associated climate (Janzen, 1967)). Beneath this new subtropical canopy many tropical species persist at elevations of an additional c. 500 m, gradually declining as frost frequency and intensity increases, while the number of subtropical species increases.

There is an analogous, albeit vastly longer evergreen forest gradient from the equatorial tropics of East Asia north to the limits of lowland evergreen forests, at 34–35° N; but in this case there is but a single major ecotone, at the Tropic of Cancer, between lowland tropical seasonal evergreen dipterocarp forest and lowland subtropical evergreen forest, again seemingly correlated with the onset of air frost. Here, though, forest with the physiognomy, structure, and composition of tropical lowland rain forest is replaced to the north by a forest with the physiognomy, structure, and much of the generic composition of lower montane tropical evergreen forest to its south, albeit with subtropical canopy species dominant. Beneath this canopy many tropical species again persist, and subtropical elements appear.

But whereas the transition to a fully temperate tree flora takes place over about 500 m in the mountains, in the subtropical lowlands it extends over <1800 km and more than ten degrees of latitude. Furthermore, on tropical mountains the ecotone from tropical soils in which termites dominate litter comminution, to temperate humic mulls in which earthworms dominate, occurs at the lowland-lower montane forest ecotone. We hypothesize that, in the lowlands at the tropical-subtropical transition, this soil ecotone occurs between the lowland tropical seasonal evergreen dipterocarp forest and the lower subtropical evergreen forests. This single massive transition is unique to the East Asian evergreen forests, in contrast to comparable forest gradients at these latitudes in other regions where the gradient has been observed to be continuous. We propose that the cause of this massive transition is the penetration of the tropical climate far north into temperate East Asia due to the Asian monsoon, which brings drenching summers but dry winters with moonlit nights bringing air frost in the lowlands south to the Tropic of Cancer. The warm temperate 'subtropical' evergreen
forests of other continents, by contrast, experience temperate climates with mild wet winters.

Critical questions remain unanswered:

- Does the lowland floristic and climatic margin coincide with an ecotone from tropical to temperate forest soils?
- At what point in their life cycle, and in their forest’s dynamic cycle, do canopy species in tropical forest formations adjacent to the frost line suffer frost-induced mortality, and what are the precise weather conditions which cause it?
- Which tropical species occurring in subtropical China manifest some level of frost resistance, and at what stage in their life cycle?
- Do localities in warm temperate China, where concentrations of tropical species have been found, have frost-free or otherwise unique climates and soils?
- How do tropical species widespread beyond the tropical margin, such as Phyllanthus emblica, Ternstroemia gymnanthera and Quercus glauca, survive towards their northernmost limits?
- What is the genetic basis to frost hardiness among such tropical species, and can it be transferred among genotypes, or to other species?
- Which of these species possess seed dormancy? The study of F.S.P. Ng in Peninsular Malaysia can serve here as an exemplary model (Ng, 1980, 1991).
- The ectone between upper montane ‘cloud’ forest and subalpine thicket on equatorial mountains is associated with periodic occurrence of frost. There, the canopy of upper montane forests at its highest limits appears to avoid frost scorching, yet juvenile frost-sensitive plants in adjacent valley grasslands are susceptible. Do such observations apply at the tropical-subtropical margin in China?
- Temperatures above and at the canopy, and in the canopy, subcanopy, understory and adjacent open ground require long-term monitoring, with their associated vegetation, along floristically defined transects. *Ex situ* monitoring of frost impact was monitored in preliminary studies at the lowland tropical margin in NW India (Nantiyal, 1934), but the need for careful rigorously designed garden experiments remains. Such research may already be in progress at stations focusing on *Hevea* rubber and tea. Species-specific comparisons of forest regeneration within the canopy of tropical-temperate transition forests, and abandoned nearby open agricultural land or grassland, will be particularly informative.

The geographical limit of the climatic and biogeographic transition line between tropical and warm temperate ecosystems and biota has likely already started to move with human-induced climate change, and will certainly continue to do so in the foreseeable future. Potentially catastrophic constraints on ecosystem and species dispersal, and even survival, can be predicted, with broad implications for future land use policy.

In this review, priorities for field and experimental research are suggested which might promote fuller understanding of the ecology of the tropical margin in southern China at this time of rapid climate change, and in formulating future land use and forestry planning and policy, ecosystem and biodiversity conservation, as well as for ornamental horticulture (Ohsawa, 2006). Research challenges remain:

- How are temperature and rainfall patterns changing along the tropical margin at Nonggang Reserve and elsewhere?
- What is the impact of current climate change on the demography and extinction risk of tropical species heretofore surviving in apparent refugia within subtropical China? Which species of plant and animal are showing evidence of retreat or advance along the margin, and in what ways?
- How are the three forest formations that variously meet at the tropical margin in South China (lowland and lower montane tropical and subtropical evergreen forests) responding to current climate change, and how will they react in future? The Nonggang Reserve would appear to present ideal conditions for rigorous long-term floristic ecological and climatic research and monitoring into the precise definition of the tropical biological margin, including *in situ* seedling transplant experiments.

China’s community of environmental scientists is presented with opportunities available to them alone: To monitor climatic and ecological changes as they occur along that most diverse of all global margins, that which marks the ecotone between tropical and temperate ecosystems in East Asia in lands where both are at their most diverse.

Declaration of competing interest

This article is no conflict of interest to anyone.

Acknowledgments

This project was funded by The National Natural Science Foundation of China (41471051, 31970223). Thuy Nguyen has greatly assisted with her knowledge of the ecology and flora of the northern Vietnamese mountains, advising and translating relevant literature; Fang Wen shared his experience of forests and landscapes in the far south-east of Guangxi autonomous regions; Shin-Ichiro Aiba provided critical information of the ecology of Okinawa forests; Leping Li provided invaluable assistance with translation, and references; while Peter Grubb and Eben Goodale commented on a draft, and the latter sought the advice of colleagues in China on our behalf. And a particular word of thanks to Peter Grubb, who provided us with extensive notes of his own on southern Chinese flora and forests, accompanied by invaluable comments from the late Len Webb and Tim Whitmore. And last, my (P.S.A.) very special thanks to Raymond Porter, who introduced discipline, precision and elegance to my unruly English presentation.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pld.2020.04.001.

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