

Research paper

Tree Population Dynamics over 12 Yr in a Warm Temperate Broad-leaved Evergreen Forest at Mt Peitungyen, Central Taiwan

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【 Summary 】

The 3-ha Peitungyen forest dynamic plot established in 1995 in a warm temperate evergreen broad-leaved forest was re-measured 12 yr later. In 2007, one species had vanished from this plot, and 5 species were newly recorded, resulting in an increase of species number from 56 to 60. In the 12-yr census interval, stem density increased from 3336.3 to 5769.0 ha⁻¹, and up to 94.5% of recruits were < 5 cm in diameter at breast height (DBH). In spite of the drastic increase in stem density, the basal area dropped from 78.7 to 71.6 m² ha⁻¹. The considerable decrease in basal area was attributed to the death of many large-DBH trees. Up to 15.7% of large trees (DBH ≥ 30 cm) were recorded as having died in 2007. Comparing the 10 most dominant species (in terms of stem density and basal area) between the 2 censuses, there was a high similarity of species composition, and the ranking only slightly differed. In other words, over the 12 yr, changes in the forest dynamics plot were mainly structural rather than compositional. A marked increment in stem density of small trees, the lack of pioneer species colonization, and little evidence of compositional changes indicate that this plot encountered medium-scale disturbances in the 12 yr. The relatively drastic changes in stem density and basal area in the Peitungyen plot might be attributed to responses of a forest with a relatively low frequency of disturbances to an abrupt increase in disturbances in recent years.

Key words: canopy gap, disturbance regime, forest dynamics plot, warm temperate forest, tree population dynamics.

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研究報告

北東眼山暖溫帶常綠闊葉林的十二年樹種族群動態

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摘要

歷經12年後，複查1995年在北東眼山建立的3公頃動態樣區。從1995到2007年間，有1物種從自樣區中移出，新增5物種，總物種數自56增為60。12年期間，植株密度從3336.3 ha⁻¹增為5769.0 ha⁻¹。94.5%新增植株的胸高直徑未及5 cm。雖然植株密度增加，而胸高斷面積卻自78.7 m² ha⁻¹減為71.6 m² ha⁻¹。胸高斷面積明顯下降，主因為不少大樹死亡。直至2007年有15.7%大樹(DBH ≥ 30 cm)死亡。比較1995與2007兩次調查，植株密度與胸高斷面積最優勢的十種，組成種類相似度頗高，僅優勢度排名稍有變動。亦即此12年中，主為結構變化，而組成改變很少。小樹大量增加、沒有先驅種移入及些微組成的改變，顯示往昔林冠層曾遭中型干擾。北東眼山樣區在植株密度及胸高斷面積上不小變動，這可歸因為一個干擾頻度較低的森林對於近年來干擾頻度增加的反應。

關鍵詞：林隙、干擾、森林動態樣區、暖溫帶林、樹種族群動態。

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INTRODUCTION

Due to the longevity of trees, conducting long-term studies is the only way to understand the dynamics of forest ecosystems. In recent decades, numerous long-term study sites were set up on nearly every continent, such as in Africa (e.g., Okali and Ooadams 1987, Swaine et al. 1987a), Asia (e.g., Manokaran and Kochummen 1987), and the Americas (e.g., Lieberman and Lieberman 1987, Condit et al. 1992). The main purposes for establishing these long-term study sites are to collect demographic data of forest communities (Swaine et al. 1987b, Condit 1995), examine the mechanisms of the successional processes of vegetation (Rees et al. 2001, Bakker et al. 2002), identify the mechanisms by which high species richness is maintained in rainforests (Hubbell and Foster 1992, Condit 1995), and examine the regeneration patterns of tree species (Clark 1986, Wills et al. 2006).

In 1989, the 1st long-term study site in Taiwan was established in a lowland area of Kenting National Park (Sun and Hsieh 2004). Compared to areas at low elevations, there is a relatively greater proportion of old-growth forests preserved at mid-elevations. In order to better understand the tree population dynamics of mid-elevation forests, which also have high species diversity, a long-term study site was set up in 1995 at Mt Peitungyen, central Taiwan (Song 1996). It was reported that the basal area was 78.7 m² ha⁻¹ and stem density was 3336.3 ha⁻¹ (Song 1996). The height of the tallest tree (*Castanopsis carlesii*) was 44 m and the diameter at breast height (DBH) of the thickest tree was 194.4 cm. The mean canopy height was 21.6 m. In term of basal area, *Castanopsis carlesii* was the most dominant species, accounting for 36.9% of total basal area. *Barthea barthei* had the highest

stem density, which accounted for 18.1% of the total stem density.

In 2007, trees in the 3-ha Peitungyen plot was remeasured. The main purpose of this article is to report the 12-yr population dynamics of tree species in this plot.

MATERIALS AND METHODS

Study site

The study site is in a temperate broad-leaved evergreen forest (24°04'41"N, 121°07'47"E, 2000 m above sea level) at Mt Peitungyen, central Taiwan (Fig. 1). The climate is warm temperate. Mean monthly temperature recorded in the nearby Meifeng Farm (24°05'10"N, 121°10'29"E, 2100 m above sea level) of National Taiwan Univ., ranges from 8.3°C (January) to 17.7°C (July). Frosts are common in winter in the open. An average annual rainfall of 2484 mm was recorded at Meifeng. The rainfall pattern there is seasonal. The wet season begins in February and ends in August. The period from September to the following January is the dry season.

Tree measurement

In 1995, a 3-ha plot was established. For ease of tree measurement, the 100 m × 300 m plot was subdivided into 300 10 m × 10 m quadrats. In each quadrat, trees with a DBH of ≥ 1 cm were measured, mapped, tagged, and identified. Species were identified by matching to voucher specimens which were collected prior to the fieldwork and housed in the Plant Ecology Laboratory, Institute of Ecology and Evolutionary Biology (previously Department of Botany), National Taiwan Univ. A re-census was conducted in the 3-ha plot in 2007, following the field methods used in 1995. Nomenclature of plant species followed the nomenclature of the 2nd edition of the *Flora of Taiwan* (Boufford et al. 2003).

Data analysis

In the present study, the annual mortality rate (m) is the loss of stems per year, which can be derived from the equation recommended by Sheil et al. (1995):

$$m = \left[1 - \left(1 - \frac{N_0 - N_1}{N_0} \right)^{\frac{1}{t}} \right] 100\%$$

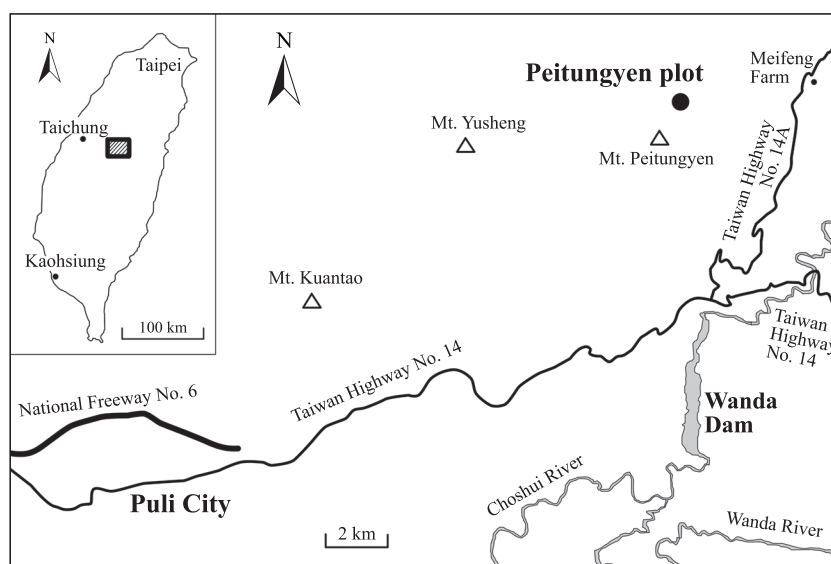


Fig. 1. Location of the Peitungyen plot.

where N_0 and N_1 are the respective numbers of stems at the beginning and end of the census interval, t . For example, with this equation, the annual mortality rate over the re-census interval 1995~2007 can be derived using the number of stems in 1995 (N_0) and the number of stems in 2007 (N_1) and 12 yr of the re-census interval (t).

RESULTS

Species richness and composition

The species richness and composition changed only slightly over 12 yr. From 1995 to 2007, the number of species rose from 56 to 60. Of 56 species found in 1995, 55 still existed in 2007 (App. 1). During the 12 yr, 1 species (*Illicium philippinense*) vanished and 5 species (*Callicarpa randaiensis*, *Daphniphyllum himalaense* ssp. *macropodum*, *Eriobotrya deflexa*, *Litsea cubeba*, and *Tricalysia dubia*) were newly recorded.

Mortality and recruitment

Over the 12 yr, the stem density drastically increased, whereas the basal area decreased (Fig. 2). Of 10009 individuals recorded in 1995, 2227 had died, and 7782 survived in 2007. There were as many as 9525 recruits, resulting in a 72.9% net increase in the total stem density (from 3336.3 to 5769.0 ha^{-1}). Recruits of < 5 cm DBH accounted for 94.5% of the newly recorded trees, resulting in a sharp increase in stem density from 1858.0 to 4353.7 ha^{-1} in the DBH class of < 5 cm (Table 1). In contrast, the basal area decreased from 78.4 to 71.6 $\text{m}^2 \text{ha}^{-1}$. Up to 15.7% (94 of 597) of large trees (DBH \geq 30 cm) had died, including the largest tree (194.4 cm DBH) in the 3-ha plot, which in total accounted for 77.3% (10.8 out of 13.9 $\text{m}^2 \text{ha}^{-1}$) of the loss of basal area. The considerable decrease of basal area was mainly attributed to the death

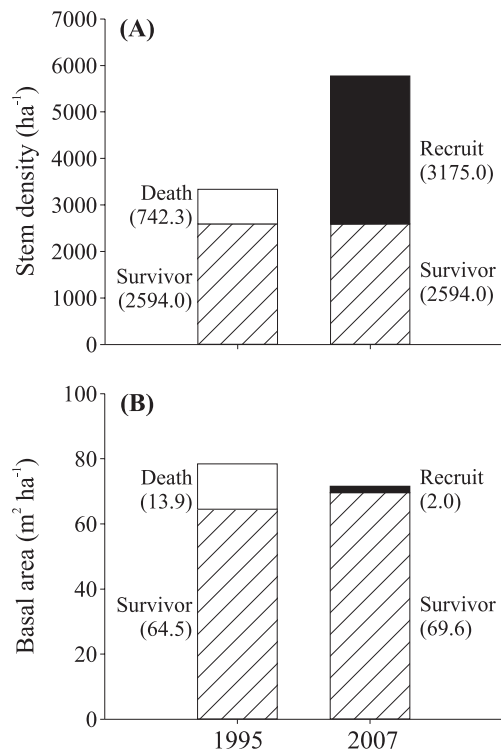


Fig. 2. Stem density (A) and basal area (B) contributed by survivors, deaths, and recruits in 1995 and 2007. The cross-hatched bars represent measurements of trees which were alive in both 1995 and 2007. Open bars represent measurements of trees which did not survive to 2007. Black bars represent measurements of new recruits in 2007. Values in brackets indicate measurements in each category. Results show that stem density increased, whereas basal area decreased.

of these large trees.

Species dominance

In terms of stem density, *Barthea barthei* was still the most dominant species over the 12 yr, the stem density of which increased from 604 to 1037.3 ha^{-1} (Table 2). Of the 10 most dominant species in 1995, only the stem densities of *Ternstroemia gymnanthera*

Table 1. Changes in stem density over the re-census interval 1995~2007

DBH class (cm)	Stem density 1995 (ha ⁻¹)	Stem density 2007 (ha ⁻¹)	Deaths 1995~2007 (ha ⁻¹)	Recruits 1995~2007 (ha ⁻¹)	Annual mortality rate (%)
< 5	1858.0	4353.7	503.7	3094.3	2.60
5~10	668.3	645.0	111.3	65.0	1.51
10~20	440.0	433.0	66.7	11.7	1.36
20~40	247.0	228.7	39.0	3.0	1.42
40~80	92.0	82.0	17.0	0.7	1.69
≥ 80	31.0	26.7	4.7	0.3	1.35
Total	3336.3	5769.0	742.3	3175.0	2.08

Table 2. Comparisons of the ranking of species dominance (stem density) between 1995 and 2007. Results show that of the 10 most dominant species in 1995 and 2007, there are 7 species (highlighted in boldface type) in common

Species	1995		2007	
	Stem density (ha ⁻¹)	Ranking	Stem density (ha ⁻¹)	Ranking
<i>Barthea barthei</i>	604.0	1	1037.3	1
<i>Cinnamomum subavenium</i>	223.7	2	252.0	6
<i>Cleyera japonica</i>	223.0	3	221.0	9
<i>Eurya loquaiana</i>	220.3	4	258.0	5
<i>Machilus thunbergii</i>	171.3	5	222.3	8
<i>Castanopsis carlesii</i>	170.7	6	232.0	7
<i>Neolitsea acuminatissima</i>	151.0	7	272.3	4
<i>Meliosma callicarpaefolia</i>	148.0	8	172.0	11
<i>Ternstroemia gymnanthera</i>	139.0	9	107.7	15
<i>Viburnum integrifolium</i>	118.7	10	155.3	12
<i>Dendropanax pellucidopunctata</i>	114.3	11	305.7	3
<i>Michelia compressa</i>	99.7	12	211.3	10
<i>Prunus phaeosticta</i>	52.3	18	842.3	2
Total	3336.3	-	5769.0	-

and *Cleyera japonica* decreased. The drastic increase in the stem densities of *Prunus phaeosticta*, *Dendropanax pellucidopunctata*, and *Michelia compressa* made these 3 species the 2nd, 3rd and 10th most dominant species in 2007 (Table 2). Comparing the 10 most dominant species in 1995 and 2007, there were still 7 species in common (Table 2). In terms of basal area, *Castanopsis carlesii* was the most dominant species over the 12 yr. Nine of the 10 most dominant species in 2007

were identical to those in 1995, and the ranking changed only slightly (Table 3). Of the 10 most dominant species in 1995, decreases in basal area were recorded for 6 species. *Ternstroemia gymnanthera* had the highest loss of basal area (up to 40.5%).

DISCUSSION

The annual mortality rate of trees in our plot was not higher than those in other

Table 3. Comparisons of the ranking of species dominance (basal area) between 1995 and 2007. Results show that in terms of basal area, the 10 most dominant species in 2007 are almost identical to those in 1995, although the rankings changed. The 10 most dominant species in common between 1995 and 2007 are highlighted in boldface type

Species	1995		2007	
	Basal area (cm ² ha ⁻¹)	Ranking	Basal area (cm ² ha ⁻¹)	Ranking
<i>Castanopsis carlesii</i>	289,637	1	242,672	1
<i>Lithocarpus lepidocarpus</i>	94,305	2	74,459	3
<i>Schima superba</i>	82,838	3	81,098	2
<i>Machilus thunbergii</i>	48,316	4	48,732	5
<i>Cinnamomum subavenium</i>	47,295	5	49,947	4
<i>Cleyera japonica</i>	26,857	6	21,089	8
<i>Ternstroemia gymnanthera</i>	26,418	7	15,725	11
<i>Neolitsea aciculata</i> var. <i>variabilima</i>	23,231	8	22,304	7
<i>Elaeocarpus japonicus</i>	22,319	9	23,045	6
<i>Neolitsea acuminatissima</i>	17,680	10	20,527	9
<i>Meliosma callicarpaefolia</i>	13,499	11	16,325	10
Total	784,253	-	715,997	-

rainforests (e.g., Hubbell and Foster 1990, Rankin-De-Merona et al. 1990, Chao 2001). Nevertheless, it is likely that the mortality rate of large trees in our plot was above the average in some years between 1995 and 2007, but it was diluted due to the long census interval. It was noted that the annual mortality rate decreases with an increase in the census interval (Lewis et al. 2004). Since our 12-yr census interval is longer than those in numerous previous studies (e.g., Hubbell and Foster 1990, Rankin-De-Merona et al. 1990, Chao 2001), the annual mortality rate in our plot as well as the scale of disturbances was likely underestimated in some years. Field observations at our study site showed that numerous trees were brought down by typhoons in 2000 and 2001 (Hou 2008). Two long-term forest dynamic studies conducted in southern Taiwan implied that the disturbances by typhoons were more intensive in the few years after 2000 than in the decade before 2000 (Yeh 2006, Chao et al. 2010). A study by Tu et al. (2009) also indicated that the typhoon counts

in the vicinity of Taiwan increased abruptly from 3.3 per year before 2000 (1970~1999) to 5.7 per year after 2000 (2000~2006). We therefore believed that the mortality of large trees in our plot had intensively occurred in some years after 2000 and consequently created substantial canopy gaps.

The most notable change over the 12 yr was the drastic increase in stem density of small-DBH trees (Table 1). This phenomenon implied that canopy gaps greater than those created by single-tree falls had occurred in the canopy layer. Small-scale disturbances caused by fallen single trees would not normally induce such a sharp increase in small trees (Smith and Nichols 2005, Smith et al. 2005, Song 2007). Song (2007) reported that the stem density barely changed over 40 yr in an Australian subtropical rainforest, in which canopy gaps were mainly created by loss of branches and the fall of single trees (see also Smith and Nichols 2005, Smith et al. 2005). Canopy gaps created by relatively large-scale disturbances are needed for a marked increase

in small trees in the understory. In our plot, the total stem density increased by > 70% (Table 2), and most of the recruits were < 5 cm in DBH (Table 1). It is very likely that the forest in our plot had encountered canopy disturbances on a scale greater than those resulting from branch losses or single fallen trees.

Two of our results indicated that from 1995 to 2007, the scale of disturbances in our study plot was not too large, either. First, there was no mass colonization of pioneer species over the 12 yr. Compared to late successional species, relatively large-scale disturbances are needed for the colonization of pioneer species. However, in our plot, no establishment of pioneer species (e.g., *Alnus formosana*) was recorded, except for a small number of early successional species (such as *Litsea cubeba* at 43 stems ha⁻¹). Second, the impact of disturbances on our plot was mainly structural rather than compositional. Disturbances can change the structure (e.g., stem density and basal area) and composition (e.g., species and dominant species) of forests (Horne and Hickey 1991, Everham and Brokaw 1996, Song 2007). Large-scale disturbances can cause both types of the changes, whereas the impact of small-scale disturbances is merely structural (Horne and Hickey 1991, Everham and Brokaw 1996, Song 2007). Although changes in stem density and basal area in our plot were dramatic, compositions of all species and dominant species changed only slightly (Tables 2, 3). The scale of disturbances was not large in our plot due to no mass colonization of pioneer species and little evidence of compositional change.

It was shown that, in selective logging, the remaining canopy cover was linearly negatively correlated with logging intensity (removal of canopy trees ≥ 70 cm DBH ha⁻¹) (Webb 1997). Webb's regression equation (1997) between disturbance scale and residual canopy cover allows us to estimate the scale

of disturbances in our plot more precisely. Disturbances in our plot resulted in a loss of 8.7 canopy trees ha⁻¹. According to the regression equation [remaining canopy cover = 91.83 - 2.80 x (logging intensity)] developed by Webb (1997), that extent of disturbance intensity could create canopy openness of as high as 32.5% if it was a operation of selective logging. With selective logging, many non-target trees are removed to make trails for the transport of harvested trees. In other words, in a given density of fallen large trees, gaps created by selective logging tends to be greater than those created by natural disturbances. Therefore, the post-disturbance canopy openness in our plot is not likely to be > 32.5%.

The considerable increase in small trees (< 5 cm DBH) (Table 1) is likely to intensify the competition between individuals in this cohort. It is expected that this will soon result in stagnant growth and a relatively high mortality rate in the understory. Although many of these small trees will die before they reach the overstory canopy layer, the species composition in our study site should not greatly vary (Hsu 2006). Due to a high similarity of species composition between the understory layer and overstory canopy layer, it is unlikely that there is going to be a high degree of composition change in our study site (Hsu 2006). The instant effects of medium-to large-scale disturbances are decreases in species richness, stem density, and basal area (Smith and Nichols 2005, Smith et al. 2005, Song 2007). Among these 3 features which are changed by disturbances, the recovery of basal area is the slowest, especially when the decrease in basal area is attributed to the loss of large-DBH trees (Smith and Nichols 2005, Smith et al. 2005, Song 2007). Even though there were no longer any signs of decreases in species richness and stem density in our plot by 2007, the basal area had still not fully

recovered. Because the decrease in basal area in the present study was mainly attributed to the mortality of large trees (≥ 30 cm DBH), it will take at least a few years more to regain the basal area to the level of 1995.

Compared to the forest dynamics of the lowland Nanjenshan plots in southern Taiwan, changes in stem density and basal area between censuses were drastic in the Peitungyen plot (Yeh 2006, Chao et al. 2010). This may be attributed to differences in their disturbance regimes and their responses to the abrupt increase of typhoon counts. The Peitungyen plot is located on the western slope of the Central Mountain Range (CMR). The adjacent ridge of the CMR is more than 3000 m in height, which can efficiently reduce disturbances of the northeast monsoon and typhoons from the east. In contrast, the Nanjenshan plots are located on the Hengchun Peninsula with no high mountains in the vicinity, so that they are exposed to frequent disturbances from the northeast monsoon and typhoons (Chao et al. in press). Even though the typhoon counts in the vicinity of Taiwan have increased abruptly since 2000 (Tu et al. 2009), the mean canopy openness before and after 2000 was consistently as high as $> 10\%$ in one of the Nanjenshan plots (SW Fan, unpublished data). That is, in forests under a disturbance regime of frequent disturbances, the effects of increased disturbances are not evident, and the responses of forests are therefore not drastic. Accordingly, the relatively drastic changes in stem density and basal area in the Peitungyen plot can be attributed to the increased disturbances exerting greater effects on forests in which the disturbance frequency used to be low.

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Appendix 1. Tree species (with individuals ≥ 1 cm DBH) in the 3-ha Peitungyen plot

Family	Species	Growth form*
Aquifoliaceae	<i>Ilex arisanensis</i>	M
Aquifoliaceae	<i>Ilex ficoidea</i>	M
Aquifoliaceae	<i>Ilex hayataiana</i>	T
Aquifoliaceae	<i>Ilex tsugitakayamensis</i>	M
Aquifoliaceae	<i>Ilex uraiensis</i>	T
Araliaceae	<i>Dendropanax pellicidopunctata</i>	M
Araliaceae	<i>Fatsia polycarpa</i>	U
Carprifoliaceae	<i>Viburnum integrifolium</i>	M
Carprifoliaceae	<i>Viburnum urceolatum</i>	U
Celastraceae	<i>Microtropis fokienensis</i>	U
Cornaceae	<i>Aucuba chinensis</i>	U
Daphniphyllaceae	<i>Daphniphyllum himalaense</i> ssp. <i>macropodum</i> ²⁾	M
Elaeocarpaceae	<i>Elaeocarpus japonicus</i>	T
Elaeocarpaceae	<i>Elaeocarpus sylvestris</i>	M
Ericaceae	<i>Lyonia ovalifolia</i>	M
Ericaceae	<i>Rhododendron formosanum</i>	U
Ericaceae	<i>Rhododendron latoucheae</i>	M
Ericaceae	<i>Vaccinium kengii</i>	U
Ericaceae	<i>Vaccinium randaiense</i>	M
Fagaceae	<i>Castanopsis carlesii</i>	T
Fagaceae	<i>Cyclobalanopsis longinux</i>	M
Fagaceae	<i>Lithocarpus amygdalifolius</i>	T
Fagaceae	<i>Lithocarpus lepidocarpus</i>	T
Fagaceae	<i>Pasania kawakamii</i>	T
Illiciaceae	<i>Illicium philippinense</i> ¹⁾	U
Juglandaceae	<i>Engelhardtia roxburghiana</i>	M
Lauraceae	<i>Cinnamomum subavenium</i>	T
Lauraceae	<i>Litsea acuminata</i>	T
Lauraceae	<i>Litsea cubeba</i> ²⁾	U
Lauraceae	<i>Machilus thunbergii</i>	T
Lauraceae	<i>Machilus zuihoensis</i> var. <i>mushaensis</i>	M
Lauraceae	<i>Neolitsea aciculata</i> var. <i>variabilima</i>	T

(con't)

Family	Species	Growth form*
Lauraceae	<i>Neolitsea acuminatissima</i>	T
Magnoliaceae	<i>Michelia compressa</i>	T
Melastomataceae	<i>Barthea barthei</i>	U
Oleaceae	<i>Osmanthus matsumuranus</i>	M
Rosaceae	<i>Eriobotrya deflexa</i> ²⁾	U
Rosaceae	<i>Malus doumeri</i>	T
Rosaceae	<i>Prunus phaeosticta</i>	T
Rubiaceae	<i>Tricalysia dubia</i> ²⁾	U
Rutaceae	<i>Skimmia reevesiana</i>	U
Rutaceae	<i>Tetradium meliaeifolia</i>	U
Sabiaceae	<i>Meliosma callicarpaefolia</i>	M
Sabiaceae	<i>Meliosma squamulata</i>	M
Saxifragaceae	<i>Itea parviflora</i>	U
Symplocaceae	<i>Symplocos arisanensis</i>	M
Symplocaceae	<i>Symplocos heishanensis</i>	T
Symplocaceae	<i>Symplocos juiyenensis</i>	M
Symplocaceae	<i>Symplocos sonoharae</i>	M
Symplocaceae	<i>Symplocos stellaris</i>	M
Symplocaceae	<i>Symplocos wikstroemiifolia</i>	M
Theaceae	<i>Cleyera japonica</i>	T
Theaceae	<i>Eurya hayatae</i>	U
Theaceae	<i>Eurya loquaiana</i>	U
Theaceae	<i>Eurya renegechiensis</i>	U
Theaceae	<i>Eurya strigillosa</i>	M
Theaceae	<i>Gordonia axillaris</i>	T
Theaceae	<i>Schima superba</i>	T
Theaceae	<i>Ternstroemia gymnanthera</i>	T
Trochodendraceae	<i>Trochodendron aralioides</i>	T
Verbenaceae	<i>Callicarpa randaiensis</i> ²⁾	U

* U, understory treelet, adults < 10 m tall; M, midstory tree, adults 10~20 m tall; T, canopy trees, adults > 20 m tall.

¹⁾ Species only recorded in the 1995 census.

²⁾ Species only recorded in the 2007 census.

