

## Research Article

# Changes in floristic composition, community structure and species diversity across a tropical coniferous-broadleaved forest ecotone

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### Abstract

Changes in an ecotone may indicate the dynamics between its two adjacent ecological systems. Most of the ecotone studies relevant to coniferous forests were conducted in temperate areas rather than in the tropics. In the low altitude tropical forest region of south China, transition zones exist between tropical coniferous forest and tropical broadleaved forest. To understand the dynamic trends of the forest stands across the ecotones, we compared the compositional and structural features of the three stand zones (the pine forest zone, the ecotone zone and the broadleaved forest zone) at 13 investigation sites, in terms of stand factors, size class distribution, growth-form, and species richness. Stem abundance and species richness increased as the vegetation zones changed from pine forest to the ecotone and then to broadleaved forest. In each stand zone, stem abundance and species richness declined as the size class increased. The coniferous-broadleaved forest ecotone revealed compositional and structural features between its adjacent forest stands. Our results will help design conservation strategies for this unique tropical coniferous forest ecosystem.

Keywords: tropical coniferous forest, ecotone, community structure, species diversity, *Pinus latteri*.

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## Introduction

Ecotones, zones of overlap between distinct vegetation types, have been recognized as sites that mediate fluxes of energy, nutrients and materials, and consequently link processes in adjoining systems [1,2]. Ecotones are viewed as natural transitions that can contribute to our understanding of the importance of biodiversity on ecosystem structure [3]. Knowledge about the features of different types of ecotones is accumulating. However, the studies are usually conducted at the landscape level. For example, some wetlands are ecotones between aquatic and terrestrial systems, and these can affect many functional landscape properties [4-6]. Many studies supported the idea that treeline trees are directly growth-limited by low temperature (environmental effect) and have suggested global temperature change could cause dynamic shifts in the ranges of these trees [7,8]. The treeline is used in a general sense to mean the altitudinal or northern limit of boreal forests, and the treeline ecotone is extremely sensitive to climate change, particularly in forest-tundra ecotones [9,10] and forest-grassland ecotones [11]. Some ecotones, such as forest-shrubland ecotones [12] and grassland-shrubland ecotones [13] provide evidence for invasion processes.

Several features have been proposed as being characteristic of ecotones [14-19]. Biodiversity may be higher in ecotones because of propagule input from adjacent communities, lower because of environmental variation, or intermediate because of gradual changes in both the abiotic and biotic environments [20,21]. The environmental gradient and interaction with multiple factors (including disturbances) are thought to constrain floristic diversity in ecotones. An ecotone may be produced by positive feedback switches between the environment and vegetation or by continuous gradual environmental changes [17,22]. Site-specific differences in a vegetation zone may be the result of environmental influences or limitations on seed productivity or dispersal and other recruitment processes [23,24]. Changing environmental conditions may affect habitat patterns within a region where an ecotone exists and thus the ecotone itself [3]. The distribution patterns of different species and functional groups across an ecotone vary [2]. Most studies focus on shifts in species composition and community structure within an ecotone [25], as well as on the distinctive ecotonal environment [26,27]. These kinds of studies can contribute to our understanding of how biodiversity affects ecosystem functioning [3]. Transition zones between two different ecosystem (or vegetation) types may contain compositional and structural characteristics found in adjacent habitats, as well as distinctive microhabitats found only in the ecotonal areas [28].

Many researchers and managers have long been interested in forest ecotones [19]. Yet most ecotonal field studies and modelling efforts have focused on transitions between forest and non-forest biomes and have mostly investigated boreal forest and savannah [29, 30]. Few studies have investigated floristic composition and patterns of species richness as you move from coniferous forest to broadleaved forest in the tropics, although there has been some research into the alpine tree line ecotones of tropical coniferous forests [31,32].

In the tropical regions of China, most of the areas are dominated by broadleaved trees and shrubs [33]. However, in some special places and habitats, where environmental conditions are stressful for broadleaved trees, a few species of conifers become dominant. Due to the special environmental and floristic conditions, tropical coniferous forests often have a distinct community structure and contain a unique biodiversity that is different from that of adjacent tropical rainforests [33]. Tropical coniferous forests play a unique role in maintaining the biodiversity and function of tropical forest ecosystems. *Pinus latteri* is a near-threatened species globally [34] and has a very limited distribution in south China, Vietnam, Laos and Burma, which are located in the tropical regions of Asia. The widest distribution of tropical natural coniferous forest is found on Hainan Island, China, most of which is concentrated in the Bawangling forest region (BFR) and is dominated by *Pinus latteri*. Only a few studies have investigated its distribution and management in China [35] and there is little or no knowledge about the

characteristics of the ecotones representing the transition between pineforest and broadleaved forest.

In this study, we hypothesized that the coniferous-broadleaved forest ecotone had distinct characteristics compared with its two adjacent forest zones, in terms of species diversity, community structure and floristic composition. Specifically, we asked: 1) Are the species present in the ecotone zone the same as the species in the adjacent forest zones, or is the floristic composition of the ecotone different from that found in the two adjacent forest zones? 2) Are the distribution patterns for woody plant abundance and species richness of different height and size classes in the ecotone different from those in the two adjacent forest zones? and 3) Is the species richness in the ecotone higher, lower or intermediate compared with the two adjacent forest zones?

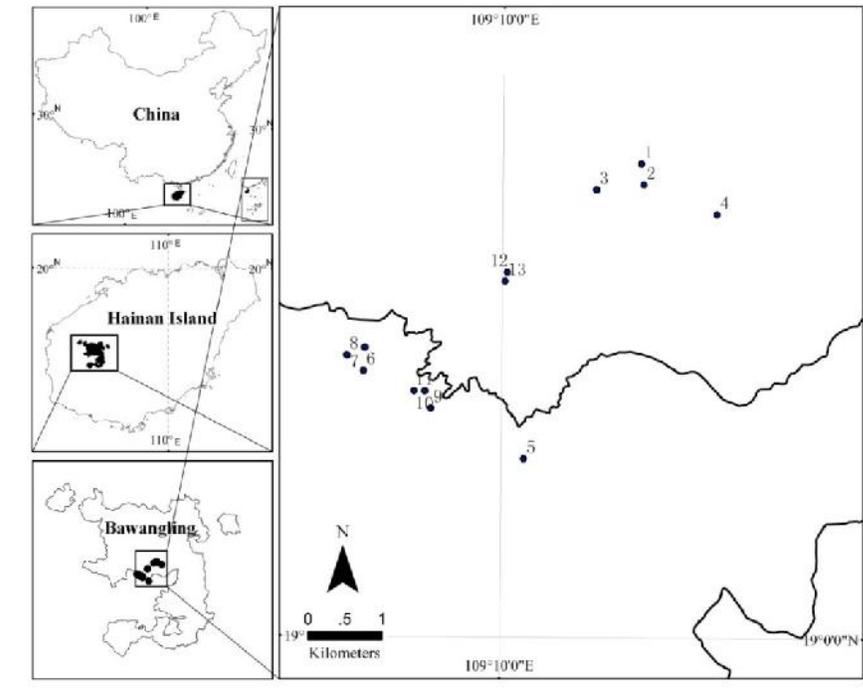


Fig. 1. Geographical location of the study sites.

## Methods

### Study area

The study was conducted in the Bawangling forest region (BFR; 18°53′–19°20′N, 108°58′–109°53′E) on Hainan Island, China (Fig. 1). The BFR is approximately 500 km<sup>2</sup>, with an elevation range of approximately 100–1,654 m asl. It has a typical tropical monsoon climate with distinct dry and wet seasons. The parent material is granite and the soils are latosols at lower elevations and mountain lateritic soils at higher elevations. Annual average temperature and precipitation is 24.2°C and 1,677.1 mm, respectively [33]. The precipitation is seasonally distributed, with a distinct wet season from May to October and a dry season (<100 mm of precipitation per month) from November to April. The natural vegetation in low elevation areas (<800 m) includes tropical lowland rainforest, tropical monsoon rainforest and tropical coniferous forest.

The coniferous forest is dominated by *Pinus latteri* and often has some broadleaved components, such as *Vatica mangachapoi*, *Quercus vestita*, *Engelhardtia roxburghiana*, *Aporosa dioica* and *Lithocarpus corneus*. The dominant herb species include *Andropogon chinensis*, *Hyparrhenia diplandra*, and *Schizachyrium sanguineum*. In the BFR of Hainan Island, the coniferous forest covers the second largest area in the low elevation areas, and

tropical lowland rainforest occupies the largest area. There are also some tropical monsoon rainforests in the low elevation areas of the BFR.

Over the past century, the BFR has experienced extensive, shifting cultivation and logging in the low elevation areas. These anthropogenic disturbances have greatly changed the structure, function and dynamics of the original vegetation. In the disturbed places, different vegetation types are often mixed up, and ecotones have formed between areas containing different vegetation types. However, a logging ban has been enforced across the whole island since the beginning of the 1990s. Following the logging ban, the BFR has recovered naturally. At present, most of the forests in the study region are secondary forests at different stages of recovery, and only a few areas of primary vegetation types have been preserved.

#### *Experimental design and data collection*

Thirteen sites were selected where coniferous-broadleaved forest ecotones had been clearly identified. The distance between each of the sites was more than 2 km. At each site, random 10 m × 10 m plots were selected along an elevational gradient oriented perpendicular to each of the ecotones (mixed coniferous-broadleaved forest surrounded by pineforest and broadleaved forest on each side). Our field observation estimated that these investigation plots were scattered along an altitude range of about 90 m–160 m, and the width of the ecotones was about 30 m–60 m, depending on the characteristics of each site.

We located three zones in each site based on field estimations of the physiognomy of the vegetation. The zones were defined as the pine forest zone (P), the ecotone zone (E) and the broadleaved forest zone (B). We estimated that the pineforest zone had > 50% of its basal area attributable to pine, while the broadleaved forest zone had < 30% of its basal area made up of pine (Zang, personal observations). The ecotone zone was considered as the transitional zone between the pineforest zone and the broadleaved forest zone. In each site, six 10 m × 10 m plots were randomly selected in each stand zone. Then each of these six plots was divided into four 5 m × 5 m sub-plots to make parameter measurements easier and for calculation of the species accumulation curves. Consequently, each of the 10 m × 10 m plots in each stand zone represented one replicate for each vegetation zone in the site. There were 78 (6 × 13) random replicates for each stand zone.

All the calculations and figures are adjusted to this basic unit of 10 m × 10 m plot, except for the accumulation curves. All the woody stems with a diameter at breast height (DBH) ≥ 1cm were identified to the species level and were classified by growth-form as trees, shrubs or lianas. For each tree, the following parameters were measured or recorded: species, DBH and height. The nomenclature follows Flora of China (English edition: <http://www.efloras.org>). All the trees were sorted into four height classes: ≤ 5 m, 5–15 m, 15–25 m and > 25 m. They were also grouped into eight DBH classes: ≤ 10, 10–20 cm, 20–30 cm, 30–40 cm, 40–50 cm, 50–60 cm, 60–70 cm and > 70 cm. The species richness was used to indicate species diversity.

#### *Data analysis*

We compared abundance and richness of the different growth-forms, tree heights and size classes among the different zones. Abundance and richness were analyzed by ANOVA and statistical significance was set at  $p < 0.05$ . All analyses were performed at the sampled plot size of 10 m × 10 m. Calculated pairwise similarities between each zone for the abundances of individuals and growth-forms (trees, shrubs and lianas) that had been identified to the species level, were used to examine species composition with Jaccard's similarity index and Sørensen's quantitative index [36].

We performed a non-metric multidimensional scaling (nMDS) analysis based on "Bray-Curtis" dissimilarity values to visualize the relationships in ordination space for all 234 plots using the metaMDS function in the "vegan"

package. We correlated the position of plots along the MDS axes, with the basal areas of all live woody vegetation as the response variable. We used ANOSIM (analysis of similarities) to compare the basal area relationships of the three zones in all the plots. ANOSIM was implemented with a maximum of 999 permutations. Area and individual-based rarefaction species accumulation curves were generated to compare species richness among the three stand zones using the entire data set of 936 sub-plots. Data transformations were made when necessary so that all analyses conformed to the assumptions of the general linear model [37]. Analyses were carried out using the R 2.15.1 Program [38].

## Results

### *Stand factors and forest structure*

One-way ANOVA showed that there were significant differences among all the three stand zones in terms of stand density, basal area, mean height, mean DBH, canopy density and litter depth (Table 1). Of the six stand factors, the basal area, mean height, mean DBH and litter depth of the E and B zones did not show any significant differences. Furthermore, there were no significant differences between the canopy density of the P and E zones either. The maximum height and maximum DBH trees were both found in the pineforest zone. Both stem abundance and species richness in the four height classes showed an inverse-J shape (Fig. 2). The order for woody stem abundance in the first two height classes for the three zones was B > E > P and B < E < P in the second two height classes. The woody stem abundances among the three zones were significantly different except for the below 5 m height class ( $F_2 = 0.726$ ,  $p = 0.484$ ). The trends for species richness in the first and second two height classes were similar. The first two height classes showed significant differences among the three stand zones, and the order was B > E > P. The second two showed no significant differences among the three stand zones, and the order was B < E < P.

**Table 1** Comparison of stand factors (mean  $\pm$  S.D.) among the three stand zones of the tropical coniferous-broadleaved forest ecotone (P: pine forest zone; E: ecotone zone; B: broadleaved forest zone). Different letters at the top right corner of the mean values indicate significant difference at  $p < 0.05$ .

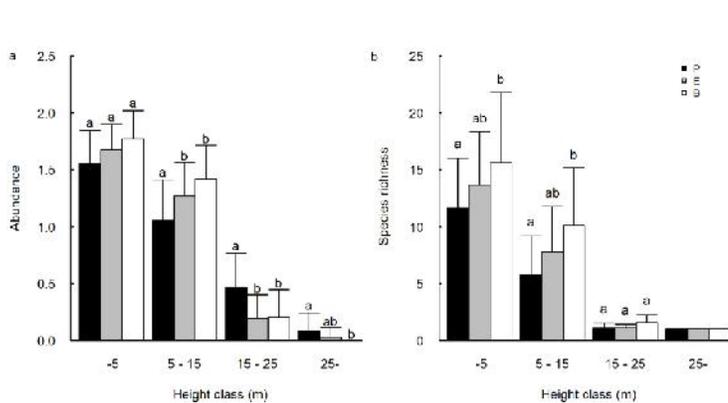
Stand factors	Zones		
	P	E	B
Density (No. stem 100 m <sup>-2</sup> )	68.97 $\pm$ 41.94 <sup>a</sup>	87.31 $\pm$ 25.61 <sup>b</sup>	115.32 $\pm$ 47.55 <sup>c</sup>
Basal areas (m <sup>2</sup> 100 m <sup>-2</sup> )	77.96 $\pm$ 65.06 <sup>a</sup>	33.82 $\pm$ 24.43 <sup>b</sup>	26.50 $\pm$ 23.78 <sup>b</sup>
Mean height (m)	5.60 $\pm$ 1.64 <sup>a</sup>	5.07 $\pm$ 1.15 <sup>b</sup>	4.97 $\pm$ 0.96 <sup>b</sup>
Maximum height (m)	31	30	23
Mean DBH (cm)	5.68 $\pm$ 2.14 <sup>a</sup>	4.51 $\pm$ 1.20 <sup>b</sup>	4.09 $\pm$ 1.08 <sup>b</sup>
Maximum DBH (cm)	100	85	64
Canopy density (%)	75.55 $\pm$ 5.59 <sup>a</sup>	76.27 $\pm$ 7.71 <sup>a</sup>	80.71 $\pm$ 5.00 <sup>b</sup>
Litter depth (cm)	5.63 $\pm$ 0.13 <sup>a</sup>	3.65 $\pm$ 0.14 <sup>b</sup>	3.01 $\pm$ 0.13 <sup>b</sup>

Similarly, both woody stem abundance and species richness in the eight size classes also had an inverse J shape (Fig. 3). The order for woody stem abundance and species richness in the first two size classes was B > E > P and in the other six, the order was B < E < P. Trees with heights above 15 m and a DBH > 30 cm were: *Pinus latteri* and *Cyclobalanopsis kerrii* in the coniferous forest zone; *Pinus latteri*, *Syzygium cumini*, *Cyclobalanopsis kerrii*, *Buchanania arborescens* and *Syzygium hancei* in the ecotone zone and *Quercus acutissima*, *Peltophorum tonkinense*, *Syzygium cumini*, *Vatica mangachapoi*, *Engelhardia roxburghiana* and *Terminalia nigrovenulosa* in

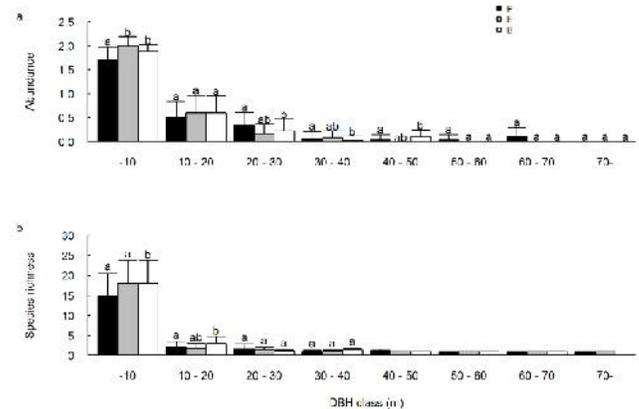
the broadleaved forest zone. Stem abundance and species richness showed significant differences among the three stand zones using one-way ANOVA. Both showed increasing trends from the P zone through the E to the B zone, reaching a maximum in B zone (Fig. 4). Stem abundance and species richness for all three growth forms in B zone were significantly higher than was found in the P zone and were occasionally higher than those in the E zone, but this was not statistically significant.

### Floristic composition and species richness

Overall, this study recorded 234 plots of 10 m × 10 m, which contained 21,185 individuals belonging to 218 species, 164 genera and 67 families (Appendix 1). Altogether, 121 species from 46 families and 94 genera, 144 species from 49 families and 112 genera and 187 species from 56 families and 144 genera, were captured in the P, E and B zones, respectively. *Pinus latteri* was the dominant tree species in the P zone where Pinaceae were clearly dominant. *Buchanania arborescens* and *Dodonaea viscosa* occurred quite often in the E zone community, but the most frequent families were the Anacardiaceae and the Sapindaceae. The B zone had many *Aporosa dioica*, *Lithocarpus corneus*, *Engelhardia roxburghiana* and *Diospyros strigosa* stems. Euphorbiaceae, Fagaceae, Ebenaceae and Juglandaceae were the four dominant families.



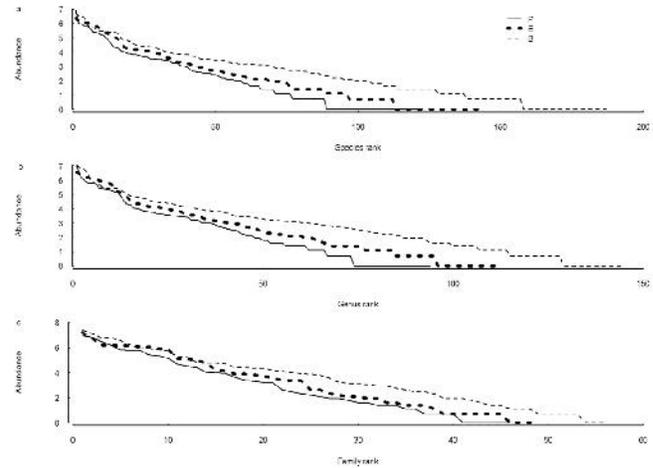
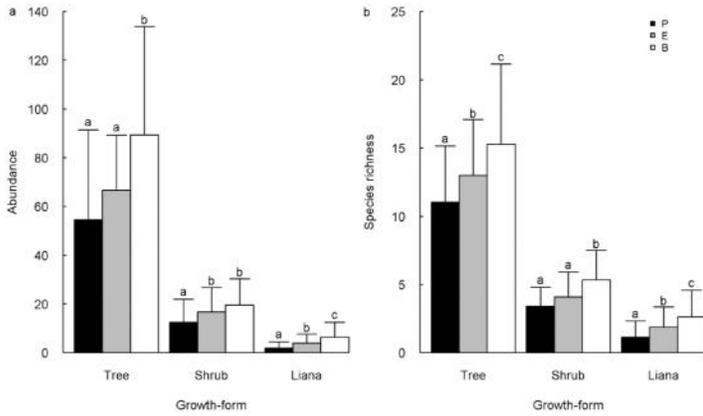
**Fig. 2.** Stem abundance and species richness (mean  $\pm$  S.D.) for the four height classes in the three stand zones (Tukey's HSD test,  $p < 0.05$ ). Black: pine forest zone (P), grey: ecotone (E) and white: broadleaved forest (B). (Abundance was transformed by  $\log_{10}$ ).



**Fig. 3.** Stem abundance and species richness (mean  $\pm$  S.D.) for the eight DBH classes in the three stand zones (Tukey's HSD test,  $p < 0.05$ ). Black: pine forest zone (P), grey: ecotone (E) and white: broadleaved forest (B). (Abundance was transformed by  $\log_{10}$ ).

The species, genus and family-rank-abundance distribution curves for the three stand zones showed that the B zone had the largest numbers of species, genera and families. The second and third were the E zone and the P zone, respectively (Fig. 5). The order for stem abundance at the species, genus and family level was  $B > E > P$ . The nMDS ordination showed that the distances between points preserved the dissimilarity values rank order between those points. Figure 6 shows that species composition according to basal area varied gradually along the stand zones gradient, with the P zone at one extreme end and the B zone at the other. There were significant differences in basal area for the three zones (ANOSIM test,  $R = 0.3514$ ,  $p = 0.001$ ). Floristic similarity between woody stem abundances was significantly higher between the E and B zones than between the E and P zones. A similar trend was found when comparing the shrub growth forms (Table 2). However, the E and P zones were more similar than the E and B zones. Species richness increased gradually from the P through the E to the B zones and showed significant differences among the three stand zones (Fig. 7a). The species richness-area curve and species richness-abundance curve revealed that the species accumulation rate rose as area and stem abundance

increased (Fig. 7b and Fig. 7c) and the order was B > E > P.



**Fig. 4.** Stem abundance and species richness (mean  $\pm$  S.D.) for the three growth forms in the three stand zones (Tukey's HSD test,  $p < 0.05$ ). Black: pine forest zone (P), grey: ecotone (E) and white: broadleaved forest (B).

**Fig. 5.** The species, genus and family-rank-abundance distribution curves for the three different stand zones (P-pine forest zone, E-ecotone zone, and B-broadleaved forest zone).

## Discussion

### *Changes in vegetation composition and structure across the tropical coniferous-broadleaved forest ecotone*

Our analyses revealed differences in tree species composition in the three stand zones and suggested that the ecotone zone was a transitional mixed forest zone, thus it had intermediate stand factor values that were between the values for the pine and broadleaved forest zones. In the ecotone zones, the main broadleaved species were: *Lithocarpus corneus*, *Aporosa dioica*, *Diospyros strigosa*, *Dodonaea viscosa*, *Engelhardia roxburghiana*, *Cratoxylum cochinchinense*, *Melastoma sanguineum*, *Phyllanthus emblica*, *Buchanania arborescens* and *Glochidion sphaerogynum*, which accounted for 59% of the total number of individuals. Woody stem abundances for these ten broadleaved species accounted for 50% and 48% of the total stem abundances in the pine forest zones and broadleaved forest zones, respectively. They are common deciduous plant species of tropical monsoon rainforests [39] and frequently appear during the early stages of recovery. They can endure intense light, drought and poor soil, can adapt to the early growth environment of the pines and can easily establish in disturbed habitats. As the canopy density increased, the shade-tolerant species of tropical lowland rainforest, such as *Quercus acutissima*, *Peltophorum tonkinense*, *Syzygium cumini*, *Vatica mangachapoi*, *Engelhardia roxburghiana* and *Terminalia nigrovenulosa*, appeared only in the broadleaved forest zones. The family rank-abundance distribution curves for the three zones showed that the largest number of individuals came from the Euphorbiaceae, while the genera containing the largest numbers were *Aporosa*, *Phyllanthus*, *Glochidion* and *Croton*.

Our study demonstrated that pine forest zones were significantly lower in stem density and higher in basal areas than those found in the ecotone and broadleaved forest zones. The woody stem abundance and species richness of the different tree height and size classes in the three zones had an inverse-J shape, which suggests that the regeneration of these zones was generally successful, since there were abundant young trees to replace old trees in the future. The different tree height classes and size classes for the three zones are probably related to past disturbances, which promoted the regeneration and invasion of broadleaved species from the adjacent secondary broadleaved forest into the margins of the pine forests. In the absence of large-scale disturbances for a sufficiently long period, natural recovery can promote canopy closure and advance the growth and regeneration of shade-tolerant species [40].

Changes in the dominant plants would strongly control the vegetation response rate and could be an agent for shifts in vegetation structure [41]. The trees with the maximum diameters and heights were mostly pines in the pine forest zones that had been subject to less severe logging disturbances in the past. Over the past century, the BFR has experienced extensive, shifting cultivation and logging in the low elevation areas. These anthropogenic disturbances have greatly changed the structure, function and dynamics of the original vegetation. In disturbed areas, different vegetation types are often mixed up and ecotones have formed between areas containing different vegetation.

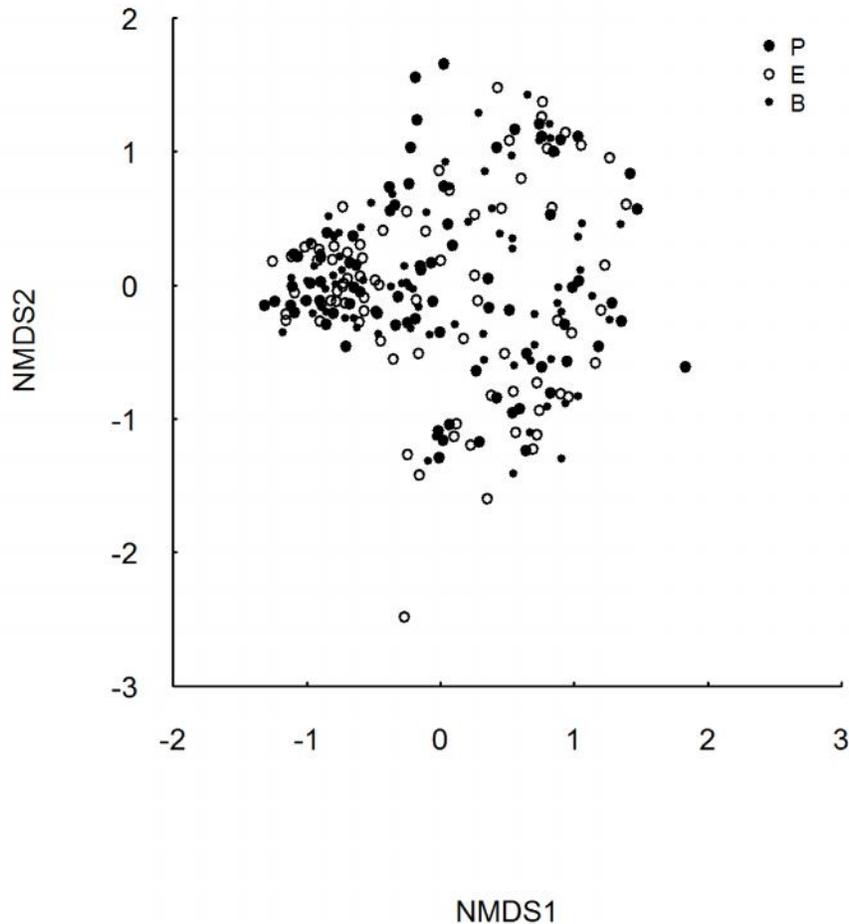
**Table 2.** Jaccard's percent similarity of all growth -forms combined, Sørensen's quantitative index (abundance) of woody plants (all size classes) in the three stand zones (Differences for lianas between the three zones was not significant,  $p = 0.397$ ).

Jaccard's percent Similarity				
All growth-forms	P	E	B	
P	1	-	-	
E	0.588	1	-	
B	0.461	0.62	1	
Sørensen's quantitative index(abundance)				
trees				
P	1	-	-	
E	0.623	1	-	
B	0.467	0.607	1	
shrubs				
P	1	-	-	
E	0.578	1	-	
B	0.47	0.624	1	

### *Changes in species diversity across the tropical coniferous- broadleaved forest ecotone*

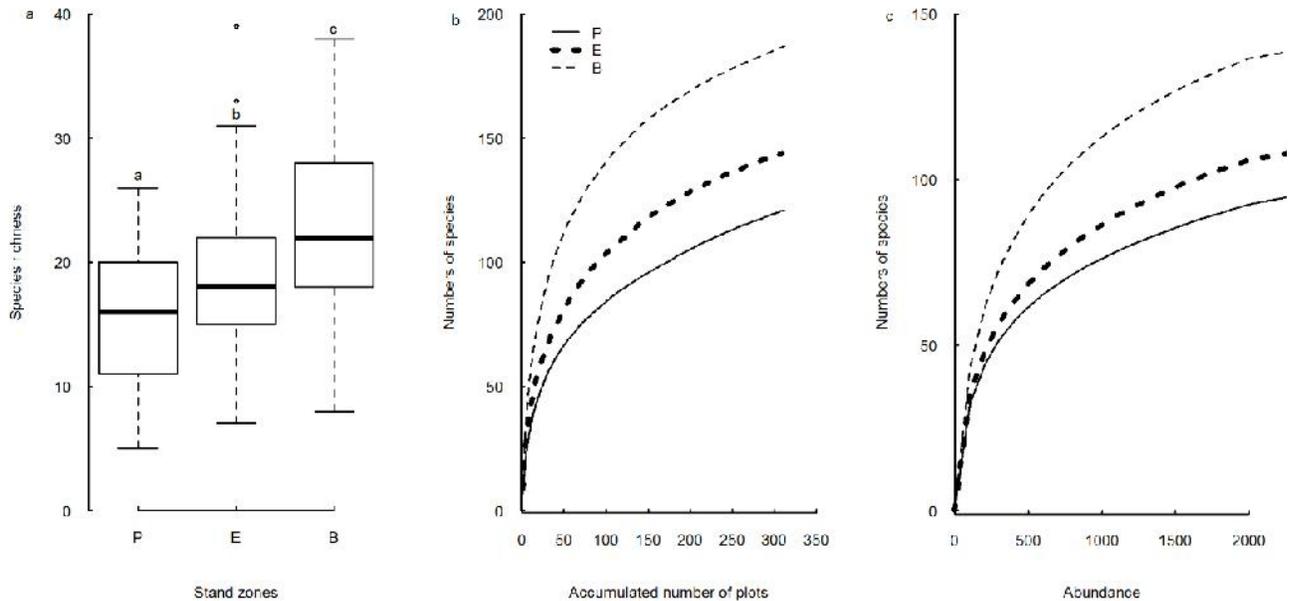
Species-area relations can provide evidence for community structure and have been used as an expression of heterogeneity [42]. The slope of the species-area curve depends on the rate at which new species are encountered. As the sample area increases, more heterogeneous areas accumulate species faster than homogenous areas. Our results indicated that the accumulation rate increased from the pine forest zone through the ecotone zone to the broadleaved forest zone, which suggested that the pine forest contained relatively

homogeneous habitats, while the broadleaved forest had more heterogeneous habitats for most species. The ecotone was intermediate in heterogeneity (Figs. 7b, 7c).



**Fig. 6. Non-metric multidimensional scaling plot for Bray-Curtis estimated similarity among the 234 plots from the 13 sites (P-pine forest zone, E-ecotone zone and B-broadleaved forest zone).**

It has often been suggested that species richness will be higher in ecotones than in adjacent communities [4, 43, 44], but occasionally it will be lower in particular types of ecotones [16, 45]. However, some studies have shown that species richness in ecotones is in the middle of their two neighbours [46]. Our results seem to deviate from the first two hypotheses, but support the latter. In our study, species richness in the ecotone zone was intermediate between the other two zones. This was probably because the ecotone was formed by the invasion of broadleaved species into the margins of the pineforest after logging or other anthropogenic disturbances, especially the invasion of the deciduous monsoon species, which can adapt to the harsh pineforest environments.



**Fig. 7. Comparison of species richness, the species-area accumulation curves and species-abundance accumulation curves for the three stand zones (P-pine forest zone, E-ecotone zone and B-broadleaved forest zone).**

Some of the reasons for the low species richness in pineforest zones are that the low nutrient concentrations and generally high acidic soil environment exclude many species [47], and that pine trees might produce more defensive phenolic and terpenic secondary metabolites [48], which are toxic to many rain forest species. However, in the ecotone zone, conifers coexisted with a large number of tropical monsoon species, such as *Cratogeomys cochinchinense*, *Aporosa dioica*, *Phyllanthus emblica* and *Dodonaea viscosa*. These species grow in open, disturbed sites, and their successful development is probably linked to their thick bark, their deciduous properties, and their capacity to adapt to intense light and drought stress. The moderate moisture and soil nutrients in broadleaved forest zones meant that tropical lowland rainforest species (e.g., *Vatica mangachapoi*, *Machilus suaveolens* and *Ardisia quinquegona*) could exist.

Like almost all the other shade-intolerant conifers, pine regeneration requires a combination of factors, such as good seed production years, favourable seeding conditions without subsequent animal damage, and fire-free periods [49]. If this occurs, they develop into an almost mono-dominant forest [50]. *Pinus latteri* has been found to require higher light intensities and can endure very poor soils. Any explanation of the coniferous-broadleaved forest ecotone needs to account for both the disturbance regimes as well as the life history characteristics of the species. The conifers that had regenerated in our studied region normally grow in open forest land, in forest gaps or at forest edges, and are highly tolerant to low soil nutrient levels and strong light intensity. These features have allowed them to thrive in the particularly harsh environment, which is stressful for most rain forest species. Where the canopy layer was dense enough, pine regeneration was limited due to low light intensity, although the light intensity and drought during this period were still limiting the regeneration of tropical broadleaved

species. However, tropical monsoon species could invade and establish at the margins of the pineforest, resulting in the formation of a mixed coniferous-broadleaved ecotone. From the patterns of diversity changes (increasing trend from P through E to B) and the above discussion, it is reasonable to assume that the broadleaved trees in the ecotone zone were invasions from the neighbouring broadleaved forest zone.

### Implications for conservation

Our study showed that the coniferous-broadleaved forest ecotone revealed compositional and structural features between its adjacent forest stands. This specificity in ecotone areas might be due to interspecific competition for resources, patterns of dispersal, the establishment of species from different sides of the adjacent communities [51] and the general features of the ecotones [52]. Furthermore, species-specific adaptive responses to the environment in different microhabitats may modulate changes in community composition of the ecotones [53].

Risser suggested that the ecotones best suited for study would be those that recover rapidly after both climate change and disturbance [3]. Disturbance leads to the invasion of species with a large ecological amplitude [54]. Tropical forests worldwide continue to face severe threats due to direct human exploitation (e.g. logging and agricultural expansion) and the indirect influence of human-accelerated environmental change [22]. Pine forests are one of the tropical forest types on Hainan Island and are found in the low elevation regions along with tropical broadleaved rainforests. Because of the area's low altitude, extensive shifting cultivation and logging, most pine forests are secondary forests in which pines are mixed with broadleaved trees.

An improved understanding of the factors that control the patterns and dynamics of plant diversity across the coniferous-broadleaved forest ecotone will contribute to the sustainable management and conservation of this special tropical pine forest and its related ecosystems. Our findings have clear implications for understanding and predicting successional dynamics in tropical coniferous forests [55]. The results may be applied in designing conservation areas and developing conservation strategies for this unique tropical coniferous forest ecosystem.

### Acknowledgements

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**Appendix 1. Alphabetical list of all the 218 species and their characteristics surveyed in the three different zones of thirteen sites. The nomenclature follows Flora of China (English edition: <http://www.efloras.org>).**

Species	Family	Growth form	Hmax
<i>Acacia pernata</i> (Linn.) Willd.	Fabaceae	Liana	-
<i>Acronychia pedunculata</i> (Linn.) Miq.	Rutaceae	Tree	19
<i>Actinodaphne pilosa</i> (Lour.) Merr.	Lauraceae	Tree	12
<i>Adinandra hainanensis</i> Hayata	Theaceae	Tree	30
<i>Aganosma schlechteriana</i> Lévl.	Apocynaceae	Liana	-
<i>Alangium chinense</i> (Lour.) Harms	Alangiaceae	Shrub	4
<i>Albizia chinensis</i> (Osbeck) Merr.	Fabaceae	Tree	25
<i>Albizia corniculata</i> (Lour.) Druce	Fabaceae	Liana	-
<i>Albizia odoratissima</i> (Linn. f.) Benth.	Fabaceae	Tree	15
<i>Albizia procera</i> (Roxb.) Benth.	Fabaceae	Tree	15
<i>Alchornea rugosa</i> (Lour.) Muell. Arg.	Euphorbiaceae	Shrub	4
<i>Alniphyllum fortunei</i> (Hemsl.) Makino	Styracaceae	Tree	20
<i>Alnus cremastogyne</i> Burkill	Betulaceae	Tree	40
<i>Alphonsea monogyna</i> Merr. & Chun	Annonaceae	Tree	20
<i>Ampelopsis cantoniensis</i> (Hook. et Arn.) Planch.	Vitaceae	Liana	-
<i>Ancistrocladus tectorius</i> (Lour.) Merr.	Ancistrocladaceae	Liana	-
<i>Antidesma bunius</i> Spreng.	Euphorbiaceae	Tree	30
<i>Antirhea chinensis</i> (Champ. O) Benth. et Hook. f.	Rubiaceae	Shrub	2
<i>Apodytes dimidiata</i> E. Meyer(ex Drege ex Bernhardi) ex Arn.	Icacinaceae	Tree	20
<i>Aporusa dioica</i> (Roxb.) Muell. Arg.	Euphorbiaceae	Tree	10
<i>Aporusa villosa</i> (Lindl.) Baill.	Euphorbiaceae	Tree	10
<i>Ardisia crassinervosa</i> Walker	Myrsinaceae	Shrub	2
<i>Ardisia quinquegona</i> Blume	Myrsinaceae	Shrub	6
<i>Arytera littoralis</i> Bl.	Sapindaceae	Tree	20
<i>Beilschmiedia longipetiolata</i> Allen	Lauraceae	Tree	20
<i>Berchemia polyphylla</i> Wall. Ex Lawson var. <i>leioclada</i> Hand	Rhamnaceae	Liana	-
<i>Breynia rostrata</i> Merr.	Euphorbiaceae	Shrub	4
<i>Bridelia insulana</i> Hance	Euphorbiaceae	Shrub	7
<i>Bridelia stipularis</i> (Linn.) Bl.	Euphorbiaceae	Liana	-
<i>Bridelia tomentosa</i> Bl.	Euphorbiaceae	Tree	12
<i>Buchanania arborescens</i> (Bl.) Bl.	Anacardiaceae	Tree	10
<i>Calamus faberi</i> Becc.	Arecaceae	Liana	-
<i>Calamus tetradactylus</i> Hance	Palmae	Liana	-
<i>Callicarpa candicans</i> (Burm.f.) Hochr.	Verbenaceae	Shrub	2
<i>Callicarpa longissima</i> (Hemsl.) Merr.	Verbenaceae	Shrub	7
<i>Callicarpa nudiflora</i> Hook. et Arn.	Verbenaceae	Shrub	3
<i>Canarium album</i> (Lour.) Rauesch.	Burseraceae	Tree	35
<i>Canthium horridum</i> Bl. Bijdr.	Rubiaceae	Shrub	5
<i>Canthium simile</i> Merr.	Rubiaceae	Tree	24
<i>Capparis hainanensis</i> Oliv.	Capparidaceae	Liana	-
<i>Capparis liangii</i> Merr.	Capparidaceae	Liana	-

<i>Carpinus londoniana</i> var. <i>lanceolata</i> (Hand.-Mazz.) P. C. Li	Betulaceae	Shrub	7
<i>Castanopsis formosana</i> Hayata	Fagaceae	Tree	15
<i>Catunaregam spinosa</i> (Thunb.) Tirveng.	Rubiaceae	Shrub	6
<i>Celastrus paniculatus</i> Willd.	Celastraceae	Liana	-
<i>Chionanthus hainanensis</i> (Merrill & Chun) B. M.	Oleaceae	Tree	12
<i>Cinnamomum porrectum</i> (Roxb.) Kosterm.	Lauraceae	Tree	25
<i>Clausena excavata</i> Burm. F.	Rutaceae	Shrub	3
<i>Cleistanthus saichikii</i> Merr.	Euphorbiaceae	Tree	8
<i>Combretum punctatum</i> Bl.	Combretaceae	Liana	-
<i>Cratoxylum cochinchinense</i> (Lour.) Blume	Guttiferae	Tree	10
<i>Cratoxylum formosum</i> (Jack) Dyer	Clusiaceae	Tree	10
<i>Croton laevigatus</i> Vahl	Euphorbiaceae	Tree	12
<i>Cryptocarya metcalfiana</i> Allen	Lauraceae	Tree	25
<i>Cyclobalanopsis hui</i> (Chun) Chun ex Y. C. Hsu & H. W. Jen	Fagaceae	Tree	20
<i>Cyclobalanopsis kerrii</i> (Craib) Hu	Fagaceae	Tree	20
<i>Cyclobalanopsis patelliformis</i> (Chun) Y. C. Hsu & H. W. Jen	Fagaceae	Tree	15
<i>Dalbergia benthami</i> Prain	Fabaceae	Liana	-
<i>Dalbergia hainanensis</i> Merr. & Chun	Fabaceae	Tree	17
<i>Dalbergia hancei</i> Benth.	Fabaceae	Liana	-
<i>Daphniphyllum calycinum</i> Benth.	Daphniphyllaceae	Tree	25
<i>Dasymaschalon trichophorum</i> Merr.	Annonaceae	Shrub	5
<i>Decaspermum gracilentum</i> (Hance) Merr. et Perry	Myrtaceae	Shrub	4
<i>Dendrolobium lanceolatum</i> (Dunn) Schindler	Fabaceae	Shrub	3
<i>Derris trifoliata</i> Lour.	Fabaceae	Liana	-
<i>Desmos chinensis</i> Lour.	Annonaceae	Liana	-
<i>Dimocarpus longan</i> Lour.	Sapindaceae	Tree	25
<i>Diospyros cathayensis</i> Steward	Ebenaceae	Tree	25
<i>Diospyros strigosa</i> Hemsl.	Ebenaceae	Tree	10
<i>Dodonaea viscosa</i> (Linn.) Jacq.Enum.Pl.Carib.	Sapindaceae	Shrub	5
<i>Dolichandrone cauda felina</i> (Hance) Benth. & Hook. f.	Bignoniaceae	Liana	-
<i>Dracaena angustifolia</i> Roxb.	Agavaceae	Shrub	3
<i>Drypetes cumingii</i> (Baill.) Pax & K. Hoffm.	Euphorbiaceae	Tree	20
<i>Drypetes hainanensis</i> Merr.	Euphorbiaceae	Tree	20
<i>Elaeagnus gonyanthes</i> Benth.	Elaeagnaceae	Liana	-
<i>Elaeocarpus sylvestris</i> (Lour.) Poir.	Elaeocarpaceae	Tree	20
<i>Ellipanthus glabrifolius</i> Merr.	Connaraceae	Tree	25
<i>Embelia ribes</i> Burm. F.	Myrsinaceae	Liana	-
<i>Engelhardia fenzelii</i> Merr.	Juglandaceae	Tree	20
<i>Engelhardia roxburghiana</i> Wall.	Juglandaceae	Tree	25
<i>Entada phaseoloides</i> (Linn.) Merr.	Fabaceae	Liana	-
<i>Epipremnum aureum</i> (Linden et André) G. S. Bunting	Araceae	Liana	-
<i>Erioglossum rubiginosum</i> (Roxb.) Bl.	Sapindaceae	Shrub	7
<i>Ervatamia hainanensis</i> Tsiang	Apocynaceae	Tree	8
<i>Euonymus geloniifolia</i> Chun & How	Celastraceae	Shrub	2
<i>Euonymus laxiflorus</i> Champ. ex Benth.	Celastraceae	Tree	10
<i>Eurya nitida</i> Korthals	Theaceae	Tree	14
<i>Evodia glabrifolia</i> (Champ. ex Benth.) Huang	Rutaceae	Tree	18
<i>Evodia leptota</i> (Spreng.) Merr.	Rutaceae	Shrub	7
<i>Ficus altissima</i> Bl.	Moraceae	Tree	35

<i>Ficus hispida</i> Linn. f.	Moraceae	Tree	15
<i>Ficus simplicissima</i> Lour.	Moraceae	Shrub	4
<i>Ficus tinctoria</i> Forst. F. subsp. <i>gibbosa</i> (Bl.) Corner	Moraceae	Tree	10
<i>Ficus variegata</i> Bl. var. <i>chlorocarpa</i> (Benth.) King	Moraceae	Tree	29
<i>Flacourtia indica</i> (Burm. f.) Merr.	Flacourtiaceae	Shrub	4
<i>Fraxinus griffithii</i> C. B. Clarke	Oleaceae	Tree	20
<i>Garcinia oblongifolia</i> Champ. ex Benth.	Guttiferae	Tree	24
<i>Girardinia cuspidata</i> (Bl.) Kurz	Ulmaceae	Tree	20
<i>Glochidion sphaerogynum</i> (Muell. Arg.) Kurz. <i>G. fagifolium</i> Miq.	Euphorbiaceae	Tree	15
<i>Glochidion wrightii</i> Benth.	Euphorbiaceae	Tree	15
<i>Gmelina hainanensis</i> Oliv.	Verbenaceae	Tree	20
<i>Gnetum montanum</i> Markgr.	Gnetaceae	Liana	-
<i>Graphistemma pictum</i> (Champ.) Benth. et Hook. f. ex Maxim.	Asclepiadaceae	Liana	-
<i>Grewia eriocarpa</i> Juss.	Tiliaceae	Tree	8
<i>Harrisonia perforata</i> (Blanco) Merr.	Simaroubaceae	Liana	-
<i>Helicteres angustifolia</i> Linn.	Sterculiaceae	Shrub	1
<i>Helicteres isora</i> Linn.	Sterculiaceae	Shrub	7
<i>Homalium paniculiflorum</i> F. C. How & W. C. Ko	Flacourtiaceae	Tree	28
<i>Ilex rotunda</i> Thunb.	Aquifoliaceae	Tree	15
<i>Illigera celebica</i> Miq.	Hernandiaceae	Liana	-
<i>Ixonanthes chinensis</i> Champ.	Erythroxylaceae	Tree	20
<i>Ixora hainanensis</i> Merr.	Rubiaceae	Shrub	4
<i>Ixora henryi</i> Lévl.	Rubiaceae	Shrub	4
<i>Lagerstroemia balansae</i> Koehne	Lythraceae	Tree	25
<i>Lannea coromandelica</i> (Houtt.) Merr.	Anacardiaceae	Tree	12
<i>Lantana camara</i> Linn.	Verbenaceae	Shrub	3
<i>Lasianthus chinensis</i> (Champ.) Benth.	Rubiaceae	Shrub	4
<i>Lindera kwangtungensis</i> (Liou) Allen	Lauraceae	Tree	25
<i>Litchi chinensis</i> Sonn. Var. <i>euspontanea</i> Hsue	Sapindaceae	Tree	30
<i>Lithocarpus chiungchungensis</i> Chun & P. C. Tam	Fagaceae	Tree	10
<i>Lithocarpus corneus</i> (Lour.) Rehd.	Fagaceae	Tree	13
<i>Lithocarpus elaeagnifolius</i> (Seemen) Chun	Fagaceae	Tree	13
<i>Lithocarpus naidarium</i> (Hance) Chun	Fagaceae	Tree	10
<i>Lithocarpus ternaticupulus</i> Hayata	Fagaceae	Tree	10
<i>Litsea cubeba</i> (Lour.) Pers.	Lauraceae	Tree	8
<i>Litsea glutinosa</i> (Lour.) C. B. Rob.	Lauraceae	Tree	15
<i>Litsea variabilis</i> Hemsl.	Lauraceae	Tree	16
<i>Machilus chinensis</i> (Champ. ex Benth.) Hemsl.	Lauraceae	Tree	25
<i>Machilus suaveolens</i> S. Lee	Lauraceae	Tree	15
<i>Maesa perlarius</i> (Lour.) Merr.	Myrsinaceae	Shrub	3
<i>Mallotus paniculatus</i> (Lam.) Muell. Arg.	Euphorbiaceae	Tree	15
<i>Mallotus philippensis</i> (Lam.) Muell. Arg.	Euphorbiaceae	Tree	15
<i>Melastoma sanguineum</i> Sims.	Melastomataceae	Shrub	3
<i>Memecylon scutellatum</i> (Lour.) Hook. et Arn.	Melastomataceae	Shrub	7
<i>Merremia boisiana</i> (Gagn.) V. Ooststr.	Convolvulaceae	Liana	-
<i>Microcos paniculata</i> Linn.	Tiliaceae	Tree	12
<i>Micromelum falcatum</i> (Lour.) Tan.	Rutaceae	Tree	10
<i>Microtropis submembranacea</i> Merr. et freem.	Celastraceae	Shrub	4

<i>Millettia nitida</i> Benth	Fabaceae	Liana	-
<i>Millettia pachyloba</i> Drake	Fabaceae	Liana	-
<i>Millettia tsui</i> Metc.	Fabaceae	Liana	-
<i>Mischocarpus hainanensis</i> H. S. Lo	Sapindaceae	Shrub	5
<i>Mussaenda hainanensis</i> Merr.	Rubiaceae	Liana	-
<i>Mussaenda hirsutula</i> Miq.	Rubiaceae	Liana	-
<i>Neolitsea oblongifolia</i> Merr. et Chun	Lauraceae	Tree	18
<i>Ochna integerrima</i> (Lour.) Merr.	Ochnaceae	Shrub	7
<i>Olea brachiata</i> (Lour.) Merr.	Oleaceae	Tree	9
<i>Ormosia pinnata</i> (Lour.) Merr.	Fabaceae	Tree	23
<i>Ormosia semicastrata</i> Hance f. <i>litchifolia</i> How	Fabaceae	Tree	19
<i>Osmanthus matsumuranus</i> Hayata	Oleaceae	Shrub	10
<i>Peltophorum tonkinense</i> (Pierre) Gagnep.	Fabaceae	Tree	28
<i>Phoebe tavoyana</i> (Meissn.) Hook. f.	Lauraceae	Tree	13
<i>Photinia benthamiana</i> Hance	Rosaceae	Tree	25
<i>Phyllanthus emblica</i> Linn.	Euphorbiaceae	Tree	23
<i>Pinus kesiya</i> var. <i>langbianensis</i> (A. Chev.) Gausson	Pinaceae	Tree	30
<i>Pinus latteri</i> Mason	Pinaceae	Tree	30
<i>Pithecellobium lucidum</i> Benth.	Fabaceae	Tree	17
<i>Pittosporum tobira</i> (Thunb.) Ait.	Pittosporaceae	Shrub	6
<i>Polyalthia cerasoides</i> (Roxb.) Benth. & Hook. f. ex Bedd.	Annonaceae	Tree	20
<i>Poncirus trifoliata</i> (Linn.) Rafin.	Rutaceae	Shrub	5
<i>Premna corymbosa</i> (Burm. F.) Rottl. et Willd.	Verbenaceae	Shrub	3
<i>Prismatomeris tetrantra</i> (Roxb.) K. Schum	Rubiaceae	Shrub	5
<i>Psychotria rubra</i> (Lour.) Poir.	Rubiaceae	Shrub	6
<i>Pterospermum acerifolium</i> Willd.	Sterculiaceae	Tree	15
<i>Pterospermum heterophyllum</i> Hance	Sterculiaceae	Tree	27
<i>Pygeum topengii</i> Merr.	Rosaceae	Tree	25
<i>Quercus acutissima</i> Carruth.	Fagaceae	Tree	25
<i>Radermachera frondosa</i> Chun & How	Bignoniaceae	Tree	20
<i>Radermachera hainanensis</i> Merr.	Bignoniaceae	Tree	20
<i>Rapanea neriifolia</i> (Sieb. et Zucc.) Mez	Myrsinaceae	Tree	20
<i>Reevesia longipetiolata</i> Merr. et Chun	Sterculiaceae	Tree	30
<i>Rhodomyrtus tomentosa</i> (Ait.) Hassk.	Myrtaceae	Shrub	3
<i>Richeriella gracilis</i> (Merr.) Pax & K. Hoffm	Euphorbiaceae	Tree	8
<i>Rourea minor</i> (Gaerth.) Leenh.	Connaraceae	Liana	-
<i>Rubus cochinchinensis</i> Tratt.	Rosaceae	Liana	-
<i>Sapium discolor</i> (Champ. ex Benth.) Muell. Arg.	Euphorbiaceae	Tree	20
<i>Sarcosperma laurinum</i> (Benth.) Hook. f.	Sapotaceae	Tree	22
<i>Schima superba</i> Gardn. & Champ.	Theaceae	Tree	25
<i>Scolopia saeva</i> (Hance) Hance	Flacourtiaceae	Tree	10
<i>Smilax amaurophlebia</i> Merr.	Liliaceae	Liana	-
<i>Smilax astroasperma</i> F. T. Wang & Ts. Tang	Liliaceae	Liana	-
<i>Smilax hypoglauca</i> Benth.	Liliaceae	Liana	-
<i>Spondias lakonensis</i> Pierre	<u>Anacardiaceae</u>	Tree	15
<i>Sterculia lanceolata</i> Cav.	Sterculiaceae	Tree	15
<i>Streblus taxoides</i> (Heyne) Kurz	Moraceae	Shrub	3
<i>Strychnos angustiflora</i> Benth.	Loganiaceae	Liana	-
<i>Styrax serrulatus</i> Roxb.	Styracaceae	Tree	12
<i>Suregada glomerulata</i> (Bl.) Baill.	Euphorbiaceae	Tree	13

<i>Symplocos cochinchinensis</i> (Lour.) S. Moore	Symplocaceae	Tree	18
<i>Symplocos euryoides</i> Hand.-Mazz.	Symplocaceae	Shrub	2
<i>Symplocos poilanei</i> Guill.	Symplocaceae	Tree	16
<i>Symplocos racemosa</i> Roxb.	Symplocaceae	Shrub	4
<i>Syzygium chunianum</i> Merr. et Perry	Myrtaceae	Tree	20
<i>Syzygium cumini</i> (Linn.) Skeels	Myrtaceae	Tree	25
<i>Syzygium hancei</i> Merr. et Perry	Myrtaceae	Tree	17
<i>Tarenna attenuata</i> (Voigt) Hutchins.	Rubiaceae	Tree	15
<i>Tarennoidea wallichii</i> (Hook. f.) Tirveng. & C. Sastre	Rubiaceae	Tree	17
<i>Terminalia hainanensis</i> Exell	Combretaceae	Tree	10
<i>Tetracera asiatica</i> (Lour.) Hoogland	Dilleniaceae	Liana	-
<i>Tetrastigma papillatum</i> (Hance) C. Y. Wu	Vitaceae	Liana	-
<i>Tetrastigma planicaule</i> (Hook.) Gagnep.	Vitaceae	Liana	-
<i>Toxicodendron succedaneum</i> (Linn.) O. Kuntze	Anacardiaceae	Tree	15
<i>Trema tomentosa</i> (Roxburgh) H. Hara	Ulmaceae	Tree	10
<i>Turraea pubescens</i> Hellen	Meliaceae	Shrub	3
<i>Urceola rosea</i> (Hook. et Arn.) D. J. Middleton	Apocynaceae	Liana	-
<i>Uvaria boniana</i> Finet et Gagnep.	Annonaceae	Liana	-
<i>Uvaria calamistrata</i> Hance	Annonaceae	Liana	-
<i>Uvaria grandiflora</i> Roxb.	Annonaceae	Liana	-
<i>Uvaria microcarpa</i> Champ. ex Benth.	Annonaceae	Liana	-
<i>Vatica mangachapoi</i> Blanco	Dipterocarpaceae	Tree	32
<i>Vernonia cumingiana</i> Benth.	Compositae	Liana	-
<i>Vitex quinata</i> (Lour.) Williams	Verbenaceae	Tree	15
<i>Wendlandia uvariifolia</i> Hance	Rubiaceae	Shrub	7
<i>Wikstroemia hainanensis</i> Merr.	Thymelaeaceae	Shrub	4
<i>Wikstroemia nutans</i> Champion ex Benth	Thymelaeaceae	Shrub	3
<i>Wrightia pubescens</i> R. Br.	Apocynaceae	Tree	20
<i>Xantolis longispinosa</i> (Merr.) H. S. Lo	Sapotaceae	Tree	15
<i>Zanthoxylum avicennae</i> (Lam.) DC.	Rutaceae	Tree	17