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# 臺灣中部蓮華池亞熱帶森林
# 木本植物多樣性與共存之研究

# Diversity and Coexistence of Woody Plants
# in a Subtropical Forest at Lienhuachih of Central Taiwan

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# 摘要

群聚生態學家常探討為何在熱帶森林中樹木多樣性如此高，以及不同物種在森林裡如何共存的問題。影響森林中物種在空間中的分布及共存，主要受棲位過程以及散佈過程的影響。近年來史密森熱帶森林研究中心在全世界設立了許多大型森林動態樣區，都不似台灣為一個亞熱帶多高山的島嶼，地形變化劇烈，且每年遭受颱風的侵襲。因此於 2008 年根據史密森熱帶森林研究中心森林動態樣區設立的方式，在台灣中部蓮華池試驗林建立了一座 25 公頃的森林動態樣區，除對於樣區內所有的樹木皆進行精確的測量及標記位置外，更收集了樣區內的地形、土壤及以干擾等環境因子資料，本研究的目的為探討棲位過程及散布過程如何影響台灣亞熱帶森林木本植物之多樣性以及共存；是否與取樣地形變化平緩且干擾較少的熱帶雨林研究所得到結果相似？

研究結果顯示，蓮華池森林動態樣區是一個以樟科和殼斗科為優勢的楠櫧森林。分析各種類的徑級結構，顯示大部份的物種以小徑级的幼樹為主，表示此森林更新狀況良好。以 alpha 多樣性而言，與台灣其他低海拔動態樣區比較，蓮華池動態樣區為最為豐富，但較世界上其他熱帶的森林動態樣區低。

以植物社會而言，蓮華池森林可以區分為四個植物社會類型:南投石櫟-茜草樹型，主要分布於山頂陵線，海拔最高、植株密度最大；白匏子-黃杞型，分布於中上坡，植株密度、胸高斷面積次之；山紅柿-厚殼桂型，主要分布在中下坡、溪谷，植株密度較少；以及大葉楠-山龍眼型，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。四型植物社會的分化及分布皆受到微地形梯度的變化所影響。

此外，比較兩個生態過程對於影響物種組成在空間中的分布時，當環境因子僅有地形因子時，散布過程為主要的影響因素，但如果加入土壤的因子的作用時，棲位過程較散布過程更顯得重要。除了地形以及土壤因子外，另在環境因子中又加入

了干擾因子，比較兩個生態過程，對於影響先驅以及非先驅幼樹組成在空間中的分布，棲位過程仍為主要的影響。然而，比較散布過程的作用，主要對於非先驅幼樹在空間上的分布影響大於先驅的幼樹。

本研究同時說明了地形因子主要影響非先驅幼樹的分布，干擾因子則影響先驅幼樹的分布，土壤因子雖然對於森林中全部物種的分布，以及先驅及非先驅的幼樹分布都相當重要，但由於植物、地形以及干擾因子都會反應於土壤的物理或化學成分之中，故對於利用土壤因子解釋物種的分布，不能過度放大其重要性。再分解多尺度的純空間變量後顯示，地形因子表現解釋反應在大尺度的空間變量，土壤及干擾因子則為增加中尺度及小尺度空間變量的重要性。總體而言，在地形變化劇烈且多干擾的蓮華池亞熱帶森林中，棲位過程主要維持了蓮華池森林樹木的多樣性與共存，並影響著植物社會的分化。

**關鍵詞**：多樣性、共存、棲位過程、散布過程、蓮華池亞熱帶森林、地形、土壤、干擾

# ABSTRACT

Why tree diversity is so high and what drives coexistence of species in a tropical forest is the central question that community ecologists concern. Niche- and dispersal-based processes are two main processes which affect distribution pattern and coexistence of trees in a forest. Recently, forest dynamics plots (FDP) established by the Smithsonian Institution Center for Tropical Forest Science (CTFS). However, none of the above is the same as in Taiwan, a subtropical and mountainous island with rough terrain and frequent disturbance. Therefore, in 2008, I used the standard protocol as the Smithsonian CTFS’s to establish a 25-ha FDP in the Lienhuachih Experimental Forest ($23^{o}$54’49”N, $120^{o}$52’43”E) in Central Taiwan. Expect precise stem mapping and topography measurement, I also collected soil and disturbance data to assess how niche- and dispersal-based processes affect coexistence of species and diversity of a subtropical forest and whether these were the same as the tropical FDPs with relative flat terrains and little disturbance.

My results show the Lienhuachih FDP is dominated by Fagaceae and Lauraceae and which is characteristic of the *Machilus-Castanopsis* forest zone of Taiwan. The size-class structure of trees show most tree species have plenty saplings, which display good recruitment in the forest. Fisher’s alpha diversity of the Lienhuachih FDP is the highest among low-elevation FDPs in Taiwan, but lower than which of other FDPs in tropical plots.

On the other hand, the Lienhuachih forest could be divided to four types, these are *Pasania nantoensis* - *Randia cochinchinensis* type locates on the ridge and the highest elevation was with the highest stem density, *Mallotus paniculatus* - *Engelhardtia roxburghiana* type locates on the upper slope was with the middle stem density and basal area, *Diospyros morrisiana* - *Cryptocarya chinensis* type locates on the lower slope and

stream side was with lower stem density and *Machilus japonica var. kusanoi* - *Helicia formosana* type locates on west stream side was with the lowest stem density and basal area. All four plant communities and species composition varied across micro-topographic gradients.

In addition, both niche process and dispersal process work together to assemble the Lienhuachih tree communities. When comparing above two processes affect community assembly, if only topography is included, dispersal-based processes prevail. But if including soil variables along with topography variables into variation partitioning, the result reverses. Furthermore, including disturbance variables with topography and soil variables, niche-based processes still prevail for both pioneer and non-pioneer saplings. However, dispersal limitation is also an important process influencing the spatial distribution of species diversity for both functional saplings, especially for the non-pioneer saplings.

My study also demonstrates that topography affects distribution of non-pioneer saplings, whereas disturbance affects distribution of pioneer saplings. Although soil is an important factor to explain distribution of both pioneer and non-pioneer saplings, it is also evident that plant species, geomorphic processes, and disturbance have different effects on the physical and chemical properties of soils. Soil and disturbance effects contribute to meso- and fine-scale spatial variations for distribution of species, whereas topographic effects contribute to broad-scale spatial variations for distribution of species. To conclude, in a rough terrain and highly disturbance area, niche-based process is the main ecological process to maintain the coexistence and diversity, and which also affect vegetation classification in the Lienhuachih subtropical forest.

***Key words*****:** diversity, coexistence, niche- and dispersal-based processes, the subtropical Lienhuachih forest, topography, soil, disturbance

# CONTENTS

CHAPTERS

# LIST OF FIGURES

# LIST OF TABLES

# LIST OF APPENDICIES

# CHAPTER 1

# GENERAL INTRODUCTION

Why tree diversity is so high and what drives coexistence of species in a tropical forest is one of the central question that community ecologists concern. In recent years, studies documenting there are two processes, niche-based process and dispersal-based process (Cottenie 2005; Legendre et al. 2009). Niche-based process claims that due to environmental heterogeneity, every species prefers a specific niche to avoid competitive exclusion (Comita et al. 2007; Gunatilleke et al. 2006; Harms et al. 2001; Wiegand et al. 2007). On the other hand, dispersal-based process argues that propagules are not able to reach every suitable site in a landscape, regardless of underlying habitat conditions or species specificities (Dalling et al. 2002; Harms et al. 2000; Hubbell et al. 1999; Plotkin et al. 2002; Seidler and Plotkin 2006).

However, trees are sessile organisms, and their growth, recruitment and mortality are influenced by the immediate neighborhood created by the abiotic environment and interactions among neighboring trees (Zhao et al. 2006). These interactions among neighboring trees and their abiotic environment usually leave spatial signatures in tree communities and create detectable spatial patterns in species diversity (Legendre et al. 2009). Hence, empirical studies demonstrated both niche- and dispersal-based processes work together responsible for community assembly (Cottenie 2005; Legendre et al. 2009).

Recently, forest dynamics plots (FDP) established by the Smithsonian Institution Center for Tropical Forest Science (CTFS) which are represented by large spatially contiguous grids of subplots with permanently tagged and georeferenced individuals of all woody species (Losos and Leigh 2004). Spatially referenced tree demographic data from these plots have profoundly advanced our understanding of the coexistence of species, studying diversity patterns, testing ecological theories, monitoring the dynamics of stand structure and function, and conserving and managing biodiversity (Condit 1995; Condit et al. 1998; Hubbell 2001; He and Legendre 2002; Losos and Leigh 2004). However, previous FDPs located at tropical area and terrains of FDPs are relative flat and with less disturbance. It is still unclear, however, whether the findings from the tropics also applicable to subtropical forest with rough terrain and frequently disturbance. Therefore, in 2008, I used the same methods to establish a 25-ha FDP in the Lienhuachih Experimental Forest (23$^{o}$54’49”N, 120$^{o}$52’43”E) in Central Taiwan. The FDP locates at extreme gradients in topography and suffers by frequent typhoon disturbance (Lin et al. 2011).

In the beginning I investigate the species composition, size-class structure, and also compare the alpha diversity with other plots in Taiwan and all over the world (Chapter 2). With the precise topography measurement, then, I classify the tree community in different types and to test if micro-topography affects classification of plant communities and species composition (Chapter 3). After I got primary analyses of tree species composition and forest types of the plot, I realized environmental data is so important for demonstrate the niche-based process that give contribution to community assembly. Next, I measured soil texture and chemical variables in 20 x 20m qudrats, and to focus on how would the conclusion about importance of niche- and dispersal-based processes change if soil variables are also included in the analysis (Chapter 4).

Except topographic and soil data, disturbance data is also important, but that has always been ignored. So, I collected past ten years disturbance variables (canopy gaps of 3 differnt years and human path road) and divided all saplings into two functional groups, pioneer saplings and non-pioneer saplings. To understand how different environmental factors contribute in explaining species composition of different functional groups, and how different ecological processes regulate the spatial distribution of species composition of different functional groups (Chapter 5). From analysis may give an insight how the environmental factors affect together to the forest diversity.

Finally, I summarized and integrated the results of each chapter in chapter 6 to reach conclusions regarding ecological processes that maintain coexistence and diversity of tree community in the Lienhuachih subtropical forest.

# CHAPTER 2

# SPECIES COMPOSITION, SIZE-CLASS STRUCTURE, AND DIVERSITY OF THE LIENHUACHIH FOREST DYNAMICS PLOT IN A SUBTROPICAL EVERGREEN BROAD-LEAVED FOREST IN CENTRAL TAIWAN

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## ABSCRAT

The Lienhuachih Forest Dynamics Plot (FDP), measured 500 m by 500 m square, is located in central Taiwan. The collected data, followed a unified method adopted for the worldwide FDP network, were analyzed for floristic composition, size-class structure, and species diversity. In total, the censused trees and shrubs belonged to 144 species in 86 genera and 39 families. The most dominant families were the Fagaceae, Lauraceae, Rubiaceae, Euphorbiaceae, and Melastomataceae. In total, 153,268 (6131 ha$^{-1}$) individuals were recorded, and the total basal area was 34.77 m$^{2}$ ha$^{-1}$. Of the 144 species, the most abundant were *Randia cochinchinensis* and *Blastus cochinchinensis*. *Pasania nantoensis* had the highest basal area (8.38%), followed by *Engelhardtia roxburghiana* (8.12%) and *Schefflera octophylla* (7.23%). Calculation of the importance value (IV, incorporating relative values of abundance and basal area) showed that *R. cochinchinensis*, *B. cochinchinensis*, *S. octophylla*, *Cryptocarya chinensis*, and *E. roxburghiana* were the most dominant species with the highest IV values in the plot. The sum of the 30 top species' IV reached 83.06% of the whole. Although the 1st 2 species were understory and very dominant due to the large number of individuals, certain numbers of rare species however increased the floristic diversity in the plot. Based on the species composition, the forest is characteristic of the *Machilus-Castanopsis* forest zone of Taiwan, with certain dominant understory species and possessing 2 pioneer species in the major canopy composition.

For the size-class structure, 102 (each with total stems $\geq$ 25) species showed 4 patterns of size-class distribution: L-shaped, inverse J-shaped, fluctuating, and bell-shaped. The former 3 patterns in a total of 98 species, including a great number of small-sized individuals, imply that most current species in this study site can display good recruitment with rich resources of saplings. The woody plant richness of the Lienhuachih FDP is the highest among low-elevation FDPs in Taiwan. Compared to other Center of

Ttropical Forest Science forest dynamics plots on islands, Fisher’s alpha diversity (ha$^{-1}$) index of the subtropical Lienhuachih FDP was similar to that of the Luquillo FDP in Puerto Rico but much lower than that of other FDPs in the tropics.

***Key words:*** species composition, size class structure, diversity, subtropical evergreen broad-leaved forest, Lienhuachih Forest Dynamics Plot.

## INTRODUCTION

In order to study spatial and temporal patterns of tree and shrub populations, recent studies of forest plots frequently adopted a large plot area. These large datasets that might encompass environmental variations can be used to examine the mechanisms that maintain species diversity, study the consequences of rarity of local species survival, and monitor long-term changes to detect effects of climate change (Hubbell and Foster 1983; Masaki et al. 1992; Tanouchi and Yamamoto et al. 1995; Condit et al. 1996; Condit 1998; Sato et al.1999; Manabe et al. 2000). Forest Dynamics Plots (FDPs) were established and used a standardized sampling methodology which allowed scientists to directly compare data collected at different sites (Losos and Leigh 2004).

Taiwan is a mountainous island with the rich ecological resources. To understand forest dynamic changes, several FDPs have been successively established since 1990 (Yang et al. 2008), but large intact FDPs of >5 ha in area in the low-elevation zone included only the Fushan FDP in northern and the Kenting FDP in southern Taiwan. Both are surrounded by intact conserved forests: the Hapen Natural Conservation area (Su et al. 2007) and Kenting National Park (Wang et al. 2004), respectively. Due to the early and sustained development in central Taiwan, it is difficult to find an intact large forest wuth no artificial disturbances. However, to monitor forest ecological changes and succession for all of Taiwan, the Lienhuachih forest is the largest one remaining at low elevations in centra Taiwan.

The Lienhuachih forest was an aboriginal hunting ground so it was conserved intact with few disturbances. More than half of the species of the Lauraceae and Fagaceae were concentrated in this area, and many rare endemic species existed in this unique habitat (Lu et al. 2001). Lienhuachih was a conserved natural broad-leaved forest representative of central Taiwan. Therefore, establishing an FDP at Lienhuachih can conserve the natural vegetation of central Taiwan, and also allow the monitoring and study of broad-leaved forest dynamics to accumulate knowledge of northern, central, and southern forests throughout all lowlands of Taiwan.

This study includes the species composition, size-class structure, and diversity of the forest of the Lienhuachih FDP. It can serve as a foundation for cross-site comparisons with other FDPs and ecosystems in Taiwan.

# MATERIALS AND METHODS

## *Study site*

In July 2008, a 25-ha (500 m × 500 m) FDP (23º54’49”N, 120º52’43”E) was established within the evergreen, broad-leaved forest in the Lienhuachih Experimental Forest (LEF), Nantou County, central Taiwan (Fig. 2.1), as part of the Taiwan Forest Dynamics Monitoring Network. The study was conducted in a 25-ha (500 m × 500 m) FDP (23º54’49”N，120º52’43”E) in a natural forest of the LEF, Nantou County, central Taiwan (Fig. 2.1). The substrate consisted of alternating argillaceous sandstone and shale. The dominant soils could be classified into 2 types, Typical Dystrochrept and Typical Hapleudults red soils (King 1986). The mean annual temperature was 20.8℃. The hottest month of the year was July with a mean temperature of 25.2℃, and the coldest was January with a mean temperature of 14.8℃. The annual precipitation was 2,285.0 mm with seasonal variation throughout the year. More than half of the annual rainfall occurred between May and September, while the dry season usually began in October and lasted through February with 5 consecutive months averaging <100 mm precipitation a month. The mean relative humidity was 87.1% (Fig. 2.2) (Lu et al. 2008). Typhoons, a common occurrence in the LEF, swept through the area with violent winds and extremely heavy rainfall, and often caused severe damage (Lee et al. 2008). Landslides also took place, mainly caused by heavy rainfall events and the reshaping of stream channels (Lee et al. 2008).

The LEF covered a total area of 461 ha with elevations ranging 576~925 m. About half of the LEF was composed of natural forests, while the other half was made up of various artificial plantations. In total, 879 vascular plant species, belonging to 177 families and 561 genera, had been recorded within the entire LEF (Hwong et al. 2002). The dominant vegetation type in the LEF was considered to be a Lauro-Fagaceous forest (Su 1984). Most of the trees were *Castanopsis* spp., *Cyclobalanopsis* spp., *Machilus* spp., and *Schima superba* (Hwong et al. 2002). Other human activities in small, widely spaced villages, with agricultural fields and small plantations, occurred within and around the LEF. Natural vegetation in the area was fragmented, degraded, and isolated (Lee et al. 2008).

### ***Field inventory***

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, each with other subsidiary points at 10-m intervals. Each 20 m × 20 m quadrat was further divided into 16 subquadrats of 5 m × 5 m.

All freestanding trees ≥ 1cm in diameter at breast height (DBH) were mapped, measured, identified, and tagged. The botanical nomenclature, life-form, and endemism of all species, following the Flora of Taiwan (Editorial Committee of the Flora of Taiwan, 1993-2003), were determined. Species rareness of fewer than 25 total individuals (< 1 individual $ha^{-1}$) was considered a rare species in the plot (Hubbell and Foster 1986).

### ***Statistical analysis***

Three parameters, stem density, basal area, and the importance value (IV, which is (relative density + relative basal area)/2), were used to describe the population structure of tree species. The relative dominance of each family and species was determined based on its IV. The main stems of plants with multiple branches at breast height were counted as 1 individual for the density calculation. However, the sum of the basal areas of all stems was used for the basal area.

For the size-class analysis, species with >25 individuals in the plot were analyzed, and each species was carried out by constructing a bar chart with DBH size classes against the numbers of individuals (Hough 1932; Tubbs 1977; McCarthy et al. 1987; Fan et al. 2005). Due to the varied growth rates, limitations of DBH sizes for different species, and non-unified size structures among species, the determination of wide-ranging size class scales followed the modified Sturges's equation instead of using a log-normal equation.

Modified Sturges' equation:

$M = 6 \times \log n_i$; where $n_i$ is the number of individuals of species $i$. The class interval of each species = (DBHmax - DBHmin)/M.

For floristic diversity, the species richness, evenness, the Shannon-Wiener diversity index, and Fisher's alpha were used (Hurlbert 1971). Fisher's alpha is a mathematical calculation for determining the diversity within a population, which is usually expressed as the species richness of an area (Fisher et al. 1943; Rosenzweig 1995). It is independent of the sample size and is used to extrapolate species richness to large areas (Losos and Leigh 2004). Richness is the number of species. Evenness is H'/ln (Richness).

The Shannon-Wiener diversity index (H') is -sum (Pi × ln(Pi)); wherePi is the ni/N; ni is the number of individuals in species i; the abundance of species i; and N is the total number of all individuals.

Fisher's alpha: $S = \alpha \ln(1 + n/\alpha)$; where S is the number of species; and n is the number of individuals.

## RESULTS

### *Topographic features*

The elevation of the plot ranged from 667 m to 845 m above the sea level. The average slop of plots was about 35.3°, so the land was very steep. The topography of the plot was characterized by hills with valleys, steep slopes, and ridges. The ridge lies between 2 slopes, a steep slope facing north and gentler slope facing south. Seepage ways, spurs, small hillocks, and several seasonal streamlets cut through these slopes (Fig. 2.3). Small streams seasonally appeared to carry water in wet seasons. When typhoons with heavy rains passed nearby, instant large amounts of rainfall particularly caused landslides and the collapse of steep slopes and stream banks. In the dry season, small streams usually showed an anhydrous state. The topographic features displayed high spatial heterogeneity within the Lienhuachih FDP (Fig. 2.3).

### *Floristic Composition*

The 153,268 (6,131 stems ha$^{-1}$) trees surveyed within the 25-ha plot included 144 species in 86 genera and 39 families. The basal area was 869.31 m$^{2}$ (25 ha)$^{-1}$ (34.77 m$^{2}$ ha$^{-1}$).With the exception of 2 gymnosperms (*Podocarpus nakaii*, and *Pinus morrisonicola*) and 1 monocotyledon (*Arecae catechu)*, all woody species were dicotyledons. These included of 27 canopy species, 72 sub-canopy species, and 45 shrubs species. Among these, 23 species are endemic in Taiwan.

The 5 most abundant species in descending order were *Randia cochinchinensis* (Rubiaceae), *Blastus cochinchinensis* (Melastomataceae), *Euonymus laxiflorus* (Celastraceae), *Cryptocarya chinensis* (Lauraceae), and *Tricalysia dubia* (Rubiaceae). The first 2 species are small trees or shrubs which are distributed throughout most of the plot.

Both accounted for 24.32% of the total abundance, but only 3.53% of the total basal area. Based on the basal area, the dominant species were large-statured, less-abundant trees, including *Pasania nantoensis* (Fagaceae), *Engelhardtia roxburghiana* (Juglandaceae), *Schefflera octophylla* (Euphorbiaceae), *Cryptocarya chinensis* (Lauraceae), and *Schima superba* (Theaceae). Most of them, except *C. chinensis*, are canopy species. The most important species as indicated by the IVs were *R. cochinchinensis, B. cochinchinensis, S. octophylla, C. chinensis*, and *E. roxburghiana*. The top 30 dominant species contributed over 80% to the total IV (Table 2.1). Among the 20 most dominant species, *Mallotus paniculatus* at 10th and *Sapium discolor* at 20th are pioneer species, and both reached the top 10 major canopy species with the highest IV.

Families with the most number of species in the plot were the Lauraceae, followed by the Rubiaceae, Fagaceae, Theaceae, and Euphorbiaceae. Families with the greatest basal areas were the Fagaceae (26.47% of the total basal area), followed by the Lauraceae, Juglandaceae, Euphorbiaceae, and Araliaceae. The Rubiaceae had the greatest density, consisting of 20.86% of the total. The top 15 families in terms of IVs are shown in Table 2.2. The most dominant families were ranked in the order of the Fagaceae, Lauraceae, Rubiaceae, Euphorbiaceae, and then the Melastomataceae.

The species-area curve shows that the number of species increased rapidly, and the curve inclined to nearly a plateau after an area of 10 ha (Fig. 2.4). The curve appears to approach an asymptote, and very few species were added to the plot beyond the point.

The species-area curve showed that the number of species increased rapidly until the incline plot area reached 2.43 ha, when about 80% of species had accumulated (Fig. 2.4). The curve inclined to nearly a plateau after an accumulated total area of 10 ha. Then, the curve appeared to approach an asymptote and very few species were added as the plot size was enlarged.

The species-abundance pattern (Fig. 2.5) showed that a few species contributed a great proportion to the stem abundance. The sum of ranks 1 and rank 2 was 37,274 individuals as 24.32% of the total. From ranks 3 to 22, the curve exhibited a shallow gradient, and the total of the top 22 species reached 80% relative abundance. Among 144 species, 43 species (29.86%) had < 25 individuals (< 1 individual ha$^{-1}$, and were considered to be rare species), and 9 of them were represented by a single stem.

***Size-class structure***

One hundred and two (each with total stems ≥ 25) out of 144 species were examined by size class. The charts exhibited 4 patterns: L-shaped, inverse J-shaped, fluctuating, and bell-shaped (Fig. 2.6). The L-shaped pattern was found in 9 species, such as *Ormosia formosana* and *Psychotria rubra*, and it showed a dramatic drop in the number of individuals in the small size-class. The inverse J-shaped pattern had a smooth, downward curve, which was shown by 60 species; for example, *E. roxburghiana* and *Helicia rengetiensis*. Twenty-nine species showed the fluctuating pattern, having the greatest number of individuals in the smallest size and a varied number of individuals in the other size classes, such as *Mallotus paniculatus* and *E. laxiflorus*. Only 4 species, such as *Antidesma japonicum* and *Rhododendron mariesii*, showed a bell-shaped pattern, and appeared to have quite a few saplings.

***Floristic diversity***

The composition and diversity of the size-classes of all woody individuals in Lienhuachih FDP showed that trees of the size class ≥ 10-cm dbh included 16,513 stems (10.77%) and made up 710.08 m$^2$ (81.68%) of the total basal area and those in the size class ≥ 30-cm dbh only included 2,267 stems (1.48%) with 370.11 m$^2$ (42.57%) in basal area. The Evenness index for those with dbh ≥ 10 cm of the 25-ha plot was 0.79, which was very high, and 0.86 ha$^{-1}$. The Shannon-Wiener diversity index (H') for those dbh ≥ 10 cm was 3.64 in the 25-ha plot and 3.40 $ha^{-1}$, which was the highest among those ≥ 1-, 10-, 30-, 60-cm dbh ranks. The Evenness index inclined with increases along the diameter of the size class, but Fisher's alpha diversity showed the opposite trend.

A comparison of CTFS FDPs on islands used Fisher's alpha diversity index to evaluate their phytodiversity. Fisher's alpha diversity index for all woody plants with DBH ≥ 1 cm was the highest at the Lienhuachih FDP among those of 4 large lowland FDPs in Taiwan (Table 2.3). Its highest number of species and the second highest abundance resulted in the richest diversity on the island of Taiwan (Table 2.3). Compared to other CTFS FDPs on islands, Fisher's alpha diversity ($ha^{-1}$) index of subtropical Lienhuachih FDP was similar to that of the Luquillo FDP in Puerto Rico but much lower than that of the Palana FDP in the Philippines, Sinhraja FDP in Sri Lanka, or Barro Colorado Island (BCI) FDP in Panama in the tropics. Meanwhile, Lienhuachih FDP was in a status between the Luquillo FDP and other tropical FDPs in terms of diversities of those large trees communities with DBH ≥ 10 cm and ≥ 30 cm. However, for those with a DBH ≥ 60cm, the canopy diversity of the Lienhuachih FDP was much higher than those of the Fushan FDP in Taiwan, Luquillo FDP in the Philippines, and Sinhraja FDP in Sri Lanka, but was lower than that of the BCI FDP in Panama.

## DISCUSSION

### *Floristic composition and size-class structure*

The vegetation of the Lienhuachih FDP is dominated by the families Fagaceae, Lauraceae, Rubiaceae, Euphorbiaceae, and Melastomataceae. These dominant families of forests are found widely in humid areas of low elevations in the Northern Hemisphere (Kira 1991, Tagawa 1995). Although my studied dominant canopy species were characterized by *P. nantoensis*, *E. roxburghiana*, *S. octophylla,* and *Cryptocarya* *chinensis*, the top 30 dominant canopy species also including *Castanopsis fargesii*, *Cast. kawakamii, Cast. cuspidata,* and *Machilus zuihoensis* were similar to species in the *Machilus*-*Castanopsis* forest zone (Su 1984). Even the sub-canopy and shrub species such as *Cryptocarya chinensis* and *B. cochinchinensis* are also common species found in this zone. These 2 species are very dominant due to the large number of individuals. Characteristics of the vegetation might be defined by the dominant families, genera or species but nearly never by non-canopy species. Prior to further analysis, the Lienhuachih FDP can be roughly recognized as a *Pasania*-*Engelhardtia*-*Schefflera* forest with dominant under-canopy of *R. cochinchinenesis, Cryptocarya chinensis* and *B. cochinchinensis,* which refer to the vegetation zone of Lauro-Fagaceous forests as well as *Machilus*-*Castanopsis* forests.

Most mature forests do not consist of pioneer species, except in area of frequent disturbances or large gaps. Among the 20 most dominant species, 2 pioneer and canopy species, *Mallotus paniculatus* and *Sapium discolor,* with a sum IV of 4.76 contributed 6~11% importance to the composition of the top 20 dorminant species and the top 10 canopy species, respectively. It is possible that new niches are created by disturbances such as typhoons and artificial plantations. Large disturbed areas might result from landslides due to heavy rains or artificial plantations. Small disturbances might be twig self-shaving, tree falls, hunting trails, medical plant collection, etc. Due to nearly no barriers between the Lienhuachih FDP and the surrounding human developments, the pioneer species can easily invade and colonize the forest gaps and disturbed areas, and then develop greater numbers. The alternate natural and artificial disturbances may also encourage the development of a great amount of sub-canopy and shrub species which are composed of rapidly growing saplings for recruitment. This is might be why the shrubby *B. cochinchinensis* and the sub-canopy *R. cochinchinensis* have great numbers of individuals resulting in major contributions to IV and dorminance.

Both L-shaped and inverse J-shaped patterns of size-class structure analysis included 69 species comprising 67.6% of the total 102 analyzed species. The great numbers of small-sized individuals in these 2 patterns imply that most current species in this study site display good recruitment with rich sapling resources. The forest stand structure had a reverse J-shaped curve for tree and for seedling/sapling size-class distributions, which indicated that the forest as a whole is probably adequately regenerating (McLaren et al. 2005). When new niches occur, those with many saplings would generally have great chances for regeneration of forests through species competition. On the contrary, species with the bell-shaped pattern with only a few saplings usually face understory inhibition of sapling development and the fate of exclusion after elimination of young trees. The fluctuating pattern, also similar to a multi-modal size-class distribution pattern, may result from the numbers of individuals in different size classes being controlled by external physical stresses or internal physiological rhythms, such as periodicity of reproduction (Fan et al. 2005).

### ***Comparisons with other lowland FDPs in Taiwan and other FDPs of the world on islands***

Among the 4 low-elevation FDPs in Taiwan, the Lienhuachih FDP has the lowest basal area per hectare, whereas the Fushan FDP has the highest (Table 2.4). This might be because of the great proportion of small trees and shrubs at the Lienhuachih FDP. However, the number of individuals is very high in the Nanjenshan FDP instead of the Lienhuachih FDP because the strong windward effect of monsoon results in numbers of small-diameter trees in high densities (Sun et al. 1996). The woody plant density of the Lienhuachih FDP was still higher than that of the Fushan FDP in the north and the Kenting FDP in the south. This is possibly due to forest management, aboriginal development of the Thao, and local agricultural reclamation at the Lienhuachih FDP (Lu et al. 2001). Both the Fushan FDP and Kenting FDP are located in conservation areas (Su et al. 2007; Wang et al. 2004), and intact forests usually contain large-sized trees but are distributed at low densities.

For the diversity of those trees with DBH ≥ 1cm and ≥ 10 cm, Fisher’s alpha diversity of the Lienhuachih FDP was the highest in Taiwan, higher than that of the Nanjenshan FDP and much higher than that of the Fushan FDP. However, it was obviously lower than the BCI, Palanan, and Sinharaja FDPs. In general, the greatest diversity occurs in humid tropical rainforests with no dry seasons. As a result, the Lienhuachih FDP with obvious dry and wet seasons should show not as high diversity. It is surprising that the diversity of those trees with DBH ≥ 30 cm and ≥ 60 cm for most canopy trees at the Lienhuachih FDP was much higher than those at the Fushan and Nanjenshan FDPs. Prior to this comparison, biodiversity and species richness of Nanjenshan and the Hengchun Peninsula were considered superior than those in other areas of Taiwan. It is also surprising that the canopy diversity of the Lienhuachih FDP was only lower than that of the BCI FDP in Panama. This indicates that the high canopy diversity at Lienhuachih results from the maintenance of natural species richness, influences of aboriginal activities and forest management, and natural disturbances by typhoons, and landslides from the steep topography generating new niches for recruitment. All disturbances including the introduction of cultivation such as *Prunus* and being too close to artificial forest management near the eastern boundary encourage pioneer species to colonize the newly generated niches. That is why 2 pioneer species were in the top 30 dominant species. The Liehuachih FDP is a forest that combines the characteristics of natural diversity and disturbed niches in succession, so its floristic diversity is high and rich.

## CONCLUSIONS

The floristic composition of the Lienhuachih FDP is dominated by the Fagaceae and Lauraceae. This is considered to be characteristic of the *Machilus-Castanopsis* forest zone. The under-canopy species, *R. cochinchinenesis* and *B. cochinchinensis,* are very dominant due to the large numbers of individuals. Two pioneer and canopy species, *M. paniculatus* and *S. discolor*, as a part of the composition of the top 20 dominant species and the top 10 canopy species indicate that the Lienhuachih FDP with mingled niches may involve natural and artificial disturbances. Certain numbers of rare species, unexpected pioneer species and waste cultivated species result in the high floristic diversity in the Lienhuachih FDP. Patterns of the size-class structure including a majority of small-sized individuals for 98 of the analyzed 102 species indicate that most current species in this study site display good recruitment with rich sapling resources. Among low-elevation FDPs in Taiwan, the Lienhuachih FDP has a higher density of individuals than the Fushan FDP and Kenting FDP, but much less than the Nanjenshan FDP. For diversity (Fisher's alpha diversity), the Lienhuachih FDP is the highest among these 4 plots. Compared to other CTFS forest dynamics plots on islands, Fisher's alpha diversity (per 1 ha) index of the subtropical Lienhuachih FDP was similar to that of the Luquillo FDP in Puerto Rico but much lower than that of other FDPs in the tropics. However, it is surprising that the canopy diversity of the Lienhuachih FDP was only lower than that of the BCI FDP in Panama. Due to the maintenance of natural species richness, influences of the aboriginal activities, forest management, and the natural disturbances by typhoons, and landslides from steep topography which generate new niches for recruitment, a high and rich floristic diversity of the Liehuachih FDP in a forest combining the characteristics of natural diversity and disturbed niches in succession can be maintained.

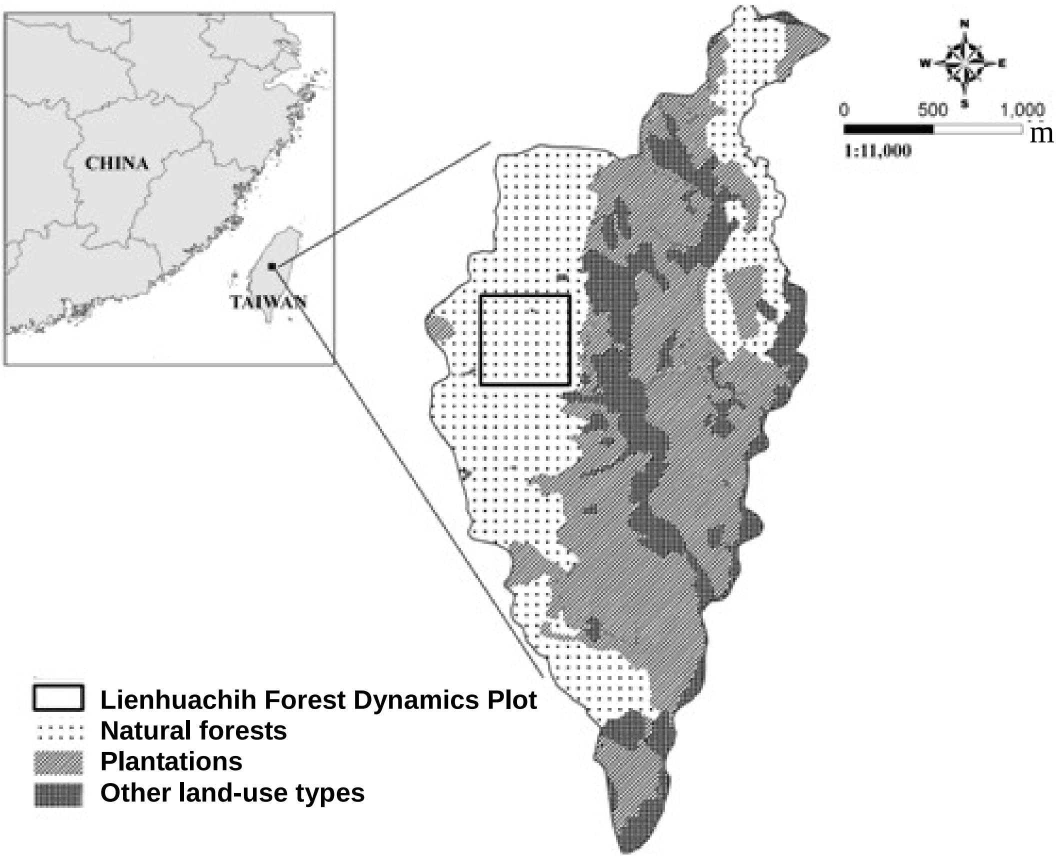

**Fig. 2.1.** Location of the 25-ha Lienhuachih Forest Dynamics Plot in the Lienhuachih Experimental Forest, Nantou County, central Taiwan.

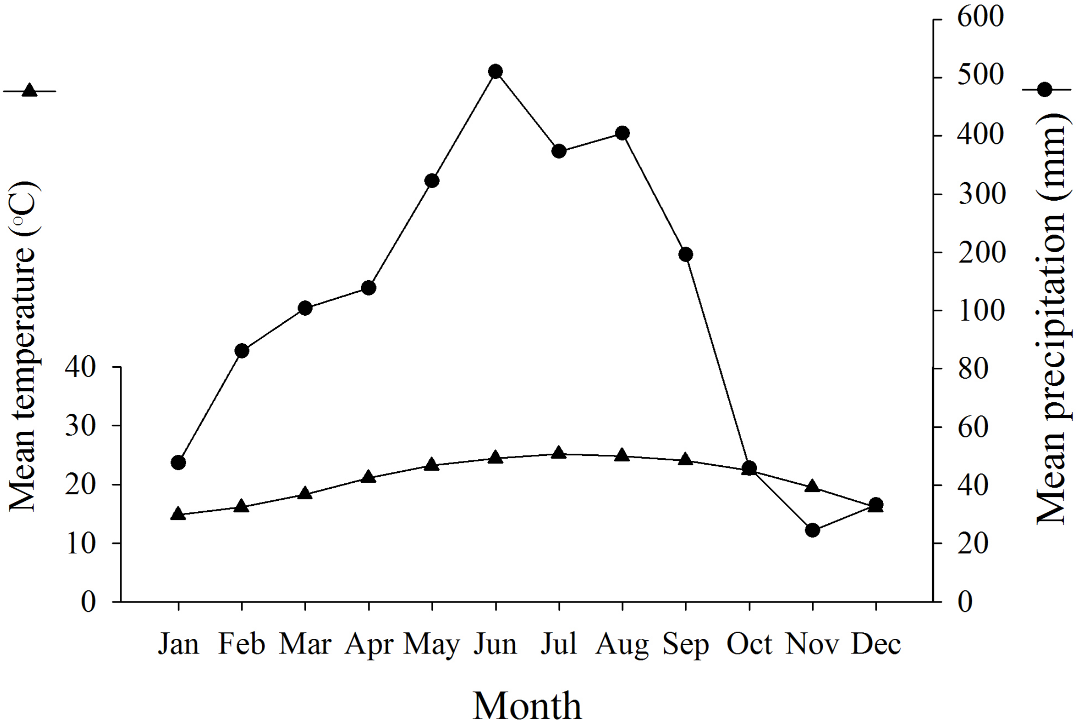

**Fig. 2.2** Climate diagram for the Lienhuachih Experimental Forest.

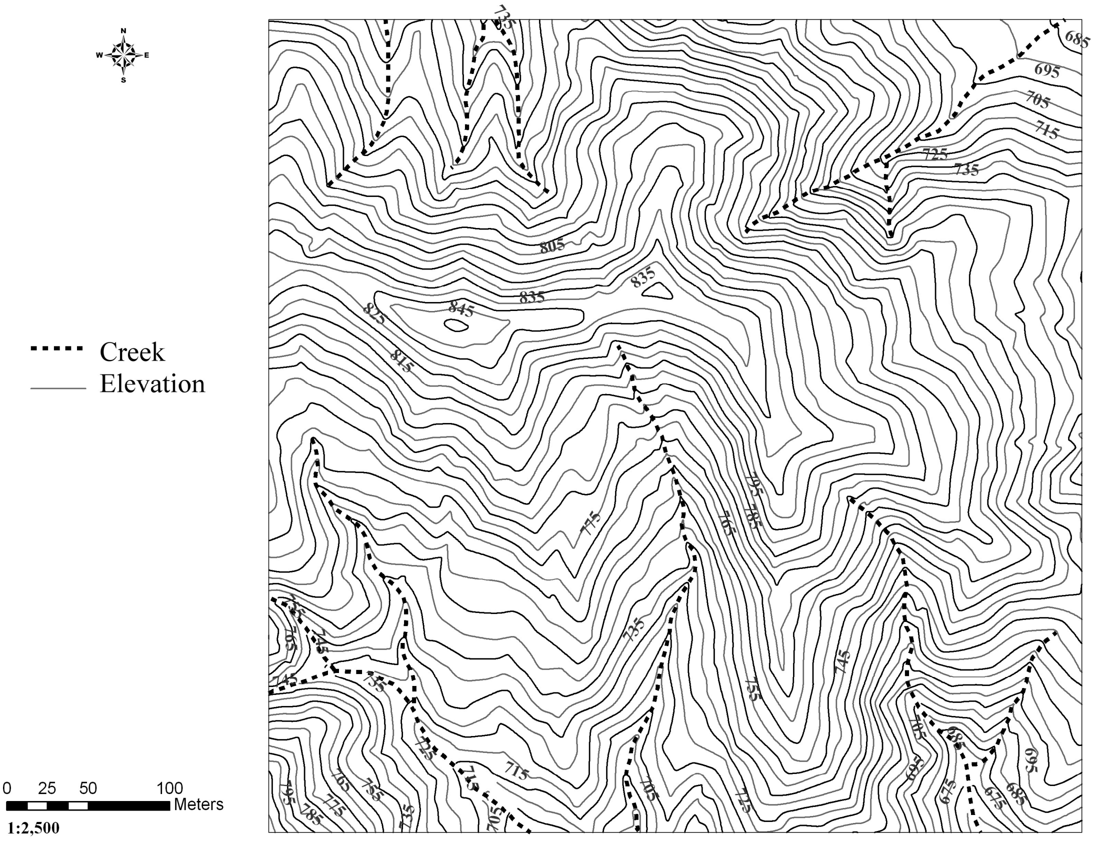

**Fig. 2.3.** Contour map of the Lienhuachih Forest Dynamics Plot with 5-m countour intervals. The dotted lines indicate creeks.

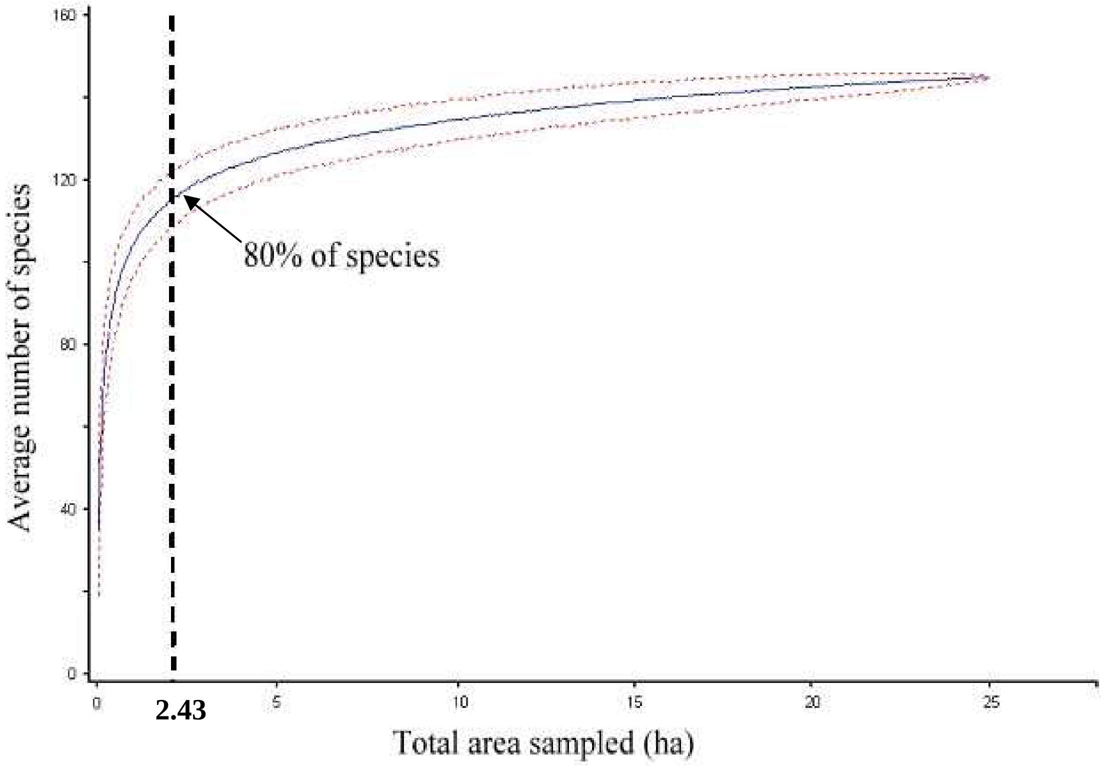

**Fig. 2.4.** Species-area curve for the 25-ha Lienhuachih Forest Dynamics Plot.

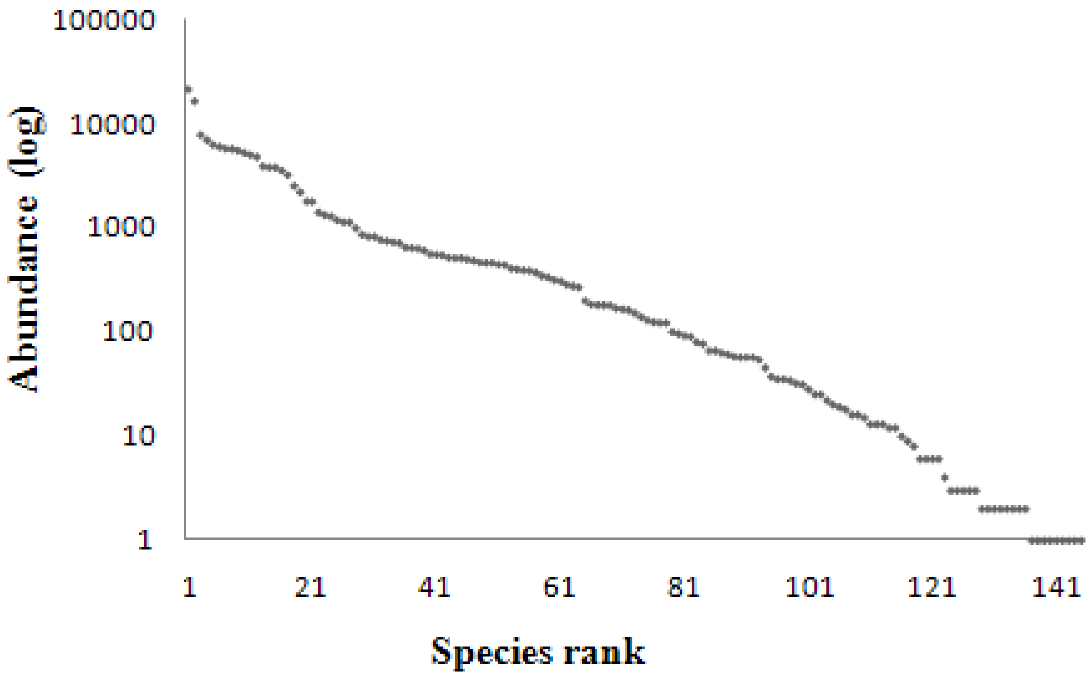

**Fig. 2.5.** Species-abundance curve for the Lienhuachih Forest Dynamic Plot.

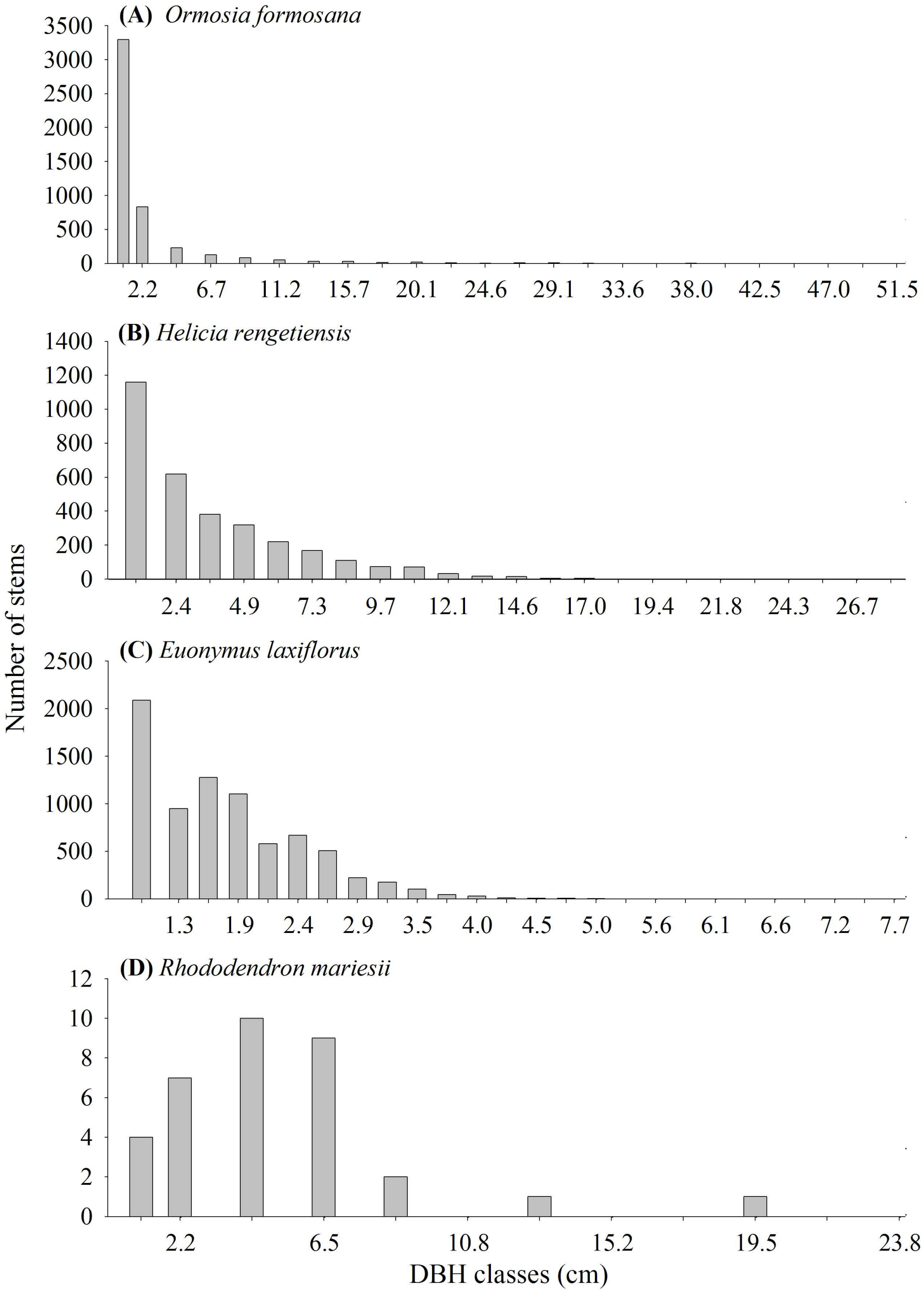

**Fig. 2.6.** Size-class structure of 4 representative species. A, L-shaped size-class pattern, representative species: *Ormosia formosana*; B, inverse J-shaped size-class pattern, representative species: *Helicia rengetiensis*; C, fluctuating size-class pattern, representative species: *Euonymus laxiflorus*; D, bell-shaped size-class pattern, representative species: *Rhododendron mariesii*.

**Table 2.1.** Top 30 species with the highest importance values in the Lienhuachih Forest Dynamics Plot

| Species | Basal area ($m^2$ (25 ha)$^{-1}$) | Relative basal area (%) | Abundance (stems (25 ha)$^{-1}$) | Relative density (%) | Importance Value (%) | Mean DBH (cm) |
|---|---|---|---|---|---|---|
| *Randia cochinchinensis*✚ | 26.95 | 3.10 | 21075 | 13.75 | 8.43 | 2.88 |
| *Blastus cochinchinensis*✱ | 3.77 | 0.43 | 16199 | 10.57 | 5.50 | 1.44 |
| *Schefflera octophylla* | 62.88 | 7.23 | 5490 | 3.58 | 5.41 | 7.34 |
| *Cryptocarya chinensis*✚ | 53.06 | 6.10 | 6936 | 4.53 | 5.31 | 5.16 |
| *Engelhardtia roxburghiana* | 70.55 | 8.12 | 1769 | 1.15 | 4.63 | 12.45 |
| *Pasania nantoensis* | 72.89 | 8.38 | 821 | 0.54 | 4.46 | 11.28 |
| *Cyclobalanopsis pachyloma* | 36.17 | 4.16 | 3875 | 2.53 | 3.34 | 6.80 |
| *Diospyros morrisiana* | 26.82 | 3.09 | 5001 | 3.26 | 3.17 | 5.16 |
| *Cinnamomum subavenium*✚ | 30.64 | 3.52 | 3800 | 2.48 | 3.00 | 5.27 |
| *Mallotus paniculatus* | 30.35 | 3.49 | 3794 | 2.48 | 2.98 | 6.40 |
| Top 10 | 414.08 | 47.63 | 68,760 | 44.86 | 46.25 | |
| *Tricalysia dubia*✚ | 15.62 | 1.80 | 6251 | 4.08 | 2.94 | 4.12 |
| *Schima superba* | 44.86 | 5.16 | 744 | 0.49 | 2.82 | 16.88 |
| *Helicia formosana*✚ | 17.47 | 2.01 | 5241 | 3.42 | 2.71 | 3.81 |
| *Euonymus laxiflorus*✱ | 2.94 | 0.34 | 7767 | 5.07 | 2.70 | 1.83 |
| *Syzygium buxifolium*✚ | 11.82 | 1.36 | 5962 | 3.89 | 2.63 | 3.59 |
| *Castanopsis fargesii* | 31.97 | 3.68 | 1277 | 0.83 | 2.26 | 7.71 |
| *Ormosia formosana* | 11.08 | 1.27 | 4779 | 3.12 | 2.20 | 2.93 |
| *Psychotria rubra*✱ | 5.09 | 0.59 | 5720 | 3.73 | 2.16 | 2.12 |
| *Ardisia quinquegona*✱ | 3.35 | 0.38 | 5693 | 3.71 | 2.05 | 2.08 |
| *Sapium discolor* | 24.32 | 2.80 | 1176 | 0.77 | 1.78 | 10.05 |
| Top 20 | 582.59 | 67.02 | 113,370 | 73.97 | 70.49 | |
| *Helicia rengetiensis*✚ | 8.23 | 0.95 | 3196 | 2.09 | 1.52 | 3.46 |
| *Litsea acuminata*✚ | 1300 | 1.49 | 2183 | 1.42 | 1.46 | 5.06 |
| *Castanopsis kawakamii* | 22.07 | 2.54 | 331 | 0.22 | 1.38 | 8.28 |
| *Neolitsea aciculata*✚ | 3.10 | 0.36 | 3514 | 2.29 | 1.32 | 2.39 |
| *Podocarpus nakaii* | 8.26 | 0.95 | 2494 | 1.63 | 1.29 | 4.69 |
| *Glochidion acuminatum* | 12.47 | 1.43 | 1396 | 0.91 | 1.17 | 7.56 |
| *Castanopsis cuspidata* | 16.58 | 1.91 | 647 | 0.42 | 1.16 | 8.04 |
| *Pasania konishii* | 11.86 | 1.36 | 1320 | 0.86 | 1.11 | 4.26 |
| *Pasania harlandii* | 13.42 | 1.54 | 986 | 0.64 | 1.09 | 7.52 |
| *Machilus zuihoensis* | 15.35 | 1.77 | 544 | 0.35 | 1.06 | 10.46 |
| Top 30 | 706.92 | 81.32 | 129,981 | 84.81 | 83.06 | |

✚ sub-canopy species; ✱ shrub species. No marks indicating canopy species. DBH, diameter at breast hight.

**Table 2.2.** Top 15 families with the highest importance values in the Lienhuachih Forest Dynamics Plot

| Family | Basal area ($m^2$/25 ha) | Relative basal area (%) | Density (stems/25 ha) | Relative Density (%) | Important Value (%) | Nomber of Species |
|---|---|---|---|---|---|---|
| Fagaceae | 230.15 | 26.47 | 21597 | 10.62 | 18.55 | 11 |
| Lauraceae | 152.41 | 17.53 | 25771 | 12.68 | 15.10 | 17 |
| Rubiaceae | 51.97 | 5.98 | 42417 | 20.86 | 13.42 | 13 |
| Euphorbiaceae | 67.60 | 7.78 | 7166 | 3.52 | 5.65 | 8 |
| Melastomataceae | 3.83 | 0.44 | 21274 | 10.46 | 5.45 | 2 |
| Araliaceae | 62.88 | 7.23 | 6359 | 3.13 | 5.18 | 1 |
| Proteaceae | 26.22 | 3.02 | 14101 | 6.94 | 4.98 | 3 |
| Juglandaceae | 70.55 | 8.12 | 2401 | 1.18 | 4.65 | 1 |
| Theaceae | 58.63 | 6.74 | 3013 | 1.48 | 4.11 | 9 |
| Ebenaceae | 27.66 | 3.18 | 5875 | 2.89 | 3.04 | 2 |
| Myrsinaceae | 8.16 | 0.94 | 8789 | 4.32 | 2.63 | 5 |
| Celastraceae | 2.95 | 0.34 | 9907 | 4.87 | 2.61 | 3 |
| Myrtaceae | 13.88 | 1.60 | 7226 | 3.55 | 2.58 | 2 |
| Leguminosae (Fabaceae) | 11.08 | 1.27 | 5180 | 2.55 | 1.91 | 2 |
| Aquifoliaceae | 6.93 | 0.80 | 5048 | 2.48 | 1.64 | 7 |
| Others | 74.41 | 8.56 | 17191 | 8.46 | 8.51 | 59 |
| Total | 869.31 | 100.00 | 203315 | 100.00 | 100.00 | 144 |

**Table 2.3.** Lowland forest dynamics plots of Taiwan

| Location | Elevation (m) | Location | Area (ha) | Number of species | Basal area ($m^2$ $ha^{-1}$) | Abundance (individual $ha^{-1}$) | Fisher's alpha |
|---|---|---|---|---|---|---|---|
| Fushan[*] | 600~733 | North | 25 | 110 | 41.40 | 4580 | 12.0 |
| Lienhuachih | 667~845 | Central | 25 | 144 | 34.77 | 6631 | 15.8 |
| Nanjenshan[+] | 300~340 | South | 3 | 118 | 36.30 | 12209 | 15.2 |
| Kenting | 280~300 | South | 10 | 110 | 45.12 | 4785 | 13.5 |

[*] Data of Fushan adopted from Su et al. 2007.

[+] Data of others than Lienhuachih and Fushan adopted from Losos and Leigh 2004.

**Table 2.4.** Fisher's alpha diversity (per 1 ha) index of different ranks of diameter at breast height for CTFS forest dynamics plots on islands

| Size class (cm) | Lienhuachih (Taiwan) | Fushan[*] (Taiwan) | Najenshan[+] (Taiwan) | Luquillo[+] (Puerto Rico) | Palanan[+] (Philippines) | Sinharaja[+] (Sri Lanka) | BCI[+] (Panama) |
|---|---|---|---|---|---|---|---|
| ≥ 1 | 15.7 | 12.1 | 15.6 | 13.5 | 43.4 | 24.4 | 34.6 |
| ≥ 10 | 14.0 | 9.9 | 14.0 | 9.3 | 36.5 | 20.4 | 35.6 |
| ≥ 30 | 10.6 | 5.9 | 5.5 | 8.8 | 16.0 | 14.1 | 23.9 |
| ≥ 60 | 8.9 | 2.8 |  | 5.8 | 4.0 | 4.3 | 17.8 |

[*] Data of Fushan adopted from Su et al. 2007.

[+] Data of others than Lienhuachih and Fushan adopted from Losos and Leigh 2004.

# CHAPTER 3

# CHANGES OF PLANT COMMUNITIES CLASSIFICATION AND SPECIES COMPOSITION ALONG THE MICRO-TOPOGRAPHY AT THE LIENHUACHIH FOREST DYNAMICS PLOT IN THE CENTRAL TAIWAN

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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, my 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 mountane 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 and Hsieh 2010 and Chao et al. 2010 both suggested monsoon exposure angle is another important micro-topographic variable to affect the species distribution and plant community classification due to the strong monsoon effect. This indicted if I 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 I 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, I have included not only the usual micro-topographic variables, but also ridge distance and stream distance, which represented water content and landslide disturbance gradient I observed in the plot. I 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 important to affect the vegetation classification and species composition.

## 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℃. The annual precipitation was 2,285.0 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), I set up a forest dynamics plot (FDP) (500m × 500m 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 caused 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 20m × 20m. 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 20m×20m 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. I used these values to calculate nine micro-topographic parameters for each 20m × 20m 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 indicates a convex terrain, whereas a negative one represents a concave terrain (Valencia et al., 2004).
4. Distance to ridge: the nearest distance from the ridge to center point of 20m × 20m quadrat.
5. Distance to stream: the nearest distance from the stream to center point of 20m × 20m quadrat.
6. Aspect ($\theta$) were then transformed trigonometrically into four indices with values from -1 to 1:

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

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

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

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

### *Plant community classification*

To investigate the plant community classification, I 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 were 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 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, diversity, and micro-topography were significantly different among community types.

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

I 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, I 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, I also applied the classification and regression tree (CART) (Therneau et al. 2009) method to examine the relationship between tree abundance data of single species and micro-topographic variables. For quantitative comparison, I 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. 3.1). Spatial distribution patterns of four plant community types (Fig. 3.2) 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. 3.2). On the other half of the TWINSPAN at the second division level (Fig. 3.1), 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. 3.2). 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. 3.1) and supportively identified by the frequency of species that occurred in each plant community type (Table 3.1), and followed by the top IVI dominant canopy tree species in each community type among the fours (Table 3.2). 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 3.3 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 3.3). This type was characterized by high stem density (8,848.17 individuals·ha$^{-1}$) and high basal area (38.65 m$^{2}$·ha$^{-1}$), on the contrary, with the lowest branch ratio (16.19%) (Table 3.3). 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 3.3). A total of 103 species was recorded for this community type, expect *P. nantoensis, Syzygium buxifolium* was another indicator specie of this type (Fig. 3.1). I 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 (Table 3.1).Shrub species were less of dominant species such as *Euonymus laxiflorus* and *Blanstus cochinchinensis* . In 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 3.3), most locating on the upper slope and some on the lower slope (Fig. 3.2). The micro-topographic features of this type were characterized by the second high elevation and the steepest slope (Table 3.3). Because of the high stem density 6055.75 stems·ha$^{-1}$, the basal area 34.18 m$^{2}$·ha$^{-1}$ was also high (Table 3.3). 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 3.3). 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 3.2). The indicator species of this type were *C. chinensis* and *M. paniculatus.* I 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 3.1).

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. 3.2). The micro-topographic features of this type were characterized by the low elevation and low convexity (Table 3.3). A total of 107,765 individuals, density, and basal area were lower than those of Type II and Type I (Table 3.3), 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 3.3). *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 3.1). The indicator species of this type were *D. morrisiana* and *E. roxburghiana.* I 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 3.1).

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 3.3), mainly located on the west stream side (Fig 3.2), with the longest distance to the ridge, and the average lowest convexity (Table 3.3). Both stem density and basal area were the lowest among all plant community types, with 139.32 individual per quadrat and 27.95 $m^2 \cdot ha^{-1}$, respectively (Table 3.3). 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*, 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 3.2). The indicator species of this type were *M. japonica* var. *kusanoi, Neolitsea konishii* and *Glycosmis citrifolia.* I 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. 3.3). 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 3.4). 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 that 27.11% of variation in erect woody species composition.

I also tested the relationship between the first three axes of DCA ordination analyses and micro-topographic variations (Table 3.4). I 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 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 3.5). 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 3.5). 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 my result, indictor 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, I assistant identified indictor species not only by the abundance of indictor 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 caused by a comprehensive factor, disturbance. Although some pervious research inferred that it was possible caused by historical disturbance events (Hara 1996b; Enoki 2003; Su et al. 2010). However, the direct evidence was irrelevant.

According to the rainfall threshold value for debris 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 maximize 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, I 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 my 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 3.3). 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 (14.38s/m) than the valley area (7.83s/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. 1996a; Wang et al. 2000). In my 2009 survey after typhoon disturbed, most of species 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, my 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. 1996b; Enoki 2003). It aslso implies that different micro-topography influences the soil formation and disturbance events. To conclude, my results support the existence of habitat association and niche divergence related to micro-topography in a subtropical evergreen broad-leaved forest.

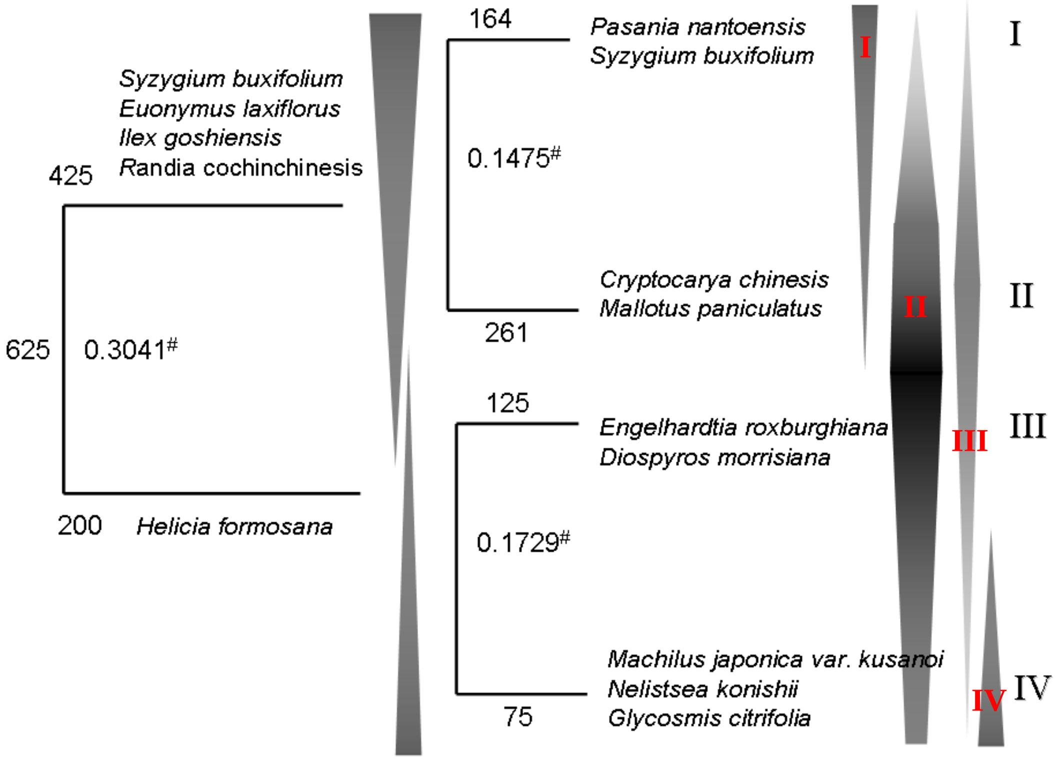

**Fig. 3.1.** Plant community types (I, II, III, and IV) in the Lienhuachih forest dynamics plot classified by TWINSPAN analysis. The number of quadrats, eigenvalues (#), and indicator species are noted in the division level. The area of black gradients are the abundance of each indicator species.

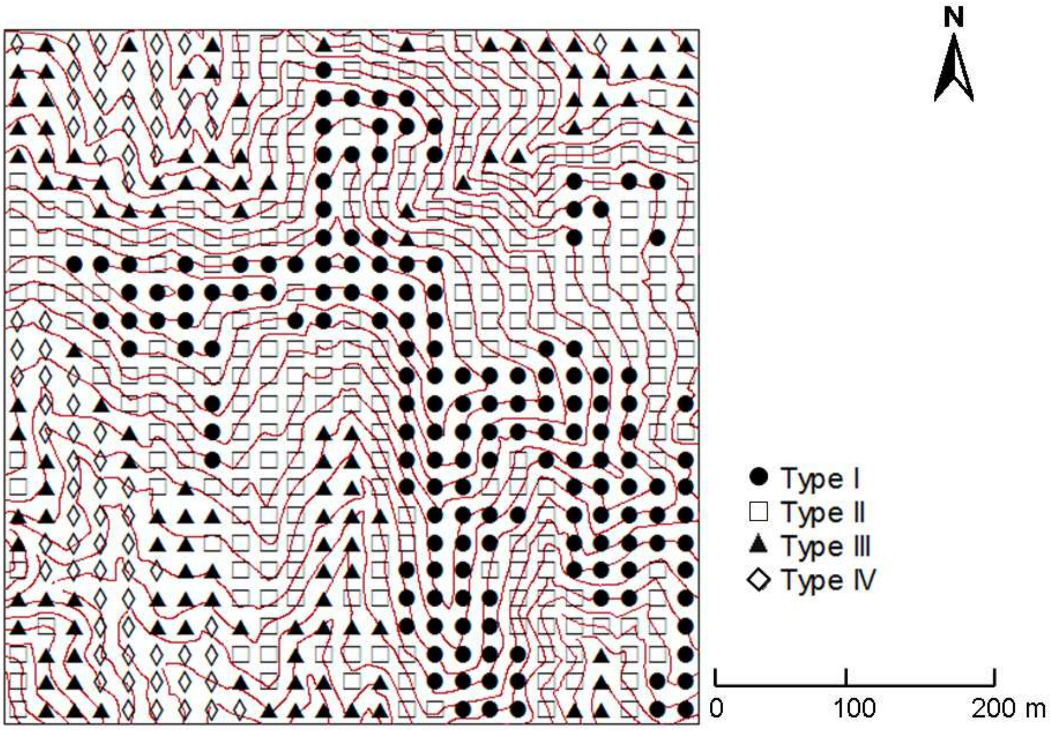

**Fig. 3.2.** Topography map and plant community types classified by TWINSPAN for the quadrats (20 × 20 m) in the Lienhuachih FDP. Type I, *Pasania nantoensis* - *Randia cochinchinensis*; Type II, *Mallotus paniculatus* - *Engelhardtia roxburghiana*; Type III, *Diospyros morrisiana* - *Cryptocarya chinensis*; Type IV, *Machilus japonica* var. *kusanoi* - *Helicia formosana*.

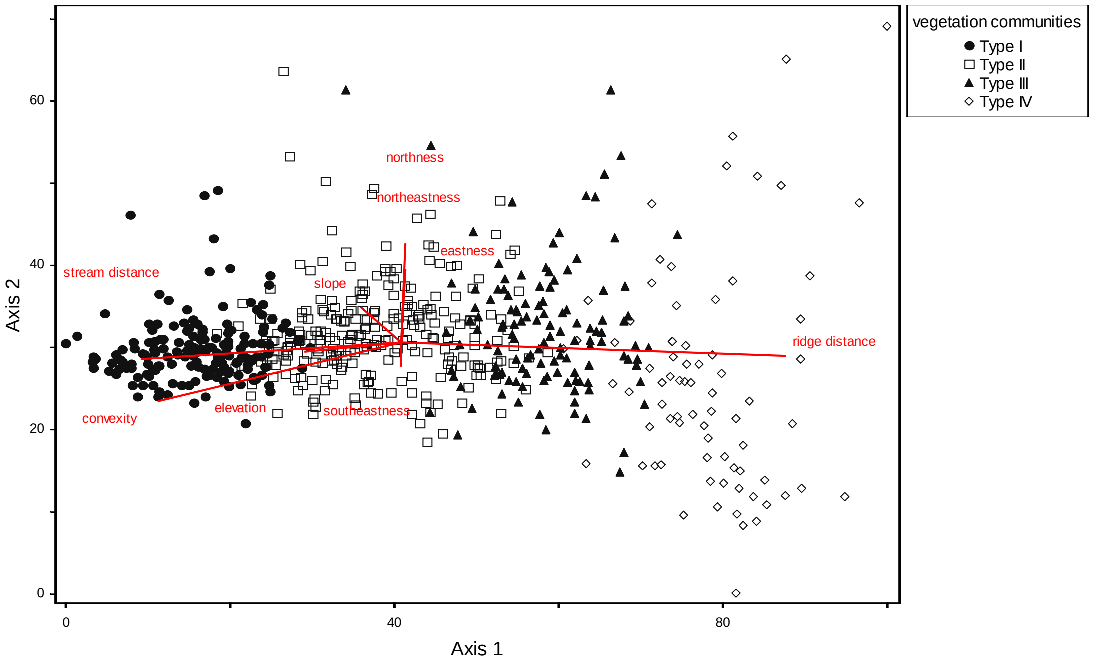

**Fig. 3.3.** DCA ordination diagram and the environmental factors of the Lienhuachih forest dynamics plot with the community types derived from TWINSPAN superimposed. The vectors represent topographic variables. The length of the vector is proportional to its importance; the angle between a vector and each axis is related to its correlation with the axis.

**Table 3.1**. Synoptic table of species with constancy ≥80 for each plant community type. 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 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*.

**Table 3.2.** The top thirty dominant species listed by IVI and the accumulated IVI values in % of the four plant community types. The abbreviation of layers include: C = canopy trees; SC = sub-canopy trees; S = shrubs. No. means ranking the dominant 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△ | *Blastus cochinchinensis,* S | *Schefflera octophylla,* C | *Blastus cochinchinensis,* S |
| 3 | *Syzygium buxifolium,* SC△ | *Randia cochinchinensis,* SC | *Blastus cochinchinensis,* S | *Schefflera octophylla,* C |
| 4 | *Cyclobalanopsis pachyloma,* C | *Cryptocarya chinensis,* C△ | *Helicia formosana,* SC | *Cryptocarya chinensis,* C |
| 5 | *Euonymus laxiflorus,* S | *Schefflera octophylla,* C | *Mallotus paniculatus,* C* | *Machilus japonica* var. *kusanoi,* C△ |
| 6 | *Cinnamomum subavenium,* SC | *Diospyros morrisiana,* C | *Engelhardtia roxburghiana,* C△ | *Mallotus paniculatus,* C* |
| 7 | *Schima superba,* C* | *Cinnamomum subavenium,* SC | *Diospyros morrisiana* C△ | *Machilus zuihoensis,* C |
| 8 | *Engelhardtia roxburghiana,* C | *Mallotus paniculatu,* C* △ | *Tricalysia dubia,* SC | *Neolitsea konishii* C△ |
| 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△ |
| 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** |

* Pioneer species; △ Indicator 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*.

**Table 3.3.** Summary statistics for the four plant community types detected by two-way indicator species analysis (TWINSPAN). 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) | $779.73 \pm 2.98^{a}$ | $767.53 \pm 2.19^{b}$ | $748.83 \pm 3.15^{c}$ | $754.07 \pm 2.80^{c}$ |
| Slope ( ◦ ) | $36.06 \pm 0.55^{a}$ | $36.55 \pm 0.47^{ac}$ | $33.87 \pm 0.69^{ad}$ | $31.74 \pm 0.75^{b}$ |
| Convexity | $2.21 \pm 0.20^{a}$ | $-0.22 \pm 0.15^{b}$ | $-1.44 \pm 0.24^{c}$ | $-1.69 \pm 0.26^{c}$ |
| Stream distance (m) | $60.60 \pm 1.77^{a}$ | $51.03 \pm 1.89^{b}$ | $26.80 \pm 1.93^{c}$ | $19.47 \pm 2.12^{c}$ |
| Ridge distance (m) | $37.37 \pm 2.91^{a}$ | $69.60 \pm 3.02^{b}$ | $122.68 \pm 5.72^{c}$ | $154.29 \pm 6.67^{d}$ |
| Basal area ($m^2$/ha) | 38.65 | 34.18 | 26.23 | 23.37 |
| Basal area ($cm^2$/quadrat) | $1.67 \pm 0.03^{a}$ | $1.45 \pm 0.03^{b}$ | $1.13 \pm 0.04^{c}$ | $1.01 \pm 0.05^{c}$ |
| Species richness (no. of species) | 103 | 124 | 125 | 113 |
| Species richness (no. of species/quadrat) | $38.01 \pm 0.47^{a}$ | $37.77 \pm 0.45^{a}$ | $30.98 \pm 0.75^{b}$ | $27.95 \pm 0.69^{c}$ |
| Species/ha | 80 | 88 | 93 | 90 |
| Density (individuals/25ha) | 8848 | 6056 | 4311 | 3483 |
| Density (individuals/quadrat) | $253.93 \pm 10.83^{a}$ | $242.23 \pm 10.83^{b}$ | $172.42 \pm 6.89^{c}$ | $139.32 \pm 5.08^{c}$ |
| 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 |

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*.

**Table 3.4.** 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 |

n.s. = coefficient not significant

**Table 3.5.** 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<br>(64.42) | 66<br>(63.46) | 62<br>(59.62) | 46<br>(44.23) | 44<br>(42.31) | 46<br>(44.23) | 38<br>(36.54) | 58<br>(55.77) | 74<br>(71.15) |

# CHAPTER 4

# BETTER ENVIRONMENTAL DATA MAY REVERSE CONCLUSIONS ABOUT NICHE- AND DISPERSAL-BASED PROCESSES IN COMMUNITY ASSEMBLY

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## ABSTRACT

Variation partitioning of species composition into components explained by environmental and spatial variables is often used to identify a signature of niche- and dispersal-based processes in community assembly. Such interpretation, however, strongly depends on the quality of the environmental data available. In recent studies conducted in forest dynamics plots, the environment was represented only by readily available topographical variables. Using data from subtropical broad-leaved dynamics plot in Taiwan, I focus on the question of how would the conclusion about importance of niche- and dispersal-based processes change if soil variables are also included in the analysis. To gain further insight, I introduced multiscaledecomposition of pure spatial component [c] in variation partitioning. My results indicate that if only topography is included, dispersal-based processes prevail, while also including soil variables reverses this conclusion in favor of niche-based processes. Multiscale decomposition of [c] shows that if only topography was included, broad-scaled spatial variation prevails in [c], indicating that other as yet unmeasured environmental variables can be important. However, after also including soil variables this pattern disappears, increasing importance of meso- and fine-scaled spatial patterns indicative of dispersal processes.

***Key words:*** Lienhuachih; Taiwan; variation partitioning; dbMEM; multiscale spatial analysis; topographical variables; soil variables; environmental control; dispersal-based processes.

## INTRODUCTION

Niche-based and dispersal-based processes were recognized as the main actors responsible for community assembly (Cottenie 2005). Continuous challenge is the development of analytical methods that are able to distinguish the relative imprint of these processes in the structure of real ecological communities. One of the most promising approaches is the partitioning of variation in community composition into environmental and spatial components (Gilbert and Lechowicz 2004). The theoretical justification behindthis is based on an assumption that environmental control on species distribution accordingto the niche theory will result in the variation of species composition explained by environmental variables, while dispersal limitation will generate spatial signatures in community structure that are detectable by spatial variables (spatial filters). The use of environmental and spatial predictors in variation partitioning results in four components being distinguished; namely, a pure environmental component [a], a spatially structured environmental component [b], a pure spatial component [c] and unexplained variation [d] (Borcard et al. 1992). In this framework, variation explained by environment (components [a+b]) represents environmental control imposed on species distribution (Chase and Leibold 2003), while variation explained purely by spatial variables (component [c]) represents partly unmeasured environmental variables with spatial structure, and partly the legacy of dispersal limitation (Legendre et al. 2009). If availableenvironmental predictors represent the most important environmental drivers of species composition, then the ratio between components [a+b] and [c] can be interpreted as the ratio between niche-based and dispersal-based processes in community assembly (e.g., Gilbert and Lechowicz 2004). However, recent simulation studies (Smith and Lundholm 2010, Gilbert and Bennett 2010) indicate that the ability of variation partitioning to disentangle these two families of processes has been overrated and the dichotomy suggested above is oversimplified. For example component [b], which is often quite large, can also carry the legacy of dispersal processes, in case that dispersal spatially coincides with some of environmental variables (such as topography, Smith and Lundholm 2010).Still, partitioning of the variation into environmental and spatial component is seen as an important step toward disentangling various processes responsible for spatial community structure (Dray et al. 2012).

Recently, the variation partitioning approach has been applied on data from forest dynamics plots established by the Centre for Tropical Forest Science (CTFS; http://www/ctfs.si.edu/) and the Chinese Forest Biodiversity Monitoring Network (http://www.cfbiodiv.org/).Forest dynamics plots are represented by large spatially contiguous grids of subplots with permanently tagged and georeferenced individuals of all woody species (Losos and Leigh 2004). Legendre et al. (2009) applied variation partitioning of tree beta diversityinto environmental and spatial components, using data from a Gutianshan forest dynamics plot (China). Their approach, based on redundancy analysis of raw abundance data, was applied by De Cáceres et al. (2012), after slight modification, on a set of 10 forest dynamics plots, distributed on three continents and ranging from tropical to temperate zones.Besides introducing the analytical framework for analysis of forest dynamics plot data using the variation partitioning method, the main goal of Legendre et al. (2009) was to “test hypotheses about the processes (environmental control and neutral) that may be responsible for the beta diversity observed in the plot, by partitioning the effects of topography and space on the distribution of species at different spatial scales ...”. Similarly, one of the aims of the study by De Cáceres et al. (2012) was to find out “what is the contribution of environmentally-related variation versus pure spatial and local stochastic variation to tree beta diversity...”.Results of such analyses, however, will be strongly dependent on the quality of environmental variables used for variation partitioning (Jones et al. 2008). The assumption that component [c] represents the role of dispersal limitationholds only in cases where all relevant environmental variables are considered; otherwise,an unknown proportion of [c] is represented by unmeasured environmental variables (Laliberté et al. 2009; Diniz-Filho et al. 2012). Both Legendre et al. (2009) and De Cáceres et al. (2012) used only topographical variables (elevation, convexity, aspect and slope) derived from the measured elevation of corners of each grid, which are the standard components of forest permanent plot datasets. Both studies acknowledged the lack of other environmental descriptors, mainly variables describing soil chemistry, which were not available at the time of their study (or not for all plots). In the Gutianshan study, Legendre et al. (2009) assumed that because of very rough terrain, topographical variables should play an important role, and that a large proportion of variation explained by spatial variables and not explained by the environment may indicate the operation of other factors such as neutral processes. De Cáceres et al. (2012) were more careful in their interpretations, arguing that the variation explained by topography contains at least some variation derived from environmental control, because, when compared between plots, it increases with increasing within-plot topographical roughness.

In my study, I focused on the question of how the quality of environmental data changes the conclusions drawn from the results of variation partitioning between environmental and spatial variables. In the context of previous studies of forest dynamics plots, based only on topographical variables, I ask whether it is reasonable to use topography as a surrogate for environment, and how variation explained by environment will be improved by also measuring soil variables. Soil properties are important(e.g., Jones et al. 2008, Baldeck et al. 2013), but not always available, while topography is easy to measure in the field. Soil and topography is partially correlated, but each may offer additional information relevant for plant growth. My aim is to evaluate how important the environmental information in soil variables is and whether inclusion of soil can change or even reverse conclusions drawn from studies based only on topography.

Additional insight can be gained from more detailed analysis of component [c], namely its scale structure. This analysis is based on an assumption that broad-scale spatial structures in species data represent imprints of environmental variables, while fine-scale autocorrelation is more likely generated by community dynamics, including dispersal (Dray et al. 2012). Diniz-Filho et al. (2012) analyzed variation represented by component [c] evaluating the shape of Moran’s I correlograms and claimed that their method can distinguish if [c] is represented by broad-scaled unmeasured environmental variables or fine-scaleddispersal processes. In this manuscript, I introduce an alternative method to analyze scale properties of the [c] component, based on its multiscale decomposition usinga scalogramapproach (Legendre and Legendre 2012). Using the available vegetation and environmental data, I attempt to evaluate whether, after including topographical variables as environmental predictors, the spatial information in component [c] is dominated by broad-scaledor fine-scaled spatial autocorrelation.Further, I tested how the pattern changes after also including soil variables, to reveal if soil and topography captured the most important ecological drivers of species composition.

My study is based on detailed information about topography, soil chemistry and soil structure, collected within 25-ha forest dynamics plot in Lienhuachih (Taiwan), which is topographically very heterogeneous (within-plot altitudinal range is 164 m). I apply the same method of variation partitioning into fractions explained by environmental and spatial variables as used by Legendre et al. (2009) and De Cáceres et al. (2012). Using these data, the main objectives are: (1) to show to what extent the increase in variation in species composition is explained by environment if I also include soil variables into the analysis andhow this changes the conclusion about the importance of niche-based and dispersal-based processes, and (2) to demonstrate the use of multiscale decomposition of [c] component to detect whether important environmental variables were included in the study.

## METHODS

### *Study site.*

The study was conducted in the Lienhuachih Experimental Forest in central Taiwan (23º54’N, 120º52’E), which is a part of international network of forest dynamics plots coordinated by CTFS. The mean annual temperature is 20.8℃ andthe mean annual precipitation is 2,285.0 mm with pronounced seasonality (89.6% of total rainfall falls in between May and September) and common typhoons (Chang et al. 2010).The forest dynamics plot of 25 ha (500 × 500 m) was set up in 2008, with methodology following the census manual of Condit (1998). All woody stems with diameter at breast height (DBH) ≥ 1 cm were measured, tagged, mapped, and identified into species. The elevation of the plot ranges from 667-845 m a.s.l, withan average slope of 35.3°. Altogether 153,268 individualsand 203,316 stems were recorded within the plot(6,131 ind/haand 8,133 stems/ha, respectively). The vegetation represents subtropical evergreen broad-leaved forest with important canopy species including *Cyclobalanopsis pachyloma*, *Engelhardia roxburghiana*, *Pasania nantoensis, Schefflera arboricola* and *Schima superba* (Chang et al. 2010).

### *Topographical, soil and spatial descriptors.*

As topographical descriptors, I used exactly the same type of variables as Legendre et al. (2009) and De Cáceres et al. (2012), namely mean elevation, convexity, slope and aspect, all derived from measured elevation of four corners of each 20×20 m cell (for details of calculations, see Appendix S2 in De Cáceres et al. 2012 and Appendix A in this paper). The aspect was further segmentedinto east-west and north-south direction, represented by the sine and cosine of the aspect, respectively. Mean elevation, convexity and slope were used to construct third-degree polynomial equations, creating a total of nine monomials (see Legendre et al. 2009); in total 11, topographical variables (nine monomials and two derivatives of aspect) were available for variation partitioning. Variables calculated here slightly differed from those used (and reported) by De Cáceres et al. (2012), probably because I used the last version of updated and corrected dataset, while De Cáceres et al. (2012) used an older version (see Appendix A for comparison).

Soil properties are described by 16 variables, including soil chemistry (total C and N, C/N ratio, pH in 1M KCl, extractable K, Ca, Mg, Fe, Mn, Cu, Zn and P), water content and texture (proportion of sand, silt and clay); see Appendix B for details. Third-degree polynomial equations were constructed for each soil variable, resulting into 48 monomials used in further analyses.

As spatial descriptors, distance-based Moran's eigenvector maps (dbMEM, previously known as PCNM) derived from spectral decomposition of the spatial relationships among grid cells were used (Borcard and Legendre 2002, Dray et al. 2006). This method produces linearly independent spatial variables covering a wide range of spatial scales and allows modeling of any type of spatial structure (Borcard and Legendre 2002). Truncation distance was selected to retain links between horizontal, vertical and diagonal neighboring cells. All eigenvectors associated with Moran's I coefficients larger than the expected values of I were kept in analysis (all together 208 eigenvectors).

***Statistical analyses***

To decompose the variation of tree beta diversity into fractions explained by topographical, soil and spatial predictors, I used variation partitioning approach based on redundancy analysis (RDA, Rao 1964). Fourvariation partitioning analyses were conducted, namely: 1) topographical vs.spatial variables, 2) soil vs.spatial variables, 3) soil and topographical vs.spatial variables, and 4) topographical vs. soil vs. spatial variables. The set of first three variation partitioning analyses was conducted on both original (i.e. not transformed) species composition matrix and on Hellinger standardized matrix (Legendre and Gallagher 2001); this dichotomy aims to make my results comparable to those of Legendre et al. (2009), who did not use any standardization, and De Cáceres et al. (2012), who used Hellinger standardization. Moreover, De Cáceres et al. (2012) compared different forest dynamics plots in terms of the amount of beta diversity attributable to particular components of variation partitioning. As a measure of beta diversity for a given forest plot, they used total variance in the Hellinger-standardized species data matrix (Legendre et al. 2005), which was consequently divided into parts according to components derived from variation partitioning. To make my results comparable, I report the results of variation partitioning of Hellinger-standardized species data by both relative values of explained variation using adjusted $R^2$ ($R^2_{\mathrm{adj}}$, Peres-Neto et al. 2006) and the absolute values of beta diversity attributable to individual components. Variation partitioning among separate topographical, soil and spatial variables was conducted only on Hellinger standardized matrix.

Multiscale decomposition of [c] component was conducted using a set of partial RDAs. I evaluated variation in species composition explained separately by each dbMEM variable in three different scenarios: 1) without any covariables (i.e., marginal variation explained by individual dbMEM variables), 2) with topographical variables as covariables (i.e., variation explained by dbMEM after accounting for topography), and 3) with topographical and soil variables as covariables (i.e. variation explained by dbMEM after accounting for all available environmental variables). The significance of each of the 208 dbMEM variables in each of the three scenarios was tested by Monte Carlo permutation test (reduced model with 9,999 permutations); Holm’s correction (Holm 1979) was applied to correct for multiple testing. Scenarios 1 to 3 differ by gradually increasing the number of environmental variables entering the analysis as covariables, from no variables, only topographical, and both topographical and soil variables. The focus of this analysis is on relative changes in the distribution of variation explained by individual dbMEM variables after including only topographical and both topographical and soil variables, namely whetherthe variation explained by broad-scaled dbMEM variables will decrease after controlling for environmental variables. Large variation explained by broad-scaled dbMEM in this analysis indicates that not all important environmental variables were included, while significant variation explained by fine-scale dbMEM variables may indicate imprints of population processes such as dispersal. Theoretically, the distribution of the explained variations will change from right-skewed, with a dominance of variation explained by broad-scaled spatial variables surrogating unmeasured environmental variables, to left skewed with a prevalence of variation explained by fine-scaled spatial variables, indicating dominance of dispersal processes.

## RESULTS

Adding soil variables along with topographical ones increases the variation explained by the environment from 20.7% explained only by topography to 47.7% explained jointly by topography and soil (Fig. 4.1 and Table C in Appendix C, considering Hellinger-standardized species data). Soil variables alone explain 43.5%, which twice as muchas the variation explained by only topographical variables. In case of non-standardized species matrix, the explained variation is slightly higher: 24.5% for topographical variables only, 43.6% for soil only and 49.0% for both (Table C in Appendix C); hereafter, only results on Hellinger-standardized species data will be reported. Almost all variation explained by environmental (either topographical or soil) variables is spatially structured, meaning that an increase in variation explained by environmental factors after including soil variables decreases the variation explained purely byspatial variables (component [c]). Component [c] decreases from 37.5% if only topography is included to 11.3% if both topography and soil are included, while unexplained variation [d] remains unaffected by selection of environmental variables. If examining topographical and soil variables separately, it becomes obvious that most of the variation explained by topography is explained also by soil variables (from the20.7% explained by topography, 16.6% is shared with soil; Fig. C in Appendix C), while soil explains a considerable amount of variation by itself (26.9% of variation is not shared with topography, from a total of 43.5%). From this I can conclude that if appropriate soil variables are measured, topographical variables become highly redundant, because, from the total variation of 47.7% explained by the environment (topography and soil), only 4.2% is explained purely by topography.

If I adopt the approach of De Cáceres et al. (2012), the absolute values of beta diversity explained by topography in Gutianshan and in Lienhuachih are comparable (0.096 and 0.092, respectively, see Table S3 in De Cáceres (2012) for the first number and Table C in Appendix C of my paper for the second), while the part of beta diversity explained by pure space in Gutianshan is lower than in Lienhuachih (0.105 and 0.166, respectively). Adding soil among environmental variables in the case of Lienhuachih increases the beta diversity explained by environment to 0.212 and decreases those explained by pure space to 0.050.

The distribution of variation explained by individual dbMEMvariables (ordered by decreasing spatial scale from broad- to fine-scaled ones) changed considerably among the three proposed scenarios. If no covariables were included, the distribution was right-skewed (Fig. 4.2a), with broad-scaled dbMEM variables being the most important (with dbMEM 1 explaining 6.8% of variation). Filtering out topographical variables as covariables has a rather minor effect on the distribution shape (Fig 4.2b), with broad-scaled dbMEM variables still prevailing. Adding soil variables along with topographical ones to the covariableschanges the distribution dramatically, decreasing the importance of broad-scaled dbMEMs in favor of meso- and partly also fine-scaled ones (Fig 4.2c).

## DISCUSSION

If I followthe reasoning of Legendre et al. (2009), who attributed the components [a+b] of variation partitioning to the signature of niche processes and component [c] signature ofdispersal-basedprocesses, and apply it to data from the Lienhuachih plot, the conclusion will be very different if I include only topographical or both topographicaland soil variables in the analysis. If environment is represented by only topographical variables, dispersal-basedprocesses prevail, as the fraction [a+b] represents 24.5% and fraction [c] represents 40.8% of explained variation (non-standardized species data in Table C in Appendix C). Including soil variables along with topographical onescompletely reverses the interpretation in favor of niche-based processes, with 49.0% becoming much more important than dispersal-basedones with 17.0%. Incomparison, in Gutianshan at the same scale, topographical variables (components [a+b]) explain30.7%, while the pure space (component [c]) explains34.8% (Table 4.1 in Legendre et al. 2009, variation in community composition at the scale 20 × 20 m). Higher variation explained by topography compared to variation explained purely by space in the case of Gutianshan can perhaps be explained by the more rugged terrain in Gutianshanwhen compared to Lienhuachih and hence the higher effect of topographical variables (De Cáceres et al.

2012). I assume that adding soil among environmental variables would considerably increase the variation explained by the environment also in the case of Gutianshan, resulting into the dominance of niche- over dispersal-basedprocesses. Although we cannot foresee how significant this increase would be, my study indicatesthat it maybe rather dramatic.

On the other hand, relatively high variation explained by soil variation can partly be an artifact. The variation-partitioning approach assumes that environmental variables have a causal effect on species composition. While this is definitely true in the case of topography, which can perhaps hardly be modified by vegetation, in the case of soil variables, the direction of the causal relationship is not so straightforward. Soil samples are usually collected in the upper part of the soil profile, which is most strongly influenced by the litter of the aboveground vegetation. In this sense, not only does the soil chemistry influence the vegetation, but thevegetation also influences the soil chemistry. The relative proportion of this feedbackchanges from species to species (e.g., Finzi et al. 1998) and is hypothesized to have evolutionary context (Binkley and Giardina 1998). Therefore, the inclusion of soil variables among environmental variables in variation partitioning effect can overestimate the real effect of environmental control at the cost of the dispersal processes. The possible indication that this overestimation exists may be drawn from detailed analysis of the importance of particular soil properties and carefully considering if the important ones are more likely to be derived from geological substrates or from the effect of aboveground vegetation. However, the real scale of this overestimation will perhaps remain unknown, and its quantification will require an experimental approach.

Multiscaleanalysis of residual spatial variationin component [c]shows that topography itself is indeed not a sufficient descriptor of environmental control on the vegetation of my study site. The distribution of variation explained by particular dbMEM variablessorted from broad-scaled to fine-scaled did not change much between analysis without any environmental variables (Fig. 4.2a) and that including topography as covariables (Fig. 4.2b).Both show that there is still a considerable amount of broad-scaled spatial variation, indicating that important environmental factors have not been considered. After including soil variables, variation explained by broad-scaledspatial variables is not much higher than that explained by meso- or fine-scaledvariables. Some of the broad-scaleddbMEM variables, however, remain significant, meaning that there is still some space for other environmental variables to play a role, although perhaps these arenot asimportant as soil.

The dichotomy of broad-scaledspatial variables equaling environmental variables and fine-scaledonesrepresenting dispersal processes is indeed simplified, and while it may be close to reality at certain scales, it cannot be applied universally. Ecologiststend to measure broad-scaled environmental variables and ignore (or are unable to measure) fine-scaled ones (Dray et al. 2012), although these may also exist. Similarly, far-distance dispersal may theoretically result in more broad-scaled spatial community patterns. Information about the spatial structure of component [c] offers additional insight in data, but does not offer a definite answer about the relative role of alternative processes causing the spatial pattern. Further studies may focus on the comparison of my method with spatial autocorrelation analysis approach proposed by Diniz-Filho et al. (2012) to see if the results are comparable, and to check its sensitivity and reliability using community data of known properties.

## CONCLUSIONS

In the case study from the Lienhuachih forest dynamics plot, I have shown that including soil variables along with topographical variables into variation partitioning results in a more than two-fold increase invariation explained by the environment, and reverses the original conclusion about the dominance of dispersal-based processes in community assembly in the prevalence of niche-based ones. Detailed multiscale decomposition of [c] component indicates that topographical variables, when included as explanatory variables, does not explain much of the broad-scaled spatial pattern in species composition, while including soil variables does, leaving meso- and fine-scaled spatial patterns unexplained. However, I also pointed out that the variation explained by soil variables may be overestimated, because not only does soil influence the vegetation, but vegetation also partly influences the soil properties.

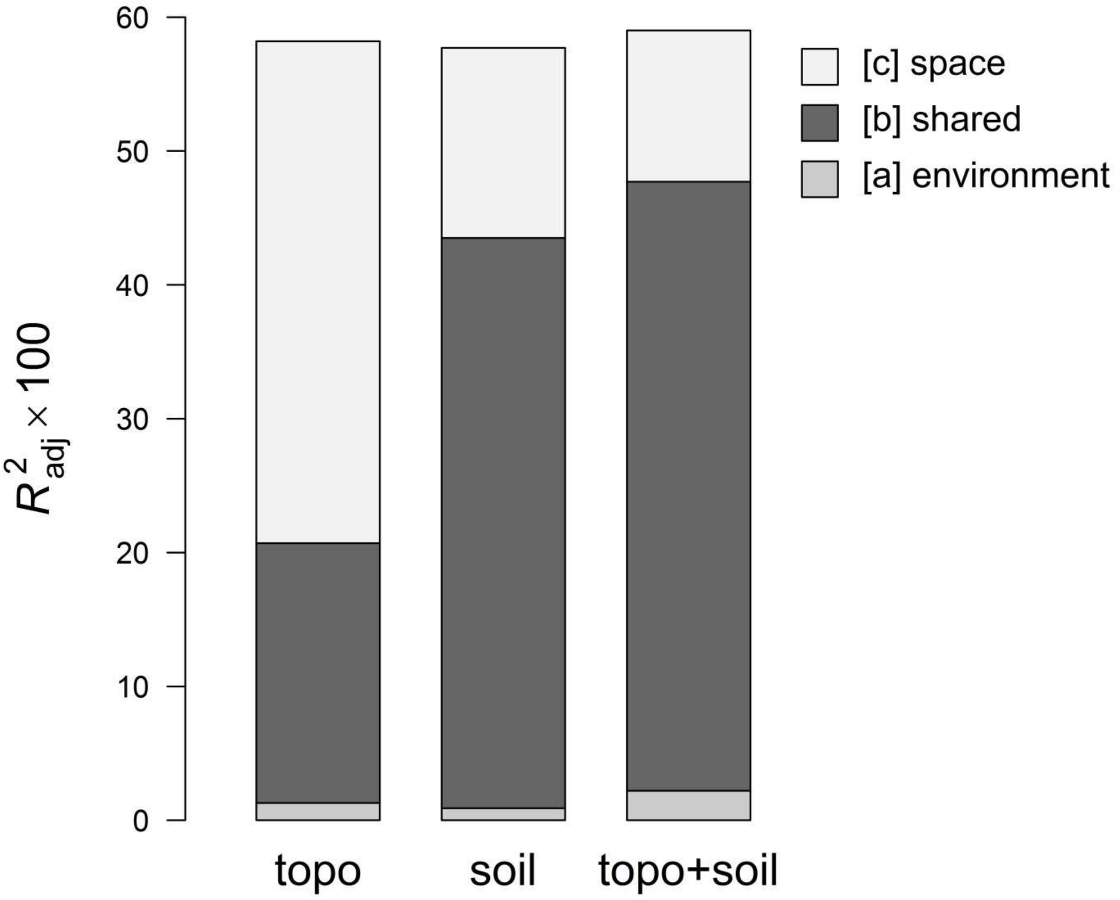

**Figure 4.1.** Results of variation partitioning of species composition into fractions explained by environmental and spatial variables, reported as adjusted $R^2$ on percentage scale ($R^2_{adj}$ × 100). Environmental variables are represented either by only topographical (first column), only soil (second column) or both topographical and soil variables together (third column).

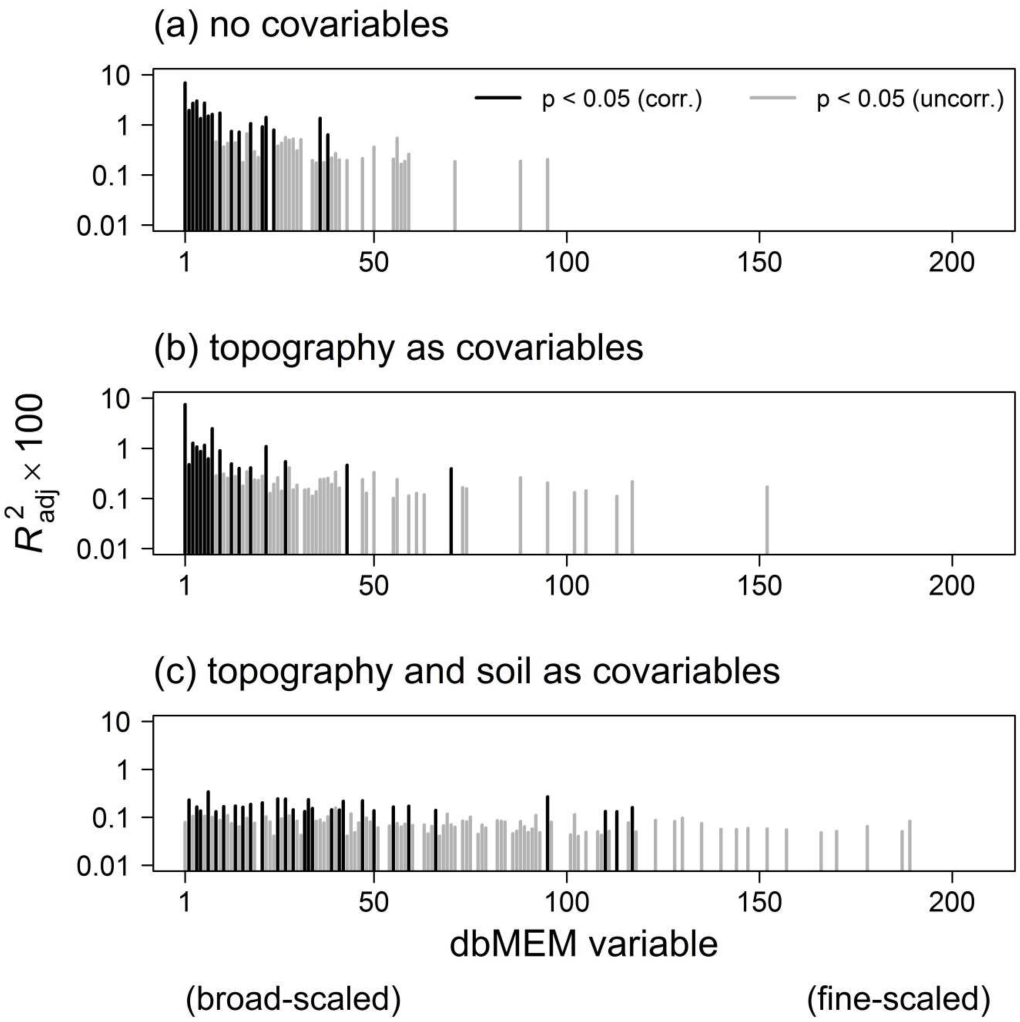

**Figure 4.2.** Variation in species composition explained in redundancy analysis ($R^2_{adj}$ × 100) by individual dbMEM variables with (a) no covariables, (b) topographical variables as covariables, and (c) topographical and soil variables as covariables. dbMEM variables are sorted from broad-scaled to fine-scaled (from left to right), and only dbMEM variables with positive $R^2_{adj}$ are presented. Significant variables ($p < 0.05$, 9999 permutations) with Holm's correction for multiple testing are black, whilevariables significant at $p < 0.05$ without correctionare dark grey;non-significant variables are not displayed. Note that to facilitate readability, values of $R^2_{adj}$ on the y-axis are multiplied by 100 and thisaxis is log-scaled.

# CHAPTER 5

# CONTRASTING SPATIAL DISTRIBUTION OF SPECIES DIVERSITY OF PIONEER VS. NON-PIONEER SAPLINGS IN A TAIWANESE FOREST: A MULTIPLE SCALE APPROACH

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# ABSTRACT

Understanding the spatial distribution of species diversity is one of the central issues in community ecology. Environmental conditions, dispersal limitation, and disturbance have been suggested to be important processes influencing spatial patterns in species diversity. At local scales, however, species distribution and habitat factors always show comparable spatial aggregation, making it difficult to understand how different processes regulate the spatial distribution of diversity and species composition. In this study, I investigated the spatial distribution of saplings belonging to two functional groups, pioneer and non-pioneer species, in a recently established 25-ha forest dynamics plot in the subtropical evergreen broad-leaved forest of central Taiwan. Spatial analysis method of principal coordinates of neighbor matrices (PCNM) was used to disentangle the contributions of these processes at different spatial scales. My results show that: (1) fine-scale spatial patterns are more important for pioneer than for non-pioneer species; (2) dispersal limitation showed stronger effects on non-pioneer saplings than pioneer saplings; (3) soil chemistry explained the greatest variations for both two functional groups, followed by disturbance for pioneer group, and topography for non-pioneer group, and then soil texture and moisture content. The results of canonical correspondence analysis indicated that species distributions were significantly correlated with topographic, soil and disturbance variables. It is also evident that plant species, geomorphic processes, and disturbance have different effects on the physical and chemical properties of soils.

***Key words:*** spatial scales; dispersal limitation; pioneer saplings; diversity; topography, soil, disturbance; PCNM analysis

## INTRODUCTION

Understanding the spatial distribution of species diversity is one of the central issues in community ecology (Chust et al. 2006; Borcard et al. 2011). Such understanding is especially important for tree communities (Legendre et al. 2009; De Cáceres et al. 2012). Trees are sessile organisms, and their growth, recruitment and mortality are influenced by the immediate neighborhood created by the abiotic environment and interactions among neighboring trees (Zhao et al. 2006). These interactions among neighboring trees and their abiotic environment usually leave spatial signatures in tree communities and create detectable spatial patterns in species diversity (Legendre et al. 2009). As a result, studying spatial distributions of species diversity and composition can be used to identify critical ecological processes that influence community assembly and species diversity (Brind'Amour et al. 2005; Legendre et al. 2009; De Cáceres et al. 2012).

In recent years, empirical studies documenting spatial patterns of species diversity in tree communities have rapidly increased (Legendre et al. 2009; De Cáceres et al. 2012, Chang et al. 2013). Principle coordinates of neighbor matrices (PCNM) is an advanced statistical method that has been widely applied to detect spatial patterns of species composition at multiple spatial scales (Chust et al. 2006; Jones et al. 2008; Legendre et al. 2009; De Cáceres et al. 2012). The overall species composition can be decomposed at several spatial scales and relevant spatial patterns can be identified. Together with the variation partitioning method, the spatial variation can be further attributed to different components, which .explained by environmental and spatial variables is often used to identify a signature of niche- and dispersal-based processes in community assembly (Legendre et al. 2009).

Many factors that influence plant distributions will generate spatial pattern in community composition. Previous studies showed that broad-scaled spatial variation dominated the spatial distribution of diversity in the forest (Jones et al. 2008; Legendre et al. 2009; De Cáceres et al. 2012). That had been explained by multiscale decomposition of pure spatial component, if only topography was included, broad-scaled spatial variation prevails in pure spatial component (Legendre et al. 2009; De Cáceres et al. 2012). However, after also including soil variables this pattern disappears, increasing importance of meso- and fine-scaled spatial patterns indicative of dispersal processes (Chang et al. 2013). When we consider environmental heterogeneity, not only topographic and soil factors are important but also as disturbance factor. While the first two factors had been studied, disturbances are often overlooked (Condit et al. 1995; van Nieuwstadt and Sheil 2005).

Canopy gaps are the most common disturbance in the forest (Tanaka et al. 1997). Comparing topographic and soil factors, gap dynamics are likely to produce spatial structure most evident at relatively fine scales (Jones et al. 2008). Gaps provide an environment in which tree species of differing competitive abilities partition heterogeneous resources. This promotes the persistence of pioneer species and maintains the diversity in the forest (Schnitzer et al. 2001). Hence, the spatial distribution of gaps also relate to distribution of pioneer species. On the other hand, the spatial distribution of species diversity of tree species, especially during the sapling stage, may reflect the distribution of canopy gaps within the forests. Therefore, the understanding factors affect distributions of pioneer and non-pioneer species help us more realize different ecological process act on diversity of the forest.

The relative importance of dispersal limitation and environmental factors, including topography, soil properties and disturbances, however, may differ among different functional groups of trees. Based on various plant attributes, tree species are usually divided into two functional groups, pioneer and non-pioneer groups. Pioneer species show adaptive traits such as small-sized, well-dispersed and dormant seeds that can survive long time in the soil bank and regenerate in large canopy gaps (Chen et al. 2003). In contrast, non-pioneer species have been considered as poor-dispersers, surviving short time in the soil seed bank, and their seedlings can tolerate the low light condition in the understory for many years (Delissio et al. 2002).

Taiwan is a mountainous island in southeastern Asia with a complex gradient in topography and experienced frequent typhoons (Lin et al. 2011). The distinction in distribution patterns between pioneer and non-pioneer saplings in subtropical evergreen broad-leaved forests has often been recognized. However, no detailed study has been done to understand the relative contribution of dispersal limitation and environmental factors (topography, soil properties, and disturbances) to the spatial distribution of species diversity. In 2008, I established a 25-ha forest dynamics plot (FDP) with precise stem mapping in the Lienhuachih forest in central Taiwan. Based upon the mapped tree data, I hypothesized that distribution of species diversity differed between pioneer and non-pioneer saplings. The main objectives of this chapter are (1) to know what the different spatial scales variations contribute to distribution of pioneer and non-pioneer saplings; (2) to understand dispersal limitation affects distribution of pioneer and non-pioneer saplings; and (3) to realize the different environmental factors contribute discriminative variation in explaining species composition of pioneer vs. non-pioneer saplings.

## METHODS

### *Study site*

The study site is located in the Lienhuachih Experimental Forest (LEF) in central Taiwan. The forest is described as a Lauro-Fagaceous forest (Su 1984). The mean annual temperature is 20.8℃. The annual precipitation is 2285.0 mm with marked seasonality (Lu et al. 2008). More than half of the rain falls in between May and September (about 89.6% of total rainfall). Typhoons, a common disturbance in the LEF, usually sweep through the area with violent winds and extremely heavy rainfall, and often cause canopy gaps and landslides (Lee 2006; Chang et al. 2010).

In 2008, following the standardized methodology developed by the Center for Tropical Forest Science, Smithsonian Institution (Condit 1998), I set up a 25-ha forest dynamics plot (FDP) (500 × 500 m, 23º54’N, 120º52’E) in the LEF. The elevation of the plot ranged from 667-845 m a. s. l. Average slope of plot was about 35.3°. Topography was characterized by hills with valleys, steep slopes, and ridges (Chang et al. 2010). All woody stems with diameter at breast height (DBH) $\geq$ 1 cm were measured, tagged, mapped, and identified to species. According to the first census there were 153,268 (6,131 ha$^{-1}$) stems within the plot, belonging to 46 families, 88 genera and 144 species. The forest is dominated by Fagaceae, Lauraceae, Rubiaceae, Euphorbiaceae and Melastomataceae (Chang et al. 2010).

### ***Data collection***

#### *Selection of pioneer and non-pioneer species and the definition of life stages*

A total of 144 species were recorded in the plot. Based on photosynthetic rates (Kuo et al. 2011), previous reports in literature (Chen et al. 2000; Chen et al. 2003) and habitat requirements such as saplings’ distribution in gaps and landslide areas which we observed in the Lienhuachih FDP, species were classified into two functional groups: pioneer and non-pioneer species. As a result, 18 pioneer species were selected. In order to make the data comparable, I also selected 18 dominant non-pioneer species.

Based on DBH, two life stages (sapling and mature stages) were distinguished separately for each of the three plant growth forms (shrub, sub-canopy tree, and canopy tree). Saplings were defined as the stems with 1.0-2.0 cm DBH for any growth form. Mature stages for canopy trees, sub-canopy trees and shrubs were defined as having a DBH ≥ 20 cm, ≥ 10 cm, and ≥ 5 cm, respectively. Dispersal modes and life forms of pioneer and non-pioneer species are listed in Appendix D.

*Topographic and soil variables*

The 25-ha LHC plot was systematically divided into 625 quadrats of 20 m × 20 m. Using laser theodolites, relative elevation was measured at each corner of the quadrat and a topographic map was generated from these data using geostatistical methods (Cressie 1991). Topographic variables derived for each quadrat included mean elevation, convexity, slope, stream distance and ridge distance. Mean elevation was obtained by averaging elevation measures from the four corners of the quadrat. Convexity was defined as elevation differences between the focal quadrat and mean elevations of the eight neighboring quadrats except for those quadrats on plot edges (Valencia et al. 2004). Slope was measured by the mean angular deviation from the horizontal plane of each of the four triangular planes by connecting three out of the four corners. Stream and ridge distances were measured from the quadrat center to the nearest stream and ridge. In order to increase the predictive ability of topographic factors, mean elevation, convexity and slope were used to construct third-degree polynomial equations for a total of 9 monomials (Legendre et al. 2009). After adding the two distance variables, a total of 11 variables were used to describe the micro-topographic environmental conditions of each quadrat.

Soil samples were collected from three randomly selected points within each quadrat at the depth of 0-10 cm. The three samples were mixed thoroughly together to obtain a composite sample. These 625 soil samples were air-dried and passed through a 2-mm sieve (10 mesh) for the following laboratory analyses. The gravimetric soil water content was determined by the weight loss at 105℃ for 24h (Gardner 1986). The sieved soil samples were subsequently analyzed for soil texture, total C and N, C/N ratio, pH, extractable K, Ca, Mg, Fe, Mn, Cu, Zn and P. Soil pH was measured in distilled water and potassium chloride (1M) at soil: solution ratios of 1:1 and 1:2.5 (McLean 1982). Extractable K, Ca, Mg, Fe, Mn, Cu, Zn and P were measured by the Mehlich-3 solution method (Helmke and Sparks 1996). Total soil C and N were determined by a dry combustion method (Nelson and Sommers 1982) using a Fisons NA-1500 analyzer. For soil texture, the Bouyoucos Hydrometer method was used for determining the soil particle size; for each sample, I obtained percentage of sand, silt and clay. The total work was done by the Soil Research Laboratory of Taiwan Forestry Research Institute. A total of 16 variables were collected, including soil chemistry and texture. For each of the 16 variables, monomials of three-degree polynomial were created, resulting in 3×16=48 soil variables.

*Disturbance variables: canopy gaps and logging road*

In this study, I applied photogrammetry and GIS techniques to collect and quantify the characteristics of forest canopy gaps. Aerial photographs of a forest canopy taken in different years provide information on canopy dynamics (Tanaka and Nakashizuka 1997; Henbo et al. 2004). Aerial photographs (1:5000) taken in 1998, 2002 and 2007 were purchased from the Aerial Survey Office, Taiwan Forestry Bureau. Elevations at every point on a 5 × 5 m grid were digitized from these photographs by Aerial Survey Office, using a stereo plotter. Two paired images were used to obtain stereo images covering the plot. Canopy gap was defined as an area where the canopy is noticeably lower than in adjacent areas or not occupied by crowns. The canopy gaps were digitized from these photographs using a stereo plotter (Leica Stereo Analyst for Arc GIS and Planar Stereoscopic Displays SD2020) and stored in the Arc/Info system. Gap area was determined by counting each quadrat where over half the quadrat was not covered by canopy. During canopy gap survey in 2008, I found a meandering logging road (180 m in length and 4 m in width) in the north middle side of the plot, which was an indicator of human disturbance. Spatial distribution of gaps and logging road at four observation times show in Appendix E.

### *Statistical analyses*

#### *Environmental variables*

For all environmental variables, 11, 48 and 4 variables were included as topography, soil, and disturbance datasets, respectively. I applied forward selection (Blanchet et al. 2008) to select those variables that significantly ($P < 0.05$ after 999 random permutations) explained the variation in species composition of pioneer and non-pioneer saplings. Only the selected variables were used in subsequent analyses.

#### *Spatial variables of sapling trees and mature trees*

Spatial variables for all saplings and mature trees and for the saplings of two different functional groups were created using the principal coordinates of neighbor matrices (PCNM) method (Borcard and Legendre 2002; Dray et al. 2006). For the 20 m × 20 m quadrats, PCNM eigenfunctions were computed across the 625 points of the spatial grids. In the present study, 324 PCNM eigenfunctions with positive eigenvalues were generated. Then I also used forward selection (Blanchet et al. 2008) to select those eigenfunctions significantly explaining variation in community composition for all species of saplings and mature trees and for the species of two functional groups. The selected PCNM eigenfunction variables were used as explanatory variables to analyze the spatial variations in community composition of saplings and mature trees. In order to understand multiple spatial structures in community composition, I arbitrary defined the first 20, 21-50, 51-100 and 101-324 of the 324 PCNM eigenfunctions representing very broad, broad, medium and fine spatial scale, respectively. Then I identified the topographic, soil and disturbance variables that significantly correspond to the different multiple spatial scales. Variation partitioning was run with each of the PCNM subsets combined with, in turn, each subset and the full set of environmental variables.

***Variation partitioning***

I conducted variation partitioning (Borcard et al. 1992), using species composition tables of pioneer, non-pioneer and all species as response matrices, and environment (topography, soil and disturbance variables), mature trees (spatial eigenfunction tables) and space (spatial eigenfunction tables of sapling trees) as explanatory matrices. I used adjusted $R^2$ ($R^2_a$ ) to measure the unbiased amount of variation explained by the PCNMs (Peres-Neto et al. 2006), and recorded the proportion of variation explained in RDA analyses by either the significant spatial (polynomial or PCNM) or environmental (simple or polynomial) variables, or both simultaneously. The results of variation partitioning were illustrated as Venn diagrams (Fig. 5.1a). This method allowed the partitioning of response matrices into the following fractions of variation: (a) pure environment, including pure topography, pure soil and pure disturbance; (b) pure mature tree space; (c) pure sapling tree space; (d) non-sapling structured mature and environment factions; (e) non-environment structured mature and sapling tree space fractions; (f) non mature tree structured space and environment factions; (g) spatially structured environment, mature tree space, and sapling tree space; and (h) residuals. In this study, I interpreted the spatially structured environmental and pure environmental fractions [a+d+f+g] as environmental control, and overlap spatial distribution fraction [e] of sapling tress and mature trees as dispersal limitation.

All analyses were done using the R statistical language (R Development Core Team 2013). Canonical analyses and PCNM eigenfunctions were computed using the “vegan” package (Oksanen et al. 2012).

### *Ordination*

For ordination quadrats or species with less than 5 individuals were eliminated resulting in a 35 species × 374 quadrats matrix. The variations in the species composition and abundance of all saplings, and their relationships with the selected environmental variables (including 16 soil, 5 topographic and 4 disturbance variables) were analyzed with Canonical Correspondence Analysis (CCA) using CANOCO 4.5 (ter Braak and Šmilauer 2002). The results of the analyses were visualized in the form of ordination diagrams in the Canodraw for Windows. Monte Carlo permutation tests (with 999 unrestricted permutations) were used to evaluate the significance of the first two canonical axes. To classify forest communities present in the FDP, the floristic data were analyzed using two-way indicator species analysis (TWINSPAN) with PC-ORD version 5 (McCune and Mefford. 2006). Differences in environmental variables between the two forest communities at the first level of TWINSPAN classification were examined by Mann–Whitney U Tests (STATISTICA. 8.0, StatSoft, Tulsa, OK, USA). Furthermore, relationship between topographic and soil variables was examined by canonical correlation analysis.

## RESULTS

### *Variation in multiple spatial scales*

The spatial structure of pioneer saplings showed a finer-scale spatial pattern than the spatial structures of all sapling and non-pioneer sapling communities. Additionally, the variation (10.6%) explained by the fine-scale PCNM eigenfunction is approximately equal to the variation (11.0%) explained by very broad-scale PCNM eigenfunction. In the cases of all saplings and non-pioneer saplings, only very broad-scale PCNM eigenfunctions accounted for the most variation (19.8% and 20.2%, respectively) (Table 5.2). When considering the environmental variables significantly related to spatial variation for different scale submodels, it was found that both topographic and soil variables contributed more at very broad, broad and medium scales, while gap disturbance variables explained more variation at fine scale.

***Environmental control and dispersal limitation processes***

Environment, sapling tree space, and mature tree space jointly explained 61.0%, 41.2% and 60.5% of the variations in sapling composition for all species, pioneer and non-pioneer species, respectively (Fig. 5.1b-d). I considered the joint non-environment fraction [e] between mature tree and space as dispersal limitation effect. The results showed that the environment fractions [a+d+f+g] explained much more of the variation than dispersal limitation fraction for all saplings and the saplings of either of the two functional groups. The adjusted $R^2$ were 0.142, 0.129 and 0.064 which accounted for 74.3%, 70.1% and 39.7% of the non-environment space fraction [e+c] for all saplings, non-pioneer and pioneer saplings, respectively. The results supported dispersal process showed a stronger effect on all saplings and non-pioneer saplings than on pioneer saplings in the Lienhuachih FDP.

The comparison between environment control [a+d+f+g] and mature tree [b+d+e+g] effects for pioneer saplings showed that environmental variables explained more variation than mature tree effects, but for all saplings and non-pioneer saplings, the pattern was reversed (Fig. 5.1b-d). In terms of pure fractions (pure environment [a], pure space [b] and pure mature tree [b] fractions), the permutation tests showed that most fractions (except pure mature trees of pioneer saplings) were significant (Fig. 5.1b-d).

***Contributions of topographic, soil and disturbance variables to saplings***

The variation partitioning of environmental submodels (topography, soil chemistry, soil texture and water content, and disturbance) showed that soil chemistry explained most of the variation in species composition for all saplings, pioneer and non-pioneer saplings, followed by disturbance for pioneer group, and topography for non-pioneer group (Table 5.2). Soil texture and water content were least important for all groups of saplings (Table 5.2).

The results of variation partitioning with respect to each environmental variable indicated that soil pH captured the largest fraction of the variation in the composition of non-pioneer saplings (14.7%) and all saplings (14.2%), whereas topographic convexity captured slightly less (10.0%, 10.4%), and ridge distance contributed the least (4.2%, 4.3%) (Table 5.2). In terms of pioneer saplings, the strongest environmental predictors were soil Mg, gap 2007, and soil P, which contributed 4.6%, 4.1%, and 3.9% of the variation, respectively (Table 5.2). Other environmental variables each contributed less than 3% (Table 5.2).

### *Ordination*

In CCA ordination, the eigenvalues of the first two CCA axes were 0.393 and 0.128, respectively. The species-environment correlations of the first two CCA axes were 0.911 and 0.680, and the cumulative percentage variance were 48.3 and 64.1%. The Monte Carlo tests ($p<0.001$) carried out for the first two canonical axes indicated that the floristic variance of saplings was significantly related to the environmental variables selected. The CCA biplot (Fig. 5.2) of species and environmental data along the first axis produced a clear segregation of quadrat and species groups classified by TWINSPAN. Quadrats (Fig. 5.2a) and species (Fig. 5.2b) of pioneer group (136 quadrats) are mainly located on the right side of the first CCA axis, wheras quadrats and species belonging to non-pioneer group (238 quadrats) are found toward the left side of the axis. Only one species (*Helicia formosana*) assigned to the non-pioneer group was misclassified by TWINSPAN as pioneer group.

The results of CCA also showed that the first axis represented a topographic-edaphic gradient; it was positively correlated with distance from the ridges and soil moisture, and negatively correlated with convexity, elevation and distance from the streams. The second axis was primarily related to disturbance-associated variables. The average values found for pH, extractable Mn, Cu, Ca, Mg Zn and clay percentage were distinctly higher in soils of pioneer communities, while C/N ratio, sand percentage, total C, total N, extractable K and Fe were higher in those of non-pioneer communities (Appendix E). There was no significant difference in extractable P between these two TWINSPAN groups.

## DISCUSSION

In this study, the explained variations for non-pioneer saplings and all saplings declined from the broad spatial scales to fine spatial scales. Similar results were found for the tree and seedling compositions in temperate and subtropical forests (Laliberté et al. 2009; Legendre et al. 2009; Yuan et al. 2011; De Cáceres et al. 2012; Lin et al. 2013). My results suggest that non-pioneer species tend to be more effective for tracking environmental variation at broader and medium spatial scales. On the other hand, the variation at fine spatial scale for pioneer saplings was greater than those for non-pioneer saplings and all saplings. This is likely to be attributable to the long-distance seed dispersal by wind and the recruitment of saplings in disturbed areas (Dalling et al. 1998). An earlier study (Lee 2006) on the same site indicated that, as a frequently disturbed forest in the Lienhuachih FDP, fine-scale disturbances resulting from the creation of canopy gaps provided more opportunities for recruitment and regeneration of pioneer species and could also influence their spatial patterns.

Both environmental variation and dispersal limitation have frequently been cited as primary determinants of species diversity and distribution across spatial scales. My analyses suggest that at broader scales, environmental control (pure environment and spatially structured environment) explained more variation than spatially structured non-environmental processes for all saplings and the two functional groups of saplings. These results implicate the importance of environmentally controlled broad-scale spatial structure, and are coincident with findings from other studies for saplings and poles in a subtropical forest (Lin et al. 2011) and overstory species in a tropical forest in southern China (Lin et al. 2013), tree species in an old growth temperate forest in northeastern China (Yuan et al. 2011), and tree seedlings in a temperate forest in Canada (Laliberté et al. 2009). On the other hand, for pioneer saplings, the increase in the proportion of spatial PCNM variables at small scales may be attributed to the influence of biotic processes such as dispersal and gap disturbance as mentioned above.

The results obtained in this study support the third hypothesis that dispersal limitation exerts stronger effects on non-pioneer saplings than pioneer ones in the Lienhuachih FDP. This can been explained by the fact that non-pioneer species dispersed their seeds over relatively shorter distances, and thus showed a stronger dispersal limitation than pioneer species with long-distance dispersal capacity. Pioneer seedlings were mostly clumped at locations with intermediate to high light availability or in recently disturbed sites, and usually occurred at some distance away from conspecific adult trees. This may have decreased the relative proportion of variation explained by the mature tree eigenfunction (Fig. 5.1). On the other hand, seedlings of non-pioneer species often showed a strong clumping around adult trees, and explained much more of the variation in mature tree space. Results from temperate and tropical forests (van Ulft 2004; Flinn et al. 2010) also suggested that dispersal limitation showed stronger effects on short-distance dispersal species than on long-distance dispersal species.

Topography associated with other environmental variables, such as drainage regimes and soil properties have been regarded as the most important abiotic factors causing variation in the composition and structure of tropical forests on a local scale (Ratter 1980; Bourgeron 1983; Foster 1988; Adámoli et al, 1990; Oliveira-Filho et al. 1990, Johnston 1992; Enoki et al. 1997). In this study, the results of CCA showed that the first axis represented mainly a topographic and edaphic gradient. Canonical correlation analysis indicated a significant overall relationship between topographic and edaphic variables (R= 0.909, p<0.001). Gradients of increasing pH, extractable Mn, Ca, Mg, Cu and Zn and decreasing C/N ratio, N, C and Fe have been shown to be associated with a microtopographic gradient from higher slopes and ridges to lower sites. This pattern may reflect an underlying gradient of soil moisture. It also points to the importance of slope processes which lead to a gradual removal of dissolved inorganic nutrients from upper slopes and the accumulation of these materials near the streamsides. As a result, upslope soils were poorer in mineral nutrients and coarser-textured than were streamside soils.

One of the the major differences in soil properties between communities of pioneer and non-pioneer saplings was C/N ratio. The C/N ratio indicated the rate of decomposition (Fisher and Binkley 2000) and the quality of the organic matter in the soils (Côté et al., 2000). There is considerable evidence that topsoil C/N ratio was significantly affected by forest types and species composition (Côté et al. 2000; Zhong and Makeschin 2004; Vesterdal et al. 2008; Gairola et al. 2012). Many studies have also documented the concomitant change of soil C/N ratio in primary and secondary chronosequences (Vitousek et al. 1989, Aravena et al. 2002, Sariyildiz et al. 2005, Dölle and Schmidt 2009), however, few researches have been examined for the broad-leaved forests along the successional sequence (Kamijo et al. 2002; Yan et al. 2009). In this study, the C/N ratios of non-pioneer soils were markedly higher than the pioneer soils. This might be attributed to the more recalcitrant (high C/N ratio) litter and a relatively low soil moisture in upslope soils. Alternatively, the fast-growing pioneer forests near streamsides had a vulnerable (low C/N ratio) litter and moistened soils. My result was consistent with other observations that soil C/N ratio increased with successional age, as a result of increasing input of partly recalcitrant organic matter with high C/N ratio (Berendse 1990; Kamijo et al. 2002; Dölle and Schmidt 2009). On the contrary, some evidences showed a lower C/N ratio of soils in later successional forests than in the earlier successional stages (Aravena et al. 2002; Yan et al. 2009). This is likely to be caused by the contribution of greater amounts of lower C/N ratio litterfall from few dominant species of later successional stages.

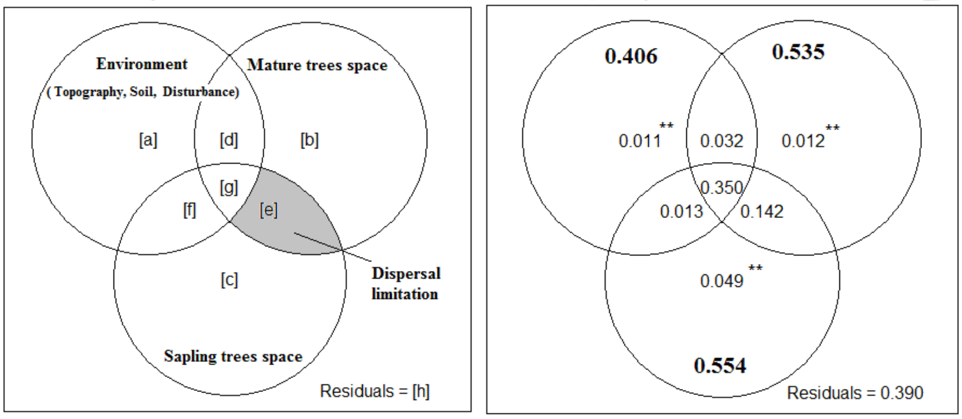
It has often been pointed out the role of gaps in maintaining pioneer species diversity in the forests (Ricklefs 1977; Denslow 1987; Brandani et al. 1988), and the empirical evidences also supported this paradigm (Schnitzer and Carson 2001). In this study, the second CCA axis represented a continuum of gap-phase regeneration, from more recently disturbed or open areas (logging road and gap 2007) in the upper portion of Fig. 5.2. to areas of later regeneration stages in the lower portion of CCA ordination. In Lienhauchih plot, landslides and treefall gaps frequently occurr on concave slopes and along streamsides, and the individuals of pioneer species such as *Melastroma candidum*, *Trema cannabina*, *Litsea cubeba*, *Tetradium glabrifolium*, etc. were abundant in those sites. The results of variation partitioning showed that the most recently created gap 2007 was the strongest predictor explaining variation in sapling composition, followed by the gap 2002. However, gap 1998 created longer than 14 years were quite closed and not suitable for using as predictor for the pioneer 1-2 cm dbh saplings. For non-pioneer saplings, gap 2007 and gap 1998 also had been selected as significant predictors, even though the contributions were weak. This is probably because the non-pioneer species included both intermediate species and shade-tolerant species. When disturbance formed, light increased, that also benefited the growth of saplings and promoted the diversity for the non-pioneer group (Yamamoto 2000).

Although there was no significant difference in extractable P between pioneer and non-pioneer groups, comparisons done separately for soil P between gap quadrats of varying ages and non-gap quadrats showed that significance levels (Mann–Whitney U-tests ) decreased with gap ages, from p=0.0003 (mean=18.437 vs 15.839) for gap 2007, through p=0.0465 (mean=17.670 vs 15.965) for gap 2002, to p=0.8949 (mean=16.534 vs 16.208) for gap 1997. Higher soil P content in gaps is most likely due to the release of P from decomposing organic debris generated by gap disturbances, with some then sorbed into geochemical soil pools (Scatena et al. 1996). The decreasing amount of P content in non-gap soils might indicate accumulation of P in the living plant biomass (Dölle and Schmidt 2009).

*H. formosana* assigned to the non-pioneer group was misclassified by TWINSPAN as pioneer group. *H. formosana* is a sub-canopy dominant specie in forest in Taiwan, which prefer lower slope and moisture habitat (Su et al. 2010). Because of landslide disturbance frequently occurred on concave area at lower slope, where was also the habitat *H. formosana* dormant. This is the reason why *H. formosana* was misclassified by TWINSPAN as pioneer group.

Overall, I observed that environment control was the main process that regulates the spatial distribution of species diversity both for pioneer and non-pioneer saplings. Disturbance effects contributed to fine-scale spatial variations for pioneer saplings, whereas topographic and soil effects contributed to broad scale spatial variations for non-pioneer saplings. At the same time, dispersal limitation was also an important process influencing the spatial distribution of species diversity for both functional saplings, especially for the non-pioneer saplings. The results also emphasize the role of disturbance process in the maintenance of pioneer species composition which simultaneously structured plant diversity. Although species distributions were significantly correlated with topography, soil and disturbance, my results showed that both topographic factors and plant species could also exert strong control over soil chemical and physical properties, and thus influenced vegetation-soil patterning.

a) Venn diagrams b) All saplings



c) Pioneer saplings d) Non-pioneer saplings

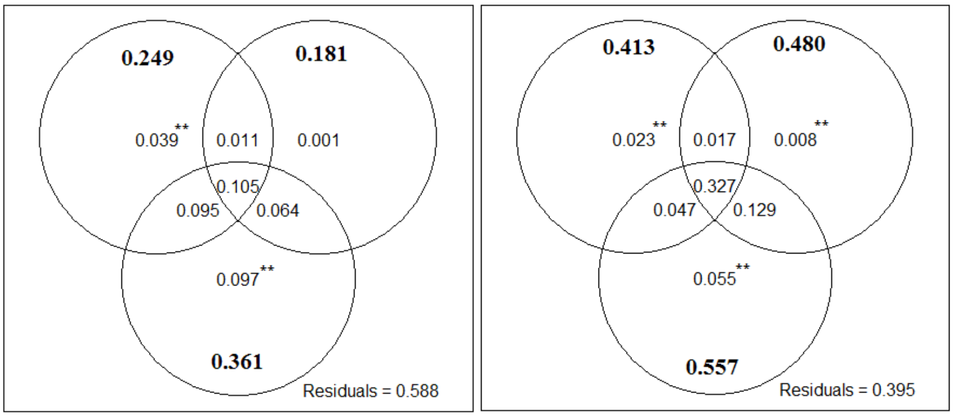


**Fig. 5.1.** Variation partitioning results. The four figure panels show Venn diagrams representing the partitioning of the variation of b) All saplings, c) Pioneer saplings and d) Non-pioneer saplings. Among three sets of explanatory variables: environment variables (upper left circle), mature trees PCNM eigenfunctions (upper right circle) and sapling trees PCNM eigenfunctions (down circle). Each box represents 100% of the variation in the corresponding response variable. The reported fractions are adjusted $R^2$ statistics. a), The figure panels show Venn diagrams.[a] pure environment (include pure topography, pure soil and pure disturbance) [b] pure mature trees space, [c] pure sapling trees space, [d] non-sapling structured mature and environment faction, [e] non-environment structured mature and sapling tree space fraction, [f] non mature tree structured space and environment faction, [g] spatially structured environment, mature tree space, and sapling tree space, and [p] residuals. The permutation test was done to test significance of pure environment, pure space and pure mature trees factions. ** significant (p<0.001); * significant (p<0.005).

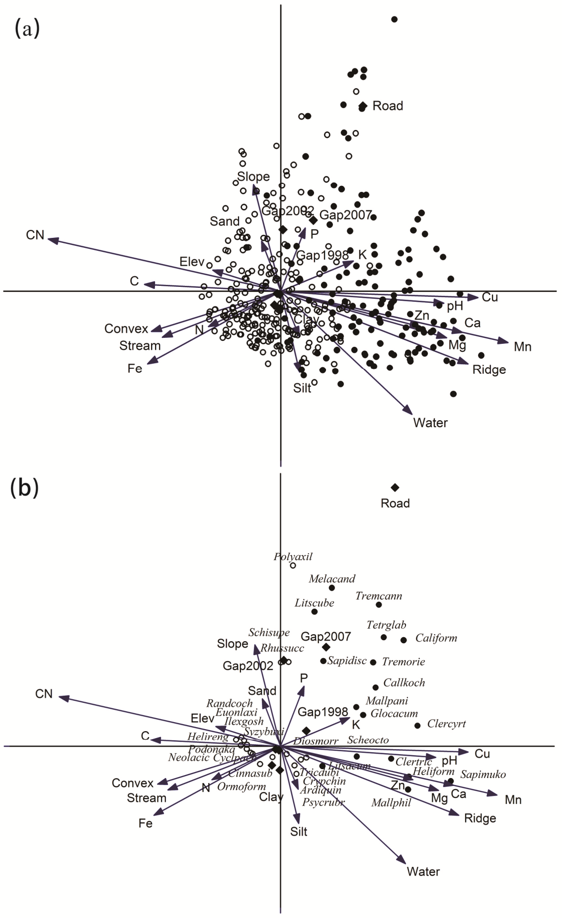


**Fig. 5.2.** Ordination diagrams of 374 quadrats (a) and 35 species (b) based on Canonical Correspondence Analysis with respect to 16 soil and 5 topographic variables represented by the arrows and 4 disturbance regimes shown by their centroids. Species are identified by their abbreviated names (the first four letters of the genus combined with the first four letters of the species: *Ardisia quinquegona*, *Callicarpa formosana*, *Callicarpa kochiana*, *Cinnamomum subavenium*, *Clerodendrum cyrtophyllum*, *Clerodendrum trichotomum*, *Cryptocarya chinensis*, *Cyclobalanopsis pachyloma*, *Diospyros morrisiana*, *Euonymus laxiflorus*, *Glochidion acuminatum*, *Gordonia axillaris*, *Helicia formosana*, *Helicia rengetiensis*, *Litsea acuminata*, *Litsea cubeba*, *Mallotus paniculatus*, *Mallotus philippensis*, *Melastroma candidum*, *Neolitsea aciculate*, *Ormosia formosana*, *Pasania nantoensis*, *Podocarpus nakaii*, *Psychotria rubra*, *Randia cochinchinensis*, *Rhus succedanea*, *Sapindus mukorossii*, *Sapium discolor*, *Schefflera octophylla*, *Schima superba*, *Syzygium buxifolium*, *Tetradium glabrifolium*, *Trema cannabina*, *Trema orientalis* and *Tricalysia dubia*. TWINSPAN classification groups are indicated by different symbols: pioneer species or quadrats (solid circle) and non-pioneer quadrats or species (open circle).

**Table 5.1**. Accumulated adjusted $R^2$ of PCNM eigenfunctions (accumulated number) and significantly correlated environmental variables in different sub models of community composition for all saplings (AS), pioneer saplings (PS) and non-pioneer saplings (NPS). Four sub models were divided: very broad-scaled: 1-20 PCNM eigenfunctions; broad-scaled: 21-50 PCNM eigenfunctions; medium-scaled: 51-100 PCNM eigenfunctions; fine-scaled: 101-324 PCNM eigenfunctions.

| | Very broad-scaled | Broad -scaled | Medium-scaled | Fine-scaled | Total |
|---|---|---|---|---|---|
| AS | 0.198 (18) | 0.165 (22) | 0.108 (25) | 0.006 (32) | 0.554 (97 ) |
| | elevation, ridge distance, silt, sand, clay, water, C/N ratio, P, Ca, Mn, Mg, K, gap1998, gap 2007 | elevation, pH, water, C/N ratio, P, Ca, Fe, Zn, Mn, Mg, K | slope, clay, water, C/N ratio, Ca, Cu, Zn, Mn, gap1998 | - | |
| PS | 0.110 (13) | 0.060 (14) | 0.068 (16) | 0.106 (50) | 0.361 (77 ) |
| | elevation, sand, clay, water, P, Ca, Fe, Mn, K, gap 2007 | elevation, ridge distance, silt, sand, water, C, P, Cu, Fe, Mn, K, gap1998 | elevation, silt, sand, clay, water, C/N ratio, Ca, Zn, Mn, K, | gap 2002, gap 2007 | |
| NPS | 0.202 (18) | 0.169 (22) | 0.111 (26) | 0.005 (50) | 0.557 (90 ) |
| | elevation, ridge distance, silt, sand, clay, water, C/N ratio, C, P, Ca, Mn, Mg, K, gap1998, gap 2007 | elevation, water, C/N ratio, P, Ca, Fe, Zn, Mn, K | slope, stream distance, silt, sand, clay, water, C/N ratio, Ca, Cu, Fe, Zn, Mg, K, gap1998 | - | |

**Table 5.2.** Variation partitioning results of environment (topography, disturbance, soil chemistry, soil texture and water content) variables for species composition of all saplings (AS), pioneer saplings (PS) and non-pioneer saplings (NPS). No.: the number of environment variables selected by forward selection. $R_a^2$, adjusted $R^2$, Acc $R_a^2$, accumulated adjusted $R^2$

| | No. | Topography | $R_a^2$ [Acc $R_a^2$] | No. | All Soil | Soil chemistry | $R_a^2$ [Acc $R_a^2$] | Soil texture and water | $R_a^2$ [Acc $R_a^2$] | No. | Disturbance | $R_a^2$ [Acc $R_a^2$] |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| AS | 8 | convexity3 | 0.100 | 26 | | C/N ratio3 | 0.142 | slit | 0.016 | 2 | gap 1998 | 0.010 |
| | | ridge distance | 0.042 | | | pH2 | 0.021 | water | 0.028 | | gap 2007 | 0.008 |
| | | | [0.191] | | 0.340 | | [0.271] | | [0.069] | | | [0.018] |
| PS | 5 | slope | 0.012 | 12 | | Mg3 | 0.046 | water3 | 0.018 | 3 | gap 2007 | 0.041 |
| | | convexity | 0.010 | | | P2 | 0.039 | sand3 | 0.008 | | gap 2002 | 0.015 |
| | | | [0.041] | | 0.161 | | [0.132] | | [0.030] | | | [0.064] |
| NPS | 8 | convexity3 | 0.104 | 26 | | C/N ratio3 | 0.147 | water | 0.029 | 2 | gap 1998 | 0.011 |
| | | ridge distance | 0.043 | | | pH2 | 0.022 | slit | 0.017 | | gap 2007 | 0.007 |
| | | | [0.196] | | 0.347 | | [0.277] | | [0.071] | | | [0.018] |

# CHAPTER 6

# SUMMARY AND CONCLUSIONS

The Lienhuachih FDP is dominated by Fagaceae and Lauraceae and which is characteristic of the *Machilus-Castanopsis* forest zone of Taiwan. The size-class structure of trees showed most tree species had plenty saplings, which displayed good recruitment in the forest. Fisher's alpha diversity of the Lienhuachih FDP was the highest among low-elevation FDPs in Taiwan, but lower than which of other FDPs in tropical plots. It indicates that the subtropical forests maintain the diversity as high as tropical ones especially in those with the good recruitment.

On the other hand, the Lienhuachih forest could be divided to four types, these are *Pasania nantoensis* - *Randia cochinchinensis* type locates on the ridge and the highest elevation was with the highest stem density, *Mallotus paniculatus* - *Engelhardtia roxburghiana* type locates on the upper slope was with the middle stem density and basal area, *Diospyros morrisiana* - *Cryptocarya chinensis* type locates on the lower slope and stream side was with lower stem density and *Machilus japonica var. kusanoi* - *Helicia formosana* type locates on west stream side was with the lowest stem density and basal area. All four plant communities and species composition varied across micro-topographic gradients. Why the Fagaceae-Lauraceae subtropical forest contained not few unique donminant species implies that Lienhuachih forest may carry on very complicated or mixed ecological processes to result in high diversity.

This may result from both niche process and dispersal process work together to assemble the Lienhuachih tree communities. When comparing above two processes affect community assembly, if only topography is included, dispersal-based processes prevail. But if including soil variables along with topography variables into variation partitioning, the result reverses. Furthermore, including disturbance variables with topography and soil variables, niche-based processes still prevail for both pioneer and non-pioneer saplings. However, dispersal limitation was also an important process influencing the spatial distribution of species diversity for both functional saplings, especially for the non-pioneer saplings.

My study also demonstrated that topography affected distribution of non-pioneer saplings, whereas disturbance affected distribution of pioneer saplings. Although soil is an important factor to explain distribution of both pioneer and non-pioneer saplings, it is also evident that plant species, geomorphic processes, and disturbance have different effects on the physical and chemical properties of soils. Soil and disturbance effects contributed to meso- and fine-scale spatial variations for distribution of species, whereas topographic effects contributed to broad-scale spatial variations for distribution of species. To conclude, in a rough terrain and highly disturbance area, niche-based process is the main ecological process to maintain the coexistence and diversity, and which also affect vegetation classification in the Lienhuachih subtropical forest.

Above conclusions, I demonstrate niche-based process is the main ecological process that regulates the coexistence and diversity of all tree community and different functional saplings, which are both community level. Further studies may focus each species level, especially on distribution of congeneric species in the plot. Because sympatric distributions of congeneric species are remarkable features which also cause high diversity in the tropical forest (Richards 1952, Ashton 1969, Whitmore 1984, Schulman et al. 2004, Sedio et al. 2012). Congeneric status as descendants of a common ancestor, are more likely to be similar in many phenotypic and ecological traits and, which means they prefer similar habitat (Ackerly and Donoghue 1998; Mooney et al, 2008). What makes them coexist is the interesting study that I would like to do in the future.

On the other hand, since 1990, the Taiwanese government has prohibited logging, timber self-sufficiency ratio gradually decreased, only 0.022%, and others 99.78% dependent on imports. Recent years, the aim of forestry department is not only try to increase timber self-sufficiency ratio but also maintain forest diversity. Based on my research, I suggest some native pioneer species are very good choices for plantation species, like T*rema orientalis, Gordonia axillaris, Litsea cubeba,* and *Sapium discolor* etc. Because those species growth fast, adapt to bad environment, and usually have short rotation. With the suitable management way, I believe those pioneer trees which I mention above are also good for timber or other uses.

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# APPENDICIES

**Appendix A.** Comparison of environmental data for Lienhuachih forest plot with those used by De Cáceres et al. (2012).

All four topographical variables in My study (elevation, convexity, slope and aspect) are derived from the dataset of measured elevation of grid corners, calculated in the same way as in Legendre et al. (2009) and De Cáceres et al. (2012). Elevation, convexity and slope are calculated according to Valencia et al. (2004). Elevation of the target cell is calculated as a mean elevation of its four corners. Convexity is calculated as elevation of target cell minus mean elevation of surrounding eight cells. Convexity of marginal cells should be calculated as elevation of the cell midpoint minus the mean of the elevation of its four corners; however, the midpoint elevation is not available (midpoint elevation cannot equal to the elevation of the cell, which is calculated as mean elevation of four corners, because the convexity of all marginal cells would become zero), and must be approximated by krigging (Valencia et al. 2004). De Cáceres et al. (2012) does not offer further details about how they dealt with the problem of the marginal cells, so the reason of the differences in convexity (Table A1) may be caused by the difference in the krigging method used. Slope was calculated as the mean angular deviation from horizontal of each of the four triangular planes formed by connecting three of its corners (Harms et al. 2001). Aspect was calculated following the formula in De Cáceres et al. (2012, Appendix S2), and thiscalculated aspect was rather similar to the real aspect measured in the field (not shown here). However, the mean and standard deviation values for sin (aspect) and cos (aspect), respectively, which were used as easterness and northerness, are different from those referred by De Cáceres et al. (2012, Table S2 in Appendix S1). The reason for this difference remains not clear.

**Table A.** Comparison of topographical variables (their mean values and variance) reported by De Cáceres et al. (2012, Table S2 in Appendix S1) and those used in my study.

| | This study | De Cáceres et al. (2012) |
|---|---|---|
| Year of the census | 2008 | 2008 |
| Number of species in the plot | 144 | 145 |
| Percentage of rare species | 75% | 75% |
| Number of individuals | 203316 | 203313 |
| Tree density (ind/$m^2$) | 0.81 | 0.81 |
| Elevation (m) – mean | 764 | 764 |
| Elevation (m) – s.d. | 35.9 | 35.9 |
| Convexity – mean | -0.108 | -0.257 |
| Convexity – s.d. | 3.83 | 7.54 |
| Slope (°) – mean | 33.4 | 33.4 |
| Slope (°) – s.d. | 8.53 | 8.69 |
| EW aspect – mean | 0.22 | 0.14 |
| EW aspect – s.d. | 0.67 | 0.73 |
| NS aspect – mean | -0.08 | -0.11 |
| NS aspect – s.d. | 0.71 | 0.66 |

**Appendix B.** Details of soil sample analyses.

In each of 625 grids, three random samples were collected from 0-10 cm depth and mixed together. Soil samples were air-dried and passed through a 2-mm sieve for the following laboratory analyses. The gravimetric soil water content was determined by the weight loss at 105°C for 24h (Gardner 1986). The sieved soil samples were subsequently analyzed for total C and N, C/N ratio, pH, extractable K, Ca, Mg, Fe, Mn, Cu, Zn, and P, and soil texture. Total soil C and N were determined by a dry combustion method (Nelson and Sommers 1982) using a Fisons NA-1500 analyzer. Soil pH was measured in 1M KCl solution (soil: solution ratio of 1:2.5 (McLean 1982). Extractable K, Ca, Mg, Fe, Mn, Cu, Zn and P were measures by the Mehlich-3 solution method (Helmke and Sparks 1996). For soil texture, the Bouyoucos Hydrometer method was used for determining the soil particle size (Gee and Bauder, 1986); for each sample, I obtained percentage of sand, silt and clay. All analyses were conducted in Taiwan Forestry Institute soil research laboratory.

**Appendix C.** Variation partitioning analysis between environmental (only topographical, only soil or both, respectively) and spatial variables.

**Figure C.** Results of variation partitioning into fractions represented by topographical (topo), soil and spatial variables, reported as adjusted $R^2$ on percentage scale ($R^2_{\mathrm{adj}}$ × 100). Topography is represented by 11 variables, soil by 46 variables and space by 208 dbMEM variables. All testable fractions are significant ($p < 0.001$, 9999 permutations).

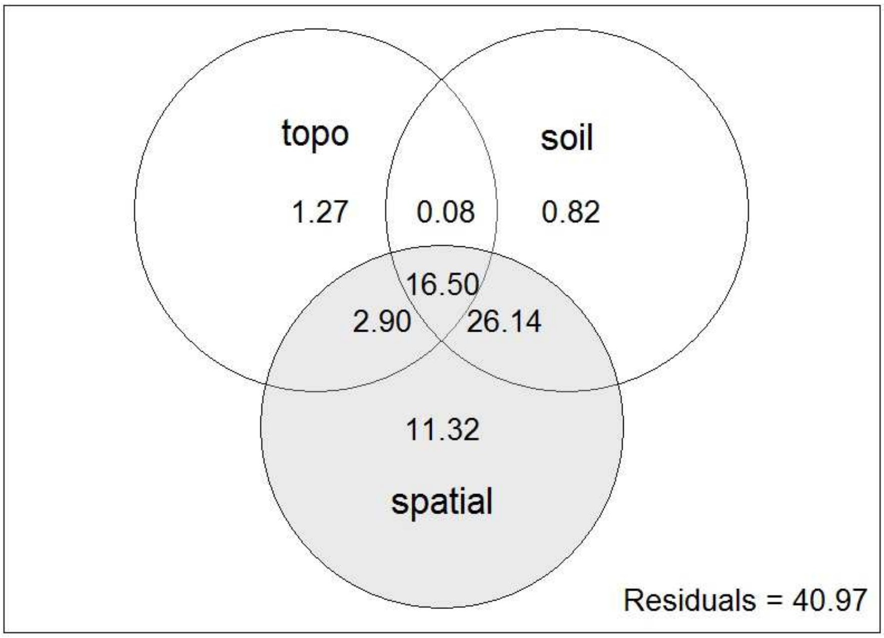


**Table C.** Reported explained variation is represented by adjusted $R^2$. All testable components ([a], [c], [a+b] and [b+c]) are significant (Monte Carlo permutation test with 9.999 permutations), mostly at $p < 0.001$, only fraction [a] explained by soil on non-standardized species data is significant at $p < 0.01$. Results of variation partitioning on non-standardized species composition matrix are provided for comparison with results of Legendre et al. (2009), while variation explained by environmental variables on Hellinger-standardized species composition matrix corrected for total beta diversity ($BD_{TOT}$) is for comparison with De Cáceres et al. (2012).

| Environmental variables | [a] | [b] | [c] | [d] | [a+b] | [b+c] |
|---|---|---|---|---|---|---|
| Hellinger-standardized species composition matrix | | | | | | |
| topographical | 0.013 | 0.194 | 0.375 | 0.418 | 0.207 | 0.569 |
| soil | 0.009 | 0.426 | 0.142 | 0.422 | 0.435 | 0.568 |
| topo + soil | 0.022 | 0.455 | 0.113 | 0.410 | 0.477 | 0.568 |
| Non-standardized species composition matrix | | | | | | |
| topographical | 0.011 | 0.234 | 0.408 | 0.346 | 0.245 | 0.642 |
| soil | 0.006 | 0.430 | 0.213 | 0.351 | 0.436 | 0.643 |
| topo + soil | 0.017 | 0.473 | 0.170 | 0.340 | 0.490 | 0.643 |
| Hellinger-standardized species composition matrix, explained variation × $BD_{TOT}$ | | | | | | |
| topographical[1] | 0.006 | 0.086 | 0.166 | 0.185 | 0.092 | 0.252 |
| soil | 0.004 | 0.189 | 0.063 | 0.187 | 0.193 | 0.252 |
| topo + soil | 0.010 | 0.202 | 0.050 | 0.182 | 0.212 | 0.252 |

[a] = variation explained by environmental and not by spatial variables, [b] = spatially structured variation explained by environmental variables, [c] = variation explained by spatial variables but not by environmental ones, [d] = unexplained variation, [a+b] and [b+c] = marginal variation explained by environmental and by spatial variables, respectively.

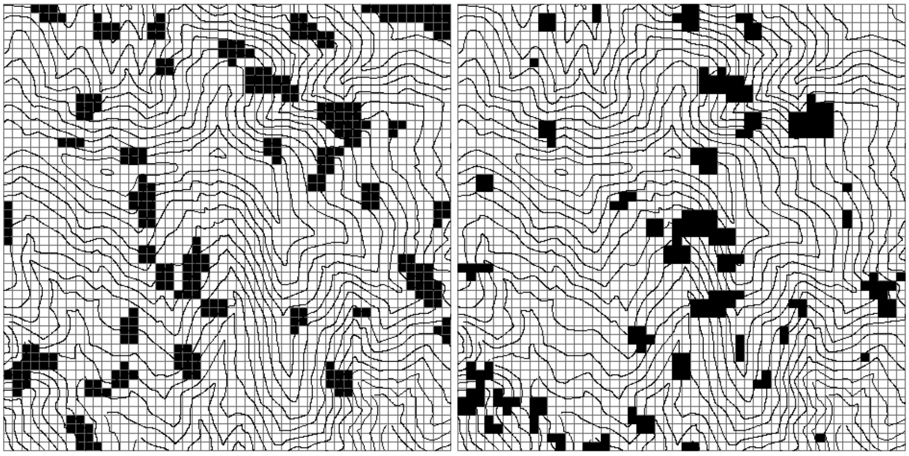
[1] Values reported for Lienhuachih by De Cáceres et al. (2012, Table S2, size 20 × 20) are slightly different: [a] 0.006, [b] 0.089, [c] 0.163, [d] 0.185, [a+b] 0.095, [b+c] 0.252.

**Appendix D.** Dispersal modes and life forms of 18 pioneer species and 18 abundance dominant non-pioneer species. C: canopy; SC: subcanopy; S: shrub.

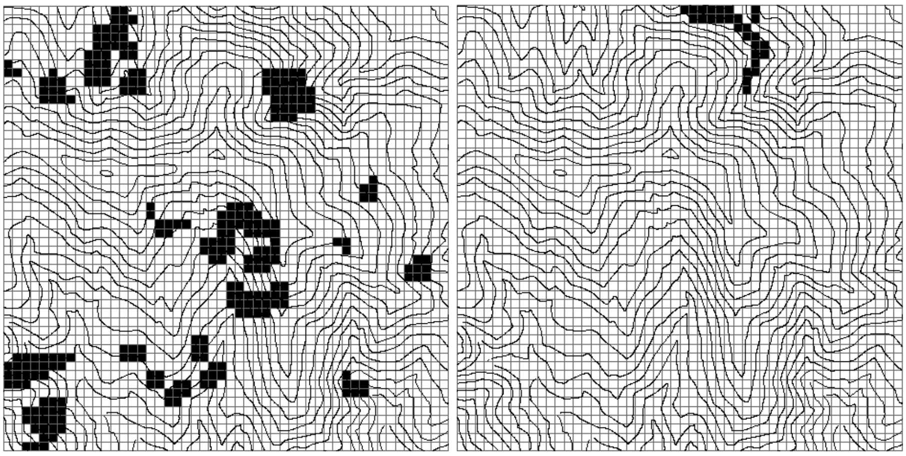
| Non-pioneer species | Dispersal mode | Life form | Pioneer species | Dispersal mode | Life form |
|---|---|---|---|---|---|
| *Euonymus laxiflorus* | Animal | S | *Clerodendrum cyrtophyllum* | Animal | C |
| *Ardisia quinquegona* | Animal | SC | *Litsea cubeba* | Animal | SC |
| *Psychotria rubra* | Animal | SC | *Trema orientalis* | Wind | C |
| *Syzygium buxifolium* | Animal | SC | *Gordonia axillaris* | Wind | C |
| *Diospyros morrisiana* | Animal | C | *Schima superba* | Wind | C |
| *Helicia formosana* | Animal | SC | *Sapium discolor* | Animal | C |
| *Cryptocarya chinensis* | Animal | C | *Mallotus paniculatus* | Wind | C |
| *Litsea acuminata* | Animal | C | *Callicarpa formosana* | Animal | SC |
| *Randia cochinchinensis* | Animal | SC | *Rhus javanica* | Animal | SC |
| *Cyclobalanopsis pachyloma* | Animal | C | *Callicarpa kochiana* | Animal | SC |
| *Ormosia formosana* | Animal | C | *Mallotus philippensis* | Animal | SC |
| *Tricalysia dubia* | Animal | SC | *Zanthoxylum ailanthoides* | Animal | SC |
| *Neolitsea aciculata* | Animal | SC | *Tetradium glabrifolium* | Animal | SC |
| *Helicia rengetiensis* | Animal | SC | *Glochidion acuminatum* | Animal | C |
| *Cinnamomum subavenium* | Animal | SC | *Trema cannabina* | Wind | SC |
| *Podocarpus nakaii* | Animal | C | *Clerodendrum trichotomum* | Animal | S |
| *Schefflera octophylla* | Animal | C | *Sapindus mukorossii* | Animal | C |
| *Pasania nantoensis* | Animal | C | *Rhus succedanea* | Animal | C |

**Appendix E.** Spatial distribution of gaps and logging road at four observation times. (a-c) Gap (black); Non- gap are (white). (d) Logging road (black); non-logging road (white). Contour lines are drawn at 10-m intervals and the quadtat size is 10 × 10 m.

a) 1998 b) 2002



c) 2007 d) 2008



■ gap □ non gap ■ logging road □ non logging road

**Appendix F.** Mann–Whitney U-tests for differences in soil properties, topographic features and disturbance regimes between pioneer and non-pioneer community types.

| Variables | Pioneer type<br>Mean ± SD (N=136) | Non-pioneer type<br>Mean ± SD (N=238) | p-level |
|---|---|---|---|
| Soil properties | | | |
| C/N ratio | 12.25 ± 1.36 | 14.42 ± 1.20 | <0.001 |
| C (cmole/kg) | 4.46 ± 1.36 | 5.87 ± 1.50 | <0.001 |
| Fe (cmole/kg) | 293.96 ± 62.55 | 338.46 ± 47.79 | <0.001 |
| Water content (%) | 15.71 ± 2.00 | 14.01 ± 2.23 | <0.001 |
| Zn (cmole/kg) | 3.56 ± 1.58 | 2.56 ± 1.01 | <0.001 |
| Cu (cmole/kg) | 0.97 ± 0.36 | 0.62 ± 0.26 | <0.001 |
| Mg (cmole/kg) | 62.34 ± 41.68 | 31.86 ± 29.03 | <0.001 |
| pH | 3.42 ± 0.22 | 3.19 ± 0.15 | <0.001 |
| Ca (cmole/kg) | 196.52 ± 170.51 | 64.40 ± 88.39 | <0.001 |
| Mn (cmole/kg) | 51.95 ± 40.70 | 10.33 ± 15.31 | <0.001 |
| K (cmole/kg) | 120.50 ± 59.72 | 104.90 ± 52.36 | <0.001 |
| N (cmole/kg) | 0.35 ± 0.08 | 0.39 ± 0.09 | <0.001 |
| Clay (%) | 14.43 ± 3.23 | 13.71 ± 2.94 | 0.006 |
| Sand (%) | 63.36 ± 5.41 | 64.43 ± 5.15 | 0.010 |
| Silt (%) | 21.92 ± 2.94 | 21.61 ± 3.00 | 0.295 |
| P | 16.51 ± 5.29 | 16.42 ± 5.02 | 0.791 |
| Topographic features | | | |
| Stream distance (m) | 27.38 ± 26.10 | 52.30 ± 27.20 | <0.001 |
| Convexity | 15.96 ± 3.36 | 18.71 ± 3.52 | <0.001 |
| Elevation (m) | 750.21 ± 29.12 | 770.77 ± 35.06 | <0.001 |
| Ridge distance (m) | 124.45 ± 65.61 | 58.67 ± 46.38 | <0.001 |
| Slope (o) | 31.65 ± 8.61 | 34.82 ± 8.35 | <0.001 |
| Disturbance regimes | | | |
| Gap2007 | 1.33 ± 0.47 | 1.13 ± 0.33 | <0.001 |
| Road | 1.07 ± 0.26 | 1.01 ± 0.11 | 0.002 |
| Gap1998 | 1.27 ± 0.45 | 1.17 ± 0.38 | 0.023 |
| Gap2002 | 1.23 ± 0.42 | 1.18 ± 0.39 | 0.318 |