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Tropical rain forest fragmentation and its ecological and species diversity changes in southern Yunnan

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Abstract. Three fragmented rain forests and one primary forest in southern Yunnan were plotted. The microclimate and soil conditions of these forests were also studied. The following conclusions were drawn: (1) The microclimatic differences between inside and outside forest are less in the fragmented forests than in the primary forest, which indicates that the buffer effects to climatic change have been reduced in the fragmented forests. The soil has deteriorated to some extent due to forest fragmentation. (2) In species composition, especially the abundance of some species and the dominant ranks of some families have changed with fragmentation. *Barringtonia macrostachya*, the most dominant species in the control primary forest, disappeared from the fragmented forests, while *Antiaris toxicaria*, which is a characteristic but not dominant species in the primary forest, is dominant in fragmented forests. (3) The total number of species per plot was reduced in the fragmented forests and the more seriously disturbed the fragment was, the more the species richness diminished. (4) In life form spectra, the liana and microphanerophyte species increased, but epiphyte, megaphanerophyte, mesophanerophyte and chamaephyte species decreased in the fragmented forests. (5) The plant species diversity is generally lower in the fragmented forests than in the primary forest, although for some life forms it could be higher. (6) The tree species with small populations could be lost first in the process of rain forest fragmentation. (7) The heliophilous or pioneer tree species increased and the shade-tolerant species were reduced in the fragmented forests.

Introduction

Studies on the biodiversity changes of fragmented tropical rain forests have been undertaken independently in many tropical areas of the world since the 1980s (Diamond et al. 1987; Laurance 1991, 1994; Newmark 1991; Williams-Linera 1992; Fonseca de Souza and Brown 1994; Kattan et al. 1994; Daily et al. 1995; Murcia 1995; Turner 1996; Fox et al. 1997; Laurance and Bierregaard 1997; Oliveira-Filho et al. 1997; Laurance et al. 1998a, b). The most representative are those in Manaus, Brazil (Lovejoy et al. 1986; Klein 1989; Bierregaard et al. 1992; Fonseca de Souza and Brown 1994; Malcolm 1994, 1997; Camargo et al. 1995; Ferreira and Laurance 1997; Benitez-Malvido 1998; Laurance et al. 1998a, b). Many interesting results have been obtained. It is commonly accepted that species richness reduces with the fragmentation of tropical forests (Lovejoy 1986; Bierregaard 1992; Chittibabu and Parthasarathy 2000). The smaller the fragments are, the less species richness the fragments display (Newmark 1991; Leigh et al.

1993; Laurance 1994; Daily and Ehrlich 1995). However, most previous studies have focused on various animal groups related to the fragmented forests. Studies on plants related to tropical forest fragments are relatively fewer, although there have been some important ones (Williams-Linera 1992, 2002; Leigh et al. 1993; Turner et al. 1996; Turner and Corlett 1996; Ferreira and Laurance 1997; Fox et al. 1997; Oliveira-Filho et al. 1997; Benitez-Malvido 1998; Laurance et al. 1998a; Cadotte et al. 2002).

In south Yunnan, southwestern China, there are some semi-natural fragments of tropical rain forests, which are remnants near local villages and usually untouched for religious reasons (Liu et al. 2002). These remnants are generally called 'holy hill' by local people. These semi-natural remnants offer us good experimental examples to examine the biodiversity change with fragmentation and to test various theories from different disciplines of studies on fragments of tropical rain forests. Some fundamental studies have been undertaken on ecological and floristic subjects, as well as plant species changes in these remnants of 'holy hill' (Xu et al. 1994; Zhu et al. 1997, 2000a, b; Ma et al. 1998), but almost none in English publications. The present paper offers a synthesis of studies on the remnants of the tropical rain forest in southern Yunnan and contributes further knowledge on studies of fragmented rain forests from the northern margin of mainland southeast Asia.

General geography of the study area

Southern Yunnan lies between 21°09′ and 22°36′ N, 99°58′ and 101°50′ E. The region, which borders Myanmar and Laos, is a mountainous area at the northern margin of mainland southeast Asia and also the southern end of the Hengdwan Mountains (part of the Himalayas). Basically, the area has a mountain–valley topography with the mountains running north–south, with lower elevations southward. Altitude varies from 480 m at the bottom of the lowest valley in the south to 2400 m at the top of the highest mountain in the north. The region is influenced by a typical tropical monsoon climate. In the areas of lower hills and valleys covered by tropical forests, the annual mean temperature is 21–22.8 °C, and frost has never been recorded. The annual cumulative temperature (the sum of daily temperature means >10 °C) is more than 7600 °C. The annual precipitation varies from 1200 to 1800 mm, of which more than 80% falls during the rainy season, which starts in May and lasts until the end of October.

Tropical rain forest occurs naturally in valleys and on lower hills below 900 m altitude as intermittent tracts or patches in local habitats with a tropical moist climate prevailing due to the particular topography. Tropical rain forest forms a mosaic pattern with montane evergreen forests and semi-evergreen forests.

The tropical rain forest of southern Yunnan occurs mainly on laterite soil developed from siliceous rocks, such as granite and gneiss. The pH values are 4.5–5.5. A small part of the tropical rain forest occurs on limestone. This paper deals with the rain forest remnants on laterite of siliceous rocks.

Methods

After an initial investigation into the remnants of 'holy hills' in southern Yunnan, three remnants were selected for plotting and complete inventory. As a control, a nearby nature reserve, with the same vegetation type as the remnants, was also plotted (see Table 1). For each remnant and the nature reserve, one plot of 50 m by 50 m was laid out. In each plot, all trees were identified and their dbh (minimum 5 cm), height and crown coverage were measured. Each plot was roughly divided into five strips, so that frequency of tree species could be calculated. Furthermore, in five subplots (in each plot) of 5×5 m, saplings and shrubs were counted, and the cover of seedlings and herbaceous plants was estimated by Braun-Blanquet's degree of abundance (Braun-Blanquet 1932). Epiphytes and lianas were identified and abundance was estimated by eye. Importance value indexes (IVI) suggested by Curtis and McIntosh (1951) were calculated and the Shannon–Wiener index (Shannon and Wiener 1949) for species diversity as well as the Evenness index of Pielou (1966) were calculated from the data of plots. For all species in plots, specimens were collected and identified.

Furthermore, a complete plant list from the three remnants was compiled for physiognomic (life forms and leaf size based on Raunkiaer's (1934) criteria) and floristic analysis.

The microclimate was observed and soil conditions were analyzed for these remnants and the control primary forest in the nature reserve.

Species authorities follow the Flora Reipublicae Popularis Sinicae. Voucher specimens are kept in the herbarium HITBC.

Results

The microclimate and soil conditions

The microclimates of the fragmented and the control primary forests were observed by Ma et al. (1998). The microclimatic disparity between the inside and outside of the forest is less in the fragmented forests than in the primary forest, that is, the buffer effect to climatic change has been reduced in the fragmented forests (see Table 2). For example, the differences of the maximum air temperature, maximum soil temperature and relative air humidity between the inside and outside of the forest are 6.1 °C, 28.2 °C and 37%, respectively in the control primary forest, and 4.3 °C, 14.3 °C and 22%, respectively in the fragment in Mane holy hill.

The soil conditions from the fragmented and primary forests were analyzed (Table 3). The differences of soil moisture% and soil pH between the edges and the interiors were larger in the primary forest than in the fragments. The differences of organic matter and extractable N between the edges and the interiors were larger in the primary forest and the slightly disturbed fragment of Chengze than in the other fragments. The extractable K was higher in the primary forest and the fragment of Chengze than in the other fragments. It seems that soil is deteriorated to some extent with forest fragmentation.

Table 1. Conditions of study sites.

Study site	Locality	E	N	Area (ha)	Alt. (m)	A.M.T.[a] (°C)	A.P[b] (mm)	Distance to the NR (km)	Surrounding situation	Disturbance history	Evaluation of disturbance
Nature Reserve	Menglun	101°14′	21°55′	75000	680	21.4	1556.8				Very slightly
Chengzi	Menglun	101°14′	21°55′	4	650	21.4	1556.8	ca. 5	Surrounded by rubber and *Cassia* plantations except for a secondary forest at the west	Never seriously disturbed	Slightly
Mane	Menglun	101°14′	21°55′	3	580	21.4	1556.8	ca. 3	Surrounded by rice fields to the south and east, road and *Cassia* plantation to the north, and connected to a village at the west	Planted *Amomum* underneath 30 years ago; humans and poultry visit frequently	More seriously
Mangyang-guan	Jinghong	100°40′	21°44′	13.3	550	21.3	1426	ca. 80	Surrounded by rubber plantation; connected to a village at the southwest	Seriously disturbed in the understory; humans and poultry visit frequently	Very seriously

[a]Annual mean temperature;
[b]Annual precipitation.

Table 2. Means of maximum air temperature (T_{max}), daily range of air temperature (ΔT), minimum relative humidity (RH), maximum soil temperature (T_s), daily range of soil temperature (ΔT_s) and velocity (V) from the fragmented and the primary forests.

Sites	Locality	T_a	ΔT_a	RH	T_s	ΔT_s	V
Fragment in Chengzi	Open (outside)	34.7	23.2	19	47.7	36.7	0.6
	Edge	29.9	18.3	26	27.7	14.0	0.1
	Interior	26.0	14.3	50	22.8	9.2	0.1
Fragment in Manyangguang	Open	35.0	25.5	19	49.4	38.5	0.6
	Edge	32.9	21.9	23	32.9	19.6	0.1
	Interior	30.1	18.9	25	29.8	15.9	0.0
Fragment in Mane	Open	29.9	16.1	43	41.0	27.2	0.9
	Edge	28.3	14.9	44	35.1	20.1	0.4
	Interior	25.6	12.2	65	26.7	11.6	0.3
Primary forest in Nature reserve	Open	31.9	20.9	27	50.7	42.1	1.1
	Edge	27.0	16.4	43	25.6	13.2	0.2
	Interior	25.8	14.5	64	22.5	8.2	0.3

From Ma et al. (1998).

Table 3. Comparison of soil conditions between the fragmented and the primary forests[a].

	Plot site							
	Manyangguang		Mane		Chengzi		Nature Reserve	
	Sample locality							
	Inter.	Edge	Inter.	Edge	Inter.	Edge	Inter.	Edge
Bulk density (g/cm^3)	0.94	0.90	1.34	1.36	1.32	1.24	1.19	1.13
Moisture% (rainy season)	32.12	31.61	20.53	22.91	27.83	28.11	27.2	30.16
pH	4.51	4.21	4.81	4.90	4.67	4.58	5.5	6.03
Organic matter%	5.72	5.71	2.5	2.47	4.29	3.22	4.5	5.48
Extractable N (mg/100 g)	24.86	22.98	13.22	12.46	19.80	16.61	24.5	18.0
Extractable P (mg/100 g)	0.60	1.32	1.91	0.69	0.87	1.09	0.68	1.39
Extractable K (mg/100 g)	7.81	9.46	7.80	7.64	17.35	11.30	14.5	14.6

[a]Data for bulk density, moisture% (rainy season) and pH are the average values of the samples from soil depths of 0–10, 20–30, and 40–50 cm. Data for organic matter%, extractable N, extractable P and extractable K are from the sample at a soil depth of 0–10 cm.

Forest structure and species composition

The original forest on the holy hills was an example of the lower hill seasonal rain forest of the region (Zhu et al. 1998). It occurred widely on the lower hills and the lower hill slopes below 800–900 m altitude. The original seasonal rain forest, for example of the plot from the nature reserve, is 35–40 m tall and has three tree layers. The top layer trees, with a crown coverage of ca. 30%, are more than 30 m tall. The second layer trees, with more continuous crown coverage (70–80%), are 18–30 m tall. The third layer trees are 5–20 m tall. Below is a sapling–shrub layer, which is 1–5 m tall and has a coverage of 30–60%, and a herbaceous layer which is less than 1 m tall and has coverage varying from site to site. The fragments on the holy hills were more or less disturbed and more or less modified in their forest profile.

The species composition of the fragmented forests is basically the same as that of the control primary forest, except for the presence of more pioneers. However, the abundance or populations of some species are conspicuously different (see Table 4).

In the control plot of primary forest, the species *Barringtonia macrostachya*, with the highest importance value index (IVI), is the most dominant species. It is a typical climax species of the tropical rain forest of the region. *Tetrameles nudiflora*, with big buttress, is the second most dominant species. Both *Barringtonia macrostachya* and *Tetrameles nudiflora* do not occur in the fragmented rain forest plots. *Gironniera subaequalis* is the third dominant species in the control plot, but is not among the dominant species in plots from fragmented forest in Chengze and Mane, except in the plot of Mangyangguan in which it appears the most dominant. The species *Antiaris toxicaria* is not dominant in the control plot, but is the dominant species in plots of fragmented forests. It is the most dominant in the plot of Chengze, the second most dominant in the plot of Mane and the third most dominant in the plot of Mangyangguan. While species composition varies from site to site even in the same tropical rain forest, the species composition, especially the dominance of some species, changes when the forest becomes fragmented.

The dominant families with species richness from the fragmented forest were compared with the ones from the control primary forest (Table 5). Most of the dominant families from the fragmented forest are still the dominant ones in the primary forest. However, the dominant ranks for some families have changed with fragmentation. For example, Papilionaceae, Rutaceae, Euphorbiaceae, Moraceae, Apocynaceae, Myrsinaceae, Asclepiadaceae, etc. had greater species richness in the fragments, while Lauraceae, Annonaceae, Ochidaceae, Fagaceae, Araceae, Piperaceae, Urticaceae, etc. had lower species richness in the fragments. Heliophilous or pioneer plants such as *Macaranga* and *Mallotus* species of Euphorbiaceae, *Millettia* species of Papilionaceae, *Clausena* of Rutaceae, and liana species of Apocynaceae and Asclepiadaceae increased in the fragments. This is the reason for the increase of species richness of these families in the fragments. The species richness of the families with more shade-tolerant species such as Piperaceae, Araceae and Urticaceae, and the families with more climax species such as Lauraceae, Fagaceae and Annonaceae, was reduced in the fragments.

Species richness and life forms

The species richness in different life forms from the plots of fragmented and primary forests are given in Table 6. The total number of species per plot diminished in the fragmented forests. The more seriously disturbed the fragment was, the more the species richness reduced. The liana species increased conspicuously, but

Table 4. Tree species composition from the fragmented forests and nature reserve plots.

Location							
Nature Reserve, Menglun		Holy hill of Chengzi, Menglun		Holy hill of Mane, Menglun		Holy hill of Mangyangguan, Jinghong	
Altitude (m)	680	Altitude (m)	650	Altitude (m)	600	Altitude (m)	550
Area of plot (m^2)	50 × 50	Area of plot (m^2)	50 × 50	Area of plot (m^2)	50 × 50	Area of plot (m^2)	50 × 50
Aspect	NE	Aspect	NE	Aspect	S	Aspect	SE
Slope (°)	25–30	Slope (°)	10	Slope (°)	3–4	Slope (°)	5
Height of canopy (m)	35	Height of canopy (m)	30	Height of canopy (m)	30	Height of canopy (m)	40
Coverage (%)	>95	Coverage (%)	>95	Coverage (%)	80	Coverage (%)	90
No. of sp. >5 cm dbh	46	No. of sp. >5 cm dbh	52	No. of sp. >5 cm dbh	37	No. of sp. >5 cm dbh	18
No. of stems	207	No. of stems	182	No. of stems	152	No. of stems	60
	IVI[a]		IVI		D + BA%[b]		D + BA%
Barringtonia macrostachya	44.50	*Antiaris toxicaria*	80.36	*Chukrasia tabularis* var. *velutina*	40.9	*Gironniera subaequalis*	84.8
Tetrameles nudiflora	40.5	*Polyalthia cheliensis*	29.41	Antiaris toxicaria	19.3	*Pterospermum lanceaefolium*	17.07
Gironniera subaequalis	23.97	*Garcinia xanthochymus*	14.2	*Knema globularia*	19.2	*Antiaris toxicaria*	14.66
Chisocheton siamensis	18.51	*Alphosea monogyna*	13.13	*Scleropyrum wallichii* var. *mengkongensis*	15.0	*Mangifera siamica*	13.61
Cinnamomum tamala	16.36	*Amoora dasyclada*	10.31	*Celtis timorensis*	14.6	*Ixonanthes cochinchinensis*	11.15
Pittosporopsis kerrii	11.66	*Xanthophyllum siamensis*	10.22	*Dysoxylum lukii*	13.2	*Pseudostroblus indica*	9.92
Millettia leptobotrya	11.49	*Dysoxylum lukii*	9.45	*Machilus tenuipilis*	5.2	*Winchia calophyla*	9.29
Ficus langkokensis	8.61	*Harpulia cupanioides*	8.35	*Beilschmiedia brachythyrsa*	5.2	*Aphananthe cuspidata*	9.07
Xanthophyllum siamensis	7.89	*Arytera litoralis*	7.83	*Millettia velutina*	4.9	*Arytera litoralis*	7.00
Randia acuminatissima	7.65	*Knema globularis*	7.76	*Syzygium szemaoense*	4.8	*Elaeocarpus sphaerocarpus*	4.11
Phoebe puwenensis	6.71	*Aphananthe cuspidata*	5.76	*Microcos paniculata*	4.0	*Scleropyrum wallichii* var. *mengkongensis*	3.54
Antidesma montana	6.26	*Microcos paniculata*	5.67	*Litsea umbellata*	3.9	*Manglietia forrestii*	3.14
Millettia pachyloba	6.23	*Gironniera subaequalis*	5.58	*Garuga floribunda* var. *gamblei*	3.7	*Pouteria grandiflora*	2.79
Pterospermum lanceaefolium	6.06	*Millettia leptobotrya*	5.06	*Dysoxylum dasyclada*	3.5	*Millettia leptobotrya*	2.19

Table 4. (continued)

	IVI[a]		IVI		D + BA%[b]		D + BA%
Baccaurea ramiflora	5.93	*Mallotus philippinensis*	5.04	*Oroxylum indicum*	3.2	*Turpinia promifer*	2.19
Metadiba trichotoma	5.7	*Syzygium tetragonum*	4.64	*Baccaurea ramiflora*	3.0	*Canarium album*	2.18
Aphananthe cuspidata	4.32	*Sapium baccatum*	4.13	*Garcinia xanthochymus*	2.7	*Elaeocarpus viridescens*	2.18
Antiaris toxicaria	3.91	*Knema furfuracea*	3.96	*Mitrephora thorelii*	2.3	*Suregada glomerulata*	2.02
Mitrephora thorelii	3.79	*Garcinia cowa*	3.65	*Ficus callosa*	2.3		
Knema furfuracea	3.57	*Castanopsis indica*	3.22	*Aporusa yunnanensis*	2.2		
Acer garrettii	3.54	*Vitex quinata*var. *puberula*	3.05	*Alangium kurzii*	2.2		
Colona thorelii	3.16	*Mallotus paniculatus*	3.04	*Canarium album*	2.2		
Litsea pierrei var. *Szemaois*	3.14	*Nephelium chryseum*	3.01	*Garcinia cowa*	1.7		
Walsura yunnanensis	3.10	*Knema cinerea* var. *glauca*	3.01	*Turpinia pomifera*	1.7		
Rapanea faber	3.08	*Dolichandrone stipulata*	3.00	*Stereospermum tetragonum*	1.3		
Garcinia xanthochymus	3.06	*Memecylon polyanthum*	2.99	*Phobe lanceolata*	1.3		
Garcinia cowa	2.79	*Phoebe lanceolata*	2.99	*Gironniera subaequalis*	1.2		
Polyalthia cheliensis	2.7	*Garuga pinnata*	2.08	*Adenanthera pavonina*	1.2		
Acronychia pedunculata	2.17	*Ailanthus fordii*	2.08	*Heteropanax fragrans*	1.2		
Ficus fulva	2.16	*Litsea panamonja*	2.07	*Mangifera siamensis*	0.9		
Trigonostemon thyrsoideus	2.11	*Amoora yunnanensis*	2.07	*Chisocheton siamense*	0.9		
Chisocheton sinensis	2.01	*Sarcosperma arboreum*	1.94	*Canthium horridum*	0.9		
Pouteria grandiflora	2.0	*Machilus tenuipilis*	1.86	*Memecylon polyanthum*	0.9		
Celtis timorensis	1.9	*Turpinia promifer*	1.71	*Goniothalamus griffithii*	0.9		
Syzygium chathayensis	1.90	*Semecarpus reticulata*	1.68	*Turpinia cochinchinensis*	0.9		
Nephelium chryseum	1.81	*Mitrephora thorelii*	1.68	*Micromelum integerrimum*	0.9		
Laportea urentissima	1.81	*Wrightia coccinea*	1.66	*Cratoxylon cochinchinensis*	0.9		
Harpulia cupanioides	1.66	*Glycosmis ferruginea*	1.66				
Syzygium sp.	1.64	*Adenanthera pavonina*	1.56				
Homalium lauticum	1.61	*Canthium horridum*	1.53				
Helicia pyrrhobotrya	1.58	*Neonauclea tsiana*	1.52				
Saprosma ternandra	1.55	*Horsfieldia glabra*	1.52				
Amoora tetrapetala	1.54	*Baccaurea ramiflora*	1.52				
Gomphandra tetrandra	1.54	*Capparis terena*	1.52				

Table 4. (continued)

	IVI[a]		IVI	D + BA%[b]	D + BA%
Turpinia promifer	1.54	*Acronychia pedunculata*	1.50		
Brassaiopsis fatsioides	1.54	*Mayodendron igneum*	1.50		
		Linociera ramiflora	1.50		
		Alangium kurzii	1.50		
		Pouteria grandiflora	1.49		
		Aporusa yunnanensis	1.49		
		Goniothalamus griffithii	1.49		
		Trevesia palmata	1.49		

[a]IVI: importance value index = relative density + relative dominance (basal area) + relative frequency.
[b]D + BA% = relative density + relative dominance (basal area).

Table 5. Comparison of dominant families between the fragmented forests on the holy hills and the primary forest in the nature reserve in Xishuangbanna.

Dominant rank	Fragmented tropical rain forest				Dominance rank	Primary tropical rain forest			
	Family	No. of species	% in fragmented forest	% in primary forest		Family	No. of species	% in primary forest	% in fragmented forest
1	Rubiaceae	35	9.67	8.32	1	Rubiaceae	53	8.32	9.67
2	Euphorbiaceae	23	6.35	4.40	2	Lauraceae	35	5.49	3.87
3	Moraceae	18	4.97	3.29	3	Euphorbiaceae	28	4.40	6.35
4	Papilionaceae	17	4.70	1.73	4	Annonaceae	28	4.40	2.76
5	Lauraceae	14	3.87	5.49	5	Moraceae	25	3.92	4.97
6	Rutaceae	14	3.87	1.88	6	Ochidaceae	23	3.61	0.28
7	Apocynaceae	13	3.59	2.04	7	Meliaceae	22	3.45	3.59
8	Meliaceae	13	3.59	3.45	8	Vitaceae	15	2.35	2.21
9	Acanthaceae	10	2.76	1.73	9	Apocynaceae	13	2.04	3.59
10	Annonaceae	10	2.76	4.40	10	Rutaceae	12	1.88	3.87
11	Myrsinaceae	9	2.49	1.41	11	Urticaceae	12	1.88	0
12	Asclepiadaceae	8	2.21	1.10	12	Fagaceae	12	1.88	0.55
13	Vitaceae	8	2.21	2.35	13	Papilionaceae	11	1.73	4.7
14	Rhamnaceae	7	1.93	0.94	14	Acanthaceae	11	1.73	2.76
15	Sapindaceae	7	1.93	0.63	15	Araceae	10	1.57	1.38
16	Araliaceae	6	1.66	1.26	16	Piperaceae	10	1.57	0.83
17	Mimosaceae	6	1.66	0.94	17	Elaeocarpaceae	10	1.57	0.83

Table 6. Comparison of species richness per plot between the primary forest and the fragmented forests. All plots had an area of 2500 m^2.

Plot	Primary forest		Fragment		Fragment		Fragment	
	Location							
	Nature Reserve		Chengzi		Mane		Mangyangguan	
	Species	%	Species	%	Species	%	Species	%
Tree								
dbh > 5 cm	46	30.3	52	38.5	37	32.7	18	18.6
dbh < 5 cm	35	23	18	13.3	24	21.2	31	32
(Tree total)	(81)	(53.3)	(70)	(51.9)	(61)	(54)	(49)	(50.5)
Shrub	14	9.2	11	8.15	11	9.7	14	14.4
Herb	25	16.4	13	9.6	7	6.2	7	7.2
Liana	26	17.1	35	25.9	31	27.4	23	23.7
Epiphyte	6	3.9	6	4.4	3	2.7	4	4.1
All life forms	152	100	135	100	113	100	97	100

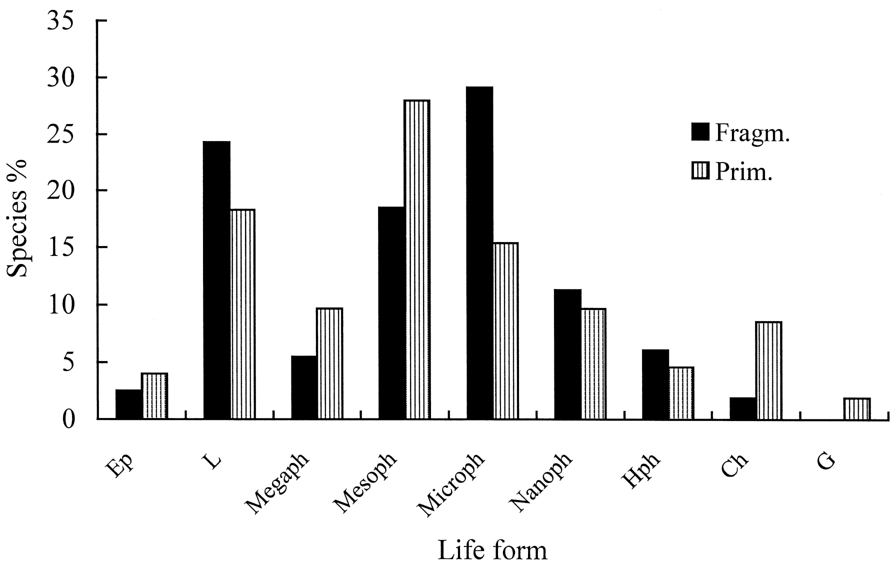


Figure 1. Comparison of life form spectra between the fragmented forest and primary forest. Fragm.: fragmented forest; Prim.: primary forest; Ep: epiphyte; L: liana; Megaph: megaphanerophyte; Mesoph: mesophanerophyte; Microph: microphanerophytes; Nanoph: nanophanerophyte; Hph: herbaceous phanerophyte; Ch: chamaephytes; G: geophyte.

the herbaceous species reduced with fragmentation. The number of tree species diminished, although its percentage in the life form spectra shows no significant change with fragmentation.

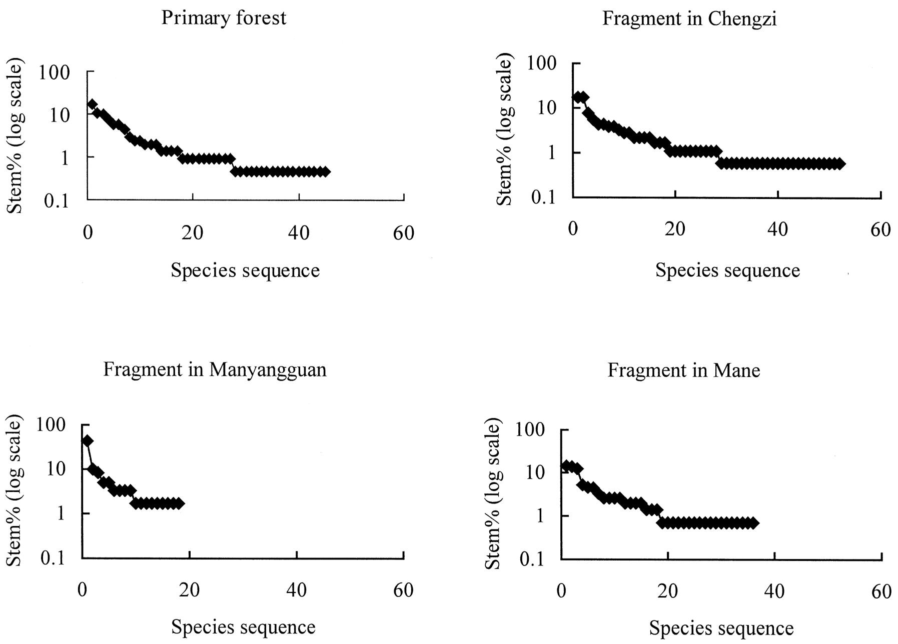
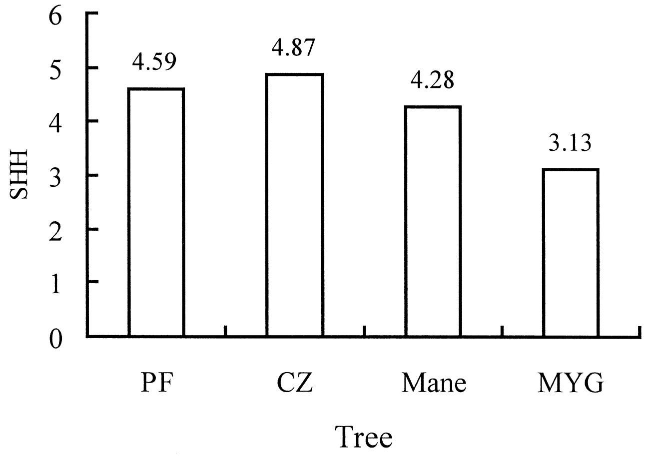


Figure 2. Tree species sequence versus stem% diagrams for the fragments and the primary forest.

From the species inventory of the three fragmented forests, the life forms based on Raunkiaer's (1934) criteria of the fragmented forests were compared with those of the control forest (see Figure 1). The liana and microphanerophyte species increased, but epiphyte, megaphanerophyte, mesophanerophyte and chamaephyte species diminished in the fragmented forest. The fact that liana plants increased in the fragments could be due to the increase of forest edges. Microphanerophytes increased in the fragments mainly because of the increase of pioneers, of which species of *Mallotus*, *Macaranga, Millettia*, and *Clausena* were microphanerophytes. The reduction of epiphyte, megaphanerophyte and chamaephytes could be the ecological results of the loss of the shaded and wet understory habitats to some extent and less differentiated microclimate in the fragmented forests. The observation that epiphytes were fewer in the disturbed fragments, is similar to the results from Venezuela (Barthlott et al. 2001).

Tree species population

In the tropical rain forest of southern Yunnan, most tree species have a small population, and some species have only one or two individuals in a forest site (such as in one of our study plots) (Cao and Zhang 1997). This is common in non-single-species dominant rain forest (consociation) and can be enumerated by their



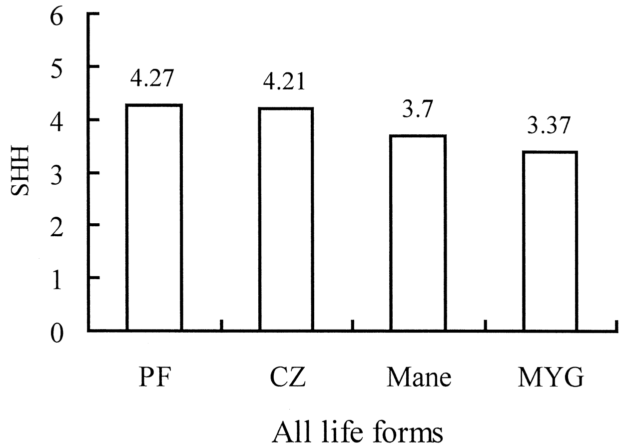


Figure 3. Comparison of plant diversity between the fragments and primary forest. PF: primary forest; CZ: fragment in Chengzi; MYG: fragment in Manyangguan; Mane: fragment in Mane; SHH: Shannon–Wiener's diversity index.

species sequence versus stem% diagrams. The species sequence/stem% diagrams from these fragment plots were compared with the one from the control plot (Figure 2). The species sequence/stem% diagram from the fragment of Chengze, with the longer tail, shows that the plot has more tree species with a small population than the plot of the primary forest. However, the species sequence/stem% diagram from the fragment of Mangyangguan, with the shortest tail, shows that the fragment has lost many of the tree species with small populations. The results imply that the tree species with small populations could be seriously affected in disturbed

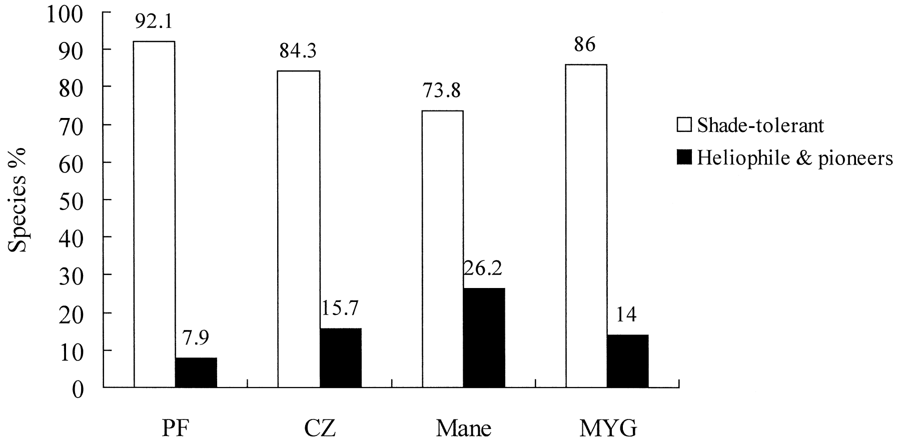


Figure 4. Comparison of ecological species groups from the fragmented and the primary forest.

rain forest. It is also concluded that tree species with small populations will be the first to be lost in the process of rain forest fragmentation.

Plant species diversity

The plant species diversity is generally higher in the primary forest than in the fragmented forests in our plots (Figure 3). However, Shannon–Wiener's diversity index for trees is higher in the fragment of Chengzi than in the primary forest.

Ecological species groups

Using Whitmore's classification of ecological species groups of tropical rain forest trees (Whitmore 1989), we roughly classified the tree species from plots of the primary and the fragmented forests into two major ecological species groups, that is, the shade-tolerant species and the heliophilous or pioneer species. Compared to the primary forest, the fragmented forests have a higher percentage of heliophilous or pioneer tree species (Figure 4). The fragment of Manyangguan, although it was the most seriously disturbed, has the lowest percentage of pioneers of the three fragments. The fragment of Mane has the highest percentage of pioneers. This could be due to its being the smallest area, which allows pioneers to invade more easily because of the relatively high forest–edge ratio. The relative amount of pioneers or heliophiles seems closely related to the size of the fragments.

Discussion

Compared to the primary rain forest, the fragmented forests have changed in various aspects, depending on the degree of disturbances to them and their areas. The fragment

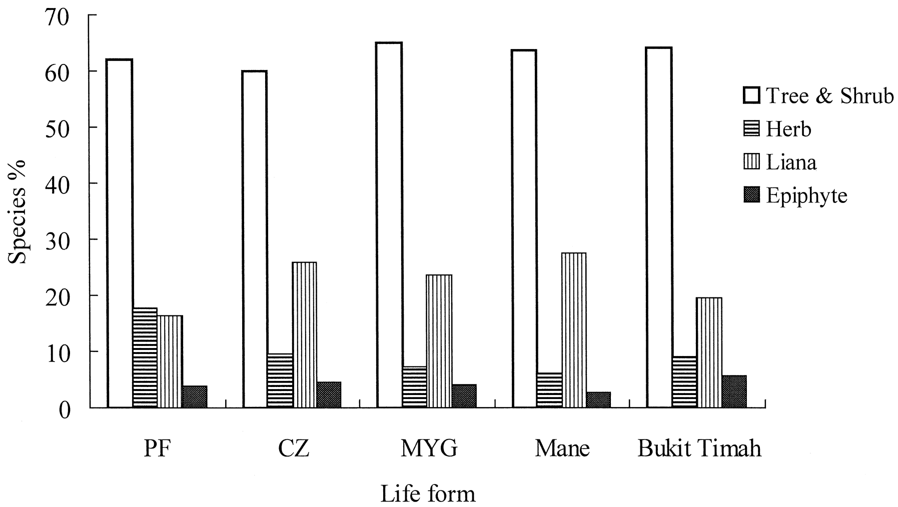


Figure 5. Comparison of life form spectra between the fragments from Xishuangbanna and a fragment from Singapore. PF: primary forest in Xishuangbanna; CZ: fragment in Chengzi; MYG: fragment in Manyangguan; Mane: fragment in Mane; Bukit Timah: fragment in Singapore.

in Chengzi holy hill, which was the most lightly disturbed, is very close to the primary forest in physiognomy and species diversity. The fragment in Mangyangguan holy hill, which was the most seriously disturbed, has the lowest species diversity. Although species diversity of some life forms could be higher in some fragments, the species diversity is generally lower in the fragmented forests than in the primary forest. Our results are similar to those from the Ghats of India (Chittibabu and Parthasarathy 2000), that is, species diversity reduced with increasing disturbance. Connell (1978), Huston (1979) and Denslow (1980) suggested that species diversity could increase in intermediate or mildly disturbed ecosystems. If we consider that the fragmented rain forests are intermediate or mildly disturbed ecosystems in our case, the species diversity is generally reduced in the fragments except for some life forms.

The Bukit Timah Nature reserve in Singapore is a typical rain forest fragment, which is 81 ha and has been isolated for more than 130 years (Corlett 1995a, b). The life form spectra from the fragmented forests in southern Yunnan were compared with those from Bukit Timah (Figure 5). Both of them have very similar life form spectra and show that the liana species increased, while the herbaceous species diminished in fragmented forests. The ecological species groups changed conspicuously with fragmentation. The heliophilous or pioneer tree species increased and the shade-tolerant species reduced in the fragmented forests.

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