



Species-habitat associations of tree species under the northeast monsoon wind-affected tropical forest at Lanjenchi Forest Dynamics Plot, Taiwan

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ABSTRACT: The spatial distribution of tree species in the forest is key to understanding species coexistence concerning their realized niche. Previous research has shown that forest community composition differs in Lanjenchi Forest Dynamics Plot (FDP) and is likely to be caused by the strength of the northeast monsoon wind. However, relationships between species and other environmental factors are not completely understood. We investigated tree species-habitat associations in Lanjenchi asking how topographic habitat affects forest structure and composition, and we classified the plot into topographic habitat using Multivariate Regression Trees based on the forest community composition and topography. Then, based on metrics of forest structure, we used the torus translation test to evaluate the degree of tree species-habitat association. Three habitats were identified in Lanjenchi and can be classified into windward, intermediate, and leeward habitats based on wind exposure value and aspect. Moreover, 81% of species had a strong positive association with one of the three habitats. Based on the strength of habitat association, the tree species can be divided into six categories. Among these categories, windward species are most abundant in Lanjenchi but are some of the rarest species in Taiwan. These results indicated that the northeast monsoon wind is an essential factor that shapes species distribution in the Lanjenchi, especially at the windward habitats. The northeast monsoon wind creates a unique niche allowing many regionally rare species to dominate these habitats in tropical Taiwan.

KEY WORDS: Environmental stress, habitat association, niche theory, tropical monsoon forests.

INTRODUCTION

Tropical forests are some of the most hyper-diverse communities in the world; numerous mechanisms cause many species to coexist within a single hectare. Niche partitioning and dispersal assemblage processes have been employed as common explanations of species coexistence and distribution in tropical rain forests (Hubbell, 2001; Wright, 2002; Potts *et al.*, 2004; Gunatilleke *et al.*, 2006). Based on the niche assembly theory, species can coexist and survive well under different environmental conditions (Chesson, 2000; Jaime *et al.*, 2015). The species spatial distributions should then reflect the structure of the underlying abiotic conditions, such as topography, through species-habitat associations at the individual species level (Whittaker, 1956).

The torus translation was the method to test the association between plants and habitat types, which generated simulated maps by applying a random toroidal rotation and reflection of the true map wrapping around the edges of the plot (Harms *et al.*, 2001). It was developed to replace traditional chi-square (Hubbell and Foster, 1986; Webb and Peart, 2000) and logistic analyses (Svenning, 1999) on species association with topographic or other environmental factors (Harms *et al.*, 2001). Harms *et al.* (2001) challenged the adequacy of the traditional analyses used to statistically test for the

species-habitat association because individual trees were not considered independent sample units. To alleviate this problem, the torus translation test was developed. Furthermore, this method has been employed successfully to evaluate the species-habitat associations of the Forest Dynamics Plot (FDP) in a semi-deciduous forest on Barro Colorado Island (BCI, Panama) (Harms *et al.*, 2001), lowland evergreen forests at Yasuni (Ecuador) (Valencia *et al.*, 2004) and Lambir (Malaysia) (Davies *et al.*, 2005), the subtropical humid forests of Gutianshan (China) (Lai *et al.*, 2009) and Nonggang (China) (Guo *et al.*, 2017), and the temperate continental forest on Liangshui (China) (Oktavia and Jin, 2019).

Topography is a first-order control on the spatial variation in hydrological conditions that structures the spatial distribution of soil moisture and nutrients, which are crucial for species spatial distribution. Habitat types used in evaluating species-habitat associations should be classified as a priori in an objective way that divides the forest into ecologically meaningful sub-unit. Multivariate Regression Trees (MRT) is a statistical extension of classification using regression tree analysis (Breiman *et al.*, 1984) that can be used to explore, describe, and predict relationships between multispecies data and environmental characteristics (De'Ath, 2002). Kanagaraj *et al.* (2011) focused on how the habitat of BCI, as defined by elevation, topographical wetness

index, and slope drives species assemblages using MRT and found that results were in close agreement with the classification results of Harms *et al.* (2001). MRT classification of habitats in the Gutianshan Forest Dynamics Plot followed by the torus translation revealed strong species-habitat associations in different habitat (Lai *et al.*, 2009). Guo *et al.* (2017) used MRT to examine species-habitat associations among eight topographically-defined habitats in a 15-ha karst tropical seasonal rain forest in the Nonggang National Natural Reserve in south China. The species association of Guo *et al.* (2017) were tested with a torus translation test, and 63 of 74 species had a significantly positive association to at least one habitat, showing that niche structure played an important role in defining the observed spatial patterns in species distributions. Therefore, the MRT is a good method for classifying habitat in forests applying topographic data.

Lanjenchi Forest Dynamics Plot (Lanjenchi FDP) is located at southern Taiwan and is affected by the northeast monsoon wind, which influences vegetation structure, stomatal conductance, morphological and physiological characteristics within the plot (Hsieh *et al.*, 2000; Chao *et al.*, 2007; Chao *et al.*, 2010; Kuo *et al.*, 2011). Due to wind stress, different tree species partition niche space in the forest. For example, Li *et al.* (2013) and Lin *et al.* (2020) showed that because of the microclimate effect, there is a mosaic pattern of vegetation types in Nanjenshan Nature Reserve, including *Ilicium*-*Cyclobalanopsis* forest, *Drypetes*-*Helicia* forest, *Ficus*-*Machilus* forest, and *Dysosylum*-*Machilus* forest. Fan and Hsieh (2010) also revealed that the seedlings of windward species have higher environmental tolerance to wind adversity. Moreover, when exposed to wind, seedlings of the windward species have higher photosynthesis rate efficiency and lower mortality rate than that of the leeward species (Fan, 2005). Chao *et al.* (2010) employed Two-Way Indicator Species Analysis (TWINSPAN) to classify the vegetation composition of Lanjenchi FDP into windward and leeward vegetation habitats and found out that the trees in windward habitat are denser, shorter and smaller than leeward habitat. Hsieh *et al.* (1992) also classified four habitat types using TWINSPAN and were able to describe the species distribution matching the particular habitat of the finer landscape scale. Although several studies have emphasized the importance of monsoon wind, the driving factors of species distribution has not been tested and verified. Moreover, it is not appropriate to use TWINSPAN to verify the species distribution because the habitat type was classified by species composition itself (Hill, 1979), without considering any underlying environmental conditions. A simultaneous procedure that can take both environmental condition and species composition into account is needed for verification of species distribution.

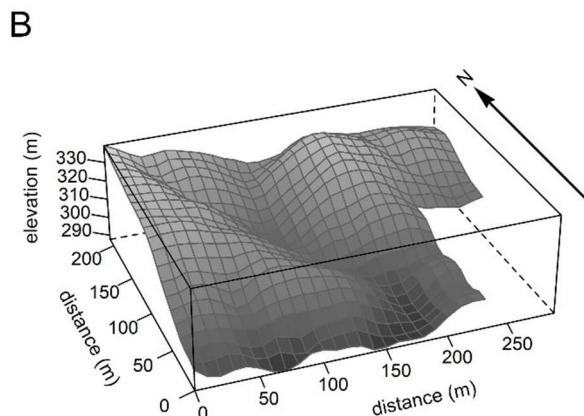
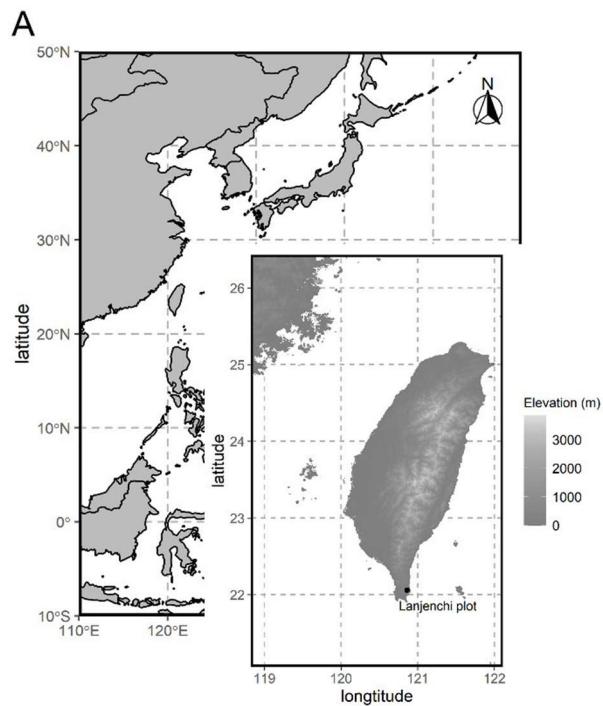


Fig. 1. Location of Lanjenchi FDP in Taiwan. **A.** Location of the island of Taiwan; **B.** the topographic map of the 5.88 ha of Lanjenchi FDP, southern Taiwan.

This research aims to classify the habitat types of Lanjenchi FDP using the topographic data and test the strength of the species-habitat associations in different habitat types of this tropical forest influenced by the northeast monsoon wind. We would like to examine the degree of habitat association among habitats, to understand whether a habitat with strong wind impacts would have a high species-habitat association or not.

METHODS

Study site

Lanjenchi FDP is located at southern Taiwan (Fig. 1A). It was established during the period from 1989 to 1991, and its trees were measured in 1991, 1997, 2005, 2013, and 2019. In this study, we used the most updated

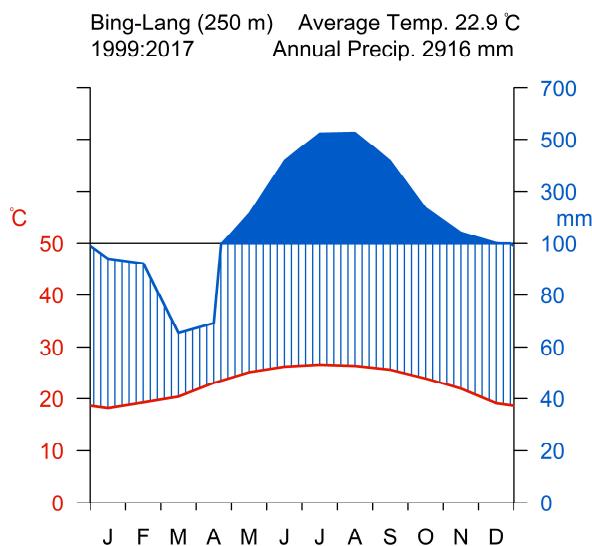


Fig. 2. Climate diagram of the nearest weather station in the Lanjenchi FDP.

census dataset collected in 2019. In 1991, it was a rectangular 3-ha plot, then in 1997, there was a southward expansion to an irregular 5.88-ha until now (Fig. 1B). Elevation in Lanjenchi FDP ranges from 284 to 341 m.a.s.l. The annual average temperature is 22.9°C, and the mean annual precipitation was 2,916 mm measured by the nearby Binglang station from 1999 to 2017 (Fig. 2). The rainy season extended from May to December, with precipitation exceeding 100 mm month⁻¹. The dominant tree species are *Castanopsis cuspidate* var. *carlesii* (Hemsl.) T. Yamaz., *Schefflera octophylla* (Lour.) Harms, *Quercus longinux* Hayata, *Illicium arborescens* Hayata, and *Schima superba* Gard. & Champ. var. *kankaoensis* (Hayata) Keng (Chao et al., 2010). Botanical nomenclature followed Flora of Taiwan, 2nd edition (Huang, 2003).

Field sampling

The 5.88-ha of Lanjenchi FDP is systematically divided into 10 × 10 m quadrats. All woody stems with the diameter at breast height (DBH) ≥ 1 cm are measured, tagged, and identified to species. Five topographic variables have been recorded in each quadrat, including elevation, slope, aspect, convexity, and wind exposure value. The elevation of each quadrat is calculated as the mean elevation of each of the four quadrat corners. Quadrat slope has been estimated from the contour maps and is calculated as the mean inclination of a quadrat. Aspect is commonly used as an index of wind stress when quadrats are oriented toward the predominant wind direction. Accordingly, quadrats directly facing northeast monsoon winds are assigned relatively high aspect values (180°) in comparison to more sheltered quadrats (0°). The convexity of a quadrat was the subtraction of the mean elevation of the outer 12 corners

(exclude the four corners shared with the focal quadrat) of its eight surrounding quadrats from the elevation of the focal quadrat (Aiba et al., 2004). A positive value of convexity represents a convex surface, while a negative value represents a concave surface. The wind exposure value is an index that can show whether topography features are blocking the northeast side of the quadrats. For the quadrats which on mountain summits or ridges, the exposure values were 90; in contrast, the quadrats in the valley were 0 (Chao et al., 2010).

Multivariate Regression Trees analysis

Multivariate Regression Trees (MRT) was used to group areas with similar species composition according to a given environmental variable, including elevation, slope, aspect, and wind exposure value. It is a method of constrained clustering, which determines clusters that are similar in a chosen measure of species dissimilarity (Bray-Curtis dissimilarity in this study), with each cluster primarily defined by the environmental values.

MRT was based on a recursive algorithm where the root node consists of all 588 quadrats. The algorithm systematically searches for the topographical variable that partitions the parent node into a left and right node, that are internally most similar in terms of species composition. The optimal size of the tree is decided by a resampling analysis and the cross-validation relative error (CVRE) which was computed to select the best tree class assignment. The CVRE varies from 0 to 1, representing the best to the worst predictor. The minimize CVRE ± 1 SE will be chosen to represent the number of cutting trees. The species composition dataset was constructed by the abundance of each species within quadrat. The data for species abundance in each quadrat will be converted through normalize data transformation before the MRT procedure. Each cluster defines a species assemblage, and the threshold values of environmental variables represent an associated habitat type. Stem density, basal area, and average DBH for each stem were calculated in each habitat type. More details about the MRT technique and its application can be found in De'Ath (2002). All the MRT procedures were conducted by using the *mpart* function of the '*mpart*' package in the R version 3.6.1 (R Core Team, 2019).

Habitat association

A torus translation was used to test the significance of species abundance in one or more habitat types of species-habitat associations proposed by Harms et al. (2001). The torus translation procedure consists of moving the true habitat map at two-dimensional torus by 10 m increments and then translating three times (Harms et al., 2001). To test the significance of a species-habitat association, the actual stem density in each habitat as compared to the distribution of stem densities obtained from the translated habitat maps under a null model in

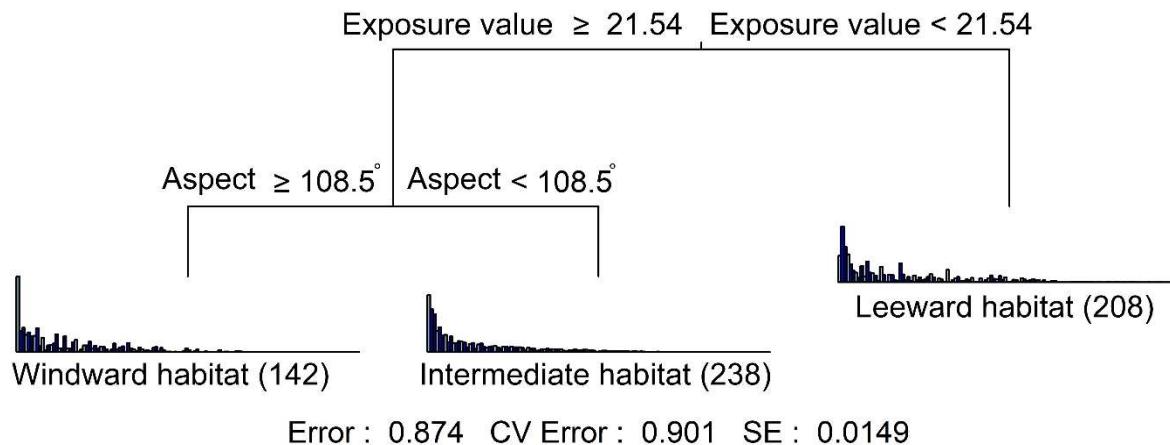


Fig. 3. Multivariate Regression Trees (MRT) for the 5.88-ha Lanjenchi FDP. Bar plots showed the multivariate species mean at each node, and the number of habitats were shown under the bar plots. The cross-validation relative error (CVRE) of the tree is 0.901 and the standard error is 0.0149.

Table 1. The parameters used to define the three habitat types and the number of species in different species-habitat associations in Lanjenchi FDP.

Habitat	Node		Number of species		
	Exposure value	Aspect	Positive association	Negative association	No association
Windward	21.54-90	>=108.5	19	29	30
Intermediate	21.54-90	<108.5	16	3	59
Leeward	<21.54		12	30	36

which the species was distributed randomly to a habitat. The p-value associated with each species was calculated by comparing the number of times the stem density in the actual map associated with a given habitat is higher or lower than the density of stems in the distribution derived from all torus-shifted maps.

Due to the restriction of the torus translation, the shape of the plot should be cut into a 5.28-ha square plot. In this study, we defined habitat based on a 10×10 m quadrat within the 5.28-ha plot, which gave one observed and 527 torus-translated habitats used for the statistical test. The significance of species-habitat association was determined by comparing the species relative density in a habitat type of the observed and simulated maps. Species relative density was positively or negatively associated with the habitat at a significance level of 5% if the density of the observed map is greater or less than at least 97.5% of those determined from the probability distribution of the simulated maps. All the torus translation tests were conducted by the *torusallsp* function, which was developed by Harms *et al.* (2001) under the R version 3.6.1 (R Core Team, 2019).

RESULTS

MRT classification result

The MRT classified Lanjenchi FDP into 3 groups, and the CVRE value was 0.901, which corresponds to the minimum CVRE $\pm 1\text{SE}$ (Fig. 3). The MRT analyses

indicated that only the wind exposure value and aspect were important determinants of species assemblages in Lanjenchi FDP (Table 1). Wind exposure value is the first node of the classification tree, which divided quadrats to less-exposed areas (wind exposure value < 21.54 ; leeward habitat) or highly exposed areas (wind exposure value ≥ 21.54) to the northeast monsoon wind. Aspect is the second node point, which divided quadrats to windward sides (Aspect $\geq 108.5^\circ$, windward habitat) and less wind-affected sides (Aspect $< 108.5^\circ$, intermediate habitat) (Fig. 3).

The windward habitat, located at the windward side of the ridge, exhibited relatively low vegetation height (Table 1, Fig. 4A). Windward habitat was named to reflect the direct influence of the northeast monsoon wind. Windward habitat had a higher stem density than the other two habitats, reaching $11,401 \pm 3,694 \text{ stems ha}^{-1}$. The basal area of this habitat was $43.00 \pm 10.50 \text{ m}^2 \text{ ha}^{-1}$. A total of 95 trees species were found in this habitat (Table 2). The most abundant species was *Illicium arborescens* Hayata, representing 16.5% of stem density in this habitat. *Castanopsis cuspidata* var. *carlesii* (Hemsl.) was the most dominant species in term of basal area (13.58% of total basal area at the windward habitat).

The intermediate habitat was at the sheltered edge of ridges, where habitat is less affected by the northeast monsoon wind in winter (Table 1, Fig. 4B). The intermediate habitat was so-named to indicate that the degree of wind effect is between that of the windward and leeward habitats. The stem density of intermediate habitat was $10,252 \pm 3,647 \text{ stems ha}^{-1}$ and the basal area was $49.80 \pm 24.50 \text{ m}^2 \text{ ha}^{-1}$ (Table 2). A total of 111 woody species were recorded in this habitat. *Illicium arborescens* Hayata was the most abundant species in this habitat, accounting for 12.17% of stem density; *Castanopsis cuspidata* var. *carlesii* (Hemsl.) T. Yamaz. was the most dominant species, representing 15.15% of the basal area at the intermediate habitat.

**Table 2.** Vegetation structure of each habitat type in the Lanjenchi 5.88-ha forest dynamics plot based on the data in 2019.

Habitat	Number of quadrats	Number of species	Stem density mean (ha^{-1}) \pm SD	Basal area mean ($\text{m}^2 \text{ ha}^{-1}$) \pm SD	Avg. DBH per stem mean (cm) \pm SD
Windward	142	95	11,401 \pm 3,694	43.00 \pm 10.50	7.14 \pm 1.35
Intermediate	238	111	10,252 \pm 3,647	49.80 \pm 24.50	7.99 \pm 1.54
Leeward	208	109	7,138 \pm 2,696	40.90 \pm 17.30	8.59 \pm 1.77

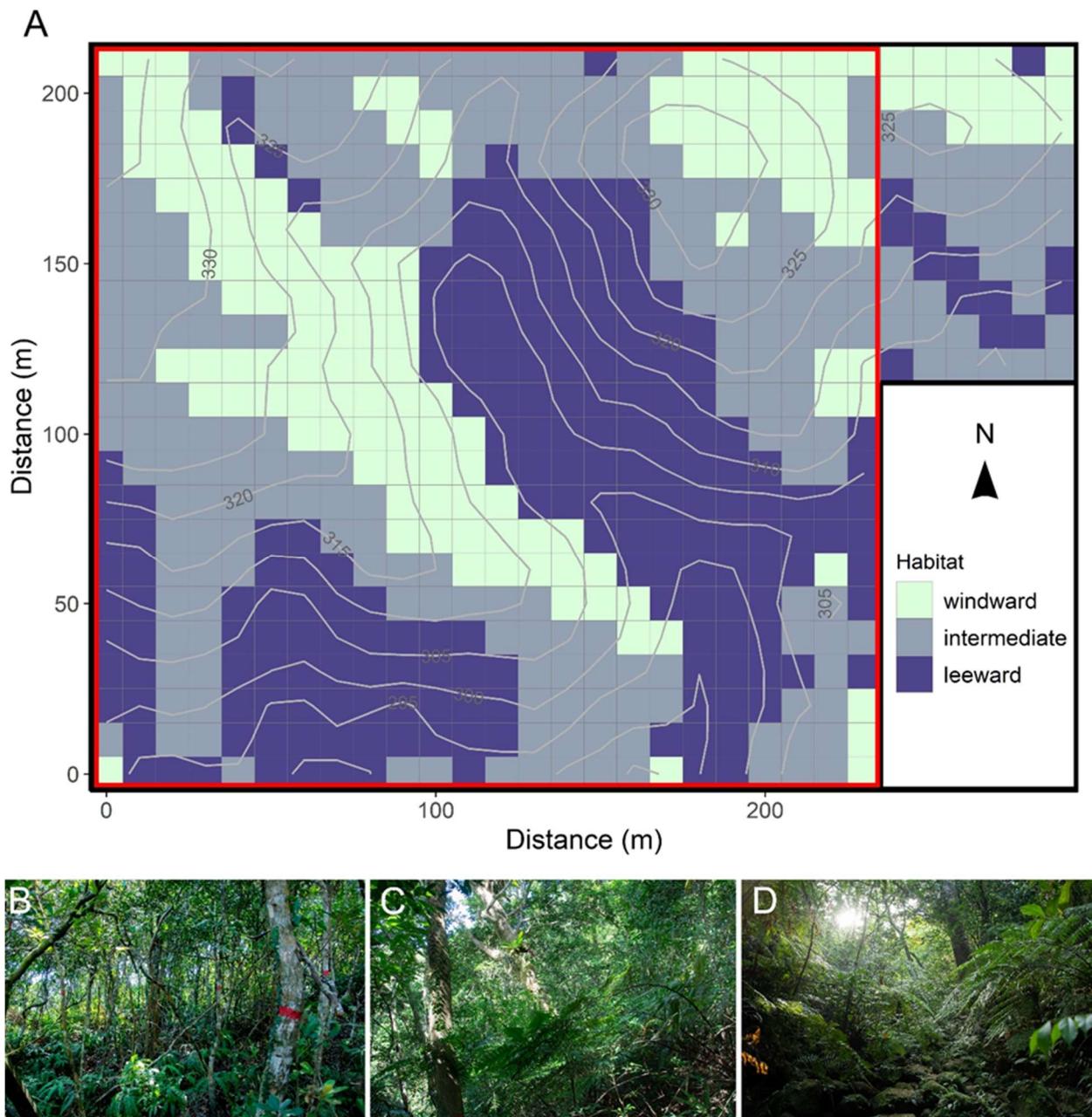


Fig. 4. Three habitat types based on the MRT classification in the Lanjenchi FDP. **A.** Distribution of the three habitats based on the MRT classification, the red square represents the 5.28-ha of the plot for the habitat association in torus translation test; **B.** Windward habitat; **C.** Intermediate habitat; **D.** Leeward habitat.



Leeward habitats were in low lying areas of the plot, where streams occasionally flow through in the summer and the vegetation is less affected by the northeast monsoon wind in winter (Table 1, Fig. 4C). The leeward habitat was so-named to reflect a relatively flat topography and the low influence of the northeast monsoon wind. The leeward habitat contained 109 species. The stem density was relatively low, measuring $7,138 \pm 2,693$ stems ha^{-1} (Table 2). The most abundant species of this habitat was *Psychotria rubra* (Lour.) Poir., which accounted for 11.75% of stem density at this habitat. The basal area of this habitat was 40.90 ± 17.30 m ha^{-1} . *Schefflera octophylla* (Lour.) Harms was the most abundant species, comprising 19.54% of basal area at the leeward habitat.

Habitat association

Based on the torus translation test, 109 significant associations (47 positive and 62 negative ones, $\alpha = 0.05$ level of significance for a one-tailed test) were observed in a total of 78 species with a count of ≥ 50 individuals. No species was positively correlated with more than two habitats. According to each species' relationship to respective habitats, species in Lanjenchi FDP can be placed into the following distribution classes: windward, leeward, intermediate, general, mid-windward, and mid-leeward (Supplementary Table).

Among these six distributed species types, three distributed types have a strong positive association in a specific habitat. For the windward distributed species, they are defined as having a positive association ($\alpha < 0.05$) with windward habitat and negative or no correlation with intermediate and leeward habitat. Among these 22 windward distributed species, there are ten species have significantly positive associations ($\alpha < 0.01$) to windward habitat. The intermediate distributed species are defined as the species which are positively associated ($\alpha < 0.05$) with the intermediate habitat and have negative or no correlation with windward and leeward habitat. There are 15 intermediate distributed species ($\alpha < 0.05$), and 8 species ($\alpha < 0.01$) have a significant positive association with the intermediate habitat. Leeward distributed species are the species that are positively associated ($\alpha < 0.05$) with leeward habitat and have negative or no correlation with intermediate and windward habitat. There are 12 leeward distributed species ($\alpha < 0.05$), and seven species ($\alpha < 0.01$) association with the leeward habitat.

The species that negatively correlate with leeward habitat and have no association with windward or intermediated habitat are defined as mid-windward distributed species. Among the four mid-windward distributed species, three species have significant negative with leeward habitat. Mid-leeward distribution species have a negative correlation with windward habitat and have no significant association with the

leeward and intermediate habitat. Among the 11 mid-leeward distributed species, six species have a significantly negative association with windward habitat. The species with no obvious positive or negative correlation with any habitat are defined as general distributed species. All the distributed species are listed in Supplementary Table.

DISCUSSION

The mechanism of the vegetation structure in Lanjenchi FDP

This study classified Lanjenchi FDP into three habitat types. Applying species data and topographic data simultaneously, our findings are in agreement with previous research (Chao *et al.*, 2010), such that the northeast monsoon wind is the major factor driving the species-habitat association in Lanjenchi FDP. From the MRT analysis with five topographic variables, we found that wind exposure value and aspect are primarily responsible for habitat structuring (Table 1, Fig. 3). Trees at the windward habitat suffer stronger northeast monsoon wind than in the other two habitats.

In response to northeast monsoon wind, the plants may alter their morphology to adapt to the wind velocity (Lawton, 1982; Grace, 1988). Trees may have smaller and thicker leaves (Martin and Clements, 1935; Grace and Russell, 1977), more flexible wood (Telewski, 1989), and higher stem hydraulic conductivity (Smith and Ennos, 2003) in wind-affected areas. Moreover, the multi-stemmed structure of mature trees can be construed as evidence demonstrating the adaptation of the community to a stressful environment (Fajardo and McIntire, 2010; McIntire and Fajardo, 2011). Therefore, the windward habitat is composed of many small trees that are responding to and are resistant to the environmental factors of the northeast monsoon wind.

Species association in Lanjenchi FDP

Varying levels of wind effect can also cause varying species composition within the forest. Our results showed that the species have various associations in different habitats of Lanjenchi FDP, and 81% of the tree species have a strong positive association in these three habitats. The different levels of wind effect within Lanjenchi FDP may cause a strong species-habitat association. In comparison, the plot on Barro Colorado Island, Panama, has 37% of species significantly associated with habitats (Comita *et al.*, 2007), and Korup Forest Dynamics Plot in Cameroon has 63% of species significantly associated with habitat (Chuyong *et al.*, 2011). In the high topographically heterogeneous area, Sinharaja in Sri Lanka (Gunatilleke *et al.*, 2006), Nonggang in China (Guo *et al.*, 2017), and Lambir in Sarawak (Davies *et al.*, 2005), 79%, 85%, and 86% of the species are significantly related to habitat,



respectively. Phillips *et al.* (2003) indicated that the high degree of habitat specialization (nearly 80%) for relatively well-sampled species in the Amazon, represents the highest record to date for similar forest studies. Chuyong *et al.* (2011) explained that the difference in the proportion of species showing significant habitat association may be partly due to variation in the strength of niche differentiation in the landscape captured within the plot area.

Previous research indicated that with the increase in fine-scale topographic and edaphic heterogeneity, there may be a concomitant increase in the proportion of habitat specialists (Harms *et al.*, 2001; Potts *et al.*, 2004). In addition to topographic factors, the strong species-habitat association might be a result of the northeast monsoon wind in the winter in our study area. This research identifies and proposes six species distributions by the species-habitat association. We found that our results support the strong wind impact would have a high species-habitat association. In a comparison of these six distribution types, the windward habitats have the highest number of distribution species. For example, *Illicium arborescens* Hayata is the most abundant species among the windward distributed species and it is also the most abundant species among the whole plot. Moreover, eight out of 22 species are rare species of Taiwan, including critical endangered (*Lithocarpus formosanus* (Skan) Hayata), endangered (*Nageia nagi* (Thunb.) Kuntze and *Podocarpus macrophyllus* (Thunb.) Sweet), vulnerable (*Camellia hengchunensis* C.E. Chang and *Symplocos shilanensis* Y.C. Liu & F.Y. Lu), and near threatened (*Eurya nitida* var. *nanjenshanensis* C.F. Hsieh, L.K. Ling & S.Z. Yang, *Myrsine seguinii* H. Lev., and *Ilex lonicerifolia* var. *matsudae* Yamamoto) species. The rarity of the species which prefer windward habitats highlights the unique environment role of the habitat for niche differentiation to species diversity. On the other hand, the leeward habitat in the valley and is not seriously affected by the northeast monsoon wind in the winter. The trees species in leeward areas tend to be large and tall, and well-adapted to the relatively high humidity in this habitat. For example, *Helicia formosana* Hemsl., *Sauraia tristyla* var. *oldhamii* (Hemsl.) Finet & Gagnep., *Melicope semecarpifolia* (Merr.) T.G. Hartley, and *Ficus fistulosa* Reinw. ex Blume are common species that tend to live in the humid lowland area in Taiwan, which also dominant the leeward area in the Lanjenchi FDP.

In comparison with this research and previous studies, Hsieh *et al.* (1992) described the distributions of four species using their abundance in each habitat and the most similar species distribution was in the windward distributions. Except for *Illicium arborescens* Hayata and *Tarennia gracilipes* (Hayata) Ohwi, the composition of windward distribution species in this research is the same as those classified by Hsieh *et al.*

(1992). In Hsieh *et al.* (1992), *Illicium arborescens* Hayata has a general distribution, and *Tarennia gracilipes* (Hayata) Ohwi has a leeward distribution. The main difference between the results of Hsieh *et al.* (1992) and this study may be attributed to the different methods and plot size. Hsieh *et al.* (1992) used the abundance of each species in each habitat as their measure of species distribution from the 3-ha Lanjenchi FDP in different habitats. Our research used the results of species-habitat association, which is likely to provide a stronger statistical evaluation of the correlation between species and habitat.

The unique species composition established in windward habitat is likely a result of the unique environmental conditions in this habitat. Several studies have described the nutrient content in the soil, including N, P, S, K, Na, Ca, Mg, and some micro-nutrients. The relative concentration of nutrients likely affects tree height, basal area, and species richness, thereby influencing forest structure (Becknell and Powers, 2014; Bunyavejchewin *et al.*, 2019; Peña-Claros *et al.*, 2012). Guo *et al.* (2017) showed that differences in soil, water, and nutrients influenced vegetation composition in complex terrains with large changes in elevation in a karst region. Tsui *et al.* (2004) found that the differences in elevation and slope caused differences in nutrients between the summit and foot-slope of transects in the Nanjenshan area, leading to different vegetation composition. In Lanjenchi FDP of the current study, the windward habitat, with strong leaching, exhibited higher Mg, Ca, and lower K, N, to which windward distribution species are adapted (Hsieh *et al.*, 1992). Conversely, within the flat leeward habitat, the relatively low leaching rate leads to higher K, N and relatively low Mg, Ca (Hsieh *et al.*, 1992).

Our research provides a new habitat classification scheme of Lanjenchi FDP based on the topography data using the MRT method. Comparing with the habitat types classified by TWINSPAN method, and correlated with environmental data using the DCA method in Chao *et al.* (2010), our classification was based on environmental data and species data simultaneously. Although the methods applied in Chao *et al.* (2010) can help to understand the correlations of environmental variables on vegetation structure and composition, we have demonstrated an independent method to support their findings. Moreover, once we need to discuss the relationships within the species-habitat association, the vegetation type should not be used to classify habitat type, to avoid self-explanation and circular arguments. Nonetheless, Chao *et al.* (2010) showed that the northeast monsoon wind mediated by topography position correlates with species composition. Our study also supports that topography niche is the key factor in determining species assemblages in Lanjenchi FDP.

In conclusion, our study has demonstrated a strong



species-habitat association relationship in Lenjenchi FDP which is directly related to topography positions and is likely to be mediated by the influences of monsoon wind. The unique niche caused by the northeast monsoon wind has allowed many regionally rare species to survive at tropical Taiwan.

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