Research paper

Community and Population Dynamics of an Evergreen Conifer-Broadleaf Forest in Southern Taiwan: Recent Trends (1999~2009)

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【Summary】

Community and population dynamics in a 1-ha permanent plot of an evergreen forest of conifer and broadleaf trees, dominated by *Pseudotsuga wilsoniana* and *Castanopsis carlesii*, in southern Taiwan were studied. All live stems with a diameter at breast height of ≥ 1 cm in this area were identified by species, tagged, and measured, first in 1999 and then again in 2009. While no changes in the floristic composition occurred between 1999 and 2009, some slight variations were evident in Shannon's diversity index. Based on a logarithmic model, the mortality, recruitment, loss, and gain rates in basal area during this period were respectively calculated to be 1.7, 0.6, -0.5, and 0.02% yr^{-1}. The stem density and especially the basal area (5.06 m^2 ha^{-1}) of *P. wilsoniana*, the most important conifer, decreased. Although the density of all dominant broadleaf trees slightly declined, 8 gained in basal area. Recent trends suggest that *P. wilsoniana* trees are now at a competitive disadvantage relative to evergreen broadleaf trees in the permanent plot, but a powerful typhoon on September 2, 2003, had a major impact on the community and population dynamics of this evergreen forest of conifer and broadleaf trees.

Key words: evergreen conifer-broadleaf forest, community dynamics, population dynamics.

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研究報告

台灣南部一個常綠針闊葉混合林的群集與族群動態：
十年(1999~2009)趨勢

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摘　要

　　本研究針對一個位於台灣南部以台灣黃杉及長尾尖葉櫧為優勢的常綠針闊葉混合林，研究此森林在10年期間群集與主要優勢族群的動態變化。我們在1999年設立1公頃永久樣區，調查樣區內1 cm以上的樹木，給予標籤、物種鑑定及胸高直徑測量，並在2009年進行重新複查的工作。在10年期間，植物組成並沒有變化，Shannon歧異度指數僅稍有變化，根據對數模式來計算林分的死亡率、補充率、失去率及獲得率，分別為每年1.7、0.6、-0.5、0.02％。台灣黃杉的族群密度與優勢度呈現下降的趨勢，大部分優勢闊葉樹的族群密度呈現微幅下降趨勢，但是有8種優勢闊葉樹的優勢度呈現增加的趨勢。本研究結果顯示台灣黃杉在此永久樣區中競爭不過常綠闊葉樹。在2003年9月2日的強烈颱風是影響此常綠針闊葉混合林的群集及族群動態的主要因子。

關鍵詞：常綠針闊葉混合林、群集動態、族群動態。

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INTRODUCTION

The study of forest dynamics focuses on changes in forest structure and composition over time, including responses to anthropogenic and natural disturbances (Pretzsch 2009). The development of sound management systems for the harvesting and/or conservation of forest resources requires an understanding of precisely such alterations. Plant ecologists have established permanent plots to study the long-term structural and compositional adaptations of woodlands, especially in late-successional and old-growth forests (Nakashizuka 1991, Falkengren-Grerup 1995, Bunyavejchewin 1999, Masaki et al. 1999, Woods 2000, McCarthy et al. 2001, Harcombe et al. 2002, Battles et al. 2003, Takahashi et al. 2003, Motta and Edouard 2005, Weckel 2006). Bakker et al. (1996) and

Herben (1996) pointed out that permanent plots can detect changes in vegetation and plant species (i.e., the parallel increase of 1 species and decrease of another) over time. Measurements of recruitment, mortality, and growth rates provide useful data for the analysis of those factors affecting stand and population dynamics. Therefore, plant ecologists strive to understand forest dynamics at the community and population levels.

Robbins (1962) placed such forests in the seral stage and suggested that although conifers have prevailed in a cooler, post-glacial climate, they are now at a competitive disadvantage relative to broadleaf trees. In Taiwan, evergreen conifer-broadleaf forests occur extensively at mid-elevations, where the conspicuous emergent conifers include

species of *Cunninghamia konishii*, *Picea morrisonicola*, *Pinus armandii*, *P. morrisonicola*, *P. taiwanensis*, *Pseudotsuga wilsoniana*, *Taiwania cryptomerioides*, *Taxus sumatrana*, and *Tsuga chinensis*. Broadleaf trees are dominated by members of the Fagaceae and Lauraceae families, with species such as *Castanopsis carlesii*, *Cyclobalanopsis longinux*, *M. thunbergii*, and *Machilus japonica*. However, few studies have been conducted in the evergreen conifer-broadleaf forests of Taiwan, explaining the insufficient data on their dynamics. We identified a mixed conifer-broadleaf forest stand in southern Taiwan with old-growth characteristics that has escaped timber cutting because of the presence of Formosan Douglas fir (*P. wilsoniana*) trees, which lack high economic value (Lin et al. 2004). We investigated the forest dynamics and tree population structure of this forest in 1999 and then reinvestigated it in 2009. Specifically, we evaluated tree demographies (mortality and recruitment rates in density and basal area) at the community and population levels and tested Robbins' (1962) hypotheses that conifers are at a competitive disadvantage relative to broadleaf trees.

MATERIALS AND METHODS

Study site

In 1999 and 2009, we conducted this study in an experimental forest (elevation 1950~2000 m; northeasterly facing slope; 22°50'N 120°46'E), which is located near Maolin Village, Kaoshiung County, southern Taiwan (Fig. 1). It belongs to the Liouguei Research Center of the Taiwan Forestry Research Institute. The mean annual temperature is 14.1℃, with monthly means ranging from 17.8℃ in July to 7.8℃ in January, and a mean annual precipitation of 2322 mm, being heavier from June to September. The weather

is often cloudy and foggy, with high relative humidity (Lin et al. 2004). The study site has the physiognomy of a subtropical evergreen conifer-broadleaf forest and is primarily dominated by *P. wilsoniana* and *C. carlesii* trees. The stand is a remnant forest with old-growth characteristics that has escaped timber cutting in the past. A powerful typhoon (a major natural disturbance) passed through Taiwan on September 2, 2003, and caused catastrophic wind damage to this forest.

Field methods

In 1999, a 1-ha (100 contiguous 10× 10 m quadrats) permanent plot was established on a gentle slope at the study site to monitor long-term forest dynamics (Lin et al. 2004). All live woody stems with a diameter at breast height (dbh) of ≥ 1 cm in the plot were identified to species, measured for dbh, mapped onto an X-Y coordinate position, and numbered with aluminum identification tags. In 2009, the permanent plot was measured again, and the status (alive, dead, or newly recruited stems ≥ 1 cm dbh), species, sizes, and positions of stems were recorded. Trees were considered dead only if the crown was fully lifeless. Finally, we inventoried trees damaged by the typhoon.

Data analysis

For parameters representing the forest's community composition and structural dynamics, we calculated the number of species, Shannon's diversity index, density of stems, basal area, and annual mortality and recruitment rates, using data for the years 1999 and 2009. Average annual changes in the 10-yr time period were estimated by demographic parameters, i.e., annual mortality and recruitment, and loss and gain rates, using a logarithmic model (Condit et al. 1995, Sheil and May 1996, Miura et al. 2001):
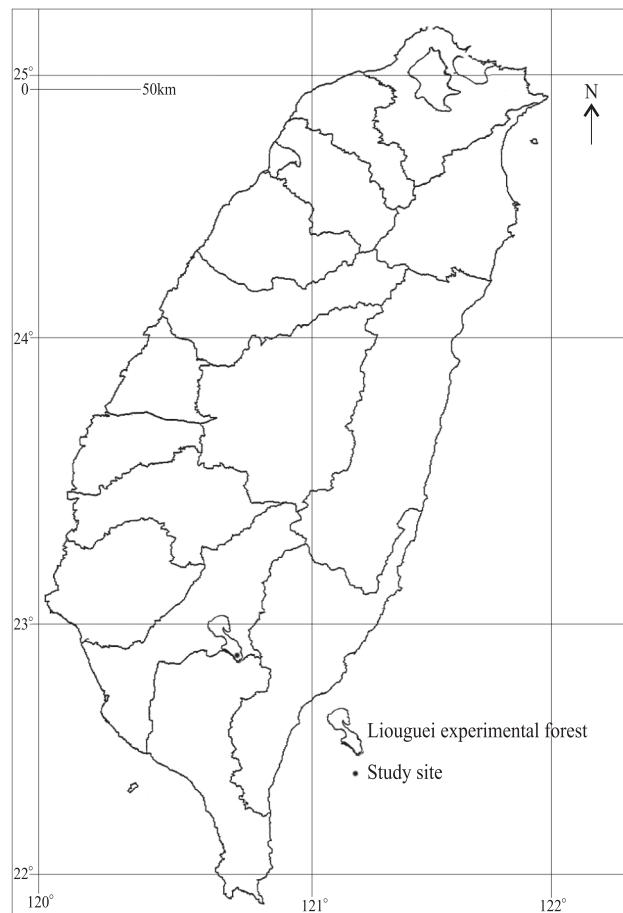
Fig. 1. Location of the study site.

Mortality rate (% $year^{-1}$) = $(\ln N_0 - \ln N_t)/T$ and Recruitment rate (% $year^{-1}$) = $(\ln N_r - \ln N_t)/T$; where N_0 is the number of live stems at the beginning of the census (in 1999), N_t is the number of live stems surviving at the end of the census interval (in 2009), T is the length of the census interval (1999~2009), and N_r = N_t + number of recruited stems during the census interval:

Loss (% $year^{-1}$) = $(\ln BA_0 - \ln BA_t)/T$ and Gain rate (% $year^{-1}$) = $(\ln BA_r - \ln BA_t)/T$; where BA_0 is the basal area of live stems at the beginning of the census (in 1999), BA_t is the basal area of live stems surviving at the end of the census interval (in 2009), and BA_r = BA_t + the basal area of recruited stems during the census interval.

In order to analyze variations in specific population parameters, we used the above equations to weigh changes in the density of stems (D) and basal area (BA), size distribution, maximum dbh, annual recruitment, and mortality, loss, and gain rates for dominant tree species during the 10-yr census period. Dominant tree species were defined as species with a relative importance value of ≥ 3%.

RESULTS

Community dynamics

Changes in the community composition and dynamic parameters for the permanent plot between 1999 and 2009 are listed in Table 1. There was no change in the floristic composition and only a slight variation (from 2.98 to 3.03) in Shannon's diversity index. Changes in stem density and basal area of the forest were -648 stems ha^{-1} and 3.48 m^2 ha^{-1}, respectively. The stem density of the forest decreased from 6349 stems ha^{-1} in 1999 to 5701 stems ha^{-1} in 2009, the result of a gain of 362 newly recruited stems and the loss of 1010 dead stems. The basal area of the forest increased from 62.04 m^2 ha^{-1} in 1999 to 65.52 m^2 ha^{-1} in 2009. The growth of surviving trees accounted for about 91% of the gain in basal area, with new recruits accounting for the rest. The annual mortality and recruitment rates were 1.7 and 0.6% yr^{-1}, respectively, and the annual loss and gain rates in the basal area equaled -0.5 and 0.02% yr^{-1}, respectively. The annual mortality was higher than the recruitment rate, suggesting a slow decline in tree density, with an accompanying increase in the basal area.

Population dynamics and diameter distribution of dominant species

For the 10 most dominant trees in the permanent plot during the census interval (1999~2009), the density change, annual mor-tality rate, and annual recruitment rate are listed in Table 2. Nine dominant trees decreased in stem density, ranging from 2 stems ha^{-1} (*P. wilsoniana*) to 199 stems ha^{-1} (*Dendropanax pellucidopunctata*), and only *Schima superba* trees showed no change. The annual mortality rate of dominant tree populations ranged from 0.8% yr^{-1} (*M. thunbergii* and *S. superba*) to 4.5% yr^{-1} (*D. pellucidopunctata*). The annual recruitment rate of dominant tree populations ranged from 1% yr^{-1} (*C. longinux*) to 4.7% yr^{-1} (*D. pellucidopunctata*).

The basal area and annual loss and gain rates of the 10 most dominant trees in the permanent plot during the census interval (1999~2009) are listed in Table 3. Eight dominant trees increased in basal area, rang-ing from 0.1 m^2 ha^{-1} (*Eurya nitida*) to 1.46 m^2 ha^{-1} (*C. longinux*), and 2 dominant trees, *C. carlesii* and *P. wilsoniana*, diminished in basal area, equaling -0.44 and -5.06 m^2 ha^{-1}, respectively. The annual loss rate of the domi-nant tree populations went from -3.85% yr^{-1} (*D. pellucidopunctata*) to 1.26% yr^{-1} (*P. wil-soniana*). Their annual gain rates ranged from 0.001% yr^{-1} (*C. carlesii*, *P. wilsoniana*, and *C. longinux*) to 0.176% yr^{-1} (*Litsea lii*).

The dbh size distributions for the live stems of the 10 most dominant trees of 1999 and 2009 are shown in Fig. 2. The size structure changes of dbh for these trees

Table 1. Changes in the community composition and dynamic parameters for the permanent plot between 1999 and 2009

Parameters	1999	2009	Change
Number of species	64	64	0
Shannon's diversity index	2.98	3.03	+0.05
Density of stems (stems ha^{-1})	6349	5701	-648
Annual mortality rate (% yr^{-1})			1.7
Annual recruitment rate (% yr^{-1})			0.6
Basal area (m^2 ha^{-1})	62.04	65.52	+3.48
Annual loss rate (% yr^{-1})			-0.5
Annual gain rate (% yr^{-1})			0.02

Table 2. Changes in stem density and dynamic parameters of the 10 most dominant trees of the permanent plot between 1999 and 2009

Tree species	Density (stems ha^{-1})			Mortality (% yr^{-1})	Recruitment (% yr^{-1})
	1999	2009	Change	1999~2009	1999~2009
Castanopsis carlesii	270	222	-48	2.3	2.5
Pseudotsuga wilsoniana	32	30	-2	2.1	3.3
Illicium tashiroi	662	568	-94	1.2	1.6
Cyclobalanopsis longinux	244	226	-18	0.9	1.0
Machilus thunbergii	377	364	-13	0.8	1.2
Dendropanax pellucidopunctata	593	394	-199	4.5	4.7
Elaeocarpus japonicus	364	298	-66	2.2	2.3
Eurya nitida	424	381	-43	1.5	1.8
Litsea lii	431	427	-4	0.9	1.6
Schima superba	170	170	0	0.8	1.5

Table 3. Changes in basal area and dynamic parameters of the 10 most dominant trees of the permanent plot between 1999 and 2009

Tree species	Basal area (m^2 ha^{-1})			Loss rate (% yr^{-1})	Gain rate (% yr^{-1})
	1999	2009	Change	1999~2009	1999~2009
Castanopsis carlesii	27.63	27.19	-0.44	-0.38	0.001
Pseudotsuga wilsoniana	30.64	25.58	-5.06	1.26	0.001
Illicium tashiroi	4.76	4.90	+0.14	-0.78	0.005
Cyclobalanopsis longinux	9.97	11.43	+1.46	-1.91	0.001
Machilus thunbergii	4.59	5.36	+0.77	-2.08	0.007
Dendropanax pellucidopunctata	1.07	1.50	+0.43	-3.85	0.091
Elaeocarpus japonicus	3.44	4.69	+1.25	-3.52	0.015
Eurya nitida	1.11	1.21	+0.10	-1.23	0.130
Litsea lii	0.41	0.60	+0.19	-3.79	0.176
Schima superba	3.91	4.24	+0.33	-1.31	0.024

were slight. All species showed decreases in the smallest dbh stem class, except for *P. wilsoniana*. The size distribution of the 7 dominant trees (*C. carlesii*, *Illicium tashiroi*, *C. longinux*, *M. thunbergii*, *D. pellucidopunctata*, *Elaeocarpus japonicus*, and *E. nitida*) of the forest showed a typical reversed, J-shaped size distribution, including abundant stems with dbh in the 5- or 10-cm classes. The size distribution of *L. lii* and *S. superba* showed a typical L-shaped size distribution, including abundant stems with a dbh in the 5- or 10-cm classes and relatively few stems in the other classes. However, the *P. wilsoniana* size distribution indicated a rough bell shape, with greater abundances in the 70~90-cm classes.

DISCUSSION

Dynamics at the community level

Recent community level changes in the permanent plot suggest that natural succession and disturbance did not wholly transform the tree composition and structure. The forest
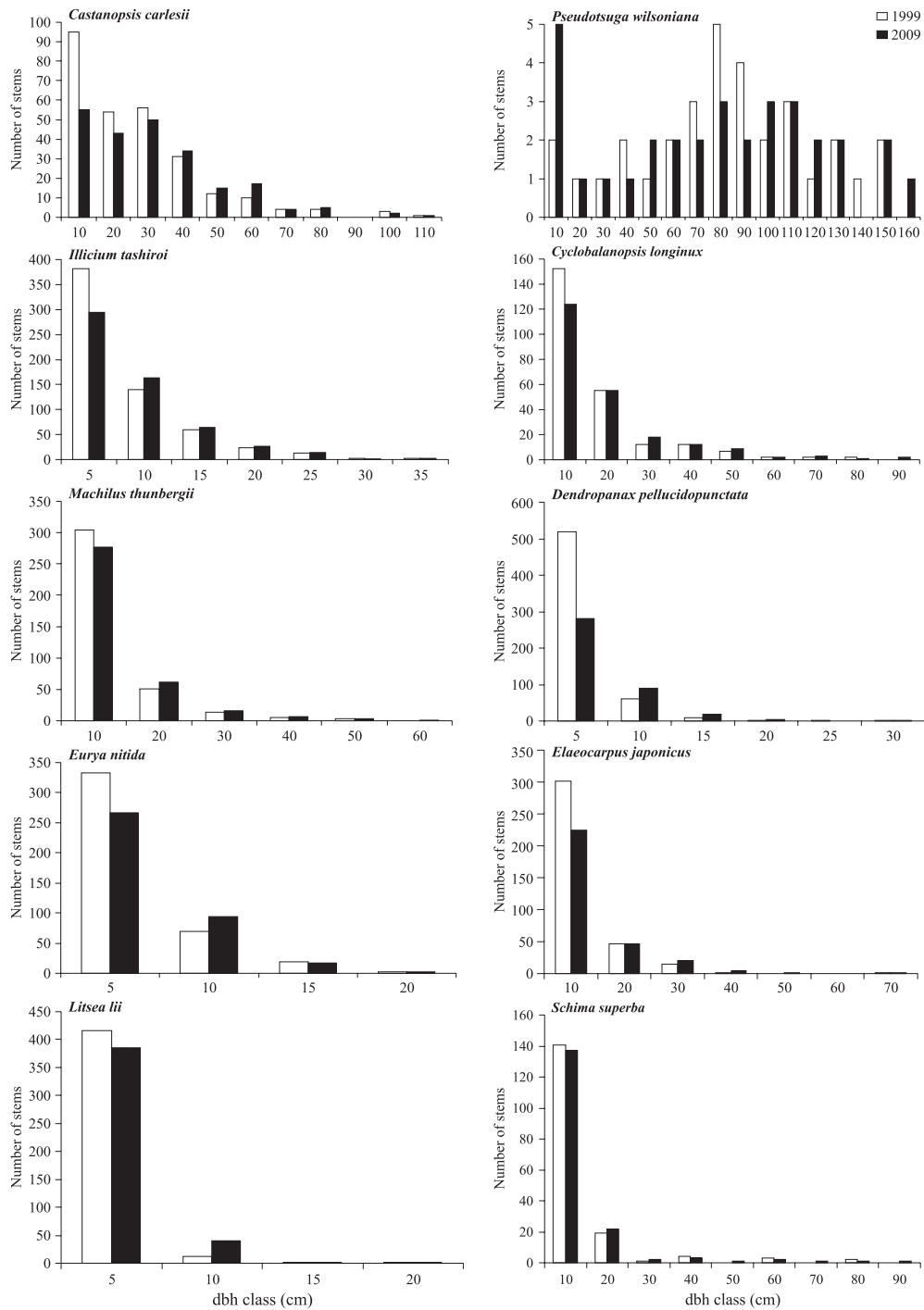
Fig. 2. Diameter distributions for live stems of the 10 most dominant trees in 1999 (light bars) and 2009 (dark bars). X-axis values are diameter of breast height (dbh) classes of sub-canopy trees, each 5-cm wide, or of canopy trees, each 10-cm wide. Y-axis values are total number of stems in the 1-ha permanent plot.

still possesses an evergreen conifer-broadleaf physiognomy. However, a decrease of 648 stems in the overall tree density, most in the smallest size class (5 cm > dbh ≥ 1 cm) occurred, although 362 newly recruited stems appeared in the same class. Most of the basal area loss was due to the death of canopy stems, especially *C. carlesii* (16.2%) and *P. wilsoniana* (13.6%), and most of the gain was used to growth of the surviving stems (91%, with the remainder due to ingrowth). Catastrophic wind damage caused stem and basal area losses, because typhoons are the major agent of natural disturbance in the study area, passing through or near Taiwan with a high frequency (2 yr^{-1}) between 1999 and 2009. A powerful typhoon on September 2, 2003 caused catastrophic wind damage to the forest. It uprooted or broke many large standing stems (76 cm ≤ dbh ≥ 124 cm) of *P. wilsoniana* and *C. carlesii*, causing large falling stems to lean and damage understory growth, because the former, located above the canopy, are more susceptible to typhoon damage. Therefore, periodic typhoons of variable breath and intensity determine the trends of the forest's dynamics; however, actual forest disturbance regimes are far too complex to quantify their effects. We should have a deeper understanding of the relationship between typhoon disturbance regimes and forest dynamics in this study area so as to predict the future of evergreen conifer-broadleaf forests. It is important to understand this process at the community level when designing programs for forest management and species preservation.

Dynamics at the population level

It is crucial to note that *P. wilsoniana* was the most dominant tree in 1999 and *C. carlesii* in 2009. The cause of this change was the decreased basal areas of the 2 spe-

cies, which were 5.06 and 0.44 m^2 ha^{-1}, respectively. The greater damage sustained by *P. wilsoniana* during the 2003 typhoon is in agreement with the tendency for conifers to be more vulnerable than evergreen broadleaf trees, because these taller trees run a higher risk of wind damage. In addition, almost all evergreen broadleaf trees increased in basal area, with the remainder caused by ingrowth. For the 10 most dominant trees in the permanent plot during the census interval (1999~2009), all decreased in density, except for *S. superba*. Although the annual mortality rate of the *P. wilsoniana* population (2.1% yr^{-1}) was lower than that of the *C. carlesii* population (2.3% yr^{-1}), the density of the former (30 stems ha^{-1}) was the lowest of all trees. Importance values were calculated for all tree species for the permanent plot as the sum of the relative density and relative dominance. Of the 2 dominant trees, *C. carlesii* decreased in importance values (IVs) from 15.96% in 1999 to 15.54% in 2009 and *P. wilsoniana* from 15.57% in 1999 to 13.06% in 2009. IVs of the other dominant evergreen broadleaf trees increased during these 10 years. In conclusion, the results support the view of Robbins (1962) that conifers are now at a competitive disadvantage relative to broadleaf trees.

Size class frequency distributions provide useful information for interpretating population dynamics between 1999 and 2009. *Pseudotsuga wilsoniana* had a roughly bell-shaped distribution, owing to the concentration of mortality in stems of small dbh (because of shading by larger trees) and in stems of large dbh (because of typhoon wind damage). Regeneration of *P. wilsoniana* was limited beneath the dense canopy; seedlings only established themselves in forest trails and in large gaps with sufficient sunlight. This species in the stand is thought to be a "pioneer,"

with "long-lived shade-intolerant" characteristics (Whitmore 1989). The strong typhoon of September 2, 2003, destroyed the previous old-growth *P. wilsoniana*, providing an opportunity for their seedlings to regenerate in the large resulting gaps. Thus, the felling of large-stemmed *P. wilsoniana* (76 cm ≤ dbh ≥ 124 cm) provided motive power for establishment of their seedlings. On the other hand, *C. longinux*, *M. thunbergii*, and *E. japonicus* had a typical reversed, J-shaped size distribution, representing strong regeneration (good reproduction and recruitment). These evergreen broadleaf trees successfully established their seedlings in the substratum with little sunlight. Hence, they appear to have "shade-tolerant" characteristics (Whitmore 1989). If the current trend is sustained, we predict a gradual change from an evergreen conifer-broadleaf forest to an evergreen broadleaf forest. In general, it is crucial to understand the relationship between typhoon disturbance regimes and forest dynamics in this study area in order to predict the future dynamics of evergreen conifer-broadleaf forests.

ACKNOWLEDGEMENTS

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