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Research paper

Floristic Composition and Diversity of the Biluxi Forest Dynamics Plot

Gaung-Pu Hsieh[1, 3], Chun-Kai Hsu[1], Hsy-Yu Tzeng[3], Sheng-Zehn Yang[4], Yen-Hsueh Tseng[2, 3]

ABSTRACT

Montane cloud forests in Taiwan are strongly influenced by topographic variation and local climatic conditions, often resulting in pronounced environmental heterogeneity and vegetation variation. However, systematic baseline information on plant composition and diversity patterns at fine spatial scales in conifer–broadleaved mixed forests of the montane *Quercus* zone in central Taiwan remains limited. In this study, a 1-ha forest dynamics plot was established in the Biluxi watershed to investigate vascular plants in the tree and understory layers. We analyzed species composition, species–area curves, dominance–diversity curves, diversity indices, Raunkiær life-form spectra, shade tolerance, and seed dispersal modes. A total of 117 vascular plant species were recorded, and no naturalized species were found within the plot. The tree layer contained 49 species, with an endemism rate of 57%, whereas the understory contained 96 species, with an endemism rate of 33%. Species–area curves revealed distinct differences in species accumulation rates between the tree and understory layers. Dominance–diversity curves indicated that the tree layer was characterized by a few dominant species, whereas the understory exhibited a greater proportion of low-abundance and rare species. Phanerophytes were the predominant life form, animal dispersal was the dominant dispersal mode, and most woody species were classified as moderately shade-tolerant to shade-tolerant. The baseline floristic data established in this study provide an important reference for long-term forest dynamics monitoring and future investigations into the relationships between environmental factors and species composition.

Keywords: conifer-broadleaved mixed forest; dominance-diversity curve; dispersal mode; species composition

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[1] 林業試驗所蓮華池研究中心，555002 南投縣魚池鄉五城村華龍巷43號 Lienhuachih Research Center, Taiwan Forestry Research Institute, No. 43, Hualong Ln., Yuchi Township, Nantou County 555002, Taiwan.

[2] 林業試驗所，100051 臺北市中正區南海路53號 Taiwan Forestry Research Institute, No. 53, Nanhai Rd., Zhongzheng Dist., Taipei 100051, Taiwan.

[3] 國立中興大學森林學系，402202 臺中市南區興大路145號 Department of Forestry, National Chung Hsing University, No. 145, Hsing-Ta Rd., South Dist., Taichung City 402202, Taiwan.

[4] 國立屏東科技大學森林系，912301 屏東縣內埔鄉學府路1號 Department of Forestry, National Pingtung University of Science and Technology. No. 1, Shuefu Rd., Neipu, Pingtung County 912301 Taiwan.

通訊作者：曾彥學 Corresponding author: Yen-Hsueh Tseng, Email: tsengyh2014@tfri.gov.tw

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INTRODUCTION

Taiwan is characterized by steep topographic relief and a monsoon climate, resulting in high environmental heterogeneity and diverse forest types (Su 1984; Chiou et al. 2010). Among these forest types, montane cloud forests (MCFs), distributed at elevations of approximately 1,500–2,500 m, are persistently shaped by cloud immersion and high humidity. These forests often consist of mixed evergreen broadleaved and coniferous tree species and exhibit pronounced heterogeneity in species composition and forest structure (Li et al. 2013; Li et al. 2015). As a key component of tropical and subtropical montane biomes, cloud forests are widely recognized as among the most vulnerable and threatened forest ecosystems globally. Beyond rainfall, their hydrological input also relies heavily on cloud-water interception (Krasilnikov 2020). The formation and distribution of cloud forests are not solely constrained by elevation, but are closely associated with local microclimatic conditions, particularly the frequency of cloud immersion and ambient humidity (Fahey et al. 2016). In the mid-elevation mountain areas of Taiwan, *Quercus* montane evergreen broadleaved cloud forests frequently form mixed stands with conifers, resulting in complex plant community composition and structure (Li et al. 2013).

Forest dynamics plots enable long-term monitoring of forest structure, species composition, and regeneration dynamics through repeated tree censuses, thereby providing an essential foundation for understanding forest community dynamics and ecological mechanisms (Anderson-Teixeira et al. 2015; Davies et al. 2021). Compared with conventional temporary plot surveys, forest dynamics plots not only enable the tracking of tree life-history events and forest structural changes but also serve as important platforms for interdisciplinary research integrating plant ecology, soil ecology, fauna, and microclimate.

Several forest dynamics plots have been established in Taiwan's montane cloud forests. For example, the Yuanyang Lake plot (Chou et al. 2000; Lai et al. 2006) and the Lala Mountain plot (Chen et al. 2024) represent *Chamaecyparis* montane mixed cloud forests, whereas the Beidongyan Mountain plot (Song et al. 2010; Hu and Tzeng 2019) and the Nantzuhsienhsi plot (Yang et al. 2008) are located within *Quercus* montane evergreen broadleaved cloud forests. Although these studies have accumulated data on forest composition and dynamics of Taiwan's cloud forests, they have focused primarily on *Chamaecyparis* forest types or evergreen broadleaved cloud forests. Accordingly, there is a lack of systematic forest dynamics plot studies on the plant community composition and structural characteristics of conifer–broadleaved mixed forests in the *Quercus* forest zone of central Taiwan.

The present study established a 1-ha forest dynamics plot in the Biluxi area of central Taiwan to generate baseline ecological data and characterize its floristic composition and community attributes. The objectives of this study were to: (1) clarify the floristic composition of the Biluxi Forest Dynamics Plot (BFDP) and evaluate species accumulation trends and plot representativeness using species–area curves (SAC); (2) describe the characteristics of species diversity and dominance distribution in the forest; and (3) analyze plant ecological traits including the Raunkiær life-form spectrum, dispersal mode, and shade tolerance, to provide a foundation for subsequent long-term monitoring and comparative studies.

MATERIALS AND METHODS

Study site

The Biluxi Forest Dynamics Plot (BFDP) (24°13′ N, 121°18′ E; 2,137–2,208 m a.s.l.) is in the Biluxi watershed, which has a total area of approximately 5,310 ha. The plot lies on a southwestward-extending spur ridge descending from Northern Mt. Pilu of the Central Mountain Range (Figure 1A), within the boundaries of Taroko National Park. Its eastern edge borders Biluxi Stream, an important upstream tributary of the Dajia River. The terrain drops steeply from west to east, with slopes dipping eastward toward the Biluxi Stream bank. According to the geoclimatic regionalization of Taiwan defined by Su (1985), the study site falls within the central west inland region and is of the summer rain type. The ecoclimatic diagram of the study area (Figure 1B; Piluxi Meteorological Station, elevation 2,100 m a.s.l.) shows that the mean annual temperature from 1972 to 2025 was 13.9℃, with the lowest and highest monthly mean temperatures recorded in January (6.4℃) and July (16.4℃), respectively. Mean annual precipitation over that period was approximately 2,967 mm, with no distinct dry season throughout the year. Rainfall was concentrated from June to August, mainly driven by plum rains and typhoons, whereas November to the following January was relatively dry. Geologically, the Biluxi watershed belongs to the Central Backbone Range geologic province and is underlain by the Miocene Lushan Formation, which consists mainly of interbedded black-to-dark-gray argillite, slate, phyllite, and dark gray graywacke (Ho 1986).

Sampling design

The boundaries of the entire plot and all quadrats were demarcated in February 2025, and the first woody plant census was completed in May of the same year. The woody plant survey and census protocols were implemented primarily in accordance with the tree census standards of the Forest Global Earth Observatory (ForestGEO) (Condit et al. 2014). The 1-ha plot was accurately laid out in the field and divided into 100 quadrats of 10 m × 10 m each. The principal axis of the BFDP was oriented due north. Quadrat corners were assigned coordinate codes, starting at (0, 0) at the plot's southwestern corner and ending at (10, 10) at its northeastern corner.

Floristic composition

The vegetation survey in the plot was stratified into the tree layer and the understory. All woody plant individuals (excluding lianas) with diameter at breast height (DBH) ≥ 1 cm in each quadrat were assigned to the tree layer and identified to species level. Herbaceous plants, ferns, lianas, and woody plants with DBH < 1 cm were classified as the understory. Plant nomenclature primarily followed the second edition of the *Flora of Taiwan* (Huang and Hsieh 2003), and the taxonomic classification system followed APG IV (The Angiosperm Phylogeny Group 2016). The conservation status of species in the plot was assessed according to the *2017 Red List of Vascular Plants of Taiwan* (Editorial Committee of the Red List of Taiwan Plants 2017). The identification of naturalized plants followed the criteria established by Wu et al. (2004) and Chang-Yang et al. (2022).

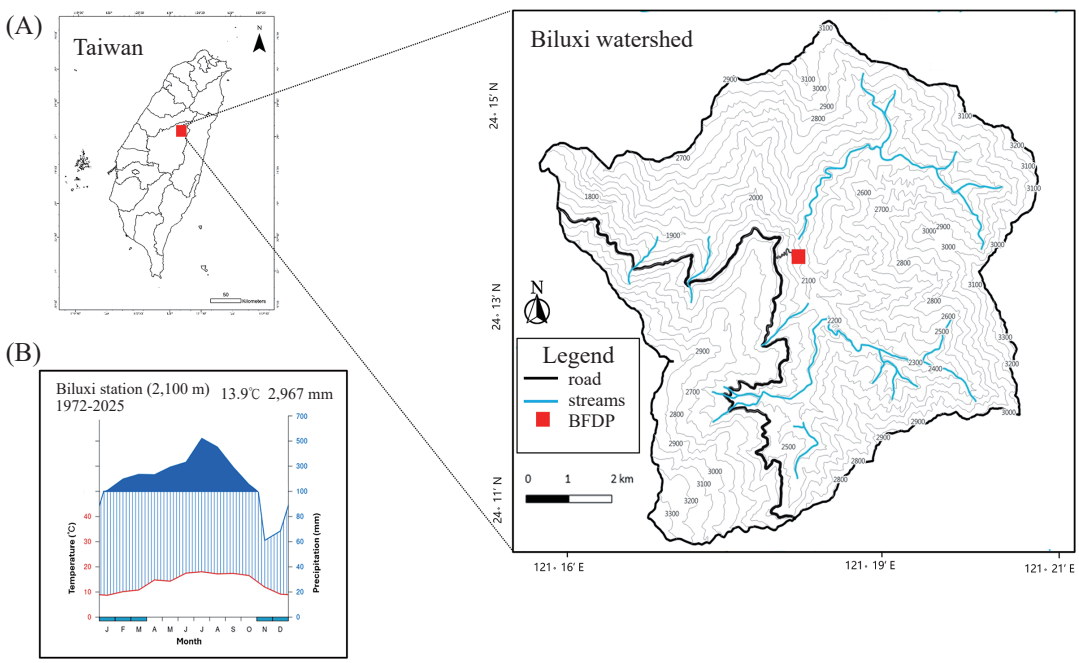

Figure 1. Location of the Biluxi Forest Dynamics Plot (BFDP). (A) Geographic location of the study area in Taiwan and the Biluxi watershed showing the location of the 1-ha forest dynamics plot (red box). (B) Climatic diagram of the Biluxi station (2,100 m a.s.l.) based on long-term records (1972–2025). The red line represents monthly mean temperature (℃), and the blue line represents monthly precipitation (mm).

Species–area curves

To compare species accumulation patterns between the tree layer and the understory, quadrats were used as sampling units, and analysis was performed using species–area curves (SAC). To reduce the effect of quadrat ordering on the cumulative number of species, quadrat order was subjected to 100 random permutations. In each permutation, quadrats were added sequentially without replacement, and the cumulative number of species at each cumulative area was calculated. The final SACs were plotted using the mean cumulative number of species from the 100 random permutations, with the 2.5th and 97.5th percentiles for each cumulative area used to construct the 95% confidence intervals. When the cumulative number of species reaches approximately 90% of the expected total, sampling is commonly considered adequate (Moreno and Halffter 2000; Willott 2001). However, SACs generally plateau once they approach 90% of the total number of species, making it difficult to distinguish differences in accumulation rates among vegetation layers. Therefore, this study adopted the area required to reach 80% of the total number of species as the saturation threshold to compare species accumulation patterns between the tree layer and the understory.

Dominance–diversity curves

To evaluate community structure and species dominance patterns, dominance–diversity curves were constructed using quadrats as sampling units. For the tree layer,

the relative dominance of each species was calculated from basal area (BA), whereas for the understory, relative abundance was calculated based on cover. To ensure a comparable scale across the two vegetation layers, each species value was standardized by dividing by the total value of its respective layer, converting it to a relative proportion within the layer. Species were then ranked in descending order of relative dominance (or relative abundance), and the relationship between species rank and relative dominance was plotted on a logarithmic scale (Whittaker 1965; Magurran 2004). The slope and shape of the resulting curves reflect community structure, the distribution of dominant species, and differences in species diversity.

Species diversity indices

To characterize species diversity in the plot, species richness, the Shannon–Wiener index (H'), Pielou's evenness (J), and Fisher's α diversity index were calculated for each quadrat. Species richness was defined as the number of species in each quadrat. The formulas for the remaining three indices were as follows:

Shannon–Wiener index (H'):

$$H' = -\sum_{i=1}^{S} P_i \ln(P_i)$$

where P_i is the relative abundance of species i (n_i/N); n_i is the number of individuals of species i; and N is the total number of individuals of all species.

Pielou's evenness (J):

$$J = \frac{H'}{\ln(S)}$$

where H' is the Shannon–Wiener index and S is the number of species.

Fisher's α diversity index:

$$S = \alpha \ln\left(1 + \frac{N}{\alpha}\right)$$

where S is the number of species, N is the total number of individuals of all species, and α is Fisher's α diversity parameter (Fisher et al. 1943).

Fruit types and dispersal modes

To characterize the functional composition of the vegetation in the plot, fruit types and dispersal modes of all vascular plant species were compiled as part of the baseline data for vegetation composition and flora. Dispersal modes were classified based on the primary dispersal mechanism of each species. For species exhibiting secondary dispersal, only the primary mode was adopted for classification. Fruit types were classified exclusively for angiosperms. Ferns and gymnosperms were excluded from fruit type classification, as they do not develop fruits from the ovary (Yang et al. 2011; Chen et al. 2017).

Dispersal modes of seed plants were determined primarily based on fruit type, seed traits, and published literature records (van der Pijl 1982; Cornelissen et al. 2003). Seed plants in the plot were classified into six dispersal types: anemochory, endozoochory, epizoochory, hoarding, barochory, and ballochory.

Evaluation of tree species shade tolerance

In this study, the shade tolerance of tree species was assessed using the classification system for native woody plants of Taiwan developed by Kuo et al. (2021). In that study, 440 woody plant species were quantified for physiological traits, including photosynthetic capacity (A_{max}), and classified into five classes: very intolerant (I), intolerant (II), moderately tolerant (III), tolerant (IV), and very tolerant (V). Tree species not covered

in the dataset of Kuo et al. (2021) were conservatively classified using the overall family-level shade-tolerance trends proposed in that study. For example, species in the Rosaceae were assigned to Class III, while species in the Fagaceae and Lauraceae were assigned to Class IV, to maintain classification consistency.

Plant life-form spectrum

Plant species were classified into five types following the Raunkiær life-form classification system (Raunkiær 1934): (1) Phanerophytes (P): perennial plants with negatively geotropic stems or branch apices, including trees and shrubs; (2) Chamaephytes (Ch): plants with perennating buds on shoots close to the ground surface (usually no more than 25 cm), such as dwarf shrubs and subshrubs; their vegetative shoots and flowering axes are negatively geotropic and produce flowers only during the growing season; (3) Hemicryptophytes (H): plants with perennating buds at the soil surface, where they are protected by winter snow, litter and soil, including most biennial and perennial herbs; (4) Geophytes (G): plants with perennating buds completely buried in the soil, protected by soil during unfavorable seasons; (5) Therophytes (T): plants without perennating buds, which complete their life cycle within a very short growing season and survive unfavorable seasons as dormant seeds. The proportion of species in each life-form type was calculated to plot the Raunkiær life-form spectrum.

RESULTS

Vascular plant composition

A total of 117 vascular plant species from 56 families and 89 genera were recorded in the Biluxi Forest Dynamics Plot (BFDP), including 44 endemic species. No naturalized plants were found in the plot. The recorded flora included 18 fern species in 8 families and 15 genera, 6 gymnosperm species in 2 families and 5 genera, 85 dicotyledonous angiosperm species in 41 families and 62 genera, and 8 monocotyledonous angiosperm species in 5 families and 7 genera.

A total of 2,379 woody plant individuals were recorded in the tree layer, belonging to 23 families, 32 genera, and 49 species. Among them, 28 were endemic species, accounting for 57% of all tree layer species. The families ranked by number of species in descending order were Pinaceae (5 species, 4 genera), Adoxaceae (4 species, 1 genus), Ericaceae (4 species, 2 genera), and Fagaceae (4 species, 2 genera). The five most dominant tree species in the plot were *Quercus stenophylloides* Hayata, *Pinus taiwanensis* Hayata, *Eurya leptophylla* Hayata, *Pseudotsuga wilsoniana* Hayata, and *Rhododendron leptosanthum* Hayata.

A total of 96 vascular plant species from 50 families and 77 genera were recorded in the understory survey, including 32 endemic species, accounting for 33% of the understory total. Among these, 18 fern species in 8 families and 15 genera were documented, along with 70 dicotyledonous seed plant species in 37 families and 55 genera, and 8 monocotyledonous species in 5 families and 7 genera. The families ranked by number of species in descending order were Rosaceae (7 species, 2 genera), Polypodiaceae (6 species, 4 genera), Araliaceae (5 species, 5 genera), and Adoxaceae (5 species, 2 genera). A total of 28 tree species in 15 families and 19 genera were shared between the tree layer and the understory.

Based on the threatened status criteria of the *2017 Red List of Vascular Plants*

of Taiwan, only one species in the plot, *Euonymus huangii* H.Y. Liu & Y.P. Yang, was assessed as Critically Endangered (CR); one species, *Taxus sumatrana* (Miq.) de Laub., was assessed as Endangered (EN); and two species, *Mahonia oiwakensis* Hayata and *Pittosporum illicioides* Makino var. *angustifolium* Huang ex S.Y. Lu, were assessed as Vulnerable (VU).

Species–area curves

The species–area curves (SAC) showed distinct differences in species accumulation patterns between the tree layer and the understory (Figure 2A). As the sampled area increased from 0.1 ha to 1 ha, cumulative number of species in the tree layer increased from approximately 20 to 49, whereas that in the understory increased from approximately 40 to 96. Using the cumulative area required to reach 80% of the total number of species as the saturation threshold, the tree layer reached this threshold at approximately 0.3 ha, whereas the understory required approximately 0.45 ha.

Dominance–diversity curves

The dominance–diversity curve of the Biluxi Forest Dynamics Plot (BFDP) exhibited a pronounced hierarchical pattern of species dominance (Figure 2B). In the tree layer, the initial segment of the curve declined steeply, indicating that the community structure was dominated by a few dominant species. The curve then gradually leveled off, forming a long-tailed distribution composed of numerous rare species. In contrast, the understory curve declined more gradually, indicating a more even distribution of species dominance and smaller differences in dominance among species. Beyond the 40th rank, however, the curve showed a distinct long-tailed pattern, reflecting the presence of a large number of low-abundance species in this layer.

Species diversity indices

In terms of species richness, values per quadrat in the tree layer (Figure 3A) generally ranged from approximately 5–15

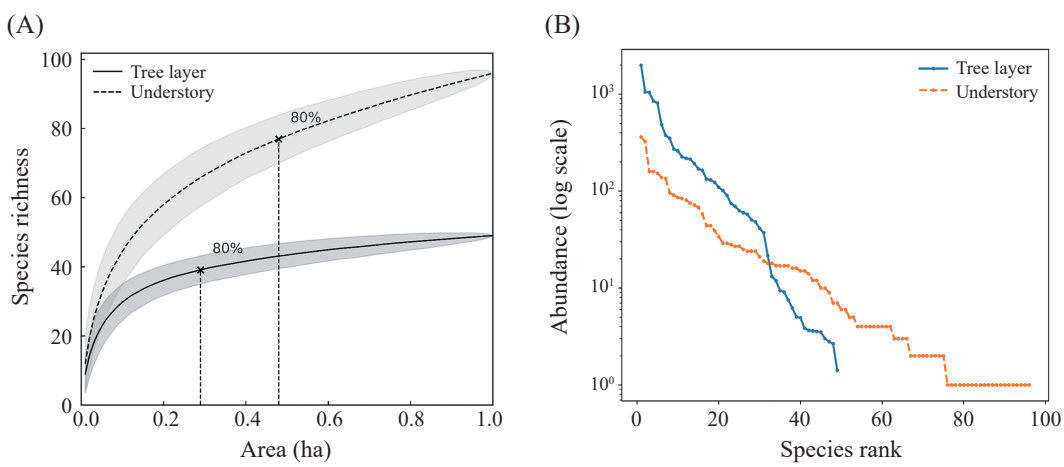

Figure 2. (A) Species–area curves for tree layer and understory vegetation. Shaded areas indicate 95% confidence intervals; dashed lines denote the area required to reach 80% of observed species richness. (B) Dominance–diversity curves for the tree layer (red) and understory layer (blue) in the BFDP.

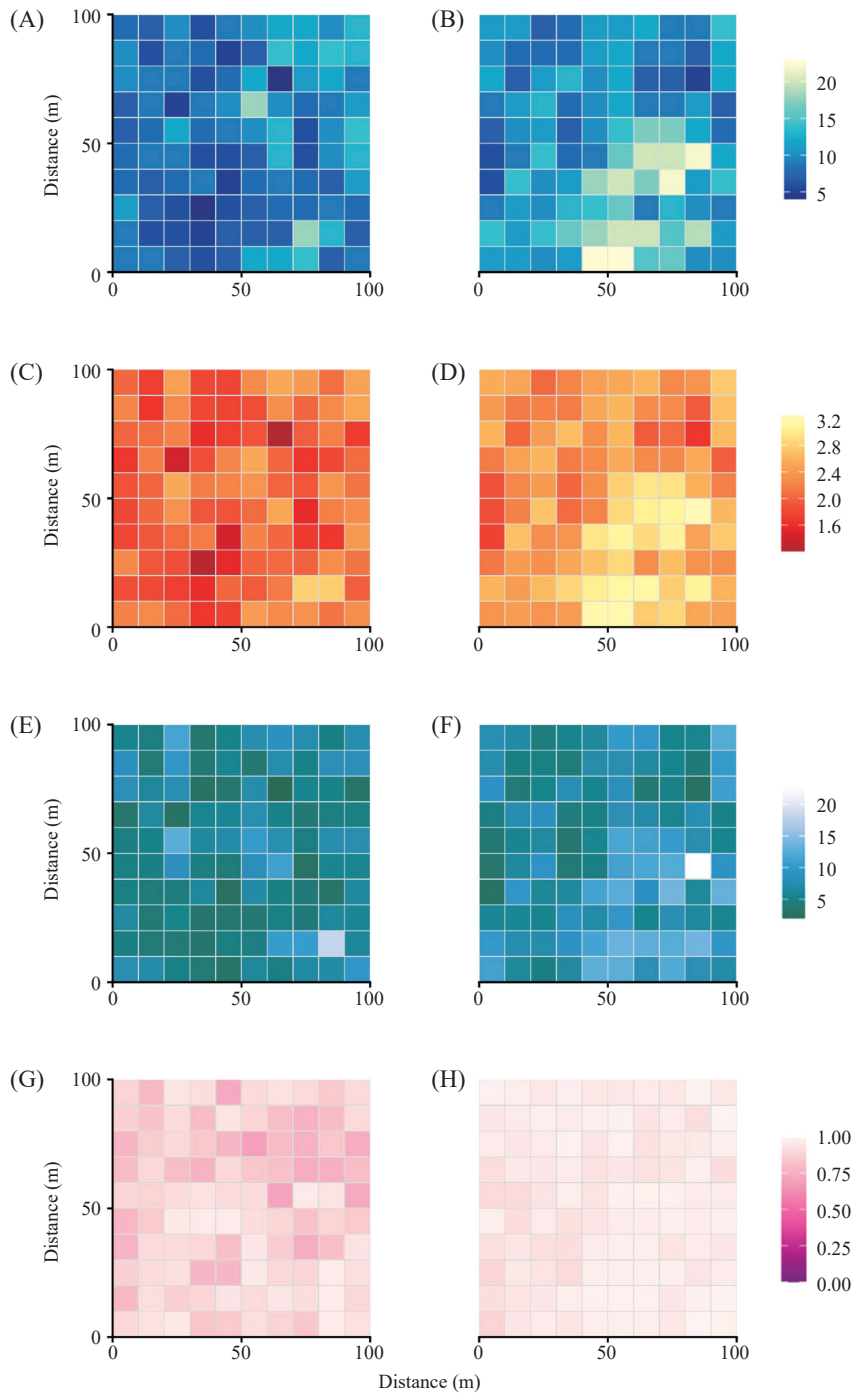

Figure 3. Spatial distributions of four diversity indices for the tree layer and the understory at the BFDP (10 m × 10 m subplots). (A, C, E, G) Tree layer: Species richness, Shannon–Wiener index (*H′*), Fisher's *α*, and Pielou's evenness index (*J*). (B, D, F, H) Understory: Species richness, Shannon–Wiener index (*H′*), Fisher's *α*, and Pielou's evenness index (*J*). Color gradients represent index values among subplots.

species. In contrast, the understory (Figure 3B) had higher overall species richness, with most quadrats containing approximately 10–20 species and several quadrats showing particularly high species richness.

The Shannon–Wiener index ranged from approximately 1.6–2.8 in the tree layer (Figure 3C). In the understory (Figure 3D), Shannon–Wiener index values were generally higher, with values in most quadrats ranging from 2.0–3.2 and several quadrats showing relatively high diversity values. Fisher's α values ranged from 5–12 in the tree layer (Figure 3E) and from 8–20 in the understory (Figure 3F).

Pielou's evenness (*J*) remained within a relatively high range in both the tree layer (Figure 3G) and the understory (Figure 3H). Most values in the tree layer ranged from 0.7–0.9, whereas those in the understory were generally close to 0.9–1.0, indicating a relatively even distribution of species dominance.

Dispersal modes

For the 49 tree species in the BFDP, the dominant fruit types were seed cones, berries, and drupes. In terms of seed dispersal modes, endozoochory within the zoochory category was the most frequent type (29 species), followed by anemochory (16 species) (Figure 4A), and a few other species (4 species) were classified as hoarding. After excluding ferns from the 96 understory species, the

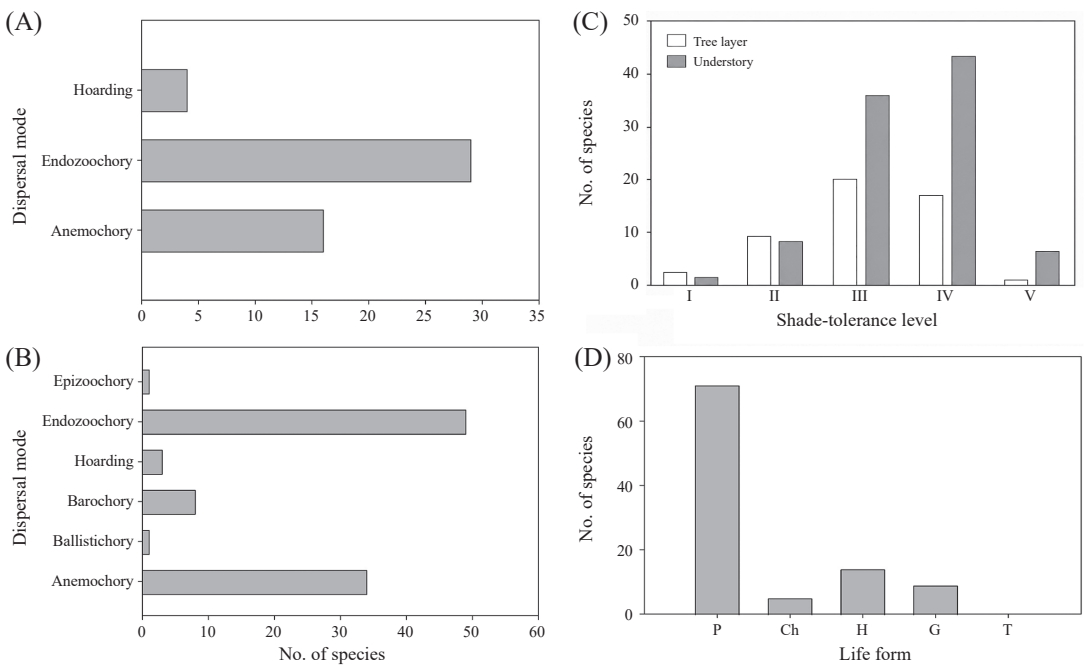

Figure 4. Seed dispersal modes of tree layer (A) and understory species (B) in the BFDP. Horizontal bar charts show the number of species belonging to each dispersal mode. (C) Species richness across five shade-tolerance levels (I–V) for the tree layer (white bars) and understory (gray bars). Both layers showed the highest species richness at intermediate shade-tolerance levels (III–IV), whereas relatively few species occurred at levels I and V. (D) The number of individuals for each Raunkiær life-form category is shown. P, phanerophytes; Ch, chamaephytes; H, hemicryptophytes; G, geophytes; T: therophytes.

remaining 78 seed plant species had dominant fruit types of berries, drupes, and capsules. Dispersal modes were clearly dominated by zoochory, accounting for 50 species: 49 with endozoochory and 1 with epizoochory. In total, zoochory accounted for 64.1% of understory seed plant species, followed by anemochory with 34 species (Figure 4B).

Evaluation of tree species shade tolerance

The distribution of tree species across shade-tolerance classes was generally consistent between the tree layer and the understory, peaking in the intermediate-high tolerance classes (Figure 4C). The highest number of species was recorded for Classes III and IV (intermediate to high tolerance), while the lowest was recorded for Class V (very tolerant) and Class I (very intolerant).

Overall, most tree species in the Biluxi forest were classified as moderately tolerant to tolerant. However, only one tree species in the tree layer fell into the very tolerant category (Class V), showing that very shade-tolerant species were relatively scarce in the tree layer. In contrast, the understory had more species than the tree layer across all shade-tolerance classes, with the most pronounced gap in Classes III and IV, indicating higher fitness and diversity of understory tree species in shaded, humid, low-light environments.

Plant life-form spectrum

The Raunkiær life-form spectrum of the plot was dominated by phanerophytes (P) with the highest number of species (71 species), and all tree layer species fell into this category (Figure 4D). Hemicryptophytes (H) were the second most species-rich group with 14 species, followed by geophytes (G) with 9 species and chamaephytes (Ch) with 5 species. No therophytes (T) were recorded in the plot.

DISCUSSION

Floristic composition

Conifer–broadleaved mixed forests are forest types where coniferous and broadleaved tree species jointly occupy a prominent position in the upper canopy of the stand. They commonly occur in ecotones between different climatic and vegetation zones, yet their delimitation is generally descriptive rather than based on a fixed proportional threshold (Su 1984; Walter 1985; Li et al. 2013). The results of this study showed that the tree layer of the Biluxi Forest Dynamics Plot (BFDP) was dominated by Fagaceae and various evergreen broadleaved tree species. Large-diameter individuals of *P. taiwanensis*, *Pseudotsuga wilsoniana* Hayata, *Picea morrisonicola* Hayata, and *Tsuga chinensis* (Franchet) Pritz. *ex* Diels var. *formosana* (Hayata) H.L. Li & H. Keng were also distributed in the plot. Overall, its floristic composition and structural features were consistent with the upper *Quercus* forest zone delimited by Su (1984). Under the vegetation classification framework of Li et al. (2013), it can be classified as a *Quercus* montane evergreen broadleaved cloud forest.

No naturalized plants were recorded in the plot, which is consistent with the elevational distribution pattern of naturalized plants in Taiwan. Wu et al. (2004) reported that most naturalized plant species in Taiwan are concentrated in low-elevation, highly disturbed habitats such as agricultural field margins, urban green spaces, and roadsides. In mid-elevation mountain areas (1,500–2,500 m), by contrast, the likelihood of non-native species establishment and invasion is markedly reduced due to the cool climate, relatively undisturbed habitats, and limited anthropogenic disturbance. Due to their cool,

humid climate, low light availability, nutrient-limited soils, and topographic isolation, cloud forests are recognized as one of the forest ecosystems with the lowest levels of plant invasion worldwide (Hamilton et al. 1995; Feeley et al. 2011).

Dominance and species diversity

The species–area curves (SACs) (Figure 2A) showed that, when compared using the 80% species saturation threshold, the tree layer required only approximately 0.30 ha to reach accumulation of most species, whereas the understory required approximately 0.45 ha to attain the same saturation level. This result indicates that the understory exhibits greater heterogeneity in species composition and supports a greater number of rare species, thus requiring a larger sampling area to fully capture its species diversity. This phenomenon is commonly explained by the understory having a larger regional species pool, typically composed of many low-dominance species and exhibiting a long-tailed distribution (He and Legendre 1996).

The dominance–diversity curves also revealed distinct differences between the tree layer and the understory (Figure 2B). In the tree layer, the top five dominant species accounted for 57% of total dominance, driving the steep initial decline of the curve. This pattern reflects that a small number of dominant species occupy most resources and shape the vegetation's physiognomic structure, representing a classic dominance hierarchy (Magurran 2004). In contrast, *E. leptophylla* was overwhelmingly dominant in the understory, while most species that were ranked below the 40th position had low cover and low occurrence frequency, forming a distinct long-tailed distribution. These species were mostly small herbaceous plants, including *Oxalis acetosella* L. subsp. *griffithii* (Edgew. & Hook. f.) Hara, *Ellisiophyllum pinnatum* (Wall. *ex* Benth.) Makino, *Peperomia reflexa* Kunth, and *Rubia lanceolata* Hayata.

The results showed that species diversity indices of both the tree layer and the understory varied across quadrats. Some quadrats with high species diversity and high evenness were concentrated in the southern and southeastern parts of the plot. Even within the small spatial scale of the 1-ha plot, species diversity still differed among quadrats, which may reflect the effects of microtopography, light environment, and local habitat heterogeneity on plant composition. However, this study presented only spatial visualizations of diversity indices at the quadrat scale, and no further spatial statistical analyses were conducted. Accordingly, the associated spatial distribution characteristics remain to be verified by follow-up studies.

Topographic heterogeneity is widely recognized as a potential factor that enhances tree species richness at small spatial scales, with species composition varying along topographic gradients, for example, from ridges to valleys and from hilltops to depressions (Enoki 2003; Masaki et al. 2007; Hortal et al. 2009; Irl et al. 2015). The spatial variation in species diversity observed in this study is most likely driven by environmental heterogeneity, particularly topographic factors. Future analyses incorporating environmental variables will help clarify the factors shaping species diversity patterns in the study area.

Dispersal modes and shade tolerance

Differences in plant diversity between the tree layer and the understory may be related to dispersal modes. Seed dispersal modes are recognized as key factors shaping plant dispersal capacity and regeneration

opportunities, and further influence community composition and species distribution patterns (Howe and Smallwood 1982; Nathan and Muller-Landau 2000). In the tree layer, 29 species with endozoochory were recorded (Figure 4A), most bearing small berries or drupes, indicating that their seeds are primarily dispersed by birds. Sixteen species were anemochorous, among which 11 (69%) were dominant canopy tree species. A similar trend was observed in the understory, suggesting that dispersal strategies may be consistent across plants of different life forms.

These findings are similar to those reported in other temperate forest studies. For example, approximately 70% of woody plant species in Chilean temperate rainforests are bird-dispersed, while 85.7% of canopy tree species are anemochorous (Armesto and Rozzi 1989). Similarly, in the subhumid temperate forests of Mexico, approximately 68% of woody plant species are zoochorous, and 32% are anemochorous (Cortés-Flores et al. 2013). Overall, montane forest plants commonly show a high proportion of fleshy fruits and zoochorous species, while canopy tree species tend toward anemochory.

The shade tolerance analysis of 440 native woody plant species in Taiwan by Kuo et al. (2021) provided an important and reliable reference basis for the shade tolerance classification in this study. Differences in light requirements and light environment responses among tree species reflect their leaf functional trait strategies, and these differences profoundly affect seedling survival, individual growth, and interspecific competition, thus serving as key drivers regulating forest regeneration, community structure, and successional stage transitions (Swaine and Whitmore 1988; Falster et al. 2017). We also observed that only 11 species in the tree layer were classified as pioneer or light-demanding tree species, including *P. taiwanensis*, *P. morrisonicola*, and *Alnus formosana* (Burkill) Makino, accounting for only 22% of all tree species. This indicates that stand composition is dominated by tree species with relatively high shade tolerance. According to forest succession and functional trait theories, pioneer species generally dominate during early successional stages, whereas shade-tolerant species gradually increase in abundance and come to dominate stand structure as the forest canopy closes and resource competition intensifies, reflecting the progression of forest communities from early to mid- and late-successional stages (Niinemets and Valladares 2006). Therefore, the low proportion of pioneer tree species observed in the tree layer of the Biluxi Forest Dynamics Plot (BFDP) aligns with the compositional features of mid- to late-successional forests.

Plant life-form spectrum

Plant life forms reflect plants' adaptive strategies in response to environmental conditions, particularly the position of perennating buds and their strategies for tolerating unfavorable conditions. As such, they are widely used to characterize the overall response of plant communities to climatic conditions (Ellenberg 1988). In the BFDP, the tree layer consisted entirely of phanerophytes, whereas the understory was dominated by hemicryptophytes and chamaephytes. Montane forests typically harbor a high proportion of near-ground life forms under cool, shaded, and humid conditions (Kitayama 1992; Körner 2003), and the results of this study align well with this documented pattern.

CONCLUSIONS

A 1-ha forest dynamics plot was established in the Biluxi watershed of central Taiwan to systematically characterize the floristic composition and diversity of a conifer–broadleaved mixed cloud forest in the *Quercus* forest zone. The results reveal distinct differences between the tree layer and the understory in species accumulation rates and dominance structure. The tree layer exhibited a hierarchical dominance pattern and relatively homogeneous species distribution, while the understory supported higher species diversity. Most species fell along the spectrum from moderately tolerant to tolerant, and the low proportion of pioneer and light-demanding tree species indicates that the forest has reached a mid- to late-successional stage. Differences in dispersal modes and shade-tolerance composition across vegetation layers reflect divergent regeneration strategies. The baseline vegetation data generated in this study provide a critical foundation for future research integrating environmental factors and spatial analyses to further explore the mechanisms underlying species assembly and forest dynamics in montane cloud forests.

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研究報告

碧綠溪森林動態樣區之植相組成與多樣性

謝光普[1, 3]、許俊凱[1]、曾喜育[3]、楊勝任[4]、曾彥學[2, 3]

摘 要

臺灣山地雲霧林受地形起伏與局部氣候條件影響，常形成顯著之環境異質性與植群變異。然而，中部櫟林帶針闊葉混合林於小尺度下之植物組成與多樣性特徵，仍缺乏系統性的基礎資料。本研究於碧綠溪集水區建立1 ha森林動態樣區，調查喬木層與地被層維管束植物，並分析其物種組成、物種–面積曲線、優勢度–多樣性曲線、物種多樣性指數、Raunkiær生活型譜、植物耐陰性及種實傳播方式等特徵。結果共記錄117種維管束植物，樣區內未發現歸化植物；其中喬木層49種(特有率57%)，地被層96種(特有率33%)。物種–面積曲線顯示，喬木層與地被層在物種累積速率上具有明顯差異。優勢度–多樣性曲線顯示，喬木層由少數優勢種主導，地被層則呈現較多低豐度與稀有物種。植物生活型以挺空植物為主，種實傳播方式以動物傳播占優勢，多數木本植物屬中度耐陰至耐陰類型。本研究建立之基礎生態資料，可作為未來森林動態監測，以及探討環境因子與物種組成關係之參考依據。

關鍵詞：針闊葉混合林、優勢度–多樣性曲線、傳播型、物種組成

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[1] 林業試驗所蓮華池研究中心，555002 南投縣魚池鄉五城村華龍巷43號 Lienhuachih Research Center, Taiwan Forestry Research Institute, No. 43, Hualong Ln., Yuchi Township, Nantou County 555002, Taiwan.

[2] 林業試驗所，100051 臺北市中正區南海路53號 Taiwan Forestry Research Institute, No. 53, Nanhai Rd., Zhongzheng Dist., Taipei 100051, Taiwan.

[3] 國立中興大學森林學系，402202 臺中市南區興大路145號 Department of Forestry, National Chung-Hsing University, No. 145, Hsing-Ta Rd., South Dist., Taichung City, 402202, Taiwan.

[4] 國立屏東科技大學森林系，912301 屏東縣內埔鄉學府路1號 Department of Forestry, National Pingtung University of Science and Technology. No. 1, Shuefu Rd., Neipu, Pingtung County. 912301 Taiwan.

通訊作者：曾彥學 Corresponding author: Yen-Hsueh Tseng, Email: tsengyh2014@tfri.gov.tw

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緒言

臺灣受劇烈地形起伏與季風氣候影響，形成高度的環境異質性與多樣化森林植群(Su 1984; Chiou et al. 2010)。其中，海拔約1,500–2,500 m之山地雲霧林(montane cloud forests, MCF)長期受雲霧覆蓋與高濕環境影響，形成由常綠闊葉樹與針葉樹混生之森林類型，並在物種組成與森林結構上表現出高度異質性(Li et al. 2013; Li et al. 2015)。雲霧林為熱帶與亞熱帶山地生物群系的重要組成之一，亦被視為全球最脆弱且最受威脅的森林生態系，其水分來源除降雨外，亦高度依賴霧水截留作用(Krasilnikov 2020)。雲霧林之形成與分布並非僅受海拔限制，而與局部微氣候條件，特別是雲霧出現頻率與濕度環境密切相關(Fahey et al. 2016)。在臺灣中海拔山區，櫟屬山地常綠闊葉雲霧林(*Quercus* montane evergreen broad-leaved cloud forest)常與針葉樹形成混合林分，呈現複雜的植群組成與結構(Li et al. 2013)。

森林動態樣區(forest dynamics plot)透過定期每木複查，可長期監測森林結構、物種組成與更新動態，為理解森林群落變遷與生態機制提供重要基礎(Anderson-Teixeira et al. 2015; Davies et al. 2021)。相較於傳統臨時樣區調查，森林動態樣區不僅能追蹤林木生活史事件與森林結構變化，亦可作為整合植物生態、土壤生態、動物相與微氣候等跨領域研究的重要平台。

臺灣山地雲霧林已建立多處森林動態樣區，例如鴛鴦湖(Chou et al. 2000; Lai et al. 2006)與拉拉山(Chen et al. 2024)代表扁柏山地混合雲霧林(*Chamaecyparis* montane mixed cloud forest)，而北東眼山(Song et al. 2010; Hu and Tzeng 2019)與楠梓仙溪(Yang et al. 2008)則位於櫟屬山地常綠闊葉雲霧林。這些研究已累積臺灣雲霧林之森林組成與動態資料，但多集中於扁柏林型或常綠闊葉雲霧林，對於臺灣中部山區櫟林帶針闊葉混合林之植群組成與結構特徵，仍缺乏系統性之森林動態樣區研究。

本研究於臺灣中部碧綠溪地區新設置 1 ha森林動態樣區，以建立樣區之基礎生態資料，並掌握森林植物組成與特徵。研究目的為：(1) 釐清碧綠溪森林動態樣區之植物組成，並利用物種-面積曲線評估物種累積趨勢與樣區代表性；(2) 描述森林之物種多樣性與優勢分布特徵；(3)分析植物生活型、種實傳播方式與耐陰性等生態特徵，以作為後續長期監測及比較之基礎。

材料與方法

研究地點

碧綠溪森林動態樣區(Biluxi Forest Dynamics Plot, BFDP; (24°13' N, 121°18' E, 海拔 2,137–2,208 m a.s.l.)位於碧綠溪集水區內，集水區總面積約為5,310 ha。樣區座落於中央山脈北畢祿山向西南延伸的支稜上(Figure 1A)，地處太魯閣國家公園範圍之內，樣區東側緊鄰碧綠溪，為大甲溪上游的重要支流。樣區地勢由西向東陡降，坡度往碧綠溪畔向東傾斜。根據Su (1985)對臺灣地理氣候區的劃分，研究地點位於中西部內陸區(central west inland region)，屬於夏雨型氣候(summer rain type)。研究區的生態氣候圖顯示(Figure 1B；碧綠溪氣象站; alt. 2,100 m)，1972-2025年的年平均氣溫為13.9℃，最低月均溫與最高月溫分別是1月(6.4℃)和7月(16.4℃)；年均降雨量約2,967 mm，全年無乾季，降雨量集中在6月至8月，主要受到梅雨及颱風影響，11月至翌年1月為相對濕潤期。碧綠溪流域屬於中央脊樑山脈地質區，地層為中新世的廬山層，大部分由黑色到深灰色的硬頁岩、板岩及千枚岩與深灰色的硬砂岩互層組成(Ho 1986)。

取樣設計

2025年2月確立樣區及所有樣方(quadrat)的邊界，並於同年5月完成首次木本植物普查。木本植物之調查與普查程序主要參考全球森林地球觀測網絡(ForestGEO)之樹木普查規範進行(Condit et al. 2014)，於現地準確放樣1 ha樣區範圍，並分為100個10 m × 10 m的樣方。BFDP 主軸的方向為北方，樣方的角落按照座標編碼，從西南角的 (0,0) 開始，到東北角的 (10,10)結束。

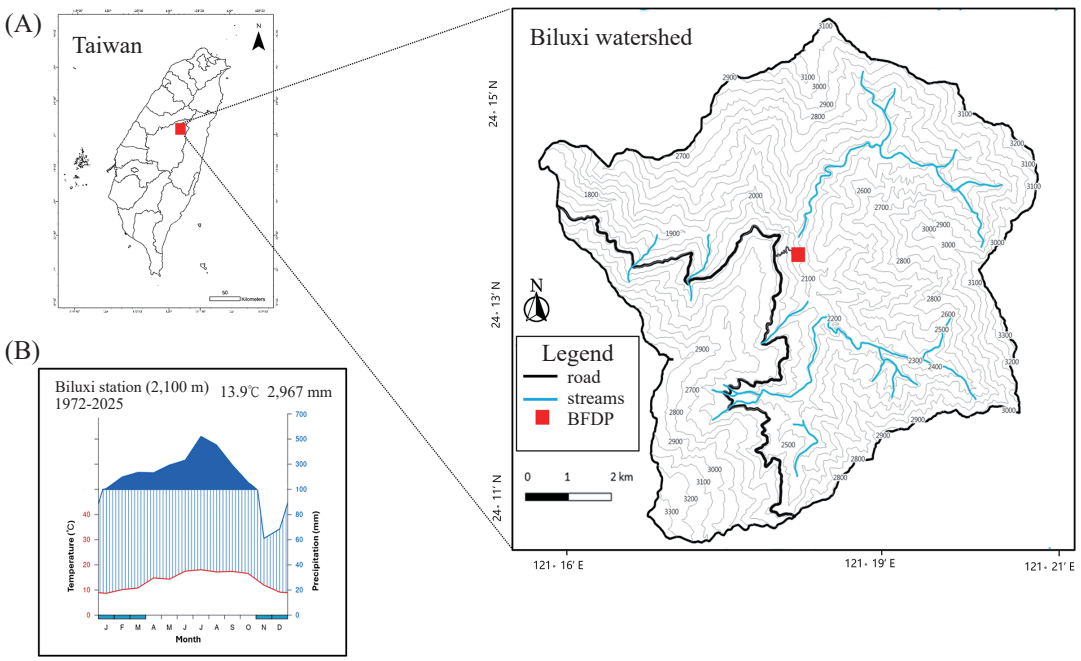

Figure 1. Location of the Biluxi Forest Dynamics Plot (BFDP). (A) Geographic location of the study area in Taiwan and the Biluxi watershed showing the location of the 1-ha forest dynamics plot (red box). (B) Climatic diagram of the Biluxi station (2,100 m a.s.l.) based on long-term records (1972–2025). The red line represents monthly mean temperature (℃), and the blue line represents monthly precipitation (mm).

植相組成

樣區內植物調查區分為喬木層(tree layer)與地被層(understory)。樣方內所有胸高直徑(diameter at breast height, DBH) ≥ 1 cm的木本植物個體(不含藤本)均列為喬木層，並鑑定至種的層級。草本植物、蕨類植物、藤本植物及DBH < 1 cm 的木本植物則歸類為地被層。植物學名主要依據臺灣植物誌第二版(Huang and Hsieh 2003)，分類系統則採用 APG IV (The Angiosperm Phylogeny Group 2016)。樣區內之物種依據「2017 臺灣維管束植物紅皮書名錄」(Editorial Committee of the Red List of Taiwan Plants 2017)進行保育等級判定；歸化植物(naturalized plants)之認定係依據Wu et al. (2004)與Chang-Yang et al. (2022)。

物種-面積曲線

為比較喬木層與地被層之物種累積特性，以樣方為取樣單位，利用物種–面積曲線(species–area curves, SAC)進行分析。為降低樣方排列順序對累積物種數之影響，將所有樣方進行100次隨機排列(random permutation)，每次皆以不放回方式依序累積樣方，並計算各累積面積下之物種數。最後以100次隨機排列所得之平均累積物種數繪製物種-面積曲線，並以各累積面積下累積物種數之2.5 %與97.5 %分位數作為95 %信賴區間。累積物種數若達到預期總物種數的約90 %，常被視為取樣已達充分程度(Moreno and Halffter 2000; Willott 2001)。然而，物種–面積曲線在接近90%後通常趨於平緩，不同植群層次之累積速率差異不易辨識，因此本研究改採累積至總物種數80%所需面積作為物種飽和指標(saturation threshold)，以比較喬木層與地被層之物種累積特性。

優勢度-多樣性曲線

為評估群落結構與物種優勢分布，本研究以樣方作為取樣單位繪製優勢度–多樣性曲線，喬木層以胸高斷面積(basal area, BA)計算各物種之相對優勢度(relative dominance)，地被層則以覆蓋度計算相對豐度(relative abundance)。為使兩植被層具有可比較的尺度，各物種數值均除以該層總量進行標準化，轉換為層內之相對比例。之後將各物種依相對優勢度(或相對豐度)由高至低排序，並於對數尺度下呈現物種序列與其相對優勢度之關係(Whittaker 1965; Magurran 2004)，曲線的斜率與形狀可反映群落結構、優勢種分布及物種多樣性差異。

物種多樣性指數

為描述樣區之物種多樣性，以樣方為單位計算物種豐富度(species richness)、Shannon-Wiener指數(H')、Pielou均勻度(J)及Fisher's α多樣性指數，物種豐富度為各樣方內物種數，其餘3個指數公式分別為：

Shannon-Wiener指數(H')，

$$H' = -\sum_{i=1}^{S} P_i \ln(P_i)$$

式中，P_i 表示物種i 之相對豐度(n_i/N)；n_i為物種i之個體數；N為所有物種個體數。

Pielou均勻度(J)，

$$J = \frac{H'}{\ln(S)}$$

H'為 Shannon–Wiener 指數，S 為物種數。

Fisher's α：

$$S = \alpha \ln\left(1+\frac{N}{\alpha}\right)$$

S為物種數、N為所有物種個體數、α為Fisher's α多樣性參數(Fisher et al. 1943)。

果實類型與種實傳播方式

為描述樣區之植物功能組成特徵，本研究整理樣區內維管束植物之果實型態(fruit type)與種實傳播型(dispersal mode)等屬性，作為植群組成與植物區系基本資料之一。種實傳播型係以物種之主要傳播機制(primary dispersal)為分類依據，若某些物種具次級傳播途徑(secondary dispersal)，則僅以主要傳播方式進行判定。果實型態僅針對被子植物進行分類，由於蕨類植物與裸子植物不形成由子房發育之果實(Yang et al. 2011; Chen et al. 2017)，故不納入果實型態分類。

種實傳播方式主要依據果實型態、種子特徵及相關文獻記載(van der Pijl 1982; Cornelissen et al. 2003)進行判定，將樣區內種子植物之傳播方式區分為風力傳播(anemochory)、內攜傳播(endozoochory)、外攜傳播(epizoochory)、儲藏傳播(hoarding)、重力傳播(barochory)及彈射傳播(ballochory)等6類。

樹種耐陰性評估

本研究樹種耐陰性(shade tolerance)之判定依據 Kuo et al. (2021)針對臺灣原生木本植物所建立之耐陰性分級系統。該研究以光合潛力(photosynthetic capacity, A_{max})等生理性狀量化440種木本植物，將其分類為5級：極不耐陰(very intolerant) (Ⅰ)、不耐陰(intolerant) (Ⅱ)、中等耐陰(moderately tolerant) (Ⅲ)、耐陰(tolerant) (Ⅳ)以及極耐陰(very tolerant) (Ⅴ)。未收錄的樹種則依據Kuo et al. (2021)所提出之科層級整體耐陰趨勢進行保守分類。例如薔薇科(Rosaceae)為第III級，殼斗科(Fagaceae)與樟科(Lauraceae)為第IV級，以維持分類之一致性。

植物生活型譜

依據Raunkiær (1934) 生活型分類方式將物種區分為5型：(1)挺空植物 (phanerophytes, P)：多年生具有背地性之莖或枝條頂端，如喬木、灌木；(2)地表植物 (chamaephytes, Ch)：生存芽位於離地面甚近之枝上 (通常不超過 25 cm)，如小灌木或

亞灌木植物，其植物體及花軸均為背地性，花只出現於生長季；(3)半地中植物 (hemicryptophytes, H)：生長芽位於土表，可受冬雪、落葉層及土壤之保護，大多數二年生或多年生草本均屬此類型；(4)地中植物 (geophytes, G)：生存芽完全埋入土中，在不良季節時可受土壤保護；(5)一年生種子植物 (therophytes, T)：無生存芽，植物在極短之生長季中完成生活週期，而以種子之休眠型態渡過不良季節，計算各生活型種類所佔比例繪製Raunkiær生活型譜(Raunkiær life-form spectrum)。

結果

維管束植物組成

碧綠溪森林動態樣區共記錄56科89屬117種維管束植物，特有種44種，樣區內未調查到歸化植物。蕨類植物8科15屬18種，裸子植物(gymnosperms)2科5屬6種，被子植物(angiosperms)的雙子葉植物(dicotyledons)41科62屬85種，單子葉植物(monocotyledons)計有5科7屬8種。

喬木層記錄2,379株木本植物，分屬於23科、32屬、49種，其中28種為特有種(endemic)，特有種比例為57%。物種數最多者的科依序分別為松科(Pinaceae)4屬5種，五福花科(Adoxaceae)1屬4種、杜鵑花科(Ericaceae)與殼斗科2屬4種，樣區中最優勢的5種優勢種分別為：狹葉櫟(*Quercus stenophylloides* Hayata)、臺灣二葉松(*Pinus taiwanensis* Hayata)、薄葉柃木(*Eurya leptophylla* Hayata)、臺灣黃杉(*Pseudotsuga wilsoniana* Hayata)、西施花(*Rhododendron leptosanthum* Hayata)。

地被層調查結果共紀錄50科77屬96種維管束植物，特有種共有32種，特有種比例33%。其中蕨類植物計有8科15屬18種，種子植物的雙子葉植物37科55屬70種；單子葉植物5科7屬8種。物種數最多的科依序分別為薔薇科(Rosaceae)2屬7種，水龍骨科(Polypodiaceae)4屬6種，五加科(Araliaceae)5屬5種與五福花科2屬5種，地被層調查有15科19屬28種樹種與喬木層為共有種。

參照「2017 臺灣維管束植物紅皮書名錄」之受脅等級標準，樣區內物種中被評定為極危(CR)的僅有黃氏衛矛(*Euonymus huangii* H.Y. Liu & Y.P. Yang)1種；瀕危(EN)者為南洋紅豆杉(*Taxus sumatrana* (Miq.) de Laub.)1種；易危(VU)等級為阿里山十大功勞(*Mahonia oiwakensis* Hayata)及細葉疏果海桐(*Pittosporum illicioides* Makino var. *angustifolium* Huang *ex* S.Y. Lu)2種。

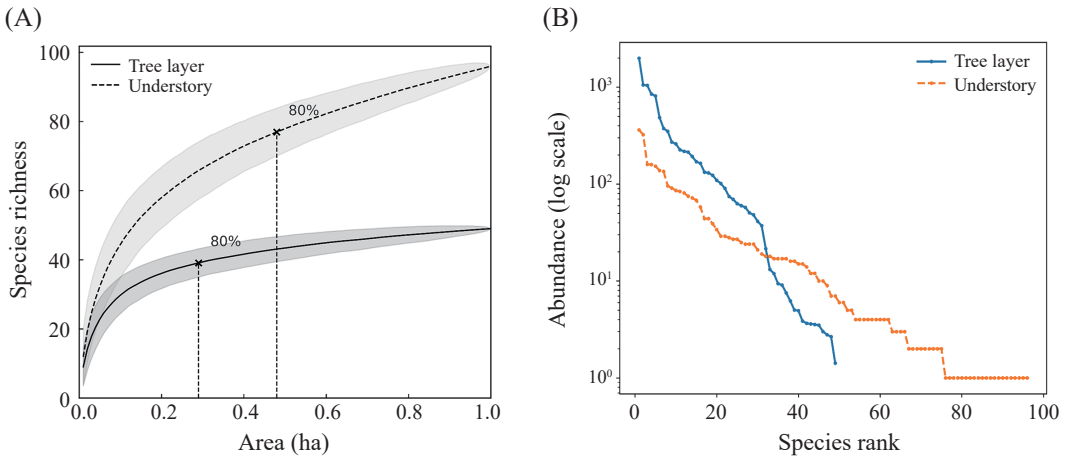

Figure 2. (A) Species–area curves for tree layer and understory vegetation. Shaded areas indicate 95% confidence intervals; dashed lines denote the area required to reach 80% of observed species richness. (B) Dominance–diversity curves for the tree layer (red) and understory layer (blue) in the BFDP.

物種-面積曲線

物種–面積曲線顯示(Figure 2A)，喬木層與地被層之物種累積速率存在明顯差異。隨取樣面積由0.1 ha增加至1 ha，喬木層累積物種數約由20種增加至49種，地被層則由約40種增加至96種，以累積達到總物種數80%所需之面積作為飽和指標，喬木層約需0.3 ha，而地被層約需0.45 ha。

優勢度-多樣性曲線

碧綠溪森林動態樣區的優勢度－多樣性曲線呈現明顯的階層化物種優勢結構(Figure 2B)，優勢度-多樣性曲線前段陡降，顯示少數優勢種主導該層群落結構；其後曲線逐漸趨緩，呈現多數稀有物種所構成的長尾分佈。相較之下，地被層曲線降幅較緩，顯示物種優勢度相對較平均，各物種間優勢差異較小；然而，在排名40名之後曲線呈明顯長尾，反映該層中同時存在大量低豐度的物種。

物種多樣性指數

在物種豐富度方面，喬木層(Figure 3A)各樣方物種數大致介於約 5–15 種之間，相較之下，地被層(Figure 3 B)物種豐富度整體較高，多數樣方約為 10–20 種，並在局部樣方呈現較高的物種豐富度。

Shannon–Wiener 多樣性指數顯示，喬木層(Figure 3C)多樣性大致介於 1.6–2.8 之間。地被層(Figure 3D）Shannon–Wiener 指數則普遍較高，多數樣方介於 2.0–3.2，且部分區域呈現較高的多樣性值。喬木層各樣方的Fisher’s α值介於5–12(Figure 3E)；而地被層(Figure 3F)Fisher’s α值介於 8–20 之間。

Pielou 均勻度(*J*)在喬木層(Figure 3G)與地被層(Figure 3H)均維持在相對較高的範圍，其中喬木層多介於 0.7–0.9，而地被層多接近 0.9–1.0，顯示各物種之相對優勢度分布較為均勻。

種實傳播方式

碧綠溪森林動態樣區49種喬木的種實類型以種毬(seed cone)、漿果(berry)、核果(drupe)為主，種實傳播方式主要以動物傳播(zoochory)類型中的內攜傳播29種為最多，風力傳播16種次之(Figure 4A)，另有少數物種屬於儲藏傳播(4種)。地被層96種組成剔除蕨類植物後，78種地被植物的果實類型以漿果、核果、蒴果(capsule)為主，種實傳播方式明顯偏向動物傳播有50種，其中內攜傳播佔49種，外攜傳播1種，總計動物傳播方式佔地被層物種數的62.2%，其次為風力傳播34種(Figure 4B)。

樹種耐陰性評估

樣區喬木層與地被層的組成在樹種耐陰性等級分布大致呈現一致，並於中高耐陰等級達到高峰(Figure 4C)。耐陰性Ⅲ與Ⅳ級的中高耐陰等級物種數最多，極耐陰(Ⅴ級)與極不耐陰(Ⅰ級)的樹種最少。

整體而言，碧綠溪森林中多數樹種屬於中度耐陰至耐陰型植物。然而，喬木層在極耐陰樹種(Ⅴ)的物種數僅剩1種，反映出屬極耐陰類別的喬木層物種相對稀少；相對地，地被層的樹種在各耐陰等級均較喬木層豐富，尤其在Ⅲ與Ⅳ區間差距最為明顯，顯示地被層樹種在陰濕、低光環境中具較高適存度與多樣性。

植物生活型譜

樣區物種的Raunkiær生活型譜以挺空植物(P)71種最多，喬木層植物均屬於此類型，半地中植物(H)14種次之，地表植物(Ch)5種、地中植物(G)9種，沒有一年生植物(T) (Figure 4D)。

討論

植相組成

針闊葉混合林係指針葉樹與闊葉樹在林分上層結構中共同占有顯著地位之森林類型，常見於氣候與植群帶之過渡區，惟其界定多採描述性而非固定比例門檻(Su 1984; Walter 1985; Li et al. 2013)。本研究結果顯示，碧綠溪森林動態樣區之喬木層以殼斗科及多種常綠闊葉樹為主要

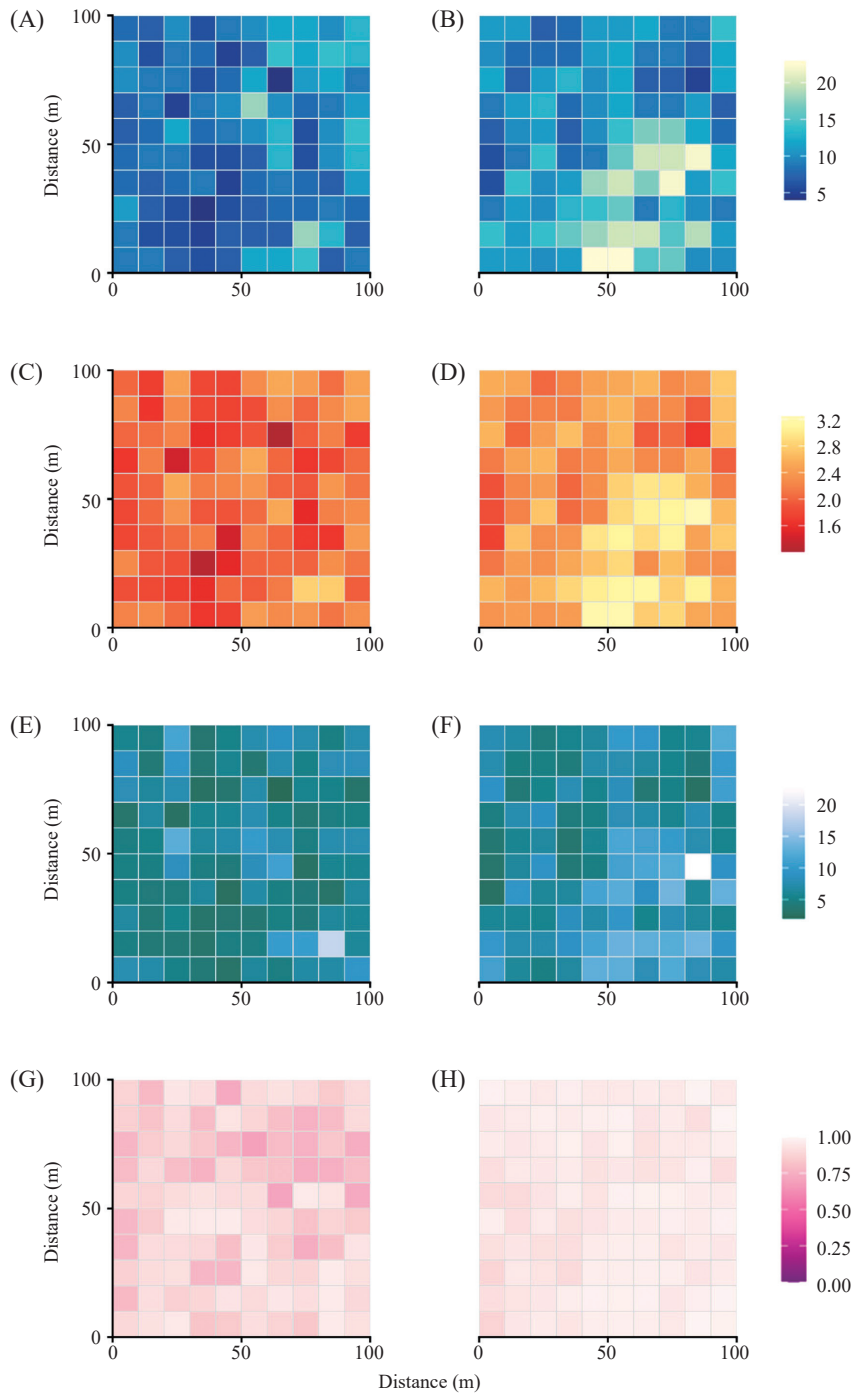

Figure 3. Spatial distributions of four diversity indices for the tree layer and the understory at the BFDP (10 m × 10 m subplots). (A, C, E, G) Tree layer: Species richness, Shannon–Wiener index (*H′*), Fisher's *α*, and Pielou's evenness index (*J*). (B, D, F, H) Understory: Species richness, Shannon–Wiener index (*H′*), Fisher's *α*, and Pielou's evenness index (*J*). Color gradients represent index values among subplots.

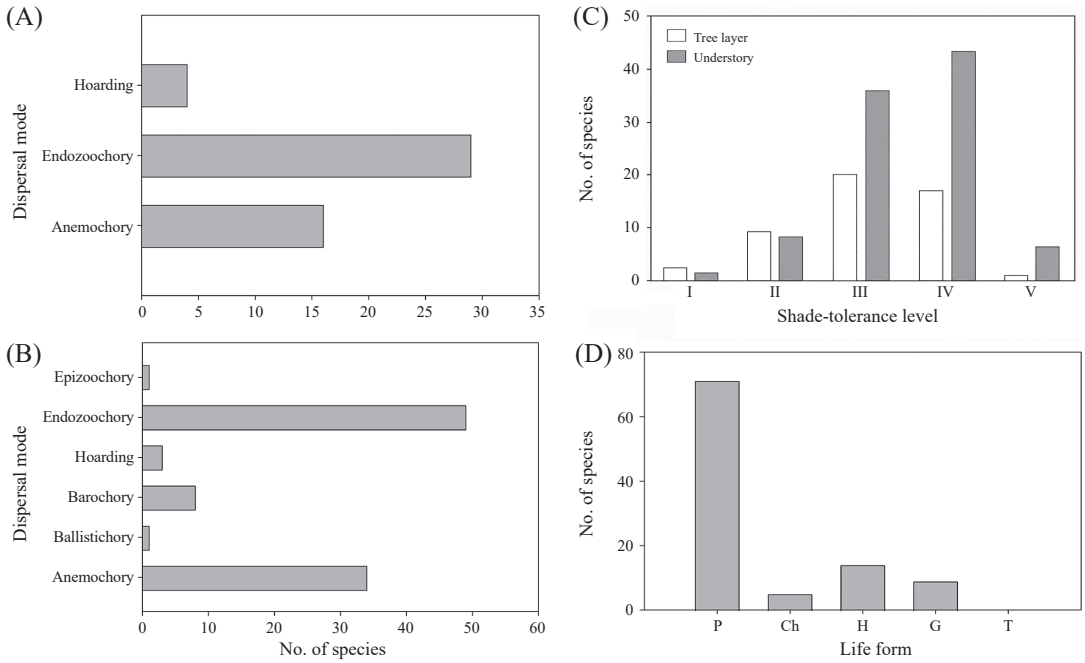

Figure 4. Seed dispersal modes of tree layer (A) and understory species (B) in the BFDP. Horizontal bar charts show the number of species belonging to each dispersal mode. (C) Species richness across five shade-tolerance levels (I–V) for the tree layer (white bars) and understory (gray bars). Both layers showed the highest species richness at intermediate shade-tolerance levels (III–IV), whereas relatively few species occurred at levels I and V. (D) The number of individuals for each Raunkiær life-form category is shown. P, phanerophytes; Ch, chamaephytes; H, hemicryptophytes; G, geophytes; T: therophytes.

組成，樣區中亦有分布臺灣二葉松、臺灣黃杉(*Pseudotsuga wilsoniana* Hayata)、臺灣雲杉(*Picea morrisonicola* Hayata)及臺灣鐵杉(*Tsuga chinensis* (Franchet) Pritz. *ex* Diels var. *formosana* (Hayata) H.L. Li & H. Keng)大徑級的林木，整體物種組成與結構特徵符合Su (1984)所界定之櫟林帶上層範圍；依Li et al. (2013)之植群分類體系，則可歸屬為櫟屬山地常綠闊葉雲霧林。

樣區未記錄到外來歸化植物，此結果與臺灣外來植物的海拔分布模式相符。Wu et al. (2004)指出臺灣絕大多數歸化植物集中於低海拔、高干擾環境，如農地邊緣、都市綠地及道路兩側；而在海拔 1,500 m-2,500 m的中海拔山區，由於氣候冷涼、棲地環境擾動較低且人為干擾有限，外來植物的建立與入侵機會顯著降低。雲霧林整體環境因氣候涼濕、光照不足、土壤養分限制及地形隔離，被視為全球外來植物入侵程度最低的森林生態系之一(Hamilton et al. 1995; Feeley et al. 2011)。

優勢度及物種多樣性

物種–面積曲線顯示(Figure 2A)以80%物種飽和點比較，喬木層僅需約0.30 ha即可達到大部分物種累積，而地被層則需約0.45 ha才達相同飽和程度。此結果顯示地被層的物種組成變化較大，且包含較多稀有物種，因此需要更大的取樣面積才能完整反映其物種多樣性。此一現象通常被解釋為地被層具有較大的區域物種庫(regional species pool)，常由大量低優勢度物種所構成，呈現典型的長尾分布(long-tailed distribution) (He and Legendre 1996)。

喬木層與地被層在優勢度–多樣性曲線亦呈現明顯差異(Figure 2B)。喬木層前5名優勢種佔全體優勢比例達57%，使曲線呈現陡降，反映少數優勢種佔據主要資源並主導植群形相結構，屬典型的階層化優勢(dominance hierarchy)變化(Magurran 2004)。相較之下，地被層最優勢的薄葉柃木佔絕對優勢，在40名之後的多數物種具有低覆蓋度與低出現頻度，曲線形成長尾分布。此類物種多為小型草本植物，如山酢漿草(*Oxalis acetosella* L. subsp. *griffithii* (Edgew. & Hook. f.) Hara)、海螺菊(*Ellisiophyllum pinnatum* (Wall. *ex* Benth.) Makino)、小椒草(*Peperomia reflexa* Kunth)、金劍草(*Rubia lanceolata* Hayata)等。

研究結果顯示樣方間之喬木層與地被層在物種多樣性指標呈現差異，部分高物種多樣性與高均勻度之樣方集中於樣區南側與東南側，即使在1 ha的小尺度範圍內，不同樣方間之物種多樣性仍存在差異，可能反映微地形、光環境或局部棲地條件差異對植物組成之影響。惟本研究主要以樣方尺度之多樣性指數進行空間圖示化呈現，尚未進一步進行空間統計分析，因此相關空間分布特徵仍有待後續研究驗證。

地形變異被認為是在小尺度範圍內提升樹木物種度豐富度的一項潛在因素，物種組成會隨著地形梯度而變化，如從山脊到山谷、從山頂到低窪地(Enoki 2003; Masaki et al. 2007; Hortal et al. 2009; Irl et al. 2015)，本研究所觀察到的物種多樣性空間變異極可能受環境異質性所驅動，特別是地形因子；未來將結合環境變數分析，以釐清研究區物種多樣性格局的因子。

種實傳播方式及耐陰性

喬木層與地被層植物多樣性差異，可能與植物之種實傳播方式有關。種子傳播方式被認為會影響植物之擴散能力與更新機會，進而影響群聚組成與物種分布特徵 (Howe and Smallwood 1982; Nathan and Muller-Landau 2000)。本研究喬木層共記錄內攜傳播植物29種（Figure 4A），果實型態多為小型漿果與核果，顯示多仰賴鳥類取食進行種子傳播；風力傳播植物共16種，其中11種(69%)為森林冠層優勢樹種。地被層植物亦呈現相似趨勢，顯示不同生活型植物之傳播策略可能具有一致性。

此結果與其他溫帶森林研究相近。例如，智利溫帶雨林約70%的木本植物屬鳥類傳播型，但冠層樹種中85.7%為風力傳播 (Armesto and Rozzi 1989)；墨西哥亞濕潤型溫帶森林木本植物則約68%屬動物傳播、32%屬風力傳播 (Cortés-Flores et al. 2013)。整體而言，山地森林植物常呈現肉質果與動物傳播占較高比例，而冠層樹種則偏向風力傳播之趨勢。

Kuo et al. (2021)分析臺灣440種原生木本植物的耐陰性，為本研究物種耐陰性之分類提供重要且可靠的參考基礎。樹種間光需求與光環境反應的差異反映其葉功能性狀策略(functional traits)，此差異深刻影響幼苗存活、個體生長與種間競爭，因而成為調控森林更新、群聚結構與演替階段轉換的重要驅動力(Swaine and Whitmore 1988; Falster et al. 2017)。另一個觀察到的現象為，喬木層僅有11種屬於先驅樹種或陽性樹種，如臺灣二葉松、臺灣雲杉、臺灣赤楊(*Alnus formosana* (Burkill) Makino)等樹種，占比僅22%，顯示林分組成以耐陰性較高之樹種為主。依據森林演替與功能性狀理論，先驅樹種多於演替初期佔優勢，而隨林冠閉合與資源競爭加劇，耐陰樹種逐漸增加並主導林分結構，反映森林由早期向中後期演替階段發展(Niinemets and Valladares 2006)。因此，碧綠溪森林動態樣區喬木層先驅樹種比例偏低的結果，符合中後期森林演替之組成特徵。

植物生活型譜

植物生活型可反映植物對環境條件之適應方式，尤其與更新芽(perennating buds)的位置及其對不利環境之耐受策略有關，因此常被用以描述植群對氣候條件之整體回應(Ellenberg 1988)。本研究碧綠溪森林動態樣區喬木層完全由挺空植物構成，相較之下，地被層則以半地中植物與地表植物占優勢。山地森林在低溫、遮蔭與高濕等環境條件下，常具有較高比例之近地表生活型(Kitayama 1992; Körner 2003)，本研究結果與此趨勢相符。

結論

本研究於臺灣中部碧綠溪集水區建立1 ha 森林動態樣區，系統性呈現櫟林帶針闊葉混合雲霧林之植相組成與多樣性特徵。結果顯示，喬木層與地被層在物種累積速率、優勢結構具有明顯差異：喬木層呈現階層化優勢格局與較均質的物種分布，而地被層則展現較高之物種多樣性。多數物種屬中度耐陰至耐陰類型，且先驅或陽性樹種比例偏低，顯示本區森林已進入中後期演替階段。不同層級在種實傳播方式與耐陰性組成上的差異，反映其更新策略之分化。本研究所建立之基礎植群資料，為後續結合環境因子與空間分析，深入探討山地雲霧林物種組成機制與森林動態提供重要依據。

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Appendix. Checklist and vegetation characteristics of vascular plants in the BFDP

Family	Scientific name	Chinese name	Layer	Life form	Fruit type	Dispersal mode	Shade-tolerance
Athyriaceae	*Diplazium pseudodoederleinii* Hayata	擬德氏雙蓋蕨	U	-	-	anemochory	Ⅳ
Davalliaceae	*Araiostegia parvipinnula* (Hayata) Copel.	臺灣小膜蓋蕨	U	-	-	anemochory	Ⅳ
Dennstaedtiaceae	*Histiopteris incisa* (Thunb.) J. Sm.	栗蕨	U	-	-	anemochory	Ⅳ
Dennstaedtiaceae	*Pteridium aquilinum* subsp. *wightianum* (J. Agardh) W.C. Shieh	巒大蕨	U	-	-	anemochory	Ⅳ
Dryopteridaceae	*Arachniodes rhomboidea* var. *yakusimensis* (H. Itô) W.C. Shieh	屋久複葉耳蕨	U	-	-	anemochory	Ⅳ
Dryopteridaceae	*Dryopteris lepidopoda* Hayata	厚葉鱗毛蕨	U	-	-	anemochory	Ⅳ
Dryopteridaceae	*Polystichum parvipinnulum* Tagawa	尖葉耳蕨	U	-	-	anemochory	Ⅳ
Dryopteridaceae	*Polystichum piceopaleaceum* Tagawa	黑鱗耳蕨	U	-	-	anemochory	Ⅳ
Gleicheniaceae	*Diplopterygium glaucum* (Thunb. *ex* Houtt.) Nakai	裏白	U	-	-	anemochory	Ⅱ
Plagiogyriaceae	*Plagiogyria euphlebia* (Kunze) Mett.	華中瘤足蕨	U	-	-	anemochory	Ⅳ
Polypodiaceae	*Lepisorus monilisorus* (Hayata) Tagawa	擬笈瓦葦	U	-	-	anemochory	Ⅳ
Polypodiaceae	*Lepisorus obscurevenulosus* (Hayata) Ching	奧瓦葦	U	-	-	anemochory	Ⅳ
Polypodiaceae	*Lepisorus pseudoussuriensis* Tagawa	擬烏蘇里瓦葦	U	-	-	anemochory	Ⅳ
Polypodiaceae	*Neolepisorus ensatus* (Thunb.) Ching	盾蕨	U	-	-	anemochory	Ⅳ
Polypodiaceae	*Polypodium amoenum* Wall. *ex* Mett.	阿里山水龍骨	U	-	-	anemochory	Ⅳ
Polypodiaceae	*Pyrrosia sheareri* (Baker) Ching	盧山石葦	U	-	-	anemochory	Ⅳ
Pteridaceae	*Coniogramme intermedia* Hieron.	華鳳丫蕨	U	-	-	anemochory	Ⅳ
Pteridaceae	*Vittaria taeniophylla* Copel.	廣葉書帶蕨	U	-	-	anemochory	Ⅳ
Pinaceae	*Picea morrisonicola* Hayata	臺灣雲杉 #	C	P	-	anemochory	Ⅰ
Pinaceae	*Pinus armandii* Franchet var. *mastersiana* (Hayata) Hayata	臺灣華山松 #	C	P	-	anemochory	Ⅰ
Pinaceae	*Pinus taiwanensis* Hayata	臺灣二葉松 #	C	P	-	anemochory	Ⅱ
Pinaceae	*Pseudotsuga wilsoniana* Hayata	臺灣黃杉 #	C	P	-	anemochory	Ⅱ
Pinaceae	*Tsuga chinensis* (Franchet) Pritz. *ex* Diels var. *formosana* (Hayata) H.L. Li & H. Keng	臺灣鐵杉 #	C	P	-	anemochory	Ⅲ

Appendix (continued)

Family	Scientific name	Chinese name	Layer	Life form	Fruit type	Dispersal mode	Shade-tolerance
Taxaceae	*Taxus sumatrana* (Miq.) de Laub.	南洋紅豆杉 (EN)	C	P	-	endozoochory	V
Adoxaceae	*Sambucus chinensis* Lindl.	接骨消	U	P	berry	endozoochory	Ⅱ
Adoxaceae	*Viburnum foetidum* var. *rectangulatum* Rehder	狹葉莢蒾	B	P	drupe	endozoochory	Ⅲ
Adoxaceae	*Viburnum parvifolium* Hayata	小葉莢蒾	B	P	drupe	endozoochory	Ⅲ
Adoxaceae	*Viburnum propinquum* Hemsl.	高山莢蒾	B	P	drupe	endozoochory	Ⅳ
Adoxaceae	*Viburnum taitoense* Hayata	臺東莢蒾	B	P	drupe	endozoochory	Ⅲ
Anacardiaceae	*Rhus ambigua* Lav. *ex* Dippel	臺灣藤漆	U	P	drupe	endozoochory	Ⅲ
Apocynaceae	*Marsdenia formosana* Masam.	臺灣牛彌菜	U	P	follicle	anemochory	Ⅲ
Apocynaceae	*Trachelospermum formosanum* Y.C. Liu & Ou	臺灣絡石 #	U	P	follicle	anemochory	Ⅲ
Aquifoliaceae	*Ilex crenata* Thunb.	假黃楊 (NT)	B	P	drupe	endozoochory	Ⅳ
Aquifoliaceae	*Ilex pedunculosa* Miq.	刻脈冬青	C	P	drupe	endozoochory	Ⅳ
Aquifoliaceae	*Ilex yunnanensis* Fr. var. *parvifolia* (Hayata) S.Y. Hu	雲南冬青 #	B	P	drupe	endozoochory	Ⅳ
Araliaceae	*Aralia bipinnata* Blanco	裡白蔥木	U	P	berry	endozoochory	Ⅱ
Araliaceae	*Fatsia polycarpa* Hayata	臺灣八角金盤 #	B	P	berry	endozoochory	Ⅲ
Araliaceae	*Hedera rhombea* (Miq.) Bean var. *formosana* (Nakai) H.L. Li	臺灣常春藤 #	U	P	berry	endozoochory	Ⅲ
Araliaceae	*Hydrocotyle setulosa* Hayata	阿里山天胡荽 #	U	H	schizocarp	barochory	Ⅳ
Araliaceae	*Sinopanax formosanus* (Hayata) H.L. Li	華參 #	B	P	drupe	endozoochory	Ⅳ
Asteraceae	*Ainsliaea latifolia* (D. Don) Sch. Bip subsp. *henryi* (Diels) H. Koyama	臺灣鬼督郵	U	H	achene	anemochory	Ⅳ
Asteraceae	*Gynura japonica* (Thunb.) Juel	黃花三七草	U	H	achene	anemochory	Ⅳ
Balanophoraceae	*Balanophora laxiflora* Hemsl.	穗花蛇菰	U	G	drupe	endozoochory	V
Berberidaceae	*Berberis kawakamii* Hayata	臺灣小檗 # (NT)	U	Ch	berry	endozoochory	Ⅳ
Berberidaceae	*Mahonia oiwakensis* Hayata	阿里山十大功勞 # (VU)	B	P	berry	endozoochory	Ⅳ
Betulaceae	*Alnus formosana* (Burkill) Makino	臺灣赤楊	B	P	nut	anemochory	Ⅱ
Betulaceae	*Carpinus kawakamii* Hayata	阿里山千金榆	C	P	samara	anemochory	Ⅱ

Appendix (continued)

Family	Scientific name	Chinese name	Layer	Life form	Fruit type	Dispersal mode	Shade-tolerance
Campanulaceae	*Peracarpa carnosa* (Wall.) Hook. f. & Thomson	山桔梗	U	H	capsule	anemochory	Ⅴ
Caprifoliaceae	*Lonicera apodantha* Ohwi	無梗忍冬 # (NT)	U	P	berry	endozoochory	Ⅲ
Celastraceae	*Celastrus kusanoi* Hayata	大葉南蛇藤	U	P	capsule	endozoochory	Ⅲ
Celastraceae	*Euonymus carnosus* Hemsl.	厚葉衛矛	C	P	capsule	endozoochory	Ⅳ
Celastraceae	*Euonymus huangii* H.Y. Liu & Y.P. Yang	黃氏衛矛 # (CR)	C	P	capsule	endozoochory	Ⅳ
Celastraceae	*Euonymus spraguei* Hayata	刺果衛矛 #	U	P	capsule	endozoochory	Ⅳ
Daphniphyllaceae	*Daphniphyllum himalaense* (Benth.) Muell.-Arg. subsp. *macropodum* (Miq.) Huang	薄葉虎皮楠	C	P	drupe	endozoochory	Ⅳ
Elaeagnaceae	*Elaeagnus glabra* Thunb.	藤胡頹子	B	P	drupe	endozoochory	Ⅲ
Ericaceae	*Lyonia ovalifolia* (Wall.) Drude	南燭	C	P	capsule	anemochory	Ⅱ
Ericaceae	*Rhododendron leptosanthum* Hayata	西施花	B	P	capsule	anemochory	Ⅲ
Ericaceae	*Rhododendron noriakianum* Suzuki	細葉杜鵑 # (DD)	B	P	capsule	anemochory	Ⅱ
Ericaceae	*Rhododendron oldhamii* Maxim.	金毛杜鵑 #	B	P	capsule	anemochory	Ⅱ
Fagaceae	*Lithocarpus hancei* (Benth.) Rehder	三斗石櫟 #	B	P	nut	hoarding	Ⅳ
Fagaceae	*Lithocarpus kawakamii* (Hayata) Hayata	大葉石櫟 #	B	P	nut	hoarding	Ⅳ
Fagaceae	*Quercus stenophylloides* Hayata	狹葉櫟 #	B	P	nut	hoarding	Ⅳ
Fagaceae	*Quercus tatakaensis* Tomiya	銳葉高山櫟 #	C	P	nut	hoarding	Ⅳ
Hydrangeaceae	*Deutzia pulchra* S. Vidal	大葉溲疏	C	P	capsule	anemochory	Ⅱ
Hydrangeaceae	*Hydrangea integrifolia* Hayata	大枝掛繡球	U	P	capsule	endozoochory	Ⅳ
Lamiaceae	*Callicarpa randaiensis* Hayata	巒大紫珠 #	B	P	drupe	endozoochory	Ⅲ
Lamiaceae	*Clerodendrum trichotomum* Thunb.	海州常山	B	P	drupe	endozoochory	Ⅱ
Lamiaceae	*Salvia arisanensis* Hayata	阿里山紫花鼠尾草 #	U	H	schizocarp	barochory	Ⅳ
Lardizabalaceae	*Stauntonia obovatifoliola* Hayata	石月	U	P	follicle	endozoochory	Ⅲ
Lauraceae	*Cinnamomum insularimontanum* Hayata	臺灣肉桂 #	B	P	drupe	endozoochory	Ⅳ
Lauraceae	*Neolitsea acuminatissima* (Hayata) Kaneh. & Sasaki	高山新木薑子 #	B	P	drupe	endozoochory	Ⅳ
Lauraceae	*Neolitsea parvigemma* (Hayata) Kaneh. & Sasaki	小芽新木薑子 #	B	P	drupe	endozoochory	Ⅳ

Appendix (continued)

Family	Scientific name	Chinese name	Layer	Life form	Fruit type	Dispersal mode	Shade-tolerance
Moraceae	*Ficus sarmentosa* B. Ham. *ex* J. E. Sm. var. *nipponica* (Franch. & Sav.) Corner	珍珠蓮	U	P	drupe	endozoochory	Ⅲ
Oleaceae	*Ligustrum sinense* Lour.	小實女貞	B	P	drupe	endozoochory	Ⅲ
Oxalidaceae	*Oxalis acetosella* L. subsp. *griffithii* (Edgew. & Hook. f.) Hara	山酢漿草	G	G	capsule	ballistichory	Ⅴ
Pentaphylacaceae	*Eurya leptophylla* Hayata	薄葉柃木 #	B	P	berry	endozoochory	Ⅳ
Piperaceae	*Peperomia reflexa* Kunth	小椒草	U	H	drupe	epizoochory	Ⅴ
Pittosporaceae	*Pittosporum illicioides* Makino var. *illicioides*	疏果海桐	C	P	capsule	endozoochory	Ⅲ
Pittosporaceae	*Pittosporum illicioides* Makino var. *angustifolium* Huang *ex* S.Y. Lu	細葉疏果海桐 # (VU)	C	P	capsule	endozoochory	Ⅲ
Plantaginaceae	*Ellisiophyllum pinnatum* (Wall. *ex* Benth.) Makino	海螺菊	U	H	capsule	barochory	Ⅴ
Polygonaceae	*Polygonum chinense* L.	火炭母草	U	H	achene	endozoochory	Ⅲ
Polygonaceae	*Polygonum multiflorum* Thunb. *ex* Murray var. *hypoleucum* (Nakai *ex* Ohwi) Liu,Ying & Lai	臺灣何首烏 #	U	G	achene	barochory	Ⅲ
Ranunculaceae	*Clematis henryi* Oliv. var. *morii* (Hayata) T.Y. Yang & T.C. Huang	森氏鐵線蓮 # (NT)	U	P	achene	anemochory	Ⅲ
Rhamnaceae	*Berchemia formosana* C.K. Schneid.	臺灣黃鱔藤	U	P	drupe	endozoochory	Ⅲ
Rhamnaceae	*Rhamnus pilushanensis* Liu & Wang	畢祿山鼠李 #	B	P	drupe	endozoochory	Ⅲ
Rhamnaceae	*Sageretia thea* (Osbeck) M.C. Johnst.	雀梅藤	U	P	drupe	endozoochory	Ⅲ
Rosaceae	*Prunus buergeriana* Miq.	布氏稠李	C	P	drupe	endozoochory	Ⅲ
Rosaceae	*Prunus phaeosticta* (Hance) Maxim. var. *ilicifolia* Yamam.	冬青葉桃仁	B	P	drupe	endozoochory	Ⅲ
Rosaceae	*Prunus transarisanensis* Hayata	阿里山櫻花 # (NT)	B	P	drupe	endozoochory	Ⅲ
Rosaceae	*Rubus buergeri* Miq.	寒莓	U	Ch	druplet	endozoochory	Ⅲ
Rosaceae	*Rubus corchorifolius* L. f.	變葉懸鉤子	U	P	druplet	endozoochory	Ⅲ
Rosaceae	*Rubus kawakamii* Hayata	桑葉懸鉤子 #	U	P	druplet	endozoochory	Ⅲ
Rosaceae	*Rubus pectinellus* Maxim.	刺萼寒莓	U	Ch	druplet	endozoochory	Ⅲ
Rosaceae	*Rubus pungens* Cambess.	刺懸鉤子	U	P	druplet	endozoochory	Ⅲ

Appendix (continued)

Family	Scientific name	Chinese name	Layer	Life form	Fruit type	Dispersal mode	Shade-tolerance
Rubiaceae	*Damnacanthus indicus* C.F. Gaertn.	伏牛花	U	Ch	drupe	endozoochory	Ⅳ
Rubiaceae	*Rubia lanceolata* Hayata	金劍草 #	U	H	berry	endozoochory	Ⅳ
Rutaceae	*Zanthoxylum scandens* Blume	藤花椒	U	P	follicle	endozoochory	Ⅲ
Sapindaceae	*Acer kawakamii* Koidz.	尖葉槭 #	C	P	samara	anemochory	Ⅲ
Sapindaceae	*Acer morrisonense* Hayata	臺灣紅榨槭 #	B	P	samara	anemochory	Ⅲ
Sapindaceae	*Acer serrulatum* Hayata	青楓 #	C	P	samara	anemochory	Ⅲ
Schisandraceae	*Schisandra arisanensis* Hayata	阿里山五味子 #	U	P	berry	endozoochory	Ⅲ
Simaroubaceae	*Ailanthus altissima* (Miller) Swingle var. *tanakae* (Hayata) Sasaki	臭椿 #	U	P	samara	anemochory	Ⅰ
Stachyuraceae	*Stachyurus himalaicus* Hook. f. & Thomson	通條樹	C	P	capsule	endozoochory	Ⅳ
Thymelaeaceae	*Daphne arisanensis* Hayata	臺灣瑞香 #	U	Ch	drupe	endozoochory	Ⅳ
Ulmaceae	*Ulmus uyematsui* Hayata	阿里山榆 #	C	P	samara	anemochory	Ⅲ
Urticaceae	*Elatostema parvum* (Blume) Miq.	絨莖樓梯草	U	H	achene	barochory	Ⅴ
Urticaceae	*Elatostema trilobulatum* (Hayata) T. Yamaz.	裂葉樓梯草 #	U	H	achene	barochory	Ⅴ
Urticaceae	*Urtica thunbergiana* Siebold & Zucc.	蕁麻	U	H	achene	barochory	Ⅲ
Vitaceae	*Tetrastigma umbellatum* (Hemsl.) Nakai	臺灣崖爬藤 #	U	P	berry	endozoochory	Ⅲ
Araceae	*Arisaema ringens* (Thunb.) Schott	申跋	U	G	berry	endozoochory	Ⅲ
Cyperaceae	*Carex makinoensis* Franch.	牧野氏薹	U	H	achene	barochory	Ⅲ
Orchidaceae	*Goodyera schlechtendaliana* Rchb. f.	斑葉蘭	U	G	capsule	anemochory	Ⅳ
Orchidaceae	*Vexillabium yakushimense* (Yamam.) F. Maek.	紫葉旗唇蘭	U	G	capsule	anemochory	Ⅳ
Poaceae	*Miscanthus transmorrisonensis* Hayata	高山芒	U	H	caryopsis	anemochory	Ⅱ
Poaceae	*Yushania niitakayamensis* (Hayata) Keng f.	玉山箭竹	U	G	caryopsis	anemochory	Ⅲ
Smilacaceae	*Smilax arisanensis* Hayata	阿里山菝葜	U	G	berry	endozoochory	Ⅲ
Smilacaceae	*Smilax discotis* Warb.	宜蘭菝葜	U	G	berry	endozoochory	Ⅲ

Notes: #: Endemic. CR: Critically Endangered; EN: Endangered; VU: Vulnerable; NT: Near Threatened; DD: Data Deficient. U: Understory; C: Canopy; B: species occurring in both the tree and understory layers. Codes for life form, dispersal mode, and shade-tolerance are defined in the Materials and Methods section.