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 ≥ 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 $2000 \sim 2008$, 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隊邊緣效 應。因此,更進一步調查颱風前後樣區內的樹冠林隊變化,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 longterm 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 for-

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,

ests change between different census periods?



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 (μ) was calculated as (Phillips and Gentry 1994):

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

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 $45.02 \text{ m}^2 \text{ ha}^{-1}$.

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

| | | Plot I | | | Plot II | | Total | | | |
|-----------|---------------------------|-----------------|---------|---------------------------|-----------------|---------|---------------------------|-----------------|---------|--|
| Census | Density | Basal area | No. of | Density | Basal area | No. of | Density | Basal area | No. of | |
| | (stems ha ⁻¹) | $(m^2 ha^{-1})$ | species | (stems ha ⁻¹) | $(m^2 ha^{-1})$ | species | (stems ha ⁻¹) | $(m^2 ha^{-1})$ | 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 | |

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

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⁻¹ in the 2008 census) in plot I and *Lasianthus obliquinervis* (764 stems ha⁻¹ 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 ≥ 1 cm diameter at breast height in the Nanjenshan Reserve, southern Taiwan

| Dlat | Conque | Total no. | Compared to the previous census | | | | | | |
|---------|--------|------------|---------------------------------|------------|--------|-------------------------------|--|--|--|
| FIOL | Census | of species | 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 | | | |

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

Table 3. Abundance [density (stems ha⁻¹)] and dominance [basal area (m² ha⁻¹)] 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

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 ≥ 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 *Mallotus 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

| | Plo | ot I | Plot II |
|--|-----------|-----------|-----------|
| | 1993~2000 | 2000~2008 | 1999~2008 |
| Time, <i>t</i> (yr) | 7 | 8 | 9 |
| Recruitment rate | | | |
| μ (%), for individuals \geq 1 cm DBH | 3.19 | 4.12 | 2.20 |
| μ_{10} (%), for individuals ≥ 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 ≥ 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) suggested 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 (≤ 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 ≥ 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 morality 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 largediameter 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 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, Dujuan, 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 ≥ 10 cm in DBH and the recruitment of new trees ≥ 1 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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