

Structure and floristics of tropical forests and their implications for restoration of degraded forests of China's Hainan Island

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Abstract: We compared vegetation structure and floristics among degraded tropical secondary forests on China's Hainan Island, representing two successional stages (SF1 and SF2), and a primary forest to provide information that would support restoration process. We observed no significant differences in total tree density among the forest types, but the total basal area was significantly higher in primary forest. Stem size class distribution differed significantly between the primary and secondary forests, but the two secondary forests did not differ significantly. SF1 was dominated by *Macaranga denticulata* and SF2 by *Cratogeomys ligustrinum*, whereas the primary forest by *Engelhardtia chrysolepis*. The Simpson and Shannon diversity indices were greater for primary forest than for secondary forests. Jaccard's similarity coefficient and the Morisita-Horn index indicated greater similarity between the two secondary forests and the lowest similarity between SF1 and the primary forest. Understanding the structural and floristic characteristics of different successional stages is important for managing forest restoration process.

Resumen: Comparamos la estructura de la vegetación y la composición florística de bosques secundarios tropicales degradados en la Isla Hainan, China, que representan dos etapas sucesionales (SF1 y SF2), y un bosque primario, para proporcionar información que podría apoyar procesos de restauración. No hubo diferencias significativas en la densidad total arbórea entre los tipos de bosque, pero el área basal total fue significativamente mayor en el bosque primario. La distribución de tamaños de los troncos difirió significativamente entre el bosque primario y los secundarios, pero los dos bosques secundarios no difirieron significativamente entre sí. SF1 estuvo dominado por *Macaranga denticulata* y SF2 por *Cratogeomys ligustrinum*, mientras que la dominancia en el bosque primario correspondió a *Engelhardtia chrysolepis*. Los índices de diversidad de Simpson y Shannon fueron mayores para el bosque primario que para los bosques secundarios. El coeficiente de similitud de Jaccard y el índice de Morisita-Horn indicaron que hay mayor similitud entre los dos bosques secundarios y que la menor similitud se dio entre SF1 y el bosque primario. Es importante entender las características estructurales y florísticas de diferentes estadios sucesionales para manejar el proceso de restauración del bosque.

Resumo: Para gerar informação capaz de suportar o processo de restauração, comparou-se a estrutura da vegetação e a florística entre as florestas secundárias degradadas da ilha chinesa de Hainan, representando dois estágios sucessionais (SF1 e SF2), e a floresta primária. Não se observaram diferenças significativas na densidade arbórea total entre os tipos florestais, mas a área basal total era significativamente mais alta na floresta primária. A distribuição das classes

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de dimensão do tronco diferiram significativamente entre as florestas primárias e secundárias, se bem que as duas florestas secundárias não diferissem significativamente. O SF1 encontrava-se dominado por *Macaranga denticulata* e o SF2 pela *Cratoxylon ligustrinum*, enquanto a espécie dominante na floresta primária era a *Engelhardtia chrysolepis*. Os índices de diversidade de Simpson e Shannon eram maiores para a floresta primária do que para a floresta secundária. O coeficiente de semelhança de Jaccard e o índice de Morisita-Horn indicaram maior semelhança entre as duas florestas secundárias e a semelhança mais baixa entre o SF1 e a floresta primária. A compreensão das características estruturais e florísticas dos diferentes estágios sucessionais é importante na gestão do processo de restauração.

Key words: Floristics, primary forest, restoration, secondary forests, successional stages, vegetation structure.

Introduction

Natural tropical forests are important because they provide many ecosystem services such as species conservation, prevention of soil erosion, and preservation of habitat for plants and animals (Armenteras *et al.* 2009; Li *et al.* 2003; Wang 2003). However, in much of the area covered by these forests, widespread deforestation and forest succession have resulted from commercial logging, human inhabitation, and agricultural activities (Álvarez-Yépiz *et al.* 2008; Brow & Gurevitch 2003; Liebsch *et al.* 2008; Romero-Duque *et al.* 2007; Trejo & Dirzo 2000; Zang & Ding 2009). In the past, China's Hainan Island was covered by virgin tropical forest with forest cover of 90 percent during the Han Dynasty (206 B.C. to 220 A.D.) and 80 percent in the Tang Dynasty (618 to 907 A.D.). Since the Qing Dynasty (1644 to 1911 A.D.), much of the tropical forest has been destroyed, and since 1949, the deforestation of this tropical forest has averaged 34,000 ha per year, representing an annual rate of decrease of 2.02 %, which is higher than the global deforestation rate (about 1 %) for tropical forests (Jiang 2006; Lin & Zhang 2001; Wang *et al.* 2005; Zhou 1995). It took nearly 375 years for the island's natural tropical forest to decrease from 2,000,000 ha at the beginning of the Qing Dynasty to only 345,600 ha in 1993 (Lin & Zhang 2001).

The main cause of degradation of the tropical forest on Hainan Island has been historically related to catastrophic anthropogenic disturbance, such as slash-and-burn cultivation, illegal logging, and excessive harvesting of wood (Chen 2007; Ding & Zang 2008; Zhou 1995). Furthermore, since the first introduction of rubber in 1906 from Malaysia,

large areas of natural forest have been cleared to permit rubber cultivation because of its high profits (Deng *et al.* 2007).

The excessive deforestation has caused many ecological problems, such as soil degradation, decreased forest quality, carbon dioxide emissions, and biodiversity loss (Achard *et al.* 2002; Fearnside 2005; Oestreicher *et al.* 2009). Due to the seriousness of these negative effects, the Hainan provincial government banned all logging in natural forests in 1994 to protect endangered plants and animals and to prevent further degradation (Davies *et al.* 2007; Zhang *et al.* 2000). The effects of the logging ban have been positive, and since 1994, the area of natural forest in various areas has remained stable or increased. The total area of natural forest increased from 345,000 ha in 1993 to 659,000 ha in 2006 and the area covered by natural forest increased to 17.0 percent of the island's area (Chen *et al.* 2007; Deng *et al.* 2007; Li *et al.* 2008). In addition, forest quality and the ecological services provided by the forest have improved. However, much of the new natural forest is secondary forest that differs dramatically from the original primary forest.

Considerable research has been done on the restoration of tropical secondary forest (Chen & Yang 2001; Jiang & Lu 1991; Jiang *et al.* 2002; Wang *et al.* 2005; Zang & Ding 2009; Zang *et al.* 2001). Zang & Ding (2009) studied the recovery of forest on three positions of abandoned logging roads: road track, road up-slope edge and road down-slope edge. Chen & Yang (2001) systematically studied the changes in floristic composition and vegetation structure after different intensities of logging. Jiang *et al.* (2002), Li *et al.* (2002), Wang *et al.* (2005) and Jiang (2006) studied the basic eco-

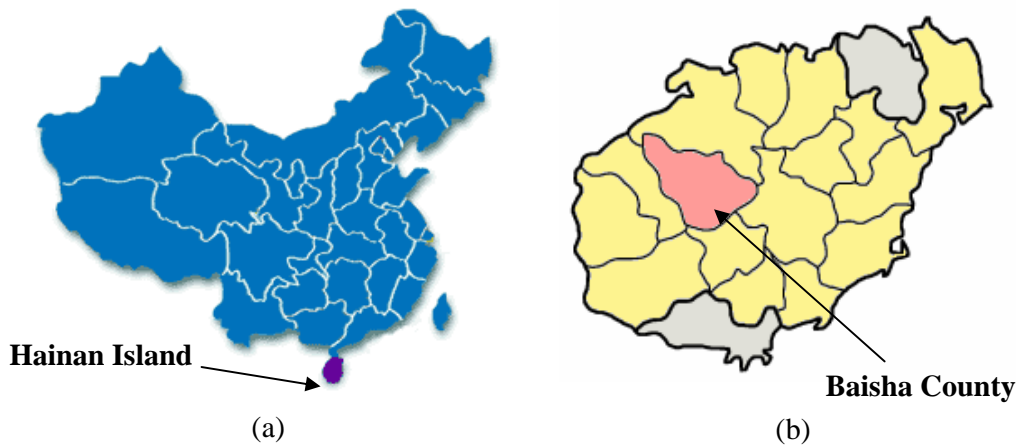


Fig. 1. The locations of (a) China's Hainan Island and (b) Baisha County on Hainan Island.

logical factors and processes in four nature reserves on Hainan Island: the Bawang Mountains, Jianfeng Mountains, Diaolu Mountains, and Wuzhi Mountains Nature Reserves.

These studies contributed greatly to forest management planning. However, each of the studies focused only on a specific successional stage and did not compare the findings with results for other successional stages. The recovery process during succession on Hainan Island has not been systematically studied, especially in mountainous forest regions populated by the local Li minority. The changes in the dynamics of the tropical forest flora and that of the vegetation structure during succession thus remain unknown. The lack of qualitative and quantitative knowledge of the composition of natural forests in different successional stages is a major problem for managers responsible for the secondary forest restoration process.

In this paper, we describe and compare the floristic composition and vegetation structure of the different successional stages. Our objectives were to examine the differences and similarities in structural and floristic characteristics among three successional stages and to consider the implications of these findings for restoration of the tropical secondary forest on Hainan Island.

Material and methods

Study area

Our study was conducted in Baisha county (18° 56' N to 19° 29' N, 109° 02' E to 109° 42' E) of

China's Hainan Island. Baisha's total population is about 164,500. This county covers an area of approximately 2118 km², and is located in the middle of western Hainan Island. It is bordered to the east by Qiongzong city, to the south by Ledong city, to the west by Changjiang city, and to the north by Danzhou city. The tropical monsoon climate provides an annual average air temperature of 23.6 °C, with maximum and minimum temperatures of 36 and 17 °C respectively. The annual precipitation ranges from 1500 to 2000 mm, with an average of 1,750 mm. Our investigation was carried out in the mountainous northern part of the county (Fig. 1), where elevations ranged from 800 to 900 m and slopes mostly ranged between 5° and 15°. The dominant parent rocks of soils in the study area are granite, sandstone and the soil supporting the forest is primarily a lateritic mountain soil (Jiang *et al.* 2002).

Plot selection and field sampling

In this study, we grouped the forests into three categories based on government historical records and interviews with the local Li minority: two categories of secondary forest (SF1 and SF2) at different successional stages, and one category of primary forest. The secondary forests, which had much simpler species compositions than the primary forest, were found in areas where the original primary forest had been felled and burned to support cultivation and cultivation was then abandoned for around 15 years (SF1) and 30 years (SF2) at the time of the study. The primary forest site was strictly protected and had never been cleared.

We established a total of 12 sample plots, each 50×50 m (0.25 ha), in representative areas of vegetation to capture most of the variability in the study parameters: four plots in SF1, four in SF2, and four in primary forest. We divided each plot into twenty-five 10×10 m sub-plots. In each subplot we recorded the diameter at breast height (dbh at 1.3 m), height and location of all trees greater than 5 cm in dbh. All trees were identified to species level and grouped into the following dbh classes: 5 to 10, 10 to 15, 15 to 20, 20 to 25, 25 to 30, 30 to 35, 35 to 40, and greater than 40 cm.

Structure and floristic indices

For all four plots in each forest type combined, we calculated the importance value Index (IVI) of each species (Magurran 2004; Müller-Dumbois & Ellenberg 1974) as follows:

$$\text{Relative dominance} = \frac{\text{Total basal area of the species}}{\text{Total basal area of all species}} \times 100$$

$$\text{Relative abundance} = \frac{\text{Number of individual of the species}}{\text{Total number of individuals}} \times 100$$

$$\text{Relative frequency} = \frac{\text{Frequency of a species}}{\text{Sum frequency of all species}} \times 100$$

$$\text{IVI} = \frac{\text{Relative dominance} + \text{Relative abundance} + \text{Relative frequency}}{3} \quad (1)$$

We estimated the total species richness using the abundance-based coverage estimator (ACE; Chao & Lee 1992; Chao *et al.* 1993; Magurran 2004; Newton 2007). As a measure of species diversity, we used the Shannon-Wiener index (H' ; Magurran 2004; Newton 2007):

$$H' = -\sum_{i=1}^s p_i \ln(p_i) \quad (2)$$

where, s is the number of species and p_i is the abundance of the i th species, which is expressed as a proportion of the total number of stems.

We estimated dominance using Simpson's index ($1/D$; Magurran 2004; Newton 2007):

$$D = \sum f_i^2 \quad (3)$$

where, f_i is the proportion of the total number of individuals accounted for by the i th species.

We determined the floristic similarity between forest types using Jaccard's coefficient of similarity (C_J ; Magurran 2004; Newton 2007) with the data for all four plots in each forest type combined:

$$C_J = \frac{a}{a+b+c} \quad (4)$$

where, a is the number of species found in both forest types, b is the number of species in forest type 1 but not in forest type 2, and c is the number of species in forest type 2 but not forest type 1.

We used the Morisita-Horn index (C_{MH} ; Magurran 2004; Newton 2007) as a quantitative measure of β diversity between types of forest:

$$C_{MH} = \frac{2\sum(a_i b_i)}{(d_a + d_b)(N_a N_b)} \quad (5)$$

where, N_a is the total number of individuals at site a, N_b is the total number of individuals at site b, a_i is the number of individuals of the i th species at site a, b_i is the number of individuals of the i th species at site b, and d_a is calculated as follows:

$$d_a = \frac{\sum a_i^2}{N_a^2} \quad (6)$$

We calculate d_b similarly, but using b_i and N_b instead of a_i and N_a . We computed all the species richness and diversity indices using version 8.0.0 of the EstimateS software (Colwell 2005).

We used a negative exponential function (Van Laar & Akça 1997) to simulate the diameter distribution of trees in the natural tropical forest:

$$N_i = k \cdot e^{-a \cdot d_i} \quad (7)$$

where, N_i is the number of trees in the i th diameter class, with midpoint diameter d_i , and k and a are regression constants.

Statistical analysis

After testing to confirm data normality and homogeneity of variance using the Shapiro-Wilk and Levene tests, we statistically compared the parameters for the three forest types. For our analysis of the forest structure and floristics, we used one-way ANOVA to test for significant differences in tree density, basal area, species density, S_{ace} , and the Simpson and Shannon-Wiener diversity indices with the four sub-plots in each forest type as independent replicates. We also used this approach to compare tree density and basal area among the three forest types within each dbh class. When the ANOVA indicated a significant difference among forest types ($P < 0.05$), we compared the means with Fisher's post-hoc LSD test. For the forest size-class structure, we used the chi-square test for the pooled plot data for each forest type and used the likelihood-ratio statistic to determine the significance of any differences. All

Table 1. Structural characteristics of the four plots (each 0.25 ha) in each of the three forest types.

	Plot no.	Secondary forest		Primary forest
		SF1	SF2	
Tree density (no.ha ⁻¹)	1	1556	1778	1478
	2	1844	1833	1511
	3	1456	2756	1544
	4	1756	1789	1633
	Mean ± SE	1653 ± 179 ^a	2039 ± 478 ^a	1542 ± 67 ^a
Basal area (m ² ha ⁻¹)	1	15.78	15.32	34.57
	2	15.79	25.94	34.26
	3	17.41	23.03	39.17
	4	19.16	20.17	37.43
	Mean ± SE	17.04 ± 1.61 ^a	21.11 ± 4.52 ^a	36.36 ± 2.35 ^b

Values for a parameter followed by different letters differ significantly ($P < 0.05$).

statistical analyses were performed using version 13.0 of the SPSS software (SPSS Inc. 2004).

Results

Forest structure

The total tree densities for all size classes combined were 1653 ± 179 , 2039 ± 478 , and 1542 ± 67 individuals ha⁻¹ (mean ± SE) in SF1, SF2, and the primary forest, respectively, and these values did not differ significantly (Table 1; ANOVA: $F_{2,9} = 3.115$, $P = 0.094$). The variation in tree densities was highest in SF1 and SF2, with coefficients of variation (CV) equal to 10.8 and 23.4 percent, respectively, but was low in the primary forest (CV = 4.3 %).

The one-way ANOVA conducted within each dbh class indicated a significantly higher density in SF2 than in primary forest only for the smallest trees (Fig. 2; 5 to 10 cm dbh, ANOVA: $F_{2,9} = 6.945$, $P = 0.015$). A significantly higher tree density was observed for trees with dbh > 25 cm in the primary forest (Fig. 2). There was no significant difference in tree density among the three forest types for dbh ranging from 10 to 20 cm (Fig. 2). The negative exponential function (equation 7) fit the diameter distribution well for all three forest types (Table 2).

Total tree basal area for all size classes combined was 17.04 ± 1.61 , 21.11 ± 4.52 , and 36.35 ± 2.35 m² ha⁻¹ in SF1, SF2, and the primary forest, respectively, and differed significantly among the three forest types (Table 1; ANOVA: $F_{2,9} = 43.51$, $P < 0.001$). Fisher's post-hoc LSD test indicated that

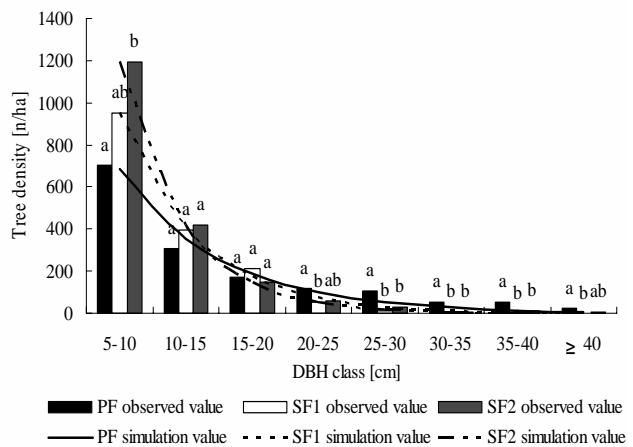


Fig. 2. Tree density in three forest types (PF, primary forest; SF1 and SF2, secondary forest) in Hainan Island's Baisha County. For each diameter class, bars labeled with different letters differ significantly ($P < 0.05$).

SF1 and SF2 did not differ significantly, but the primary forest had a significantly higher basal area than the two degraded secondary forests ($P < 0.001$). The mean total basal areas of SF1 and SF2 were 47.1 and 58.3 % of the primary forest's basal area. The highest variation in basal area was for SF2 (CV = 21.4 %), followed by SF1 (CV = 9.4 %) and the primary forest (CV = 6.5 %).

The difference in basal area within each dbh class was similar to the pattern for tree density. The basal area in SF2 was only significantly greater than that in the primary forest in the smallest trees (Fig. 3; 5 to 10 cm dbh; $F_{2,9} = 6.272$,

Table 2. Regression results (based on equation 7) for the diameter distribution of the three tropical forests.

	Model	R^2	MSE	F -value	P -value
Primary forest	$N = 1804.74 \cdot \exp(-0.13d)$	0.974	1165.36	206.595	< 0.001
Secondary forest					
SF1	$N = 3373.66 \cdot \exp(-0.17d)$	0.997	299.91	1151.70	< 0.001
SF2	$N = 5692.69 \cdot \exp(-0.21d)$	1	35.93	16980.57	< 0.001

In the models, d represents the midpoint of each diameter class.

$P = 0.02$). The basal area was significantly greater in primary forest than in the two degraded secondary forests when dbh was more than 20 cm. There was no significant difference among the three forest types for dbh ranging from 10 to 20 cm (Fig. 3).

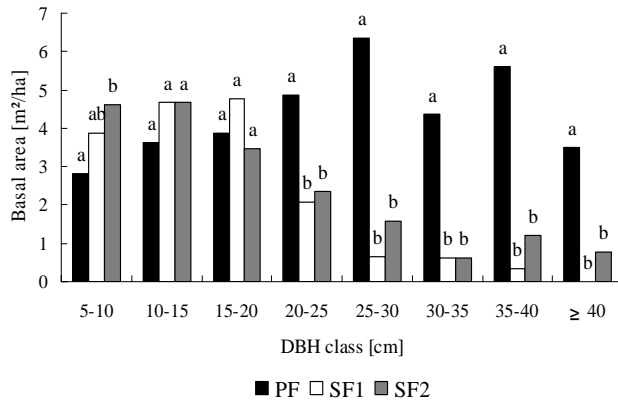


Fig. 3. Basal area of trees in three forest types (PF, primary forest; SF1 and SF2, secondary forest) for each diameter class. For each diameter class, bars labeled with different letters differ significantly ($P < 0.05$).

The size class structure differed significantly among the three forest types ($\chi^2 = 25.156$, $P = 0.024$), but there was no significant difference between SF1 and SF2 ($\chi^2 = 3.568$, $P = 0.738$). In contrast, primary forest differed significantly from both SF1 ($\chi^2 = 13.683$, $P = 0.026$) and SF2 ($\chi^2 = 25.156$, $P = 0.024$). Small trees (DBH = 5 to 10 cm) dominated both secondary forests (58.2 % of total tree number in SF1, versus 63.8 % in SF2), but the extent of this dominance was lower (46.0 %) in the primary forest (Fig. 4). The secondary forests had the lowest percentages of large-diameter trees. Trees with dbh greater than 20 cm accounted for just 4.6 and 6.1 % of the total in SF1 and SF2, versus 23 % in the primary forest (Fig. 4).

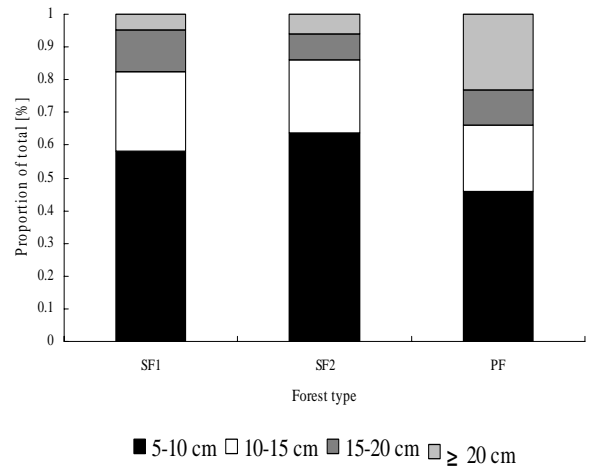


Fig. 4. Proportion of total number of stems in each diameter class for the three forest types (PF, primary forest; SF1 and SF2, secondary forest).

Forest composition and species importance value

Table 3 presents the contributions of each taxonomic family to the tree species diversity in the three forest types. The most common families in SF1 in terms of the number of stems were the Euphorbiaceae (37.5 %), Guttiferaceae (9 %), and Fagaceae (7.8 %). In terms of basal area, the highest values were for the Euphorbiaceae (35.9 %), Hamamelidaceae (13.4 %), and Fagaceae (9.5 %). In SF2, the most common families in terms of the number of stems were the Hamamelidaceae (30 %), Lauraceae (17.4 %), and Euphorbiaceae (12 %). In terms of basal area, the highest value was for Hamamelidaceae (49.7 %), followed by the Euphorbiaceae (11.5 %) and Myrtaceae (9.4 %). This contrasts markedly with the primary forest, in which the commonest families in terms of the number of stems were the Fagaceae (19.3 %), Ebenaceae (12.4 %), and Theaceae (11.8 %). In terms of basal area, the highest values were for the Fagaceae (35.3 %), Juglandaceae (17 %), and Moraceae (6.8 %).

Table 3. Percentage of total tree density and basal area by families in SF1, SF2 and the primary forest.

Family	Secondary forest				Primary forest	
	SF1		SF2		Stems	Basal area
	Stems	Basal area	Stems	Basal area		
Aceraceae	0.00	0.00	0.00	0.00	0.07	0.03
Actinidiaceae	0.39	0.14	0.00	0.00	0.21	0.04
Alangiaceae	0.10	0.02	0.00	0.00	0.00	0.00
Anacardiaceae	6.51	5.83	2.29	1.12	0.00	0.00
Annonaceae	0.68	0.66	0.86	0.30	0.00	0.00
Apocynaceae	0.29	0.22	1.29	0.45	0.07	0.08
Aquifoliaceae	0.39	0.17	0.14	0.48	0.69	0.25
Araliaceae	0.00	0.00	1.00	1.44	0.07	0.01
Bignoniaceae	0.10	0.02	0.00	0.00	0.07	0.01
Bombacaceae	0.58	0.92	0.00	0.00	0.00	0.00
Burseraceae	0.00	0.00	0.00	0.00	0.28	0.06
Dilleniaceae	6.22	4.20	0.57	0.27	0.55	0.40
Ebenaceae	0.00	0.00	0.00	0.00	12.39	2.90
Elaeocarpaceae	0.00	0.00	0.00	0.00	2.49	2.78
Euphorbiaceae	37.48	35.91	12.00	11.51	2.77	1.90
Fagaceae	7.77	9.53	0.14	0.44	19.31	35.34
Flacourtiaceae	0.10	0.05	0.00	0.00	0.00	0.00
Guttiferae	9.03	4.05	10.57	3.86	9.62	5.76
Hamamelidaceae	6.70	13.39	30.01	49.66	0.00	0.00
Icacinaceae	0.19	0.05	0.00	0.00	0.00	0.00
Juglandaceae	3.88	2.65	0.00	0.00	7.47	17.01
Lauraceae	3.11	1.91	17.43	9.32	8.79	5.71
Leguminosae	1.75	4.27	1.43	1.11	0.90	0.37
Magnoliaceae	0.00	0.00	0.00	0.00	0.14	0.11
Melastomataceae	0.00	0.00	0.00	0.00	0.07	0.01
Meliaceae	0.00	0.00	0.00	0.00	0.48	0.32
Mimosaceae	2.04	1.54	0.00	0.00	0.00	0.00
Moraceae	1.65	0.96	1.29	0.96	5.40	6.79
Myrsinaceae	0.00	0.00	0.00	0.00	0.48	0.20
Myrtaceae	3.79	7.88	5.00	9.37	5.47	3.02
Oleaceae	0.00	0.00	0.14	0.40	1.59	2.26
Polygalaceae	0.00	0.00	0.00	0.00	1.31	0.69
Proteaceae	0.00	0.00	0.00	0.00	0.07	0.01
Rubiaceae	0.68	0.31	0.00	0.00	1.59	0.53
Rutaceae	2.62	2.38	0.14	0.04	0.07	0.01
Sabiaceae	0.00	0.00	0.00	0.00	0.48	0.14
Samydaceae	0.00	0.00	0.00	0.00	0.42	0.21
Sapindaceae	0.00	0.00	0.00	0.00	0.14	0.26
Sapotaceae	0.00	0.00	0.00	0.00	0.69	0.70
Sterculiaceae	0.19	0.07	1.00	0.41	2.49	4.99
Styracaceae	0.00	0.00	0.00	0.00	0.14	0.18
Symplocaceae	2.62	1.86	6.43	4.01	0.90	0.21
Theaceae	0.58	0.32	6.57	3.96	11.76	6.41
Tiliaceae	0.00	0.00	0.43	0.12	0.00	0.00
Verbenaceae	0.58	0.67	1.29	0.77	0.55	0.31

Table 4. Abundance, relative abundance, relative frequency, relative dominance and importance value (IVI) for all trees with dbh > 5 cm for the dominant species in each forest type.

Species	Abundance (no.ha ⁻¹)	Relative abundance (%)	Relative frequency (%)	Relative dominance (%)	IVI	Rank
Secondary forest SF1						
<i>Macaranga denticulata</i>	336	23.93	12.99	26.30	63.22	1
<i>Liquidambar formosana</i>	92	6.55	4.53	13.18	24.26	2
<i>Lannea grandis</i>	89	6.36	7.68	5.74	19.78	3
<i>Lithocarpus corneus</i>	96	6.84	4.13	8.78	19.75	4
<i>Cratoxylon ligustrinum</i>	124	8.83	6.89	3.99	19.71	5
<i>Dillenia pentagyna</i>	85	6.08	6.50	4.14	16.71	6
<i>Syzygium cumini</i>	52	3.70	5.12	7.76	16.58	7
<i>Antidesma ghaesembilla</i>	63	4.46	4.13	2.37	10.97	8
<i>Antidesma bunius</i>	57	4.08	3.54	2.17	9.79	9
<i>Engelhardtia colebrookiana</i>	45	3.23	4.33	1.81	9.37	10
Secondary forest SF2						
<i>Liquidambar formosana</i>	583	30.00	10.42	49.67	90.08	1
<i>Cratoxylon ligustrinum</i>	203	10.43	7.99	3.57	21.99	2
<i>Cinnamomum porrectum</i>	142	7.29	9.38	3.29	19.95	3
<i>Syzygium cumini</i>	86	4.43	5.21	9.20	18.84	4
<i>Glochidion sphaerogynum</i>	108	5.57	6.94	4.47	16.98	5
<i>Symplocos cochinchinensis</i>	125	6.43	6.25	4.01	16.69	6
<i>Phoebe zhennan</i>	81	4.14	5.56	3.48	13.18	7
<i>Antidesma ghaesembilla</i>	53	2.71	4.51	4.20	11.43	8
<i>Eurya loquaiana</i>	78	4.00	3.82	2.81	10.63	9
<i>Actinodaphne pilosa</i>	64	3.29	4.86	1.41	9.56	10
Primary forest						
<i>Engelhardtia chrysolepis</i>	108	7.13	6.43	16.73	30.29	1
<i>Diospyros discolor</i>	175	11.56	7.50	2.64	21.69	2
<i>Garcinia multiflora</i>	99	6.54	4.42	4.76	15.72	3
<i>Cleyera japonica</i>	102	6.74	3.75	4.14	14.62	4
<i>Cyclobalanopsis nemoralis</i>	51	3.37	2.41	7.62	13.40	5
<i>Castanopsis hystrix</i>	32	2.11	2.95	6.49	11.55	6
<i>Castanopsis hainanensis</i>	31	2.05	2.01	5.83	9.89	7
<i>Castanopsis fabri</i>	50	3.30	2.68	3.31	9.29	8
<i>Artocarpus styracifolius</i>	28	1.85	2.14	5.10	9.09	9
<i>Cinnamomum porrectum</i>	39	2.58	3.21	1.33	7.12	10

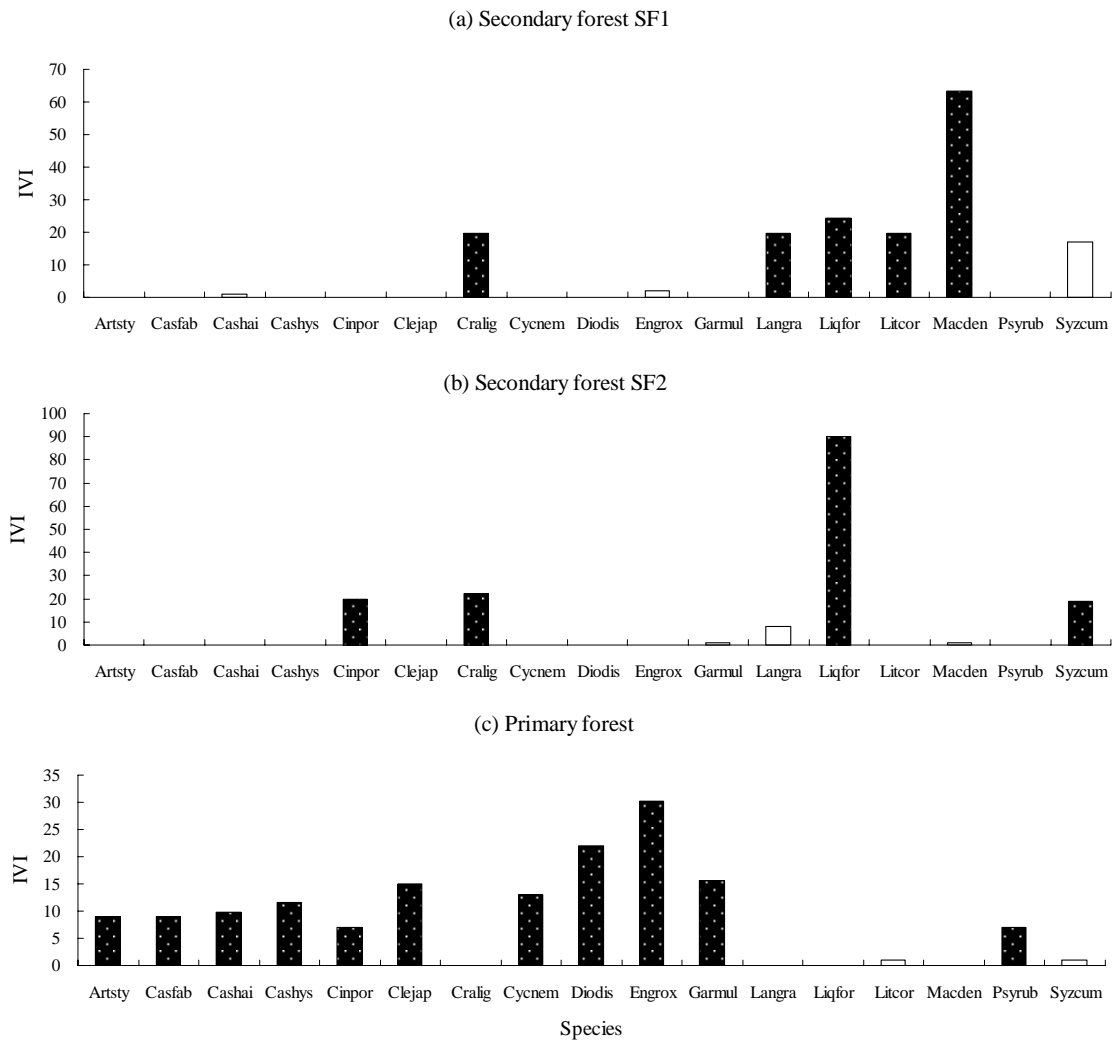


Fig. 5. Relative importance values (IVI) of the species that together accounted for ~50 % of total IVI in each forest type (black bars). White bar indicate species present but not contributing to 50 % of IVI in each forest type. Species abbreviations: Artsty = *Artocarpus styracifolius*; Casfab = *Castanopsis fabri*; Cashai = *Castanopsis hainanensis*; Cashys = *Castanopsis hystrix*; Cinpor = *Cinnamomum porrectum*; Clejap = *Cleyera japonica*; Cralig = *Cratoxylon ligustrinum*; Cycnem = *Cyclobalanopsis nemoralis*; Diodis = *Diospyros discolor*; Engrox = *Engelhardia roxburghiana*; Garmul = *Garcinia multiflora*; Langra = *Lannea grandis*; Liqfor = *Liquidambar formosana*; Litcor = *Lithocarpus corneus*; Macden = *Macaranga denticulata*; Psyru = *Psychotria rubra*; Syzcum = *Syzygium cumini*.

Notably, the two degraded secondary forests were dominated by the same two families (Euphorbiaceae and Hamamelidaceae) in terms of either the number of stems or the basal area. However, different families dominated the primary forest.

Macaranga denticulata was the dominant species in SF1 (IVI = 63.2) accounting for 21.1 % of total IVI (Table 4). The co-dominant species was *Liquidambar formosana* (IVI = 24.26) accounting for 8.1 % of total IVI. The other species with IVI

values greater than 10 include *Lannea grandis*, *Lithocarpus corneus*, *Cratoxylon ligustrinum*, *Dillenia pentagyna*, *Syzygium cumini*, and *Antidesma ghaesembilla*, which accounted for 3.7 to 6.6 % of total IVI. Although these eight species accounted for just 14.3 % of the total number of species, they accounted for 63.7 % of total IVI.

In SF2, *Liquidambar formosana* was the dominant species (IVI = 90.1) accounting for 30 % of total IVI. *Cratoxylon ligustrinum* was the co-

Table 5. Species density (number of species per plot), total richness estimator (S_{ace}) and the Simpson and Shannon diversity indices for each of the four plots per forest type.

Forest type	Plot no.	Species density	S_{ace}	Simpson ($1/D$)	Shannon (H')
Primary forest	1	28	22.85	13.93	2.92
	2	22	17.64	16.15	3.09
	3	32	19.17	16.14	3.24
	4	29	18.48	15.53	3.25
	Mean \pm SE	27.75 \pm 4.19 ^a	19.54 \pm 2.29 ^a	15.44 \pm 1.05 ^a	3.13 \pm 0.16 ^a
Secondary forest SF1	1	24	18.83	11.09	2.67
	2	21	14.9	8.72	2.79
	3	23	15.92	11.45	2.98
	4	26	14.82	11.65	2.99
	Mean \pm SE	23.5 \pm 2.08 ^a	16.12 \pm 1.88 ^a	10.73 \pm 1.36 ^b	2.86 \pm 0.16 ^b
Secondary forest SF2	1	24	16.50	11.69	2.67
	2	20	14.38	10.06	2.71
	3	22	13.58	8.55	2.69
	4	27	17.80	11.33	2.94
	Mean \pm SE	23.25 \pm 2.99 ^a	15.57 \pm 1.93 ^a	10.41 \pm 1.42 ^b	2.75 \pm 0.13 ^b

Values for a parameter followed by different letters differ significantly ($P < 0.05$).

dominant species (IVI = 22.0) accounting for 7.3 % of total IVI. The other species with IVI greater than 10 include *Cinnamomum porrectum*, *Syzygium cumini*, *Glochidion sphaerogynum*, *Symplocos cochinchinensis*, *Phoebe zhennan*, *Antidesma ghaesembilla*, and *Eurya loquaiana*. These nine species accounted for just 22 % of the total number of species, but accounted for 73.3 % of total IVI.

In the primary forest, *Engelhardtia chrysolepis*, *Diospyros discolor*, *Garcinia multiflora*, *Cleyera japonica*, and *Cyclobalanopsis nemoralis* and *Castanopsis hystrix* had IVI values greater than 10. *Engelhardtia chrysolepis* had the largest IVI, with a value of 30.3, accounting for 10.1 % of total IVI, followed by *D. discolor* with IVI = 26.19, accounting for 8.7 % of total IVI. The IVI of the other four species ranged from 11.6 to 15.7, accounting for 3.8 to 5.2 % of total IVI. These six species accounted for 5 % of the total number of species, but accounted for 35.8 % of total IVI.

In the two degraded secondary forests, four to five species, most of which were fast-growing trees, accounted for ~50 percent of total IVI (Fig. 5). *Cratogeomys ligustrinum* (Cralig in the figure) and *Liquidambar formosana* (Liqfor) appeared in both secondary forests, accounting for 14.7 percent of the total IVI in SF1 and 37.3 percent in SF2. In contrast, a total of 11 species in the primary forest

accounted for ~50 percent of total IVI, and these species were mostly climax and sub-climax species. *Cinnamomum porrectum* (Cinpor) appeared both in SF2 and in primary forest among the species that accounted for ~50 percent of total IVI, indicating the high potential of this species to persist and remain important during future succession in SF2.

Diversity

The Simpson and Shannon-Wiener diversity indices were significantly greater in primary forest than in the secondary forests (Table 5; ANOVA, $F_{2,9} = 19.184$, $P = 0.001$; $F_{2,9} = 6.915$, $P = 0.015$). The species density and S_{ace} value were also greater in primary forest, but the differences among the forest types were not significant (Table 5). The Jaccard coefficient for differences between forest types revealed that the species similarity values ranged from 0.089 to 0.263 for the comparisons of all pairs of forest types. The highest similarity was observed between SF1 and SF2 ($C_J = 0.263$) and the lowest was between primary forest and SF1 ($C_J = 0.089$). In contrast, the Morisita-Horn index showed a much higher probability ($I_{MH} = 0.277$) of finding an individual of the same species in a given random sample from SF1 and SF2 than in such a sample from primary forest and SF1 ($I_{MH} = 0.014$) or from primary forest and SF2 ($I_{MH} = 0.037$).

Discussion

Forest structure

Our results showed that the two degraded secondary forests had similar structural and floristic characteristics, but differed significantly from the primary forest in their structural characteristics (basal area and size-class structure).

The total density of all individuals ≥ 5 cm in dbh in the two secondary forests (1653 to 2039 individuals ha^{-1}) lies within the range of values for other secondary forests on Hainan Island (1640 to 4376 individuals ha^{-1} , Chen & Yang 2001; Jiang & Lu 1991; Jiang *et al.* 2002; Zang *et al.* 2001), but the basal area in the secondary forests (17.04 to 21.11 $\text{m}^2 \text{ha}^{-1}$) is well above the values of 9.91 to 15.13 $\text{m}^2 \text{ha}^{-1}$ reported by Chen & Yang (2001) and Wang *et al.* (2005). This could be related to differences among the sampled locations in the severity of disturbance, history of land use prior to abandonment, and climatic factors (Romero-Duque *et al.* 2007).

The total density (1542 individuals ha^{-1}) and basal area (36.36 $\text{m}^2 \text{ha}^{-1}$) in the primary forest fall within the range of values for other primary forests on Hainan Island (1942 to 2094 individuals ha^{-1} and 16.4 to 55.19 $\text{m}^2 \text{ha}^{-1}$; Fang *et al.* 2004; Wang *et al.* 2005; Zang *et al.* 2001).

Individuals of 5 to 10 cm dbh constituted 58.2 % of the total number of individuals in SF1, 63.8 % in SF2, and 46 % in the primary forest. In contrast, large trees (≥ 35 cm dbh) constituted 4.6 % of the individuals in SF1, 6.1 percent in SF2, and 23 % in the primary forest, which is far more than in the two secondary forests. This shows that the proportion of large trees increases as succession progresses.

After 15 years of natural succession, SF1 had attained only 46.9 % of the primary forest's basal area, versus 58.1 % for SF2 after 30 years of succession. The basal areas of individuals ≥ 10 cm in dbh in SF1 and SF2 accounted for, respectively, just 40.8 % and 45.7 % of the corresponding basal area in the primary forest. The percentages in SF1 and SF2 were much lower for large trees (≥ 35 cm dbh), attaining only 3.6 and 21.9 % of the values for primary forest in this region. Therefore, structural differences between secondary and primary forests were greater for larger trees.

Diversity and floristic characteristics

Li *et al.* (2002) and Jiang *et al.* (2002) grouped the main taxonomic families of Hainan Island into

five subfamilies: monotypic families (with only one species), oligotypic families (with 2 to 10 species), mesotypic families (with 11 to 20 species), plurotypic families (with 21 to 50 species), and plurimotypic families (with 51 or more species).

Plurimotypic families such as the Lauraceae, Euphorbiaceae, Fagaceae, and Myrtaceae were the main families that comprised the forest communities in previous studies in four nearby regions: the Jianfeng Mountains National Nature Reserve (Fang *et al.* 2004; Jiang & Lu 1991; Li *et al.* 2003); the Diaoluo Mountains National Nature Reserve (Jiang *et al.* 2002; Jiang 2006; Li *et al.* 2002, 2006); the Bawang Mountains National Nature Reserve (Jiang *et al.* 2002); and the Wuzhi Mountain National Nature Reserve (An *et al.* 1999; Jiang *et al.* 2002; Zhu *et al.* 1997). We found the same results. The Fagaceae and Euphorbiaceae were the main plurimotypic families in SF1, the Lauraceae, Euphorbiaceae, and Myrtaceae were the main plurimotypic families in SF2, and the Fagaceae was the main plurimotypic family in the primary forest. Interestingly, species belonging to some oligotypic and mesotypic families were the dominant species in terms of either stem number or basal area. For instance, *Liquidambar formosana* (oligotypic family, Hamamelidaceae) and *Cratogeomys ligustrinum* (mesotypic family, Guttiferae) were dominant in SF1 and SF2, whereas *Diospyros discolor* and *Diospyros hainanensis* (mesotypic family, Ebenaceae) and *Garcinia multiflora* (mesotypic family, Guttiferae) were dominant in the primary forest. Similar results were reported for nearby regions by Li *et al.* (2002) and Jiang *et al.* (2002).

The differences in the IVI sequence in the three forest types (Table 4) revealed that the ecological position of the species was changing as succession progressed. This suggests that the ecological position of each species in different successional stages and in the climax successional stage is significant, and can reveal the identity of the climax species in the region. Succession theory suggests that early-successional species will be replaced by other species during the next successional stage. Therefore, late-successional species that are present during earlier successional stages have the potential to develop further as succession progresses. This is significant for forest management because understanding the ecological position of each species during different successional stages allows forest managers to decide which species should be protected or encouraged in the current stand. This knowledge can also reveal which

species will gradually disappear from the stand and which will remain relatively stable during succession.

In SF1, late-successional species such as *Lithocarpus corneus* and *Syzygium cumini* had the potential to develop further. In contrast, early-pioneer species such as *Macaranga denticulata* would gradually disappear. In SF2, late-successional species such as *Cinnamomum porrectum*, *Syzygium cumini*, and *Phoebe zhennan* would develop further whereas the pioneer species *Liquidambar formosana* had no potential to develop further.

The Shannon-Wiener and Simpson diversity indices were significantly higher in primary forest than in the two secondary forests, suggesting that the primary forest had greater diversity and evenness. During the process of natural succession towards the climax community, diversity generally increased, although the diversity in intermediate stages may be greater than that in the climax community. Jiang *et al.* (2002) reached at the same conclusion for forests in the Jianfeng Mountains.

The time since forest regeneration began is important because it determines the degree of similarity among forest types at different successional stages (Álvarez-Yépiz *et al.* 2008). In the present study, floristic similarity (measured by Jaccard's similarity index) between secondary and primary forest was extremely low, indicating a significant difference in floristics. The relatively short time during which forest regeneration has occurred in the secondary forests (≤ 30 years) might account for the low similarity. Brearley *et al.* (2004) argued that even 55 years of succession may be insufficient to restore most primary forest species in old secondary forest in Central Kalimantan, Indonesia. Other factors such as differences in seed dispersal, rates of herbivory, soil degradation, and drought resistance must be considered to fully explain differences in the return intervals for certain species or in the successional trajectories toward different species mixtures during succession in tropical forests (Álvarez-Yépiz *et al.* 2008; Holl 2007; Vieira & Scariot 2006). Therefore, in addition to the short time during which secondary forests have been regenerating, and poor seed dispersal may be responsible for the low similarity between the primary and secondary forests. The current secondary forest originally developed at sites where the primary forest had been clear-felled and then burned for cultivation, providing little chance for propagules to survive. Moreover, clear-felled areas were too large for

propagules to reach most parts of these sites from nearby primary forest. In contrast, SF1 and SF2 had similar floristics. This could be because both were subjected to similar land use and conversion histories, even though they differed in their successional stages.

Implication for the restoration of tropical secondary forest

Hainan's government has designated the island as an Eco-province, making environmental and economic performance the basis of its government policy (Deng *et al.* 2007). This decision requires management of the island's forests for multiple purposes— not just for its timber production, but also for its ecological functions. The concept of nearly natural forest, which originated in Europe, may be the best way to satisfy these multiple demands. In general, nearly natural forest management is a model based on emulating the natural stability mechanisms of an ecosystem, which are supported by high biological diversity, and on attempting to harmonize the economic requirements with ecological requirements so as to attain the multiple benefits offered by sustainable development (Höfle 2000; Lu *et al.* 2004; Lu 2006). The principle of a nearly natural forest is based on a full understanding of the natural forest's structure and the natural successional processes. Janzen (1988), Finegan (1992), and Finegan & Delgado (2000) also noted that management of the restoration process for secondary forests must be based on an understanding of the dynamics of secondary succession.

The stand information that we obtained for the primary forest provides a reference model for the management of SF1 and SF2. Primary forest can tell us what the climax tree species will probably be in the study area and thus, which tree species in SF1 and SF2 have the most probability to survive the succession progress.

In SF2, *Cinnamomum porrectum*, *Syzygium cumini*, and *Phoebe zhennan* are the major tree species and are likely to form the future stand. During forest management, these species should be prioritized because they are climax tree species in primary forest and hence have the most potential for development. In contrast, *Liquidambar formosana* is dominant in the current stand, but is a pioneer species that does not exist in the primary forest and is therefore likely to disappear during succession. This means that no management activities are required for this species.

Similarly, because SF2 is in a later successional stage than SF1, it can serve as a model for the management of SF1. In SF1, species such as *Lithocarpus corneus*, *Syzygium cumini*, and *Castanopsis hainanensis* are the main future tree species that should be favored by forest management. This is because these trees species are also found in the primary forest, with a high IVI value, which suggests that these are climax or sub-climax tree species. In contrast, species such as *Macaranga denticulata* are likely to gradually disappear because they appear neither in SF2 nor in the primary forest, possibly because they are highly shade-intolerant. Although *Liquidambar formosana* in SF1 will disappear during the succession progress, this species should be favored during early succession because it is the most dominant species in SF2 and has high value. The species may show good development throughout the SF1 and SF2 successional stages and possibly even longer.

The results of our basic research on natural succession in tropical forests of Hainan Island can be used to guide the development of practical silvicultural diagnostic techniques to support the restoration of forests by local managers by permitting appropriate silvicultural interventions in the right places, at the right times, in the island's spatially complex forests (Finegan & Delgado 2000).

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