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Changes of Plant Communities Classification and Species Composition along the Micro-topography at the Lienhuachih Forest Dynamics Plot in the Central Taiwan

Li-Wan Chang[1,2], Shau-Ting Chiu[1,3*], Kuoh-Cheng Yang[4], Hsiang-Hua Wang[5], Jeen-Lian Hwong[6], Chang-Fu Hsieh[1]

1. Institute of Ecology and Evolutionary Biology, National Taiwan University, 1 Roosevelt Rd., Sec. 4,Taipei 10617, Taiwan.
2. Taiwan Forestry Research Institute, No. 53, Nan-Hai Road , Taipei 10014, Taiwan.
3. Department of Botany, National Museum of Natural Science, 1 Kuan Chien Rd., Taichung 40453, Taiwan.
4. Department of Ecology, Providence University, 200 Chung Chi Rd., Taichung 43301, Taiwan.
5. Fushan Research Center, Taiwan Forestry Research Institute, 1 Shuangpi Rd., Hushi Vil., YuanshanTownship, Yilan 26445, Taiwan.
6. Lienhuachih Research Center, Taiwan Forestry Research Institute, 43 Hualong Ln., Wucheng Vil., Yuchih Township, Nantou 55543, Taiwan.
** Corresponding author. Tel: 886-4-2322-6940 ext. 505; Fax: 886-4-2325-8684; E-mail:stchiu@mail.nmns.edu.tw*

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ABSTRACT: How micro-topography affecting plant communities classification and species composition at one stand-level was investigated through the plant communities and species composition varied across fine-scale environmental heterogeneity at the 25-ha Lienhuachih broad-leaved forest dynamics plot (FDP). All free-standing woody plants with diameter at breast height ≧1 cm were identified, measured, tagged and mapped. Four plant communities were identified and represented with dominant and indicating species based on two-way indicator species analysis (TWINSPAN). Type I, *Pasania nantoensis - Randia cochinchinensis*, locating on the ridge and the highest elevation was with the highest stem density; Type II, *Mallotus paniculatus - Engelhardtia roxburghiana*, locating on the upper slope was an ecotone between type I and type III, with the middle stem density and basal area among four plant community types; Type III, *Diospyros morrisiana - Cryptocarya chinensis*, locating on the lower slope and stream side was with lower stem density but the highest species heterogeneity; and Type IV, *Machilus japonica* var. *kusanoi - Helicia formosana* locating on west stream side was with the lowest stem density and basal area. Detrended Correspondence Analysis (DCA) results showed nearly 27.11% of the plant species composition was attributable to micro-topographic variables. Ridge distance, stream distance and convexity were the most important factors effected the changes of plant community and species composition. Classification and regression tree (CART) method was also used to examine the relationship between each single specie and micro-topographic variables. Over 70% species had more than 27.11 % variations which explained by DCA results. To conclude, our results support the existence of habitat association and niche divergence related to micro-topography in a subtropical evergreen broad-leaved forest.

KEY WORDS: Habitat association, niche divergence, plant communities, species composition, micro-topography, subtropical evergreen broad-leaved forest.

INTRODUCTION

Topography is one of the most important factors affecting the vegetation pattern within a climatic region. In hilly or mountane areas, the vegetation pattern is closely related to the pattern of micro-topography (Hack and Goodlet, 1960; Miura and Kikuchi, 1978; Ishizaki and Okitsu, 1988). It not only creates a gradient of water and nutrient availability in the soil (Zak *et al.*, 1991; Enoki *et al.*, 1997; Hirobe *et al.*, 1998), but also affects the pattern of disturbances such as landslides, windstorms and fires (Kilgore and Taylor, 1979; Foster, 1988).

The fine-scale heterogeneity may affect the establishment of tree seedlings, which in turn influence the spatial distribution of tree species (Beatty, 1986; Núñez-Farfán and Dirzo, 1988; Harmon and Franklin, 1989; Nakashizuka, 1989). Resulting from niche differentiation, a micro-site could be important in maintaining species composition in a community. Closely related species may coexist in a non-uniform environment that permits partitioning among species, or even restriction to special microhabitats (Harper and Sagar, 1953; Harper ,1957, 1958).

Taiwan's montane areas are very steep and rugged. Previous vegetation studies in Taiwan have indicated that variations of forest composition at medium to large scales are primarily governed by climatic factors and reflect among different altitudinal or geographic regions (Su, 1984; Su, 1985; Hsieh *et al.*, 1997). However, there have been few direct and quantitative analyses that focused on relationships between the forest composition and environmental gradients at a stand-level scale, except for investigations performed with small dispersed sample plots (Su *et al.*, 2010).

Since 1990, in order to understanding forest dynamic changes, several large Forest dynamics plots (FDP) (total area > 5 ha) have been successively established (Yang *et al.*, 2008; Chang *et al.*, 2010). (e.g. Nanjenshan FDP located at south, Nantzuhsienhsi FDP located at median altitude in central, and Fushan FDP located at south). Previous studies showed the plant community changed along micro-topography, however used limited micro-topography variables, such as elevation, slope and aspect (Chao *et al.*, 2010; Yang *et al.*, 2008; Su *et al.*, 2010). For the continuous sampling FDP, Fan (2010) and Chao *et al.* (2010) both suggested that monsoon exposure angle was another important micro-topographic variable to affect the species distribution and plant community classification due to the strong monsoon effect. This indicated if we can find different micro-topographic variable which especially represented at unique site that could contribute more effects on understanding diversity and plant community classification in FDP.

In order to investigated how the plant communities and species composition varied across fine-scale environmental heterogeneity. Here we set up a forest dynamics plot (FDP) at the Lienhuachih broad-leaved forest dynamics 25-ha plot in central Taiwan in 2008. The Lienhuachih FDP was extremely steep, with slopes as steep as 35.3°, and had great topographical variation, with multiple dry ditch and gully features. In this study, we have included not only the usual micro-topographic variables, but also ridge distance and stream distance, which represented water content and landslide disturbance gradient we observed in the plot. We investigated: 1. how the plant community classification and species composition changed along the micro-topography gradient and 2. which micro-topographic factors were the great importance to affect the vegetation classification and species composition.

MATERIALS AND METHODS

Study site

The study site has been a Lauro-Fagaceous forest (Su, 1984) in the Lienhuachih Experimental Forest (LEF) in central of Taiwan. The mean annual temperature was 20.8°C. The annual precipitation was 2285.0 mm with seasonality (Lu *et al.*, 2008). More than half of the rain falls in between May and September (about 89.6% total rainfalls). The dominant soils could be classified into 2 types, Typic Dystrochrept and Typic Hapleudults red soils (King, 1986).

In 2008, following the census manuals developed by the CTFS's long-term research for forest dynamics plots (Condit, 1998), we set up a forest dynamics plot (FDP) (500 m × 500 m with projected area of 25 hectares) (23º54'49"N, 120º52'43"E) in the sampling area. The elevation of the plot ranged from 667 m to 845 m above sea level. Average slope of plots was about 35.3°. Topography of the plot was characterized by hills with valleys, steep slopes, and ridges. When typhoons with heavy rains passed near by this region, instant and large amounts of rainfall would particularly cause landslides and the collapse of steep slopes and stream banks. In the dry season, small streams usually without water showed an anhydrous state. The topographic features displayed a high spatial heterogeneity within the Lienhuachih FDP (Chang *et al.*, 2010).

Topography survey and tree census

Electronic total-station thedolites were used for precise topographic measurements. The field teams measured all horizontal points at 20-m intervals within the 25-ha plot. The plot was divided into 625 quadrats of 20 m × 20 m. All free-standing woody plants with diameter at breast height ≧ 1 cm of a 25-ha Lienhuachih FDP were identified, measured, tagged and mapped at every 20 m×20 m quadrat. In terms of plant identification, voucher specimens were collected from individuals that could not be determined in the field. The identification of plant species was based on the Flora of Taiwan (Editorial Committee of the Flora of Taiwan, 1993–2003). Detailed methods of the field inventory followed the unified protocol adopted by the CTFS plots network. (Condit, 1998; Su *et al.*, 2007; Chang *et al.*, 2010).

Data analysis

Micro-topography variables

Through the topographic survey, the elevation of each intersection point was measured. We used these values to calculate nine micro-topographic parameters for each 20 m × 20 m quadrat.

1. Mean elevation: the mean value of elevations at the four corners.
2. Slope: the mean angle of inclination of four triangular planes composed of any three quadrat corners.
3. Index of convexity (IC): the mean elevation of the focal quadrat minus the mean elevation of its eight surrounding quadrats. A positive IC indicated a convex terrain, whereas a negative one represented a concave terrain (Valencia *et al.*, 2004).
4. Distance to ridge: the nearest distance from the ridge to center point of 20 m × 20 m quadrat.
5. Distance to stream: the nearest distance from the

stream to center point of 20 m × 20 m quadrat.

6. Aspect (θ) were then transformed trigonometrically into four indices with values from -1 to 1:

(1) Northness (N) = *cos* (θ);
(2) Eastness (E) = *sin* (θ);
(3) Northeastness (NE) = *sin* (θ+45°);
(4) Southeastness (SE) = *sin* (θ-45°)

Plant community classification

To investigate the plant community classification, we used two-way indicator species analysis (TWINSPAN) (Hill, 1979). Importance value index (IVI, mean of both relative abundance and basal area in 100 %) of each species in each quadrat was complied into 144 species × 625 quadrats matrix. Eigenvalues (contribution of data variation) acquired in the program were used to determine the final results of community classification. The classification divisions were retained for those with eigenvalues > 0.14. Analyses using PC-ORD Version 5 (McCune and Medfford, 1999). Univariate analysis of means and Tukey's analysis ($\alpha = 0.05$) were used to determine whether number of species, density and basal area, diversity, and micro-topography were significantly different among community types.

Ordination of plant communities and species composition changing along the micro-topographic variables

We used Detrended Correspondence Analysis (DCA) (Hill and Gauch, 1980) in the PC-ORD program to summarize the trend in floristic composition. No data transformation was conducted. Species IVI values were utilized to determine DCA axes coordinates. For better ecological interpretation of DCA axes, we created a secondary matrix with micro-topographic factors of each quadrat and analyzed it with each DCA axis by utilizing Pearson's correlation.

The preceding DCA analysis focused on the global pattern of plant community along micro-topography gradient. To investigate niche differentiation of individual species further, we also applied the classification and regression tree (CART) (Therneau *et al.*, 2012) method to examine the relationship between tree abundance data of single species and micro-topographic variables. For quantitative comparison, we used "the proportion of variation explained by CART model" as a measure of the strength of micro-topographic differentiation.

RESULTS

Plant community classification

According to the TWINSPAN analysis four plant communities were identified. Classification was halted at the first division level, leaving all the divisions with eigenvalues > 0.14 (Fig. 1). Spatial distribution patterns of four plant community types (Fig. 2) in the Lienhuachih FDP showed that quadrats along stream side and those on the slope and close to ridge area separated at the first division level eigenvalues = 0.3041. Quadrats on the slope and close to ridge were further divided into two types: Type I, those were mainly close to the ridge and locating on high elevation; Type II, those mainly located on slope and under the ridge area (Fig. 2). On the other half of the TWINSPAN at the second division level (Fig. 1), stream side quadarts were further classified into two types: Type III, those mainly located on the lower slope above Type IV, and some of those located along east stream side; and Type IV, those were mainly on west stream side (Fig. 2). These four types respectively consisted of 196, 261, 125 and 75 quadrats.

Plant community types

Each community is named by the indicator species, which based on the TWINSPAN classification (Fig. 1) and supportively identified by the frequency of species that occurred in each plant community type (Table 1), and followed by the top IVI dominant canopy tree species in each community type among the fours (Table 2). Lienhuachih broad-leaved forest dynamics plot (FDP) represented four plant community types identified as *Pasania nantoensis* - *Randia cochinchinensis* type, *Mallotus paniculatus* - *Engelhardtia roxburghiana* type, *Diospyros morrisiana* - *Cryptocarya chinensis* type, and *Machilus japonica* var. *kusanoi* - *Helicia formosana* type. Pioneer species were noted, based upon regeneration requirements of species reported in the literature (Chang, 1996; Chen *et al.*, 2000; Chen *et al.*, 2003; Kuo *et al.*, 2011). The species diversity, characteristics of plant community structure and micro-topographic features listed in Table 3 were significantly differed.

Type I: *Pasania nantoensis - Randia cochinchinensis* type

This type was mainly located on the highest convexity, the highest elevation, steep slope, the shortest distance to ridge and the longest distance to stream (Table 3). This type was characterized by high stem density (8848.17 individuals·ha^{-1}) and high basal area (38.65 m^{2}·ha^{-1}), on the contrary, with the lowest branch ratio (16.19%) (Table 3). For the species richness, the average species number per quadrat was significantly higher than that of other types, but with the lowest species heterogeneity (Fisher's α 12.29). The evenness was with similarity between Type III and Type IV but that was lower than the Type II's (Table 3). A total of 103 species was recorded for this community

Table 1 Synoptic table of species with constancy ≥80 for each plant community type; Type I, *Pasania nantoensis - Randia cochinchinensis*; Type II, *Mallotus paniculatus - Engelhardtia roxburghiana*; Type III, *Diospyros morrisiana - Cryptocarya chinensis*; Type IV, *Machilus japonica* var. *kusanoi - Helicia formosana*. Constancy = frequency of species i in a vegetation unit (Chytry and Tichy, 2003).

Species	Type I	Type II	Type III	Type IV
Euonymus laxiflorus	**99**	**92**	26	4
Syzygium buxifolium	**△99**	**84**	18	4
Cinnamomum subavenium	**⊕99**	**⊕93**	71	32
Randia cochinchinensis	**○99**	**○95**	70	33
Diospyros morrisiana	**98**	**98**	**△90**	59
Ormosia formosana	**98**	**89**	58	16
Ardisia quinquegona	**98**	**93**	**86**	79
Tricalysia dubia	**○98**	**○95**	**○86**	64
Cyclobalanopsis pachyloma	**◇98**	**◇90**	47	17
Ilex goshiensis	**97**	56	3	0
Neolitsea aciculate	**⊕96**	**⊕89**	52	13
Pasania nantoensis	**△◇94**	32	2	1
Elaeocarpus japonicus	**90**	59	12	0
Podocarpus nakaii	**89**	72	29	12
Psychotria rubra	**○87**	**○87**	79	79
Helicia rengetiensis	**▼85**	51	6	0
Cryptocarya chinensis	**⊕84**	**△⊕97**	**⊕97**	**⊕95**
Schefflera octophylla	**80**	**96**	**100**	**99**
Castanopsis fargesii	**◇80**	71	42	21
Engelhardtia roxburghiana	77	**86**	△69	24
Blastus cochinchinensis	69	**◎94**	**◎98**	**◎95**
Litsea acuminata	65	**⊕86**	77	63
Glochidion acuminatum	61	77	***83**	***89**
Mallotus paniculatus	51	**△*88**	***94**	***93**
Helicia formosana	5	42	**▼91**	**▼97**
Neolitsea konishii	0	5	33	**△⊕81**
Glycosmis citrifolia	0	2	26	**△88**

***Pioneer species; △ Indicator species; ◇ Species belonging to Fagaceae, ⊕ Lauraceae, ○ Rubiaceae, ◎ Melastomataceae, and ▼ Proteaceae**

type, expect *P. nantoensis, Syzygium buxifolium* was another indicator specie of this type (Fig1). We chose *P. nantoensis* indicating this type, because Fagaceae was the most dominant family (e.g. *P. nantoensis, Cyclobalanopsis pachyloma*, and *Castanopsis fargesii*). For other canopy species such as, *Engelhardtia roxburghiana*, *Schima superba* and *Ormosia formosana* were with the high IVI. *Randia cochinchinensis, S. buxifolium* and *Cinnamomum subavenium* were the dominant species of sub-canopy layer (Table1). Shrub species were less of dominant species such as *Euonymus laxiflorus* and *Blanstus cochinchinensis* . In

Table 2. The top thirty dominant species listed by IVI and the accumulated IVI values in % of the four plant community types. No. means ranking the dominant species. Type I, *Pasania nantoensis - Randia cochinchinensis*; Type II, *Mallotus paniculatus - Engelhardtia roxburghiana*; Type III, *Diospyros morrisiana - Cryptocarya chinensis*; Type IV, *Machilus japonica* var. *kusanoi - Helicia formosana*. The abbreviation of layers include: C = canopy trees; SC = sub-canopy trees; S = shrubs. Symbols indicate “*” as pioneer species and “△” as indicator species.

No.	Type I	Type II	Type III	Type IV
1	*Randia cochinchinensis,* SC	*Engelhardtia roxburghiana,* C	*Cryptocarya chinensis,* C	*Helicia formosana,* SC
2	*Pasania nantoensis,* C$^{\triangle}$	*Blastus cochinchinensis,* S	*Schefflera octophylla,* C	*Blastus cochinchinensis,* S
3	*Syzygium buxifolium,* SC$^{\triangle}$	*Randia cochinchinensis,* SC	*Blastus cochinchinensis,* S	*Schefflera octophylla,* C
4	*Cyclobalanopsis pachyloma,* C	*Cryptocarya chinensis,* C$^{\triangle}$	*Helicia formosana,* SC	*Cryptocarya chinensis,* C
5	*Euonymus laxiflorus,* S	*Schefflera octophylla,* C	*Mallotus paniculatus,* C*	*Machilus japonica* var. *kusanoi,* C$^{\triangle}$
6	*Cinnamomum subavenium,* SC	*Diospyros morrisiana,* C	*Engelhardtia roxburghiana,* C$^{\triangle}$	*Mallotus paniculatus,* C*
7	*Schima superba,* C*	*Cinnamomum subavenium,* SC	*Diospyros morrisiana* C$^{\triangle}$	*Machilus zuihoensis,* C
8	*Engelhardtia roxburghiana,* C	*Mallotus paniculatu,* C* $^{\triangle}$	*Tricalysia dubia,* SC	*Neolitsea konishii* C$^{\triangle}$
9	*Tricalysia dubia,* SC	*Tricalysia dubia,* SC	*Litsea acuminata,* SC	*Ficus fistulosa,* C
10	*Diospyros morrisiana,* C	*Schima superba,* C*	*Machilus zuihoensis,* C	*Glycosmis citrifolia* SC$^{\triangle}$
11	*Ormosia formosana,* C	*Cyclobalanopsis pachyloma,* C	*Ardisia quinquegona,* SC	*Glochidion acuminatum,* C*
12	*Castanopsis fargesi,i* C	*Castanopsis fargesii, C*	*Glochidion acuminatum,* C*	*Ardisia sieboldii,* SC
13	*Helicia rengetiensis,* SC	*Psychotria rubra,* SC	*Psychotria rubra,* SC	*Ficus nervosa,* C
14	*Sapium discolor,* C*	*Ardisia quinquegona,* SC	*Cinnamomum subavenium,* C	*Cinnamomum camphora,* C
15	*Neolitsea aciculata,* SC	*Ormosia formosana,* C	*Schima superba,* C*	*Litsea acuminata,* C
16	*Schefflera octophylla,* C	*Euonymus laxiflorus,* S	*Cinnamomum micranthum,* C	*Psychotria rubra,* SC
17	*Podocarpus nakaii,* C	*Sapium discolor,* C*	*Sapium discolor,* C*	*Ardisia quinquegona,* SC
18	*Psychotria rubra,* SC	*Pasania nantoensis,* C	*Styrax suberifolia,* C	*Trema orientalis,* C*
19	*Ardisia quinquegona,* SC	*Castanopsis kawakamii,* C	*Castanopsis kawakamii,* C	*Tricalysia dubia,* SC
20	*Blastus cochinchinensis,* S	*Litsea acuminata,* SC	*Castanopsis fargesii,* C	*Styrax suberifolia,* SC
21	*Castanopsis cuspidata,* C	*Helicia rengetiensis,* SC	*Randia cochinchinensis,* SC	*Beilschmiedia erythrophloia,* C
22	*Gordonia axillaris,* C	*Podocarpus nakaii,* C	*Cyclobalanopsis pachyloma,* C	*Sapindus mukorossii,* C*
23	*Pasania konishii,* SC	*Pasania harlandii,* C	*Wendlandia formosana,* SC	*Ilex formosana,* SC
24	*Ilex goshiensis,* SC	*Neolitsea aciculata,* SC	*Limlia uraiana,* C	*Clerodendrum cyrtophyllum,* S*
25	*Elaeocarpus japonicus,* C	*Pasania konishii,* SC	*Ormosia formosana,* C	*Syzygium formosanum,* C
26	*Cryptocarya chinensis,* C	*Castanopsis cuspidate,* C	*Ardisia sieboldii,* SC	*Pasania harlandii,*,C
27	*Castanopsis kawakamii,* C	*Syzygium buxifolium,* SC	*Pasania harlandii,* C	*Saurauia tristyla* var *oldhamii* , SC
28	*Meliosma squamulata,* C	*Styrax suberifolia,* C	*Illicium arborescens,* C	*Diospyros morrisiana,* C
29	*Pasania harlandii,* C	*Glochidion acuminatum,* C*	*Ilex formosana,* SC	*Sapium discolor,* C*
30	*Pasania synbalanos,* SC	*Machilus thunbergii,* C	*Beilschmiedia erythrophloia,* C	*Cinnamomum subavenium,* C
IVI%	**92.12**	**85.21**	**86.91**	**89.99**

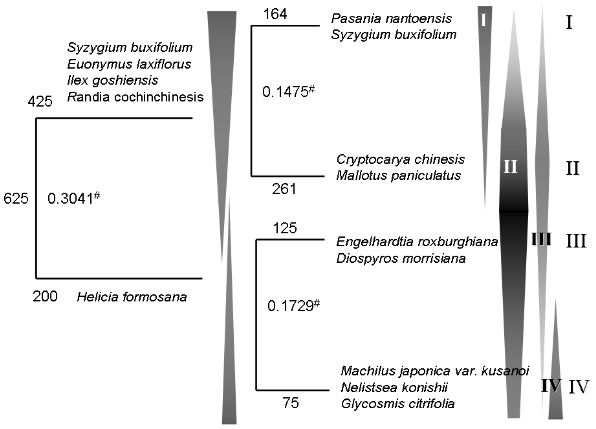

Fig. 1. Plant community types (I, II, III, and IV) in the Lienhuachih forest dynamics plot classified by TWINSPAN analysis. The number of quadrats, eigenvalues (#), and indicator species are noted in the division level. The areas of black gradients are the abundance of each indicator species.

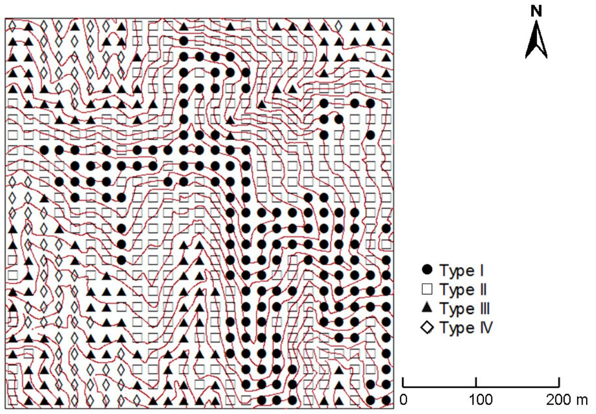

Fig. 2. Topography map and plant community types classified by TWINSPAN for the quadrats (20 × 20 m) in the Lienhuachih FDP. Type I, *Pasania nantoensis - Randia cochinchinensis*; Type II, *Mallotus paniculatus - Engelhardtia roxburghiana*; Type III, *Diospyros morrisiana - Cryptocarya chinensis*; Type IV, *Machilus japonica* var. *kusanoi - Helicia formosana*.

terms of pioneer species, *Schima superba* and *Sapium discolor* were the only two pioneer species among dominant species.

Type II: *Mallotus paniculatus - Engelhardtia roxburghiana* type

This type had the largest area of the plot (10.44 ha, 41%) (Table 3), most locating on the upper slope and some on the lower slope (Fig. 2). The micro-topographic features of this type were characterized by the second high elevation and the steepest slope (Table 3). Because of the high stem density 6055.75 stems·ha^{-1}, the basal area 34.18 m^{2}·ha^{-1} was also high (Table 3). There were 151, 393 individuals belonging to 124 species recorded for this community type. Although with the second high species number, Fisher's α diversity was only 14.97. However, the evenness was the highest of four types (Table 3). The 5 most dominant species, in descending order of IVI were *E. roxburghiana* (canopy), *B. cochinchinensis* (shrub), *R. cochinchinensis* (subcanopy), *Cryptocarya chinensis* (subcanopy) and *Schefflera octophylla* (canopy) (Table 2). The indicator species of this type were *C. chinensis* and *M. paniculatus.* We chose *M. paniculatus* represented this type, because of its' frequency occurred in Type II was much lower than in Type I. *S. discolor, M. paniculatus* and *Glochidion acuminatum* were the pioneer species of the top 30 dominant species of this type (Table 1).

Type III: *Diospyros morrisiana - Cryptocarya chinensis* type

Most quadrats in this type distributed along stream side, and a small part on lower slope within the plot (Fig 2). The micro-topographic features of this type were characterized by the low elevation and low convexity (Table 3). A total of 107,765 individuals, density, and basal area were lower than those of Type II and Type I (Table 3), but branch ratio was the second high among four types. For the species richness, this plant community type included 125 species, with the highest Fisher's α diversity (Table 3). *C. chinensis, S. octophylla* , *M. paniculatus*, *E. roxburghiana,* and *Diospyros morrisiana* were the dominant canopy species. Sub-canopy and shrubs species included,*B. cochinchinensis, Helicia formosana, Tricalysia dubia* and *Litsea acuminata* (Table 1). The indicator species of this type were *D. morrisiana* and *E. roxburghiana.* We chose *D. morrisiana* represented this type, because of its' frequency occurred in Type III was much higher than in Type IV. Four pioneer species of the dominant species in this type, these were *M. paniculatus, G. acuminatum, S. superba* and *S. discolor* (Table 1).

Type IV: *Machilus japonica* var. *kusanoi - Helicia formosana* type

This plant community type only included 75 quadrats occupying the least area within the plot (Table 3), mainly located on the west stream side (Fig 2), with the longest distance to the ridge, and the average lowest convexity (Table 3). Both stem density and basal area were the lowest among all plant community types, with 139.32 individual per quadrat and 27.95 m^{2} ·ha^{-1}, respectively (Table 3). A total of 113 species was recorded for this type and the species α is similar to Type III which was the second high among these four types. This type with the highest branch ratio was dominated by *H. formosana*,

Table 3. Summary statistics for the four plant community types detected by two-way indicator species analysis (TWINSPAN); Type I, *Pasania nantoensis - Randia cochinchinensis*; Type II, *Mallotus paniculatus - Engelhardtia roxburghiana*; Type III, *Diospyros morrisiana - Cryptocarya chinensis*; Type IV, *Machilus japonica* var. *kusanoi - Helicia formosana*. Micro-topographic variavles, species richness, density, basal area, and proportion of multi-stemmed trees were calculated on quadrat basis (mean value ± standard error). Values with different superscripts in each row denote significant differences at P <0.05 (Tukey's test).

	Type I	Type II	Type III	Type IV
Area (ha) [no. of quadrats]	6.56 [164]	10.44 [261]	5 [125]	3 [75]
Elevation (m)	779.73 ± 2.98^{a}	767.53 ± 2.19^{b}	748.83 ± 3.15^{c}	754.07 ± 2.80^{c}
Slope (◦)	36.06 ± 0.55^{a}	36.55 ± 0.47^{ac}	33.87 ± 0.69^{ad}	31.74 ± 0.75^{b}
Convexity	2.21 ± 0.20^{a}	-0.22 ± 0.15^{b}	-1.44 ± 0.24^{c}	-1.69 ± 0.26^{c}
Stream distance (m)	60.60 ± 1.77^{a}	51.03 ± 1.89^{b}	26.80 ± 1.93^{c}	19.47 ± 2.12^{c}
Ridge distance (m)	37.37 ± 2.91^{a}	69.60 ± 3.02^{b}	122.68 ± 5.72^{c}	154.29 ± 6.67^{d}
Basal area (m^2/ha)	38.65	34.18	26.23	23.37
Basal area (cm^2/quadrat)	1.67 ± 0.03^{a}	1.45 ± 0.03^{b}	1.13 ± 0.04^{c}	1.01 ± 0.05^{c}
Species richness (no. of species)	103	124	125	113
Species richness (no. of species/quadrat)	38.01 ± 0.47^{a}	37.77 ± 0.45^{a}	30.98 ± 0.75^{b}	27.95 ± 0.69^{c}
Species/ha	80	88	93	90
Density (individuals/25ha)	8848	6056	4311	3483
Density (individuals/quadrat)	253.93 ± 10.83^{a}	242.23 ± 10.83^{b}	172.42 ± 6.89^{c}	139.32 ± 5.08^{c}
Fisher's α	12.29	14.97	17.74	17.71
Branch ratio (%)	16.19	18.66	22.3	27.27
Evenness	0.68	0.73	0.68	0.67

with 7.36% IVI. Other dominant species, in a descending order of IVI value were *B. cochinchinensis, S. octophylla, C. chinensis, M. japonica var. kusanoi* and *M. paniculatus* (Table 2). The indicator species of this type were *M. japonica* var. *kusanoi, Neolitsea konishii* and *Glycosmis citrifolia.* We chose *M. japonica* var. *kusanoi* represented this type, because Lauraceae was the dominant family of this type. One fifth of dominant species are pioneer species, there were *M. paniculatus, G. acuminatum, Trema orientalis, Sapindus mukorossii, Clerodendrum cyrtophyllum,* and *S. discolor.*

Ordination of plant communities and species composition changing along the micro-topographic variables

The results of DCA ordination showed that the four communities located along a major compositional gradient (Fig. 3). The eigenvalues for the first three DCA axes were 0.460, 0.138 and 0.113, and the corresponding gradient lengths were 3.852, 2.501 and 2.103 (Table 4). Communities were well separated on the first DCA axis, in general in consistence with the results of the TWINSPAN classification. The first DCA axis explained 15.27% of the total variance in the data. The communities from left to right of DCA axis 1 were Type I, Type II, Type III and Type IV. The second DCA axis only explained 4.60% of the total variance in the data. The results of the DCA ordination demonstrated 27.11% of variation in erect woody species composition.

We also tested the relationship between the first three axes of DCA ordination analyses and micro-topographic variations (Table 4). We explored, the main correlated factors of the first DCA axis were ridge distance (correlation coefficient = - 0.627), stream distance (0.523) and convexity (0.516), whereas the main correlated factors of the second axis were northness (0.341), southeatness (-0.309) and slope (-0.207).

For quantitative comparison, the proportion of variation explained by CART model indicated the measurement of the strength of micro-topographic differentiation. Among 144 species excluding the 41 rare species whose individuals were less than 25, the

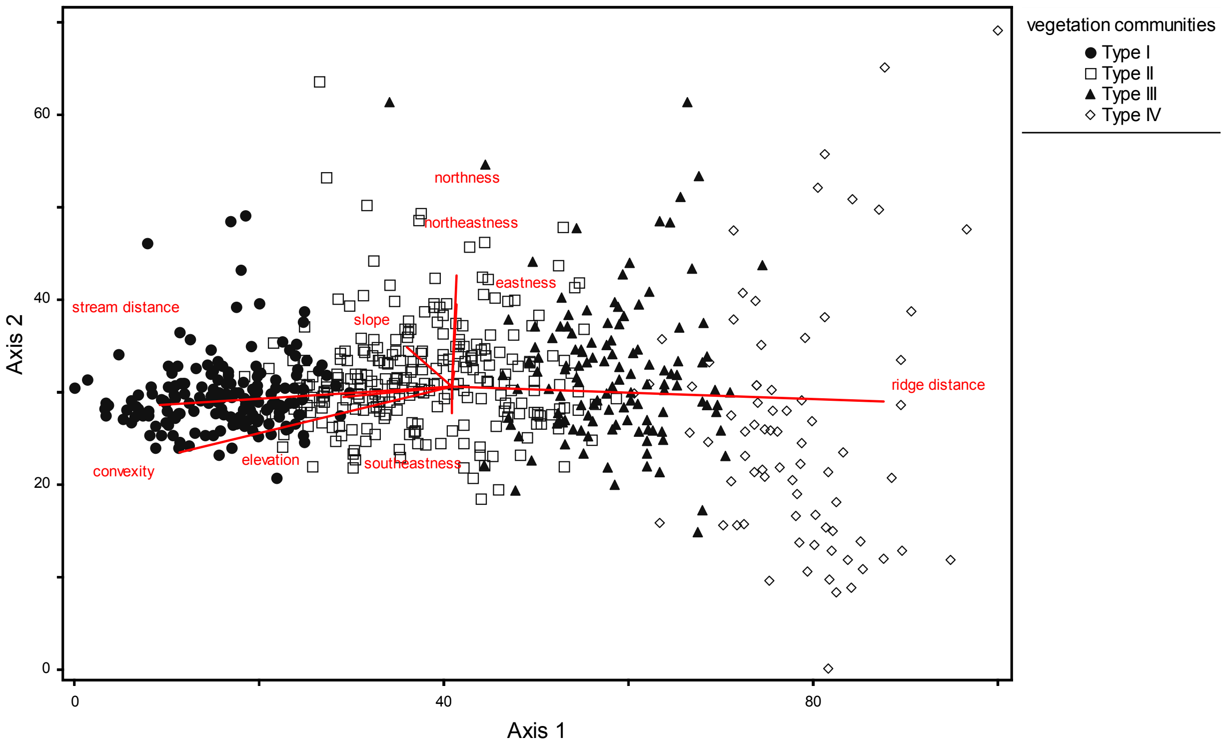

Fig. 3. DCA ordination diagram and the environmental factors of the Lienhuachih forest dynamics plot with the community types derived from TWINSPAN superimposed. The vectors represent topographic variables. The length of the vector is proportional to its importance; the angle between a vector and each axis is related to its correlation with the axis.

variation of 103 species distribution explained by model ranged as *S. buxifolium* and *Ilex goshiensis* each with a maximum of 65.2%, in contract *Melastoma candidum* with a minimum of 15.66% (Table 5). 79 out of 103 species (76.70%) displayed >27.1% (DCA, global pattern) variation of species distribution explained by CART model.

In terms of micro-topographic variables spited by these CART models, ridge distance, slope, elevation, convexity and stream distance showed the most prevalent influences, and were included in 74 (71.15%), 67 (64.42%), 66 (63.46%), 62 (59.62%), and 58 (55.77%) cases, respectively (Table 5). The proportions of explained variation revealed a positive correlation with the species' total abundance (person correlation $r = 0.40$, $P < 0.001$); i.e. the more individuals of certain species the higher proportions of variation in micro-topography could fit the explanation on the spatial differentiation of species distribution. Besides, there was no significant difference of explainable variation among different vertical forest layers of species by ANOVA examination ($P > 0.001$).

DISCUSSION

Plant community classification

For plant community classification, the continuous large plot was more difficult to separate clearly than small dispersed plots, because of niche obviously overlap in the same region (Wang *et al.*, 2000). It is also showed in our result, indicator species from TWINSPAN analysis of Type II and Type III separated from Type I and Type IV, respectively. But those did not indicate the species only occurred in each plant community type. In the study, we assist identified indicator species not only by the abundance of indicator species of TWINSPAN results but also the frequency of species in different plant community types. This could help us choose the suitable indicator species which represented in each type.

This study presented how plant community, species diversity, species abundance, branch ratio and species composition varied along the gradients of micro-topography at the Lienhuachih broad-leaved FDP. The ridge distance, stream distance and convexity were accounted for the top three variation factors of the erect woody species composition among the 9 micro-topographic variables. That could be caused by a comprehensive factor, disturbance. Although some pervious research inferred that it was possibly caused by historical disturbance events (Hara *et al.*, 1996; Enoki, 2003; Su *et al.*, 2010). However, the direct evidence was irrelevant.

According to the rainfall threshold value for debris

Table 4. Summary of the results of detrended correspondence analysis (DCA) of Lienhuachih species data from 625 quadrats. Correlation coefficients of micro-topographic variables with the first third axes.

	Axis1	Axis 2	Axis 3
Eigenvalue	0.460	0.138	0.113
Lengths of gradient	3.852	2.501	2.103
Cumulative % variance of species data	15.27	19.87	23.6
Slope	0.202	-0.207	0.147
Elevation	0.320	n.s.	n.s.
Convexity	0.516	.139	-0.228
Ridge distance	-0.627	-0.117	-0.173
Stream distance	0.523	0.167	n.s.
Eastness	n.s.	n.s.	n.s.
Northness	n.s.	0.341	0.521
Northeatness	n.s.	0.181	0.331
Southeatness	n.s.	-0.309	-0.400

flow warning, the precipitation > 350mm might possibly cause landslide in the steep slope at the LEF (Soil and Water Conservation Bureau, Debris Flow disaster prevention information). During 1958–2009, 67 typhoons went through the LEF where the average was 1.2 typhoons per year (Lu *et al.*, 2008; Lu *et al.*, 2010; Central Wheatear Bureau: Typhoon Database). For the maximum precipitation, 8 times > 350mm, 6 times > 400mm and 3 times > 500mm in 24 hours, respectively. (Lu *et al.*, 2008; Lu *et al.*, 2010). In 2008, a strong typhoons devastated the Lienhuachih FDP, brought 520mm heavy rainfall in 24 hours. After typhoon, we recensused landslide area, in a total of 1.22 ha damaged, more than 3300 tree were removed. About 93% of the disturbance area was nearby the stream side. That could reflect micro-topography variables, such as stream distance and convexity in the importance variables for species composition and plant community classification of the plot.

The quadrats close to stream: Type III and Type IV (lower slope and valley area, usually the concave terrain), was the most steep and unstable part of the whole plot. Therefore, it had the most active processes of soil erosion and the most frequent landslides or slope failures (Tamura, 1987; Lee, 2006). Unstable surface may limit species distribution. These two types had low tree density, the small basal area, and more pioneer species, such as *M. paniculatus* and *G. acuminatum* which indicated for these types. Because of the fast species turnover rate, species heterogeneity is relatively high among other plant community types, which could also explain these types have the high α diversity. Even some species might regenerate depending on landslide disturbance on unstable topography (Enoki, 2003). Species growth on unstable area usually do not become large trees but small trees or shrubs, and frequently sprout in natural conditions (Sakai and Ohsawa, 1993, 1994). That could explain, in our study, the branch ratio on the stream side and lower slope is higher than those on the ridge and upper slope area. Sprouting from the base of leaning trunks is also common in *H. formosana* and *B. cochinchinensis.* Other common species like *M. zuihoensis, L. acuminata* and *M. japonica* belong to Lauraceae which was the most dominant family indicator of these two types.

Type III and type IV both distributed in low elevation close to stream, but for the spatial pattern, they were separated. Type IV distributed on the stream bank and mostly on the west stream. In contrast, type III distributed above the stream bank or on the valley. In terms of micro-topographic variables, slope is the most important variable that showed the significant difference between these two types. The stream bed on the west side was wider than the east side, in part, slope steepness of type III was significant steeper than that of type IV (Table 3). It might cause different exposure of sun light in the stream bed habitat. Su (1987) interpreted environmental variables such as solar incidence angle (aspect) and slope might work together to regulate the strength of sun light. This could be another hidden environmental factor to verify the difference of these two plant community types. Slope was an important factor that affected establishment and growth of different spices (Enoki, 2003), but it might be other abiotic (soil nutrient distribution) or biotic (species interaction) factors which limit these two types spatial distribution.

On the other hand, the area closed to the ridge (usually the convex terrain), generally reveals greater wind-stress (Noguchi, 1992), lower soil moisture (Chen and Ho, 2001) and relatively stable in terms of soil surface disturbance. This stability may explain the greater density and large basal area found on type I and type II than other two types. When the typhoon came, the meteorological station on the ridge in the Lienhuachih FDP showed much greater wind speed (14.38 s/m) than the valley area (7.83 s/m). The effect of strong winds resulting from typhoon disturbances is severe on ridge positions (Lee, 2006). Fagaceae dominated in type I on the ridge and this similar pattern was also found in other forest in Asia (Hara *et al.*, 1996; Wang *et al.*, 2000). In our 2009 survey after typhoon disturbed, most of species

Table 5. The summary results of classification and regression tree (CART) analyses of 103 woody species. Percent variation explained >50 are listed in a descending order. The abbreviations of micro-topographic parameters are as follows: E = eastness; N = northness; NE = northeastness; SE = southeastness. The parameters marked with circles denoted the effective explanatory variables selected by CART models for individual species. The abbreviations of layer include: C = canopy trees; SC = sub-canopy trees; S = shrubs.

Species	Percent variation explained	Individual	Layer	Slope	Elevation	Convexity	E	N	NE	SE	Stream distance	Ridge distance
Syzygium buxifolium	65.2	5962	SC	○	○	○	○	○			○	○
Ilex goshiensis	65.2	1778	SC	○		○		○	○	○		○
Saurauia tristyla var. oldhamii	62.3	458	SC	○							○	○
Helicia formosana	60.9	5241	SC	○	○	○	○				○	○
Randia cochinchinensis	60.3	21075	SC	○	○	○		○		○	○	○
Pasania nantoensis	56.2	821	C	○		○	○	○	○		○	○
Meliosma squamulata	55.5	711	SC	○	○	○		○	○	○	○	○
Cyclobalanopsis pachyloma	54.6	3875	C	○	○	○	○	○	○	○	○	○
Trema orientalis	54.1	35	C			○				○		○
Glycosmis citrifolia	53.9	630	SC	○	○	○					○	○
Ficus nervosa	53.8	161	SC	○	○			○			○	○
Elaeocarpus japonicus	52.4	1129	C	○		○	○		○		○	○
Tricalysia dubia	52.1	6251	SC	○		○	○	○	○		○	○
Ilex formosana	52.1	602	SC	○	○	○		○	○		○	○
Meliosma squamulata	51.9	4779	C			○	○	○	○		○	○
Neolitsea aciculata var. variabillima	51.8	3514	SC	○	○	○	○	○			○	○
Saurauia tristyla var. oldhamii	51.1	168	SC	○	○						○	○
Cinnamomum subavenium	50.8	3800	SC	○	○	○		○	○		○	○
Gordonia axillaris	50.2	1320	C	○	○		○	○			○	○
Sum of the above (Percent variation explained >50)		62310		17	12	15	9	13	9	5	17	19
Other species (Percent variation explained < 50)		82929		50	54	47	37	29	37	33	41	55
Total (Proportion of total 103 species)		145239		67 (64.42)	66 (63.46)	62 (59.62)	46 (44.23)	44 (42.31)	46 (44.23)	38 (36.54)	58 (55.77)	74 (71.15)

like *C. pachyloma* and *P. nantoensis* did not die but sprouted from the base. Many authors also have reported that species growing on the ridge or upper slope in natural forests usually comprise longer-lived, climax species (Kikuchi, 1981; Tanaka, 1985; Kikuchi and Miura, 1991, 1993; Sakai and Ohsawa, 1993, 1994; Shimada, 1994). Therefore, Type I and Type II have relatively less pioneer species than Type III and Type IV.

Micro-topography association of individual tree species

The results from the CART analyses provide a more specific test of micro-topographical variable association for individual species because the DCA was derived from the whole community composition and may not be capably fit to every species populations. Among 103 species populations, 79 species had more than 27.1% variation of their distribution explained by micro-topographic variables. These species certainly display stronger niche differentiations than the whole species pool. In particular, the ridge distance, stream distance, and convexity variables were still the dominant factors in models, but slope showed the second dominant factor. That could explain slope was an important factor affecting the species distribution and as well the spatial distribution of plant community types III and type IV.

Besides, the positive correlation between explanatory power of models and species abundance further suggests that the distributions of more abundant species are more likely differentiated among various micro-topographic conditions. These results indicate pervasive habitat associations of tree species in this plant community. Although there was no significant difference of explainable variation among different vertical forest layers of species by ANOVA examination ($P > 0.001$), there was still a tendency of poor explainable variation in shrub. The results showed the same as the previous study (Su *et al.*, 2010). These species at the low-statured layer might be affected by other factors that further differentiae the micro environment below the shelter of canopy trees, e.g. light condition.

Over all, our result showed the strong relationship between plant community types, species composition and varied topographic features in the Lienhuachih FDP. In a niche-driven community, more heterogeneity of environment generally results in greater habitat specialization and hence stronger associations with species distributions (Potts *et al.*, 2004). Other researches in subtropical Asia forests also showed the same pattern, such as Lanjenchi plot (Chao *et al.*, 2007) in south Taiwan, Lopei plot (Lin *et al.*, 2005) and Fushan plot (Su *et al.*, 2010) in northern Taiwan and some plots in Japan forest (Hara *et al.*, 1996; Enoki, 2003). It also implies that different micro-topography influences the soil formation and disturbance events. To conclude, our results support the existence of habitat association and niche divergence related to micro-topography in a subtropical evergreen broad-leaved forest.

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台灣中部蓮華池森林動態樣區依微地形影響之植物社會分類與植物組成改變

張勵婉(1,2)、邱少婷(1,3*)、楊國禎(4)、王相華(5)、黃正良(6)、謝長富(1)

1. 國立台灣大學生態學與演化生物學研究所，10617 台北市羅斯福路 4 段 1 號，臺灣。
2. 行政院農業委員會林業試驗所技術服務組，10014 台北市南海路 55 號，臺灣。
3. 國立自然科學博物館，40453 台中市館前路 1 號，臺灣。
4. 私立靜宜大學生態系，43301 台中沙鹿鎮中棲路 200 號，臺灣。
5. 行政院農業委員會林業試驗所福研究中心，26445 宜蘭縣員山鄉湖西村雙埤路 1 號，臺灣。
6. 行政院農業委員會林業試驗所蓮華池研究中心，55543 南投縣魚池鄉五城村華龍巷 43 號，臺灣。

* 通信作者。*Tel: 886-4-2322-6940 轉 505; Fax: 886-4-23258684; Email: stchiu@mail.nmns.edu.tw*

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摘要：單一地點其微地形如何影響植物社會分類及物種組成，可藉由調查25公頃蓮華池闊葉林森林動態樣區的植物社會及物種組成沿著異質性微地形的變化而了解。測量樣區內胸高直徑達到1cm以上的樹木種類及標定其位置，採用雙向指標法(TWINSPAN)，依優勢種及指標種分成不同植物社會類型: 第Ⅰ型: 南投石櫟-茜草樹型 (*Pasania nantoensis* - *Randia cochinchinensis* type) 主要分布於山頂陵線，海拔最高、植株密度最大；第Ⅱ型: 白匏子-黃杞 (*Mallotus paniculatus* - *Engelhardtia roxburghiana* type) 是屬於第I型及第Ⅲ型的過渡帶，分布於中上坡，植株密度、胸高斷面積次之；第Ⅲ型:山紅柿-厚殼桂型 (*Diospyros morrisiana* - *Cryptocarya chinensis* type)主要分布在中下坡、溪谷，植株密度較少，但物種種類的異質性最高；及第Ⅳ型:大葉楠-山龍眼型(*Machilus japonica* var. *kusanoi* - *Helicia formosana* type)，分布於樣區西側溪谷附近，植株密度及胸高斷面積皆為最低。另利用降趨對應分析(DCA)排序法並與微地形等環境因子檢測後發現，有27.11%的物種組成在空間上分化可以被微地形因子所解釋，又以距稜線距離、距溪溝距離及凹凸度為重要影響的因子。在單一物種數量變化與微地貌的關係檢測則利用分類與迴歸樹(CART)方法，結果顯示超過70%的物種受微地形因子影響可解釋變異量大於利用降趨對應分析方法可解釋的27.11%變異量。總體而言，本研究支持在亞熱帶常綠闊葉林中，各種微地形因子確實會影響生境的分化以及各物種分布與生育地的關聯性。

關鍵詞：生育地關聯性、生境分化、植物社會、物種組成、微地形、亞熱帶常綠闊葉林。