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Species Composition and Structure of the Lowland Subtropical Rainforest at Lanjenchi, Southern Taiwan

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ABSTRACT: The forest in Lanjenchi is a remnant patch of subtropical rainforests in southern Taiwan. In 1998, the previous Lanjenchi plot was enlarged from 3 ha to 5.88 ha in order to include more topographical variation and understand how the gradient of wind stress controls forest structure and species composition. All free-standing woody plants in these plots with diameter ≥ 1 cm were identified, measured, tagged and mapped. A total of 60,146 individuals belonging to 136 vascular tree species in 83 genera and 42 families was recorded. Families with the largest cumulative basal areas were Fagaceae, Theaceae, Araliaceae, Aquifollaceae, Lauraceae and Illiciaceae. The size-class distribution of all species showed that most species were in good recruitment patterns with the most stems in small size classes. The results of two-way indicator species analysis (TWINSPAN) classified the sampling plots into four forest and habitat types: 1. *Rhaphiolepis indica* var. *hiiranensis* - *Illicium arborescens* (Windward I) type; 2. *Cinnamomum brevipedunculatum* - *Illicium arborescens* (Windward II) type; 3. *Sloanea formosana* - *Ilex cochinchinensis* (Leeward) type; and 4. *Glycosmis citrifolia* - *Helicia formosana* (Creek) type. The forest composition changes formed a sequence on the topographic gradient from the most exposed windward ridges and north-east-facing slopes to more sheltered leeward footslopes and creeks. Further studies using detrended correspondence analysis (DCA) and canonical correspondence analysis (CCA) confirmed the results of TWINSPAN, and showed the important roles of the topographic variables in the distribution of most tree species.

KEY WORDS: Nanjenshan forest dynamics plot, DCA, forest structure, monsoon, Taiwan, tree species composition, species distribution pattern, TWINSPAN.

INTRODUCTION

Rainforest ecosystem has attracted lots of ecologist´s attention due to its richness in biodiversity and stratification (Black et al., 1950; Richards, 1952; Poore, 1968; Ashton, 1969; Gentry, 1982, 1992; Phillips et al., 1994; Whitmore, 1998). In order to better understand the structure and population dynamics of rainforests, several "Forest Dynamics Plots (FDP)" have been established (Losos and Leigh, 2004). The first FDP site was established in BCI (Barro Colorado Island), Panama in 1980. To find a place which can compare with BCI in Asia, the Pasoh Forest Reserve, Malaysia was established in 1985. To provide a contrast to BCI under a drier climate, Mudumalai, India was subsequently established in 1987 (Losos and Leigh, 2004). Both the similarities and the differences among the first three plots aroused widespread interests in establishing Forest Dynamics plots in other forests, such as subtropical forests. To understand the structure, composition, and dynamics of the forests at the margin of the tropics, four forest dynamics plots and a transect have been established since 1989 in the Nanjenshan Nature Reserve of the southernmost Taiwan.

Previous studies have shown that both monsoon and topography significantly determine the species composition and forest structure (Sun, 1993; Sun and Hsieh, 2004), species spatial patterns (Chao, 1997), soil properties (Chen et al., 1997), leaf structure (Su, 1993), litterfall decomposition (Liu, 1994) and physiological characteristics of plants (Wang, 1995; Yang, 1997) in this plot. This plot has been recensused twice (Wu, 1998; Yeh, 2006). However, it seems that the area of the Lanjenchi plot is not large enough to include a sufficient number of tree species for both creek and leeward forest types. Therefore, the aim of this study was to enlarge the Lanjenchi plot to include more creek and leeward subplots and to examine again the species composition, structure and vegetation pattern of the forest in the plot. The

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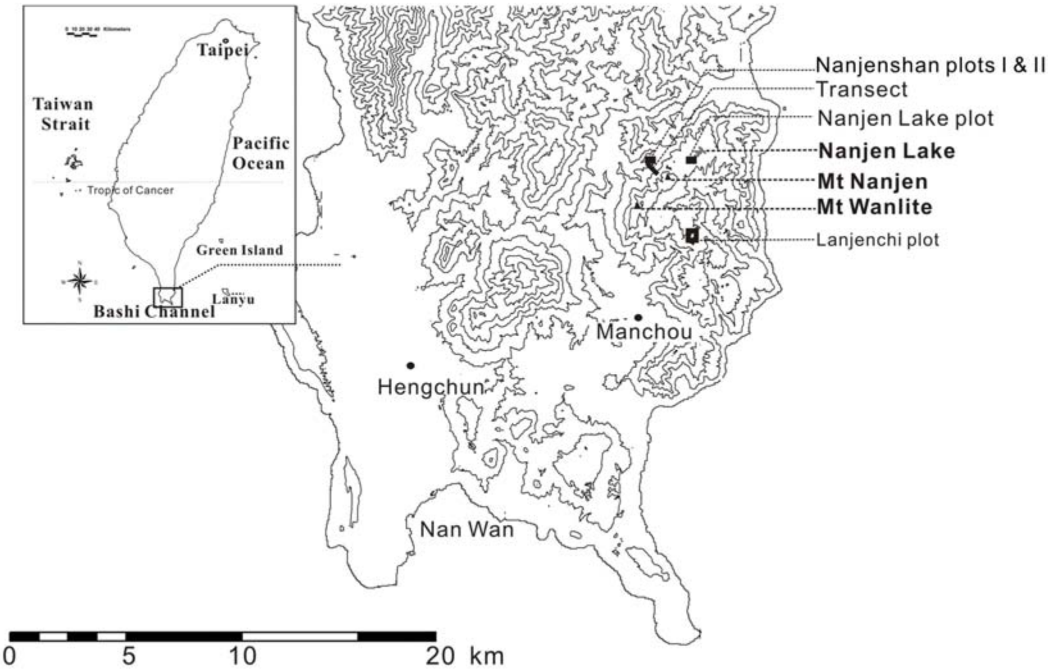

Fig. 1. Location of the Lanjenchi plot (bottom right). The other three plots (Nanjenshan plot I, Nanjenshan plot II, and Nanjen Lake plot) and a transect are also shown.

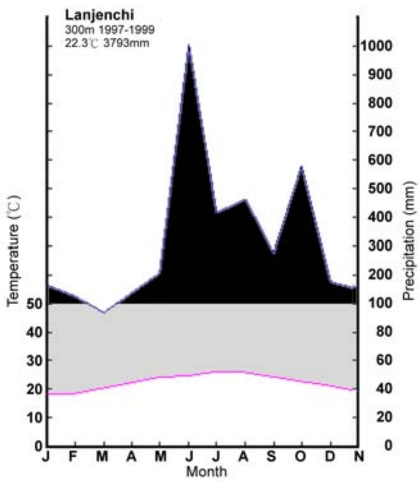

Fig. 2. The climate diagram of the Lanjenchi plot.

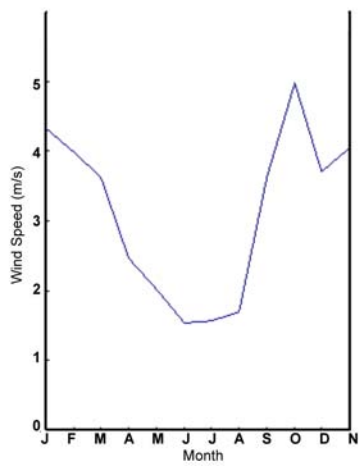

Fig. 3. Monthly average wind speeds of the Lanjenchi plot.

differences in species composition between the Lanjenchi plot and other three nearby permanent plots and a transect were also examined.

MATERIALS AND METHODS

Study site

The Lanjenchi plot is located on the eastern slope of Mt Wanlite (Fig. 1) in the southernmost Taiwan, and it is one of the four permanent study sites previously established in the Nanjenshan area. Slope ranges from 10 to 30 degrees and altitude ranges from 284 to 341 m. The average annual rainfall is 3,793 mm. The mean monthly precipitation varies from 60 to 1,200 mm depending on the patterns of typhoons and southwest monsoon winds. The climate here is warm and humid with a mean annual temperature of 22.3°C, a minimum mean temperature of 17.1°C during January and a maximum temperature of 26.8°C in July (Fig. 2). The mean wind velocity is 3.0 m s^{-1} and can be up to 8.4 m s^{-1} during monsoon season (Fig. 3).

Vegetation sampling

The previously established 3-ha Lanjenchi plot was enlarged to 5.88 ha to include more creek and leeward subplots. The plot was mapped into 588 10×10 m^2 quadrats (subplots). All free-standing trees $\geq$ 1 cm DBH (diameter at 1.3 m) in the newly expanded 2.88 ha were tagged, mapped, and measured (both DBH and height) from 1998 to 1999. Tree species were identified following the Flora of Taiwan (Huang, 2003). The general structural patterns were analyzed, including stem density, basal area and importance value index (IVI, by relative density and basal area).

Plant communities were classified using the Two-Way Indicator Species Analysis (TWINSPAN, Hill, 1979). Quadrats would not be classified into different communities unless the eigenvalues between them were greater than 0.14. Detrended correspondence analysis (DCA, Hill and Gauch, 1981) was performed to ordinate vegetation samples. Canonical Correspondence Analysis (CCA, Ter Braak, 1986) was used to explore the relationship of the vegetation and community structure to the recorded topographic variables (elevation, slope, aspect and surface curvature). Monte Carlo permutation tests were performed to test the significance of the first two canonical axes and each topographic variable. All multivariate analyses were analyzed using PC-ORD Version 4 (McCune and Medford, 1999). Univariate analysis of means and Tukey's analysis ($\alpha = 0.05$) were used to determine whether number of species, density and basal area are significantly different among community types.

The analysis of DBH-class distributions was generated to infer the population structures of species (McLaren et al., 2005). DBH-class distributions were plotted using histograms for species with more than 15 individuals in the plot. The interval of each diameter class is decided by the Sturges' formula which considers the total individuals of species *i* (Hough, 1932; Tubbs, 1977; McCarthy et al., 1987). The number of DBH classes (M) for each species was determined by the equation:

$M=6 \times \log (N_i)$ (modified from Sturges' formula)

where N_i is number of individuals of species i.

The interval of each class (R) was calculated by:

$R = (DBH_{max} - DBH_{min}) / M$ where DBH_{max} is the maximum DBH of the species *i* and DBH_{min} is the minimum DBH of the species.

For comparison of floristic composition between Lanjenchi plot and other nearby plots, Dice's index and Motyka's index of similarity (described by Mueller-Dombois and Ellenberg, 1974) were used.

RESULTS

Floristic composition

A total of 60,146 individuals was recorded, representing 136 species, 83 genera and 42 families. The average tree species per quadrat (10×10 m^2) was 32 ± 8 and varied from 11 to 52. Families with the most abundance species in the plot were Lauraceae, Euphorbiaceae, Rubiaceae, Fagaceae, Moraceae and Theaceae (Fig. 4A). Families with the greatest basal areas were Fagaceae (31.9% of total basal area), followed by Theaceae, Araliaceae, Aquifollaceae, Lauraceae and Illiciaceae (Fig. 4B). These six most important families accounted for about 70% of the total basal area.

The average stem density was 102 ± 55 per quadrat, with a minimum of 13 and a maximum of 383 stems per quadrat. Stem densities were considerably higher on the northeastern slopes and ridges than those on the southwestern slopes (Fig. 5A). The species-abundance pattern exhibited a typical inverse J-distribution (Fig. 6). This indicates that only a few species contributed a great proportion of stem density. The most abundance species was *Illicium arborescens*, a subcanopy tree species, accounting for about 11.1% of the total number of individuals. The second most abundant species was *Psychotria rubra*, a shrub species, accounting for 7.4% of the total stem density. Both of them are small-sized but high-density species. The other dominant species included *Ilex cochinchinensis* (6.6%), *Ilex uraiensis* (3.7%), *Antidesma hiiranense* (3.5%), *Eurya nitida* var. *nanjenshanensis* (2.8%), *Daphniphyllum glaucescens* subsp. *oldhamii* (2.8%), *Microtropis japonica* (2.7%), *Castanopsis cuspidata* var. *carlesii* (2.5%) and *Osmanthus marginatus* (2.3%). These ten most abundant species collectively contributed 45.3% of stem density and the first 36 species contributed 80.4% of all stems in the plot.

The mean basal area was 43.31 m^2 ha^{-1}. In terms of per quadrat, basal area was relatively high on the southwestern slopes and relatively low along the creek (Fig. 5B). The most dominant species, in terms of basal area $\geq$ 1 m^2 ha^{-1}, were *Castanopsis cuspidate* var. *carlesii*, *Schefflera octophylla*, *Illicium arborescens*, *Cyclobalanopsis longinux*, *Schima superba* var. *kankoensis*, *Cyclobalanopsis championii*, *Daphniphyllum glaucescens* subsp. *oldhami, Ilex cochinchinensis*, *Osmanthus marginatus, Lithocarpus amygdalifolius, Castanopsis fabric* and *Elaeocarpus sylvestris.* These twelve species accounted for 56.6% of the total basal area (Table 1).

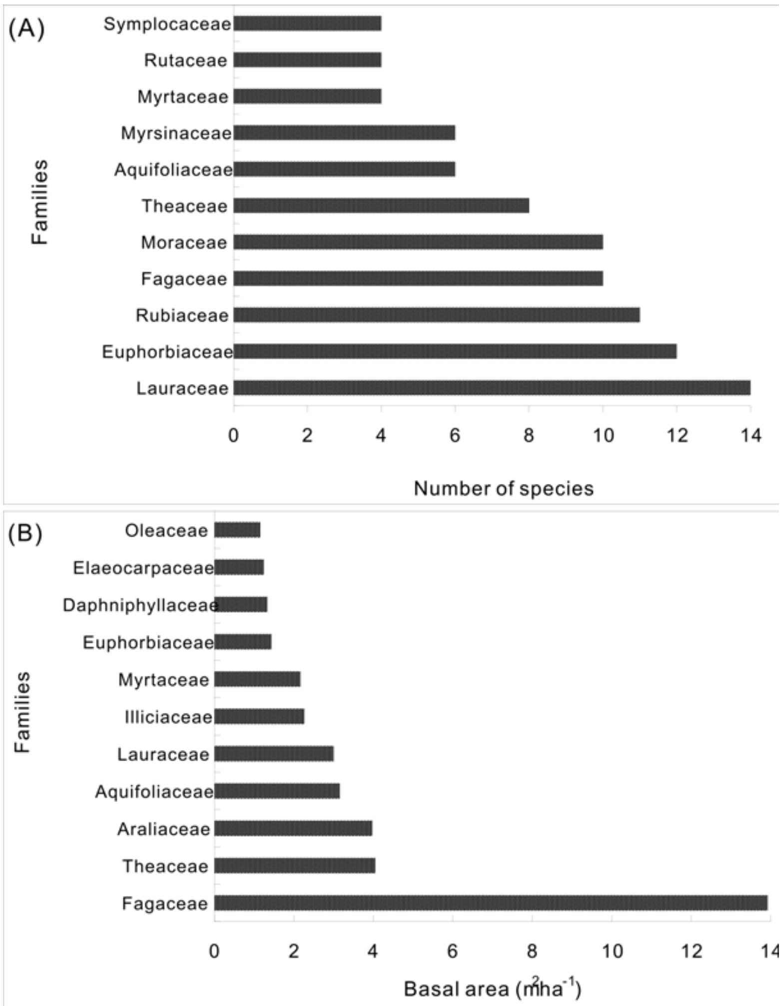

Fig. 4. Families with (A) the most species and (B) the highest basal area.

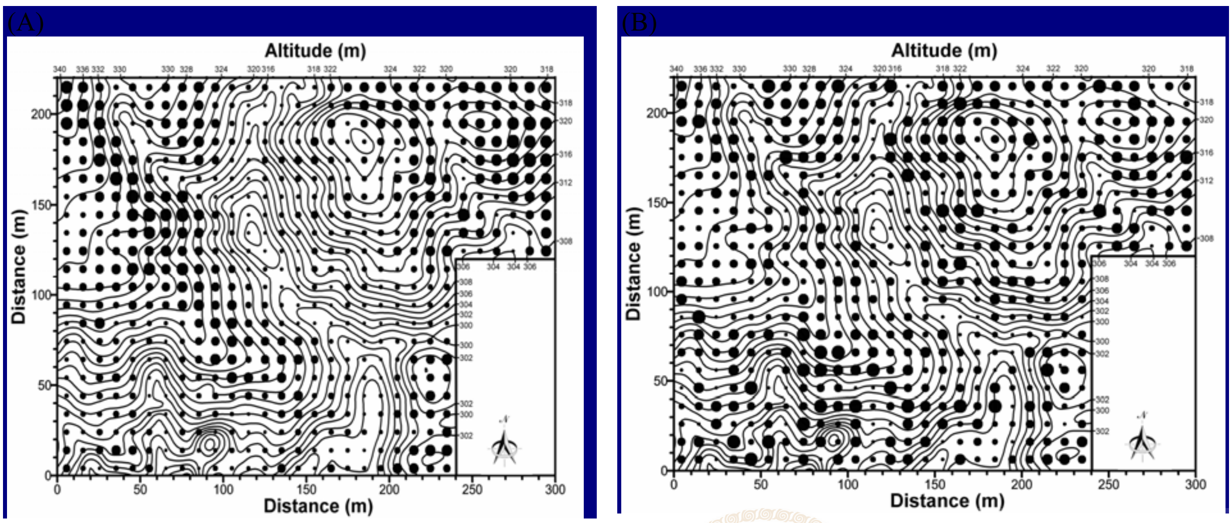

Fig. 5. The spatial distribution patterns of (A) number of stems and (B) total basal areas (m^2ha^{-1}) per 10 square quadrat in the Lanjenchi plot (the larger the solid circle, the higher the value).

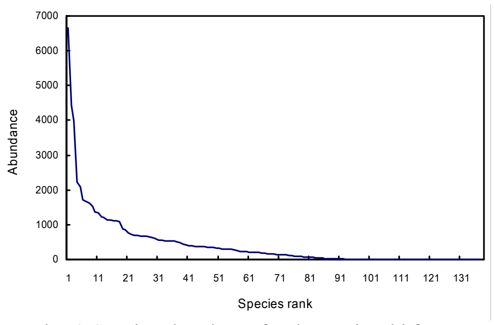

Fig. 6. Species abundance for the Lanjenchi forest.

Size-class structure

The size-class structure of 88 (each with total stems ≥ 15) out of 136 species were examined. The size-class distribution charts exhibited four patterns: Inverse J-shaped, L-shaped, fluctuated and bell-shaped distributions. Thirty-nine species showed an inverse J-shaped regeneration pattern, such as *Illicium arborescens* (Fig. 7A), *Psychotria rubra*, *Ilex uraiensis* and *Eurya nitida* var. *nanjenshanensis*. The L-shaped pattern was found in 36 species, such as *Ilex cochinchinensis* (Fig. 7B), *Antidesma hiiranense*, *Microtropis japonica* and *Beilschmiedia tsangii*. Both patterns show a decrease of abundance with increasing DBH class, but the inverse J-shaped curved indicating a steep decline in numbers with increasing size. The fluctuated pattern was shown by 12 species, such as *Rhododendron simsii* (Fig. 7C), *Castanopsis cuspidata* var. *carlesii*, *Lithocarpus amygdalifolius* and *Pasania formosana*. This type of structure implies periodic regeneration. Only one species showed a bell-shaped pattern, the *Alniphyllum pterospermum* (Fig. 7D), suggesting the species has certain difficulties in recruitment.

Classification

Four plant communities were identified using the TWINSPAN analysis. Each community is named by the characteristic species followed by the most dominant species. Relationships between these vegetation types and slope positions were found, such that four classified communities also can be named by their topographic types (Fig. 8). The first community is *Rhaphiolepis indica* var. *hiiranensis* - *Illicium arborescens* type (or Windward type I), the second is *Cinnamomum brevipedunculatum* - *Illicium arborescens* type (or Windward type II), the third is *Sloanea formosana* - *Ilex cochinchinensis* type (or Leeward type) and the fourth community is *Glycosmis citrifolia* - *Helicia formosana* type (or Creek type). These four types consisted of 86, 176, 230 and 96 quadrats, respectively (Table 2).

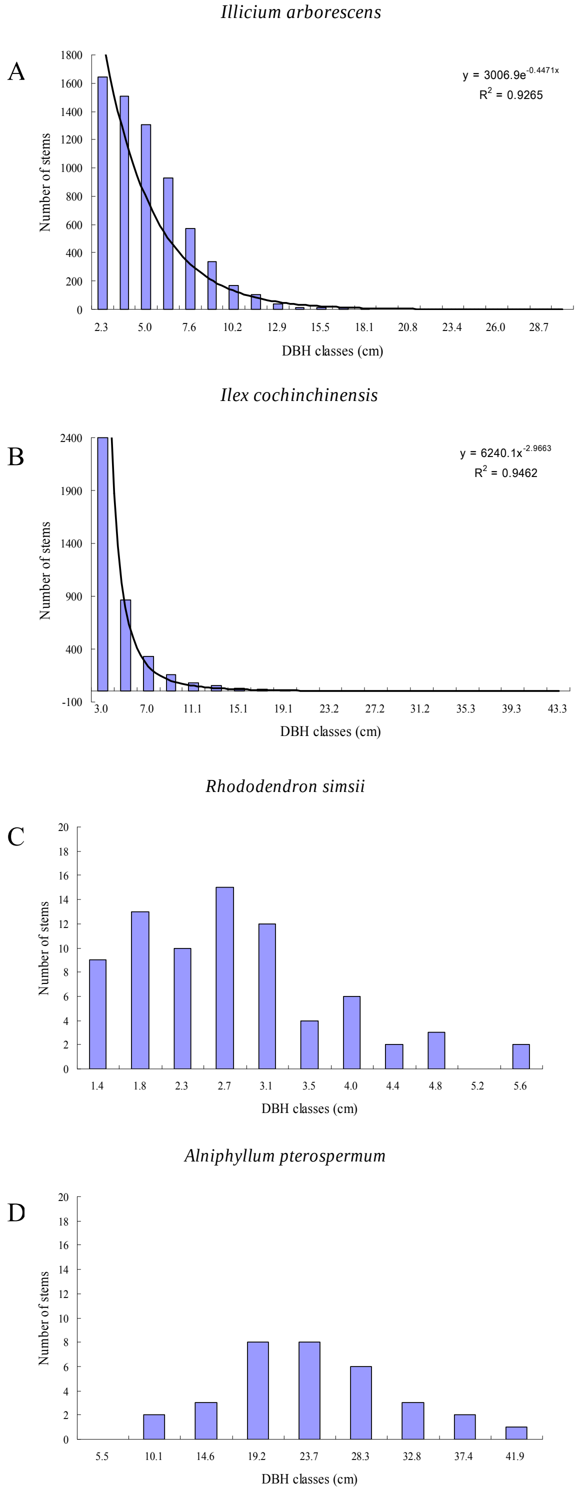

Fig. 7. Size-class distributions of four representative species. X-axis represents upper limits of DBH. A: Inverse J-shaped size-class distribution, typical species is *Illicium arborescens*; B: L-shaped size-class distribution, representative species is *Ilex cochinchinensis*; C: fluctuating size-class distribution, representative species is *Rhododendron simsii*; and D: bell-shaped size-class distribution, typical species is *Alniphyllum pterospermum*.

Table 1. Woody species composition of the Lanjenchi plot. Only the 30 most dominant species (based on basal area) are shown.

Species	Basal area (m^2 ha^{-1})	Relative cumulative basal area (%)	Density (stems ha^{-1})
Castanopsis cuspidata var. *carlesii*	6.68	15.4	259
Schefflera octophylla	3.97	24.6	194
Illicium arborescens	2.26	29.8	1132
Cyclobalanopsis longinux	1.99	34.4	204
Schima superba var. *kankoensis*	1.37	37.6	110
Cyclobalanopsis championii	1.36	40.7	64
Daphniphyllum glaucescens subsp. *oldhamii*	1.33	43.8	284
Ilex cochinchinensis	1.15	46.4	676
Osmanthus marginatus	1.15	49.1	232
Lithocarpus amygdalifolius	1.12	51.7	105
Castanopsis fabri	1.09	54.2	53
Elaeocarpus sylvestris	1.06	56.6	62
Ilex uraiensis	0.96	58.9	379
Gordonia axillaris	0.89	60.9	119
Eurya nitida var. *nanjenshanensis*	0.83	62.8	291
Beilschmiedia tsangii	0.83	64.7	187
Syzygium kusukusense	0.71	66.4	89
Sapium discolor	0.71	68.0	35
Cyclobalanopsis pachyloma	0.65	69.5	61
Syzygium euphlebium	0.62	71.0	95
Pasania harlandii	0.62	72.4	31
Ilex lonicerifolia var. *matsudae*	0.60	73.8	229
Machilus thunbergii	0.59	75.1	115
Adinandra formosana	0.54	76.4	93
Astronia formosana	0.54	77.6	41
Syzygium buxifolium	0.52	78.8	193
Neolitsea hiiranensis	0.38	79.7	146
Psychotria rubra	0.37	80.6	752
Magnolia kachirachirai	0.37	81.4	91
Pasania formosana	0.37	82.3	17
Others	7.68	17.7	3890
Total	43.31	100.0	10229

Table 2. Number of species, density and basal area of each of the four community types of the Lanjenchi plot. Values with different superscripts are significantly different at $\alpha \leq 0.05$ (Tukey's analysis).

Community type	No. of quadrats	Total species number	Mean species number per quadrat	Stem density per quadrat	Basal area (m^2) per quadrat (0.01ha^{-1})
Windward I	86	86	$36±5.5^a$	$178±58.6^a$	$0.488±0.116^a$
Windward II	176	107	$37±5.5^a$	$123±41.1^b$	$0.458±0.102^a$
Leeward	230	122	$31±5.6^b$	$81±26.9^c$	$0.449±0.154^a$
Creek	96	104	$23±5.7^c$	$47±16.6^d$	$0.306±0.147^b$

The DCA ordination results showed that the four communities are located along a major compositional gradient (Fig. 9). The eigenvalues for the first three DCA axes were 0.481, 0.248 and 0.199, and the corresponding gradient lengths were 4.708, 3.129 and 2.722 (Table 3). Communities were well separated on the first DCA axis with 95% confidence intervals of DCA site scores. The communities from left to right of DCA axis 1 were the Creek type, Leeward type, Windward type II and Windward type I.

The results of the CCA ordination showed that 6.6% of the variance in species data are accounted by the first two axes and 87.7% of the variation could be explained by the topographic variables (Table 4). Monte Carlo permutation test revealed that both the first axis and second axis were highly significant at the 1% level. The intraset correlation coefficients indicated that the first axis (species-environment correlation = 0.823) mainly correspond to elevation, surface curvature and slope. The second axis (species-environment correlation = 0.549) corresponds primarily to aspect. The results of correlation analysis and CCA suggested that variables associated with exposure were the most highly correlated factors with species distribution.

Forest types

Species compositions and structures are different for these four forest types (Tables 2 and 5). The Windward Type I (*Rhaphiolepis indica* var. *hiiranensis* - *Illicium arborescens* type) has the highest stem density and highest basal area, with 178 stems and 0.488 m^2 basal area per quadrat (17,762 stems ha^{-1}

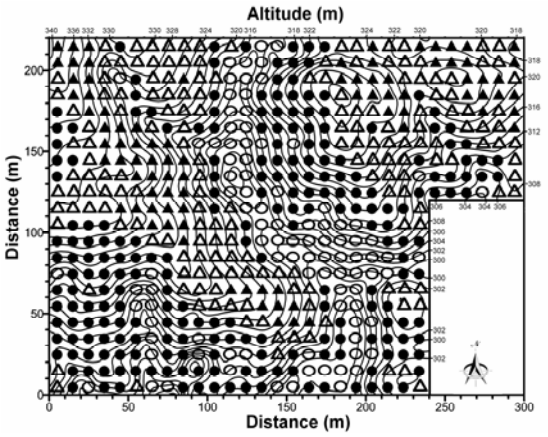

Fig. 8. Topographic map of the Lanjenchi plot with four community types identified by TWINSPAN superimposed. Windward type I (▲), Windward type II (△), Leeward type (●) and Creek type (○).

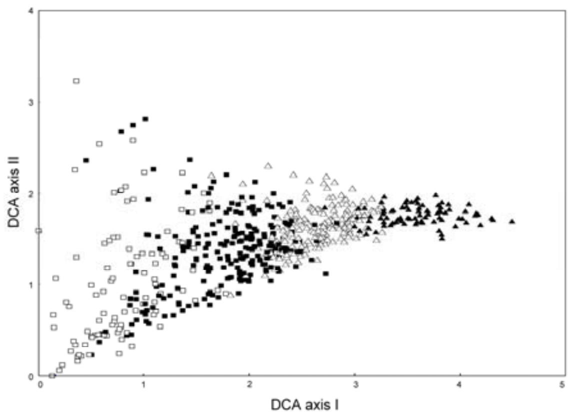

Fig. 9. DCA ordination of 588 quadrats from Lanjenchi plot. The TWINSPAN groups are indicated by symbols. Windward type I(▲); Windward type II (△); Leeward type (■); and Creek type (□).

Table 3. The eigenvalues, gradient lengths and 99% confidence intervals for the first three axes of DCA scores.

Axis	DCA		99% confidence intervals of DCA scores for each community type			
	Eigen-value	Gradient length	Windward type I	Windward type II	Leeward type	Creek type
1	0.481	4.708	3.71-3.92	2.77-2.87	1.88-2.04	0.99-1.18
2	0.248	3.129	1.79-1.87	1.63-1.71	1.33-1.48	1.01-1.34
3	0.199	2.722	1.13-1.29	1.01-1.17	0.97-1.12	1.13-1.31

Table 4. Summary of the results of canonical correspondence analysis (CCA) of Lanjenchi species data from 588 plots constrained to four topographic variables. Correlation coefficients of topographic variables with four axes are also provided.

Axis	1	2	3	4
Eigenvalue	0.294	0.042	0.029	0.018
Species-environment correlation	0.823	0.549	0.523	0.497
Cumulative % variance of				
species data	5.8	6.6	7.2	7.6
species-environment relation	76.6	87.7	95.2	100.0
Elevation	-0.605	0.258	-0.255	0.016
Surface curvature	-0.528	-0.325	0.248	-0.057
Slope	0.397	0.078	-0.072	-0.424
Aspect	-0.574	0.393	-0.026	0.013

and 48.8 $m^2 ha^{-1}$, respectively). On the contrary, the Creek Type (*Glycosmis citrifolia* - *Helicia formosana* type) has the lowest stem density, basal area and also number of species per quadrat, due to some quadrats of this type are on small gullies or bare rocks.

1. The Windward Type I (*Rhaphiolepis indica* var. *hiiranensis* - *Illicium arborescens* type)

A total of 15,277 individuals belonging to 86 species was recorded. These quadrats are mainly located on the northeastern and eastern slopes within the plot. The average species number was 36 per quadrat, which was higher than those of the leeward and creek types. Stem density was the highest among the four types. Most trees were relatively thin with 75.5% of individuals thinner than 5 cm in DBH and only 1.0% of individuals ≥ 20 cm in DBH (Fig. 10). The basal area of this type was significantly higher than that of the Creek type, but was similar to other two types. The most important species (highest IVI) was *Illicium arborescens*, followed by *Cyclobalanopsis championii*, *Castanopsis cuspidata* var. *carlesii*, *Eurya nitida* var. *nanjenshanensis* and *Syzygium buxifolium* (Table 5). The characteristic species of this type was *Rhaphiolepis indica* var. *hiiranensis*, which is an endemic variety in southern Taiwan.

2. The Windward Type II (*Cinnamomum brevipedunculatum* - *Illicium arborescens* type)

A total of 21,699 individuals belonging to 107 species was recorded for this community type. Stem density was significantly lower than the Windward Type I, but significantly higher than the Creek and Leeward types. The DBH-class structure was the same with the Windward Type I but with more trees

Table 5. Species composition for the four community types of the Lanjenchi plot. For each community type, only 20 species with the highest IVI are listed in a descending order.

Windward type I			
Species	Density (stems ha^{-1})	Basal area (m^{2}ha^{-1})	IVI (%)
Illicium arborescens	2836	3.85	11.93
Cyclobalanopsis championii	353	7.94	9.13
Castanopsis cuspidata var. *carlesii*	490	6.18	7.70
Eurya nitida var. *nanjenshanensis*	1250	3.07	6.66
Syzygium buxifolium	1014	2.62	5.54
Osmanthus marginatus	729	2.83	4.95
Ilex lonicerifolia var. *matsudae*	881	1.45	3.97
Microtropis japonica	974	0.84	3.61
Gordonia axillaris	414	2.18	3.40
Rhaphiolepis indica var. *hiiranensis*	341	1.72	2.73
Ilex cochinchinensis	683	0.75	2.69
Lithocarpus amygdalifolius	223	1.70	2.37
Daphniphyllum glaucescens subsp..*oldhamii*	412	1.09	2.28
Podocarpus macrophyllus	409	1.04	2.21
Ilex maximowicziana	335	1.15	2.12
Pasania formosana	71	1.55	1.79
Myrsine sequinii	422	0.54	1.74
Ilex uraiensis	447	0.38	1.65
Antidesma hiiranense	521	0.16	1.63
Cyclobalanopsis longinux	257	0.80	1.55
Others	4700	6.97	20.37
Total	17762	48.82	100.00

Windward type II			
Species	Density (stems ha^{-1})	Basal area (m^{2}ha^{-1})	IVI (%)
Illicium arborescens	1757	3.83	11.32
Castanopsis cuspidata var. *carlesii*	354	8.67	10.90
Ilex cochinchinensis	821	1.10	4.54
Cyclobalanopsis longinux	283	2.65	4.04
Psychotria rubra	797	0.30	3.56
Daphniphyllum glaucescens subsp. *oldhamii*	385	1.67	3.38
Ilex uraiensis	532	1.09	3.35
Osmanthus marginatus	266	1.87	3.12
Lithocarpus amygdalifolius	172	2.20	3.10
Eurya nitida var. *nanjenshanensis*	314	1.18	2.57
Antidesma hiiranense	572	0.22	2.56
Gordonia axillaris	166	1.62	2.45
Ilex lonicerifolia var. *matsudae*	280	1.05	2.28
Schefflera octophylla	182	1.38	2.24
Schima superba var. *kankoensis*	144	1.40	2.11
Microtropis japonica	320	0.43	1.77
Elaeocarpus sylvestris	73	1.23	1.64
Cyclobalanopsis	91	1.03	1.50
Syzygium kusukusense	96	0.90	1.37
Tricalysia dubia	238	0.34	1.34
Others	4477	11.60	30.84
Total	12322	45.78	100.00

Leeward type			
Species	Density (stems ha^{-1})	Basal (m^{2}ha^{-1})	IVI (%)
Castanopsis cuspidata var. *carlesii*	198	7.89	10.05
Schefflera octophylla	235	5.47	7.57
Ilex cochinchinensis	750	1.54	6.35
Psychotria rubra	928	0.50	6.28
Illicium arborescens	463	1.31	4.32
Cyclobalanopsis longinux	179	2.28	3.66
Ilex uraiensis	340	1.32	3.57
Daphniphyllum glaucescens subsp. *oldhamii*	250	1.52	3.24
Castanopsis fabri	77	1.81	2.49
Schima superba var. *kankoensis*	84	1.73	2.45
Litsea acutivena	282	0.39	2.17
Neolitsea hiiranensis	207	0.72	2.08
Ardisia quinquegona	300	0.16	2.02
Elaeocarpus sylvestris	67	1.40	1.98
Machilus thunbergii	155	0.87	1.93
Beilschmiedia tsangii	186	0.58	1.79
Syzygium euphlebium	116	0.92	1.75
Syzygium kusukusense	116	0.92	1.74
Antidesma hiiranense	251	0.11	1.67
Sapium discolor	43	1.16	1.56
Others	2883	12.11	31.32
Total	8110	44.69	100.00

Creek type			
Species	Density (stems ha^{-1})	Basal (m^{2}ha^{-1})	IVI (%)
Schefflera octophylla	219	8.60	16.76
Psychotria rubra	606	0.42	7.20
Helicia formosana	338	0.54	4.52
Archidendron lucidum	268	0.52	3.75
Astronia formosana	100	1.57	3.71
Ilex cochinchinensis	226	0.67	3.54
Castanopsis fabri	58	1.68	3.44
Wendlandia formosana	193	0.79	3.39
Cyclobalanopsis longinux	69	1.12	2.62
Machilus thunbergii	80	1.03	2.58
Ardisia quinquegona	178	0.13	2.12
Beilschmiedia tsangii	105	0.55	2.05
Ilex uraiensis	130	0.35	1.99
Ficus fistulosa	119	0.42	1.98
Schima superba var. *kankoensis*	44	0.88	1.94
Pasania harlandii	24	0.94	1.84
Alniphyllum pterospermum	18	0.94	1.76
Litsea acutivena	124	0.21	1.68
Syzygium kusukusense	71	0.47	1.55
Sloanea formosana	38	0.68	1.54
Others	1659	7.32	30.04
Total	4666	29.83	100.00

in the larger DBH classes. Basal area of trees per unit area was not significantly different from the Windward Type I. The same with the Windward Type I, *Illicium arborescens* was the most important species of this type with IVI = 11.32, followed by *Castanopsis cuspidata* var. *carlesii*, *Ilex cochinchinensis, Cyclobalanopsis longinux* and *Psychotria rubra*. The characteristic species of this type was *Cinnamomum brevipedunculatum*, which is an endemic species in southern Taiwan.

3. The Leeward Type (*Sloanea formosana - Ilex cochinchinensis* type)

There were 18,681 individuals belonging to 122 species recorded for this community type. Although with the highest species number, on average only 31

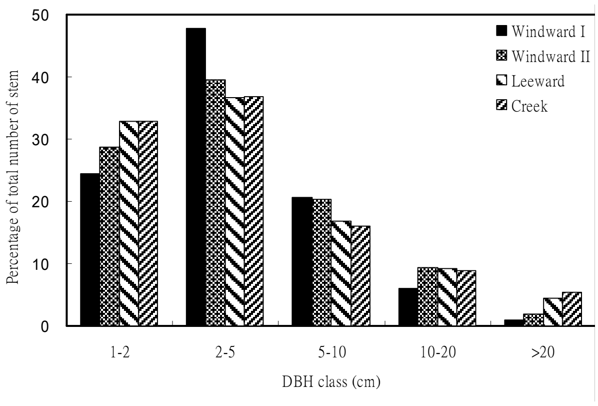

Fig. 10. Percentage of stems in different size classes for the four community types of the Lanjenchi plot.

species can be found in a quadrat. Stem density was 81 stems per quadrat, and there were more trees with larger DBH (about 4.4% of stems with DBH ≥ 20 cm). Basal area per unit area was not significantly different from the Windward Type I and II. The most important species was *Castanopsis cuspidata* var *carlesii* (IVI = 10.05), followed by *Schefflera octophylla*, *Ilex cochinchinensis*, *Psychotria rubra* and *Illicium arborescens*. The characteristic species of this type was *Sloanea formosana*, which is an endemic species in Taiwan and distributed in lowland forests.

4. The Creek Type (*Glycosmis citrifolia* - *Helicia formosana* type)

A total of 4,489 individuals belonging to 104 species was recorded for this type. Due to lacking tree individuals on some small gullies and bare rocks, both stem density and basal area per quadrat were the lowest for all forest types, with 47 stems per quadrat and 30.1 $m^2 ha^{-1}$ basal area. Comparing with other forest types, there were more large trees in the Creek Type (5.44% of individuals with DBH≥ 20 cm). This type was dominated by *Schefflera octophylla*, with an important value of 16.76. Other dominant species, in a descending order of importance, were *Psychotria rubra*, *Helicia formosana*, *Archidendron lucidum* and *Astronia formosana*. The characteristic species of this type was *Glycosmis citrifolia*, which was a relatively few species in the Lanjenchi plot, but was abundant in the adjacent Nanjenshan plot.

Spatial pattern

Based on the distribution maps of species, most species were patchily distributed and others were randomly distributed. Among those patchily distributed species, most were associated with specific topographic positions like northeastern slope, southwest slope, creek or others. *Elaeocarpus sylvestris* (Fig. 11A) and *Ilex uraiensis* (Fig. 11B) appeared to be randomly or near-randomly distributed within the plot, whereas *Myrsine sequinii* (Fig. 11C) and *Osmanthus marginatus* (Fig. 11D) were locally abundant on the northeastern slopes. *Helicia formosana* (Fig. 11E) and *Wendlandia formosana* (Fig. 11F) were prone to grow along the creeks or on the southwestern slopes of the plot.

DISCUSSION

This study presented how forest communities varied along the gradients of wind-stress and topography. We expanded the Lanjenchi plot from 3 to 5.88-ha to increase the sample size of the creek and leeward types and the range of elevation. The elevation of the original 3-ha plot is from 300 to 341 m, and the current 5.88-ha plot is from 284 m to 341 m. There are 35,633 stems in the original plot and 24,513 stems in the expanded part of the plot. Eleven out of the 136 species in the whole plot only appeared in the southern expanded part. Except for *Aucuba chinensis*, all other ten species had less than 14 stems within the whole plot. The relative abundance of species has changed slightly due to the increase of leeward and creek habitats. An increase or decrease in relative abundance was also observed for some habitat-associated species. For example, *Ardisia quinquegona* had more individuals in the southern part than in the northern part of the plot, whereas *Ilex lonicerifolia* var. *matsudae* was more common in the northern (Fig. 12).

There are four plots and a transect established in the Nanjenshan area (Fig. 1, Table 6). Hsieh et al. (2000) showed that marked differences of species composition and forest structure were observed between 3-ha Lanjenchi plot and the Nanjenshan plot. Fan et al. (2005) showed that the dominant families in Nanjen Lake plot are similar to those in the Lanjenchi plot. Both Dice and Motyka similarity values were calculated here for all pairs of plots in terms of the species presence. The results (Table 7) shows that the Lanjenchi and Nanjen Lake plots have a very similar floristic composition, whereas the Nanjenshan plots I and II are similar to each other. However, the Lanjenchi and Nanjen Lake plots were quite distinct from the Nanjenshan plots I and II. These results are very similar to those obtained earlier (Hsieh et al., 2000).

The most abundant species in the study, *Illicium arborescens*, was also the most abundant species in the Nanjen lake plot (Fan, 2005), but was not distributed in the Nanjenshan plots I and II, and the

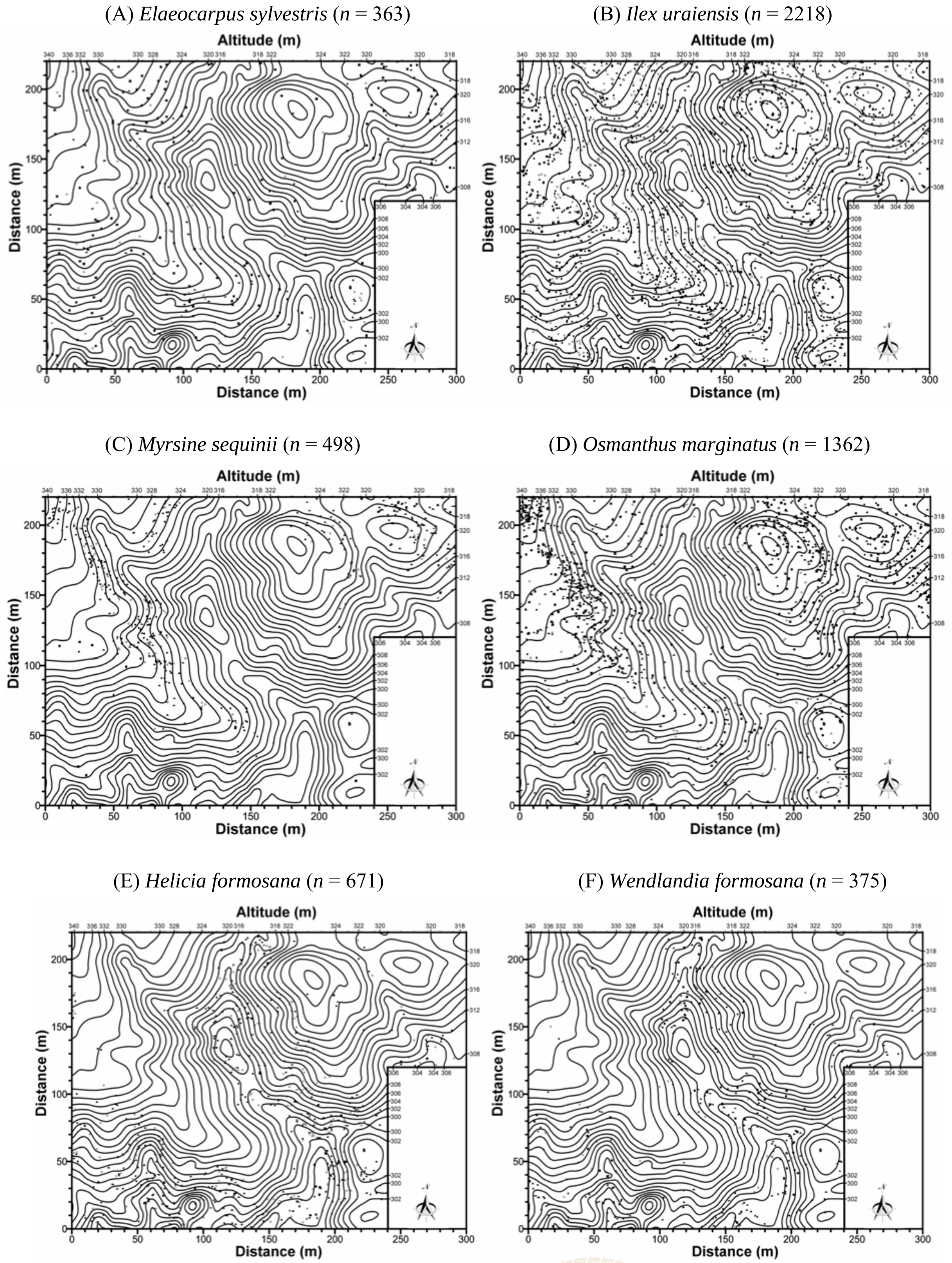

Fig. 11. Distribution maps of the six representative species in the Lanjenchi plot. (A) and (B) species distributed randomly in the whole plot, while (C) and (D) species occurring only on the windward slopes. (E) and (F) species limited to leeward slopes and creak sides.

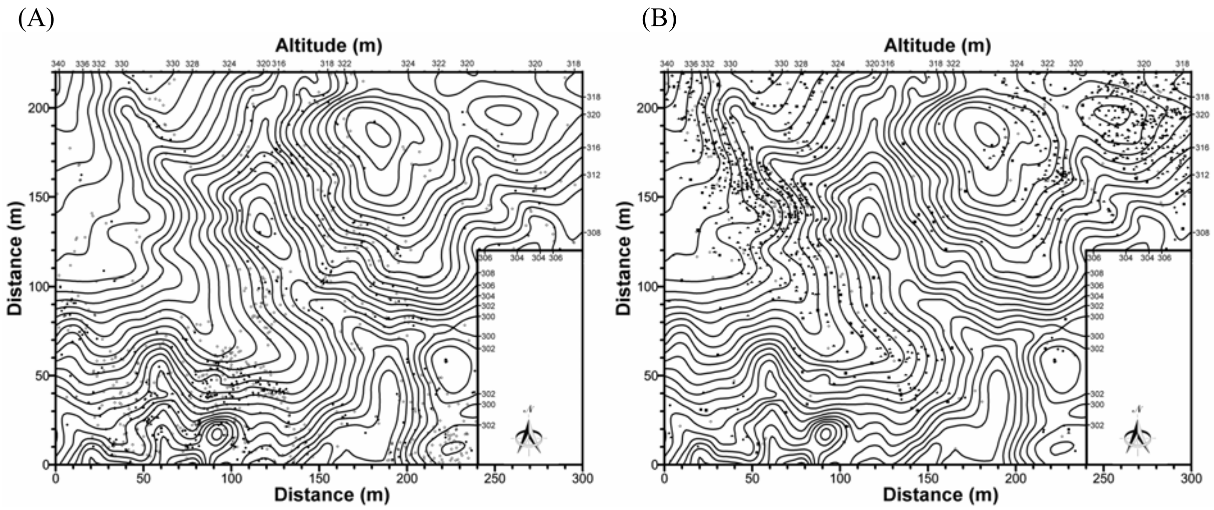

Fig. 12. Distribution maps of (A) *Ardisia quinquegona* (n = 1,087) and (B) *Ilex lonicerifolia* var. *matsudae* (n = 1,330), note that *Ardisia quinquegona* has more individuals in the southern part of the plot compared with *Ilex lonicerifolia* var. *matsudae*.

Table 6. Summary of Nanjenshan forest dynamics plots. All plots have been fully censused at least once. The years for which data were used in this study are underlined.

Plot	Plot size (ha)	Fully censused	Altitude (m)	Wind stress/ Topography	Number of Species	Number of Species per quadrat	Number of Individuals per quadrat	Basal area per quadrat (m^2/ha)
Lanjenchi	5.88	1989-1991 1996-1997 1998-1999	High (284-341)	Windward slope Leeward slope Valley	136	32±7.5	102±54.5	43.2±14.63
Nanjen Lake*	2.21	1998	High (326-358)	Windward slope Leeward slope Valley	120	34±8.9	114±50.0	44.8±17.78
Nanjenshan plot I	2.10	1993-1994 2000	Low (225-275)	Valley	102	15±4.6	37±17.5	43.1±38.20
Nanjenshan plot II	0.64	2000	Low (196-226)	Valley	67	16±3.4	50±32.2	53.7±36.51
Transect	0.76	1995	Low to High (291-475)	Leeward slope	122	22±7.8	66±38.2	49.0±24.08

*The size of the Nanjen Lake plot was 2.21 ha, but data from the 0.35 ha swamp area within the plot were excluded from the analysis.

Table 7. Dice (lower-left) and Motyka (upper-right) similarity indices calculated for all pairs of plots in the Nanjenshan area.

	Lanjenchi	Nanjen Lake	Nanjenshan plot I	Nanjenshan plot II	Transect
Lanjenchi	-	0.46	0.10	0.04	0.20
Nanjen Lake	0.84	-	0.16	0.09	0.43
Nanjenshan plot I	0.62	0.61	-	0.53	0.26
Nanjenshan plot II	0.45	0.47	0.75	-	0.28
Transect	0.73	0.74	0.66	0.52	-

transect (which included the highest summit of Mt. Nanjen, 385m). The species was also the most dominant species in the Lopei plot, ca 200 km north of the Nanjenshan Reserve (Lin et al., 2005). Other species such as *Cyclobalanopsis longinux*, *Meliosma squimulata* and *Syzygium buxifolium* exhibited similar distribution patterns. These species represent a downward-migration pattern of their altitudinal distribution in the study area.

On the basis of TWINSPAN classification and DCA ordination, four groups of subplots were identified along the topographic gradient. While these groups were associated with topographic position, and also reflected the wind effects. In subtropical Asia forests influenced by strong northeastern monsoon winds in the winter season often have specific forest structures and species composition (Chen et al., 1997; Sun et al., 1998; Lin et al., 2005; Fan et al., 2005; Kubota et al., 2004). On the windward sides, forest canopies are relatively low and uniform, and stems densities are higher than that of the leeward sides, which are also shown in the

Lanjenchi (this study) and Nanjen Lake plots in Nanjenshan area, Lopei plot in northern Taiwan (Lin et al., 2005) and Lanyu Islet (Hsieh et al., unpublished data). Topographic variables (elevation, slope, aspect, etc.), therefore, has a strong influence on structure and composition of the forests in the Nanjenshan area, and also contribute to the maintenance of species richness for these forests.

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Appendix. Woody species of the study plots at Nanjenshan area.

Species	Lanjenchi	Nanjen Lake	Nanjenshan plot I	Nanjenshan plot II
Gymnosperms				
Podocarpaceae				
Podocarpus macrophyllus	Y	N	N	N
Podocarpus nagi	Y	Y	Y	N
Dicotyledons				
Acanthaceae				
Strobilanthes longespicatus	N	N	Y	Y
Actinidiaceae				
Saurauja oldhamii	Y	Y	Y	N
Anacardiaceae				
Rhus succedanea	N	Y	N	N
Aquifoliaceae				
Ilex asprella	Y	N	Y	N
Ilex cochinchinensis	Y	Y	Y	N
Ilex lonicerifolia var. *matsudae*	Y	Y	N	N
Ilex maximowicziana	Y	Y	Y	N
Ilex rotunda	Y	Y	Y	Y
Ilex uraiensis	Y	Y	Y	Y
Araliaceae				
Schefflera octophylla	Y	Y	Y	Y
Bignoniaceae				
Radermachia sinica	Y	Y	Y	Y
Boraginaceae				
Ehretia longiflora	Y	Y	Y	N
Capparaceae				
Crateva adansonii subsp. *formosensis*	N	N	Y	Y
Caprifoliaceae				
Viburnum arboricola	Y	N	N	N
Viburnum luzonicum	N	Y	N	N

Appendix. Continued.

Viburnum odoratissimum	Y	Y	Y	Y
Celastraceae				
Euonymus pallidifolia	Y	Y	N	N
Microtropis japonica	Y	Y	Y	N
Clusiaceae				
Calophyllum inophyllum	Y	N	N	N
Garcinia multiflora	Y	Y	Y	N
Cornaceae				
Aucuba chinensis	Y	Y	N	N
Daphniphyllaceae				
Daphniphyllum glaucescens subsp. *oldhamii*	Y	Y	Y	N
Ebenaceae				
Diospyros eriantha	Y	Y	Y	Y
Diospyros maritima	N	Y	Y	Y
Diospyros morrisiana	Y	Y	N	N
Elaeocarpaceae				
Elaeocarpus sylvestris	Y	Y	N	N
Sloanea formosana	Y	Y	Y	Y
Ericaceae				
Rhododendron simsii	Y	Y	N	N
Euphorbiaceae				
Acalypha suirenbiensis	N	N	Y	Y
Antidesma hiiranense	Y	Y	Y	N
Bischofia javanica	N	Y	Y	Y
Bridelia balansae	Y	Y	Y	Y
Drypetes karapinensis	Y	Y	Y	Y
Drypetes littoralis	Y	N	N	N
Glochidion philippicum	N	N	Y	Y
Glochidion rubrum Blume	Y	Y	Y	Y
Glochidion zeylanicum var. *lanceolatum*	Y	N	N	N
Glochidion zeylanicum	Y	Y	Y	N
Liodendron formosanum	N	N	Y	Y
Macaranga tanarius	N	N	Y	Y
Mallotus japonicus	Y	Y	Y	N
Mallotus paniculatus	Y	Y	Y	Y
Mallotus philippensis	Y	N	Y	N
Melanolepis multiglandulosa	N	Y	Y	Y
Sapium discolor	Y	Y	Y	N
Sapium sebiferum	Y	N	N	N
Fabaceae				
Archidendron lucidum	Y	Y	Y	N
Ormosia hengchuniana	Y	Y	N	N
Fagaceae				
Castanopsis cuspidata var. *carlesii*	Y	Y	N	N
Castanopsis fabri	Y	Y	N	N
Castanopsis formosana	Y	Y	N	Y
Castanopsis indica	Y	Y	Y	Y
Cyclobalanopsis championii	Y	Y	N	N
Cyclobalanopsis longinux	Y	Y	N	N
Cyclobalanopsis pachyloma	Y	Y	N	N
Lithocarpus amygdalifolius	Y	Y	Y	N
Pasania formosana	Y	N	N	N
Pasania harlandii	Y	Y	Y	N
Flacourtiaceae				
Casearia membranacea	N	N	Y	N
Illiciaceae				
Illicium arborescens	Y	Y	N	N
Juglandaceae				
Engelhardtia roxburghiana	Y	Y	N	N
Lauraceae				
Beilschmiedia erythrophloia	Y	Y	Y	Y
Beilschmiedia tsangii	Y	Y	N	N
Cinnamomum brevipedunculatum	Y	Y	N	N
Cinnamomum kanehirae	Y	N	N	N
Cryptocarya chinensis	Y	Y	N	N
Cryptocarya concinna	Y	N	Y	Y

Appendix. Continued.

Litsea acutivena	Y	Y	Y	N
Litsea akoensis	N	N	Y	Y
Machilus japonica var. *kusanoi*	Y	Y	Y	Y
Machilus obovatifolia	Y	Y	Y	N
Machilus thunbergii	Y	Y	Y	Y
Machilus zuihoensis	Y	Y	Y	N
Neolitsea buisanensis	Y	Y	N	N
Neolitsea hiiranensis	Y	Y	Y	N
Neolitsea parvigemma	Y	N	N	N
Leeaceae				
Leea guineensis	N	N	Y	Y
Loganiaceae				
Fagraea ceilanica	Y	N	N	N
Lythraceae				
Lagerstroemia subcostata	Y	N	Y	Y
Magnoliaceae				
Magnolia kachirachirai	Y	Y	N	N
Michelia compressa	Y	Y	Y	Y
Melastomataceae				
Astronia formosana	Y	Y	N	N
Melastoma candidum	Y	Y	N	N
Meliaceae				
Aglaia elliptifolia	N	N	Y	Y
Dysoxylum hongkongense	N	Y	Y	Y
Melia azedarach	N	N	Y	N
Moraceae				
Ficus ampelas	N	N	Y	Y
Ficus benjamina	Y	Y	Y	Y
Ficus erecta var. *beecheyana*	Y	N	N	N
Ficus fistulosa	Y	Y	Y	Y
Ficus formosana	Y	Y	Y	Y
Ficus irisana	Y	N	Y	Y
Ficus microcarpa	N	N	Y	N
Ficus nervosa	Y	N	Y	N
Ficus ruficaulis var. *antaoensis*	Y	Y	N	N
Ficus septica	Y	N	Y	Y
Ficus superba var. *japonica*	Y	Y	Y	N
Ficus variegata var. *garciae*	N	N	Y	Y
Ficus virgata	Y	N	Y	N
Morus australis	N	N	Y	N
Myricaceae				
Myrica adenophora	N	Y	N	N
Myrsinaceae				
Ardisia cornudentata	Y	Y	N	N
Ardisia quinquegona	Y	Y	Y	Y
Ardisia sieboldii	Y	Y	Y	Y
Ardisia virens	N	N	Y	Y
Maesa japonica	Y	N	N	N
Maesa perlaria var. *fomosana*	Y	Y	Y	N
Myrsine seguinii	Y	Y	N	N
Myrtaceae				
Decaspermum gracilentum	Y	Y	Y	N
Syzygium buxifolium	Y	Y	N	N
Syzygium euphlebium	Y	Y	Y	Y
Syzygium kusukusense	Y	Y	Y	N
Oleaceae				
Fraxinus insularis	Y	N	N	N
Osmanthus marginatus	Y	Y	Y	N
Opiliaceae				
Champereia manillana	Y	Y	Y	Y
Proteaceae				
Helicia formosana	Y	Y	Y	N
Helicia rengetiensis	N	Y	N	N
Rosaceae				
Pourthiaea lucida	N	N	Y	N
Prunus phaeosticta	Y	Y	Y	N

Appendix. Continued.

Rhaphiolepis indica var. hiiranensis	Y	Y	N	N
Rubiaceae				
Gardenia jasminoides	N	Y	Y	N
Lasianthus chinensis	Y	N	N	N
Lasianthus cyanocarpus	Y	Y	N	Y
Lasianthus fordii	Y	Y	N	N
Lasianthus hiiranensis	Y	N	Y	Y
Lasianthus obliquinervis	Y	Y	Y	Y
Lasianthus wallichii	Y	Y	Y	Y
Neonauclea reticulata	Y	N	Y	Y
Psychotria rubra	Y	Y	Y	Y
Tarenna gracilipes	Y	Y	Y	Y
Tricalysia dubia	Y	Y	Y	N
Wendlandia formosana	Y	Y	Y	Y
Rutaceae				
Glycosmis citrifolia	Y	Y	Y	Y
Melicope semecarpifolia	Y	Y	Y	Y
Tetradium glabrifolium	Y	Y	Y	N
Zanthoxylum ailanthoides	Y	N	Y	Y
Sabiaceae				
Meliosma rigida	N	Y	N	N
Meliosma squimulata	Y	Y	N	N
Sapindaceae				
Sapindus mukorossii	N	N	Y	Y
Saxifragaceae				
Hydrangea chinensis	Y	Y	Y	N
Itea parviflora	Y	Y	N	N
Staphyleaceae				
Turpinia formosana	Y	N	N	N
Turpinia ternata	Y	Y	Y	Y
Sterculiaceae				
Reevesia formosana	Y	Y	Y	Y
Styracaceae				
Alniphyllum pterospermum	Y	N	N	N
Styrax suberifolia	Y	N	N	N
Symplocaceae				
Symplocos congesta	Y	Y	N	N
Symplocos modesta	Y	Y	Y	Y
Symplocos sasakii	N	N	N	Y
Symplocos shilanensis	Y	Y	N	N
Symplocos theophrastaefolia	Y	Y	N	N
Theaceae				
Adinandra formosana	Y	Y	Y	Y
Anneslea lanceolata	N	Y	N	N
Camellia hengchunensis	Y	Y	N	N
Cleyera japonica var. *morii*	Y	Y	N	N
Eurya chinensis	Y	Y	Y	Y
Eurya natida	N	N	Y	Y
Eurya nitida var. *nanjenshanensis*	Y	Y	N	N
Gordonia axillaris	Y	Y	N	N
Schima superba var. *kankoensis*	Y	Y	Y	N
Ternstroemia gymnanthera	Y	Y	N	N
Thymelaeaceae				
Wikstroemia taiwanensis	Y	Y	N	N
Ulmaceae				
Celtis formosana	N	N	Y	Y
Trema orientalis	N	N	Y	N
Urticaceae				
Dendrocnide meyeniana	N	Y	Y	Y
Verbenaceae				
Callicarpa remotiflora	Y	Y	N	N
Callicarpa remotiserrulata	Y	Y	Y	Y
Clerodendrum cyrtophyllum	Y	Y	Y	N
Premna octonervia	N	N	Y	Y

臺灣南部欖仁溪樣區之森林結構與物種組成

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摘　　要

南仁山區為臺灣南部保留之低地亞熱帶雨林。為了包含更多的地形變異及瞭解季風對森林結構及物種組成的影響，本研究將原先 3 公頃的欖仁溪樣區擴大至 5.88 公頃。樣區內所有胸高直徑大於 1 公分之木本植物均加以標定、鑑定、測量及記錄。整個樣區共記錄 60,146 株木本植物，分屬於 42 科 83 屬及 136 種。樣區中樹種累積底面積以殼斗科、茶科、五加科、冬青科、樟科及八角茴香科最為優勢。大多數的物種在徑級上呈現反 J-型或 L-型分佈，表示這些種類在樣區中皆能良好的更新。雙向指標種分析法 (TWINSPAN) 及降趨對應分析法(DCA)同時清楚的將樣區分成四類型，其分佈與地形位置有關，此四型依照特徵種-優勢種（生育地類型）命名分別為：恆春石斑木-紅花八角林型（迎風型），小葉樟-紅花八角林型（緩風型），猴歡喜-革葉冬青林型（背風型）及石苓舅-山龍眼林型（溪谷型）。本研究之結果顯示植物組成與先前之 3 公頃樣區類似，且同時呈現出地形變化及其導致的風力梯度對此森林物種組成及結構之影響甚深。

關鍵詞：降趨對應分析法、雙向指標種分析法、森林結構、季風、臺灣、南仁山、物種、植物組成。

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