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Vegetation Pattern and Woody Species Composition of a Broad-Leaved Forest at the Upstream Basin of Nantzuhsienhsi in Mid-southern Taiwan

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ABSTRACT: A 8.37-ha plot of the broad-leaved forest at an elevation of about 2000 m in the upstream basin of the Nantzuhsienhsi River in mid-southern Taiwan was set up for long-term monitoring of forest dynamics. All stems with diameter at breast height (d.b.h.) ≧ 1 cm were identified, measured, tagged, and mapped to analyze the forest composition, structure and species diversity of the plot. A total of 18,790 woody plant individuals, belonging to 64 species in 27 families, were recorded. The dominant families were Lauraceae, Fagaceae, and Theaceae, accounting for 78.8% of total individuals. The dominant species were *Castanopsis carlesii*, *Machilus japonica*, *Listea acuminate*, and *Cyclobalanopsis stenophylloides*. The most abundant species in the canopy layer was *Castanopsis carlesii*, in the subcanopy layer was *Listea acuminate*, and in the shrub layer were *Machilus japonica* and *Listea acuminata*. Four plant communities were identified based on Two-way Indicator Species Analysis (TWINSPAN) classification, including three evergreen forest types and one deciduous forest type. The three evergreen types are *Machilus japonica* type, locating on the east and west valleys and partial lower slopes, *Machilus japonica-Castanopsis carlesii* type, locating on middle to lower slopes and the central dry valley, and *Schima superba-Castanopsis carlesii* type, locating on eastern ridge and upper slopes. The deciduous type is *Alnus formosana* forest which is distributed on mid-west and southwestern ridges. The means of species number, density and basal area for different forest types declined gradually from ridge to valley habitats. These results reveal that topography is an important factor which is closely related to the distribution of evergreen broad-leaved forest types in the plot.

KEY WORDS: Broad-leaved forest, vegetation pattern, species composition, Forest Dynamics Plot, Nantzuhsienhsi.

INTRODUCTION

In order to study spatial and temporal patterns of tree population and forest community, many Forest Dynamics Plots were set up for long-term monitoring of large numbers of trees. For example, there are seven large tropical Forest Dynamics Plots located in the Neotropics and Plaeotropics (Wills et al., 2006), and some on Japanese islands in East Asia (Enoki, 2003; Manabe et al., 2000; Masaki et al., 1992; Tanouchi and Yamamoto, 1995; Yamamoto et al., 1995). Across Taiwan, there are 14 Forest Dynamics Plots with size more than 1 ha, but only two of them are larger than 4 ha: one is a 25-ha broad-leaved forest plot in Fushan (Chang et al., 2004) and the other is a 10-ha Karst forest plot in Kenting (Wang et al., 2000). According to vegetation zones of Taiwan (Su, 1984), the Kenting plot is approximately in the *Ficus-Machilus* forest zone and the Fushan plot belongs to the *Machilus-Castanopsis* forest zone. There is yet no large-area forest dynamic study based on the *Quercus* forest zone.

Broad-leaved forests in the upstream basin of the Nantzuhsienhsi River are located in the middle elevation of mid-southern Taiwan and are well protected from human disturbances by Yushan National Park since 1985 (Chen, 2001). The aim of this study was to establish a larger Forest Dynamics Plot in the upstream basin of the Nantzuhsienhsi

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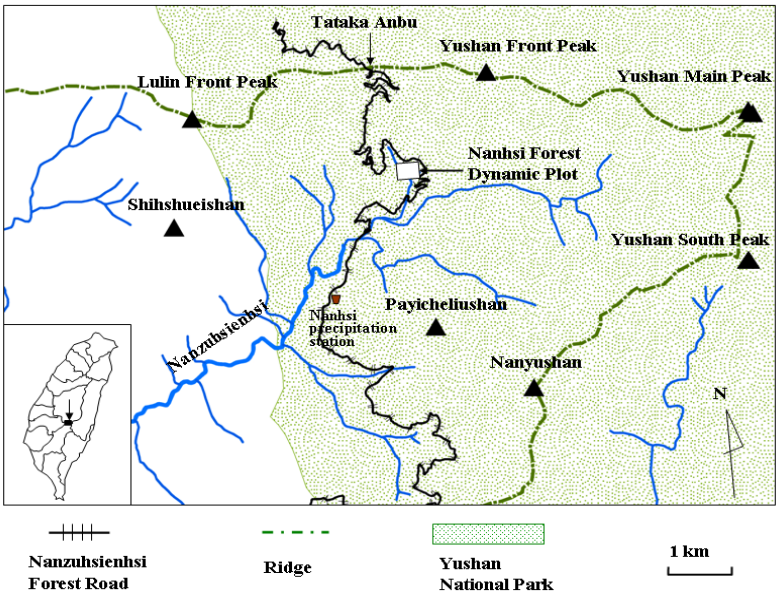

Fig. 1. Location of the Nanhsi Forest Dynamic Plot in mid-southern Taiwan.

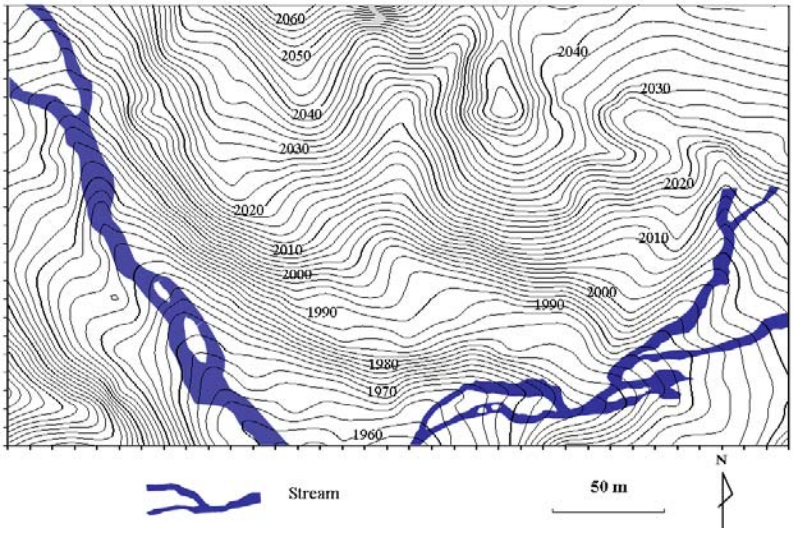

Fig. 2. The contour map of the Nanhsi Forest Dynamics Plot.

River, and to provide information useful for a better understanding of the broad-leaved forests located in the *Quercus* forest zone. The results of this study presented the vegetation patterns, species composition, floristic structures and the relationships between forest communities and topographic positions in this plot. This study also can serve as a basis for cross-site comparisons with other Forest Dynamics Plots in Taiwan and other ecosystems.

Study area

A 8.37-ha Forest Dynamics Plot, Nanhsi plot, near the 9.5 K to 10.0 K of Nantzuhsienhsi forest road, centered approximately at 23°27'40.7" N and 120°54'22.2" E was designated in 2003 and achived in 2006 (Fig. 1). This plot is about 5 km southwest away from Yushan (also called Mt. Yushan, Mt. Morrison or Mt. Jade) and situated in the broad-leaved forests in the upstream basin of the western part of the Yushan National Park, mid-southern Taiwan. The topography types of this plot include valleys, slopes and ridges. One stream ran through the plot from northwest to south all year round and the other from east to southwest parts. The two streams joined outside the south of this plot (Fig. 2) and formated the Nantzuhsienhsi, (also called

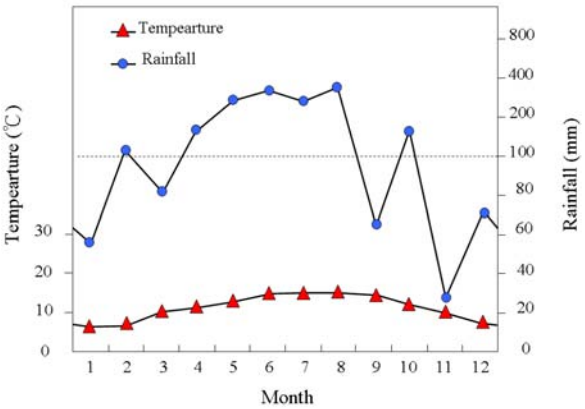

Fig. 3. Monthly average temperature and rainfall estimated from weather station records near the Nanhsi Forest Dynamics Plot. Mean annular temperture = 11.5 ºC and mean annular rainfall = 2007 mm.

River Nantzuhsien) and Elevation here ranged from 1,955 to 2,064 m above sea level. The bedrock was slate with mixed metamorphic sandstone of Shihpachungchi Formation of early middle Eocene, and the soil was forest brown soil. The climate condition (Fig. 3) between 1998 and 2002, estimated by combined data from nearby weather stations, showed that the mean annual temperature of 11.5 ºC and the monthly means ranged from 7.2 ºC in January to 14.5 ºC in July (Alishan weather station, 2,406 m above sea level). The mean annual rainfall was 2007 mm, estimated by Nanhsi precipitation station. The 63% of total rainfalls are caused by *Meiyu* (spring monsoon rain), summer southwest monsoons, typhoons and thundershowers.

METHODS

The Nanhsi Forest Dynamics Plot was divided into 837 quadrats, each with 10 m × 10 m in size. Within each quadrat, all free-standing woody plants with stems of diameters at breast height (d.b.h.; 1.3 m above ground) ≧ 1 cm were tagged, measured, mapped, and identified from January 2005 to February 2006. Botanical nomenclature was adopted from the Flora of Taiwan (Huang, 1993-1998). All individuals were classified into three groups according to their crown position and height. These groups are 'canopy layer' for trees reached forest canopy, 'subcanopy layer' for tree crowns below the canopy layer and > 5 m in height, and 'shrub layer' for trees ≦ 5 m in height.

The relative dominance of each species in this plot was determined based on its Important Value (IV_{total} = (individuals of one species in this plot / total individuals in this plot + basal area of one species in this plot / total basal area in this plot) / 2). Diameter records of a multiple-stemed tree were recalculated as if from a single tree, by assuming the same total basal area value derived from summing up all stems of one individual. Two-way Indicator Species Analysis (TWINSPAN) was applied to classify vegetation types (Hill, 1979) using PC-ORD (McCune and Mefford, 1999). The analysis was based on a primary matrix of 64 species × 824 quadrats, excluding 13 quadrats that without any tree records. The parameter in the primary matrix were species Important Value by quadrats: $IV_{quadrat}$ = (individuals of one species in the quadrat / total individuals in this plot + basal area of one species in the quadrat / total basal area in this plot) / 2. All 837 quadrats were assigned to one of the five habitat categories (ridge, upper slope, middle slope, lower slope and valley) in order to access the relationships between vegetations and habitat types. Ridges are defined as quadrats located on a relatively higher elevation than adjacent quadrats; upper slopes are slopes below the ridges; lower slopes are slopes near to the bottom of mountain hills; middle slopes are those transition slopes between upper and lower slopes. Valleys are those located at the foot slopes and bottomlands which with flat and concave topography and/or near ravines. The correlations between TWINSPAN and topography types of all 837 quadrats were tested by chi-square goodness-of-fit statistics to determine whether topographic heterogeneity is related to the vegetation types in the Nanhsi plot.

Following TWINSPAN classification, dominant species of each forest type were determined by its Important Value within each type ($IV_{within\ type}$ = (individuals of one species in that forest type / total individuals in that forest type + basal area of one species in that forest type / total basal area in that forest type) / 2). The character species for different vegetation types were chosen by using the first indicator species of serial hierarchy of TWINSPAN classificationand by using the Important Value between types > 50% ($IV_{between\ types}$ = (density of one species in one forest type / total amount density of this species in four forest types + mean basal area of this species in this forest type / total amount of mean basal area of this species in four forest types) / 2). The unit of density is stem/ha and that of mean basal area is m^2/ha.

Species diversity was measured by using the Simpson's index $D = 1 - \Sigma(n_i / N)^2$, and the Shannon-Wiener index $H = - \Sigma(n_i / N)\log(n_i / N)$, where n_i = number of individuals of species i in the plot or the forest type, and N = Total number of individuals in the plot or the forest type.

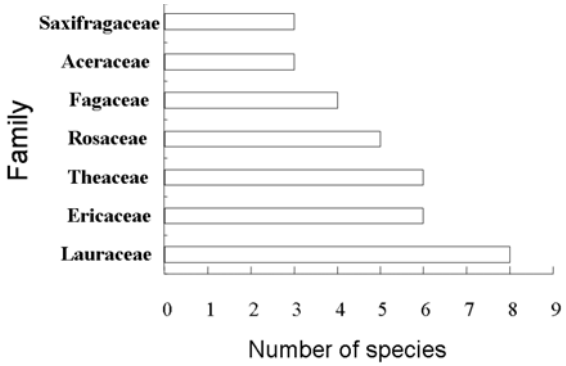

Fig. 4. Families with more than three species in the Nanhsi Forest Dynamics Plot.

RESULTS

Woody floristic composition and structure

A total of 64 species belonging to 51 genera and 27 families were found in this plot. It was composed of one evergreen conifer, and 44 evergreen and 19 deciduous, broad-leaved angiosperms. There were 48 tree species and 16 shrub species. The family with the most species number was Lauraceae, followed by Theaceae, Ericaceae, Rosaceae, Fagaceae, Aceraceae, and Saxifragaceae (Fig. 4). These 7 families contained 53 species and accounted for 82.8% of total species numbers.

In terms of individual numbers, the density of this plot was 2,245 individual/ha and a total of 18,790 individuals were recorded. Individual numbers per quadrat ranged from 0 to 80 and the average is 22 individuals. Density was high on the steep slopes, especially in the southwestern slope of the mid-west ridge and southeastern slope of mid-east ridge (Fig. 5). Lauraceae was the most abundant family, followed by Fagaceae and Theaceae. These three families accounted for 78.8% of total individuals in the plot. *Listea acuminata* was the most abundant species, followed by *Machilus japonica*, *Eurya leptophylla*, *Castanopsis carlesii*, *Eurya loquaiana*, *Cyclobalanopsis stenophylloides*, *Neolitsea sericea*, *Rhododendron latoucheae*, *Pasania kawakamii*, and *Pourthiaea beauverdiana* var. *notabilis* (Table 1). The five most abundant species together accounted for 61.13% of total individuals.

The basal area was 54.64 m^2/ha in the plot. Family with the highest basal area is Fagaceae (accounted for 55.93% of total basal area), followed by Lauraceae (20.58%) and Betulaceae (7.69%). Other families all had less than 5% of total basal area. The top ten species with the highest basal area values were *Castanopsis carlesii*, *Cyclobalanopsis stenophylloides*, *Pasania kawakamii*, *Machilus japonica*, *Alnus formosana*, *L. acuminata*, *Schima superba*, *N. sericea*, *Machilus zuihoensis var. mushaensis*, and *Michelia compressa* (Table 1). Cumulative basal area of these ten species was 86.73%.

The four most important families, based on IV_{total}, were Fagaceae, Lauraceae, Theaceae, and Betulaceae. These four families collectively comprised 84.63% of IV_{total} in this plot. *Castanopsis carlesii* (IV_{total} = 20.67%) was the most dominant species, followed by *Machilus japonica*, *L. acuminata*, *Cyclobalanopsis stenophylloides*, *Pasania kawakamii*, *Eurya leptophylla*, *A. formosana*, *Eurya loquaiana*, *N. sericea*, and *S. superba* (Table 1). These ten species together represented 78.56% of total IV_{total}.

Species composition in vertical structure

In the canopy layer, 35 species and 1,356 individuals were found in this census. The most abundant families were Fagaceae (48.53% of total individuals of this layer), Lauraceae (19.25%), and Betulaceae (15.56%). The species had greatest number of individuals was *Castanopsis carlesii*, followed by *A. formosana*, *Pasania kawakamii*, *Cyclobalanopsis stenophylloides*, *Machilus japonica*, *L. acuminata*, *Machilus zuihoensis var. mushaensis* , *N. sericea*, *S. superba*, and *Michelia compressa* (Table 1). These ten species cumulatively comprised 86.28% of total individuals in this canopy layer.

In the subcanopy layer, there were 52 species and 4,167 individuals. Lauraceae and Fagaceae were the most abundant species in this layer, accounting for 48.07% and 22.58% of individuals, respectively. *L. acuminata* was the most abundant species, followed by *Machilus japonica*, *Castanopsis carlesii*, *Cyclobalanopsis stenophylloides*, *N. sericea*, *Pourthiaea beauverdiana* var. *notabilis*, *Osmanthus matsumuranus*, *Pasania kawakamii*, *R. latoucheae*, and *Michelia compressa* (Table 1). These ten species together accounted for 79.91% of individuals of the subcanopy layer.

In the shrub layer, 56 species and 13,267 individuals were recorded. Lauraceae (40.76%), Theaceae (26.77%), and Fagaceae (12.89%) were the most abundant families. *Machilus japonica*, *L. acuminata*, *Eurya leptophylla*, *Castanopsis carlesii*, *Eurya loquaiana*, *R. latoucheae*, *Callicarpa formosana*, *N. sericea*, *Viburnum taitoense*, and *Cyclobalanopsis stenophylloides* (Table 1) were the abundant species and accounted for 80.49% of individuals in this layer.

Most species presented more individuals in the shrub layer than in other layers. However, *A. formosana*, *Tetradium meliaefolia*, *Ulmus uyematsui*, and *Acer insulare* showed more individuals in the

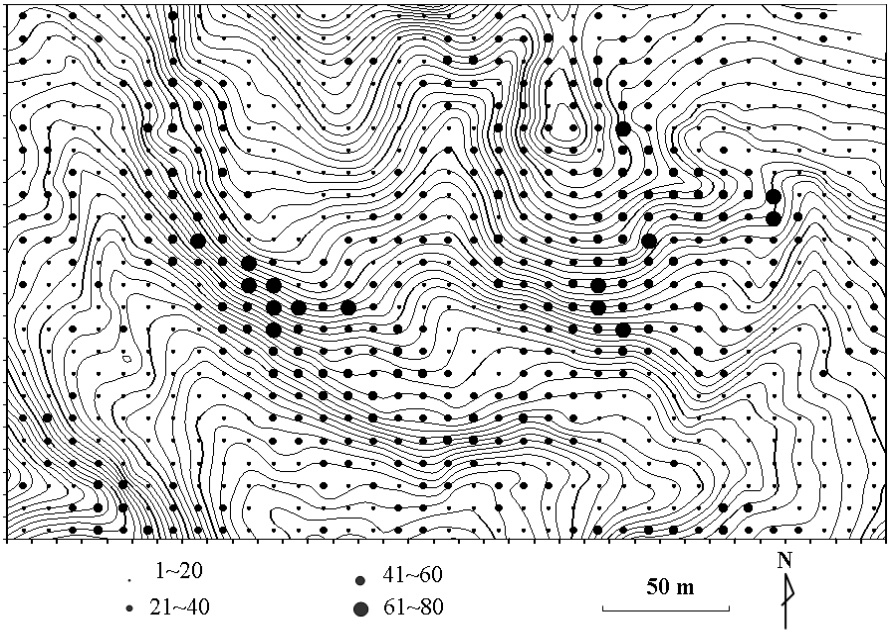

Fig. 5. Distribution map for the number of individuals per quadrat in the Nanhsi Forest Dynamics Plot.

Table 1. Woody species composition in the Nanhsi Forest Dynamics Plot: number of individuals of each forest layer, total number, basal area (BA), and important value (IV=(relative density+relative basal area)/2). Only the species with IV ≧ 0.25% are presented.

Species	Number of individuals				BA	IV
	Canopy	Subcanopy	Shrub	Total	(m^2ha^{-1})	(%)
Castanopsis carlesii	372	525	1093	1990	16.80	20.67
Machilus japonica	89	612	2320	3021	4.68	12.32
Litsea acuminata	65	1026	2204	3295	3.29	11.78
Cyclobalanopsis stenophylloides	136	270	311	717	7.76	9.01
Pasania kawakamii	137	135	298	570	5.44	6.49
Eurya leptophylla	3	13	2086	2102	0.20	5.77
Alnus formosana	207	33	4	244	4.14	4.44
Eurya loquaiana	-	31	1048	1079	0.17	3.02
Neolitsea sericea	43	204	387	634	1.32	2.89
Schima superba	42	72	122	236	1.68	2.17
Machilus zuihoensis var. mushaensis	49	89	142	280	1.26	1.90
Rhododendron latoucheae	-	118	508	626	0.20	1.85
Pourthiaea beauverdiana var. *notabilis*	8	184	293	485	0.43	1.68
Gordonia axillaris	26	78	293	397	0.64	1.64
Callicarpa formosana	1	68	411	480	0.35	1.60
Michelia compressa	30	110	98	238	1.03	1.58
Osmanthus matsumuranus	18	146	126	290	0.60	1.32
Viburnum taitoense	-	14	311	325	0.05	0.91
Cinnamomum insulari-montanum	13	38	78	129	0.55	0.85
Litsea akoensis	-	20	268	288	0.07	0.83
Elaeocarpus sylvestris	13	36	44	93	0.57	0.77
Quercus tatakaensis	13	11	8	32	0.56	0.60
Tetradium meliaefolia	23	7	1	31	0.57	0.60
Vaccinium randaiense	1	44	98	143	0.14	0.51
Malus doumeri	12	42	26	80	0.32	0.51
Eriobotrya deflexa	3	49	72	124	0.14	0.46
Ulmus uyematsui	11	4	1	16	0.42	0.43
Viburnum luzonicum	-	11	133	144	0.02	0.41
Acer insulare	16	14	2	32	0.32	0.38
Acer albopurpurascens	5	13	19	37	0.28	0.36
Symplocos konishii	-	27	56	83	0.03	0.25
Others	20	123	406	549	0.61	2.00
Total	1356	4167	13267	18790	54.64	100.00

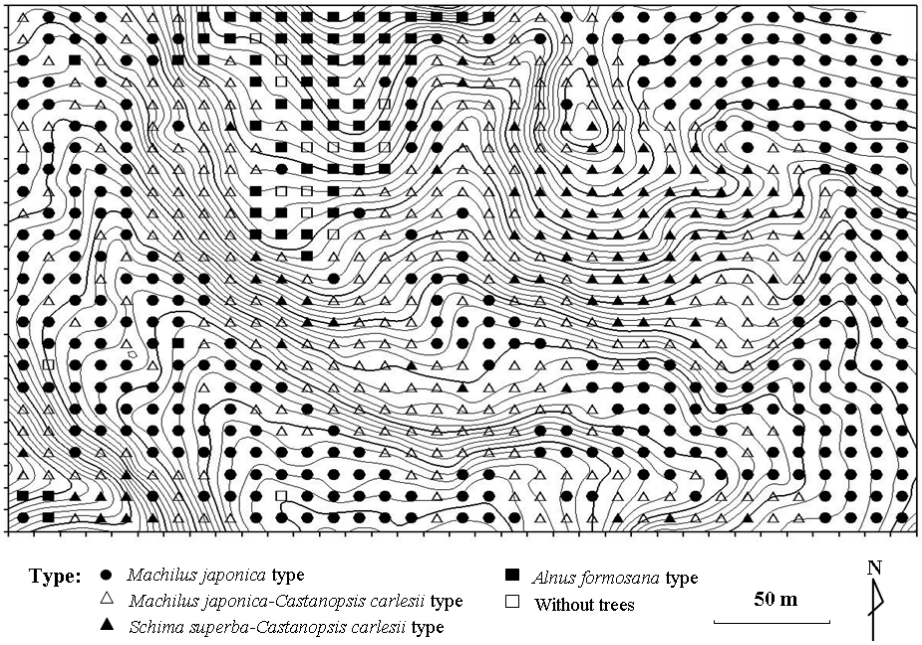

Fig. 6. Distribution patterns of four woody plant community types in the Nanhsi Forest Dynamics Plot.

canopy and subcanopy layers than in the shrub layer (Table 1).

Classification of plant community

The indicators presented by TWINSPAN classification were chosen as the character species of each vegetation type. In addition, species with IV $_{\text{between types}}$ > 50% in each vegetation type were also candidates for character species, because these species presented a relatively high proportion in the vegetation type. The results of TWINSPAN classification showed four plant communities, including three types of the evergreen forest (*Machilus japonica* type, *Machilus japonica-Castanopsis carlesii* type, *Schima superba-Castanopsis carlesii* type) and a deciduous forest (*Alnus formosana* type) (Fig. 6). Except for those quadrats without any tree individuals, habitat association were tested for each TWINSPAN types (Table 2).

I. *Machilus japonica* type (Lauraceae / Fagaceae type)

This forest type included 364 quadrats, mainly located on the east and west valley, and partial lower slope, and few quadrats appearing on central dry valley (Fig. 6). Chi-square test indicated that *Machilus japonica* type was significantly, positively associated with lower slope and middle slope (Table 2); especially the lower slope. In addition, this was the major forest type of valley (foot slope-bottomland; Table 2). There were 50 species and 5,347 individuals recorded in this type. This type had relatively low density and mean basal area (Table 3). Lauraceae was the most dominant family (51.93% of IV $_{\text{within type}}$), followed by Fagaceae (31.53%). *Machilus japonica* was most dominant species, based on IV $_{\text{within type}}$, and followed by *Pasania kawakamii*, *L. acuminata*, and *Cyclobalanopsis stenophylloides* (Table 4). The character species were *Machilus japonica* (selected by TWINSPAN) and *L. akoensis* (Table 5). Both species had IV $_{\text{between types}}$ > 50% in this forest type (Table 5).

II. *Machilus japonica-Castanopsis carlesii* type (Fagaceae / Lauraceae type)

This forest type included 303 quadrats mostly appeared on middle and lower slope, and central dry valley in this plot (Fig. 6, Table 2). Most quadrats in this type distributed in topography position above *Machilus japonica* type and below *Schima superba-Castanopsis carlesii* type (Fig. 6). This forest type included 56 species and 8,637 individuals. Density and mean basal area were between those of *Machilus japonica* type and *Schima superba-Castanopsis carlesii* type (Table 3). Fagaceae was the most dominant family with 41.55 % in IV $_{\text{within type}}$, followed by Lauraceae (36.76%). The 5 most dominant species, in descending order of IV $_{\text{within type}}$, were *Castanopsis carlesii*, *L. acuminata*, *Cyclobalanopsis stenophylloides*, *Eurya leptophylla*,

Table 2. Chi-square goodness-of-fit test for habitat associations for the Nanhsi Forest Dynamics Plot. Most observed values of the quadrats with no recorded plants were less than 5 and not included in the analysis. The first rows of each set are numbers of quadrats associated with a forest type, the second rows display the percentage of quadrats within each vegetation type and the third rows indicate the percentage of quadrats within each habitat category. Pearson chi-square value is 498.25 (df=12), likelihood ratio is 482.71 (df=12), and p value (2-sided asymptotic significance) is less than 10^{-94}. For each forest type, '+' indicates a significant positive association, '++' indicates a strongly significant positive association and '-' indicates a significant negative association ($\alpha \leqq 0.05$). The quadrats without any woody plants are not correlated with any habitat association.

Habitat category	Forest type				Total	N
	I	II	III	IV		
Ridge	1^{-}	8^{-}	19	26	54	4
% within forest type	0.28	2.63	19.59	43.33	6.55	
% within habitat type	1.85	14.81	35.19	48.15	100	
Upper slope	9	54	20^{+}	21^{+}	104	7
% within forest type	2.48	17.76	20.62	35.01	12.62	
% within habitat type	8.66	51.92	19.23	20.19	100	
Middle slope	55^{+}	151^{+}	53^{+}	11	270	0
% within forest type	15.15	49.67	54.64	18.33	32.77	
% within habitat type	20.37	55.93	19.63	4.07	100	
Lower slope	227^{++}	57^{+}	4	0	288	1
% within forest type	62.53	18.75	4.12	0	34.95	
% within habitat type	78.82	19.79	1.39	0	100	
Foot slope-bottomland	71	34	1^{-}	2	108	1
% within forest type	19.56	11.19	1.03	3.33	13.11	
% within habitat type	65.74	31.48	0.93	1.85	100	
Total	363	304	97	60	824	13
% within forest type	100	100	100	100	100	
% within habitat type	44.053	36.89	11.77	7.28	100	

Forest type: I: *Machilus japonica* type (Lauraceae / Fagaceae type), Ⅱ: *Machilus japonica-Castanopsis carlesii* type (Fagaceae / Lauraceae type), Ⅲ: *Schima superba-Castanopsis carlesii* type (Fagaceae / Theaceae type), Ⅳ: Deciduous *Alnus formosana* forest type, N: number of quadrats without any individuals.

Table 3. Density, basal area and diversity of the four forest types in the Nanhsi Plot.

	Forest type				Whole Plot
	I	II	III	IV	
Number of quadrats	364	303	97	60	824
Species no.	50	56	49	28	64
Species no. (per 0.01 ha)	6	11	13	4	8
Density (individuals / ha)	1,469	2,850	4,406	887	2,245
Basal Area (m^2 / ha)	41.21	62.49	93.11	46.17	54.64
Simpson's index	0.81	0.90	0.90	0.84	0.91
Shannon-Wiener index	2.34	2.78	2.73	2.30	2.86

Forest type: I: *Machilus japonica* type (Lauraceae / Fagaceae type), Ⅱ: *Machilus japonica-Castanopsis carlesii* type (Fagaceae / Lauraceae type), Ⅲ: *Schima superba-Castanopsis carlesii* type (Fagaceae / Theaceae type), Ⅳ: Deciduous *Alnus formosana* forest type.

and *Machilus japonica* (Table 4). The character species were *Machilus japonica* (selected by TWINSPAN), *Castanopsis carlesii* (TWINSPAN indicator of the traced-up hierarchy), *Viburnum taitoense* and *Machilus zuihoensis var. mushaensis* . Only $IV_{between\ types}$ of *Viburnum taitoense* and *Machilus zuihoensis var. mushaensis* in this forest type having $IV_{between\ types} > 50\%$ (Table 5).

III. *Schima superba-Castanopsis carlesii* type (Fagaceae / Theaceae type)

This forest type included 97 quadrats, appearing on eastern ridge, upper and middle slope within the plot (Fig. 6). Chi-square test indicated that Type III tended to distribute in upper and middle slope, but not in lower slope and valley (Table 2). A total of 49 species and 4,274 individuals were recorded. This forest type contained higher density and basal area than other three types (Table 3). Fagaceae, with 43.82% of $IV_{within\ type}$, was the most dominant family and Theaceae with 27.63% was after it. The three most dominant species in descending order of $IV_{within\ type}$ were *Castanopsis carlesii*, *S. superba*, and *L. acuminata* (Table 4). TWINSPAN classification indicated that *S. superba* and *Castanopsis carlesii* were indicators of this forest type. The $IV_{between\ types}$ of *S. superba*, *R. latoucheae*, *Vaccinium randaiense*, *Viburnum luzonicum Gordonia axillaris*,

Table 4. Important values ($IV_{within\ type}$) of woody species within each forest type in the Nanhsi Plot. The underlined values indicate those critical species with IV values just > 7% within each forest type. Species listed above the underlined values are the major species.

I. *Machilus japonica* (Lauraceae / Fagaceae) type		II. *Machilus japonica-Castanopsis carlesii* (Fagaceae / Lauraceae) type		III. *Schima superba-Castanopsis carlesii* (Fagaceae / Theaceae) type		IV. *Alnus formosana* (Deciduous forest) type	
Species	IV (%)	Species	IV (%)	Species	IV (%)	Species	IV (%)
Machilus japonica	29.53	*Castanopsis carlesii*	26.19	*Castanopsis carlesii*	36.68	*Alnus formosana*	58.23
Pasania kawakamii	12.90	*Litsea acuminata*	13.08	*Schima superba*	9.45	*Callicarpa formosana*	9.84
Litsea acuminata	12.53	*Cyclobalanopsis stenophylloides*	9.94	*Litsea acuminata*	9.07	*Eurya leptophylla*	7.91
Cyclobalanopsis stenophylloides	11.64	*Eurya leptophylla*	8.18	*Rhododendron latoucheae*	5.75	*Litsea acuminata*	5.56
Castanopsis carlesii	6.46	*Machilus japonica*	7.24	*Eurya leptophylla*	5.20	*Deutzia pulchra*	2.29
Neolitsea sericea	5.32	*Pasania kawakamii*	4.88	*Cyclobalanopsis stenophylloides*	5.09	*Clerodendrum trichotomum*	2.09
Callicarpa formosana	2.32	*Eurya loquaiana*	3.83	*Eurya loquaiana*	4.91	*Pourthiaea beauverdiana* var. *notabilis*	1.97
Litsea akoensis	2.19	*Machilus zuihoensis var. mushaensis*	2.71	*Gordonia axillaris*	3.68	*Eurya loquaiana*	1.42
Eurya leptophylla	2.16	*Alnus formosana*	2.67	*Michelia compressa*	2.43	*Acer insulare*	1.35
Machilus zuihoensis var. mushaensis	1.71	*Neolitsea sericea*	2.47	*Pourthiaea beauverdiana* var. *notabilis*	2.17	*Pasania kawakamii*	1.29
Pourthiaea beauverdiana var. *notabilis*	1.65	*Gordonia axillaris*	1.70	*Vaccinium randaiense*	1.51	*Gordonia axillaris*	1.26
Michelia compressa	1.23	*Osmanthus matsumuranus*	1.68	*Cinnamomum insulari-montanum*	1.05	*Vaccinium randaiense*	0.78
Osmanthus matsumuranus	1.15	*Michelia compressa*	1.60	*Quercus tatakaensis*	1.03	*Debregeasia edulis*	0.74
Tetradium meliaefolia	1.14	*Pourthiaea beauverdiana* var. *notabilis*	1.39	*Pasania kawakamii*	1.01	*Neolitsea sericea*	0.58
Viburnum taitoense	1.03	*Viburnum taitoense*	1.27	*Osmanthus matsumuranus*	1.00	*Litsea akoensis*	0.54
Ulmus uyematsui	0.89	*Rhododendron latoucheae*	1.24	*Alnus formosana*	0.97	*Tetradium meliaefolia*	0.51
Other 34 species	6.16	Other 40 species	9.94	Other 33 species	9.00	Other 12 species	3.64
Total	100	Total	100	Total	100	Total	100

Castanopsis carlesii, *Michelia compressa*, *Eriobotrya deflexa*, *Eurya loquaiana*, and *Cinnamomum insulari-montanum* in this forest type were with $IV_{between\ types}$ > 50%, suggesting this forest type had more character species than other three types (Table 5). Among them, *S. superba* and *R. latoucheae* with 95.36% and 87.38% of $IV_{between\ types}$ (Table 5) were the top two indicators of this forest type.

Ⅳ. *Alnus formosana* type (Deciduous forest type)

A total of 60 quadrats were classified as this forest type, locating in the mid-western and southwestern ridges (Fig. 6). This forest type showed significant positive association with upper slope (Table 2). In addition, most ridge quadrats belonged to this forest type (Table 2). This type contains 28 species and 532 individuals, and about 3/4 of $IV_{within\ type}$ (78.29%) were deciduous species (n =12). Density and mean basal area of this type were less than those of other three types (Table 3). *A. formosana*, the first indicator selected by TWINSAPN, was also the most dominant species ($IV_{within\ type}$ = 58.23%; Table 4). *Callicarpa formosana* and *Eurya leptophylla* also dominated in this type, but their $IV_{within\ type}$ was much less than *A. formosana* (Table 4). *A. formosana* and *Callicarpa formosana* were also the character species of this type (Table 5). None of the six character species in Type II or III (e.g., *Castanopsis carlesii*, *R. latoucheae*, *Viburnum taitoense*, *Michelia compressa*, *S. superba*, and *Cinnamomum insulari-montanum*) were presented in this forest type. Moreover, *Osmanthus matsumuranus* that generally presented in other three types was also not in this forest type.

Species diversity

Species number within a quadrat ranged from 1 to

Table 5. Important values ($IV_{between\ type}$) of woody species in the four forest types in the Nanhsi Plot.

Species	$IV_{between\ types}$ (%)				Total abundance
	I	II	III	IV	
Litsea acuminata	22.63	38.59	33.09	5.69	3295
Machilus japonica	**68.31**	26.55	4.62	0.52	3021
Eurya leptophylla	5.59	39.07	34.53	20.81	2102
Castanopsis carlesii	4.64	29.11	**66.25**	0.00	1990
Eurya loquaiana	2.13	34.89	**55.35**	7.62	1079
Cyclobalanopsis stenophylloides	25.14	37.02	37.15	0.69	717
Neolitsea sericea	49.70	34.67	12.34	3.29	634
Rhododendron latoucheae	0.03	12.59	**87.38**	0.00	626
Pasania kawakamii	46.31	35.11	13.75	4.83	570
Pourthiaea beauverdiana var. *notabilis*	16.66	20.27	41.84	21.24	485
Callicarpa formosana	16.40	13.99	6.34	**63.27**	480
Gordonia axillaris	1.14	20.70	**71.45**	6.71	397
Viburnum taitoense	27.89	**62.50**	9.62	0.00	325
Osmanthus matsumuranus	19.52	43.33	37.14	0.00	290
Litsea akoensis	**57.00**	22.06	1.20	19.74	288
Machilus zuihoensis var. mushaensis	19.27	**50.73**	28.45	1.55	280
Alnus formosana	0.50	5.98	4.65	**88.87**	244
Michelia compressa	12.01	26.72	**61.27**	0.00	238
Schima superba	0.27	4.37	**95.36**	0.00	236
Viburnum luzonicum	2.89	22.92	**73.13**	1.06	144
Vaccinium randaiense	0.47	10.92	**74.93**	13.67	143
Cinnamomum insulari-montanum	11.45	35.81	**52.74**	0.00	129
Eriobotrya deflexa	7.53	37.59	**53.34**	1.54	124

Numbers in bold indicate $IV_{between\ types} \geqq 50.00$. Those indicate species with very high possibility to occur in unique forest type as additional character species. Forest type, I: *Machilus japonica* type, Lauraceae / Fagaceae type, II: *Machilus japonica-Castanopsis carlesii* type, Fagaceae / Lauraceae type, Ⅲ: *Schima superba-Castanopsis carlesii* typ, Fagaceae / Theaceae type, Ⅳ: Deciduous *Alnus formosana* forest type.

20, and the average was 8 species. Most diversity indexes differed among these four forest types (Table 3). Type II had the greatest species number, and Type Ⅲ had the greatest number of species per quadrat. Both numbers were lowest for Type Ⅳ. Type II and III had higher Simpson's index than the other two, but the numbers of these four types were all close to 1. Type II had the greatest number of Shannon-Wiener index, followed by Type III, Type I and Ⅳ. The deciduous forest type (Type IV) showed lower diversity than the other evergreen forests, according to most of the indexes in Table 3. Species-area curves showed that at the 0.01 ha scale (1 quadrat) the range of species number was 4 to 13 and it was 16 to 31 species at the 0.1 ha scale (10 quadrats). Each curve presented that the number of species was approaching an asymptote, but was still increasing (Fig. 7). Type III forest had the fastest increasing rate of species number, followed by Type II, Type I and Type Ⅳ. The patterns of species-area curves were similar for the Type III and Type II forests.

DISCUSSION

The altitudinal gradient of vegetation zones in Taiwan represents a large scale variation of montane vegetations of Taiwan (Liu, 1968; Su, 1984). The Nanhsi Forest Dynamics Plot was regarded as the upper *Quercus* vegetation zone in Taiwan (Su, 1984), in terms of its altitude range (1,955 to 2,064 m a. s. l.) and dominant floristic composition (*Castanopsis carlesii*, *Machilus japonica*, *L. acuminate*, and *Cyclobalanopsis stenophylloides*) (Hsieh et al., 1997; Su, 1984). Our studied forests were also similar to the forests dominated by *Cyclobalanopsis stenophylloides*/-*Castanopsis carlesii*/-*Machilus japonica*/-*Schima superba* and *Chamaecyparis formosensis* in the west ridge of Mt. Chunta, central Taiwan (Chen, 1995). Locally, the altitude position of this plot, 1,955 to 2,064 m above sea level, belonged to the border of the upper *Quercus* zone that the low limits of the elevation at about 1,900 m in the Nantzuhsienhsi valley (Su, 1984).

In a landscape scale, topography position is one of the important factors that can influence vegetation patterns (Chou, 2004; Fan et al., 2005; Hara et al., 1997; Hsieh et al., 2000; Lin et al., 2005; Song, 1996; Wang et al., 2000). These have been documented in Taiwan (Fan et al., 2005; Hara et al., 1997; Wang et al., 2000) and also some East Asian islands (e.g. Okinawa (Enoki, 2003) and Honshu (Nagamatsu, 2003) in Japan). Our study showed that vegetation types based on the first census of Nanhsi Forest Dynamics Plot were significantly related to their topography positions, suggesting the effects of

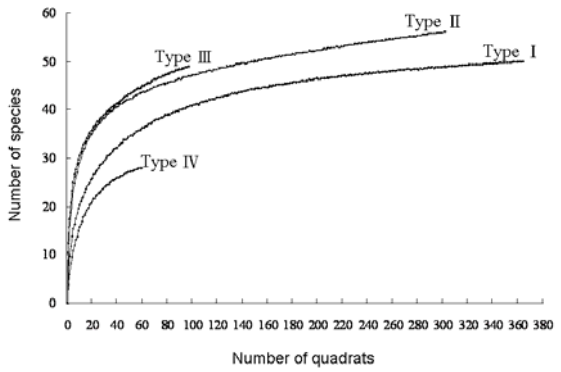

Fig 7. Species-area curves for four forest types of the Nanhsi Forest Dynamics Plot. I: *Machilus japonica* type, Ⅱ: *Machilus japonica-Castanopsis carlesii* type, Ⅲ: *Schima superba-Castanopsis carlesii* type, Ⅳ: Deciduous *Alnus formosana* forest type.

habitat (niche) differentiations. To further evaluate spatial patterns of specific species, analyses of species distributions within microtopographic positions, such as canopy gaps, or of wind disturbance patterns during typhoon and monsoon seasons will give insights into the forest dynamics in this region.

The deciduous forest (*A. formosana*) type in the Nanhsi plot is likely to be caused by both natural and anthropogenic disturbances, such as fire or landslide (caused by paving forest road) in about 40 to 50 years ago (Chen, 2001). Large *A. formosana* individuals mainly present in the northern quadrats of the plot, suggesting a past disturbance event in this part. Among the top ten dominant canopy species of the plot, *A. formosana* was the only species with very few individuals in the shrub layer, indicating a problem of regeneration. Forest structure may help to reflect forest disturbance history. For example, approximately 35-40 years after disturbances in the Techi Reservoir, there are more large individuals of *A. formosana* than small ones, suggesting *A. formosana* cannot regenerate well (Hsieh et al., 1989). Hsieh et al. (1989) also suggested that *A. formosana* is an early successional species and will gradually be replaced by other evergreen broad-leaved tree species. A long term observation of forest composition can help to reveal the role of *A. formosana* in this plot.

The other three evergreen broad-leaved forest types classified by TWINSPAN in the Nanhsi plot were related to the topographical position. For the most dominant species of the plot, *Castanopsis carlesii* was also a character species of the *Schima superba-Castanopsis carlesii* type (Type III). This type located in eastern ridge, upper and middle slope, and the character species, *S. superba*, was extremely prone to distributed in this habitat (Table 5). It may be because *S. superba* adapts to the sunny and windy environment conditions at the ridge and upper slopes. In comparison, the second dominant species, *Machilus japonica*, was the character species of the *Machilus japonica* type (Type I). This type favored the east and west valley, and partial lower slope within this plot. The relationships between the species distribution and topographic features are similar to the patterns reported in the lower elevation montane forests in south and north Taiwan (Hara et al., 1997). Hara et al. (1997) suggested that Fagaceae, including the *Castanopsis* and *Quercus* genera, was the most dominant taxon of upper slopes, whereas Lauraceae, represented by the *Machilus* genus, was the most dominant taxon in the lower slope.

The *Machilus japonica-Castanopsis carlesii* type (Type II), topographically in-between *Machilus japonica* type (Type I) and *Schima superba-Castanopsis carlesii* type (Type III), showed higher species diversity than the other two types (Table 3). The proportions of the top two dominant species (*Castanopsis carlesii* and *Machilus japonica*) of the whole plot were also in-between the Type I and III forests. In comparison, *Viburnum taitoense* and *Machilus zuihoensis var. mushaensis* were the characteristic species of this type. Therefore, Type II can be considered as an ecotone type between Type III and Type I.

This study provides a new combined method for selecting character species, using both traditional indicator species chosen by TWINSPAN and by $IV_{between\ types} > 50\%$. This is due to the traditional definition of character species based on TWINSPAN may sometimes appear in more than one vegetation types. Therefore, we suggest a new method in selecting character species using $IV_{between\ types}$ to choose species that specific to a certain vegetation type. This can help to avoid widely distributed character species and to indicate the specific character species for a vegetation type. The new method also helps to understand whether an ecotone vegetation would present many character species with high $IV_{between\ types}$.

Forest structure, tree density and basal area, of the studied evergreen forest types related to topographic positions, such that density and basal area were the highest in ridge, upper and middle slopes (Type III), and gradually decreased toward middle and lower slopes (Type II), and valley (Type I). In other forests, similar patterns were also found and suggested to be caused by soil disturbance correlated to topographic positions (Hara et al., 1996; Wang et al., 2000). The

other possible explanation may be due to a longer lifespan of trees in the upper slope than those in the foot slope and valley (Nagamatsu et al., 2003).

The basal area, 93.11 m^2/ha in ridge and upper slope area (Type III), of the Nanhsi plot is higher than that of the *Quercus* forests (68.67-80.65 m^2/ha) in Chungtzekuan (Chou, 2004) and Mt. Peitungyen (Song, 1996), both situated in similar elevation as our study. It is also higher than that of a lowland *Machilus-Castanopsis* forest (38.12-42.70 m^2/ha) in Nanjenshan (Hsieh et al., 2000). The Chungtzekuan and Peitungyen plots locate on the northwestern ridge of Mt. Kuhanuosin and southwestern ridge of Hehuanshan, respectively, whereas the forests of the Nanhsi plot locates in, southwestern valley of Yushan. The great basal area of the Nanhsi plot may be due to its sheltered topographic position, which relatively protects the plot from strong wind disturbances from typhoons.

For plots of the *Quercus* forest, species diversity is different even in a similar elevation. Diversity of the Nanhsi plot (H=2.86), upper *Quercus* forest, is higher than that of the Peitungyen plot (H=2.2), upper *Quercus* forest, but lower than that of the Chungtzekuan plot (H=3.4), lower *Quercus* forest (Chou, 2004). However, the diversity of evergreen forest types in the Nanhsi plot (H=2.34-2.78) compared to that of a lower *Quercus* forest plot in Mt. Lopei (H=2.61-2.67, 1,132-1,164 m a. s. l., Lin, 2005) showed similar floristic diversity. The results of this study suggest that the vegetation types of montane evergreen forests in Taiwan are related to topographic position and the high diversity here may be partially caused by the topographic heterogeneity in this landscape.

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臺灣中南部楠梓仙溪上游集水區闊葉森林的植被類型及物種組成

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摘　　要

為了瞭解中海拔闊葉森林的組成、結構及物種多樣性，本研究於臺灣中南部楠梓仙溪上游集水區設立一處 8.37 公頃的森林動態樣區，樣區內所有胸高直徑大於 1 公分之木本植物都登錄其物種、胸高直徑、位置，並給予編號。結果紀錄了 27 科 64 種，共 18,790 棵木本植物。其中三個優勢的科別為樟科、殼斗科與茶科，共佔了總數的 78.8%；樣區中優勢的物種分別為長尾栲、假長葉楠、長葉木薑子及狹葉櫟；森林結構方面，樹冠層以長尾栲為最優勢種類，次冠層以長葉木薑子為最優勢，灌木層則為假長葉楠與長葉木薑子。將資料以雙向指標種分析法（TWINSPAN）進行植群分類後，呈現出四型植物社會：假長葉楠型位於樣區東面及西面的底坡谷地，以及部分的下坡處；假長葉楠-長尾栲型位於樣區中至下坡處，以及樣區中央乾涸的底坡谷地；木荷-長尾栲型出現在東側的稜脊與上坡的區域，這三型屬於常綠闊葉森林，另外尚有臺灣赤楊型的落葉森林，位於樣區中偏西側的稜脊與西南角的稜脊上。樣區三種常綠闊葉林型的分佈與地形有密切相關，且各類型的平均物種數、密度及底面積，從稜脊到底坡谷地呈現逐漸下降的趨勢。顯示在楠溪樣區中，地形是影響常綠闊葉樹種分佈的重要因素。

關鍵詞：闊葉森林、植被類型、物種組成、森林動態樣區、楠梓仙溪。

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