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Research paper

Tropical deciduous forest in Yunnan, southwestern China: Implications for geological and climatic histories from a little-known forest formation

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ABSTRACT

In the southern mountain ranges of Yunnan province, China, deep valleys of several large rivers create rain shadows with hot dry summers, and are locally designated tropical; towards the north, notably in the Lancang (Upper Mekong) valley, these regions may experience frost during winter. The woody forest canopy of these valleys is predominantly deciduous, with evergreen elements in the north, where the canopy is open and the forest savanna-like. However, we here present tall forest with a closed deciduous canopy and semi-evergreen subcanopy observed in hot dry valleys of these rivers and their tributaries in the tropical south. The structure and physiognomy of these forests resemble the tall (moist) deciduous forest formation widespread in South Asia and Indo-Burma. Furthermore, these forests are largely composed of tropical elements at both the generic (80%) and the species level (>70%), indicating that these forests are indeed tropical. We originally hypothesized that these isolated forests represent refugia of a pre-Holocene extension of tall (moist) deciduous forest formation of South Asia and Indo-Burma. The sample plot we established to test this hypothesis confirmed that these forests share the structure and physiognomy of the tall (moist) deciduous forest formation; however, the plots also showed that these forests lack the characteristic and dominant species of the formation's Indo-Burmese range. The tree flora, in particular, indicates that both deciduous and evergreen elements are instead mostly derived from the adjacent tropical semi-evergreen forests of tropical southern China; yet they also include an important endemic element, which implies that these forests have survived as refuges possibly since the Pliocene. The exceptional representation of evergreen elements in these forests indicates that they have rarely been subject to hot fires or domestic cattle browsing, adding to the unique nature of the forests and further justifying their strict conservation.

1. Introduction

Southern Yunnan, which is located on the northern margin of mainland Southeast Asia, is dominated by tropical lower montane broad-leaved evergreen forest. Most widespread are the lower montane forests of dry slopes dominated by *Pinus kesiya*. These forests represent the easternmost extension of a savanna formation widespread in seasonal Indo-Burma west of Assam. These Yunnan forests are accompanied by many of the same fire-prone invasive lower montane broad-leaved evergreen species. To the north-east, replacement of *P. kesiya* by *P. yunnanensis*, as indicated on the vegetation map of China (Hou et al., 1979; Hou 1983; Wu, 1980, 1987), marks the transition from tropical to subtropical lower montane forests (Ashton and Zhu, 2020). However, in the drier river valleys and their tributaries, tropical deciduous forests occur, bordered by seasonal evergreen and semi-evergreen rain forests which occur in more limited wet ravines and lower hills (Zhu et al., 2019). Although Zhu et al. (2006, 2015) have clarified key differences between lowland tropical evergreen forest and tropical deciduous forest, these tropical deciduous forests in Yunnan remain little known to science.

The lowland tropical deciduous forests of Yunnan have been studied using plot data. Previous research has analyzed secondary *Anogeissus acuminata*-dominated forest (Wang and Zhu, 1990), a

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riparian *Bombax ceiba*-dominated forest and a tropical-subtropical *Pterocarya tonkinensis* forest (Li et al., 1993, 1999), as well as a *Lannea coromandelica - Sterculia pexa* community in a notably dry section of the valley of the lower Lancang (Upper Mekong) River (Zhou et al., 2006). In addition, researchers have studied uncategorized tropical mixed deciduous forest in the lower reaches of the Luozha River, a tributary of the lower Lancang River (Li et al., 2007), and a mixed deciduous forest at Luzhi River, a tributary of the Red River (Gu and Zhu, 2015). Based on some plot data, Wu (1980, 1987) described these mixed deciduous forests as monsoon forest. Although previous research has characterized the topical deciduous forests in Yunnan (Zhu, 2005, 2006, 2007, 2011; Zhu et al., 2006, 2015), no clear floristic or structural categorization of these forests has been recognized.

Researchers have yet to reach a consensus on a classification system for pantropical vegetation or for forests (Corlett, 2014). In Chinese botanical literature, "tropical monsoon forest" is described, but the term is used inconsistently and often confused with— and includes— tropical evergreen rain forest (Zhu, 2011). Schimper (1903) defined *tropical monsoon forest* as being more or less leafless during the dry season, noting that the physiognomy and distribution of these forests represented a transitional vegetation type between tropical rain forest and tropical fully deciduous forest and savanna. Champion (1936) recognised three lowland tropical forest formations within Schimper's monsoon forest category, in which there are major deciduous tree species components, successively declining in stature and occurring in successively dry climates: (1) Semi-evergreen forest, in which deciduous and evergreen species co-dominate the canopy, the deciduous playing the major part in forest succession while the evergreen gradually increase in dominance as the individual forest stand matures; (2) moist deciduous forest, in which deciduous elements dominate the canopy, while the evergreen element, always present, is subordinate and predominant in the subcanopy; and (3) dry deciduous forest, in which evergreen woody species are rare or absent, excepting succulent elements such as *Euphorbia.* Moist deciduous forest has been renamed Tall Deciduous Forest by Ashton (2014), who also renamed dry deciduous forest Short Deciduous Forest, following the current ecological practice of removing inferred but untested links between a forest type's name and its habitat expressed in its name. This scheme remains in current use by regional forest services and ecologists from South Asian countries east to Myanmar and Thailand. In addition to renaming these forest types Ashton (2014) noted that these formations experience varying mean annual rainfall, especially towards the high rainfall maxima, but are more closely correlated with the length of their dry seasons, as indicated by the number of continuous months experiencing less than an expected open pan evaporation rate (i.e., ~100 mm).

The Indo-Burma floristic province includes the seasonal tropics of northern East India, Myanmar (Burma), Thailand, and the Indochinese nations. The vegetation of Indo-Burma comprises seasonal evergreen dipterocarp, semi-evergreen, thorn woodland, and (secondary) savanna, as well as tall deciduous and short deciduous forests, depending on habitat, especially length of dry season (Ashton, 2014; Morley, 2018). Indo-Burmese tall deciduous forests are divided into two floristically and environmentally distinct formations (Ashton, 2014): (1) Tall teak forests, in which teak *(Tectona grandis*), *Xylia xylocarpus* ssp. *kerrii,* and *Lagerstroemia calyculata* are variably dominant, and mostly occur on tropical yellow-red loam soils; and (2) Deciduous dipterocarp forests, in which the dipterocarps *Dipterocarpus obtusifolius, D. tuberculatus, Shorea siamesnsis* and *S. obtusa* are variably dominant along with *Buchanania lanzan*, and which occur on freely draining drought-prone soils of varying clay content. Neither teak, *X. xylocarpus* ssp. *kerrii,* nor any of these dipterocarps have yet been recorded in China.

Our previous studies on the vegetation in southern Yunnan, southwestern China and on the Indochinese peninsula showed that so-called tropical monsoon forests in South China comprise tropical deciduous or semi-evergreen forests under the influence of a strong monsoon climate (Zhu, 2011, 2018, 2019; Zhu et al., 2015). These forests, which occur mainly on the deep, drier valleys and river banks of several large rivers below 1300 m, mostly appear to represent intermediate formations between seasonal evergreen rain forest and savanna, some of them successional, and most resemble tall (moist) deciduous forests in both form and habitat.

In this paper, we describe these tall deciduous forests of southern Yunnan. The forest canopy is predominantly deciduous, especially on limestone, but evergreen elements dominate the subcanopy (see Figs. S1 and S2). Their climate has an annual mean temperature between 20 and 25 °C, annual precipitation of 600–1100 mm, and is characterized by a dry season of about six months (Table 1). One key question is whether these tall deciduous forests of southern Yunnan represent refugia of one or both of the two regionally widespread Indo-Burmese forest formations, or whether, as we propose here, they are autochthonous and have originated independently. The present article aims to resolve this historical biogeographic issue by clarifying the species composition, physiognomy and biogeography of the tropical deciduous forests in Yunnan. Because tropical deciduous forest is not represented immediately at the high mountain range to the south of the Red River valley in Vietnam and adjacent Laos, we predicted that if the tall deciduous forests of southern Yunnan originated independently, the tropical southern part of their rain shadows would have a shared history; also, their flora would be derived from adjacent evergreen and semi-evergreen forest. This work will also allow us to make important recommendations regarding conservation.

2. Methods

We established four sampling plots of tropical tall deciduous forests in southern Yunnan: one each in deep valleys in the lower Lancang (Upper Mekong) River at Nuozhadu and its tributary at Luozahe, and two in the Red River and its tributary at Luzijiang (see Fig. 1). Sampling plot size was 1 ha for the sites of the Red River and its tributary, but 0.25 ha for the sites of the lower Lancang River and its tributary due to the difficult rocky topography. Although no meteorological stations operate in close proximity to our sample plots, climatic conditions of plots were recorded from the nearest meteorological stations (Table 1). Forest stature and physiognomy of the plots are consistent with that of the Indo-Burmese formations, suggesting that the plots share similar climatic conditions with the latter, which experience variable total mean annual rainfall, and for 5–7 months receive less-than-expected evapotranspiration (100 mm). Our plots sample forests at elevations between 500 and 1000 m, which is within the elevational range of tropical lowland forest formations. Soils in the plots are tropical yellow-red ultisolic, and of moderate clay content.

In each plot, all plants, including understory shrubs, herbs, lianas and epiphytes, were surveyed for life forms. All trees in each plot were identified and their DBH (minimum 1 cm for the plots of the Red River and its tributary, and 5 cm for the plots of the lower Lancang River and its tributary) and height were measured. We also documented tree leaf size, whether leaves were pinnate (compound) or single, and whether trees were evergreen or deciduous.

Importance value indices (IVI) (Curtis and McIntosh, 1951) were calculated for each tree species in all four plots. Physiognomy (life forms for all plants and leaf size for trees) was analyzed using Raunkiaer's criteria (Raunkiaer, 1934) as revised by Mueller-Dombois and Ellenberg (1974). Biogeographical elements

Table 1
Climatic features from available meteorological stations in the vicinity of the plot sites.

Locality of meteorological stations near our plot sites	Latitude & Longitude	Alt.(m)	AMT (°C)	ACT (°C)	MTH (°C)	MTC (°C)	AP (mm)	NDM (month)	DMP (mm)
Yuanjiang, Red River[a]	N 23°28′17″ E 102°10′58″	497	24.9	8709	29.9	16.5	666.6	7	87
Nuozhadu, Lancang River[b]	N 22°40′ E 100°28′	700	22	7851	25.6	14.9	1100	6	165

AMT: Annual mean temperature; ACT: Annual cumulative temperature ≥10 °C; MTH: Mean temperature of the hottest month (June); MTC: Mean temperature of the coldest month (January); AP: Annual precipitation; NDM: Number of dry months (Nov. to April next year); DMP: Dry months precipitation in total.
[a] Data from Yuanjiang Ecological Station of Xishuangbanna Tropical Botanical Garden, CAS.
[b] Data from Cao, S.S. ed. Nuozhadu Nature Reserve, Kunming: Yunnan Science and Technology Press, 2004, pp.1–378.

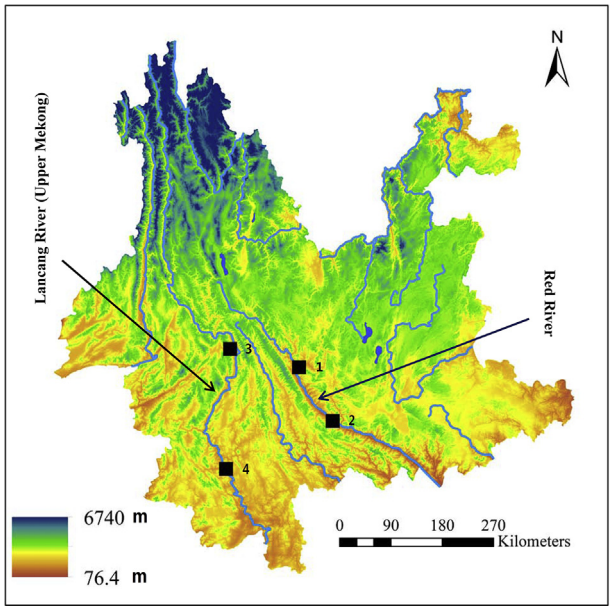

Fig. 1. Location of four plots with dark squares. 1, Luzhijiang; 2, Yuanjiang; 3, Luozahe; 4, Nuozhadu.

(attributes) of the forests at the generic and species levels were analyzed based on their geographical distributions following the work of Wu (Wu, 1991; Wu et al., 2006), which documented and categorized biogeographical elements for Chinese seed plants at the generic level based on their global distributions. We obtained the authority and distributions of all seed plant species in the plots from *Flora of China*, and documented biogeographical elements at the species level by referring to Wu's classification.

3. Results

3.1. Species composition

The tropical tall deciduous forest in Yunnan is 20–30 m tall and has one or two tree layers; trees of the top canopy layer, at least, are deciduous in the dry season. The canopy trees usually have an umbrella crown and thick, rough bark.

Species composition of these tropical deciduous forests is diverse. Table 2 lists dominant species and important value indices. The most common dominant species in all plots, especially in the deciduous forest plots of the lower Lancang River and its tributary, is the deciduous subcanopy tree *Lannea coromandelica*, which is widespread and characteristic of tall deciduous forest throughout tropical Asia. The most dominant evergreen subcanopy species identified in the plots is *Trigonostemon tuberculatus,* a newly published and local endemic species found in the Red River plot, and the widely distributed deciduous species *Cipadessa cinerascens*, which is found in Red River tributary plot. The subdominant species in the plot of the Red River tributary plot is the Chinese endemic understory evergreen tree species *Pistacia weinmannifolia,* whose distribution extends into subtropical limestone forests in Yunnan; in the Red River valley plot, the subdominant species is the succulent and thorny shrub *Euphorbia royleana*. The presence of *P. weinmannifolia* and *E. royleana* imply that these sites may experience a somewhat lower annual precipitation and a stronger foehn effect due to their cliffy and deeper valley topography. In the lower Lancang River, the subdominant deciduous canopy species is *S. pexa*, and in the Lancang River tributary, it is *Colona floribunda*. One frequent deciduous canopy species in the forest of the Red River is *Garuga forrestii*, which is also endemic. Among deciduous canopy species common in both valleys are *B. ceiba, Chukrasia tabularis* var. *velutina*, *Erythrina stricta*, *S. pexa*, *Albizia odoratissima*, *P. tonkinensis*, *Albizia chinensis*, *Eriolaena kwangsiensis*, *Dalbergia fusca*, *Dalbergia obtusifolia*. Frequent deciduous subcanopy species in both the valleys of the Red River and the lower Lancang River include *Lagerstroemia intermedia*, *Phyllanthus emblica*, and *Woodfordia fruticosa*. Common deciduous subcanopy species include *Bauhinia variegata*, *Grewia eriocarpa*, *Mayodendron igneum* and *Mitragyna brunonis*.

The tropical tall deciduous forests in southern Yunnan also contain several endemic species to Yunnan or endemic to southwestern China. Specifically, deciduous canopy endemic species include *Terminalia franchetii, Dolichandrone (Markhamia) caudafelina, D. obtusifolia, E. kwangsiensis*, and *Garuga forrestii*. The evergreen subcanopy endemic species include *Pistacia weinmannifolia, Beilschmiedia purpurascens,* and *Himalrandia lichiangensis.* However, the species *Trigonostemon tuberculatus* is endemic to the Red River and its tributary.

3.2. Physiognomy

The plant life forms of the tropical deciduous forest are shown in Table 3. Slightly more than 50% of all life forms documented are phanerophytes. Most of the phanerophytes in the lower Lancang River (Nuozhadu plot) are mesophanerophytes, whereas most in the Red River (both in the mainstream and tributary plots) are microphanerophytes. Most of the other life forms in our plots are lianas and hemicryptophytes. Notably, epiphytes are almost absent, except in one plot in the lower Lancang River tributary.

Leaf features of tree species from the four forest plots are reported in Table 4. Surprisingly, more than half the tree and shrub species recorded in the plots in both valleys are evergreen, and these overwhelmingly belong to the subcanopy or understory at maturity. In contrast, the canopy is almost entirely deciduous. In the lower Lancang River plots, the great majority of plants have mesophyll leaves (63.46%–68.0%), whereas in the Yuanjiang plot, the mainstream of the Red River, the majority of plants have microphyll leaves (60%).

Table 2
Dominant tree species in the tropical deciduous forests.

Tributary of the Red River (Luzhijiang) (Plot 1) N 24°16′15″,E 101°35′19″ Alt.: 630m Plot size: 1 ha Total tree species (>1 cm dbh): 36	IVI[a]	The Red River (Yuanjiang) (Plot 2) N 23°28′17″,E 102°10′58″ Alt.: 497m Plot size: 1 ha Total tree species (>1 cm dbh): 30	IVI[a]	The lower Lancang River (Nuozhadu) (Plot 3) 22°40′N, 100°28′E Alt.: 700 m Plot size: 0.25 ha Total tree species (>5 cm dbh): 25	IVI[a]	Tributary of the lower Lancang River (Luozahe) (Plot 4) 24°29′59″N,100°25′11″E Alt.:1000m Plot size: 0.25 ha Total tree species (>5 cm dbh): 22	IVI[a]
Cipadessa cinerascens (=baccifera) P, D[b]	56.96	*Trigonostemon tuberculatus* E	54.19	*Lannea coromandelica* P, D	52.94	*Lannea coromandelica* P, D	44.22
Pistacia weinmannifolia P, E	37.52	*Euphorbia royleana* E	46.70	*Sterculia pexa* P, D	45.86	*Colona floribunda* D	38.45
Lannea coromandelica P, D	34.92	*Lannea coromandelica* P, D	39.81	*Stereospermum colais* P, D	17.60	*Mallotus philippensis* E	33.08
Polyalthia cerasoides E	27.93	*Vitex negundo* f. *laxipaniculata* P, D	29.74	*Pistacia weinmannifolia* P, E	15.99	*Beilschmiedia purpurascens* E	23.27
Albizia odoratissima P, D	16.47	*Tarenna depauperata* E	24.42	*Albizia odoratissima* P, D	15.85	*Grewia eriocarpa* E	22.44
Haldina cordifolia D	16.13	*Strophioblachia fimbricalyx* E	22.03	*Eriolaena kwangsiensis* D	14.86	*Cipadessa cinerascens* (=baccifera) P, D	19.30
Mallotus philippensis E	15.42	*Garuga forrestii* P, D	14.13	*Dendrocalamus membranaceus* E	13.94	*Bauhinia variegata* var. *candida* D	17.37
Garuga forrestii P, D	14.14	*Murraya exotica* P, E	12.62	*Cipadessa cinerascens* P, D	13.35	*Oroxylum indicum* P, D	14.72
Chukrasia tabularis var. *velutina* P, D	11.29	*Falconeria insignis* D	9.72	*Eriolaena spectabilis* D	12.75	*Bombax cambodiense* P, D	14.45
Dolichandrone cauda-felina P, D	9.66	*Polyalthia cerasoides* E	8.26	*Phyllanthus emblica* D	10.16	*Phyllanthus emblica* D	12.91
Mangifera indica E	8.29	*Bridelia tomentosa* E	7.15	*Colona floribunda* D	9.86	*Albizia odoratissima* P, D	11.86
Phyllanthus emblica D	6.79	*Capparis cantoniensis* E	5.70	*Dalbergia obtusifolia* P, D	9.77	*Casearia graveolens* D	11.48
Stereospermum colais P, D	6.60	*Clausena excavata* P, E	3.95	*Grewia eriocarpa* E	9.70	*Dalbergia obtusifolia* P, D	7.37
Morus australis D	6.05	*Bauhinia variegata* D	3.60	*Grewia abutilifolia* E	9.31	*Wendlandia tinctoria* subsp. *barbata* E	5.54
Falconeria insignis D	5.10	*Sterculia pexa* P, D	3.28	*Sterculia villosa* D	8.62	*Wendlandia tinctoria* subsp. *intermedia* E	5.09
Grewia eriocarpa E	3.88	*Flueggea suffruticosa* D	3.14	*Woodfordia fruticosa* E	7.11	*Litsea glutinosa* E	3.61
Diospyros dumetorum E	2.64	*Bauhinia brachycarpa* E	2.34	*Casearia graveolens* D	6.27	*Eriolaena spectabilis* D	3.53
Ficus racemosa D	2.29	*Pistacia weinmannifolia* P, E	2.03	*Dalbergia cultrata* (*Dalbergia fusca*) P, D	5.28	*Bridelia stipularis* E	3.19
Woodfordia fruticosa E	2.19	*Diospyros dumetorum* E	1.21	*Bauhinia acuminata* E,	5.23	*Casearia balansae* var. *balansae* D	2.41
Himalrandia lichiangensis E	2.09	*Ficus concinna* E	0.80	*Hymenodictyon flaccidum* D	4.76	*Mayodendron igneum* P, D	2.01
Syzygium leptanthum E	1.97	*Albizia kalkora* P, D	0.80	*Mallotus philippensis* E	3.50	*Wrightia pubescens* E	1.88
Antidesma acidum E	1.96	*Fraxinus floribunda* P, D	0.77	*Bombax ceiba* P, D	2.35	*Ficus hispida* E	1.83
Ficus hispida E	1.30	*Phyllanthus emblica* D	0.77	*Ziziphus rugosa* E	1.72		
Colona floribunda D	1.18	*Terminalia franchetii* D	0.52	*Flacourtia montana* E	1.65		
Jatropha curcas E	1.00	*Ficus orthoneura* E	0.43	*Markhamia stipulata* var. *stipulata* P, D	1.58		
Bombax ceiba P, D	0.84	*Vitex peduncularis* P, D	0.39				
Maytenus berberoides (*Gymnospora orbicukata*) E	0.80	*Ficus microcarpa* E	0.39				
Sterculia pexa P, D	0.79	*Ficus maclellandii* E	0.38				
Bridelia tomentosa E	0.79	*Haldina cordifolia* D	0.37				
Eriolaena spectabilis D	0.50	*Millettia erythrocalyx* E	0.37				
Buchanania latifolia E	0.49						
Oroxylum indicum P, D	0.43						
Dolichandrone stipulata P, D	0.39						
Colebrookea oppositifolia E	0.39						
Vitex negundo var. *microphylla* P, D	0.39						
Fraxinus malacophylla P, D	0.39						
Total	300		300		300		300

[a] IVI (Importance Value Indices) = %Density + %Frequency + %Dominance.
[b] P=Pinnate or compound leaf; E = Evergreen; D = Deciduous.

These microphylls are mostly leaflets of pinnate-leaved species, all but a few of which are deciduous. However, the majority of plants in this forest are single leaves in leaf types.

3.3. Floristic characteristics and geographical elements

The most species-rich family in the plot sites is Fabaceae, which comprises 10.77%–11.93% of the total species (Table 5). Other species-rich families are Poaceae, Euphorbiaceae, Asteraceae and Rubiaceae.

Excluding ferns, we analyzed the biogeographical attributes of 175 seed plant species in 147 genera from the two plots of the Red River and its tributary, 601 species in 360 genera from the mainstream (Nuozhadu) of the lower Lancang (Upper Mekong) River, and 244 species in Luozahe plot of a tributary of the lower Lancang (see the Methods section). Tropical elements (types 2–7 in Table 6)

Table 3
Plant life forms in the four sites of the tropical deciduous forests.

Location	Luzhijiang[1] (1 ha)		Yuanjiang[1] (1 ha)		Nuozhadu[2] (0.25 ha)		Luozahe[3] (0.25 ha)	
Life forms (including understory saplings)	No. of sp.	% of sp.	No. of sp.	% of sp.	No. of sp.	% of sp.	No. of sp.	% of sp.
Megaphanerophytes	0	0	0	0	1	1.4	1	1.09
Mesophanerophytes	18	15.52	12	13.19	20	27.8	19	20.65
Microphanerophytes	21	18.10	18	19.78	4	6.6	9	9.78
Nanophanerophytes	10	8.62	10	10.99	10	13.9	16	17.39
Chamaephytes & Herbaceous phanerophytes	14	12.07	8	8.79	4	5.6	6	6.52
Phanerophytes in total	**63**	**54.31**	**48**	**52.75**	**39**	**55.3**	**51**	**55.43**
Geophytes	3	2.59	0	0	5	7.0	3	3.26
Hemicryptophytes	18	15.52	15	16.48	12	16.7	11	11.96
Therophyte	9	7.76	9	9.89	4	5.6	9	9.78
Liana	21	18.10	19	20.88	12	16.7	13	14.13
Epiphytes	2	1.72	0	0	0	0	5	5.43
Total species	116	100	91	100	72	100	92	100

1: from Gu, B.J. 2015. Community ecology study on the monsoon forest and savanna in lower Luzhi River and Pupiao of Yuanjiang dry-hot valley. Thesis for Master of Botany, University of Chinese Academy of Sciences; 2: from Zhu (2011); 3: from Li. Q.H. 2007. The flora of lower reaches of Luozha River and the community ecology study on deciduous monsoon forest in Yunxian County. Thesis for Master of Botany, University of Chinese Academy of Sciences.

Table 4
Leaf features of tree species in the four sites of the tropical deciduous forests[a].

Location	Luzhijiang (1 ha) Total tree species (>1 cm dbh): 36		Yuanjiang (1 ha) Total tree species (>1 cm dbh): 30		Nuozhadu (0.25 ha) Total tree species (>5 cm dbh): 25		Luozahe (0.25 ha) Total tree species (>5 cm dbh): 22	
	No. of sp.	%	No. of sp.	%	No. of sp.	%	No. of sp.	%
Leaf size[a]								
Macrophyll	1	2.78	0	0	2	8.0	1	4.55
Mesophyll	17	47.22	10	33.33	17	68.0	14	63.64
Microphyll	15	41.66	18	60.00	6	24.0	6	27.27
Nanophyll	3	8.33	2	6.67	0	0	1	4.55
Leaf type								
Compound (Pinnate)	14	38.89	10	33.33	10	40.00	7	31.18
Single	22	61.11	20	66.66	15	60.00	15	68.18
Seasonal aspect								
Evergreen	16	44.44	17	56.66	9	36.00	9	40.91
Deciduous	20	55.55	13	43.33	16	64.00	13	59.09

[a] Webb (1959) split off the lower end of Raunkiaer' big mesophyll class (2025–18225 mm^2) as notophylls (2025–4500 mm^2). Although it is better for detailing categories of leaf size spectrum, Chinese botanists are more familiar with Raunkiaer' big mesophyll class, and here we use Raunkiaer' big mesophyll class for the tropical deciduous forest in Yunnan.

Table 5
Dominant families of the tropical deciduous forests in three sites.

Mainstream of the Lancang River (Nuozhadu) (based on 612 seed plant species)		Tributary of the Lancang River (Luozahe) (based on 251 seed plant species)		Red River (Yuanjiang) (based on 195 seed plant species)	
Family	%	Family	%	Family	%
Fabaceae	11.93	Fabaceae	13.94	Fabaceae	10.77
Poaceae	5.07	Asteraceae	7.17	Euphorbiaceae	10.77
Euphorbiaceae	4.58	Euphorbiaceae	5.58	Asteraceae	6.15
Asteraceae	3.76	Poaceae	4.78	Poaceae	5.64
Rubiaceae	3.10	Rubiaceae	3.98	Moraceae	4.10
Lamiaceae	2.94	Moraceae	2.79	Asclepiadaceae	3.59
Menispermaceae	2.61	Urticaceae	2.79	Convolvulaceae	3.59
Sterculiaceae	2.45	Tiliaceae	2.79	Oleaceae	3.59
Lauraceae	2.29	Vitaceae	2.39	Anacardiaceae	2.56
Convolvulaceae	2.29	Fagaceae	2.39	Rubiaceae	2.56

contribute 85.6% of the total genera of all life forms in the plot sites of the Red River and its tributary, 83.4%–81.8% in the Nuozhadu and Luozahe sites of the lower Lancang River. Pantropic elements constitute the highest ratio for both places.

Tropical biogeographical elements at the species level are shown in Table 7. With the exception of *Pistacia wenmanniifolia*, which is also characteristic of the Mediterranean savanna towards the north in the Lancang rain shadow, all tree and shrub species are tropical. In both the Red River and Lancang plots, the majority of elements consists of tropical Asia species (45.1% and 60.6% respectively), although there are higher ratios of Old World tropical, and tropical Asia to tropical Australia elements in the Red River sites than in the lower Lancang River sites (Table 7). The majority of trees and shrubs documented also occur in South China in seasonal evergreen forest and/or southern subtropical evergreen, as well as tropical and subtropical semi-evergreen forests. Nearly 20% of the total species at the sites of the lower Lancang River consist of tropical Asian elements from the mainland SE Asia distribution subtype. In the Red River and its tributary, 17% of the total species are endemic to China, whereas in the lower Lancang River elements

Table 6
Geographical elements of seed plants at the generic level of the three floras of the deciduous forests.

Compared regional floras	Luzijiang + Yuanjiang[1]. (2 ha plots with 147 genera)	Nuozhadu[2] (360 genera)	Luozahe[3] (180 genera)
Geographical elements at generic level	%	%	%
1 Cosmopolitan	6.1	4.4	6.7
2 Pantropic	33.3	28.6	33.9
3 Tropical Asia and Tropical America disjunct	0.0	4.2	2.78
4 Old World Tropic	19.0	12.2	10
5 Tropical Asia to Tropical Australia	7.5	6.4	6.11
6 Tropical Asia to Tropical Africa	9.5	11.4	10.56
7 Tropical Asia	16.3	20.6	17.78
Tropical elements (types 2–7) in total	**85.6**	**83.4**	**81.1**
8 North Temperate	2.0	4.7	4.4
9 East Asia and North America disjunct	0.7	2.8	2.2
10 Old World Temperate	0.7	0.8	0.0
11 Temperate Asia	0.7	0.3	0.6
12 Mediterranean, W Asia to C Asia	1.4	0.3	0.6
13 Center Asia	0.0	0.0	0.0
14 East Asia	2.7	3.1	2.8
15 Endemic to China	0.0	0.3	1.7
Temperate elements (types 8–15) in total	**8.2**	**12.3**	**12.2**
Total	100.00	100.00	100.00

1: from Gu, B.J. 2015. Community ecology study on the monsoon forest and savanna in lower Luzhi River and Pupiao of Yuanjiang dry-hot valley. Thesis for Master of Botany, University of Chinese Academy of Sciences; 2: from Zhu (2011); 3: from Li, Q.H. 2007. The Flora of lower reaches of Luozha River and the Community Ecology Study on Deciduous Monsoon Forest in Yunxian County. Thesis for Master of Botany, University of Chinese Academy of Sciences.

Table 7
Geographical elements at specific level for each of the sites of the deciduous forests.

Compared regional floras	Luzijiang + Yuanjiang[1]. (2 ha plots with 175 species)		Nuozhadu[2] (601 species)		Luozahe[3] (244 species)	
Geographical elements at specific level	No. of sp.	%	No. of sp.	%	No. of sp.	%
Cosmopolitan	4	2.3	12	2.0	8	3.3
Pantropic	12	6.9	37	6.2	11	4.5
Tropical Asia and Tropical America disjunct	0	0.0	5	0.8	7	2.9
Old World Tropic	13	7.4	12	2	4	1.6
Tropical Asia to Tropical Australia	13	7.4	13	2.2	13	5.3
Tropical Asia to Tropical Africa	7	4.0	29	4.8	13	5.3
Tropical Asia	(79)	(45.1)	(364)	(60.6)	(145)	(59.5)
Indo-Malesia	32	18.3	131	21.8	37	15.2
S Asia to mainland SE Asia	31	17.7	108	18	59	24.2
Mainland SE Asia	16	9.1	125	20.8	49	20.1
(Tropical elements in all)	**(124)**	**(70.8)**	**(460)**	**(76.6)**	**(193)**	**(79.1)**
North Temperate	1	0.6	5	0.8	0	0.0
East Asia and North America disjunct	0	0	0	0	0	0.0
Old World Temperate	0		0	0	1	0.4
East Asia	9	5.1	37	6.3	7	2.9
Endemic to China	30	17.1	64	10.9	25	10.2
Endemic to Yunnan	7	4.0	23	3.9	10	4.1
(Temperate elements in all)	**(47)**	**(26.2)**	**(129)**	**(21.9)**	**(43)**	**(17.6)**
Total	175	100	601	100	244	100

endemic to China represent only c. 10%. Elements endemic to Yunnan (i.e., the local endemic species) comprise 4%–10% of the total species in these two river regions.

Aside from these forests, no other tall deciduous forests in southern China are known to us. Thus, their endemic elements are particularly noteworthy because many also variously extend to semi-evergreen and seasonal evergreen, tropical, and subtropical forest formations in the seasonally dry climate of the mountains of southwestern China (Fang et al., 2009).

4. Discussion

The deciduous forests of tropical Asia are currently possibly all successional owing to anthropogenic influences, especially fire, and overgrazing by domestic cattle. Their deciduous tree species are, in general, more fire- and drought-hardy than their evergreen components, which are fire-sensitive as seedlings and particularly prone to crown fire mortality. Deciduous species dominate early succession following windthrow and fire, and are more resistant to browsing, readily coppicing even from mature felled individuals as in the case of the important timber tree teak (*Tectona grandis*) (Champion, 1936). Higher frequency and greater intensity human activity has increased successional deciduous over evergreen species, and consequently altered forest structure from semi-evergreen to tall deciduous and tall deciduous to short deciduous in the former ranges of each formation. But there is as yet little evidence that the characteristic species of the formations of each successively more seasonal climate have invaded these degraded seres.

We here report the first record of tropical lowland tall deciduous forest in China, and confirm that it represents a pristine and primary example of the tropical tall deciduous forest formation which dominates regions of tropical Asia that experience 5–7 dry months. This is the predominant formation in Indo-Burma, but does not extend continuously north to South China. The two examples documented here are confined to rain shadows in deep valleys of the two major rivers in southern Yunnan, which have likely been

isolated since the Pleistocene epoch, when low sea levels increased continentality in equatorial Southeast Asia, thereby weakening the summer rainy monsoon. The tall deciduous forest in the deep valleys occurs on dry red soil or so-called savanna red soil (Gong et al., 1999). It formed under dry hot climate in deep sedimentary valleys of Yunnan, and from granite in the Red River and its tributary (Zhang and Zhou, 1986). This kind of soil is also widely distributed in Indo-Burma with savanna vegetation, which implies that the tall deciduous forest in Yunnan could have evolved from much drier habitats, possibly from a savanna vegetation before or during the Pleistocene. As possible evidence, *Tsaiodendron* is a new genus that has been recently found in the hot dry valley of the Yuanjiang (Zhou et al., 2017). Phylogenetic analyses revealed that this genus originated in the late Miocene (10.42 Mya), suggesting that vegetation in the dry hot valley of the Red River has a long history. The higher rainfall in Yunnan during the later Pleistocene and early Holocene (Walker, 1986) likely explains the development of the tall deciduous forest in deep rain shadow valleys.

The forest types described here are unique due to the exclusive dominance of deciduous species in their closed canopies, yet abundance and diversity of their overwhelmingly evergreen subcanopy. The canopy dominance of deciduous species implies the prevalence of a dry season long enough to give taller deciduous species the competitive advantage in late succession. The evergreen subcanopy could only have survived over a long period in the absence of both crown fires and domestic cattle, the latter of which, in contrast to ethnicities elsewhere further south and west in tropical Asia, were never adopted by the Han and related ethnicities physiologically unadapted to habitual consumption of milk and milk products.

It is possible, therefore, that these stands in southwestern China represent the sole survivors of tropical tall deciduous forest in Asia, and that they have survived in a pristine state since domestic cattle were first introduced into India, and extended during the spread of Indianised cultures in Southeast Asia. These forests therefore not only represent ecosystems of extraordinary theoretical and practical importance for conservation and research, but also merit consideration for UNESCO World Heritage status as natural monuments.

The dominant species of the two Indo-Burmese lowland tall deciduous forest formations are absent from our plots and their immediate vicinity. Overall, the tree flora of our plots is composed of generalized tall deciduous forest species, but two features stand out. These plots contain few of the endemic woody flora elements characteristic of tropical lowland Guangxi and Guangdong, elements which also characterize the tropical evergreen and semi-evergreen forests of the region (Ashton and Zhu, 2020). Second, these plots contain a significant endemic woody element, implying that this formation has developed over a long period in the rain shadow. Aside from these endemic elements, the woody flora of these plots mostly comprises widespread components of southern Chinese semi-evergreen forests and of Indo-Burmese forests to their south. Taken together, these findings support an autochthonous origin for these isolated forests.

As expected, the majority of species in the plots have single leaves in leaf types, although species with compound leaves do make up a higher ratio of the total species in the tropical deciduous forest than do those in evergreen forests in wetter habitats in the region (e.g., the tropical seasonal evergreen rain forest, see Zhu, 1997; the tropical lower montane evergreen broad-leaved forest, see Zhu et al., 2005).

Species composition in our tropical deciduous forests, especially dominant species composition, differs from site to site. Except for the common-shared dominant species *Lannea coromandelica,* different subdominant species form diverse forest formations or communities locally. In the plots of the lower Lancang River, most species are mesophanerophytes, while in the plots of the Red River and its tributary microphylls are well-represented.

This could be because the lower Lancang River plot sites are much wetter (annual precipitation 900–1100 mm) than the Red River plot sites (annual precipitation 750 mm at the tributary Luzhijiang, while only 666.6 mm at the mainstream of the Red River), although the length of the dry season is almost the same in both. High annual precipitation may support the development of mesophanerophytes (tall trees), whereas lower annual precipitation may support development of microphylls, which predominate in taxa with pinnate leaves.

We found that the flora of the deciduous forest largely consists of tropical elements (80% of the genera and 70% of the species), providing indisputable evidence that this forest is tropical. However, at the species level the two sites of deciduous forest have different ratios of geographical elements. For example, although the flora at both sites consists of tropical Asia elements, at the Red River sites these elements contribute to only 45% of the flora, whereas at the lower Lancang (Upper Mekong) River sites they contribute to c. 60% of the flora. Similarly, in the sites of the lower Lancang River 20% of total species are the SE Asia mainland element, but in the sites of the Red River and its tributary this subtype constitutes only 9% of the total species. One explanation for this finding is that the lower Lancang River (Upper Mekong) is in a core area of the Indochina geoblock, whereas the Red River and its tributary follow the rift between Indochina and South China tectonic geoblocks that has survived since Tertiary times. Another feature of the flora of the deciduous forest is that the element endemic to China is present at higher ratios in the sites of the Red River and its tributary than in the sites of the lower Lancang River. This difference may also be explained by the geological history, as the Red River evolved from the paleo-Red River following a major tectonic rift, and is the oldest paleo river in Yunnan (Clark et al., 2004; Zhu et al., 2020).

Comparative ecological evidence implies that the widespread Asian *Euphorbia royleana* in the main Red River site is more characteristic elsewhere in tropical Asia of short deciduous forest and thorn woodland. The endemic canopy species *Terminalia franchetii* and subcanopy *Pistacia weinmanniifolia* also imply drier conditions, while the canopy *Garuga forrestii* and subcanopy *Trigonostemon paniculatus*, in particular, further imply a history of local speciation analogous to that of the well-known flora of the of the northern Irrawaddy valley rain shadow of Myanmar (Champion, 1936). Whereas South Asia experienced aridity during the Pleistocene temperate ice ages when the Indian south-west monsoon is thought to have periodically abated, southern China seems to have experienced higher rainfall, at least in the later Pleistocene and early Holocene (Walker, 1986), implying persistence, or even, strengthening of the Far Eastern wet summer monsoon. It is therefore improbable that the Indo-Burmese lowland deciduous forests could have extended as far north as China at that time. Instead, the distinct if modest endemic arboreal element, consisting of long-lived life forms, must have originated in the early Pleistocene, if not Pliocene, providing evidence of the persistence of their rain shadows through the Pleistocene. Furthermore, the Chinese endemic element in these forests, in particular, occurs also in adjacent tropical and subtropical formations, from which we infer that the origin of these forests predates their likely Holocene isolation.

Our finding that Chinese endemic species are present at higher ratios at the Red River and its tributary than at the lower Lancang River leads us to recommend that conservation priority should be given to the tropical deciduous forest of the Red River and its tributary.

5. Conclusion

In this paper, we have described two separately isolated areas of tropical tall deciduous forest in China for the first time. The tropical deciduous forests observed in Yunnan have a diverse species composition. Both forests have exceptionally rich evergreen tree flora, consistent with the historical absence of domestic cattle or frequent anthropogenic fire such that, unlike tall deciduous forest in South Asia, their form is unique and possibly aboriginal. The physiognomy and biogeography of these forests differ in the habitats at the Red River and its tributary, and those at the lower Lancang River. Furthermore, the physiognomy of the forest is correlated more with climate, especially the length of the dry season (November to April), whereas their biogeography shows a connection with the geological and climatic history of these two regions. Ecological and floristic analysis support our hypothesis that these represent the autochthonous assembly of tall deciduous forest islands from the flora of the regionally widespread and adjacent semi-evergreen forest formation; the presence of a distinct endemic element of a long-lived life form, tree species, implies an early Pleistocene or pre-Pleistocene origin of both these isolated communities and the rain shadows in which they have survived. Finally, our finding that Chinese endemic species are present at higher ratios at the Red River and its tributary than at the lower Lancang River leads us to recommend that conservation priority should be given to the tropical deciduous forest of the Red River and its tributary.

Author contributions

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Appendix A. Supplementary data

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