

東海大學生命科學系
碩士論文

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墾丁熱帶喀斯特森林中紅柴(*Aglaia formosana*)

與黃心柿(*Diospyros maritima*)之棲地關聯

Habitat associations of *Aglaia formosana* and *Diospyros maritima*
populations in Kenting tropical karst forest

研究生：蕭逸柔

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中華民國 107 年 6 月

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墾丁熱帶喀斯特森林中紅柴(*Aglaia formosana*)與黃
心柿(*Diospyros maritima*)之棲地關聯

(英文)

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maritima* populations in Kenting tropical karst forest

經本委員會審定通過，特此證明。

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中文摘要

熱帶樹種的空間分布及形成過程可以反映出樹種之間或是與環境因子之間的交互關係，而這也被認為是樹種共存的機制之一。熱帶森林樹種在空間上大多呈現聚集分布，這可能是源自於樹種具有棲地偏好，使其在各類棲地間存活率不同，進而導致樹種在空間分布上並不均勻。因此，樹種族群的生長表現與棲地的關聯，是研究森林生態過程的重要問題。此外，植物的生理反應常被用於檢視環境因子對植物的影響，透過生理反應，可能可以輔助說明棲地對植物的影響。因此，本研究從族群與生理層次，探討熱帶喀斯特森林中的紅柴(*Aglaia formosana*)及黃心柿(*Diospyros maritima*)的棲地偏好。本研究的主要問題如下：(1)不同棲地下的小苗、小樹及大樹族群是否具有不同的存活表現及新增？(2)小樹族群在不同棲地下的生理表現是否有差異？並檢視在該森林中，不同季節的生理反應是否有差別。研究結果顯示，紅柴與黃心柿大樹死亡率，在不同棲地間沒有顯著差異。但在小樹階段，紅柴死亡風險在谷地較高，礁頂較低；而黃心柿小樹死亡風險則在礁頂較低。紅柴的小苗新增數量，在棲地間也有同樣的趨勢。因此，新增及存活率在兩樹種的小苗及小樹可看出具有棲地關聯，但是在大樹則無趨勢。在生理層次，小樹族群的有效光量子產量($\Delta F/F_m$)，

在谷地顯著較低，且有效光量子產量與土壤水分具備顯著二次式函數關係。透過這個結果，我們可以推斷小樹及小苗族群與棲地具有關聯，且土壤深度可能為重要的因子。綜合族群存活、新增表現與生理反應，可以更完整的解釋棲地關聯。本研究將有助於以生理生態學觀點出發的森林動態研究，並探討生理表現對解釋熱帶森林物種的族群動態、棲地與空間分布的可能性。

關鍵字：族群生態假說、葉綠素螢光、生長階段

Abstract

Spatial distribution and the formative process of tropical tree species can reflect the interaction between tree species or correlation with environmental factors. It is considered as one of the coexistence mechanisms for tropical forests. Many tropical tree species are aggregated in space. Such aggregation pattern may originate from habitat preference of tree species. Survival rates and recruitment of trees species may differ among habitats and lead to an uneven distribution among habitats. Therefore, understanding the habitat association of tree species is important to study forest dynamics. In addition, physiological performances have been using to evaluate the effect of environmental factors which may be used as indices to explore habitat association of tree species. The aim of this study is to understand the habitat association of two dominant species, *Aglaia formosana* and *Diospyros maritima*, at both demographic and physiological levels in a tropical karst forest. The specific objectives include (1) to compare mortality and recruitment rates of seedlings, saplings, and trees among habitat, (2) to study the physiological performance of saplings among habitats. Seasonal changes in environmental factors are also considered. The results indicated that mortality of trees did not differ significantly among habitats. Saplings of *A. formosana* in valleys were at a higher risk of mortality than those on slopes and top-reefs; saplings of *D. maritima* were at lower risk of mortality on top-reef. Recruitment of *A. formosana* exhibited a similar pattern with saplings. Therefore, the demographic hypothesis was supported with

saplings and seedlings. Moreover, effective quantum yield ($\Delta F/Fm'$) of saplings was significantly lower in valleys than the other two habitats. It can be best described by quadratic functions of soil moisture. In this study, we demonstrated that demographic performances of saplings and seedlings associated with habitat. Further, soil depth is critical for two study species in this forest. An integration of demographic and physiological data is usefully to explain habitat association of tree species. This study is valuable to evaluate researches of forest dynamics with eco-physiological perspective and understand coexistence mechanism of tree species in the tropical forest.

Keyword: Demographic hypothesis, Chlorophyll fluorescence, life stages

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Introduction

Understanding patterns and processes underlying spatial distributions of tree species has been one of the key tasks in plant ecology. Especially, the spatial distribution of tree species is suggested to contain spatial signatures of interactions between individual plants and their neighborhood. Studying spatial patterns and their formation, therefore, have been applied to understand coexistence mechanisms of tree species (Harms et al. 2001). Many tree species are not distributed randomly but aggregated in space. This aggregation was observed in both tropical and temperate forests worldwide (He et al. 1997, Clark et al. 1999, Russo et al. 2005, Yamada et al. 2007, Zhang et al. 2010, Chuyong et al. 2011, Kanagaraj et al. 2011, Kenfack et al. 2014, Lan et al. 2016, Guo et al. 2017). Multiple mechanisms, including both neutral- and niche- based processes have been proposed to explain the aggregation distributions, such as habitat association and dispersal limitation (Gilbert and Lechowicz 2004, Lin et al. 2011).

Among many mechanisms underlying tree distribution, habitat association was suggested to be an important mechanism. It is suggested that non-random distributions of trees were, in part, determined by habitat preference of tree species (Harms et al. 2001, Guo et al. 2017). Abiotic conditions in favorable habitats of a certain species are suitable for the species and lead to tree aggregation in the habitat. Such habitat association of tree species may be

reinforced by differential demographic performances of individual plants among habitats. Higher recruitment and survival of individual plants were expected in their favorable habitats. As a result, habitat-specific demography would be observed. For example, Russo et al. (2005) proposed that spatial distribution of tree species is correlated with soil types, defined by soil texture, moisture, and fertility, in a Malaysian tropical forest. Survival and growth rates were parallel to their spatial distributions. Tree species were predicted to grow and survive better in their specialized habitats. A similar hypothesis was suggested by Kenfack et al. (2014). They sought to explain demographic variation among different habitats defined by topographic factors.

However, the proposed demographic advantages in favorable habitats were not fully supported by the previous two studies. Despite different survival and growth rates were detected among habitats, the differential demographic patterns were not consistent with species' habitat association (Russo et al. 2005, Kenfack et al. 2014). Several reasons were proposed to explain these inconsistent results. First, habitat-specific demography may mainly occur in early life stages (Kanagaraj et al. 2011). Seedlings and saplings are more vulnerable to environmental stresses than trees and may be more sensitive to variation in habitat quality and form a stronger species-habitat relationship than trees. Secondly, the immediate impact of habitat conditions on plant performance may not be able to be demonstrated by demographic variation among habitats. Demographic performances represent cumulative effects over

time. When environmental stresses occur, trees may not die immediately. In this case, impacts of environmental stresses may not be reflected in demographic patterns. Especially, habitat quality may differ seasonally or annually. Habitat differences in demography may be more pronounced with environmental stresses, such as drought (Fortunel et al. 2016, Levine et al. 2016, Zuleta et al. 2017). Thirdly, habitat association of some tree species may result from habitat-specific recruitment (Comita et al. 2007). It is suggested that higher seedling establishment in favored habitats of certain tree species may occur, although such association may decrease along with life stages (Comita et al. 2007). Thus, it is necessary to understand habitat association of tree species during different life stages.

To reconcile the existing inconsistency, two approaches are proposed. First, demographic variation among habitats should be studied during different life stages, from seedling, sapling to tree. This way, critical life stages for habitat-specific demography may be identified. Secondly, physiological indices may be used to detect a short-time impact of habitats on individual plants. Physiological performances of plants are expected to decrease before they die. Therefore, I suggested that physiological indices can be used to recognize stressed plants and serve as complementary variables to study habitat association of tree species.

Quantum yields, estimated by chlorophyll fluorescence technique, have been used to measure the photosynthetic efficiency of photosystem II (PSII).

Quantum yields are sensitive to environmental stresses, such as drought and flood (Zheng et al. 2009, Anjum et al. 2011, Polacik and Maricle 2013, Yu et al. 2015, Lukatkin et al. 2017). Furthermore, it is widely applied as indicators to evaluate the response of plants to abiotic factors for decades. When chlorophyll absorbs light energy, photosynthesis will be driven and the other energy will be emitted as heat and fluorescence (Maxwell and Johnson 2000, Baker 2008, Murchie and Lawson 2013). These three processes are in competition and influenced by ambient lighting and other environmental factors. Such processes can be estimated through chlorophyll fluorescence technique. Quantum yield as one of the key parameters obtained by chlorophyll fluorescence technique, therefore, has been suggested to be used an indicator of physiological performances of plants (Zheng et al. 2009, Anjum et al. 2011, Polacik and Maricle 2013, Yu et al. 2015, Lukatkin et al. 2017).

We predicted that physiological performances of plants vary with habitats since individuals may experiences habitat-specific stress. Plants perform better in their favorable habitats, and they are correlated with key environmental factors. Besides, physiological differences among habitats may be enhanced by means of seasonal changes. For instance, plants on the ridge may undergo stronger water-shortage than in the valley during dry seasons. Comparing physiological changes within a year may reveal the influence of seasonal changes in different habitats. Photosynthetic parameters, which are measured by chlorophyll fluorescence devices, can be used to estimate the rate of electron

transport in photochemical reactions and photochemical quenching of light energy in PSII (Appendix S1.). In this study, to understand the influence of habitat on photosynthetic efficiency of woody plants, the proportion of electron transport in PSII in the nature light condition was used to represent physiological state of plant.

The Kenting Uplifted Coral Reef Nature Reserve, also known as Kenting Karst Forest, is topographically heterogeneous and characterized by uplifted coral reefs. Spatial distribution of many tree species is determined by habitat heterogeneity and dispersal limitation in the forest (Lin et al. 2011). Mechanisms that may contribute to the spatial patterns, however, have not been explored. Studying impacts of habitat heterogeneity on demographic and physiological performances can be a critical step to understand the formation of spatial patterns in the forest.

The objective of this study is to understand habitat association of two dominant species, *Diospyros maritima*, and *Aglaia formosana*, from demographic and physiological perspectives in a tropical karst forest. Specifically, the following questions were addressed: (1) Did demographic performances (recruitment and survival) of seedlings, saplings, and trees vary among habitats? (2) Were physiological performances different among habitats and correlated with environmental factors? (3) Were seasonal changes in abiotic factors enhance physiological differences among habitats? It was predicted that

habitat-specific demography would be detected. Such demographic differences were expected to be stronger in earlier life stages. Finally, physiological performances were predicted to be reduced in plants' unfavorable habitat during different seasons.

Methods & Materials

Study site & species

This study was carried out in the Kenting Karst Forest Dynamics Plot (Kenting FDP) which is categorized as a tropical seasonal forest. The Kenting FDP (21°57'58" N, 120°49'7" E, Fig. 1a) is located in the Hengchun Peninsula, Taiwan. The Hengchun Peninsula is characterized by tropical monsoon climate with warm temperatures year-round. According to the weather data provided by the Central Weather Bureau, the mean temperature of January is 20.9°C and mean temperature of August is 28.4°C. They represented the coldest and hottest month, respectively (Wu et al. 2011). The average annual precipitation is about 2000 mm, 87% of which concentrates in June to November. A 6 months dry season occurs from October to April. The topography of this forest was formed by Miocene rock and uplifted coral reef of middle to last Pleistocene age (Wu et al. 2011).

The Kenting FDP is 10 ha in size (400 m × 250 m) that was established in 1996 by Dr. I-Fang Sun. All woody stems with breast height (DBH) ≥ 1 cm within the plot was tagged, mapped and identified to species (Condit 1998). Three censuses were completed up to date in the FDP (2001, 2008, and 2013). The first census was completed by Dr. I-Fang Sun and Taiwan Forestry Research Institute (TFRI) in 2001. Fully re-censuses were finished by TFRI in 2008 and 2013 respectively (Wu et al. 2011).

According to the 2008 census, dominant family within the Kenting FDP belong to Euphorbiaceae and Moraceae (Wu et al. 2011). The most abundant species was *Diospyros maritima* in the 2008 census within the 10-ha plot. During the census, 21823 individuals of *D. maritima* were recorded. In addition, *Aglaia formosana* was also abundant in the plot. It was recorded that 1635 individuals of *A. formosana* are monitored in the Kenting FDP. Besides, a seedling survey (see below for details) indicated that 1035 seedlings of *D. maritima* and 4085 seedlings of *A. formosana* were recorded in 144 seedling plots (1.5 m x 1 m) during 2014-2018 (Lin et al. 2011). Based on the above two datasets, only *D. maritima* and *A. formosana* have sufficient sample sizes across different life stages (seedling, sapling, and trees). Thus, these two species were chosen as the study species in this study (Figure 2, Appendix S2).

Topographic variables and habitat classification

The Kenting Karst Forest Dynamics Plot (250 m × 400 m, 10 ha) was divided into 1000 quadrats (10 m × 10 m). Elevation of the corners of each quadrat was measured (Sun, unpublished data). Three topographic variables, mean elevation, convexity, and slope, were derived from the elevation measurements for each quadrat (Lin et al. 2011).

Mean elevation of each quadrat was obtained by averaging elevation measurements of four corners of each quadrat. Convexity was defined as the

elevational difference between the target quadrat and 8 neighboring quadrats. The slope was measured with a horizontal plane of four triangular planes and estimated the mean angular deviation (Harms et al. 2001, Su et al. 2010). Soil depth was measured within a radius of 1 m from the coordinate post of each quadrat (Wang and Chang, unpublished data). Due to the length limitation of the soil-digger, the deepest depth was recorded at 100 cm. Depth was recorded as 0 cm, if the plot was rocky and soilless.

These four variables, mean elevation, convexity, slope and soil depth, were included in Multivariate Regression Tree (MRT) analysis for habitat classification. The MRT analysis divided the habitat by referring critical and efficient topographic variables. The processes of division were constructed as a tree model with critical variable and the estimated value. In this classification, “mvpart” R packages was used for MRT analysis (De’ath 2002, De’ath 2007). According to the result of the MRT analysis, Kenting FDP was classified into three different habitats: valley, slope, and top reef (Figure 3). The valley habitat has the deepest soil (mean soil depth ≥ 67.19 cm) and negative convexity (mean convexity = -0.843 m) and gentle slope (mean slope = 12.768 degree) in the Kenting FDP. Negative convexity refers to concave surfaces that may be flooded during rainy seasons (From April to October). The top-reef habitat is characterized by shallow soil (mean soil depth < 26.69 cm), convex surfaces (mean convexity = 0.925 m) and steep slope (slope = 31.187 degrees). The slope habitat (26.69 cm < mean soil depth < 67.19 cm, mean convexity = -0.351 m,

mean slope= 24.78 degrees) has intermediate level of topographic heterogeneity in comparison with the other two habitats (Appendix S3). A total of 166 quadrats belonged to the valley habitat; 505 quadrats were classified into the slope habitat and 329 quadrats belonged to top-reef (Figure 4).

Habitat-specific demography

1) Habitat-specific demography during the seedling stage

To study demography of seedlings, 144 seedling plots were established in 2007 centering 72 seed traps along 4 transects within the FDP (Lin et al. 2017). Two seedling plots were established adjacent to each of the 72 seed traps (1 m × 1.5 m, Figure 1c). Seedlings were defined as DBH less than 1 cm. All woody seedlings within seedling plots were tagged, identified and mapped every three months since July 2007. Survival status of each seedling was also checked. Height and number of leaves of each seedling were measured (Lin et al. 2017). Sixteen seedling censuses during January 2014- April 2018 were used for this study.

All seedling plots were assigned to one of the three habitats based upon the same definition as above. The locations of the center seed trap of each pair of seedling plots were used to define the habitat. Among the 144 seedling plots, 36 plots located in valleys, 66 plots belonged to the slope habitat and 42 plots located in the top reef.

2) Habitat-specific demography during the sapling and tree stages

The 2008 and 2013 censuses by Taiwan Forestry Research Institute (Wu et al. 2011) were used to study demography of saplings and trees. Median DBH of each species in the 2008 census was used to distinct saplings and trees. Median DBH of *D. maritima* and *A. formosana* was 3.6 cm and 3.1 cm respectively.

All individuals of two species, *D. maritima*, and *A. formosana*, in Kenting FDP, were assigned to one of three habitats by their locations in the 2008 census. Newly recruited saplings were defined as individuals that were first tagged in 2013. Survival rates of tree and sapling were evaluated based on the status of the two censuses.

Physiological measurements: Effective quantum yield

Effective quantum yield (ϕ_{PSII} ; $\Delta F/F_m$ ') of 250 individuals were measured in July 2017 and February 2018. For each of individual, we chose 3 mature and shade leaves to measure effective quantum yield following method in Lukatin *et al.* (2017). The effective quantum yield was measured with MINI-PAM (Heinz Walz GmbH, Effeltrich, Germany). Individuals of *D. maritima* and *A. formosana* were subsampled from 1000 quadrats (Figure 5). In sampling

quadrats, 15 quadrats were valley habitat, 14 quadrats were slope habitats and 13 quadrats were top-reef habitats (Table 1).

Environmental factors correlated with effective quantum yield

Effective quantum yield of PSII are sensitive to the temperature, soil moisture, and light quantity. Three environmental factors mentioned above were measured to explore their relationships with effective quantum yield. Leaf temperatures were measured with MINI-PAM while measuring effective quantum yield. Light quantities near each individual were also measured for an average of 15 seconds by using LI-190R quantum sensor (LI-COR, USA). Soil moisture of each sampling quadrats was measured at depths of 10 cm and 20 cm. Soil moistures were measured in both Jul. 2017 and Jan. 2018. The location of soil measurement (i.e. soil dig) was within a 3 m radius of the sampled individual. If there were more than one sampled individual in the plot, we took the center of all of sampled individuals as the location of soil measurement. A hole was dug at each sampling quadrat at depths 10 cm and 20 cm, and soil moistures were measured by using GS3 sensor (Decagon, USA).

Data analysis

1) Demography of seedlings

Survival analyses were used to analyze seedling survival in the seedling plots. The Kaplan-Meier method was used to estimate survival curves of

seedlings. Effects of habitat type on seedlings were evaluated by mixed effects Cox models. Survival analyses were conducted by Packages of Survival (Therneau and Grambsch 2013) in R.

2) *Demography of saplings and trees*

General Linear Mixed Model (GLMM) was constructed to analyze survival of trees and saplings. Survival of trees and saplings during 2008-2013 was included in the GLMM as the response variable; Habitat type was treated as a fixed factor and quadrats were used as random effects. A binomial error was used in the GLMM. Recruitment of seedlings, saplings, and tree among habitats were compared using χ^2 test. lme4 package in R was used to run GLMM.

3) *Effective quantum yield*

The comparisons of effective quantum yield among habitats were examined by one-way Analysis of variance (ANOVA). Before using ANOVA, Shapiro-Wilk test was used to check for normality. The comparison of effective quantum yield between seasons was tested by paired *t*-test (adjusted *p*-value = 0.017). Seventeen individuals were wilted, dead, missing or covered by lianas when the second field survey was conducted in February 2018. Thus, their effective quantum yields were not measured (Table 1). Relationships between effective quantum yield and two environmental variables, soil moisture, and light, were explored by polynomial Regressions. Several plants were eliminated from the regression analysis with soil depth of 20 cm due to missing values. One of

quadrats on the top-reef was difficult to dig at depth 20 cm because of the roots of plants. Eight individuals at the same quadrat were eliminated from the regression. Besides, the deepest soil depth of a quadrat on the top-reef habitat is 18 cm, therefore, soil moisture at 18 cm was measured, instead of soil moisture at 20 cm. A set of full models was first constructed and the best model was selected by a stepwise procedure. R was used for data analysis (R Core Team 2013).

Results

Demographic performances

Overall, 1,035 and 4,084 new recruited seedlings of *D. maritima* and *A. formosana* were identified in the seedling plots during 2014-2018, respectively (Table 1). In the 2008 census, there were 11,018 saplings of *D. maritima* and 823 saplings of *A. formosana* (Table 1). Meanwhile, 10,805 and 812 trees were found for *D. maritima* and *A. formosana*.

1) Habitat-specific recruitment during the seedling and sapling stages

Habitat-specific recruitments were detected for both species (Figure 6). Recruitment of *D. maritima* was few at most times, but it reached a peak in July 2015. A test of goodness-of-fit indicated that the number of recruited seedling differed significantly among habitats in July 2015 ($\chi^2 = 8.53$, $df=2$, $p=0.01$, Figure 6a). The density of newly recruited seedlings was the highest on slopes. In contrast, the highest density of recruits of *A. formosana* occurred on top-reefs (Figure 6b). Recruitments of *A. formosana* peaked every October during 2014-2018. Results of goodness-of-fit during the annual peaks indicated that recruitment of *A. formosana* varies significantly among habitats.

On the other hand, the number of newly recruited saplings of *D. maritima* and *A. formosana* differed significantly among habitats according to χ^2 tests (Table 2). For both species, a higher density of recruits was detected on top reefs.

2) Habitat-specific survivorship during different life stages

Habitat-specific survivorship was demonstrated during the seedling and sapling stages, but not for the tree stage (Tables 3-5). The patterns, however, varied between the two study species. During the seedling stage, habitat-specific survivorship was only detected in *D. maritima* (Figure 7, Table 3). Results of mixed effects Cox model showed that mortality hazard of *D. maritima* was significantly lower on top-reefs than slopes (Table 3). In contrast, seedling survivorship of *A. formosana* did not differ among habitats significantly. During 2014-2018, median survival time for seedlings of *D. maritima* was 8-10 months and 15-18 months for *A. formosana* according to the Kaplan-Meier method (Figure 7). For saplings, results of GLMM suggested that survival of both species was significantly higher on top reefs than the slope habitat. Survival rates of *A. formosana* saplings showed the lowest survival rate in valleys, but survival rates of *D. maritima* saplings in valleys were not differing from slope habitat (Table 4). During the tree stage, survival rates of both *D. maritima* and *A. formosana* did not differ significantly among habitats (Table 5).

Physiological performances

Effective quantum yield ($\Delta F/Fm'$) were measured in 131 individuals of *D. maritima* and 119 individuals of *A. formosana* in 42 quadrats (Table 1).

1) *Effective quantum yield among habitats*

Similar trends of effective quantum yield ($\Delta F/F_m'$) was found for *D. maritima* and *A. formosana*. Effective quantum yields were significantly lower in the valley habitat than the other two habitats for both species (Figure 8). Such patterns were consistent during two seasons (Figure 8).

2) *Seasonal variation in effective quantum yield*

Seasonal variation in effective quantum yield was low for both species (Figure 9). Compared with the July, *D. maritima* exhibited significantly higher effective quantum yield ($\Delta F/F_m'$) on slopes during February, and yet effective quantum yield did not differ significantly between two seasons in valleys and on top-reefs (Figure 9). For *A. formosana*, $\Delta F/F_m'$ in valleys displayed significantly higher value during February. Conversely, $\Delta F/F_m'$ on top-reefs were higher in July, but not reaching a significance level after Bonferroni adjustments (paired *t*-test, $p=0.03$).

3) *Correlation between effective quantum yield and environmental factors*

Using stepwise quadratic polynomial models, soil moisture was selected as an important environmental factor that was correlated with quantum yield (Figures 10-11). Between these two species, R^2 was higher for *A. formosana*. The relationship was stronger for soil moisture at 10 cm (Figures 10-11).

Discussion

Our results suggested that demographic and physiological performances for both *D. maritima* and *A. formosana* varied among habitats (Table 6). Such habitat-specific demography was especially pronounced during the seedling and sapling stages, but trees performed equally among different habitats. At the physiological level, the effective quantum yield of saplings differed among habitats and the lowest in the valley habitat for *D. maritima* and *A. formosana*. The effects of habitats, however, were slightly different for the two study species.

For *D. maritima*, habitat-specific recruitment was detected during both seedling and sapling stages (Table 6). In spite of the significant effects, the impact of habitats on recruitment was not consistent between the seedling and sapling stages. More seedling recruited on slopes than the other habitats, while most saplings recruited on top-reefs (Table 2). On the other hand, the pattern of survival was similar during these two life stages. The highest survival rates were demonstrated on top reefs for both of seedlings and saplings. Based upon survival rates, it was inferred that top reefs were likely to be a better habitat for *D. maritima* than the other habitats. Such pattern may be correlated with drought tolerance of *D. maritima*. A previous suggest that *D. maritima* is able to adapt to drought well (Tsai 2011).

This pattern may also arise from ungulate herbivory. Seedlings of *D. maritima* were heavily browsed by sika deer (*Cervus nippon taiwanus*) during the study period (Lin, unpublished data). Sika deer mostly foraged in the valley and slope areas (Chen 2002). Their activities were particularly high in the valleys (Wu 2007). They consumed a good proportion of vegetation in the habitats. Survival rates of *D. maritima* in the valley and slope areas may be reduced by deer browsing. As a result, survival of seedlings and saplings on the top reefs may be relatively higher than the other habitats. However, *D. maritima* has been considered as a habitat generalist since saplings and trees of *D. maritima* are widely distributed in the Kenting FDP (Figure 2a). The pattern of habitat association for *D. maritima* may not be as distinct as habitat specialists.

For *A. formosana*, habitat-specific recruitment and survival were detected during the seedling and sapling stages (Table 6). The highest density of newly recruited seedlings and saplings occurred on the top reef. Moreover, survival of saplings was significantly higher on the top reef than the other habitats (Table 6). The only exception to the pattern was survival of seedlings. Survival rates of seedlings did not differ significantly among habitats. This demographic advantage on top reefs may result from several potential processes. First, high density of newly recruited seedlings on the top reef may be highly correlated with locations of parent trees on the top reef. It was suggested that the majority of tree species have dispersal limitation (Lin et al. 2011). Seedlings are likely to establish near their parents. Second, the top-reef habitat may be a favorable

habitat for *A. formosana*. According to the 2008 census, the density of *A. formosana* tree was higher on top-reefs than the other two habitats (Figure 2, Table 1).

The observed patterns of habitat association of *A. formosana* were probably driven by abiotic factors of the habitats that reflect habitat requirements of *A. formosana*. The contribution of biotic factors, especially ungulate herbivory, was limited. Previous studies suggested that *A. formosana* was not a preferred species for sika deer (Chen 2002). Sika deer did not browse as heavily as the other studied species in the Kenting FDP. An enclosure experiment suggested that survival rates of *A. formosana* did not differ significantly between deer accessible and excluded plots (Lin, unpublished data).

The results supported our prediction that differential demography among habitats was stronger during the early life stages than the tree stage. Such results were consistent with other studies. For example, Metz (2012) showed that survival of newly recruited seedlings significantly differed among topographic habitats in a tropical forest in Ecuador (Metz 2012). Demographic hypothesis, therefore, should be examined during the seedling or sapling stages. Combining individuals from various life stages or testing the hypothesis with trees only may lead to inappropriate conclusions. One possible reason for the lack of habitat association during the tree stage is the occurrence of density dependence. Density dependence has been widely demonstrated in tropical and subtropical

forests (Webb and Peart 1999, Piao et al. 2013, Zhu et al. 2015, LaManna et al. 2017). The occurrence of negative density-dependence may reduce tree density at a local scale and lessen the degree of tree clustering. As a result, habitat association of trees cannot be detected.

This study was one of the few studies that the hypothesis was tested by individuals in different life stages. And yet, only two species in the Kenting FDP have sufficient sample sizes for the tests across different life stages. It was not clear whether the patterns may be applicable to other species. Alternative statistical methods may be necessary to overcome small sample sizes for such studies.

Habitat-specific physiological performances were found in the study. The pattern was consistent for the two species during the experiment. It was demonstrated that efficiency of photochemistry, which was represented by effective quantum yield, was the lowest in valleys. The results contradicted our prediction. We predicted that saplings performed the worst on the top reefs since plants may experience the highest level of drought stress on top reefs, especially during a dry season (Wu et al. 2011, Lin et al. 2017). Instead, plants perform the worst in valleys. One potential explanation is that soils in the Kenting FDP contain a high proportion of clays (Hseu et al. 2004, Wu et al. 2011). Soils may be poorly drained in the valley. Floods were commonly observed during Aprils to Octobers. Seasonal flooding occurred may create hypoxia stress for roots and

cause effective quantum yield to decrease (Dreyer 1994, Polacik and Maricle 2013, Yu et al. 2015). On the other hand, this high proportion of clays may slow water drainage and maintain a reasonable level of soil moisture on top reefs despite its shallow soil depth.

Furthermore, seasonal variation in physiological performance was detected in one of the three habitats for each species. Significantly seasonal variation in effective quantum yield ($\Delta F/F_m'$) was shown on slopes for of *D. maritima* and in the valley habitat for *A. formosana*, respectively. It is speculated that effect of seasonal changes on different habitats depends on species. The slope habitat is an intermediate habitat for *D. maritima*, and the valley is considered as a stressful habitat for *A. formosana*, especially in February.

Habitat association of tree species may be shaped by multiple environmental factors, such as soil moisture and light availability. In the Kenting FDP, light availability did not differ among habitats; leaf temperatures was not correlated with the parameter (Appendix S4. and Appendix S5.). According to the annual precipitation, July was during a rainy season while February was in the middle of a dry season. However, the measurements of soil moisture in this study were higher during the dry season than the rainy season (Appendix S6.). Such results may be contributed by short-term effects. It rained a few days before the field survey in February. The rainfall may increase soil moisture at the time of measuring. It was not clear whether the level of soil moisture could

last for the whole dry season. Hence, monitoring soil moisture continuously is necessary when studying habitat association in the Kenting FDP.

Conclusion

In this study, habitat-specific demographic and physiological performances were demonstrated for two species, *D. maritima* and *A. formosana* in this study. It was suggested that soil moisture, topography, and adaptation of species are correlated with both demographic and physiological performances. This study suggested that habitat association can be explained sophisticatedly with multiple aspects. To further understand coexistence mechanisms of tree species, and develop management of forest conservation, long-term research in forest dynamics and environmental monitoring are necessary.

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Figures

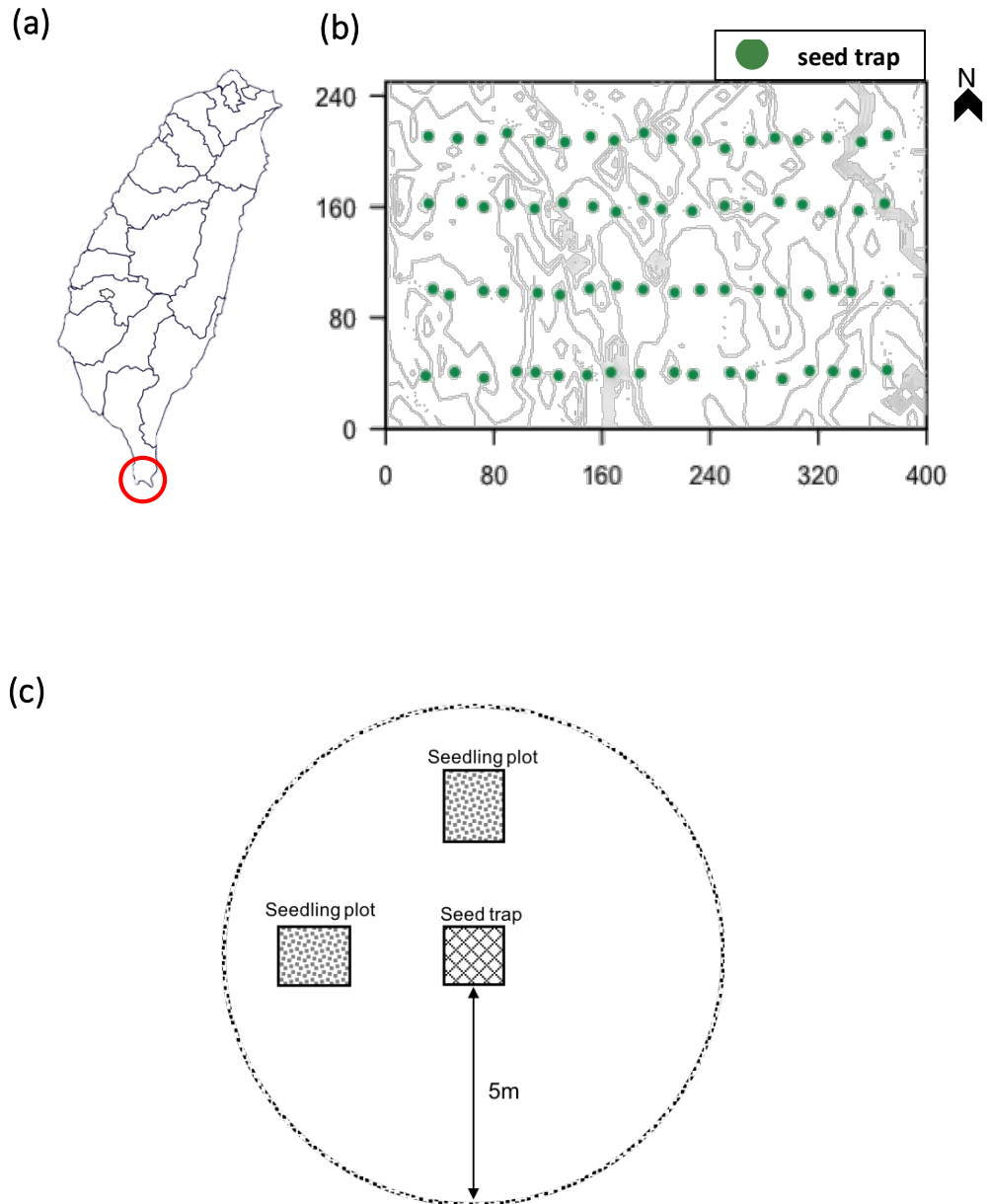


Figure 1. Location of the Kenting Forest Dynamics Plot in Taiwan (a) and spatial arrangement of seed traps and seeding plots (b, c). Seed traps were established along four transect lines (b), and two seedling plots (1 m × 1.5 m) were set up adjacent to each seed trap within a 5-m radius (c).

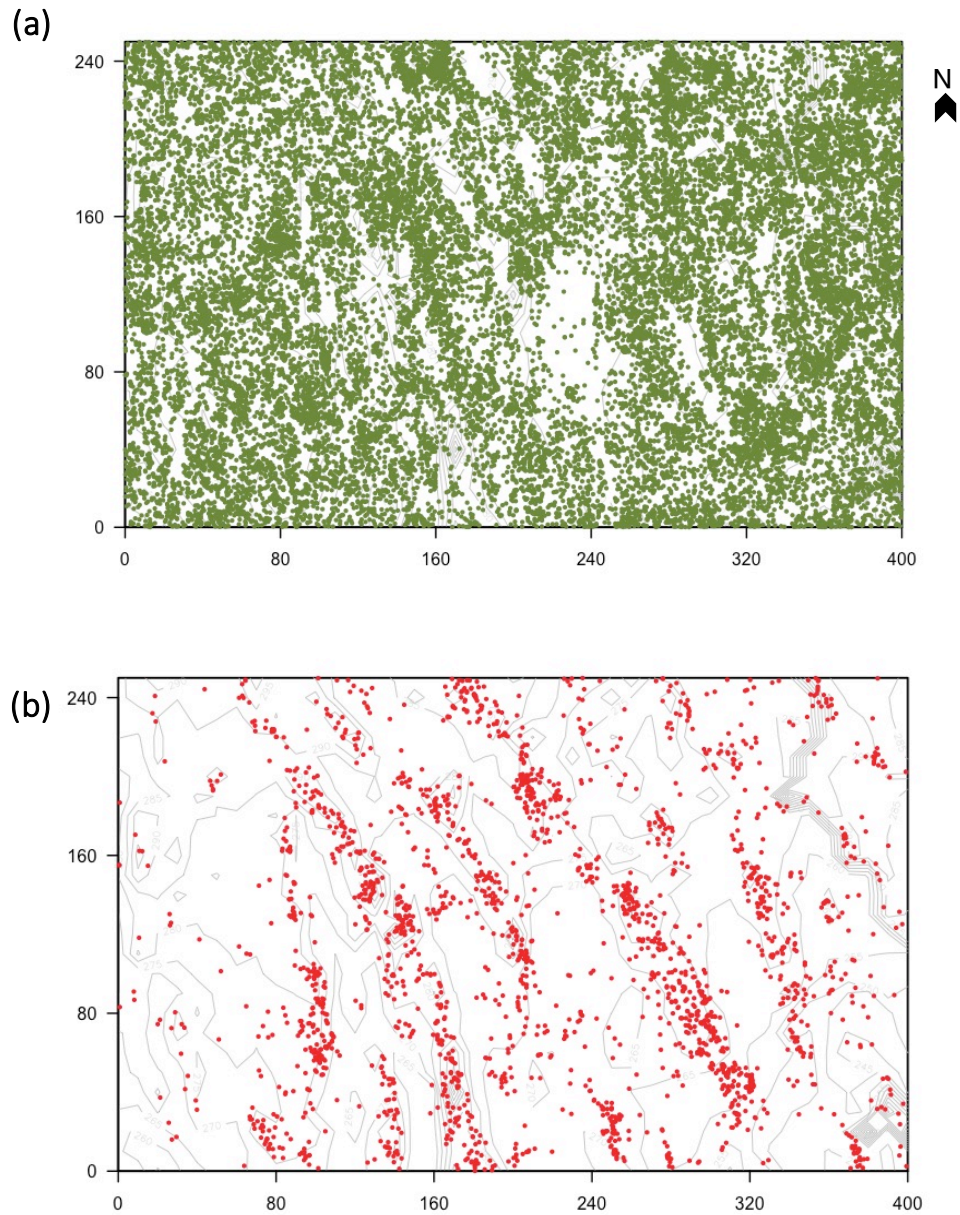


Figure 2. Spatial distribution of *Diospyros maritima* (a) and *Aglaia formosana* (b) in Kenting Karst Forest Dynamics Plot (Kenting FDP). Each point represents a woody plant with $DBH \geq 1$ cm (Data source: Wu et al. 2011).

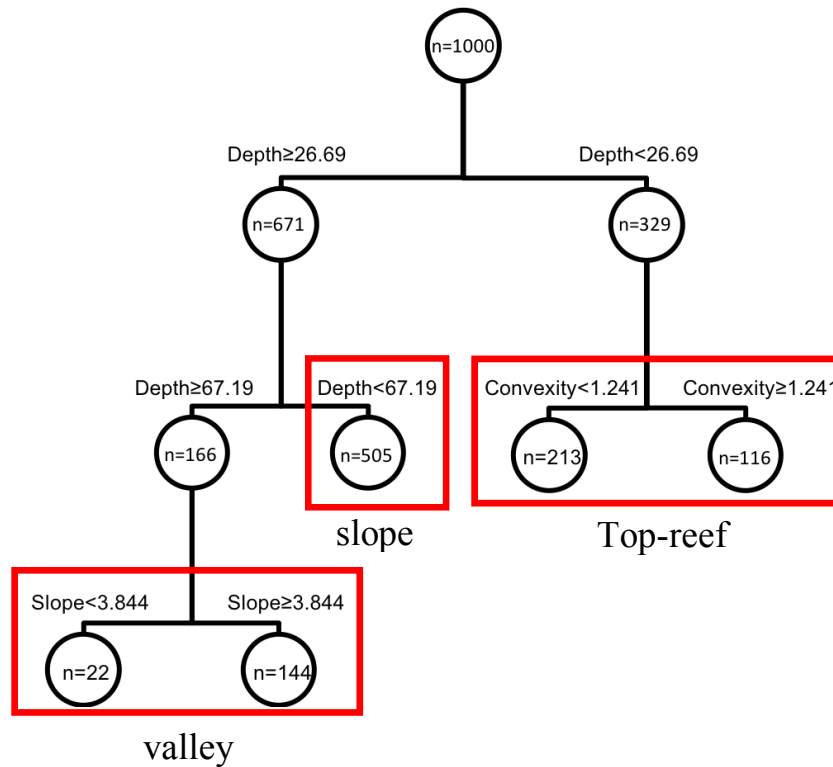


Figure 3. Results of multiple regression analysis used for habitat classification in the Kenting Forest Dynamics Plot. Four habitat variables of each 10×10 m quadrat were considered in MRT analysis and the 2008 census was used (See methods for details).

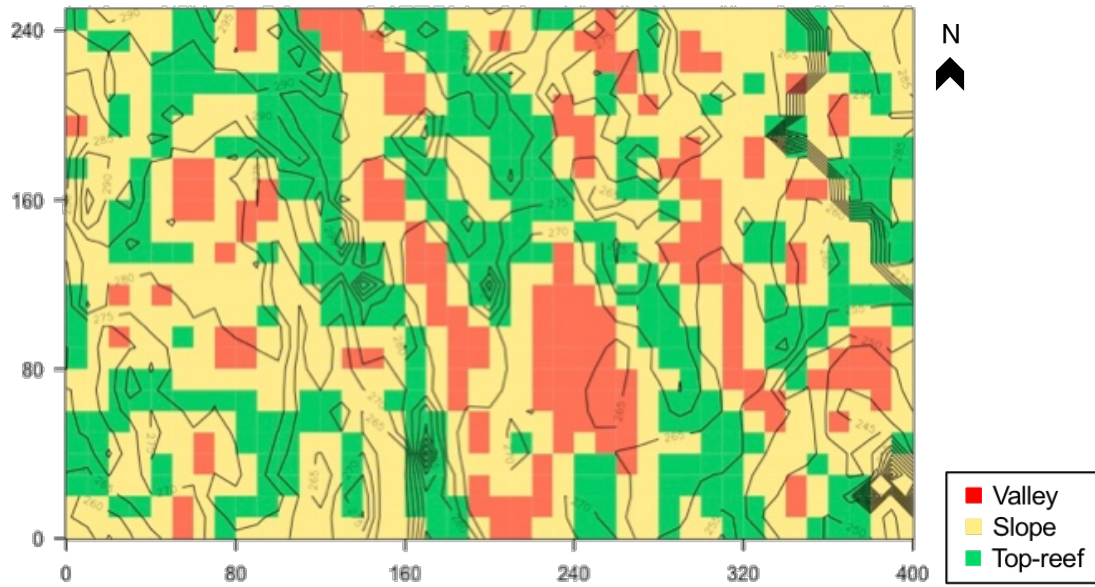


Figure 4. The Kenting Forest Dynamics Plot was divided into three different habitats. Background is contour map of Kenting FDP at a 5 m interval. Each quadrat represents is 10 m × 10 m in size. Red quadrats are valleys habitats, yellow quadrats are slopes habitats and green quadrats are top-reef habitats.

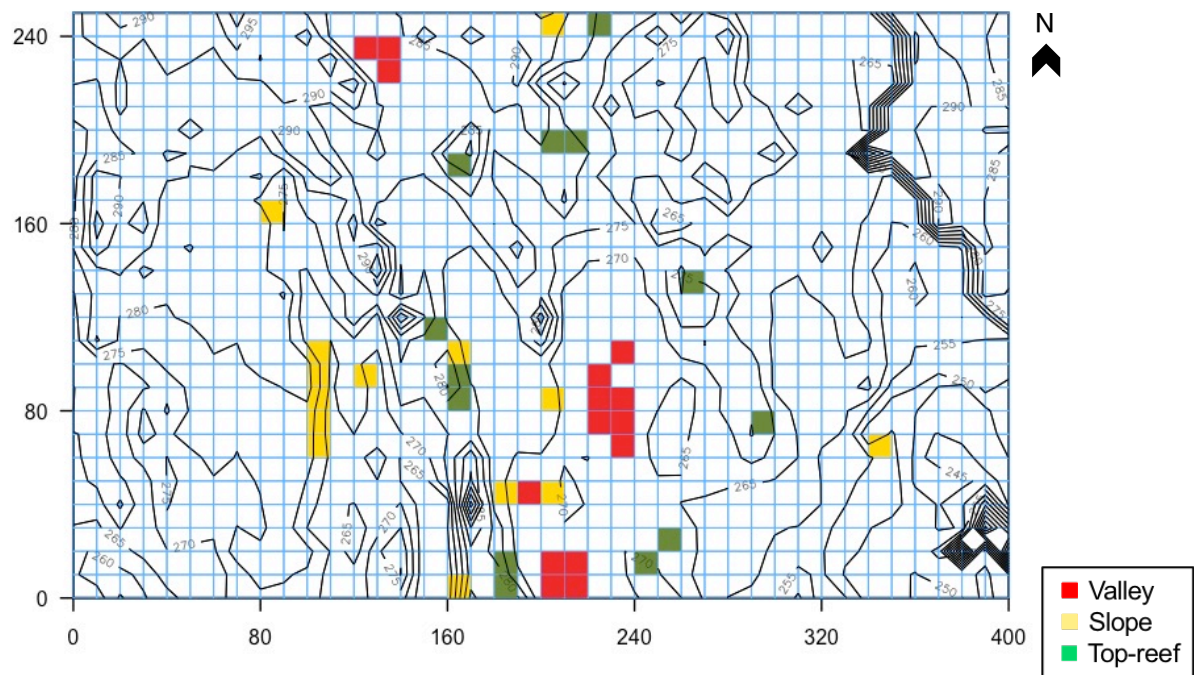


Figure 5. Sampling quadrats of saplings for physiological measurements in the three different habitats in the Kenting Forest Dynamics Plot. Red quadrats refer to the valley habitat; yellow quadrats belong to the slope habitat and green quadrats indicate top reefs.

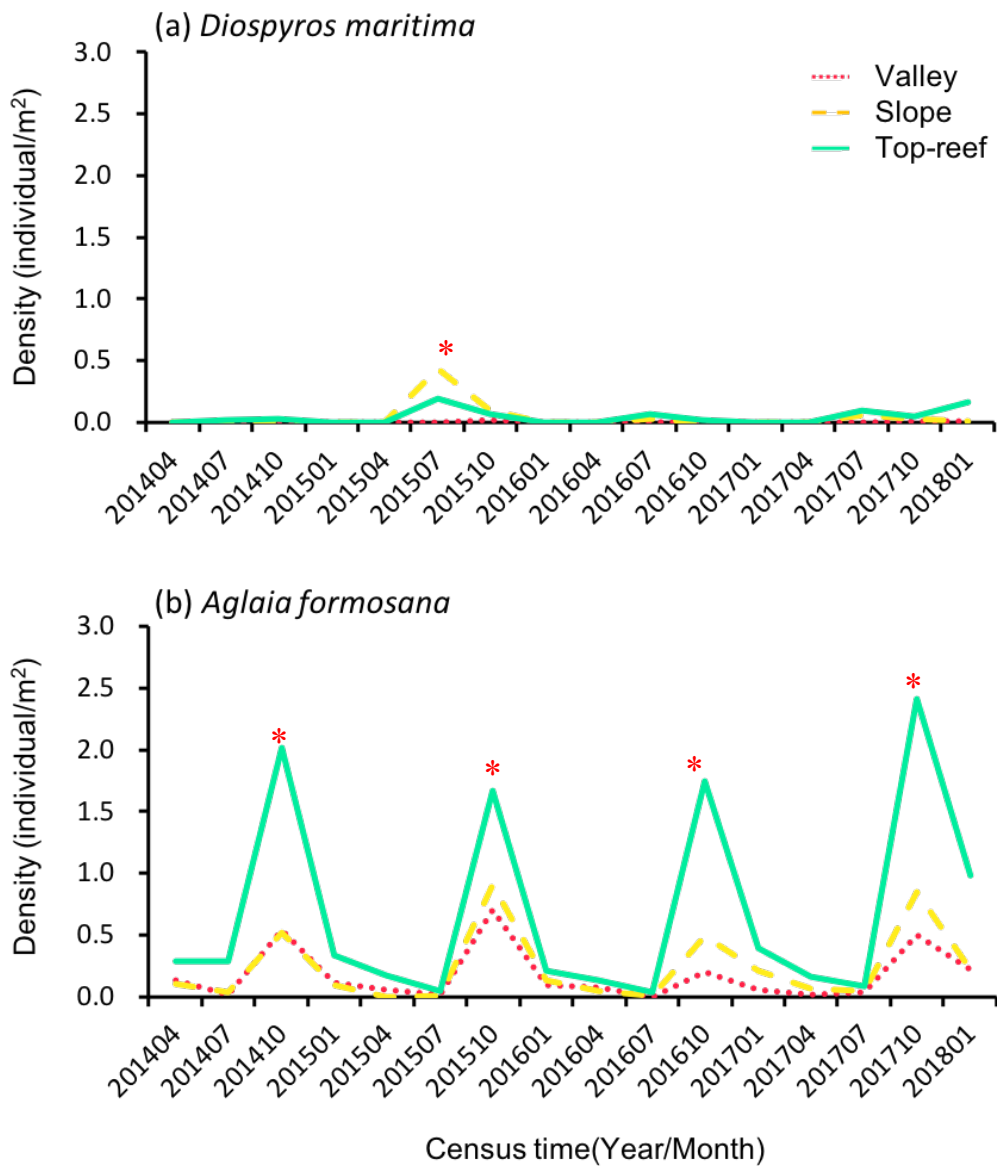


Figure 6. Density of newly recruited seedlings of *Diospyros maritima* (a) and *Aglaia formosana* (b) among different habitats during 2014-2018 in the Kenting Forest Dynamics Plot. Asterisks indicate that significant differences among habitats were detected ($P < 0.05$) using chi-square analysis.

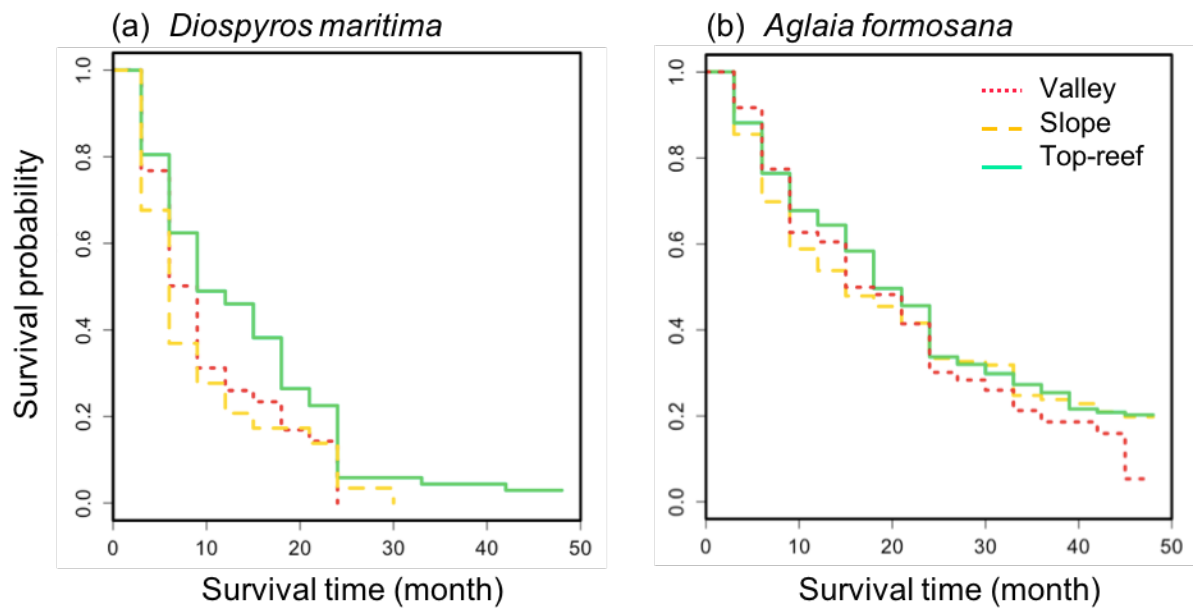


Figure 7. Estimated survival probabilities of seedlings of *Diospyros maritima* (a) and *Aglaia formosana* (b) among different habitats in the Kenting Forest Dynamics Plot. Seedling survivorships were estimated by the Kaplan-Meier method.

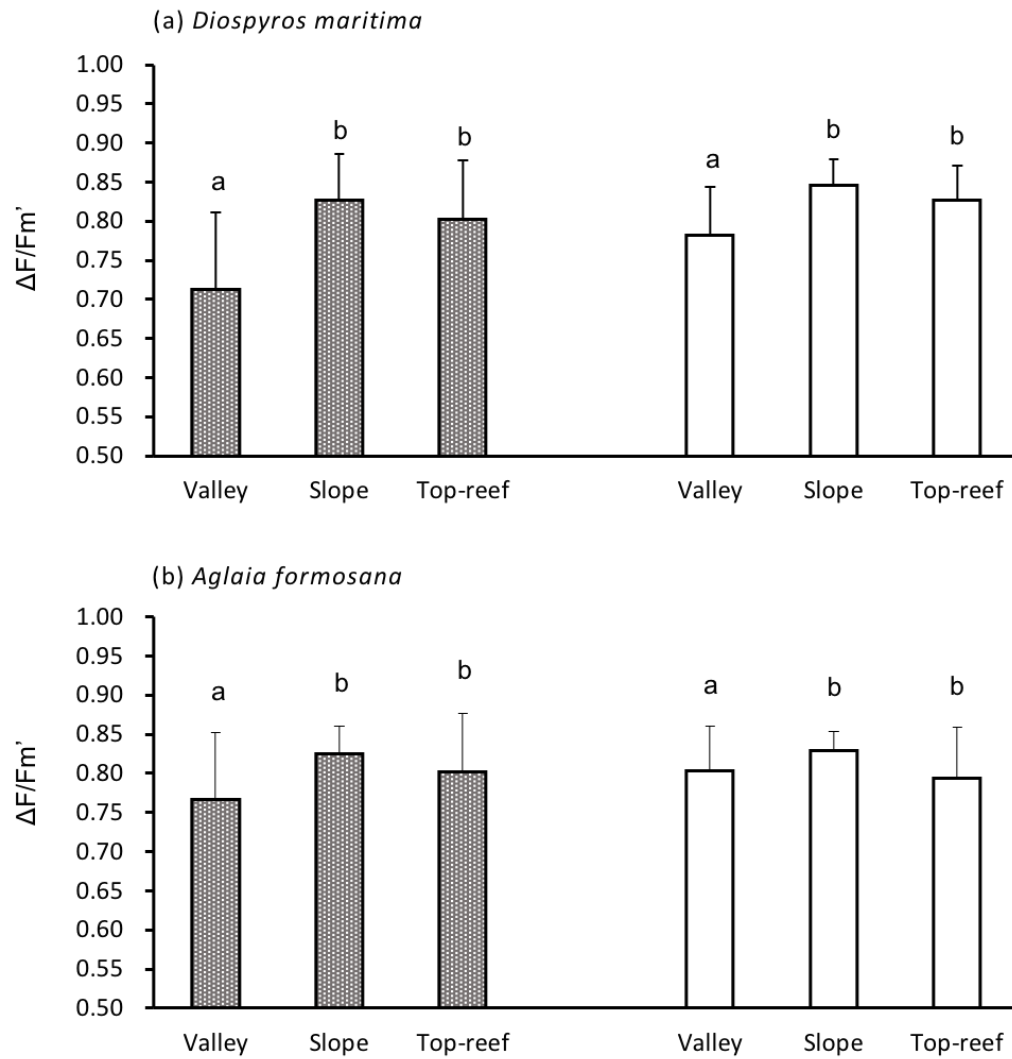


Figure 8. Effective quantum yield ($\Delta F/F_m'$) of *Diospyros maritima* (a) and *Aglaia formosana* (b) among habitats in different seasons in the Kenting Forest Dynamics Plot. Grey bars represent means of effective quantum yield in July; blank bars indicate means in February. Error bars are standard error (SE).

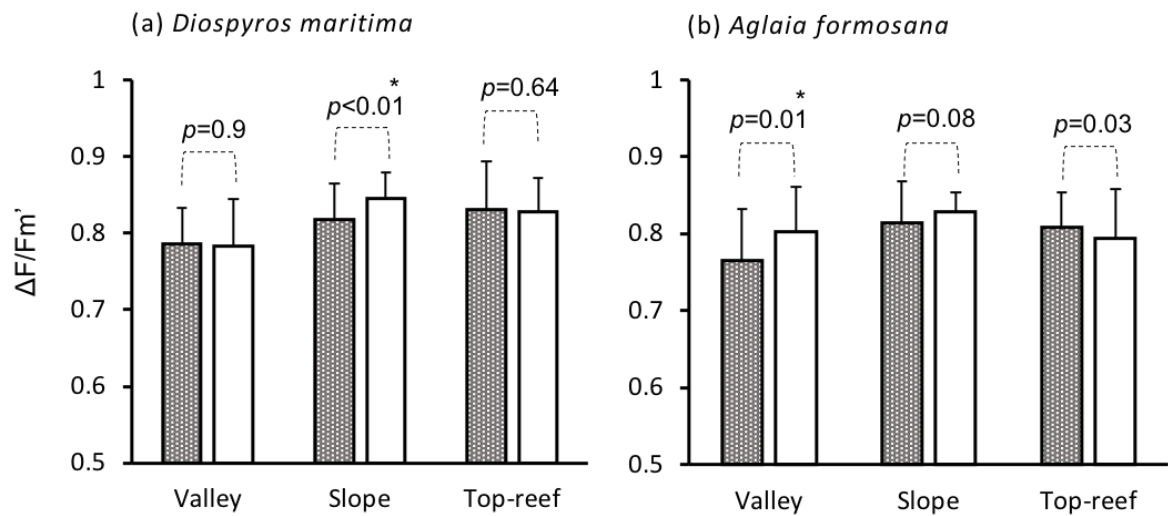


Figure 9. Seasonal comparison of effective quantum yield ($\Delta F/F_m'$) of the same individuals among three different habitats in the Kenting Forest Dynamics Plot (Mean \pm SE). The significance level used in the analyses was 0.017 after Bonferroni corrections. Grey bars represent means of effective quantum yield in July; blank bars indicate means in February.

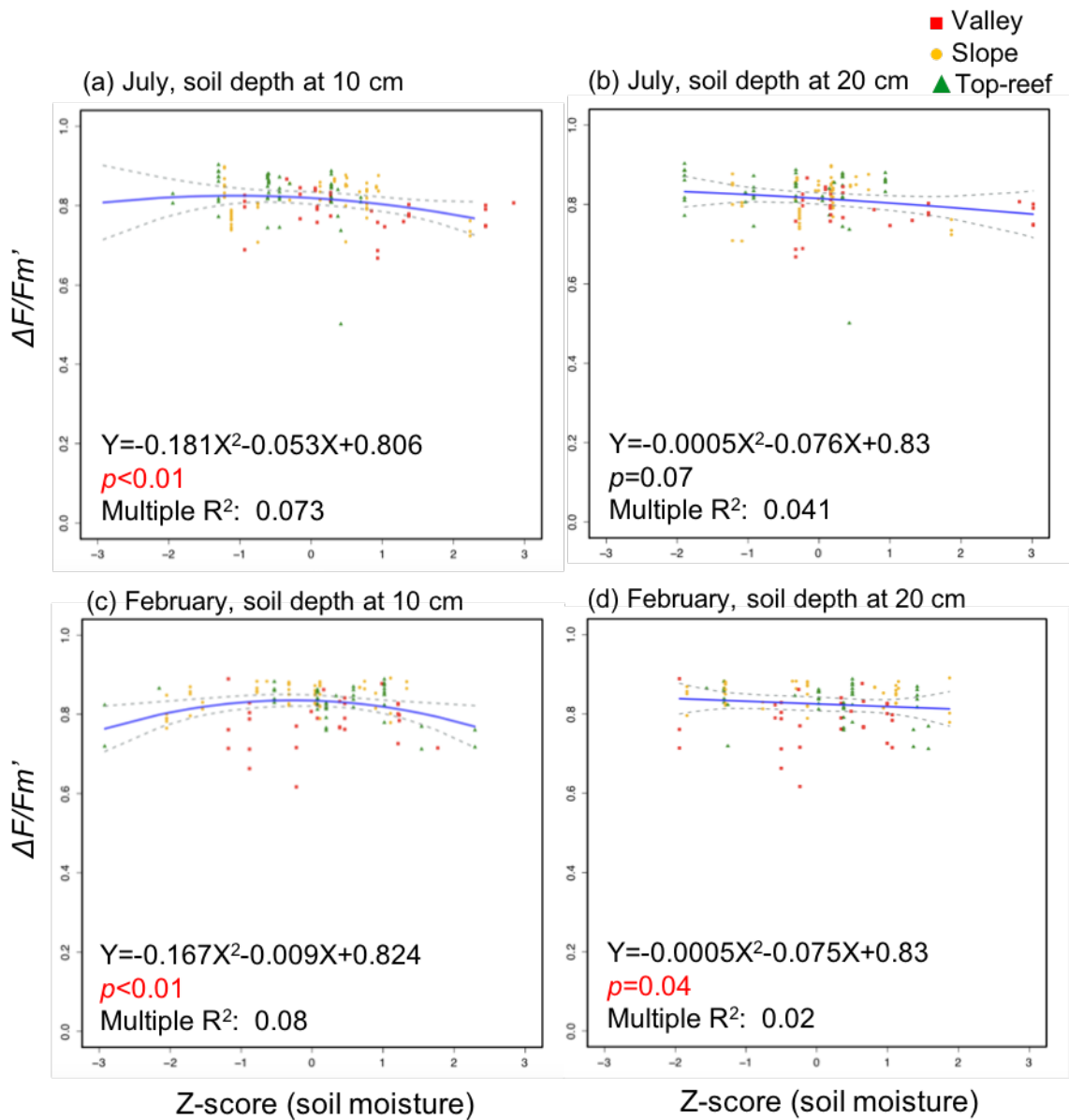


Figure 10. Relationships between soil moisture and effective quantum yield ($\Delta F/F_m'$) of *Diospyros maritima* at two different soil depths in July (a, b) and February (c, d). The fitted lines were derived from quadratic polynomial models. The dashed lines represent 95% confidence intervals.

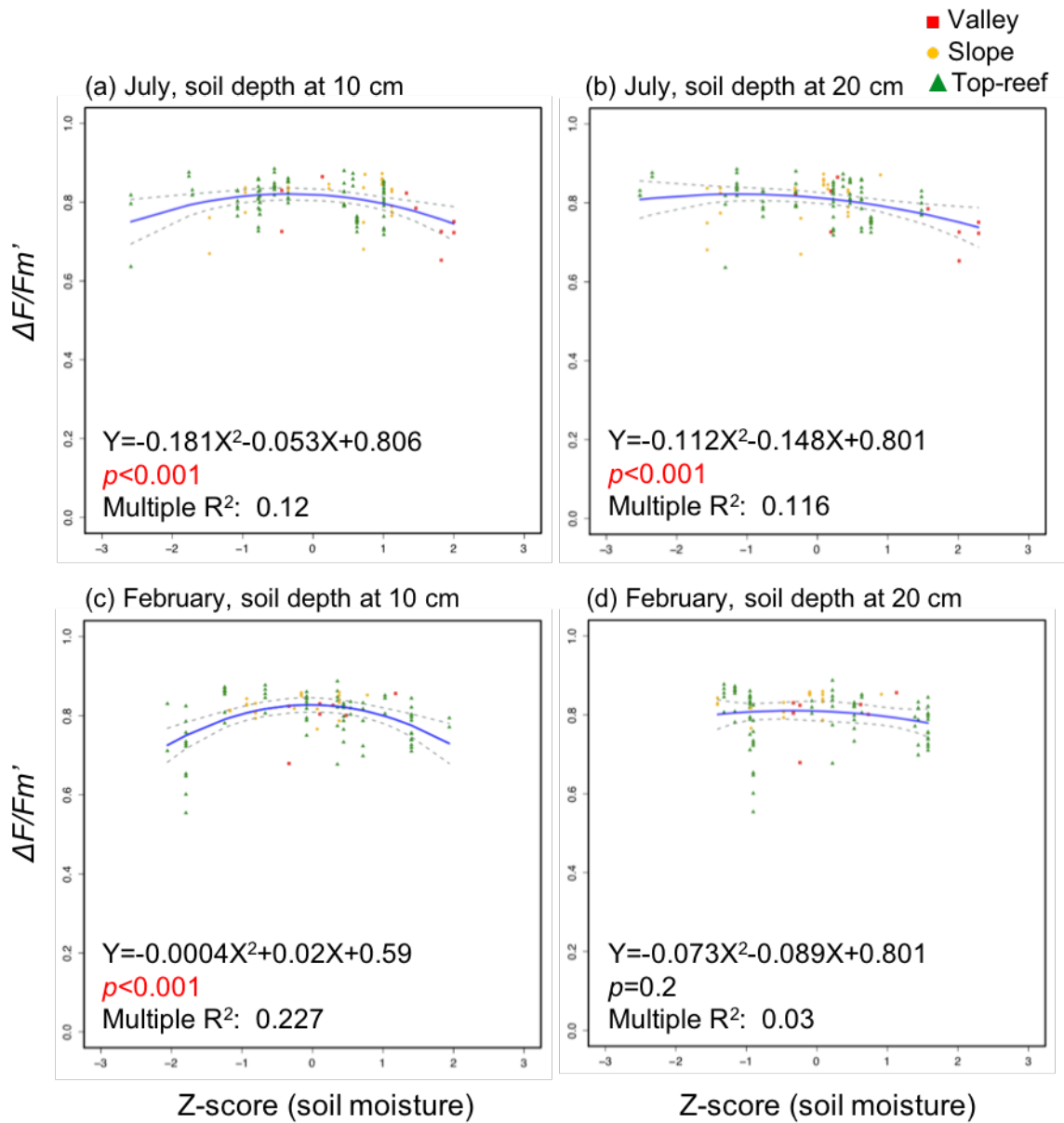


Figure 11. Relationships between soil moisture and effective quantum yield ($\Delta F/F_m'$) of *Aglaia formosana* at two different soil depths in July (a, b) and February (c, d). The fitted lines were derived from quadratic polynomial models. The dashed lines represent 95% confidence intervals.

Tables

Table 1. Summary of sample sizes used for demographic and physiological analysis in this study.

	2008 tree census ¹		2014-2018	2017	2018
	Trees	Saplings	Seedlings	July ²	Feb. ²
				Saplings used for physiological measurements	
<i>Aglaia formosana</i>					
Valley	27	49	523	9	7
Slope	231	269	1302	26	23
Top-reef	554	505	2259	84	79
<i>Diospyros maritima</i>					
Valley	1315	2012	198	31	29
Slope	5639	5994	506	54	52
Top-reef	3851	3012	331	46	43

Note: 1. Wu et al. 2011

2. Differences in sample sizes between July 2017 and February 2018 were due to wilting, death and missing of some tagged saplings. Besides, some target saplings were covered by lianas in February 2018.

Table 2. Results of goodness-of-fit for sapling recruitment among habitats in the Kenting Forest Dynamics Plot in 2013. Number of saplings among habitats were compared by using χ^2 test (Data source: Wu et al. 2011).

	χ^2	Degrees of freedom	p
<i>Diospyros maritima</i>	11.22	2	0.004**
<i>Aglaia formosana</i>	43.71	2	<0.001***

*** $p < 0.001$, ** $p \leq 0.01$

Table 3. Results of mixed effects Cox models of seedlings among habitats in Kenting Forest Dynamics Plot. The values are estimated hazard coefficients of the fixed factors in the mixed effects Cox models.

	Hazard ratio	<i>z</i>	<i>p</i>
<i>Diospyros maritima</i>			
Top-reef	0.685	-2.580	0.01**
Valley	1.096	0.445	0.657
<i>Aglaia formosana</i>			
Top-reef	0.888	-1.726	0.084
Valley	0.996	-0.042	0.966

*** $p < 0.001$, ** $p \leq 0.01$

Table 4. Estimated effects of habitats by a general linear mixed-effect model (GLMM) on sapling survival during 2008-2013 in the Kenting Forest Dynamics Plot. The slope habitat was used as a standard for parameter comparison.

	Parameter	Standard		
	Estimate	error	<i>z</i>	<i>p</i>
<i>Aglaia formosana</i>				
Top-reef	1.078	0.243	4.441	<0.001***
Valley	-1.041	0.404	-2.580	<0.001***
<i>Diospyros maritima</i>				
Top-reef	0.380	0.075	5.086	<0.001***
Valley	-0.064	0.086	-0.745	0.456

*** $p < 0.001$, ** $p \leq 0.01$

Table 5. Estimated effects of habitats by a general linear mixed-effect model (GLMM) on tree survival during 2008-2013 in the Kenting Forest Dynamics Plot. The slope habitat was used as a standard for parameter comparison.

	Parameter	Standard	z	p
	Estimate	error		
<i>Aglaia formosana</i>				
Top-reef	0.446	1.095	0.407	0.684
Valley	-0.681	1.950	-0.349	0.727
<i>Diospyros maritima</i>				
Top-reef	0.056	0.130	0.430	0.664
Valley	-0.123	0.177	-0.960	0.488

Table 6. Summary demographic performance of *Diospyros maritima* (a) and *Aglaia formosana* (b) during different life stages in Kenting Forest Dynamics Plot.

(a) Diospyros maritima

	Recruitment density	Survival rate
Tree	--	No difference among habitats (Table 5)
Sapling	Top-reef > slope > valley (Table 2)	Top-reef > slope = valley (Table 4)
Seedling	Slope > top-reef > valley (Figure 6a)	Top-reef > slope = valley (Figure 7a; Table 3)

(a) Aglaia formosana

	Recruitment density	Survival rate
Tree	--	No difference among habitats (Table 5)
Sapling	Top-reef > slope > valley (Table 2)	Top-reef > slope > valley (Table 4)
Seedling	Top-reef \geq slope > valley (Figure 6b)	Top-reef = slope = valley (Figure 7b; Table 3)

Appendix

Appendix S1

Several parameters obtained by chlorophyll fluorescence technique have been used as indices of stress tolerance. They are F_v'/F_m' (maximum quantum yield in the light), ϕ_{PSII} ($\Delta F/F_m'$; effective quantum yield in the light), qP (photochemical quenching) and qN (non-photochemical quenching). These parameters represent different parts of photochemical reaction and demand specific treatment (Maxwell and Johnson 2000, Baker 2008, Murchie and Lawson 2013).

Among all, ϕ_{PSII} ($\Delta F/F_m'$) can be used to estimate the proportion of electron transport in PSII in the nature light condition. In terms of this parameter, we may estimate the physiological state of the plant immediately. Equations of the parameter is listed as below (Murchie and Lawson 2013):

$$\phi_{PSII} = \Delta F/F_m' = (F'm - F') / F'm$$

where $F'm$ is maximal fluorescence in the light adapted state; F' is the steady-state level of fluorescence in the light.

Appendix S2. Abundance of top 10 dominant species during tree, sapling, and seedling stages in the Kenting Forest Dynamics Plot.

Species	Total of individuals ¹	Tree	Sapling	Seedling ²
<i>Diospyros maritima</i> (黃心柿)	21823	10805	11018	1035
<i>Drypetes littoralis</i> (鐵色)	3452	1711	1741	671
<i>Aglaia formosana</i> (紅柴)	1635	812	823	4085
<i>Champereia manillana</i> (山柚)	963	473	490	229
<i>Dendrocnide meyeniana</i> (咬人狗)	920	460	460	60
<i>Cryptocarya concinna</i> (土楠)	756	375	381	84
<i>Melanolepis multiglandulosa</i> (蟲屎)	752	375	377	45
<i>Macaranga tanarius</i> (血桐)	676	337	339	1
<i>Palaquium formosanum</i> (大葉山欖)	606	303	303	166

¹ Based on the 2008 census of the Kenting Forest Dynamics Plot (Wu et al. 2011)

² Based upon seedling survey during Apr. 2014 to Apr. 2018 (Lin, unpublished data)

Appendix S3. Topographic features among the three habitats in the Kenting Forest Dynamics Plot.

Valley

	Mean elevation (m)	Convexity (m)	Slope	Depth (cm)
Min	0.657	-7.57	0.33	67.25
Median	25.46	-0.73	8.99	77.50
Max	50.68	-1.55	57.94	100.00
Mean	26.78	-0.84	12.77	80.20

Slope

	Mean elevation (m)	Convexity (m)	Slope	Depth (cm)
Min	1.51	-9.06	0.618	26.75
Median	29.91	-0.23	21.93	45.00
Max	54.32	-12.19	80.95	67.12
Mean	29.80	-0.35	24.78	44.95

Top-reef

	Mean elevation (m)	Convexity (m)	Slope	Depth (cm)
Min	5.14	-6.80	4.12	0.00
Median	33.95	0.71	29.19	12.75
Max	53.55	9.49	75.04	26.62
Mean	33.18	0.93	31.19	13.59

Appendix S4.

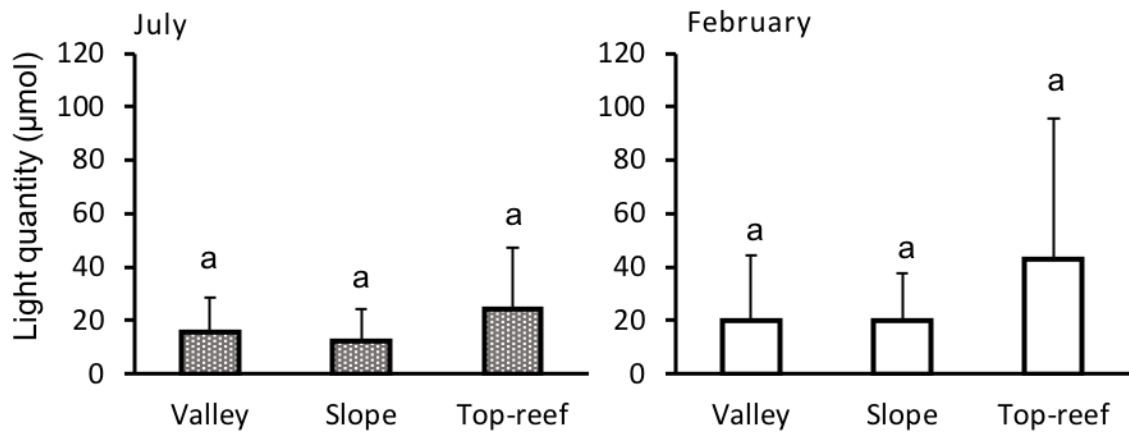


Figure: Light quantities among habitats in July and February in Kenting Forest Dynamics Plot.

Appendix S5.

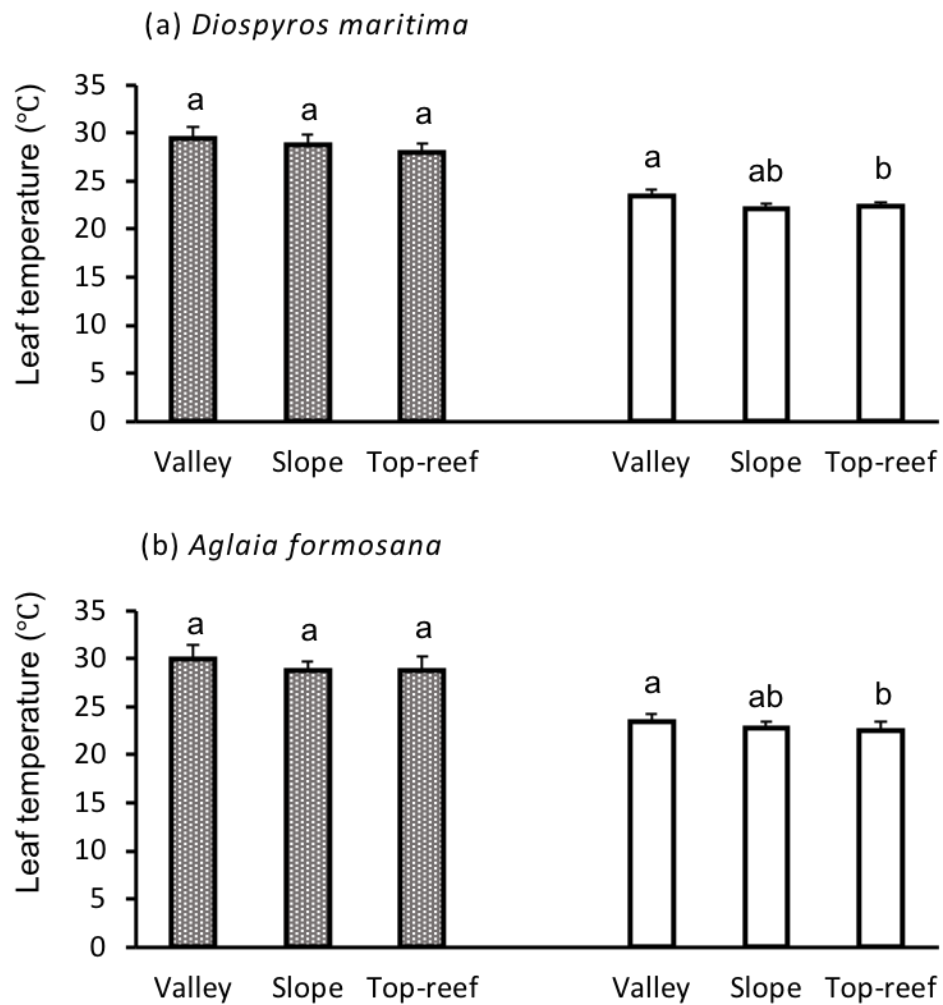


Figure: Leaf temperature compared between seasons in Kenting Forest Dynamics Plot. Values were compared among habitats by using one-way ANOVA. Dark bars were the value measured in July; light bars were the value measured in February.

Appendix S6.

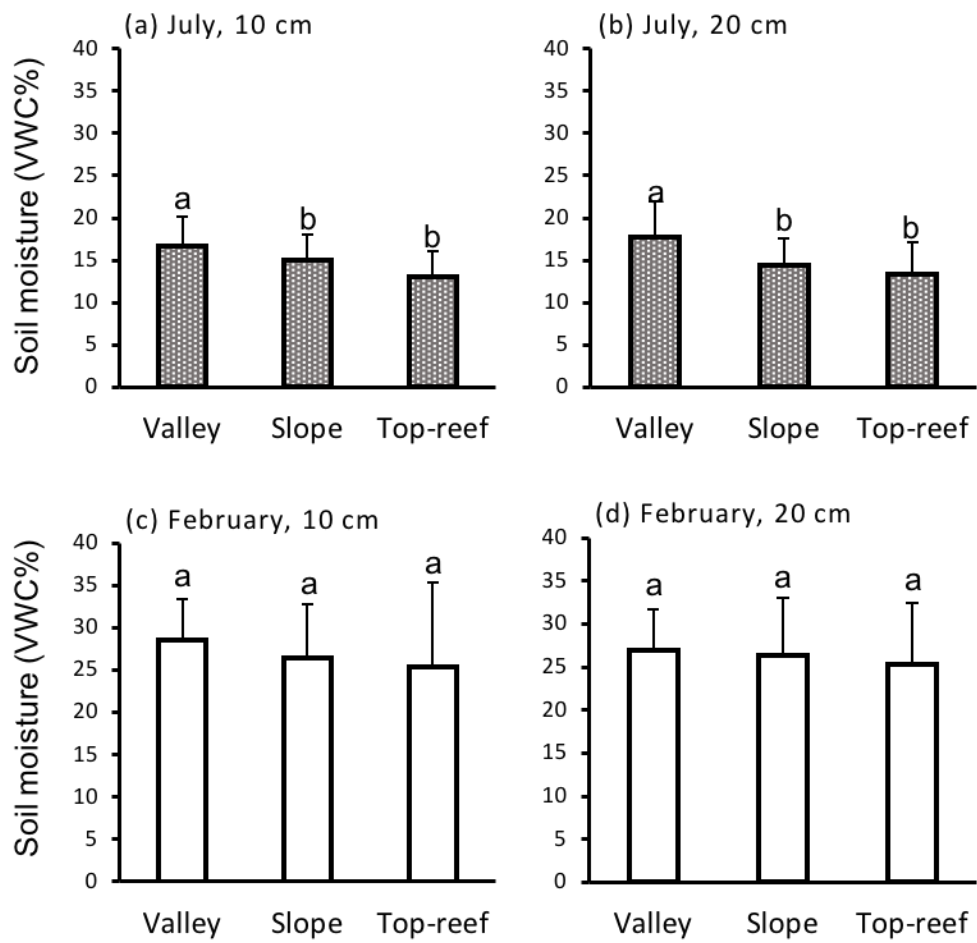


Figure: Soil moisture in different depth compared between seasons in Kenting Forest Dynamics Plot. Values were compared among habitats by using one-way ANOVA.