Research paper

Micro-topographic Differentiation of the Tree Species Composition in a Subtropical Submontane Rainforest in Northeastern Taiwan

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【Summary】

In this study, we investigated how the forest composition varies across fine-scale environmental heterogeneity. We established a 25-ha permanent plot, surveyed the micro-topography, and censused all trees with diameter at breast height of ≥ 1 cm within a natural broad-leaved forest in northeastern Taiwan. The micro-topographic differentiation of the forest composition and habitat association of individual species were analyzed using regression tree models and indicator species analysis. Our results demonstrated that nearly 30% of the variation in the tree species composition was attributable to micro-topographic factors in this contiguous forest region. Slope curvature, inclination, and aspect were the decisive factors of micro-topographic niche differentiation. Over 9/10 of the examined species were shown to be indicative of a specific habitat, but each species performed dissimilarly in both the magnitude and breadth of its habitat associations. In addition to niche differentiation, other underlying processes might also be jointly regulating this forest community. In conclusion, our results confirm the control of the niche-assembly rule on tree species diversity and forest structure along micro-topographic gradients in this subtropical rainforest.

Key words: niche differentiation, micro-topography, indicator species, habitat association, Fushan Forest Dynamics Plot.

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研究報告

台灣東北部亞山地雨林樹木組成之微地形分化現象

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摘　要

為了探討森林組成在細微尺度異質環境下的變化，本研究於台灣東北部天然闊葉林中設立一處25公頃的永久樣區，進行微地形高程測量工作，並完成區內所有胸高直徑達到1 cm以上樹木的每木調查工作。本研究採用迴歸樹狀模式與指標種分析法，以分析森林組成在微地形上的分化以及個別樹種對於生育地的關聯性。分析結果顯示，在這個連續的森林區域內，近30％的樹木組成變化可歸因於微地形因子。其中以坡面曲度、坡度與方位角為最關鍵的生境分化因子。而在所有的受測樹種中，超過九成的樹種對於特定的生育地具有指標能力，但是在不同樹種之間則呈現強弱與幅度不等的生育地關聯性。而除了微地形分化作用之外，其他潛在的生態過程亦可能共同影響此處森林的樹木分布變化。綜言之，本研究證實在這處亞熱帶雨林中，微地形上的變化梯度可反映出生境組合律對於樹種多樣性與森林結構的影響力。

關鍵詞：生境分化、微地形、指標種、生育地關聯性、福山森林動態樣區。

INTRODUCTION

Investigating species assemblage rules is an important topic in plant community ecology. Among dozens of mechanisms documented by theoretical and empirical studies, dispersal-assembly and niche-assembly processes are currently the main points being debated (Hubbell 2001, Whitfield 2002, Potts et al. 2004). The dispersal-assembly theory claims that forest communities are formed through continuous random processes of seed and propagule dispersal and seedling establishment (Hubbell and Foster 1986, Wang and Smith 2002); species assemblages have little dependence on environmental variations. On the contrary, the niche-assembly theory argues that a forest community structure is subject to environmental heterogeneity and species interactions; every tree species adapts to a specific niche to avoid competitive exclusion (Grubb 1986, Wright 2002). Due to the distinct properties and predictions of these theories, detecting and quantifying the effects of the underlying mechanisms on a forest community are essential for forest management and species conservation.

In a niche-driven forest community, tree species evolve to adapt to specific environments and reveal certain habitat associations (Enoki 2003, Tuomisto et al. 2003, Kubota et al. 2004, Gunatilleke et al. 2006). Hence the associated habitat types can be properly defined by the presence/absence or abundance of corresponding indicator species. Conversely, species would have little relation to environmental factors or the distribution of other species in a dispersal-driven community (Hubbell and Foster 1986,

Hubbell et al. 1999). Results from earlier studies demonstrated that niche differentiation plays an influential part of plant community assemblages at the geographic-, regional-, and stand-level scales (Clark et al. 1999, Tuomisto et al. 2003, Potts et al. 2004). Moreover, topographic effects on forest structure, tree distribution, and forest dynamics were well documented in several forests (Harms et al. 2001, Enoki 2003, Kubota et al. 2004, Potts et al. 2004, Valencia et al. 2004, Gunatilleke et al. 2006).

Previous vegetation studies in Taiwan indicated that variations of the forest composition at medium to large scales (> 10 km) are primarily governed by climatic factors and reflect different altitudinal or geographic regions (Su 1984, 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 (usually 0.01~0.1 ha in size). In this study, we attempted to investigate relationships between the tree species composition and micro-topographic gradients on a fine scale, using data from a 25-ha permanent plot that is situated in a natural forest with a heterogeneous topography. The study attempted to answer the following questions:

1. How is the tree species composition associated with micro-topography? ;
2. Which micro-topographic factors are of great importance? ; and
3. Do different species show distinct associations with certain habitats?

MATERIALS AND METHODS

Study site

We conducted this study in the Fushan Forest Dynamics Plot (FFDP), a 25-ha permanent plot located in northeastern Taiwan (24°45'40"N, 121°33'28"E) (Fig. 1). The FFDP is a subtropical site of the worldwide forest monitoring plot network organized by the Center of Tropical Forest Science of the Smithsonian Tropical Research Institute (CTFS) (Losos and Leigh 2004). The plot is situated in an old-growth submontane rainforest which can be categorized as the *Machilus-Castanopsis* zone of broad-leaved forests in Taiwan (Su 1984). The forest reveals a strong dominance concentration, where the leading 5 species account for more than 50% of the total basal area (Su et al. 2007).

The climate at Fushan is strongly influenced by typhoons during summer and autumn (Mabry et al. 1998) and the northeastern monsoon in winter, with an average temperature of 18.2℃, a mean annual precipitation of 4271 mm, and a mean relative humidity of 95.1% (Su et al. 2007). Rain falls throughout the year (no dry months with < 100 mm of precipitation), but is heaviest during the typhoon season from July to September.

Topographically, the FFDP is situated in a small upstream watershed. The plot encompasses a hill in the western part and a permanent creek traversing the eastern and southern parts (Fig. 1). The soils are extremely acidic (pH 3.3~4.3) with low organic carbon content and fertility (Su et al. 2007). The morphological features, physical conditions, and chemical properties of the soils vary across different topographic locations (Liao 2005, Su et al. 2007).

Topographic survey and tree census

The 25-ha FFDP was designed as a 500×500-m grid system composed of 625 20×20-m quadrats. The plot region and
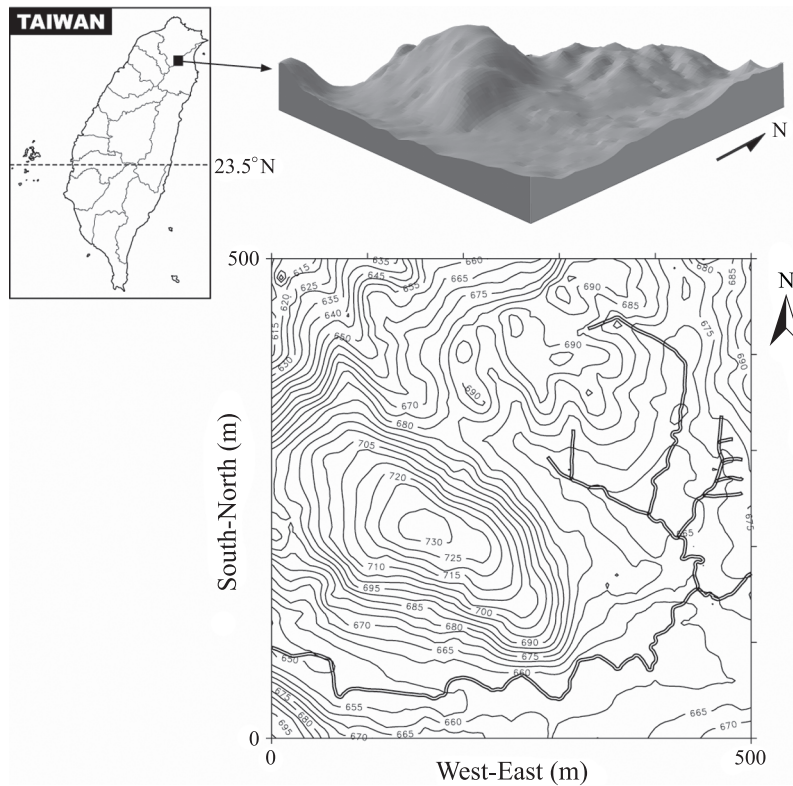
Fig. 1. Location, perspective diagram, and contour map of the Fushan Forest Dynamics Plot. The contour lines are drawn at 5-m intervals in elevation. The zigzag double-line indicates creeks within the plot.

each intersection of the grid system were demarcated and staked during 2002~2003, through topographic survey work implemented with electronic theodolites. Following that, the tree census work was carried out in 2003~2004. All shrubs, trees, and tree ferns (hereafter jointly called "tree species") with a diameter at breast height (DBH) of ≥ 1 cm were tagged, identified, measured, and mapped. Branches of multi-stemmed individuals were also counted and measured. Detailed methods of the topographic survey and tree census followed the unified protocol adopted by the CTFS plots network (Condit 1998, Su et al. 2007). The identification of tree species was based on the *Flora of Taiwan* (Editorial Committee of the Flora of Taiwan 1993~2003).

Data processing and statistical methods

Through a topographic survey, the elevation of each intersection point was measured. We used these values to calculate 7 micro-topographic parameters for each 20 × 20-m quadrat and compiled them into a "quadrat × environment" matrix.

1. Mean elevation: the mean value of elevations at the 4 corners of the 20 × 20-m quadrat.
2. Slope: the mean angle of inclination of 4 triangular planes composed of any 3 quadrat corners (Harms et al. 2001).
3. Index of convexity (IC): the mean elevation of the focal quadrat minus the mean elevation of its 8 surrounding quadrats. A positive IC indicates a convex terrain, whereas a negative one indicates a concave

terrain (Valencia et al. 2004).

4. Four indices of aspect: the aspect, defined as the steepest downslope direction of a slope surface, was geometrically computed from the plane composed of the 4 quadrat corners instead of field measurements. Due to its circular property (counting from 0° to 359°), aspects (θ) were then transformed trigonometrically into 4 indices with values from -1 to 1:

(1) Northness (N) = $cos(\theta)$;

(2) Eastness (E) = $sin(\theta)$;

(3) Northeastness (NE) = $sin(\theta + 45°)$; and

(4) Southeastness (SE) = $sin(\theta - 45°)$.

During the tree census, a total abundance of 114508 individuals comprising 110 species was recorded in 625 20×20-m quadrats. The tree abundance data were then compiled into a "quadrat×species" matrix. On account of the minimum sample size for data analysis, rare species (< 10 individuals ha^{-1}) were excluded, leaving 48 species for the subsequent analyses, which comprised 97% of the total abundance.

To investigate the niche differentiation of the tree species composition, we applied the classification and regression tree (CART) method to examine the relationship between tree abundance data of single species and environmental factors. CART explains the variation of a response variable by repeatedly partitioning the data into more-homogeneous subsets through various combinations of explanatory variables (Breiman 1984, De'ath and Fabricius 2000). This creates a tree-like diagram that illustrates the relationship and hierarchy of variables in a straightforward way. Therefore, it was proposed as being suitable for exploring complex ecological data (De'ath and Fabricius 2000). The multivariate regression tree (MRT) analysis is a multivariate extension of CART (De'ath 2002). It is a constrained clustering method

that constructs a dichotomous tree model for multidimensional data in response to selected explanatory variables. This nonparametric technique was shown to be more robust than traditional ordination methods and capable of handling nonlinear relationships within data (De'ath 2002). In this study, we used the MRT to analyze the "quadrat×species" and "quadrat×environment" matrices. For parsimony reasons, we adopted the 1-S.E. rule to determine the size of the tree model (Breiman 1984, De'ath 2002). The MRT helped detect habitat types among which the tree community composition and micro-topographic factors correspondingly varied. Species associated with habitat types were then identified using the indicator value (INDVAL) method (Dufrêne and Legendre 1997). INDVAL calculations combine the relative abundance and frequency for a species occurring in a specific MRT-defined habitat type and then test its statistical significance. INDVAL ranges from 0 (for species not present in a given group of quadrats) to 100 (for species occurring in all quadrats within 1 specific group only), indicating both the specificity and fidelity of selected species.

The above data processing and analyses were carried out on an R statistical platform (R Development Core Team 2008). In addition, we used the "rpart" (Therneau et al. 2009), "mvpart" (De'ath 2007), "labdsv" (Roberts 2007), and "npmc" (Helms and Munzel 2008) R packages for the CART, MRT, INDVAL, and nonparametric multiple comparison analyses, respectively.

RESULTS

Topographic features

Elevations in the FFDP range 600~733 m with an uneven terrain. The topographic

components of hills, ridges, slopes, gullies, flats, and the creek create complex relief in the plot (Fig. 1). The distributions and summary statistics of micro-topographic variables are shown in Fig. 2. Although the leptokurtic distribution of the mean elevation indicated over 85% of the region fell into a 60-m range (640~700 m), minor parts at both edges implied the existence of precipitous terrain within the plot. More than 82% of the area was inclined at > 10° in slope. The IC value represents the curvature of the surface within a 20×20-m localized area. It showed a roughly symmetric unimodal distribution with 45.4 and 54.6% of convex and concave landforms, respectively. If we defined flat regions as areas within 1-unit IC deviation from 0, 78.7% of the plot was uneven. The 4 indices of aspect similarly displayed U-shaped distributions, featured by low flat central parts and 34.1~48.5% allocations at the 2 tail bins. All these data features not only
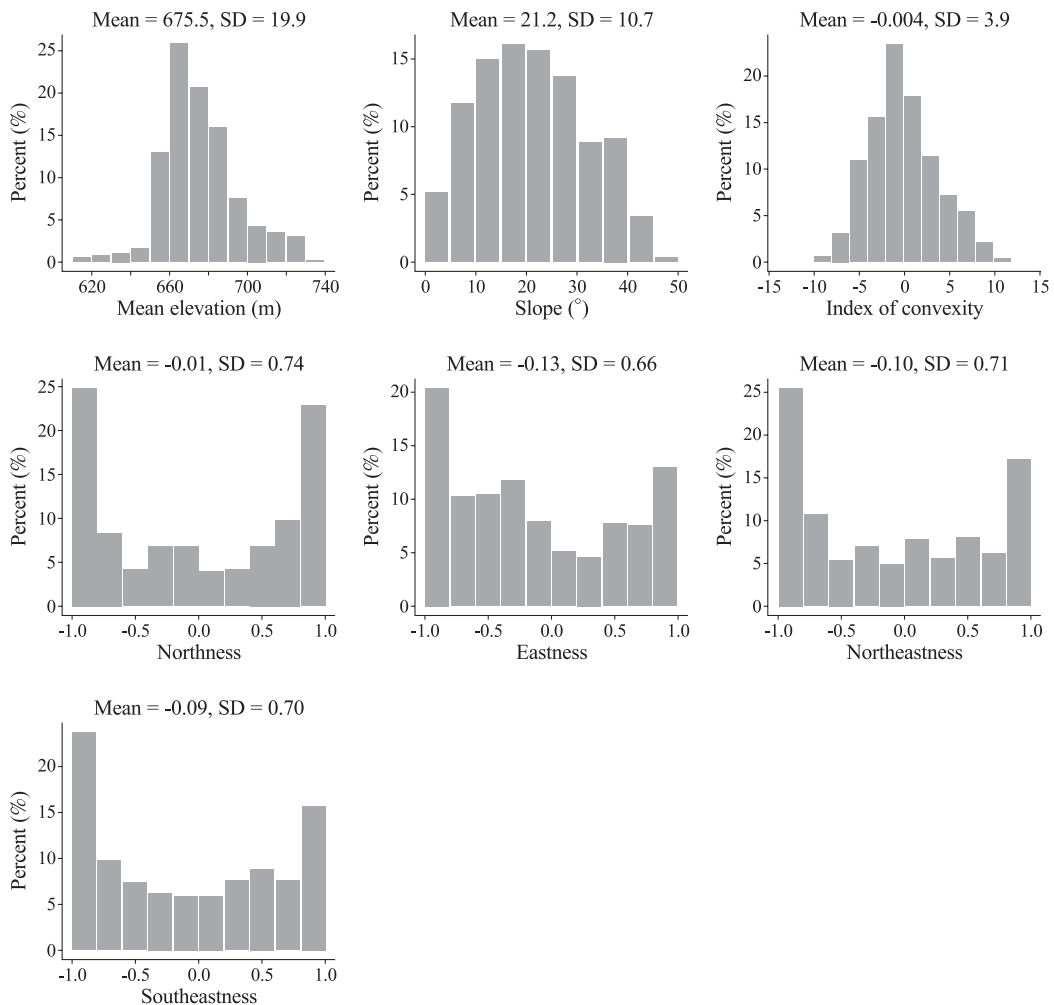

Fig. 2. Histograms of micro-topographic variables. The information above each panel shows the mean value and standard deviation (SD) of the variable. The bins in each histogram denote right-open (left-closed) intervals of the focal variable.

showed departures from normality ($p <$ 0.001, Shapiro-Wilk normality test; thus non-parametric analyses were preferred) but also indicated a highly heterogeneous micro-topography within the FFDP.

Tree species composition in response to micro-topography

For the forest composition, the MRT defined 7 habitat types by the IC, SE, and slope factors (Fig. 3). This tree model explained 29.3% of the total variation in the species assemblage in the FFDP. First of all,

40 quadrats (6% of all) with the most convex terrain were separated from the others. This branch was then divided into types 1 and 2 by a threshold of SE of 0.38; type 1 was found in the southeast-oriented ridge at the main hill of the plot, while type 2 occurred on the opposite part of the ridge and in several protrudent patches (Fig. 4). The left primary branch of the tree model contained less-convex to concave landforms. Types 3 and 4 were steep slopes differing from types 5~7 with slopes of ≥ 30.35º; type 3 occupied the southeastern bisection of the steep slope region, and type
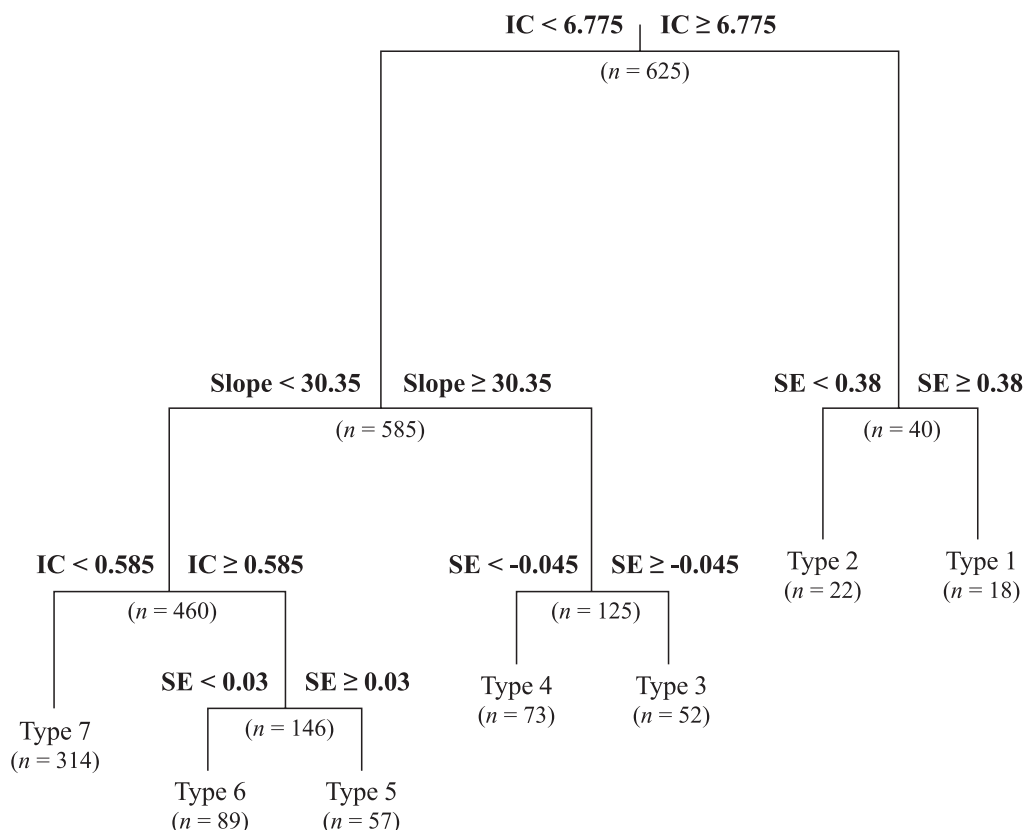
Fig. 3. Multivariate regression tree (MRT) for the tree species composition against micro-topographic factors in the Fushan plot. The information above each node denotes the selected factor and rule for the division of the quadrats. Numbers in parentheses below each node and terminal give the number of quadrats in that branch. The length of the branch is proportional to the variation explained by tree splitting. The abbreviations of factors are as follows: IC, index of convexity; SE, southeastness index.

4 existed in the northwestern part. Types 5~7 had somewhat gentler slopes which could be further categorized into 3 groups: types 5 and 6 represented moderately convex southeastern and northwestern surfaces, respectively, while type 7 represented for most of the flat and concave terrains (77%) and also comprised the greatest part of the plot (50% of all), which includes flat, creek-side, lower-slope, and gully regions (Fig. 4).

Among the 7 habitat types, the species diversity and characteristics of the forest structure significantly differed (Table 1). Species richness and tree density were highest in type 1 and lowest in type 7. The summation of basal area, an approved predictor of forest biomass, was also lowest in type 7, but highest in type 2, but without significant differences among types 1~6. Conversely, the multi-stemmed architecture of the trees was most common in type 7 and occurred least in type 1.

Indicator species for habitat types

In total, 44 of 48 species (92%) were detected to be statistically significant indicator species in association with the MRT habitat classification. We sorted out 39 indicator species with INDVAL ≥ 25 to represent eligible characteristic species (Dufrêne and Legendre 1997). The results of the indicator species analysis can be interpreted in a 2-way manner. One is to find the best indicator species for each habitat type, and the other focuses on species performances across different habitats.
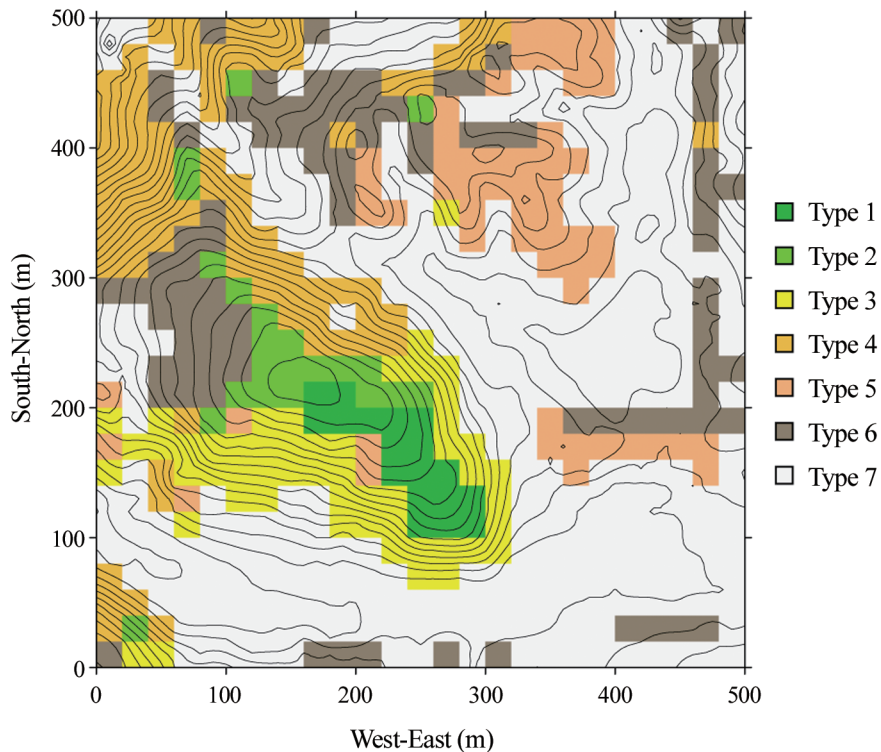

Fig. 4. Map of the habitat types classified by the multivariate regression tree at a 20×20-m scale. Considering visual clarity, elevation values of the contour lines were omitted (see Fig. 1).

Table 1. Summary statistics for the 7 habitat types detected by a multivariate regression tree (MRT) analysis. The species richness, density, basal area, and proportion of multi-stemmed trees were calculated on a quadrat basis (mean value±standard error). Values with different superscripts in a row denote significant differences at *p* < 0.05 (Behrens-Fisher type nonparametric multiple-comparison test; Munzel and Hothorn 2001). For easy interpretation, density and basal area are scaled up to a per-hectare basis

	MRT habitat classification						
	Type 1	Type 2	Type 3	Type 4	Type 5	Type 6	Type 7
Area (ha) [no. of quadrats]	0.72 [18]	0.88 [22]	2.08 [52]	2.92 [73]	2.28 [57]	3.56 [89]	12.56 [314]
Shannon's index of diversity	3.19	3.45	3.48	3.24	3.34	3.06	2.92
Species richness (no. of species quadrat^{-1})	39.9 ± 0.9^a	38.0 ± 1.0^{ab}	35.1 ± 0.9^{bcd}	32.6 ± 0.9^{ce}	38.7 ± 0.6^{ad}	31.1 ± 0.7^e	27.5 ± 0.4^f
Density (individuals ha^{-1})	8971 ± 393^a	6684 ± 371^b	5054 ± 245^c	4625 ± 226^c	6697 ± 232^b	4543 ± 160^c	3719 ± 84^d
Basal area (m^2 ha^{-1})	42.7 ± 1.2^a	48.7 ± 2.5^a	44.0 ± 1.3^a	43.9 ± 1.6^a	48.3 ± 1.8^a	42.7 ± 1.4^a	38.1 ± 0.9^b
Proportion of multi-stemmed trees (%)	18.9 ± 1.4^a	21.5 ± 1.0^{ab}	28.0 ± 0.7^{ce}	26.4 ± 1.0^{bc}	21.7 ± 0.6^{ad}	25.3 ± 0.8^{bd}	30.1 ± 0.5^e

Among the 7 MRT-generated habitat types, the indicator species analysis selected 11 habitat groups defined by a single type or a combination of several types (Table 2). For solitary habitat types, type 1 displayed the most indicator species, while type 6 had no indicator species at all. On the other side, 5 composite groups of habitats at various levels of the MRT hierarchy were detected (see Fig. 3). However, albeit statistically significant, these INDVAL values considerably varied among habitat types, and some species were counted in more than 1 habitat, e.g., *Litsea acuminata* and *Helicia formosana*.

Methodologically, associations with higher INDVAL values would represent more-proper habitat categories (Dufrêne and Legendre 1997). Therefore, for species associated with more than 1 habitat type, we selected a combination of maximum INDVAL values as the species' best indicative power of habitat discrimination (Table 3). From this viewpoint, the habitat type "1 + 2" could be characterized by 28 indicator species, which was the largest number across all habitat categories. From the aspect of species performance, *Myrsine seguinii* showed the highest INDVAL (nearly 90) with habitat type "1 + 2" (Fig. 5). In second place, *Syzygium buxifolium* presented a distinct specificity to the solitary habitat type 1. Unexpectedly, *H. formosana*, a widespread species with the second largest population in the plot, was well representative of habitat type "3 + 4 + 5 + 6 + 7", appearing to be a complement to *M. seguinii*'s distribution pattern on the map (Fig. 5).

Differentiation of species distributions

The preceding MRT and INDVAL analyses focused on the global pattern of differentiation in the forest community and its corresponding indicator species. To further investigate the niche differentiation of individual species, we applied the CART analysis, i.e., a univariate regression tree, to the single-species abundance data and micro-topographic variables. For quantitative comparisons, we used "the proportion of variation explained by the CART model" as a measure of the strength of micro-topographic differentiation.

Table 2. Detected habitat types associated with indicator species of indicator values (INDVAL) ≥ 25. For each habitat, the number of indicator species and INDVAL values of the primary indicator species (with the highest value) are listed here. The codes for the habitat types are consistent with those of the multivariate regression tree model (see Fig. 3). The asterisks with INDVAL denote the significance levels of the permutation tests ($p <$ 0.01; *** $p <$ 0.001)**

Habitat type	No. of indicator species	Primary indicator species	INDVAL
1	20	*Syzygium buxifolium*	88.9***
2	7	*Cinnamomum subavenium*	40.3**
3	1	*Prunus phaeosticta*	25.1***
4	3	*Saurauia tristyla*	31.2***
5	3	*Litsea acuminata*	32.7***
7	1	*Helicia formosana*	37.4***
1 + 2	30	*Myrsine seguinii*	89.9***
3 + 4	5	*Cyathea podophylla*	47.5***
5 + 6	3	*Litsea acuminata*	32.0**
5 + 6 + 7	4	*Helicia formosana*	59.3***
3 + 4 + 5 + 6 + 7	4	*Helicia formosana*	77.8***

Thirty-four of 48 species (71%) displayed > 10% variation of species distributions explained by the model, with a maximum of 64.6% in the species *S. buxifolium* (Appendix 1). Among these effective models, the IC, mean elevation, SE, and slope factors showed the most prevalent influences, and were included in 26 (77%), 14 (41%), 12 (35%), and 9 (27%) cases, respectively. The proportions of explained variation revealed a positive correlation with the species' total abundance (Spearman's $\rho = 0.34$, $p < 0.05$). In addition, species with greater explainable distributions tended to reveal higher INDVAL values (Spearman's $\rho = 0.74$, $p < 0.001$), except several widespread species such as *Blastus cochinchinensis*.

DISCUSSION

Micro-topographic differentiation of the forest composition

Micro-topographic factors in the plot demonstrated a large environmental variation in landforms (Fig. 2). In a niche-driven community, a greater heterogeneity of the environment generally results in greater habitat specialization and hence stronger associations with species distributions (Potts et al. 2004). In the FFDP, nearly 30% of variation in the tree species composition was explained by the selected micro-topographic factors through the MRT model. Comparing our results with similar studies conducted in other regions, Clark et al. (1999) investigated a tropical rain forest across a "mesoscale" landscape (~1 to 100 km^2) in Costa Rica and found that only 2.2% of the variation in the species composition could be accounted for by edaphic and topographic factors taken together. Kubota et al. (2004) reported that 41% and 74% of the variance in tree density and species richness, respectively, could be explained by topography in a 1.2-ha subtropical forest on Okinawa Island. Although the spatial scales, resolution of field sampling, and analytical methods differed among these studies, our results

Table 3. Thirty-nine indicator species for habitat types categorized by the multivariate regression tree (MRT). Indicator values (INDVAL) and corresponding habitats of each species are given. The codes for habitat types denote different hierarchy levels of MRT groupings (see Fig. 3). For species associated with more than 1 habitat type, only the records with the maximum INDVAL are listed here. The asterisks with INDVAL denote the significance levels of permutation tests (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$)

Species	INDVAL	Habitat type
Syzygium buxifolium	88.9***	1
Ilex ficoidea	44.5***	1
Litsea acuminata	32.7***	5
Cryptocarya chinensis	31.0***	5
Myrsine seguinii	89.9***	1 + 2
Elaeocarpus japonicus	85.9***	1 + 2
Pyrenaria shinkoensis	84.5***	1 + 2
Cinnamomum subavenium	81.1***	1 + 2
Randia cochinchinensis	80.1***	1 + 2
Cyclobalanopsis longinux	79.7***	1 + 2
Meliosma squamulata	79.2***	1 + 2
Cyclobalanopsis sessilifolia	77.5***	1 + 2
Diospyros morrisiana	76.5***	1 + 2
Castanopsis cuspidata var. *carlesii*	75.0***	1 + 2
Daphniphyllum glaucescens	74.6***	1 + 2
Cleyera japonica	73.3***	1 + 2
Machilus thunbergii	72.5***	1 + 2
Limlia uraiana	72.4***	1 + 2
Ardisia quinquegona	68.8***	1 + 2
Tricalysia dubia	65.3***	1 + 2
Antidesma japonicum	62.1***	1 + 2
Symplocos theophrastifolia	59.1***	1 + 2
Eurya loquaiana	56.9***	1 + 2
Engelhardtia roxburghiana	56.5**	1 + 2
Cyathea podophylla	52.9*	1 + 2
Symplocos glauca	52.5**	1 + 2
Elaeocarpus sylvestris	51.6***	1 + 2
Cinnamomum austrosinense	50.5***	1 + 2
Pasania harlandii	50.2**	1 + 2
Adinandra formosana	48.9***	1 + 2
Prunus phaeosticta	45.9*	1 + 2
Ilex pubescens	40.3**	1 + 2
Schefflera octophylla	45.1**	3 + 4
Machilus mushaensis	26.9*	5 + 6
Ilex formosana	28.7*	5 + 6 + 7
Helicia formosana	77.8***	3 + 4 + 5 + 6 + 7
Blastus cochinchinensis	69.1***	3 + 4 + 5 + 6 + 7
Machilus zuihoensis	36.5*	3 + 4 + 5 + 6 + 7
Saurauia tristyla	35.7**	3 + 4 + 5 + 6 + 7
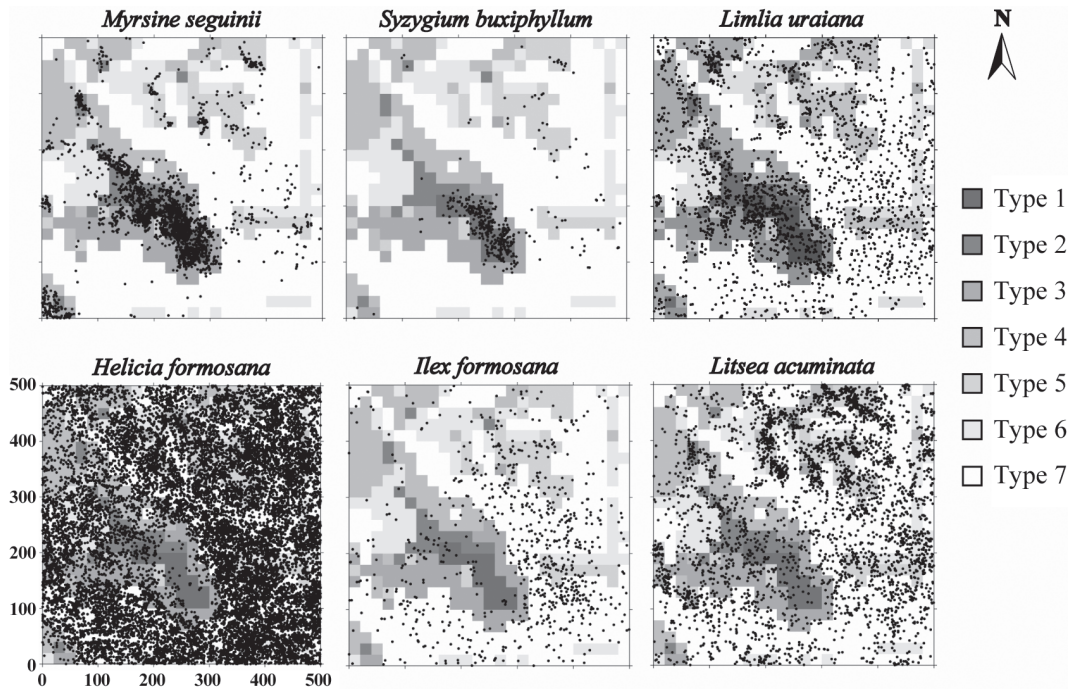
Fig. 5. Selected distribution maps of indicator species for the various habitat types. The units of the axes are in meters. For the associated habitat type of each species and a colored habitat map, readers are referred to Table 3 and Fig. 4.

unequivocally detected niche differentiation of the tree community in a subtropical forest in Taiwan using direct and quantitative variables of micro-topography alone.

The IC factor accounted for the most variation of the tree species composition among the 7 micro-topographic variables (Fig. 3). By definition, the index represents the curvature of the local landform and may reflect varied environmental settings. A convex terrain (usually the summit, ridge, or slope areas) generally reveals faster water drainage, lower soil moisture (Chen and Ho 2001), and greater wind-stress (Noguchi 1992a) than a concave landform. Therefore, different soil formation processes may be accordingly invoked (Chen et al. 1997). In the MRT model, the most convex and the most concave regions were sorted out to be at the 2 extremes, which represented the largest

differentiation of the forest composition. In other words, they defined the beta-diversity on this fine-scale compositional gradient (Legendre et al. 2005).

The slope factor sieved out the steepest areas in the plot. On inclined ground, the slope factor determines the surface space per unit horizontal area and the repose angle of its substrates, hence providing various physical conditions for tree growth (Barnes et al. 1998). Soil properties may also be influenced by the inclination of a slope (Chen et al. 1997). Moreover, the extent of slope steepness is usually related to the magnitude of disturbances caused by water runoff, soil erosion, and consequent tree-falls (Barnes et al. 1998; Enoki 2003). Wang et al. (2002) showed that more gaps were found with steep landforms than in the flatter region at Fushan. Therefore, with the highly variable slope

factor, more micro-topographic niches might be created in the Fushan forest which could favor certain tree species.

The aspect of the slope further seg-regated the compositional variation of the forest by means of a southeastern tendency. In sloping areas, the aspect factor affects the reception of insolation and the magnitude of wind-stress against the prevailing winds, hence modifying the vegetation structure and composition (Sun et al. 1998, Kubota et al. 2004). The MRT model had 3 nodes split by the SE index, indicating the asymmetry of forest vegetation along a southeast-northwest gradient (Fig. 3). More specifically, types 1 and 2 were divided in an uneven manner at the cutoff point far from 0. The result suggests an asymmetrical development of habitats in the summit and ridge regions. Similar phenomena were observed in other wind-affected forests (Noguchi 1992b, Sun et al. 1998). Meteorological records at the Fushan station (ca. 4 km from the FFDP) indicate that the prevailing wind directions are from the east or west (Lu et al. 2000). Therefore, the uneven patterns on the hilltops might be attributed to wind stresses and local atmospheric circulation altered by the surrounding landforms.

Although micro-topographic dif-ferentiation only accounted for a part of the community constitution in the MRT model, significant differences were found in species richness, forest structure, and tree architecture among habitat types (Table 1). This indicates the accompanying effects of micro-topography on the forest physiognomy and diversity. In addition, the control of niche-assembly in this forest may have been underestimated partly due to the coun-teraction or interference of multi-species performances in the modeling process, and partly due to a lack of data on other decisive environmental factors, e.g., soil properties (Clark et al. 1999, Poulsen et al. 2006, John et al. 2007) and micro-climatic conditions (Lin et al. 2003). However, the results might also imply the existence of other driving forces underlying this contiguous forest region, such as dispersal-assembly, historical events (e.g., typhoon disturbances), and random drift (Hubbell and Foster 1986, Hubbell et al. 1999, Lin et al. 2003).

Habitat associations of individual tree species

Individual species demonstrated different magnitudes and breadths of specificity among various MRT-classified habitat types and their groupings (Table 3). Some species were indicative of higher-level combinations of habitat types, which suggested that they were more eurytopic than other indicator species along the micro-topographic gradient. Among the 39 selected indicator species, most species were most highly associated with the summit and ridge areas (habitat type "1 + 2" or "1"; Table 3). To our knowledge, none of these indicator species was recognized as a typical pioneer species before. Therefore, the uniqueness and asymmetry of this region should have developed under certain localized conditions (e.g., soil properties) or constant stress (e.g., wind), rather than under gaps created by catastrophic disturbances.

The results from the CART analyses provide a more-specific test of habitat associations of individual species because the MRT model is derived from the entire community composition and might not ca-pably fit every species' population. Among 48 species populations, 14 species had > 30% variation of its distribution explained by micro-topographic variables. These species certainly display stronger niche dif-ferentiations than the entire species pool. In

particular, the IC, SE, and slope variables were still the dominant factors in the models, with the addition of a mean elevation factor. In addition, the positive correlation between the explanatory power of the models and species abundances 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 forest community.

The 5 leading dominant species in the canopy, which accounted for 54% of the total basal area, showed a moderate to great extent of habitat association (28~63% explainable variation; see Appendix 1). The lower levels observed for *Limlia uraiana* and *Castanopsis cuspidata* var. *carlesii* might have been due to their vegetative growth and recruitment limitations. Both of these species vigorously sprouted (Su et al. 2007), and a scarcity of seedling establishment was observed in the Fushan forest (unpublished data). Hence, trees of these 2 species might persist at their initial sites once they are successfully established and then pass through environmental filtering. This persistence strategy may counteract the environmental control to a certain extent (Bond and Midgley 2001). As for understory species, *B. cochinchinensis* and *H. formosana*, which together accounted for 34% of the total abundance and dominated the sub-canopy and shrub layers, performed quite differently. They both showed considerable INDVAL values with habitat "3 + 4 + 5 + 6 + 7" but merely low to moderate explainable variations. Similar results were found for other eurytopic species such as *Machilus zuihoensis* and *Ilex formosana*. These might have been due to the intraspecific distributional variations over their broad habitats. In addition, there was also a tendency of the variations in shrub species to be poorly explained (Appendix 1). These low-statured species might be affected by other factors that further differentiate the microenvironment below the shelter of canopy trees, e.g., light conditions.

CONCLUSIONS

Our study demonstrated the niche differentiation of the tree species composition along micro-topographic gradients in subtropical Taiwan. The forest vegetation revealed distinct yet asymmetrical patterns among different micro-topographic units, accompanied by divergences in tree diversity and forest physiognomy. Slope curvature (convex, flat, or concave), inclination, and aspect were the decisive factors of micro-topography that determined the forest composition.

Most species were shown to be indicative of specific habitats but performed dissimilarly both in the magnitude and breadth of the habitat association. Importantly, the major canopy tree species displayed a moderate to great extent of habitat association. Some species even revealed stronger differentiations of tree distributions than the entire forest community. In addition, a moderately positive correlation existed between the species abundance and the extent of micro-topographic differentiation. These results clearly indicate pervasive habitat associations for populations of species within the forest.

Although there might be other potential processes co-regulating the forest community, our results verify the control of niche-assembly by directly examining relationships between the community structure and micro-topographic gradients. The findings presented here may be of great importance for both the conservation of natural broad-leaved forests and further community ecological studies in Taiwan.

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Appendix 1. Summary results of the classification and regression tree (CART) analyses of 48 tree species. The abbreviations of micro-topographic parameters are as follows: IC, index of convexity; E, eastness index; N, northness index; NE, northeastness index; SE, southeastness index. The parameters marked with circles denote the effective explanatory variables selected by CART models for individual species. The abbreviations of lifeform include: C, canopy trees; SB, sub-canopy trees; S, shrubs; F, tree ferns

Family	Species	Chinese name	Lifeform category	Abundance	Basal area (m² ha⁻¹)	Percent variation explained	Mean elevation	IC	slope	E	N	NE	SE
Myrtaceae	*Syzygium buxifolium*	小葉赤楠	SB	396	0.03	64.6		○					○
Theaceae	*Pyrenaria shinkoensis*	烏皮茶	C	4725	2.20	62.5		○					○
Theaceae	*Cleyera japonica*	紅淡比	SB	1528	0.59	59.3	○	○	○		○		○
Elaeocarpaceae	*Elaeocarpus japonicus*	薯豆	C	1327	0.80	59.3	○	○	○	○			
Lauraceae	*Machilus thunbergii*	紅楠	C	2984	2.72	46.3	○	○	○				○
Cyatheaceae	*Cyathea podophylla*	鬼桫欏	F	2524	1.79	46.3	○		○			○	
Myrsinaceae	*Myrsine seguinii*	大明橘	SB	2735	0.45	45.4		○					
Elaeocarpaceae	*Elaeocarpus sylvestris*	杜英	C	581	0.09	44.6	○	○	○		○		
Sabiaceae	*Meliosma squamulata*	綠樟	C	3633	2.61	41.0		○					
Fagaceae	*Cyclobalanopsis longinux*	錐果櫟	C	820	0.36	36.5		○		○			
Fagaceae	*Castanopsis cuspidata* var. *carlesii*	長尾栲	C	4681	3.91	33.9		○		○			
Proteaceae	*Helicia formosana*	山龍眼	SB	18614	1.68	33.0	○		○				
Rubiaceae	*Randia cochinchinensis*	茜草樹	SB	1876	0.17	31.9		○					
Lauraceae	*Cinnamomum subavenium*	香桂	C	654	0.15	30.0		○					
Daphniphyllaceae	*Daphniphyllum glaucescens*	奧氏虎皮楠	SB	688	0.10	28.1		○					
Fagaceae	*Limlia uraiana*	烏來柯	C	2172	10.30	27.5	○				○		
Lauraceae	*Litsea acuminata*	長葉木薑子	C	3719	2.03	27.0	○						○
Myrsinaceae	*Ardisia quinquegona*	小葉樹杞	S	1383	0.02	24.8	○						○
Rubiaceae	*Tricalysia dubia*	狗骨仔	SB	1102	0.12	24.6	○						○
Melastomataceae	*Melastoma candidum*	野牡丹	S	371	0.00	22.7	○				○		○
Fagaceae	*Cyclobalanopsis sessilifolia*	毽子櫟	SB	355	0.02	19.4	○						
Ebenaceae	*Diospyros morrisiana*	山紅柿	C	2256	0.89	18.1	○						
Symplocaceae	*Symplocos theophrastifolia*	山豬肝	SB	3057	0.33	17.9	○						
Myrsinaceae	*Maesa perlaria*	台灣山桂花	S	317	0.01	17.4		○	○				○
Actinidiaceae	*Saurauia tristyla*	水冬瓜	SB	660	0.02	17.3	○						
Saxifragaceae	*Itea parviflora*	小花鼠刺	SB	354	0.04	16.6	○	○		○			
Euphorbiaceae	*Antidesma japonicum*	密花五月茶	S	996	0.02	13.5	○						
Fagaceae	*Pasania harlandii*	短尾柯	C	1552	0.21	13.3	○						
Verbenaceae	*Callicarpa kochiana*	鬼紫珠	S	305	0.01	12.9	○	○			○	○	
Aquifoliaceae	*Ilex formosana*	糊樗	SB	814	0.10	12.8							○
Araliaceae	*Schefflera octophylla*	江某	C	2373	0.98	12.7		○	○				○
Juglandaceae	*Engelhardtia roxburghiana*	黃杞	C	8204	1.54	11.2		○	○			○	
Theaceae	*Eurya loquaiana*	細枝柃木	S	1596	0.06	10.2	○						
Aquifoliaceae	*Ilex ficoidea*	台灣糊樗	SB	489	0.02	10.1							○
Lauraceae	*Cryptocarya chinensis*	厚殼桂	SB	295	0.19	9.5		○					○
Rubiaceae	*Lasianthus fordii*	琉球雞屎樹	S	308	0.00	9.0	○						
Symplocaceae	*Symplocos glauca*	山羊耳	SB	1579	0.10	8.8		○					
Lauraceae	*Cinnamomum austrosinense*	牡丹葉桂皮	SB	436	0.03	8.2		○					○
Fagaceae	*Cyclobalanopsis gilva*	赤皮	C	272	0.31	8.1							○
Melastomataceae	*Blastus cochinchinensis*	柏拉木	S	20660	0.15	7.4	○						
Euphorbiaceae	*Glochidion acuminatum*	裏白饅頭果	SB	2343	0.60	7.3							○
Rosaceae	*Prunus phaeosticta*	黑星櫻	SB	1116	0.37	7.1			○				○
Lauraceae	*Machilus mushaensis*	霧社楨楠	C	2322	2.19	6.4	○						
Aquifoliaceae	*Ilex pubescens*	密毛冬青	S	400	0.01	5.9			○				
Lauraceae	*Machilus zuihoensis*	香楠	C	702	0.61	5.2	○		○	○		○	
Oleaceae	*Osmanthus matsumuranus*	大葉木犀	SB	321	0.02	5.0	○						
Lauraceae	*Cinnamomum micranthum*	冇樟	C	385	1.01	4.3			○				
Theaceae	*Adinandra formosana*	台灣楊桐	SB	517	0.12	4.2	○						