

Research paper

Composition, Structure, and Preliminary Restoration Efforts of a Tropical Coastal Forest at Siangjiaowan, Southern Taiwan

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【 Summary 】

In recent years, the tropical coastal forest of the Siangjiaowan Ecological Reserve has been severely invaded by shade-intolerant species and *Leucaena leucocephala* due to road construction which created adverse edge effects along the forest. In addition, many valuable tree species lack new recruits. The composition and structure of this forest are dramatically altered compared to those 40 yr ago. To understand the current status of this coastal forest, we established a 1.55-ha sampling plot (300 m long, 40~60 m wide) in the forest in January 2012. Each individual of a woody species was identified and tagged, and its height, diameter at breast height (DBH), and location were recorded. In total, 1765 trees ha⁻¹ belonging to 58 species with a DBH of ≥ 1 cm were recorded; among them, *Aglaia formosana* and *Macaranga tanarius* had the highest species abundances. For trees with a DBH of < 1 cm, a total of 3023 stems ha⁻¹ belonging to 53 woody species was recorded, with 934 stems belonging to *Aglaia formosana*. Among the 58 species with individuals with a DBH of ≥ 1 cm, e.g., *Hernandia nymphiifolia* and *Barringtonia asiatica*, most of them appeared to have a fluctuating diameter structure, indicating that many disturbance events had occurred during their regeneration process. Sorted by the Importance Value Index (IVI) of this stand, *Bar. asiatica* and *Her. nymphiifolia* were listed as nos. 1 and 3. However, *Mac. tanarius* and *Melanolepis multiglandulosa*, both very shade-intolerant species, were nos. 2 and 6 in the IVI. Furthermore, *Mac. tanarius* and *Leu. leucocephala* rapidly occupy tree-fall gaps created by disturbances from typhoons. From 1974 to 2012, species abundances of *Her. nymphiifolia* and *Bar. asiatica* were respectively reduced by 31 and 21%, and those of *Murraya paniculata* and *Morinda citrifolia* were reduced 51 and 55%, while those of *Mac. tanarius* and *Mel. multiglandulosa* increased 56- and 4 fold. The leaf area index of this tropical forest decreased from 3.96 to 1.73 after 2 typhoons hit in August 2012, but had rebounded to 3.02 in only 75 d after the second typhoon. Preliminary

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ecological restoration efforts of this forest were initiated in July 2012. We reduced the density of 3 invasive shade-intolerant species in a wind-disturbed site and planted *Bar. asiatica* and other native species of this coastal forest, in an effort to improve the stand structure of this tropical coastal forest.

Key words: *Barringtonia asiatica*, diameter structure, ecological restoration, invasive shade-intolerant species, species abundance.

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研究報告

香蕉灣熱帶海岸林森林組成結構及初步復育工作

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摘要

香蕉灣生態保護區的熱帶海岸林，近年來因人類開路造成邊際效應，林緣環境惡化，陽性樹種及銀合歡入侵嚴重。此外，許多珍貴樹種缺乏更新植株，林分組成結構與過40年比較已有很大的改變。本研究於2012年1月，在該處設置長300 m，寬40~60 m，面積1.55 ha的調查樣區，將樣區內所有木本植物予以編號，記錄種類、高度、胸徑(≥ 1 cm者)，並標記其空間分布位置。2012年植群普查共記錄到58種胸徑≥ 1 cm的樹種，共計1765株ha⁻¹，以紅柴及血桐的株數最多。胸徑< 1 cm的木本植物有53種，共3023株ha⁻¹，以紅柴934株最多。胸徑≥ 1 cm的58種樹種中，大多數樹種的徑級結構為波動型，蓮葉桐及棋盤腳族群即屬此型，顯示此處過去常遭擾動。此區樹種的重要值指數排序，棋盤腳與蓮葉桐分別為第1及第3位，但是陽性樹種血桐及蟲屎分別已達第2及第6位，且血桐與銀合歡會佔據颱風擾動所形成的孔隙。由1974到2012年，蓮葉桐及棋盤腳的物種豐量分別減少31及21%，月橘及檫樹分別減少51及55%，而血桐及蟲屎則分別增加56倍及4倍。在2012年8月有2個颱風侵襲南台灣，此海岸林葉面積指數由3.96降至1.73，但颱風過後75天已回升至3.02，林冠枝葉生長恢復甚快。2012年7月起在此處進行初步生態復育工作，已減少3種入侵陽性樹種在風災擾動區的密度，並人為栽植棋盤腳及其他海岸林原有樹種，期望能改善此海岸林的林分結構。

關鍵詞：棋盤腳、徑級結構、生態復育、入侵陽性樹種、物種豐量。

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INTRODUCTION

Effects of fragmentation on the composition, structure, and biodiversity of forests are important issues in global ecology (Oliveira-Filho et al. 1997, Bierregaard et al. 2001). Many factors, such as road construction,

deforestation, and range operations, may contribute to forest fragmentation. Prolonged (lasting over 32 yr) research about forest fragmentation in the Amazon rainforest pointed out that the increased death rate at the edge

of a rainforest might be one of the most important processes leading to fragmentation (Laurance et al. 2006, 2011). The death rate of plants at the edge of a fragmented forest might increase as a result of high light, more-severe drought, or recruitment of invasive species; consequently, the turnover rate of species at the edge was significantly higher than that in the inner core of a forest (Laurance et al. 1998, 2006). Changes in the species composition at a fragmented forest edge vary depending on the ecological characteristics of each species. Abundances of shade-tolerant species decrease, while light-demanding and r-selected species increase due to edge effects (Laurance et al. 2006).

The forest of the Siangjiaowan Ecological Reserve in Kenting National Park, southern Taiwan is the only tropical coastal forest that exists in Taiwan. Many valuable coastal tree species are found in this forest, for example, *Barringtonia asiatica*, *Hernandia nymphiifolia*, *Hibiscus tiliaceus*, *Morinda citrifolia*, *Terminalia catappa*, *Thespesia populnea*, *Allophylus timorensis*, *Excoecaria agallocha*, *Tournefortia argentea*, *Millettia pinnata*, *Pisonia umbellifera*, *Premna serratifolia*, *Heritiera littoralis*, *Cerbera manghas*, *Calophyllum inophyllum*, and *Guettarda speciosa*. This coastal forest once extended 12 km in length with the widest part being 0.6 km and a total area of 500 ha (Wang 1975). Unfortunately since the 1950s, this coastal forest has been severely degraded by local inhabitants in order to plant cash crops (e.g., sisal). The originally intact coastal forest had become fragmented, with only a limited extent of the forest remaining. The only portion of the coastal forest that still remains is a narrow strip of 28 ha of 1.5 km in length along the coast from Chuanfanshih to Siangjiaowan. It is divided by Highway 26 into 2 parts; the seaside part has a width of only

50~80 m. Moreover, the seaside fragmented forest along the road suffers from hostile environmental conditions of especially strong winds and high light caused by edge effects.

According to a survey of the floral composition of the Siangjiaowan coastal forest in around 1960, there were 42 tree species, 30 shrub species, and 33 herbaceous species (Chang 1960). However, the abundance of understory juveniles was a lot less than the abundance of adult trees, inferring that the succession of this plant community was in doubt (Chang 1960, 1984). Researchers at the Taiwan Forestry Research Institute (TFRI) established a 1.46-ha plot in this coastal forest in 1974, and recorded 41 tree species with a density of 507 trees ha⁻¹ (Chang et al. 1985). Then the same plot was re-censused in 1980, 1984, and 2005. In the 2005 census, 51 tree species were recorded, and the density had increased to 1158 trees ha⁻¹, mostly mid- and small-diameter-class individuals (Hsu et al. 2012). Chang et al. (1985) found that old growth *Bar. asiatica* trees had diminished, but no recruits were found in this forest. Once the *Bar. asiatica* old growth trees died, the canopy was opened, accelerating invasion by shade-intolerant species. Individuals of *Melanolepis multiglandulosa* and *Macaranga tanarius* had respectively expanded 3.5- and 61-fold in the 2005 census compared to numbers in the 1974 census (Wang et al. 2007). These 2 species had progressively invaded from the roadside into the coastal forest, and colonized tree-fall gaps. *Leucaena leucocephala*, an exotic invasive tree, did not appear in the 1974 census of this coastal forest, but 110 adult trees were found mainly distributed at the roadside along the forest edge in 2005 (Wang et al. 2007). That report also pointed out that half of this coastal forest area had been seriously invaded by native or exotic shade-intolerant species over the previous 30

yr. They suggested eliminating the invasive species, rehabilitating the old growth species, and monitoring the population dynamics of the stand, such that further deterioration of the coastal forest could be prevented (Wang et al. 2007).

The current research investigated the vegetation structure of the Siangjiaowan coastal forest in 2012. Our purposes were to understand the composition, abundance, and diameter structure of tree species in this forest, and thereby be aware of the transitions in the composition and structure over the past 40 yr. We also surveyed young saplings and seedlings with diameter at breast height (DBH) of < 1 cm to understand the status of natural regeneration of the stand. In addition, by periodically taking fisheye photographs, we also observed seasonal variations in the leaf area index and the recovery status of this coastal forest after typhoon disturbances. In addition to ecological studies, we also report on ecological restoration efforts conducted in this forest and the preliminary progress.

MATERIALS AND METHODS

General description of the study site

The Siangjiaowan Ecological Reserve is located between Chuanfanshih and Shadao on the Hengchun Peninsula at the southern tip of Taiwan (Fig. 1). There were 200 species of vascular plants, with a typical composition of tropical coastal vegetation (Chang et al. 1985). According to statistics provided by the Central Weather Bureau, the annual precipitation was 2022 mm, the average temperature was 25.1°C, and the average relative humidity was 75.2% in the Hengchun area in 1981 to 2010. Rainfall is mainly concentrated from May to October, accounting for 91% of the total annual precipitation, while November to April is the dry season, with only 9% of the

total annual precipitation. June to September is the season of higher temperatures with an average of 28°C, while December to February is the season of lower temperatures with an average of 21°C.

Sampling plot

A sampling plot (300 m long, 40~60 m wide) was established in 2012 at a location west of Highway 26 and within the coastal forest of the Siangjiaowan Ecological Reserve (Fig. 1). This plot covered the sampling area of the 4 previous censuses conducted in 1974, 1980, 1985, and 2005 by the TFRI. Thirty transects (40~60 long and 10 m wide) for inventorying the plants were established (Fig. 2). The inventory was carried out in smaller subplots (5×5 m) within each transect. The total area of the sampling plot was 1.55 ha.

Plant census

In January to March 2012, we identified, marked, and measured the height and DBH (at 1.3 m above the ground) of each woody individual with a DBH of ≥ 1 cm. The location of each individual in this sampling plot was marked (see an example of *Bar. asiatica* in Fig. 2). The height of each tree was measured with a 12-m-long altimeter rod. Upon completion of the above inventory, we then determined the abundance of each species and the number of transects on which each species was distributed, and thereby calculated the density per hectare and frequency of each species. The total basal area (calculated by the DBH) of each species was summed from the basal area of each individual to represent the dominance of a species. With the acquired density, frequency, and dominance of all species, we calculated the relative values of these 3 parameters for each species, and summed them as an Importance Value Index (IVI) of a species. Young saplings (with a DBH of < 1 cm and a

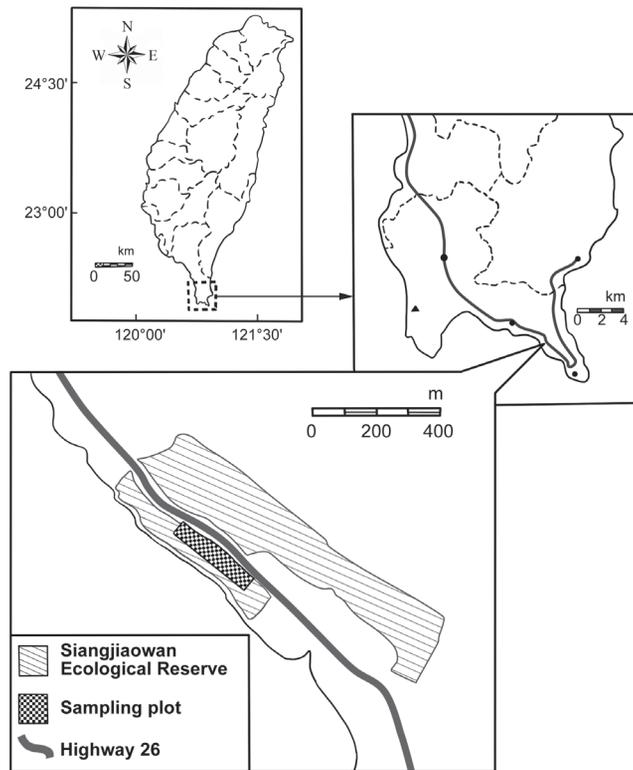


Fig. 1. Location of the Siangjiaowan Ecological Reserve in Kenting National Park and the sampling plot in the coastal forest.

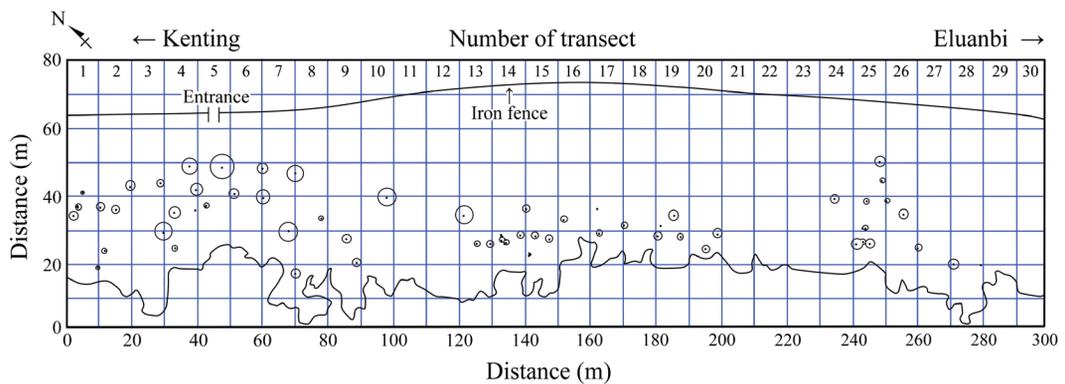


Fig. 2. The range of the sampling plot in the Siangjiaowan coastal forest and the distribution of *Barringtonia asiatica* in the sampling plot. The total sampled area was 1.55 ha with 30 transects. Circles in the graph depict positions of *Bar. asiatica* individuals with a diameter at breast height (DBH) of ≥ 1 cm. A larger circle indicates a larger DBH.

height of ≥ 1 m) and seedlings (with a height of < 1 m) of woody plants were also identified, measured, and marked in this census.

Shade-tolerance classification

Kuo (2014) classified 180 species of native broadleaf trees into 5 shade-tolerance

classes, with class 1 the least and class 5 the most shade tolerant, based on the photosynthetic capacity of each species as well as referencing the opinions of experts. The corresponding photosynthetic capacities of each respective class were ≥ 26.0 , 25.9~21.0, 20.9~15.5, 15.4~12.5, and < 12.5 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. Among species investigated in this study, the shade tolerance class of 48 of them had previously been classified by Kuo (2014) as shown in Table 1. In addition, although *Scaevola sericea*, *Cinnamomum reticulatum*, *Antidesma pentandrum*, and *Champereia manillana* were not listed in Kuo (2014), their photosynthetic capacities had respectively been measured to be 24.1, 14.7, 13.5, and 11.2 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (unpublished data). Thus, these 4 species were respectively classified into shade-tolerance classes 2, 4, 4, and 5 (Table 1). The photosynthetic capacity of *Leu. leucocephala* was 29.5 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (Yang 2011), belonging to class 1 as a very shade-intolerant species.

Canopy openness and leaf area index

A fisheye photographic technique was used to monitor the dynamics of canopy openness and the leaf area index. A fisheye lens was placed at the center position of each transect, across the sampling plot at an interval of 10 m; thus, in total, 30 photographic sites were established. Photographs at these 30 places were taken on a cloudy day, or before sunset of a sunny day, every other month from February 2012. A Nikon D90 camera equipped with a fisheye F2.8 lens (Sigma 4.5 mm) was set up 1 m above the ground. Photographs were analyzed by Gap Light Analyzer 2.0 software (Simon Fraser University, Canada) to assess the canopy openness and leaf area index. Two typhoons (Typhoons Saola and Tembin) affected the Hengchun Peninsula in August 2012. We took immediate aftermath

images of the canopy to monitor the influence of typhoon disturbances.

Management measures to reduce the abundance of invasive shade-intolerant species

There was a disturbed site of 0.22 ha on the roadside of transect #21~30 along the forest edge. It was created by wind disturbance from Typhoon Parma on 6 October 2009, which caused 31 trees to fall down and created a large-sized tree-fall gap. This disturbed site had been severely invaded by shade-intolerant species such as *Mac. tanarius*, *Mel. multiglandulosa*, and *Leu. leucocephala* and had become a secondary forest.

To reduce abundances of invasive shade-intolerant species at the disturbed site, we first removed all stems of *Leu. leucocephala*, but not all individuals of *Mac. tanarius* or *Mel. multiglandulosa*, in order to leave some crown to provide shading. Then, we transplanted seedlings of coastal forest species, including *Mil. pinnata*, *The. populnea*, *Her. littoralis*, *Bischofia javanica*, *Pre. serratifolia*, *Pistacia chinensis*, *Firmiana simplex*, *Ter. catappa*, and *Ficus superba*, into the wind-disturbed site along the stand edge of transect #26~30. Seedlings of these species were cultivated from seeds collected in the Hengchun area, and were planted in pots (9 cm in diameter and 15 cm high) in a nursery for 1~2 yr. In total, 109 seedlings were transplanted in July 2012 for the restoration operation. In the process of the transplanting operation, we faced the problem of the ground substrate of this coastal forest being coral reef not mineral soil. To resolve this problem, we removed part of the base of the pot, and then placed the potted plants on top of the forest floor, with the expectation that their roots could develop through cracks in the coral reef. We constantly removed sprouts of the aforementioned invasive species during the restoration opera-

tion to facilitate the growth of the planted young trees.

Restoration of *Bar. asiatica* and other coastal tree species

In July 2012, we found that some fruits of *Bar. asiatica* had sprouted new roots yet had not extended into the forest floor. We collected 48 of those rooting fruits of *Bar. asiatica* and placed them at the disturbed site of transect #26~30 in order to increase its abundance.

In addition, saplings of *Bar. asiatica*, *Her. nymphiifolia*, *Her. littoralis*, *Pis. umbellifera*, and *Cal. inophyllum* were cultivated from seeds collected in the Kenting area and planted in pots (33 cm in diameter and 28 cm high) in a nursery for 3 yr. The potted saplings were transplanted to transect #1~12 in July 2012. For *Bar. asiatica*, *Her. nymphiifolia*, *Her. littoralis*, *Pis. umbellifera*, and *Cal. inophyllum*, there were 21, 12, 30, 10, and 10 saplings respectively transplanted. The bottoms of these pots were also cut open to allow the roots to extend freely into the forest floor. Lastly, we placed another 50 potted saplings of *Bar. asiatica* (1.0~1.5 m tall) at transect #13~19 in June 2014. Seeds of these saplings were from mother trees near the office of the Kenting National Park Administration and had been cultivated in a nursery at Kenting National Park for 2~3 yr.

RESULTS

Composition of woody plants and species abundances

From January to March 2012, we recorded 68 species of naturally regenerated dicot woody plants and 3 species of monocot woody plants (including *Pandanus odoratisimus*, *Dracaena angustifolia*, and *Arenga tremula*) in the 1.55-ha sampling plot. Fifty-

eight of the 68 dicot species had individuals with a DBH of ≥ 1 cm. Among the 58 species, the top 6 most abundant species included *Aglaia formosana* (302 trees ha⁻¹), *Mac. tanarius* (301 trees ha⁻¹), *Mel. multiglandulosa* (154 trees ha⁻¹), *Hib. tiliaceus* (152 trees ha⁻¹), *Cha. manillana* (121 trees ha⁻¹), and *Her. nymphiifolia* (101 trees ha⁻¹) (Table 1). The total summed number of trees of these 6 species was 1131 trees ha⁻¹, accounting for 64% of all trees (1765 trees ha⁻¹ in total). There were 10 species with abundances of 30~100 trees ha⁻¹, including *Gue. speciosa* (63 trees ha⁻¹), *Diospyros philippensis* (58 trees ha⁻¹), *Planchonella obovata* (52 trees ha⁻¹), *Murraya paniculata* (48 trees ha⁻¹), *Leu. leucocephala* (48 trees ha⁻¹), *Bar. asiatica* (39 trees ha⁻¹), *Mil. pinnata* (39 trees ha⁻¹), *Fic. septica* (34 trees ha⁻¹), *Pre. serratifolia* (34 trees ha⁻¹), and *Ter. catappa* (30 trees ha⁻¹). There were 12 species with abundances of 5~30 trees ha⁻¹, among which *Dendrocnide meyeniana*, *Mor. citrifolia*, and *Sca. sericea* had more trees than the others. There were 12 species with abundances of 1~5 trees ha⁻¹, while as many as 18 species had only 1 individual (0.6 tree ha⁻¹) in the plot (Table 1).

Among woody plants with individuals with a DBH of < 1 cm, 53 species were noted. The most abundant species was *Agla. formosana*, which had as many as 934 stems ha⁻¹ of such small individuals. Other species with more than 125 stems ha⁻¹ of small individuals included *Her. littoralis* (287 stems ha⁻¹), *Dio. philippensis* (272 stems ha⁻¹), *Cha. manillana* (191 stems ha⁻¹), *Leu. leucocephala* (191 stems ha⁻¹), *Mel. multiglandulosa* (173 stems ha⁻¹), and *Mac. tanarius* (148 stems ha⁻¹) (Table 1). Species abundances of small individuals with 60~125 stems ha⁻¹ included *Her. nymphiifolia* (125 stems ha⁻¹), *Pla. obovata* (117 stems ha⁻¹), *Hib. tiliaceus* (78 stems ha⁻¹), *Pis. umbellifera* (69 stems ha⁻¹),

and *Mil. pinnata* (61 stems ha⁻¹), which are 5 common tree species of this coastal forest. There were 11 species with abundances of

small saplings of 5~50 stems ha⁻¹, including *Bar. asiatica* (9 stems ha⁻¹) and *Ter. catappa* (23 stems ha⁻¹). Fifteen tree species had only

Table 1. Numbers of small (diameter at breast height (DBH) < 1 cm, S) and large (DBH ≥ 1 cm, L) individuals per hectare of woody species in the Siangjiaowan coastal forest. STC, shade tolerance class based on Kuo (2014): 1, very shade-intolerant; 2, shade-intolerant; 3, moderately shade-tolerant; 4, shade-tolerant; 5, very shade-tolerant. * A typical coastal species. § An exotic invasive species

Species	STC	S/L (ratio)	Species	STC	L/S (ratio)
<i>Heritiera littoralis</i>	3*	287/7.1 (40.5)	<i>Scolopia oldhamii</i>	*	2.6/1.3 (2.0)
<i>Pisonia umbellifera</i>	4*	69/9 (7.6)	<i>Calophyllum inophyllum</i>	3*	2.6/1.3 (2.0)
<i>Antidesma pentandrum</i>	4	22/3.9 (5.7)	<i>Indigofera zollingeriana</i>		1.9/1.3 (1.5)
<i>Diospyros philippensis</i>	5*	272/58 (4.7)	<i>Colubrina asiatica</i>		1.3/1.3 (1.0)
<i>Leucaena leucocephala</i>	1§	191/48 (4.0)	<i>Celtis formosana</i>	3	0.6/1.3 (0.5)
<i>Aglaia formosana</i>	3*	934/302 (3.1)	<i>Liidendron formosanum</i>	5	7.7/0.6 (12)
<i>Planchonella obovata</i>	3*	117/52 (2.3)	<i>Cinnamomum reticulatum</i>	4	2.6/0.6 (4.0)
<i>Goniothalamus amuyon</i>	4	3.2/1.9 (1.7)	<i>Ehretia resinosa</i>	2	1.3/0.6 (2.0)
<i>Champereia manillana</i>	5	191/121 (1.6)	<i>Leea guineensis</i>	3	1.3/0.6 (2.0)
<i>Ficus virgata</i>	2	18/12 (1.6)	<i>Melicope triphylla</i>	3	1.3/0.6 (2.0)
<i>Millettia pinnata</i>	3*	61/39 (1.5)	<i>Glochidion philippicum</i>		0.6/0.6 (1.0)
<i>Diospyros maritima</i>	5	9.7/6.5 (1.5)	<i>Eriobotrya deflexa</i>	3	0/0.6 (0)
<i>Pittosporum pentandrum</i>	3*	3.9/2.6 (1.5)	<i>Neolitsea parvigemma</i>	4	0/0.6 (0)
<i>Hernandia nymphiifolia</i>	4*	125/101 (1.2)	<i>Ficus irisana</i>		0/0.6 (0)
<i>Melanolepis multiglandulosa</i>	1	173/154 (1.1)	<i>Drypetes littoralis</i>	5	0/0.6 (0)
<i>Morinda citrifolia</i>	2*	24/21 (1.1)	<i>Firmiana simplex</i>	1	0/0.6 (0)
<i>Gelonium aequoreum</i>	3	4.5/4.5 (1.0)	<i>Sophora tomentosa</i>	*	0/0.6 (0)
<i>Ficus microcarpa</i>	2	9.7/11 (0.9)	<i>Broussonetia papyrifera</i>	1	0/0.6 (0)
<i>Terminalia catappa</i>	2*	23/30 (0.7)	<i>Callicarpa formosana</i>		0/10.6 (0)
<i>Murraya paniculata</i>	3	31/48 (0.6)	<i>Bridelia tomentosa</i>	2	0/0.6 (0)
<i>Macaranga tanarius</i>	1	148/301 (0.5)	<i>Ardisia sieboldii</i>	4	0/0.6 (0)
<i>Hibiscus tiliaceus</i>	1*	78/152 (0.5)	<i>Cerbera manghas</i>	3*	0/0.6 (0)
<i>Ficus septica</i>	2	15/34 (0.5)	<i>Vitex negundo</i>	1	0/0.6 (0)
<i>Ficus benjamina</i>	2	2.6/6.5 (0.4)	<i>Croton cascarilloides</i>		110/0
<i>Dendrocnide meyeniana</i>	2	7.7/30 (0.3)	<i>Litsea hypophaea</i>	3	15/0
<i>Guettarda speciosa</i>	2*	13/63 (0.2)	<i>Ficus pedunculosa</i>	*	9.7/0
<i>Barringtonia asiatica</i>	3*	9/39 (0.2)	<i>Ficus tinctoria</i>	*	4.5/0
<i>Bischofia javanica</i>	2*	1.9/9.7 (0.2)	<i>Flueggea virosa</i>		2.6/0
<i>Excoecaria agallocha</i>	2*	1.9/8.4 (0.2)	<i>Ehretia acuminata</i>	3	1.9/0
<i>Premna serratifolia</i>	1*	3.9/34 (0.1)	<i>Ehretia dicksonii</i>		1.3/0
<i>Scaevola sericea</i>	2*	2.6/18 (0.1)	<i>Maytenus diversifolia</i>		1.3/0
<i>Tournefortia argentea</i>	1*	0.6/4.5 (0.1)	<i>Neolitsea hiiranensis</i>		0.6/0
<i>Allophylus timorensis</i>	3*	0/9 (0)	<i>Clerodendrum inerme</i>		0.6/0
<i>Ficus superba</i>	2*	0/3.9 (0)	Total individuals		3023/1765 (1.71)
<i>Thespesia populnea</i>	2*	0/2.6 (0)	Total species		53/58

large individuals with no young recruits, such as *All. timorensis*, *The. populnea*, *Drypetes littoralis*, *Firmiana simplex*, and *Cer. manghas* (Table 1). On the other hand, 10 woody species had only juveniles but no large-sized trees, such as *Litsea hypophaea*, *Ehretia acuminata*, and *Ehr. dicksonii*.

We further analyzed the ratio of small (S) vs. large (L) individuals (S/L ratio, Table 1). The 6 species of *Her. littoralis*, *Pis. umbellifera*, *Ant. pentandrum*, *Dio. philippensis*, *Agl. formosana*, and *Pla. obovata*, are moderately shade-tolerant to very shade-tolerant species and had S/L ratios of 2.3~40.5 (Table 1), indicating that they could recruit well in this stand. There were 15 species with more than 3 large individuals and S/L ratios of 0.1~0.9, such as *Fic. microcarpa*, *Ter. catappa*, *Bis. javanica*, and *Tou. argentea*, indicating that these 4 shade-intolerant species recruited poorly in this stand. However, *Mur. paniculata* and *Bar. asiatica* were not shade-intolerant species but did not have many small individuals (Table 1). Overall, the 1.55-ha sampling plot as a whole had an average S/L ratio of 1.71 (Table 1).

Changes in species abundance over time

Comparing species abundances (for individuals with a DBH of ≥ 4 cm) of the same species in different censuses, *Her. nymphiifolia* had 127 trees ha^{-1} in 1974, which subsequently decreased in each successive census to only 82 trees ha^{-1} in 2012, an overall 31% reduction (Fig. 3a). *Barringtonia asiatica* showed a similar trend, with 50 trees ha^{-1} in 1974 and only 37 trees ha^{-1} in 2012, a 21% reduction (Fig. 3g). In addition, *Mur. paniculata* (Fig. 3h) and *Mor. citrifolia* (Fig. 3n) showed 51 and 55% reductions, respectively. On the other hand, 11 species showed significant increases in species abundances in 2012 compared to 1974. Among these 11 species,

3 shade-intolerant species, *Mac. tanarius* (Fig. 3d), *Gue. speciosa* (Fig. 3l), and *Mel. multiglandulosa* (Fig. 3e), had respectively increased 56-, 26-, and 4-fold. Species abundances of 5 other shade-intolerant species, *Hib. tiliaceus*, *Fic. septica*, *Pre. serratifolia*, *Den. meyeniana*, and *Ter. catappa* had increased 1~3-fold. Yet, species abundances of the shade-tolerant species, *Agl. formosana*, *Cha. manillana*, and *Dio. philippensis*, had also increased 2~3-fold over the years. *Leucaena leucocephala* was not found in this stand before 1984, but had surged to 75 trees ha^{-1} in the 2005 census (Fig. 3f). In 2012, its abundance had drastically dropped to 10 trees ha^{-1} , probably due to the shading effects by surrounding taller trees. Several coastal species of this forest showed no obvious changes in their abundances over the past 40 yr, including *Mil. pinnata*, *Tou. argentea*, *Exc. agallocha*, *All. timorensis*, *Pis. umbellifera*, *The. populnea*, *Scolopia oldhamii*, and *Cal. inophyllum*; while other coastal species, including *Pla. obovata*, *Bis. javanica*, and *Her. littoralis*, exhibited slight increases in their abundances (Fig. 3).

Stand structure

Vegetative parameters of 58 major species, which had individuals with a DBH of ≥ 1 cm, are listed in Table 2. Among them, *Bar. asiatica* exhibited the highest IVI of 41.0, due mainly to the fact that 50 individuals of this species had DBHs of > 64 cm (Fig. 4), and its basal area summed up to 15.9 m^2 (Table 2). There were 9 species in the sampling plot that grew into the upper canopy (12~15 m), including *Bar. asiatica*, *Her. nymphiifolia*, *Ter. catappa*, *Bis. javanica*, *Fic. superba*, *Fic. septica*, *Fic. benjamina*, *Her. littoralis*, and *Mac. tanarius*. *Barringtonia asiatica*, and *Fic. superba* were the 2 tallest trees with mean heights of > 9 m (Table 2). Species with

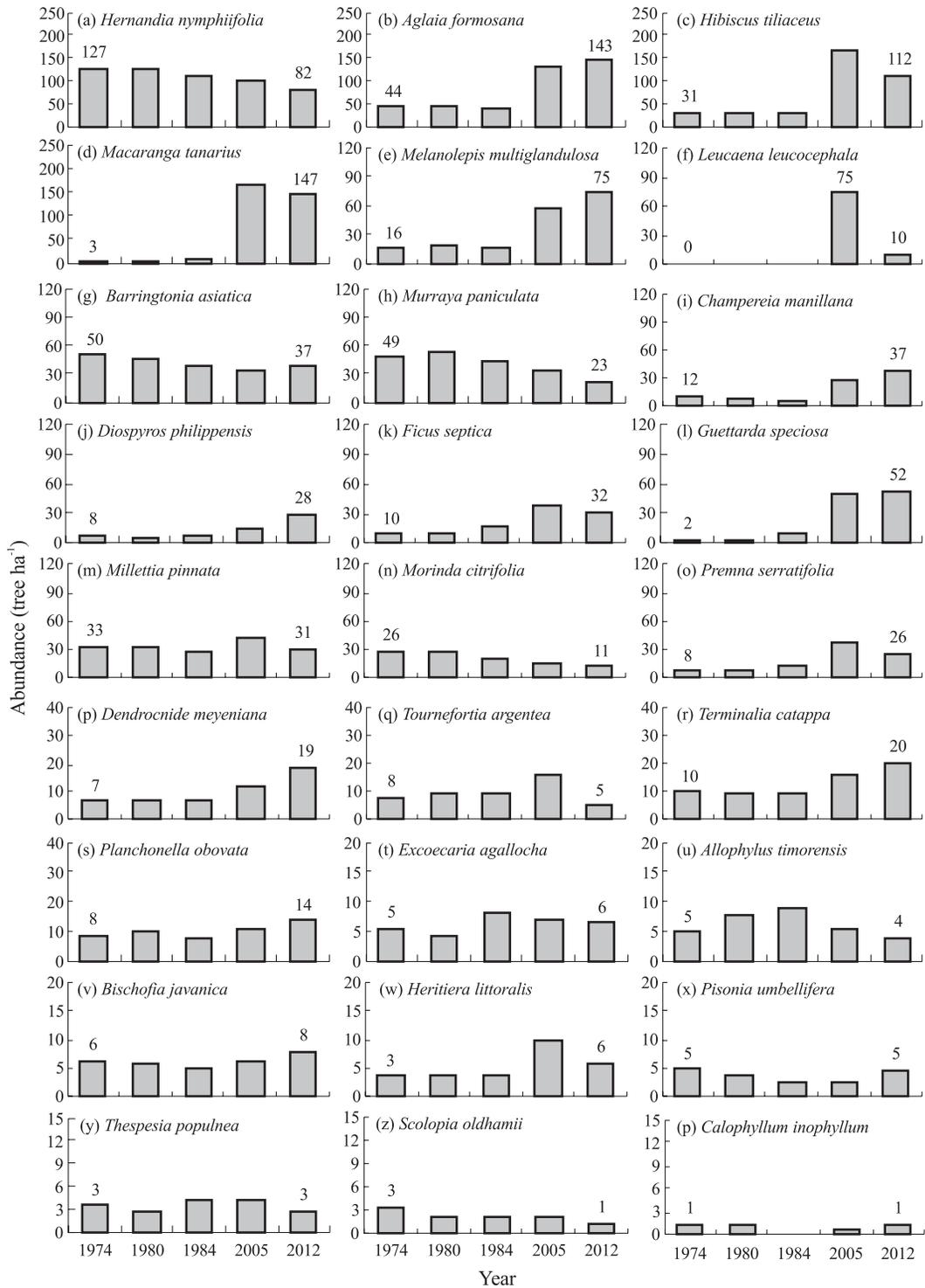


Fig. 3. Numbers of trees per hectare with a diameter at breast height (DBH) of ≥ 4 cm of 27 species in the Siangjiaowan coastal forest from censuses in different years.

Table 2. Importance value index (IVI) and vegetative parameters of the Siangjiaowan coastal forest in 2012. The following characteristics were calculated for saplings with a diameter at breast height (DBH) of ≥ 1 cm: H_m, mean height; D_m, mean diameter; D_{md}, median diameter; Trns, no. of transects on which the species occurred; Freq, frequency; BA, basal area; R_d, R_f, and R_{ba}, relative density, relative frequency, and relative dominance, respectively

Species	IVI	H _m (m)	D _m (cm)	D _{md} (cm)	Density (tree ha ⁻¹)	Trns	Freq (%)	BA (m ² ha ⁻¹)	R _d (%)	R _f (%)	R _{ba} (%)
<i>Bar. asiatica</i>	41.0	9.9	61.5	54.0	39.4	23	76.7	15.86	2.2	4.2	34.6
<i>Mac. tanarius</i>	30.7	6.7	9.2	4.4	300.7	30	100.0	3.73	17.0	5.5	8.1
<i>Her. nymphifolia</i>	27.9	7.7	24.6	21.1	100.7	30	100.0	7.65	5.7	5.5	16.7
<i>Agl. formosana</i>	26.1	4.3	5.6	3.8	301.9	29	96.7	1.66	17.1	5.3	3.6
<i>Hib. tiliaceus</i>	16.5	4.5	8.0	6.2	151.6	29	96.7	1.19	8.6	5.3	2.6
<i>Mel. multiglandulosa</i>	15.3	5.3	6.0	3.8	153.6	26	86.7	0.85	8.7	4.8	1.8
<i>Cha. manillana</i>	12.2	3.2	4.1	3.0	120.7	26	86.7	0.29	6.8	4.8	0.6
<i>Ter. catappa</i>	12.1	7.3	24.0	10.9	30.3	21	70.0	2.99	1.7	3.9	6.5
<i>Gue. speciosa</i>	9.7	5.8	9.6	9.5	62.6	26	86.7	0.63	3.6	4.8	1.4
<i>Pla. obovata</i>	8.6	3.8	6.1	2.5	51.6	23	76.7	0.68	2.9	4.2	1.5
<i>Dio. philippensis</i>	8.2	4.7	8.2	3.8	58.1	15	50.0	0.97	3.3	2.8	2.1
<i>Mil. pinnata</i>	7.9	5.3	11.3	7.8	39.4	23	76.7	0.65	2.2	4.2	1.4
<i>Fic. septica</i>	6.9	7.3	13.9	11.7	34.2	19	63.3	0.67	1.9	3.5	1.5
<i>Mur. paniculata</i>	6.7	3.5	5.0	3.8	48.4	20	66.7	0.14	2.7	3.7	0.3
<i>Bis. javanica</i>	6.7	8.4	39.6	57.0	9.7	9	30.0	2.07	0.6	1.7	4.5
<i>Pre. serratifolia</i>	6.2	4.5	9.7	7.5	33.6	19	63.3	0.37	1.9	3.5	0.8
<i>Den. meyeniana</i>	5.6	4.5	10.1	6.3	29.7	15	50.0	0.52	1.7	2.8	1.1
<i>Leu. leucocephala</i>	5.5	4.0	3.3	2.4	48.4	14	46.7	0.06	2.7	2.6	0.1
<i>Fic. superba</i>	4.9	9.2	60.7	56.5	3.9	4	13.3	1.80	0.2	0.7	3.9
<i>Fic. virgata</i>	3.8	5.4	13.3	3.9	11.6	12	40.0	0.43	0.7	2.2	0.9
<i>Mor. citrifolia</i>	3.7	3.1	4.5	4.1	21.3	13	43.3	0.05	1.2	2.4	0.1
<i>Fic. microcarpa</i>	3.7	4.1	11.6	3.9	11.0	12	40.0	0.39	0.6	2.2	0.9
<i>Fic. benamina</i>	3.5	6.4	29.8	24.9	6.5	7	23.3	0.85	0.4	1.3	1.9
<i>Sca. sericea</i>	3.3	3.2	5.1	4.4	18.1	12	40.0	0.05	1.0	2.2	0.1
<i>Exc. agallocha</i>	2.6	4.0	12.3	13.8	8.4	10	33.3	0.13	0.5	1.8	0.3
<i>Pis. umbellifera</i>	2.6	4.6	14.9	4.0	9.0	6	20.0	0.44	0.5	1.1	1.0
<i>Her. littoralis</i>	1.9	7.5	16.9	10.6	7.1	4	13.3	0.34	0.4	0.7	0.8
<i>Dio. maritima</i>	1.9	3.6	3.7	3.5	6.5	8	26.7	0.01	0.4	1.5	0.0
<i>Tou. argentea</i>	1.8	5.1	17.9	15.2	4.5	7	23.3	0.12	0.3	1.3	0.3
<i>Gel. aequoreum</i>	1.4	5.7	8.0	7.6	4.5	6	20.0	0.03	0.3	1.1	0.1
<i>Ant. pentandrum</i>	1.3	4.5	4.2	2.9	3.9	6	20.0	0.01	0.2	1.1	0.0
<i>The. populnea</i>	1.1	6.7	21.0	20.5	2.6	4	13.3	0.10	0.2	0.7	0.2
<i>All. timorensis</i>	1.1	3.1	3.9	3.4	9.0	3	10.0	0.01	0.5	0.6	0.0
<i>Pit. pentandrum</i>	0.7	3.6	5.9	5.7	2.6	3	10.0	0.01	0.2	0.6	0.0
<i>Gon. amuyon</i>	0.7	3.0	4.9	4.5	1.9	3	10.0	0.00	0.1	0.6	0.0
Other 23 species	5.2				15.6			0.12	0.9	4.2	0.1
Sum of 58 species	300							45.87	100	100	100

Abbreviations of species names are spelled out in Table 1.

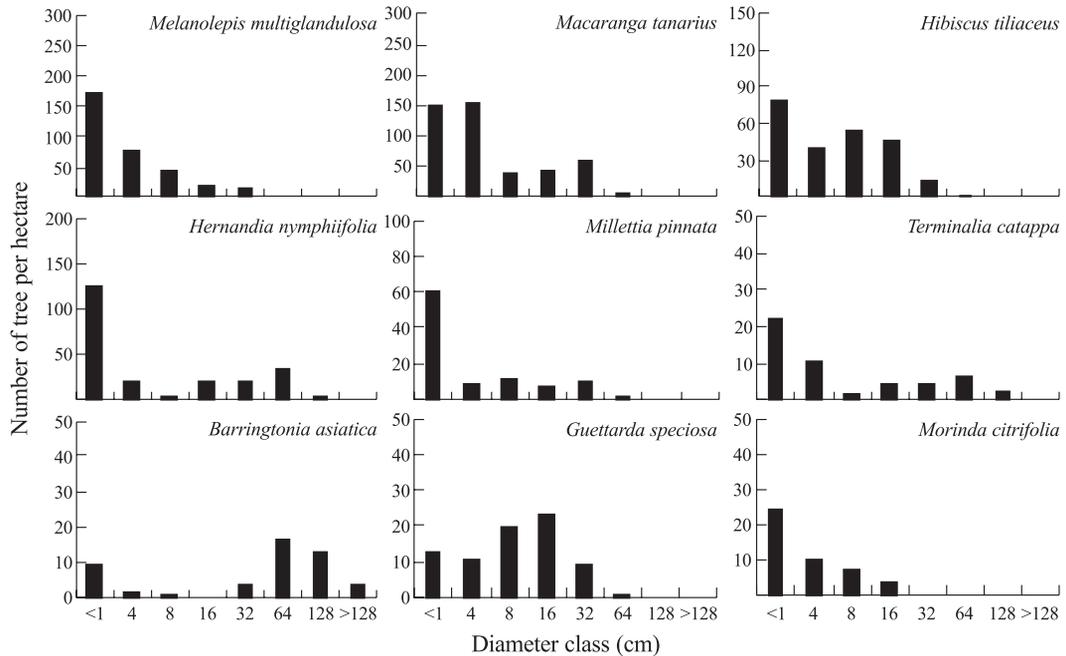


Fig. 4. The diameter structure of some major tree species in the Siangjiaowan coastal forest.

larger mean DBHs in descending order were *Bar. asiatica*, *Fic. superba*, *Bis. javanica*, *Fic. benjamina*, and *Her. nymphiifolia*; yet if the median of DBH was considered, *Bis. javanica* was the largest one (Table 2). The largest individuals of *Bar. asiatica* and *Fic. superba* had DBHs of 189 and 150 cm, respectively; and for *Bis. javanica*, *Dio. philippensis*, *Her. nymphiifolia*, *Her. littoralis*, and *Pis. umbellifera*, their largest individuals had respective DBHs of 94, 85, 73, 69, and 69 cm.

Of 28 tree species that had more than 10 large individuals, we found that 19 of them exhibited a fluctuating type of diameter structure, including typical coastal species of *Her. nymphiifolia*, *Bar. asiatica*, *Hib. tiliaceus*, *Mil. pinnata*, *Gue. speciosa*, and *Pre. serratifolia*, as well as *Ter. catappa*, *Pis. umbellifera*, *All. timorensis*, and *Exc. agallocha* (Fig. 4). Of all coastal tree species, only 1 species, *Mor. citrifolia*, showed an anti-J type of diameter structure (Fig. 4). The 2 dominant shade-intolerant species of this stand, *Mel.*

multiglandulosa and *Mac. tanarius*, respectively showed an anti-J type and a fluctuating type of diameter structure (Fig. 4).

Dynamics of canopy openness and the leaf area index

Canopy openness of this coastal forest was in the range of 5.1~19.8% (with an average of 11.2%) and the mean leaf area index was 2.44 in February 2012. The average canopy openness decreased to 6.8 and 3.3% while the leaf area index increased to 3.12 and 3.96 in April and June, respectively (Fig. 5). Typhoon Saola hit the Hengchun Peninsula on 2 August 2012, severely damaging the forest canopy. The canopy openness had surged to 18.8% and the leaf area index had dropped to 1.83 the next day. Unfortunately, this coastal forest was hit by a second typhoon, Typhoon Tembin, in the same month twice on 25 and 28 August. When we investigated on 30 August, the canopy openness had further increased to 20.1%, and leaf area

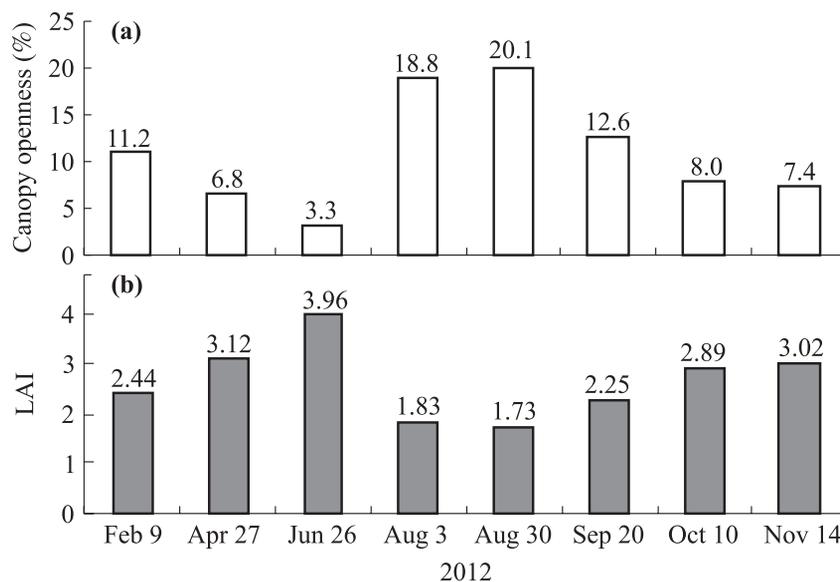


Fig. 5. Canopy openness and the leaf area index of the Siangjiaowan coastal forest in various months of 2012. Note that Typhoon Saola hit southern Taiwan on 2 August, and Typhoon Tembin hit twice on 25 and 28 August 2012.

index had decreased to 1.73. However, the openness had been reduced to 7.4%, and the leaf area index had increased to 3.02 by 14 November, 75 d after Typhoon Tembin had struck (Fig. 5). Compared to data obtained on 26 June before the typhoon disturbance, the leaf area index of this stand had recovered to 76% of the original value, indicating a high resilience capacity.

Preliminary progress of restoration efforts

Initially, there were 109 seedlings of 9 coastal tree species transplanted to the wind-disturbed site (transect #26~30) in July 2012. By September 2014, there were 5 species with survival rates of >70% (Table 3). Among them, *The. populnea*, *Bis. javanica*, and *Pis. chinensis* all showed good growth performances in that some individuals had reached 250 cm in height. As for the rooting fruits of *Bar. asiatica*, 40 of the 48 rooting fruits had survived and successfully become established by November 2014. Most of these juveniles

had grown to 60~130 cm in height, with the tallest one reaching 224 cm.

After 2 yr of placement, saplings of *Bar. asiatica*, *Her. Nymphiifolia*, *Her. littoralis*, and *Pis. umbellifera* had respective survival rates of 86, 67, 33, and 40%, in transect #1~12. These saplings did not grow well in height since most plants had only about a 10-cm height increment under the low-light canopy (Table 3). The other 50 *Bar. asiatica* saplings transplanted to transect #13~19 in June 2014 were not harmed by Typhoon Fung-Wong which hit southern Taiwan on 20 September 2014, and were still vigorously growing.

DISCUSSION

Changes in the species composition and forest structure

The species composition of the coastal forest in Siangjiaowan has changed since the 1960s. Hu (1961) reported that the main

Table 3. Surviving individuals (*n*) and the mean height (HT) of transplanted seedlings and saplings in 2 sections of the sampling plot of the Siangjiaowan coastal forest

Species	July 2012		Dec. 2013		Sept. 2014		Survival rate
	<i>n</i>	HT (cm)	<i>n</i>	HT (cm)	<i>n</i>	HT (cm)	
Disturbed site (transect #26~30)							
<i>Millettia pinnata</i>	30	67±2	24	128±8	22	132±9	73%
<i>Thespesia populnea</i>	30	59±2	26	153±13	21	197±18	70%
<i>Heritiera littoralis</i>	10	54±3	6	65±9	5	88±15	50%
<i>Bischofia javanica</i>	10	64±4	8	128±26	6	179±33	60%
<i>Premna serratifolia</i>	10	73±5	6	98±23	1	224	10%
<i>Pistacia chinensis</i>	6	68±15	4	204±15	3	230±32	50%
<i>Firmiana simplex</i>	5	53±9	4	87±18	4	135±10	80%
<i>Terminalia catappa</i>	4	48±5	4	87±16	3	127±65	75%
<i>Ficus superba</i>	4	60±13	3	165±18	3	191±33	75%
Transect #1~12							
<i>Barringtonia asiatica</i>	21	122±6	21	130±6	18	133±7	86%
<i>Hernandia nymphiifolia</i>	12	150±8	10	158±8	8	156±10	67%
<i>Heritiera littoralis</i>	30	52±3	14	58±4	10	65±7	33%
<i>Pisonia umbellifera</i>	10	87±4	5	95±11	4	100±8	40%
<i>Calophyllum inophyllum</i>	10	92±6	2	141±26	1	173	1%

species of the coastal forest west to Eluanbi were *Bar. asiatica*, *Her. nymphiifolia*, *Cal. inophyllum*, *Ter. catappa*, *Bis. javanica*, and *Agl. formosana*. However, the species abundance of *Cal. inophyllum* was very low; in fact, only 2 trees with DBHs of 7.7 and 9.2 cm were found in the 2012 census. It was also noted that *Cal. inophyllum*, *Palaquium formosanum*, and *Gonocaryum calleryanum* were gradually disappearing since the 1920s (Chang et al. 1985). *Erythrina variegata* var. *orientalis* once occurred in this coastal forest in the 1960s to 1980s (Chang 1960, Chang et al. 1985), but was not found in the either 2005 or 2012 censuses. The erythrina gall wasp *Quadrastichus erythrinae* severely threatened the survival of any remaining *Ery. variegata* var. *orientalis* in Kenting National Park in 2004 (Chang 2009). This species of the Siangjiaowan coastal forest might have been infected as well and died during that time.

We found that the number of larger trees (i.e., individuals with a DBH of ≥ 4 cm) of

some species had significantly increased from 1974 to 2012. These species included the shade-tolerant species of *Agl. formosana*, *Cha. manillana*, and *Dio. philippensis*, as well as the shade-intolerant species of *Hib. tiliaceus*, *Mac. tanarius*, *Mel. multiglandulosa*, and *Leu. leucocephala* (Fig. 3). One reason for the increases in their species abundance might be that they all had numerous small saplings (Table 1). With more small saplings, the chances of having large trees would be raised, and thus the species abundance would increase. Species like the moderately shade-tolerant *Bar. asiatica* and *Mur. paniculata*, and shade-intolerant *Mor. citrifolia*, had fewer and fewer larger trees over the years, possibly due to fewer small saplings. Species abundances of the other 5 shade-intolerant species, *Fic. septica*, *Gue. speciosa*, *Pre. serratifolia*, *Den. meyeniana*, and *Ter. catappa*, had increased, but with smaller rates of increase compared to *Hib. tiliaceus* or *Mac. tanarius*, probably due to the fact that the densities of

small saplings of these 5 species were only 4–23 stems ha⁻¹. Yet, the consistent increase in the number of larger trees of shade-intolerant species indicated that the canopy of this stand was frequently disturbed, and incident light was greatly raised so that young saplings had a chance to grow.

Some species did not show obvious changes in their species abundance from 1974 to 2012: for example, the moderately shade-tolerant species of *All. timorensis* and *Cal. inophyllum*, as well as the shade-intolerant species of *Tou. argentea*, *Exc. agallocha*, *Bis. javanica*, and *The. populnea* (Fig. 3). One reason for not having obvious changes might be that numbers of larger trees of these species were originally small, as were numbers of small saplings; consequently, the species abundance of these species did not significantly increase. However, there were many larger trees and small saplings of some shade-tolerant species, including *Mil. pinnata*, *Pis. umbellifera*, *Pla. obovata*, and *Her. littoralis*, but their species abundances still did not significantly change over the years. Reasons for this phenomenon need to be further investigated.

The composition and structure of the Siangjiaowan coastal forest face 2 major hurdles. First, there is an imbalanced age structure of dominant species which consist of only larger old-growth trees but lack juveniles (Chang et al. 1985, Hsu et al. 2012). Although *Bar. asiatica*, the dominant and representative species of this coastal forest, ranked no. 1 in the IVI of this stand, its diameter structure appeared to be of the fluctuating type (Fig. 4g). The number of individuals with a DBH of < 8 cm was less than that of larger trees, indicating that this species does not possess a successful regenerating process. In particular, there were only 3 juveniles ha⁻¹ (with a DBH of 1–8 cm) plus 9 seedlings ha⁻¹ with a DBH

of < 1 cm. This species extremely lacked young trees, a phenomenon repeatedly noted by researchers in the past (Wang 1975, Chang 1984, Chang et al. 1985, Hsu et al. 2012). *Barringtonia asiatica* bears large-sized fruits of a unique shape. It has become an expensive ornamental plant, especially sprouted seedlings attached to a fruit. In the coastal forest, its fruits are thus frequently collected by people. This is 1 reason for the lack of *Bar. asiatica* juveniles in this forest (Chang et al. 1985). With regard to this situation, the Kenting National Park Administration closed the entrance to the Siangjiaowan Ecological Reserve in 2013. By the spring of 2014, we had discovered new recruits of *Bar. asiatica* near the entrance. Restricting entry to the forest had effectively minimized human disturbance and benefited the regeneration of this species. The photosynthetic capacity of *Bar. asiatica* is 16.1 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (Kuo 2014), indicating that it is a moderately shade-tolerant (shade tolerance class 3, Table 1) but not a very shade-tolerant species. Whether or not its natural recruits can survive and become established under the low-light environments of this stand requires further monitoring. On the other hand, *Her. nymphiifolia* ranked no. 3 in the IVI of this forest. It had many large trees (with a DBH of > 32 cm) as well as juveniles (with a DBH of < 1 cm) but lacked mid-sized individuals (with a DBH of 1–16 cm) (Fig. 4d), indicating a non-smooth process of growing from seedlings to saplings. Furthermore, the abundance of individuals with a DBH of ≥ 4 cm had decreased over the past 40 yr for *Her. nymphiifolia* (Fig. 3a). Therefore, both *Bar. asiatica* and *Her. nymphiifolia* require further restoration measures.

The second threat to the Siangjiaowan coastal forest is the invasion of shade-intolerant species into disturbed tree-fall gaps (Wang et al. 2007). These gaps, mostly along the

roadside at the forest edge, were created by fallen trees due to wind disturbances caused by frequent typhoons that hit this coastal area. This coastal forest encounters typhoon disturbances almost every year. If the disturbances only caused leaf falls and branch snaps, then this forest would have a good resilience characteristic. The original leaf area index was restored within 3 mo after a typhoon disturbance (Fig. 5). It would be difficult to restore, however, if serious typhoon disturbances caused large-sized tree-fall gaps. Environmental conditions of these gaps are highly favorable for species that prefer intense light and high temperatures. Brothers and Spingarn (1992) pointed out that many exotic species had invaded into a fragmented old growth forest. Laurance et al. (2001) found that the number of *Cecropia sciadophylla*, a pioneer species in the Amazon rainforest, had increased 33-fold in a residual fragmented forest over a period of 22 yr. In our study, we also obtained a similar result that the pioneer species of *Leu. leucocephala*, *Mac. tanarius*, and *Mel. multiglandulosa* as well as 2 vine species of *Mikania micrantha* and *Flagellaria indica* had invaded the Siangjiaowan tropical coastal forest. Many researchers have highlighted the need for management measures and ecological restoration plans for this deteriorating tropical forest ecosystem (Wang 1975, Chang et al. 1985, Wang et al. 2007, Hsu et al. 2012). We constantly removed sprouts of the aforementioned invasive pioneer species during the restoration operation to facilitate the growth of planted young trees. So far, this disturbed and invaded area has been transformed into a stand dominated by its original tree species instead of invasive species. The ecological restoration has thus achieved preliminary effectiveness. We eliminated all large-sized individuals of *Leu. leucocephala* that previously occurred in the sam-

pling plot. Yet, there are still numerous large-sized individuals of *Mac. tanarius* and *Mel. multiglandulosa*, which had even reached the uppermost canopy. Appropriate measures still need to be deliberated to decrease the dominance of these shade-intolerant trees in this coastal forest.

CONCLUSIONS

The Siangjiaowan Ecological Reserve is the only tropical coastal forest that exists in Taiwan, preserving many valuable plant species. In 2012, this research recorded 58 tree species with a DBH of ≥ 1 cm; among them, *Agl. formosana* and *Mac. tanarius* had the highest abundances. As representative species of this coastal forest, *Bar. asiatica* and *Her. nymphiifolia* ranked nos. 1 and 3, respectively, in the IVI of this stand. However, the species abundances of these 2 species had decreased 21 and 31%, respectively, compared to values in 1974. Their diameter structure was of the fluctuating type with fewer medium- and small-sized individuals. On the contrary, species abundances of *Mac. tanarius* and *Mel. multiglandulosa* had respectively increased 56- and 4-fold compared to values in 1974. These 2 species ranked nos. 2 and 6 in the IVI of this stand, which had caused the gradual deterioration of the structure of this forest. The leaf area index of this forest dropped from 3.96 to 1.73 after 2 typhoons hit in August 2012, but soon recovered to 3.02 in just 75 d, indicating the high resilience of this forest. To improve the stand structure of this coastal forest, we artificially transplanted saplings of *Bar. asiatica*, *Her. nymphiifolia*, and other coastal tree species into the forest. In addition, we reduced the abundances of invasive shade-intolerant species in tree-fall gaps, and planted several coastal tree species instead. These ecological restoration mea-

tures have already shown preliminary effects, yet require many more ongoing, long-term efforts.

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