

Research paper

## Vegetation Dynamics of a Lowland Rainforest at the Northern Border of the Paleotropics at Nanjenshan, Southern Taiwan

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### [ Summary ]

Long-term forest dynamic studies are vital for revealing how forests function. We conducted tree-by-tree censuses on 2 plots located in a valley of a lowland rainforest at Nanjenshan, southern Taiwan, which is located at the northern border of the Paleotropics. All free-standing trees  $\geq 1$  cm diameter at breast height (DBH) were identified, measured, and mapped for Nanjenshan plot I in 1993, 2000, and 2008, and for Nanjenshan plot II in 1999 and 2008. In 2008, 10,581 individuals in total were recorded in the 2 plots, belonging to 106 species, 75 genera, and 41 families. The community similarity index (Motyka's index of similarity) showed that the 2 plots had 93~95% similarities to prior census. During 2000~2008, individuals in plot I increased by 10.0%, but the basal area decreased by 1.6%, and the plot was dominated by the broken mode of death (46.3%). During a similar period (1999~2008), individuals in plot II only decreased by 0.4%, the basal area increased by 2.6%, and the plot was dominated by the standing mode of death (66.7%). In addition, a higher proportion of large trees had died and more pioneer species were recruited in the same period in plot I. These results indicate that during the 2000~2008 census period, plot I might have experienced an increased frequency of disturbances, which could be caused by typhoons. In the meantime, the relatively low-elevation, small-sized plot II might have been better sheltered and less influenced by the gap-edge effect. Advanced studies of canopy gaps before and after typhoon seasons can help elucidate the disturbance mechanisms of lowland rainforests in Taiwan.

**Key words:** Forest Dynamics Plot, Paleotropical lowland rainforests, re-census, species composition, tree mortality and recruitment.

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## 研究報告

## 南台灣南仁山舊熱帶北緣之低地雨林植被動態

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## 摘要

長期森林動態研究有助於瞭解森林運作的模式。本研究針對舊熱帶域邊緣，一座位於台灣南部溪谷邊的低地雨林(南仁山)，設置兩調查樣區，定期進行每木調查。所有胸高直徑大於1公分的木本植物都加以測量直徑、鑑定物種以及繪製分布圖。至今，南仁山樣區I已有3次調查紀錄，分別於1993、2000及2008年，而南仁山樣區II則已有2次調查，分別於1999及2008年。於2008年時，此兩樣區植株數共計有10,581株，物種計有106種，分屬41科75屬。在物種組成方面，兩樣區變動不大，和其前一次調查的林分相似性(Motyka's index of similarity)皆達93~95%。但是，在2000~2008年間，樣區I增加了10.0%的個體，減少了1.6%的底面積，並且樹木死亡的方式主要方式為斷折(46.3%)。於近似的調查年間(1999~2008)，樣區II則個體只減少了0.4%，底面積增加了2.6%，而樹木的主要死亡方式為立枯(66.7%)。除此之外，樣區I於2000~2008年間，有較高比例的大樹死亡，以及較多先驅物種進入。這些結果顯示，樣區I於最近一期的調查年間(2000~2008)，曾遭遇到頻度較高的擾動，其有可能是颱風造成。在同一時期，樣區II可能因為海拔較低和面積較小，而受到較良好的遮蔽效應和較低的林隙邊緣效應。因此，更進一步調查颱風前後樣區內的樹冠林隙變化，將有助於釐清此台灣低地雨林的干擾機制。

關鍵詞：森林動態樣區、舊熱帶低地雨林、複查、物種組成、樹木死亡出生率。

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## INTRODUCTION

Long-term and repeated inventories of permanent plots can provide better information on how forests function (Swaine et al. 1987, Phillips and Gentry 1994, Condit 1995). Moreover, such studies can provide background knowledge for when unusual scenarios occur (e.g., Condit et al. 1995, Phillips et al. 2009). In several tropical and temperate regions, this kind of research has been conducted for several years (e.g., Phillips et al. 2004, Coomes and Allen 2007). However, in the transition zone between tropical and temperate regions, which may be more susceptible to climate change, there are relatively few long-term studies (but see Yeh 2006).

In the northern border of the Paleotropics

(*sensu* Takhtajan 1986), there are some long-term Forest Dynamics Plots in southern Taiwan (Chao et al. in press). Some of the plots were found to be similar to tropical rainforests, Nanjenshan plot I and plot II. Compared with typical tropical rainforests, these forests are relatively low in canopy height (15~20 m), less stratified, and lacking the Paleotropical dominant family (Dipterocarpaceae), which was likely caused by stress from the northeast monsoon and biogeographical barriers (Chao et al. in press). Stress from the monsoon in the southern part of Taiwan is distinct, but is relatively weak at Nanjenshan plot I and plot II (Chao et al. in press), as the plots are located at the northwestern mountain foot of

Mt. Nanjen.

In terms of biogeography, although the 2 plots are located to the south of the Tropic of Cancer, their biogeographical components of woody plants include not only tropical-related species (29%), but also Eastern Asiatic-related species (46%) (Chao et al. in press), which may have resulted from continental bridges between Taiwan and China during the Pleistocene (0.02~0.015 mya, Ota 1998). These studies show that Nanjenshan forests are in a transition zone between tropical and temperate regions.

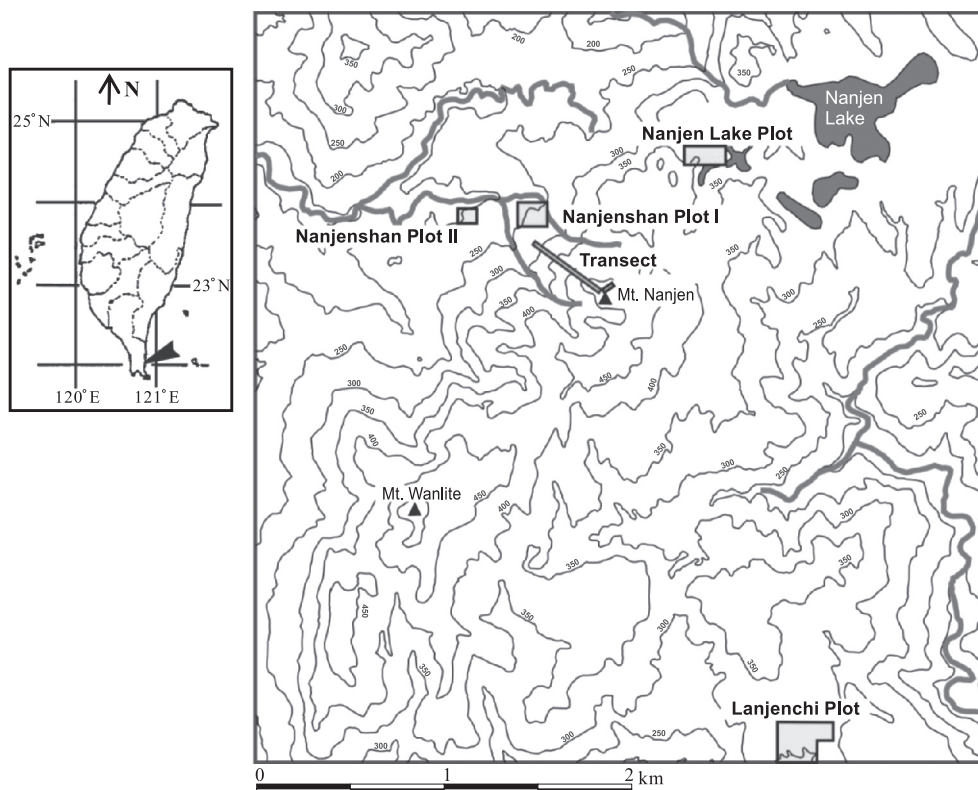
The aim of our study was to disentangle the dynamics of forests in a valley which is relatively sheltered from the influences of the monsoon, located at the northern border of the Paleotropics. We conducted 3 censuses for

Nanjenshan plot I (1993, 2000, and 2008) and 2 censuses for Nanjenshan plot II (1999 and 2008). The questions we asked were: (1) does the composition of the Nanjenshan forests vary through time; and (2) did the dynamic patterns (mortality and recruitment) of the forests change between different census periods?

## METHODS

### Study plots

The study plots are located in a valley on the northwestern foot of Mt. Nanjen in the Nanjenshan Reserve, southern Taiwan (Hsieh et al. 2000, Chao 2001, Chao et al. in press) (Fig. 1). The 2 plots are sheltered from the influence of the monsoon winds (Chao et al. in press). Nanjenshan plot I (2.1 ha,



**Fig. 1.** Map of Taiwan and Nanjenshan plots I and II (other plots in the same reserve are also shown).

120°50'51"E, 22°04'54"N) was established in 1993, and was censused in 2000 and 2008. The elevation ranges 224–275 m. Nanjenshan plot II (0.64 ha, 120°50'36"E, 22°04'52"N) was established in 1999 and was re-censused in 2008. Its elevation is lower than plot I, ranging 196–229 m. (Fig. 1). In this region, the average annual temperature is 23°C and annual precipitation is about 3300 mm. All free-standing trees within the study plots with a diameter at breast height (DBH, measured at 1.3 m)  $\geq 1$  cm were recorded, including their diameter, height, species name, and location. In 2008, the mode of tree death was also recorded in 4 major categories, including broken, standing, uprooted, and unknown, following Chao et al. (2009). Some trees that were strangled to death by lianas or *Ficus* spp. were also recorded.

#### Data analysis—dominance and abundance

Dominance was indicated by the basal area (BA), which was calculated as:  $BA = ((DBH/2)^2 \times \pi)$ . For any individual having more than 2 branches, its basal area was the sum of all branches. The abundance was indicated by the density, which was defined as the number of individuals per hectare. The overall importance was indicated by the importance value (IV), which was calculated as:  $IV\% = [(relative\ BA\% + relative\ density\%)/2]$ .

#### Data analysis—similarity

To compare the similarity through time for both plots, we used 2 kinds of similarity indexes: one is a species composition similarity index, the Sørensen similarity index (Sørensen 1948, cited in Looman and Campbell 1960), and the other is a community similarity index, Motyka's index of similarity (Motyka et al. 1950, cited in Mueller-Dombois and Ellenberg 1974). The Sørensen similarity index is calculated as  $IS (\%) = 2C/(A + B) \times 100\%$ ,

where  $A$  and  $B$  are the number of species in plots A and B, respectively, and  $C$  is the number of shared species in both plots. Motyka's index of similarity ( $IS_{MO}$ ) is calculated as:  $IS_{MO} (\%) = 2c/(a + b) \times 100\%$ , where  $a$  and  $b$  are the focal parameters of species in plots A and B, respectively, and  $c$  is the sum of the smaller value of the parameter for shared species in the 2 plots. In this study, we used the basal area and density as our focal parameters.

#### Data analysis—dynamics

Mortality was the annual mortality rate ( $m$ ) (Sheil et al. 1995):

$$m = (1 - (N_s/N_0)^{(1/t)}) \times 100\%,$$

where  $N_0$  is the number of individuals at the beginning, and  $N_s$  is the number of surviving individuals at the end of measurement interval,  $t$ . Those individuals with no measurable points at 1.3 m height were treated as dead in the calculation.

The recruitment rate ( $\mu$ ) was calculated as (Phillips and Gentry 1994):

$$\mu = \ln(N_f/N_s)/t \times 100\%,$$

where  $N_f$  is the total number of individuals at the end of measurement interval,  $t$ .

## RESULTS

#### Species composition, dominance, abundance, and similarity

Taking all censuses into account, 113 species, belonging to 78 genera and 41 families were recorded within the 2 plots. In 2008, 10,581 individuals, belonging to 106 species, in 75 genera and 41 families were recorded in the 2 plots, with 103 species found in plot I and 61 species in plot II (Table 1). In the 2008 census, the total density of the studied plots was 3862 stems  $ha^{-1}$ , and the basal area was 45.02  $m^2 ha^{-1}$ .

The density of trees in Nanjenshan plot I in the 2 census periods gradually increased

**Table 1. Summary of Nanjenshan plots I (2.1 ha) and II (0.64 ha) in different census years, for trees  $\geq 1$  cm diameter at breast height**

Census	Plot I			Plot II			Total		
	Density (stems ha <sup>-1</sup> )	Basal area (m <sup>2</sup> ha <sup>-1</sup> )	No. of species	Density (stems ha <sup>-1</sup> )	Basal area (m <sup>2</sup> ha <sup>-1</sup> )	No. of species	Density (stems ha <sup>-1</sup> )	Basal area (m <sup>2</sup> ha <sup>-1</sup> )	No. of species
1993	3276	38.59	103	-	-	-	-	-	103
1999/2000	3413	42.75	101	4225	53.34	66	3603	45.22	105
2008	3756	42.06	103	4208	54.75	61	3862	45.02	106

from 4.2~9.1% (Table 1). However the basal area increased 10.8% during the 1993~2000 census period, and then decreased 1.6% during the 2000~2008 census period. For plot II, densities were similar between the censuses (decreased by 0.4%), but the basal area increased by 2.6%. These results indicate that during the 2000~2008 census period, plot I experienced the death of some large trees and recruited a lot of individuals. In contrast, changes in plot II were not as distinct.

Species composition slightly varied between censuses (Table 2), with similarity ranging 94.1~97.1% (Sørensen similarity index). Changes in species composition mostly occurred for rare species. For example, some species were extirpated in 2008, including 5 species in plot I (*Ilex maximowicziana*, *Mallotus japonicus*, *Litsea acutivena*, *Neolitsea hiiranensis*, and *Decaspermum gracilentum* (all  $n = 1$ )), and 5 species in plot II (*Glochidion rubrum*, *Machilus thunbergii*, *Lasianthus cyanocarpus*, *Zanthoxylum ailanthoides*, and

*Adinandra formosana* (all  $n = 1$ )). As for recruited species, in 2008, there were 5 species recorded for the 1st time in plot I, including *Cordia aspera* subsp. *kanehirai*, *Cryptocarya chinensis*, *Melastoma candidum*, *Maesa japonica*, and *Murraya paniculata* (all  $n = 1$ ). However, two species, *Clerodendrum trichotomum* ( $n = 26$ ) and *Microtropis japonica* ( $n = 1$ ) were extirpated within plot I in 2000, but were recorded again in 2008 (both  $n = 1$  in 2008). These species were mostly rare species within the plots, except for 1 pioneer species, *Clerodendrum trichotomum*.

Both *Bischofia javanica* and *Ficus benjamina* were the top 2 dominant species in the 2 plots, although with different ranking orders (Table 3). The top 15 dominant species accounted for 75~78% of the total basal area. The most abundant (by number of individuals) species were *Psychotria rubra* (595 stems ha<sup>-1</sup> in the 2008 census) in plot I and *Lasianthus obliquinervis* (764 stems ha<sup>-1</sup> in the 2008 census) in plot II, both of which are shrub species.

**Table 2. Number of species in Nanjenshan plots I (2.1 ha) and II (0.64 ha) found in different censuses and compared with the previous census, for trees  $\geq 1$  cm diameter at breast height in the Nanjenshan Reserve, southern Taiwan**

Plot	Census	Total no. of species	Compared to the previous census			
			Recruited	Extirpated	Shared	Sørensen similarity index (%)
Plot I	1993	103				
	2000	101	2	4	99	97.1
	2008	103	7	5	96	94.1
Plot II	1999	66				
	2008	61	0	5	61	96.1

**Table 3. Abundance [density (stems ha<sup>-1</sup>)] and dominance [basal area (m<sup>2</sup> ha<sup>-1</sup>)] of species in Nanjenshan plots I and II in different census years, arranged in descending order of their basal area in plot I in 2008**

Family	Species	Plot I							Plot II				
		Density			Basal area			Rank	Density		Basal area		Rank
		1993	2000	2008	1993	2000	2008		2000	2008	2000	2008	
Euphorbiaceae	<i>Bischofia javanica</i>	42	42	47	6.64	7.36	7.67	1	28	25	4.34	4.05	2
Moraceae	<i>Ficus benjamina</i>	9	9	9	3.74	5.32	5.47	2	27	28	10.75	12.63	1
Meliaceae	<i>Dysoxylum hongkongense</i>	320	324	325	3.08	3.34	3.26	3	319	297	2.85	2.92	5
Urticaceae	<i>Dendrocnide meyeniana</i>	160	143	156	2.04	2.22	2.07	4	120	105	3.75	3.67	3
Aquifoliaceae	<i>Ilex rotunda</i>	20	20	19	2.03	1.84	1.98	5	19	17	1.50	1.55	11
Araliaceae	<i>Schefflera octophylla</i>	50	53	62	1.76	1.77	1.88	6	38	42	0.66	0.86	17
Elaeocarpaceae	<i>Sloanea formosana</i>	69	64	61	1.86	1.90	1.63	7	70	61	3.20	2.78	7
Fagaceae	<i>Castanopsis indica</i>	26	28	31	1.10	1.44	1.60	8	34	27	3.43	3.43	4
Lythraceae	<i>Lagerstroemia subcostata</i>	29	23	23	1.80	1.58	1.44	9	20	19	1.02	0.83	19
Lauraceae	<i>Machilus japonica</i> var. <i>kusanoi</i>	33	32	24	1.61	1.79	1.26	10	30	23	2.98	2.71	8
Staphyleaceae	<i>Turpinia ternata</i>	180	215	262	0.70	0.84	1.07	11	303	297	1.45	1.58	10
Magnoliaceae	<i>Michelia compressa</i>	22	25	26	0.71	0.81	0.91	12	14	14	0.79	0.91	16
Rubiaceae	<i>Psychotria rubra</i>	600	578	595	0.65	0.79	0.89	13	430	441	0.66	0.73	21
Myrsinaceae	<i>Ardisia sieboldii</i>	46	48	45	0.82	0.90	0.83	14	30	31	0.84	0.94	14
Moraceae	<i>Ficus ampelas</i>	33	31	33	0.92	0.88	0.75	15	72	66	2.33	2.63	9
	Subtotal	1639	1636	1718	29.47	32.78	32.70		1553	1492	40.53	42.22	
	Total	3276	3413	3756	38.59	42.75	42.06		4225	4208	53.34	54.75	

Compared with prior census, community similarities (Motyka's index of similarity) ranged 93~95% for either density- or basal area-based results (Table 4), indicating high similarity between censuses. In addition, the indices between the 2 plots were all > 60%, showing that both plots were composed by similar communities (as defined by Mueller-Dombois and Ellenberg 1974) (Table 4).

### Dynamics

The dynamic rates, especially mortality, were high for plot I during the 2000~2008 census period (Table 5). Trees  $\geq 10$  cm DBH experienced the highest mortality rate during 2000~2008 in plot I (Table 5). During this period, the loss of basal area caused by tree death was not compensated for the increment from recruits and growth of survivors (Fig. 2). Proportions of dead individuals were highest

for trees < 2 cm DBH, regardless of the plot or census time (Fig. 3). Notably, a relatively high proportion of large trees ( $\geq 32$  cm) died in plot I during the 2000~2008 census period, compared to other same-sized trees.

The major mode of death (excluding unknown) for trees  $\geq 10$  cm in plot I was broken (46.3%), followed by standing (27.8%), uprooted (24.1%), and strangled (1.9%), whereas in plot II, it was standing (66.7%), followed by broken (16.7%) and uprooted (16.7%).

Most species had similar numbers of dead and recruited individuals (Fig. 4). Species with the most dead and recruited individuals were mostly shrub and sub-canopy species, including *Lasianthus obliquinervis*, *Psychotria rubra*, and *Aglaia elliptifolia*. However, some pioneer species, such as *Malotus paniculatus*, *Leea guineensis*, and *Ficus*

*fistulosa* had net increases in individual numbers during 2000~2008 in plot I, indicating

that there were more open-canopy areas during this period (Fig. 4).

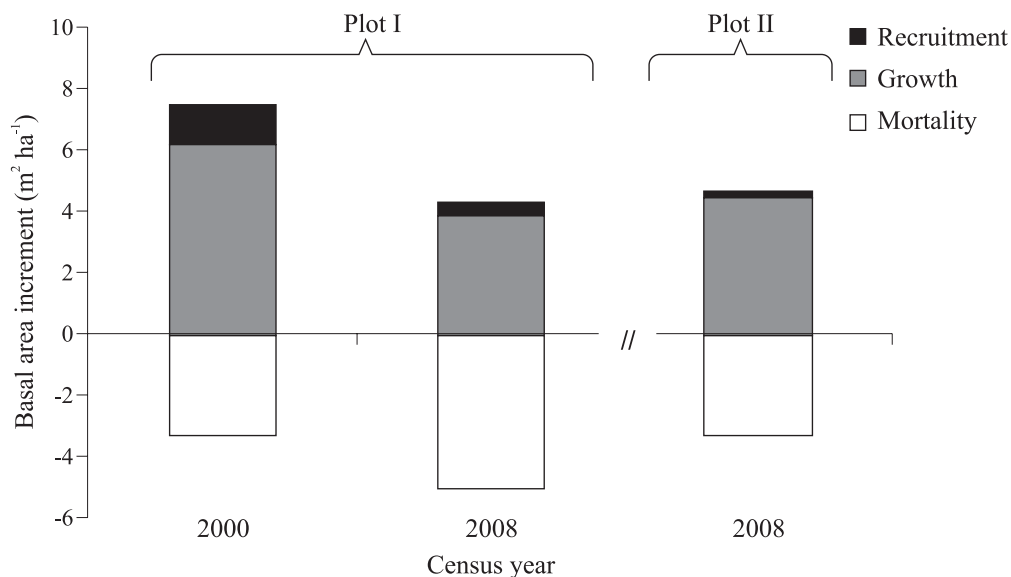
**Table 4. Motyka's index of similarity ( $IS_{MO}\%$ ) for Nanjenshan plots I and II in different census years, in the Nanjenshan Reserve, southern Taiwan. Results above the diagonal used basal area as a comparison parameter, whereas results below the diagonal used density**

	Plot I 1993	Plot I 2000	Plot I 2008	Plot II 1999	Plot II 2008
Plot I 1993	-	93	89	64	63
Plot I 2000	94	-	95	68	66
Plot I 2008	90	93	-	67	65
Plot II 1999	71	75	75	-	94
Plot II 2008	70	74	74	94	-

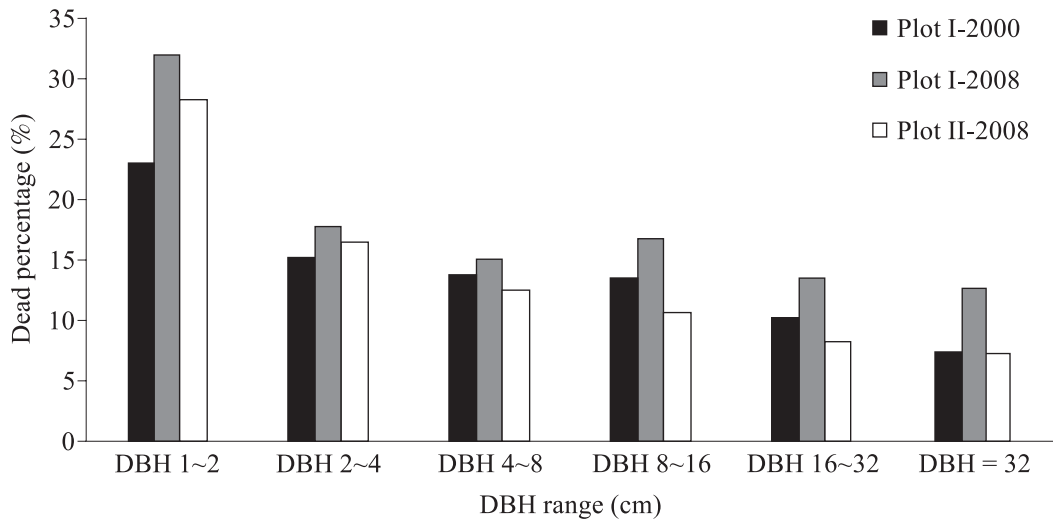
**Table 5. Recruitment and mortality rates of Nanjenshan plots I and II during different census periods**

	Plot I		Plot II
	1993~2000	2000~2008	1999~2008
Time, $t$ (yr)	7	8	9
Recruitment rate			
$\mu$ (%), for individuals $\geq 1$ cm DBH	3.19	4.12	2.20
$\mu_{10}$ (%), for individuals $\geq 10$ cm DBH	2.60	2.29	1.89
Annual mortality rate			
$m$ (%), for individuals $\geq 1$ cm DBH	2.57	2.88	2.22
$m_{10}$ (%), for individuals $\geq 10$ cm DBH	2.22	2.83	1.77

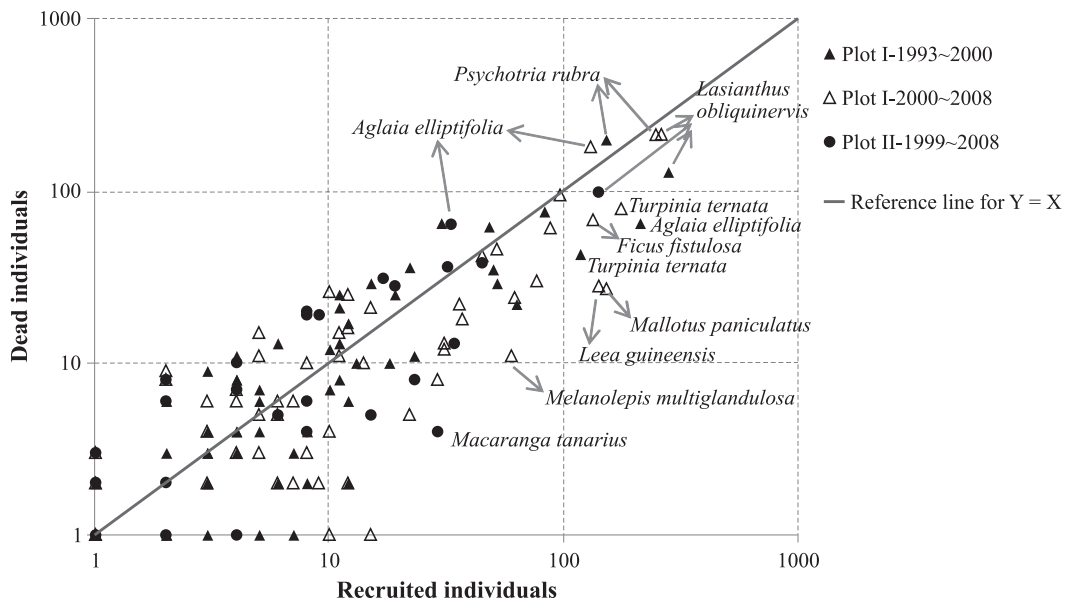
DBH, diameter at breast height.



**Fig. 2. Basal area dynamics for Nanjenshan plots I and II in different census years.**



**Fig. 3.** Percentage of dead individuals in size classes for Nanjenshan plots I and II in different census years. DBH, diameter at breast height.



**Fig. 4.** Recruited and dead individual scatter plot for Nanjenshan plots I and II in different census periods. Names of species with the most or unbalanced recruited and dead individuals are indicated.

## DISCUSSION

For Nanjenshan forests which are close to the border of the Paleotropics (*sensu* Takhtajan 1986), Chao et al. (in press) sug-

gested that the canopy structure and species composition were shaped by a gradient of stresses from the monsoon. Our study furthered revealed the temporal patterns of community composition and dynamics, and



discuss the possible causes for these patterns.

### Species composition, dominance, and abundance

Species of Nanjenshan plot I were similar to those of its prior censuses during 1993~2008, as was the case for plot II during 1999~2008 (Table 4). These results showed that both plots have a relatively stable status in terms of species composition. Only some of the rare ( $n = 1$ ) or pioneer species were found to have been extirpated from the plots. Similar results were also found in a temperate broadleaved evergreen forest in a re-census after 12 yr (Song et al. 2010). However, 2 species (*Clerodendrum trichotomum* and *Microtropis japonica*) were found to have been extirpated in plot I during the 1993~2000 census period, but were found again in the 2008 census, indicating that these species are still available in the surrounding forests and their extirpation was not an irreversible event. Therefore, the species composition of the study plots showed no dramatic changes during the study period ( $\leq 15$  yr), resulting in high species similarities of both plots to their prior censuses (Table 2).

In terms of basal area and stem density, plot II showed relatively stable patterns, with a slight increase in the basal area, and a decrease in density. However, results for plot I showed a large increase in individual numbers but a decrease in the basal area during the 2000~2008 census period. This is due to a high proportion of large trees that died in this period in plot I (Fig. 3), which then provided chances for the recruitment of pioneer species (Fig. 4). Therefore, during the 2000~2008 census period, the dynamics of Plot I were relatively unstable.

### Dynamics

The dynamic rates of our studied plots

did not greatly differ from those of other tropical forests. For most tropical forests, the mortality rates and recruitment rates for trees  $\geq 10$  cm DBH ranged 0.6~3.3% and 0.4~3.4%, respectively (Swaine et al. 1987, Phillips and Gentry 1994). The dynamic rates of our study plots were all in the middle of those ranges (Table 5), showing they did not have unusual dynamic rates.

There were temporal changes in mortality patterns for Nanjenshan plot I. Patterns of mortality across diameter classes can indicate vital mechanisms controlling forest dynamics and structure (Coomes et al. 2003). These mechanisms can include competition, exogenous disturbances, or both competition and exogenous disturbances. (1) Competition: when the mortality is driven by competition, the risk of mortality is the highest for the smallest stems and declining for largest stems, as mortality depends on the ability of trees to access resources (i.e., stem size). (2) Exogenous disturbances: when the rate of mortality is proportional to the number of stems (invariant among sizes), this indicates that disturbances are the major sources of stem mortality, as individuals are killed regardless of their size. (3) Both competition and exogenous disturbances: the mechanism is that smaller stems are subject to competitive exclusion, whereas intermediate- to large-diameter stems are killed by disturbance. Therefore, both ends of the size class show high proportions of dying.

Our results in Fig. 3 show that the mortality pattern for plot I during the 2000~2008 census period was similar to type 3 (controlled by both competition and disturbances) as suggested by Coomes et al. (2003). In comparison, patterns for plot II and the other period for plot I were similar to type I: mainly controlled by competition. These results show that plot I suffered some disturbances during

the 2000~2008 census period.

The mode of death can also be an indicator of disturbance patterns (Denslow 1980, Krasny and Whitmore 1992, Chao et al. 2009). For example, Carey et al. (1994) proposed that standing death can indicate intrinsic loss of vigor and/or a senescence mechanism. On the other hand, trees that suffer from disturbance by wind, rain-load, or another treefall may die by being uprooted or broken (Van der Meer and Bongers 1996). The major mode of death was broken in plot I and standing in plot II, again, suggesting that Nanjenshan plot I experienced disturbances during the 2000~2008 census period.

#### **Possible causes: stress or disturbance?**

The major climatic stress in the Nanjenshan region is the northeast monsoon, and major disturbances come from typhoons (Chao et al. in press). The stress of the northeast monsoon likely influences the forest canopy structure and composition in the Nanjenshan region (Chao et al. in press), as trees surviving here must have adapted to the gradient of annual stress from the monsoon. Therefore, the species compositions were similar between censuses (Table 2). However, fluctuations in dynamic patterns in our studied plots showed that this annual, regular stress is less likely to be the major causal force for the variation between censuses. Thus, we suspect that the irregular patterns (frequency and intensity) of typhoons could be the major force that determines vegetation dynamics in our studied plots, as typhoons can significantly change the understory light environment (e.g., Kuo et al. 2007).

During 1985~2008, there were several strong typhoons (maximum wind speeds near the center  $> 51.0 \text{ m sec}^{-1}$ ), including Gerald (1987), Sarah (1989), Amy (1991), Nat (1991), Tim (1994), Bilis (2000), Hai-

tang (2005), Talim (2005), and Longwang (2005) (Central Weather Bureau, Taiwan). Four of them occurred prior to the 1st census (1985~1992), only 1 of them occurred during the 1st census period (1993~1999), but 4 of them occurred during the 2nd census period (2000~2008). In addition, based on a satellite image study during 2000 to 2004, Chunag (2005) found that a medium typhoon, Dujan, also caused serious impacts on forests at Nanjenshan in 2003. The varied frequency of strong typhoons provides a possible explanation for why the dynamic patterns differed between census periods in the studied region.

Some other studies also found relatively high dynamic rates during a similar period (Yeh 2006, Song et al. 2010). For example, Yeh (2006) studied a nearby plot, Lanjenchi (Fig. 1), which suffers from both the stress of the monsoon and disturbances of typhoons. He concluded that tree mortality during the 1997~2005 census period was higher than that during the 1991~1997 census period. However, compared to our study, the mortality in Yeh (2006) was mainly contributed by small trees, and their recruitment rates decreased in the 2nd census period. That could have been because Yeh (2006) conducted that study right after a major disturbance in 2005 (typhoon Haitang; Central Weather Bureau, Taiwan), while our study was conducted 3 yr later in 2008. There could be a delay between disturbances and the death of trees  $\geq 10 \text{ cm}$  in DBH and the recruitment of new trees  $\geq 1 \text{ cm}$ , as suggested by Whigham et al. (1991).

As for why plot II did not suffer the same degree of disturbance, this could have been because it is better sheltered and less influenced by the gap-edge effect. Plot II is located on a lower slope (196~229 m in elevation) of Mt. Nanjen than is plot I (224~275 m in elevation), so it may be better sheltered by nearby ridges (Fig. 1). Moreover, a small-

sized plot may be biased to mature-phase and gap-free sites (Phillips et al. 2002). This is evident from Table 1 where the plot-level average density and basal area were relatively high for plot II. Thus, the bias would result in a relatively low rate of disturbances that happened at the edge of canopy gaps or fragmented areas (c.f., Laurance et al. 2000).

## CONCLUSIONS

Our study found that the forest compositions of Nanjenshan plot I and plot II were similar after a 15-yr investigation. However, the dynamic patterns were likely to be related to the frequency of typhoons. An increased frequency of typhoons can result in increased mortality and recruitment and the broken mode of tree death. Therefore, for forests close to the border of the Paleotropics, although their canopy structure and composition are likely shaped by the gradient of stress from the monsoon, their dynamics are likely controlled by the disturbance frequency of typhoons. More studies on gap dynamics before and after typhoon seasons would help elucidate the regeneration and restoring mechanisms for the Nanjenshan forests.

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