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Biotic vs. Abiotic Drivers of Seedling Persistence in a Tropical Karst Forest

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Abstract

Question: Quantifying the duration and drivers of seedling persistence is critical for understanding seedling dynamics and species coexistence in plant communities. In this study, we incorporated data from multiple seedling censuses to characterize patterns of seedling persistence in a tropical karst forest. Specifically, we evaluated the effects of density dependence, habitat heterogeneity, and recruitment timing on seedling persistence.

Location: A tropical karst forest in Taiwan

Methods: Using data from 144 seedling plots censused every three months from 2007 to 2012, we examined persistence times of 6399 seedlings of 36 species. Seedling survival was estimated by the Kaplan-Meier method. Mixed effects Cox models were used to identify significant biotic (i.e., initial height, conspecific and heterospecific seedling and adult densities) and abiotic (i.e., mean elevation, convexity, slope, effective soil depth, and recruitment time) drivers of seedling persistence at the community, guild and species levels.

Results: At the community level, newly recruited seedlings had a median survival time of 6 months. Median survival time was higher for seedlings in the shade-tolerant guild compared to seedlings in the shade-intolerant guild (9 vs. 3 months). When all species were analyzed together, seedling persistence significantly increased with increasing initial size and soil depth and significantly decreased with increasing density of conspecific and heterospecific seedling neighbors. Drivers of seedling persistence tended to be guild- and species-specific, however negative effects of conspecific seedling neighbors were consistently detected in all models, indicating strong and pervasive

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conspecific negative density dependence. Significant effects of recruitment time, soil depth and convexity were revealed by guild- and species-specific models, suggesting abiotic niche differences.

Conclusions: This study highlights the importance of multiple ecological processes for seedling persistence. Both abiotic and biotic factors may play an important role in species coexistence in this forest via niche partitioning and negative density dependence. Among these factors, negative conspecific density dependence had the strongest and most consistent effect. In addition, soil depth played a key role in shaping seedling regeneration, likely through effects of soil moisture. Overall, this study contributes to a better understanding of the ecology of karst forests. Analyzing seedling persistence in karst forest expands our general understanding of forest dynamics and species coexistence in tropical forests as a whole, especially at sites with high spatial heterogeneity.

Key-words: density-dependence; forest dynamics; forest regeneration; Janzen-Connell hypothesis; limestone; maintenance of diversity; survival analysis; tropical seasonal forest

Nomenclature: Huang (ed) 2003

Introduction

Tree seedlings may persist in the understory for long periods of time, sometimes decades, waiting for increased light provided by canopy gaps to reach maturation (Canham 1985; Delissio et al. 2002). Only seedlings that persist long enough to encounter gaps are able to move to subsequent life stages and ultimately reach the canopy layer. It has been shown that seedlings usually require multiple canopy gap episodes to receive sufficient light to reach maturation (Canham 1985; Delissio et al. 2002). However, the formation of canopy gaps is episodic and infrequent (Brokaw 1985a; Runkle & Yetter 1987; Runkle 2000). Long intervals between gap formation highlight the advantage of persisting for a long time in the understory. Furthermore, when a canopy gap is created by the falling of trees or branches, the gap is likely to be filled by existing seedlings rather than from newly germinated seeds (Brokaw 1985b; Runkle & Yetter 1987; Brokaw & Busing 2000). Seedling

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communities available at the time of gap formation serve as the template for tree communities. Therefore, quantifying the duration of seedling persistence in the understory is critical for understanding forest dynamics.

Seedling persistence can be considered a dimension of seedling survival, but it emphasizes the length of time that an individual survives. Thus, seedling persistence presents a continuing process starting with seedling emergence to subsequent seedling survival. Seedling persistence may not only be affected by factors operating during a given point in time, but also by cumulative effects of multiple factors over a period of time. Despite intensive studies of seedling survival, the majority of studies have focused on identifying factors that influence the probability of a seedling surviving over a single time interval (e.g. Comita et al. 2009; Chen et al. 2010). The length of time a seedling can persist in the understory and the factors that affect species' persistence time are also ecologically relevant, but have received relatively less attention. This is likely because estimating persistence time requires considerably more effort in the form of repeated censuses over time. While focusing on seedling survival over a single period helps to clarify factors causing seedling mortality at that time, studies of seedling persistence emphasize persistence as a continuous process over multiple periods. These two approaches may provide complementary perspectives and expand our understanding of patterns and drivers of seedling dynamics.

What limits long-term persistence of seedlings in the understory? Biotic and abiotic factors in the understory environment pose many challenges for seedlings, potentially increasing mortality risk and reducing persistence time (Augsburger 1984). A number of these variables are also thought to act as mechanisms that promote species coexistence. For example, conspecific negative density-dependent mortality of seedlings caused by pathogens or herbivores has been widely detected in both tropical and temperate forests (Webb & Peart 1999; Harms et al. 2000; Comita et al. 2009; Comita et al. 2010; Comita et al. 2014; Johnson et al. 2014). Such conspecific negative density dependence has been identified as an important mechanism structuring plant communities, especially in species-rich forests (Janzen 1970; Connell 1971, Queenborough et al. 2007; Chen et al. 2010). In addition, ecologists have demonstrated that seedling survival in forests varies as a result of habitat heterogeneity, namely spatial variation in light (Beckage et al. 2000; Beckage & Clark 2003), soil water (Comita & Engelbrecht 2009) and nutrient availability (Salinas-Peba et al. 2014). Tree species often vary in their responses to these abiotic variables, suggesting that niche differentiation

and habitat partitioning may be important mechanisms promoting tree species coexistence (Harms et al. 2001; Comita et al. 2007; Lai et al. 2009).

Furthermore, seedling persistence may be strongly affected by the timing of recruitment, which demonstrates significant cohort effects. It has been shown that seedling survival is highly influenced by seedling height, with taller seedlings typically having higher survival rates than shorter ones (Metz et al. 2008; Bai et al. 2012). Seedlings established during a favorable season may grow faster during the initial phase and therefore acquire a survival advantage. This is likely to be the case in seasonal forests, where seedlings that establish during wet seasons may gain an initial size advantage over seedlings that establish during dry seasons, when low water availability may limit growth. Seedlings established during wet seasons, therefore, may persist longer than those established during dry seasons. Such timing effects may also result in temporal variability in recruitment, which can contribute to species coexistence (Chesson 2000). In addition, most seedling studies only have an annual return time and that timing censuses to coincide with seasons will help determine the mechanisms effecting survival as well as timing of germination.

Ultimately, seedling persistence will reflect interactions between ecological factors and the biology of species. It has been shown that the relative importance of density dependence and habitat heterogeneity on seedling survival varies among species (Bai et al. 2012), resulting in guild- and species-specific patterns of seedling persistence. In particular, seedlings of shade-tolerant species typically persist in the understory longer than light-demanding species since seedlings of shade-tolerant species have morphological and physiological traits that enhance their survival in low light environments (Kitajima & Myers 2008). Such differences in seedling persistence time are expected to reflect trade-offs in survival and growth of tree species (Kobe 1996; Kitajima & Myers 2008).

While a number of recent long-term studies have examined abiotic and biotic drivers of seedling survival in tropical and subtropical forests (Queenborough et al. 2007; Comita & Engelbrecht 2009; Comita & Hubbell 2009; Comita et al. 2009; Queenborough et al. 2009; Chen et al. 2010; Metz et al. 2010; Lin et al. 2012; Metz 2012; Paine et al. 2012), these have been largely restricted to lowland moist and wet forests. In the present study, we use survival analysis to assess factors influencing seedling persistence time in a tropical karst forest. Karst forests are widely distributed worldwide and are a unique forest type (Kelly 1986; Ford & Williams 2007), yet empirical data on the ecology of karst forests are limited. These forests are associated with karst topography, a distinctive landscape formed by layers of carbonate bed rocks, such as limestone. Karst terrain is

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characterized by steep rocky hills and outcroppings interrupted by depressions with thick and fertile soils. In general, soils of karst forests are more basic than most forest soils due to leaching of the limestone (Kelly 1986; Wu et al. 2011). Such geological features make karst forests highly spatially heterogeneous and create sharp contrasts in environmental conditions. In karst forests, some valley areas are severely light-limited due to shading by limestone formations. At the same time, other areas mostly associated limestone outcrops may be relatively open since trees in many karst forests tend to be short and have small crown radii, likely due to low soil water availability and nutrient limitation.

As a result of such unique topography in karst forests, patterns of seedling persistence may be quite different from the other forest ecosystems. In particular, we expected topographic and edaphic factors to play a key role in karst forests due to the extreme environmental heterogeneity, with the biotic neighborhood playing a more limited role in determining persistence. Finally, there may be significant effects of recruitment time on seedling persistence, because environmental conditions vary greatly over time due to strong seasonality in rainfall. A study of seedling persistence in karst forests not only expands our general understanding of forest dynamics and mechanisms of species coexistence in tropical forests as a whole, but also provides an opportunity to examine how abiotic and biotic factors interact in plant communities with high spatial heterogeneity.

In this study, we incorporated data from multiple seedling censuses to characterize patterns of seedling persistence in a Taiwanese karst forest. Specifically, we evaluated the effects of density dependence, habitat heterogeneity, and timing of recruitment on seedling persistence in this forest. We hypothesized that habitat heterogeneity, and to a lesser degree, the local biotic neighborhood has significant impacts on seedling persistence times in this forest. Furthermore, we predicted that seedlings that recruited during the wet season would have longer persistence times than seedlings that recruited during the dry season because of an initial survival advantage due to relatively favorable conditions in the wet season (i.e. moist soils). In addition, we examined the interaction between ecological factors and species' biology by comparing guild- and species-specific patterns of seedling persistence.

Materials and methods

Study site

This study was carried out in the Kenting Uplifted Coral Reef Natural Reserve in the Hengchun Peninsula, Taiwan (21°58'N, 120°48'E; Fig. 1a). This site is underlain by coral reef limestone of Pleistocene age (Wang et al. 2004; Wu et al. 2011). Due to its karst topography, soils in the forest are

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mainly calcareous, neutral loam or light clay with a clay content over 30%. Soil pH values range from 5.3 to 7.4 (Wu et al. 2011). The forest experiences a distinct dry season annually, lasting from November to April (Wu et al. 2011). Although prevailing northeast and southwest monsoons occur during the winter, precipitation is low since the Kenting Forest is located on the leeward side of the Hengchun Peninsula (Wu et al. 2011). The average mean temperature is 25.4 °C with the annual precipitation being about 2000 mm from 2000 to 2010, which occurred mostly from June to November (Wu et al. 2011). In some years, a good proportion of precipitation during the wet seasons is associated with typhoons. Most typhoons occur between June and September in Taiwan. Typhoons are considered to be an important disturbance agent, but no major damage was caused by typhoons in the forest during the study period. The Kenting Karst Forest Dynamics Plot, which is 10 ha in size (400 m x 250 m), was established in 1996 with the first census conducted in 1997. The second census took place in 2008 (Wu et al. 2011). In each census, all trees and shrubs ≥ 1 cm in diameter at breast height (DBH; 1.3 m above ground) were mapped, measured and identified to species using standardized methodology (Condit 1998). Ninety-five woody species of 34 families, all Angiosperms, were identified in the 2008 census of the plot (Wu et al. 2011). The community is dominated by species from Ebenaceae, Euphorbiaceae, and Moraceae. Coast persimmon, *Diospyros maritima*, is especially abundant and accounts for 56.4 % of the individuals within the plot (Wu et al. 2011). Other common species include *Ficus benjamina*, *Melanolepis multiglandulosa*, *Bischofia javanica*, *Palaquium formosanum*, and *Aglaiia formosana*. The mean canopy height is ~10 m (Lin, unpublished data). The census data are currently owned and managed by Taiwan Forestry Research Institute. The data are available for researchers upon request (Wu et al. 2011).

Seedling census

We established four east-west transects within the Kenting Karst Forest Dynamics Plot in July 2007 (Fig. 1b). Each transect was 340 m in length and started 30 m from the western edge and ended 30 m from the eastern edge of the plot. At 20 m intervals along each of the four transects, we established seedling survey stations consisting of two 1.5 m x 1 m seedling plots located within 5 m from the center of each seedling survey station (Fig. 1c). In total, 144 seedling plots were established (2 seedling plots x 18 research stations x 4 transects). All seedlings within the seedling plots were censused every three months. Seedlings were defined as woody plants with DBH < 1 cm at 1.3 m. There was no minimum size for seedlings. Each seedling was tagged, mapped and identified to species. All identifiable seedlings were included in the census. Unidentifiable seedlings accounted for

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only 2 % of total seedlings and were excluded from the analyses. The height and the number of leaves or cotyledons of the seedling were measured. Finally, the status of seedlings was also recorded (alive, dead, or missing). If a seedling remained missing or leafless for two consecutive census periods, it was defined as dead.

From 2007 to 2012, we tagged 9407 seedlings of 57 woody dicot species, including 8099 seedlings of 42 tree/ shrub species and 1308 seedlings of 15 liana species. Among seedlings of tree and shrubs, 6399 seedlings of 36 species recruited after the first census so that the ages of these seedlings were known. These individuals were used as focal seedlings in our survival analyses (Appendix S1). The 36 target species account for 92.4 % of the overall stems with DBH \geq 1 cm in the 2008 forest census. Although seedlings of the initial census with unknown age and liana species were not treated as focal individuals, they were included in calculations of neighboring seedling density.

Quantifying habitat heterogeneity

Four abiotic factors, mean elevation, convexity, slope and effective soil depth, were used to quantify habitat heterogeneity in this study. The first three variables were considered as topographic variables and derived from elevation measurements. Elevation was measured at the four corners of each of the 10 x 10 m quadrats within the Kenting Karst Forest Dynamics Plot using electronic total station theodolites in 1997 (Sun, unpublished data). Mean elevation of a quadrat was obtained by averaging elevation measures from the four corners of the quadrat. Convexity was defined as elevation differences between the focal quadrat and mean elevation of the eight neighboring quadrats, except for those quadrats on the edges of the Dynamics Plot. Slope was measured by the mean angular deviation from the horizontal plane of each of the four triangular planes by connecting three out of the four corners (Lin et al. 2011a). Effective soil depth was measured at the scale of individual seedling plot. Soil depth at 9 points within each seedling plot was measured in July 2007 (Malanson et al. 2002). The 9 points were the four corners, midpoints of each side, and the center point of each seedling plot. For a given point, a steel rod was used to penetrate through the soil surface until underlying limestone was reached. The penetrating depth was defined as the effective soil depth at the point. The mean effective soil depth of the 9 points was calculated for each seedling plot.

Classification of species guilds

In this study, we classified species into guilds based on their shade tolerance. After measuring photosynthetic rates of a wide range of native species in Taiwan, species were defined as shade-tolerant or shade-intolerant based on photosynthetic capacity as a physiological index for shade-tolerance (Kuo 2012). Species with photosynthetic capacity $\geq 17 \mu\text{mol}\cdot\text{CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ were classified as shade-intolerant, while species with photosynthetic capacity $< 17 \mu\text{mol}\cdot\text{CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ were classified as shade-tolerant species (Appendix S1). Field measurements of the photosynthetic capacity were available for 25 of our focal species. In the guild-specific models, only species with photosynthetic measurements were included (Kuo 2012).

Statistical analysis

We used the Kaplan-Meier method to estimate survival time (Lee & Wang 2003). In addition, we compared survivorship curves among different guilds (i.e. shade-intolerant vs. shade-tolerant) and species using logrank tests (Lee & Wang 2003). Finally, effects of density dependence, habitat heterogeneity, and recruitment timing on seedling persistence were explored using mixed effects Cox models (Cox 1972; Therneau & Grambsch 2000).

In the mixed effects Cox models, independent variables were classified into three groups representing density dependence, habitat heterogeneity, and recruitment timing. Initial height of the seedling was included as a covariate. Four variables were used to estimate effects of density dependence: basal area of conspecific neighbors, basal area of heterospecific neighbors, average density of conspecific seedling neighbors and average density of heterospecific seedling neighbors. Basal area of conspecific neighbors and basal area of heterospecific neighbors were estimated by summing the basal area of neighboring individuals with DBH ≥ 1 cm within a 10-m radius of each seedling plot based on the 2008 census. Basal area of conspecific and heterospecific neighbors only varied slightly over time during the study period since no major disturbances occurred. Average seedling density was calculated using neighbor densities in the same seedling plot as the focal seedling. Average seedling neighbor density was obtained over the period in which the seedling survived and was used to represent the average neighbor density that the focal seedling experienced during its lifetime. Preliminary analyses indicated that average seedling density generated similar results in the Cox models as using dynamic seedling densities. Average basal area of conspecific adult neighbors around a given seedling was $5.21 \pm 7.18 \text{ cm}^2/\text{m}^2$, while that of heterospecific adult

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neighbors was $41.38 \pm 13.75 \text{ cm}^2/\text{m}^2$. There was a weak negative relationship between conspecific and heterospecific adult neighbor basal area (Pearson's Correlation Coefficient = -0.28). As for seedling neighbors, average conspecific and heterospecific densities were 29.80 ± 53.06 and 8.94 ± 9.82 seedlings/ m^2 , respectively. The ranges of conspecific and heterospecific seedlings differed. Therefore, we ran models where the densities were restricted to a similar range and found that differences in density ranges were not producing spurious results. Similar to adult neighbors, weak negative correlations were detected between conspecific and heterospecific densities (Pearson's Correlation Coefficient = -0.20). The second group of variables included abiotic factors. Four variables were used to quantify habitat heterogeneity: mean elevation, convexity, slope, and effective soil depth. They were included in the models as continuous variables. Lastly, the census in which the seedling initially recruited (January, April, July, or October) was included as a categorical variable. The July and October censuses were conducted during the wet season, while the January and April censuses took place during the dry season.

Values of each continuous independent variable were standardized by subtracting the mean of the variable and then dividing by its standard deviation. To account for species variability and spatial autocorrelation, species and seedling plot were included in the mixed effects Cox models as random effects. Seedling plots were nested within each research station. Right censoring was applied in the survival analyses, because some seedlings survived beyond the last census and therefore their exact mortality dates are not known (Therneau & Grambsch 2000; Lee & Wang 2003 2010).

Three sets of analyses were constructed: overall, guild-specific, and species-specific models. The overall analysis included all individuals of all focal species combined (i.e. community-level analysis). The guild-specific analyses involved separate models for shade-tolerant and shade-intolerant species groups. Finally, species-specific models were constructed for species that had more than 200 new recruits with an exception of *Gonocaryum calleryanum*. The distribution of *Gonocaryum calleryanum* is restricted to a limited area. All seedlings of *Gonocaryum calleryanum* were only found in one seedling plot. It is not possible to construct a species-specific model for *Gonocaryum calleryanum* that include all biotic and abiotic factors.

We used backward elimination to select the most parsimonious model. The full models were first run, and then independent variables with $P > 0.1$ were gradually removed one by one. This procedure was repeated until all variables in the final models had P values < 0.1 . Survival analyses were performed using the packages 'survival' and 'coxme' in the R statistical software package (R Development Core Team 2013).

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Results

Seedling persistence

During the 5-year study period, the number of newly recruited seedlings varied significantly between dry and wet seasons (Appendix S2; ANOVA: $F_{1,17} = 19.80$, $P < 0.001$, log transformation). Higher recruitment occurred during wet seasons (July and October) than dry seasons (January and April). In particular, the number of recruits was lower in April than in the other months (Appendix S2). The highest number of recruits occurred in October 2008, while the lowest number of recruits occurred in April 2010.

The median survival time of seedlings was 6 months according to the Kaplan-Meier method (Fig. 2). Only 11% of seedlings persisted longer than 24 months (Fig. 2). Shade-tolerant species survived significantly longer than intolerant species ($\chi^2 = 679$, $df = 1$, $P < 0.001$, Fig. 3). Median survival time for shade-tolerant seedlings was 9 months, compared to only 3 months for shade-intolerant seedlings (Fig. 3).

Median survival intervals of individual species ranged from 3 to 33 months. The longest survival time occurred in *Excoecaria formosana* (Appendix S1). The shortest median survival time of 3 months was exhibited by eight species (Appendix S1). The median persistence interval differed significantly among species ($\chi^2 = 1646$, $df = 35$, $P < 0.001$).

Community-level model

For all species combined, four variables were significant in the most parsimonious model: initial height, density of conspecific seedling neighbors, density of heterospecific seedling neighbors and effective soil depth (Table 1). Initial height and effective soil depth had negative hazard coefficients, which indicated that the instantaneous mortality risk of an individual seedling was significantly reduced by these variables (Table 1). In other words, seedlings that were taller and growing on deeper soils had a better chance of surviving. In contrast, mortality risk significantly increased with densities of conspecific and heterospecific seedling neighbors. The negative effect of conspecific neighbors on survival was stronger than that of heterospecific neighbors (Table 1).

Guild-specific models

Our mixed effects Cox models identified different sets of significant variables for shade-intolerant and shade-tolerant species (Table 1). For shade-intolerant species, survival was significantly impacted by initial height, basal areas of conspecific and heterospecific neighbors, density of conspecific seedling neighbors and recruitment time. Specifically, mortality risk significantly decreased with initial height, but increased with conspecific and heterospecific neighbor basal area, conspecific seedling neighbor density, and recruitment in July (Table 1). For shade-tolerant species, mortality risk of seedlings significantly increased with densities of both conspecific and heterospecific seedling neighbors (Table 1), while initial height, basal area of conspecific neighbors, effective soil depth and recruitment in January significantly reduced the mortality risk.

Species-specific models

Variability among species was demonstrated by the species-specific models. We detected one to five significant variables for individual species (Table 1). For example, only conspecific seedling neighbor density had a significant effect on *M. japonica* var. *kusanoi*, while persistence of *A. formosana* was significantly impacted by initial height, densities of conspecific and heterospecific seedling neighbors, soil depth and recruitment timing (Table 1). Despite the variability among species, increasing density of conspecific seedling neighbors significantly increased mortality risk for all study species (Table 1). In contrast, basal area of conspecific neighbors resulted in a reduced mortality risk for *D. maritima* and *D. littoralis*. Compared to biotic factors, abiotic factors were not significant in most models. Only soil depth and convexity were significant for the models of *A. formosana* and *P. umbellifera*, respectively (Table 1). Finally, recruitment timing was important for two species, *A. formosana* and *B. javanica* (Table 1).

Discussion

We used survival analyses to estimate seedling persistence and determine which abiotic and biotic factors affected persistence time in a Taiwanese karst forest. Our results indicated that seedlings persisted for relatively short periods. Median survival time for newly recruited seedlings was 6 months. Even for shade-tolerant species, which are expected to show longer survival times in the understory, median survival time was only slightly longer. Our overall survival model indicated that

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only 11% of individual seedlings could persist longer than 2 years. This is in contrast to studies in which seedlings were found to have survived for decades (Hubbell 1998; Connell & Green 2000; Delissio et al. 2002). The discrepancy between these results suggests that the early seedling stage might act as a bottleneck, and that the small proportion of seedlings that do manage to survive beyond this stage can likely persist for longer periods. Thus, understanding the factors influencing persistence time of small seedlings is critical for determining species composition and diversity of adult trees. Our study revealed that both abiotic and biotic factors influenced persistence. However, contrary to our predictions, biotic factors had stronger and more consistent effects on seedling persistence compared to abiotic factors in this tropical karst forest.

Biotic and abiotic factors determining persistence time

According to our overall model, seedling persistence was significantly affected by several biotic and abiotic factors, specifically conspecific seedling density, heterospecific seedling density and soil depth. Among all of the factors examined, conspecific seedling neighbors had the strongest effect on seedling persistence (i.e. the highest hazard coefficient). This result is consistent with other studies from tropical and temperate forests that found strong negative conspecific density dependence during early life stages (Harms et al. 2000; Hille Ris Lambers et al. 2002; Queenborough et al. 2007; Chen et al. 2010; Comita et al. 2010; Metz et al. 2010) and confirms that conspecific density dependence can play an important role in structuring tree communities even in forests with high spatial and temporal heterogeneity in environmental conditions. As in other forests, negative conspecific neighbor effects may be strong due to strong local spatial aggregations of seeds and seedlings that have been shown to result from dispersal limitation in this forest (Lin et al. 2011a; Lin et al. 2011b).

Host-specific natural enemies, such as pathogens and insect herbivores, have been identified as important causes of negative density dependence in many tropical forests (Janzen 1970; Connell 1971; Terborgh 2012; Bagchi et al. 2014). Intraspecific competition for resources may also be a potential cause, although previous studies suggest that intraspecific competition is weak among tree seedlings in tropical forests (Paine et al. 2008; Terborgh 2012). The causes of conspecific negative density dependence have yet to be examined in the Kenting forest, although a recent study reported abundant herbivorous insects at the site (Lan 2010).

In addition to conspecific neighbors, we detected significant, but weaker effects of heterospecific seedling density. This finding is in contrast to some previous studies in which heterospecific neighbors had little or positive effects on seedling survival in tropical forests (Comita et al. 2010; Metz et al. 2010). One likely cause of negative heterospecific seedling density effects may be generalist herbivores, including large mammals. Although not explicitly examined in this study, large mammals can have large impacts on seedling persistence in forest understories (Côté et al. 2004). There is a reintroduction program of Formosan sika deer (*Cervus nippon taiouanus*) in the area surrounding our study site, which started in 1990 and aims to return the extinct deer to the natural ecosystems (Pei 2009). The deer population has experienced a rapid increase recently (Yen et al. 2012). We observed many browsed seedlings and saplings in the Kenting karst forest, with the number of browsed stems increasing rapidly in the past few years. In addition to sika deer, several mammals in the Kenting forest may be potential predators for seedlings (Pei 2002), such as Formosan wild boar (*Sus scrofa taiwanus*), red-bellied squirrels (*Callosciurus erythraeus*), and spinous country-rat (*Niviventer coxingi*), as well as escaped feral goats. In particular, soil disturbances by wild boars were observed a few times during the study period (Lin, personal observation). Effects of soil disturbance caused by large mammals, such as peccaries, have also been observed in other tropical forests (Queenborough et al. 2012). Given the potentially large impacts of mammals on seedling persistence, future studies in this forest should include measures of herbivory. Of the abiotic factors examined, only effective soil depth had a significant impact on seedling persistence. Soils in karst forests tend to be thin near limestone outcrops (Kelly 1986; Wu et al. 2011). Such thin soils do not have good water holding capacity and create a harsh environment for seedlings to establish and survive. Furthermore, the Kenting forest is a seasonal forest, and water may be particularly limiting in the dry season. Areas with thicker soils may help preserve water for seedlings during the dry season and therefore enhance seedling survival. This is consistent with our field observations where wilting was one of the common causes of seedling mortality. Dry and leafless seedlings were widely observed during the study period. These observations, combined with the model results, suggest that soil water availability is likely to be an important limiting factor for seedling survival in the karst forest.

The importance of soil water availability for seedling dynamics has also been found in studies at other seasonal tropical forests (Comita & Engelbrecht 2009; Lin et al. 2012). For example, at Barro Colorado Island, Panama, mortality and growth rates of seedlings varied among habitats with different water availability (Comita & Engelbrecht 2009). Similarly, seedling mortality increased

during the dry season in a Chinese forest (Lin et al. 2012). Such results indicate the critical role of soil water availability in driving spatial and temporal patterns of seedling survival.

Surprisingly, the topographic variables had no effect on seedling persistence at the community level and for all but one of the focal species included in our analyses. The Kenting forest is very heterogeneous in topography, and we expected to detect strong topography effects. Critical resources in the forest such as light, soil water, and soil nutrients are expected to be associated with topography. Our findings run contrary to our prediction that topographic variables would have strong effects on seedling persistence. A potential reason for the insignificant role of topography may be that the main influence of topography on seedling persistence could be through soil depth, which we included explicitly in the models. Additionally, the 10 x 10m scale at which topography was measured may be too coarse for capturing appropriate abiotic factors. In some parts of the forest, sharp changes in elevation are observed within a short horizontal distance (Wang et al. 2004; Wu et al. 2011).

Differences among ecological guilds and among species

Patterns of seedling persistence differed significantly among guilds and species. Shade-intolerant species had shorter persistence time than shade-tolerant species. This is expected given that most seedlings plots were located in the shaded understory. Median survival time of shade-intolerant species was only three months. In other words, many seedlings were not able to survive to the next season. Usually, large quantities of seedlings of shade-intolerant species recruited in each census. However, these seedlings were typically small. Our model results indicated that, for all groups, smaller seedlings had a higher mortality risk. Thus, small seedling size likely contributes to the short persistence time for shade-intolerant species.

In addition, seedling persistence of shade-intolerant and shade-tolerant species was affected by different abiotic factors. In particular, seedlings of shade-tolerant species were affected by soil depth and had a lower mortality risk when growing in deep soils. No such soil effects were found for shade-intolerant species. The differences between guilds may be attributed to their patterns of seedling establishment. Seedlings of shade-tolerant species may be able to establish in a wide range of habitats, while seedlings of shade-intolerant species may only establish in gaps and are more limited by light availability than soil resources. Significant effects of soil depth for shade-tolerant species suggest the occurrence of edaphic habitat preferences. This is further supported by the fact

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that conspecific adult basal area was positively related to seedling persistence for shade tolerant seedlings, suggesting that these seedlings survive best in preferred habitats of adult trees of their species. Habitat associations of adult trees can result from non-random mortality across multiple life stages. Some studies have found evidence for such topographic habitat specialization beginning at early seedling stages (Metz 2012), while others have found that adult tree habitat associations result predominantly from non-random mortality of larger, established seedlings and saplings (Comita et al. 2007; Comita & Engelbrecht 2009; Lai et al. 2009; Baldeck et al. 2013). Our results suggest that some of the species at our site begin to form habitat associations in the first few months after seedlings germinate.

Seedlings of both shade-tolerant and shade-intolerant species were negatively affected by conspecific seedling neighbors, confirming the prevalence of conspecific negative density dependence in this forest. As discussed above, such effects likely result from host-specific pathogens and herbivores, but could also be due to intraspecific resource competition. Despite the significant negative effects on conspecific seedling neighbors, seedling survival for the shade-tolerant guild was positively related to conspecific adult basal area. This suggests that areas of high conspecific tree basal area reflect favorable microhabitats or positive plant-mycorrhizal associations. In contrast, seedlings of the shade-intolerant guild were negatively impacted by both heterospecific and conspecific tree basal area. This is consistent with the idea that above-ground competition for light is a key determinant of seedling survival for shade-intolerant species. Shade-tolerant seedlings were also negatively impacted by heterospecific seedling neighbors, but this likely reflects interspecific competition for below-ground resources or generalist natural enemies.

Significant effects of recruitment time were also found in our guild-specific models. For shade-intolerant species, seedlings that recruited during the wet season (July) persisted for a significantly shorter period of time than seedlings that recruited in the dry seasons. Also, seedlings of shade-tolerant species that recruited in the middle of dry season (January) persisted longer than seedlings recruiting during the other seasons. These results are contrary to our prediction that moist soils in the wet season would result in longer persistence for seedlings that recruited during that time. The advantage of higher water availability in the wet season may have been canceled out by negative effects of herbivores and pathogens, which have been shown to cause more damage in wet compared to dry seasons in tropical forests (Coley & Barone 1996; Marod et al. 2002).

At the species level, significant effects of recruitment time were only detected for two species, *A. formosana* and *B. javanica*. However, the other four focal species all had low numbers of recruits

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during the dry season. Thus, the lack of significant recruitment time effects for these species may be attributed to low statistical power associated with small sample sizes during the dry season.

Even for species in the same guild, we found differences in persistence times, as well as the factors influencing mortality risk. Nonetheless, a significant negative effect of conspecific seedling density was detected in all species-level models. Such results indicate that negative density-dependent seedling survival is strong and pervasive not only at the community level, but also at the species level in this karst forest. While significant were found for all focal species, the coefficients for conspecific seedling neighbor effects varied widely in the species-specific models, consistent with recent studies that reported a wide range of variation among tree species in the strength of conspecific density dependence (Comita et al. 2010; Johnson et al. 2012).

Conclusions

By focusing on the understudied karst forest ecosystem, our study expands general understanding of the factors influencing seedling survival in tropical forests worldwide. At our site, we found contributions of density dependence, soil depth and recruitment timing to patterns of seedling persistence. Such factors may play an important role in species coexistence in this forest via niche partitioning and negative density dependence. The simultaneous contribution of biotic and abiotic variables is consistent with the findings of recent studies of seedling survival in tropical, as well as subtropical and temperate forests (Comita et al. 2009; Chen et al. 2010 ; Bai et al. 2012; Johnson et al. 2014). These results highlight the importance of multiple ecological processes for seedling survival. Among the factors found to influence seedling persistence in our study, negative conspecific density dependence had the strongest and most consistent effect on seedling persistence. Our results also suggest that soil water availability, mediated by soil depth, plays a key role in influencing seedling dynamics in this karst forest. Overall, the short persistence time of newly recruited seedlings suggests that this life stage serves as a bottleneck in the life cycle of tree species in this forest.

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Description

Appendix S1. Biological characteristics, seedling abundance and the medians of survival intervals of seedlings for the focal species in the Kenting Karst Forest Dynamics Plot during 2007-2012.

Appendix S2. Temporal variation in newly recruited seedlings from July 2007 to April 2012 in the Kenting Karst Forest Dynamics Plot.

Table 1. Summary for the most parsimonious models of mixed effects Cox models. Final models were determined by backward selection. Effects of density dependence, habitat heterogeneity and recruitment timing on seedling persistence were evaluated. Initial height of seedlings was included in all models as a covariate. The values are estimated hazard coefficients of the fixed factors in the mixed effects Cox models. All independent variables listed in the table had significant effects ($P < 0.05$). Coefficients > 0 indicate that the hazard increased as the independent variable increased, while coefficients < 0 indicate that the hazard decreased as the independent variable increased. Each continuous independent variable was standardized prior to analysis by subtracting the mean and then dividing by its standard deviation.

Model	Initial Height	ConBA ¹	HetBA ₁	ConDe _{n¹}					
				HetDe _{n¹}					
				Soil Dept h	Convexit y ²	RT ^{3,4} (Jan)	RT ^{3,4} (July)	RT ^{3,4} (Oct)	
Overall model	-0.135			0.926	0.262	-0.142			
Guild-specific models									
<i>Shade-intolerant species</i>	-0.171	0.137	0.152	0.935			-0.053 _a	0.702 _b	0.135 ^a
<i>Shade-tolerant species</i>	-0.139	-0.120		0.963	0.279	-0.159	-0.310 _b	0.008 _a	-0.003 ^a
Species-specific models ⁵									
<i>Aglaia formosana</i> (S)	-0.285			2.122	0.371	-0.232	-0.815 _b	0.456 _a	-0.475 _b
<i>Bischofia javanica</i> (I)				0.745			0.164 ^a	0.605 _b	0.341 ^a

Table 1 (Continued)

<i>Model</i>	Initial Height	ConBA	HetBA	ConDen	HetDen	Soil Depth	Convexity	RT (Jan)	RT (July)	RT (Oct)
<i>Diospyros maritima</i> (S)		-1.366	-1.045	16.482	1.471					
<i>Drypetes littoralis</i> (S)	-0.387	-1.604	0.354	3.189						
<i>Machilus japonica</i> var. <i>kusanoi</i> (S)				3.875						
<i>Pisonia umbellifera</i> (S)	-0.483		0.567	0.954			-0.506			

1. ConBA/HetBA refers to basal area of conspecific/heterospecific neighbors within a 10 m radius of the seedling plots. ConDen/HetDen refers to average densities of conspecific/heterospecific seedling neighbors within the same seedling plot during the persistence of the focal seedling.
2. Two abiotic variables (mean elevation and slope) were not significant in any of the models so that they were not listed in the table.
3. RT: recruitment timing, which is a categorical variable. The April census is treated as the baseline for comparison (i.e. hazard coefficient = 0).
4. Different letters indicate significant differences between pairwise comparisons of hazard ratios for different recruitment times (month) based on 95% confidence intervals. Values that were not significantly different from the baseline (April) are denoted by the letter a.
5. Shade-intolerant (I) and tolerant species (S)

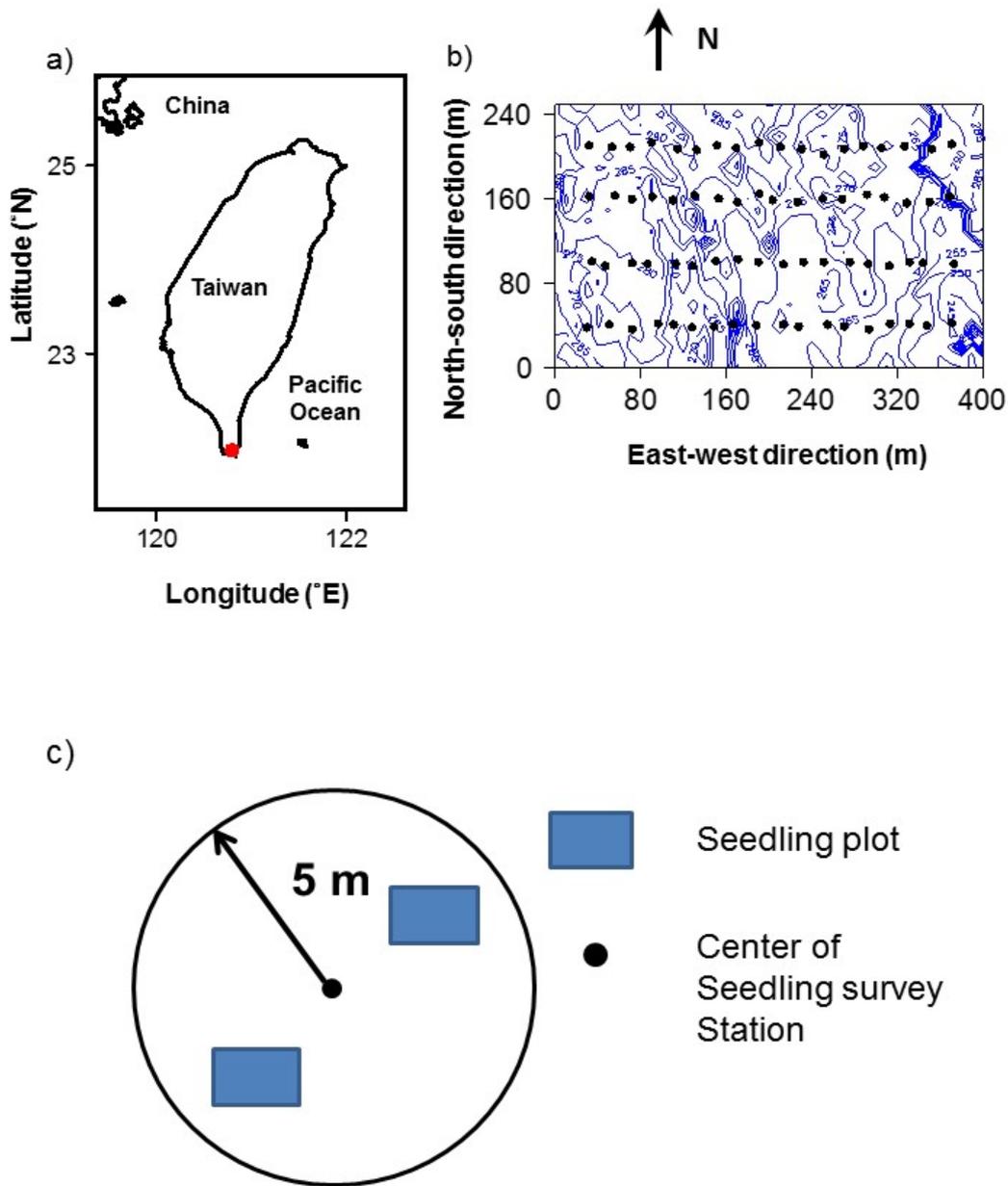


Fig. 1. The location of the Kenting Karst Forest Dynamics Plot (a), the distribution of seedling survey stations within the plot (b) and the arrangement of seedling plots (c). The location of the Kenting Karst Forest Dynamics Plot is indicated by a red dot (a). The black dots represent seedling survey stations (b, c). Contour lines in the background are at 5-m intervals. At each station, two seedling plots were established within a 5-m radius from the center of each station (c).

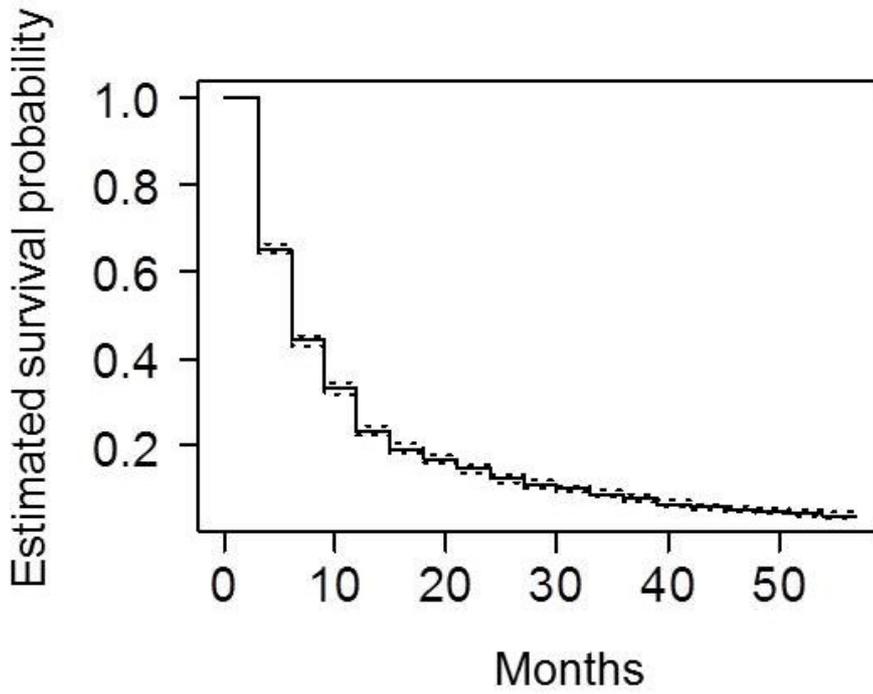


Fig. 2. Estimated survival functions of all species combined in the Kenting Karst Forest Dynamics Plot based on seedling censuses from July 2007 to April 2012. Estimated survival average probabilities (solid lines) and 95 % confidence intervals (dotted lines) are shown. Survival functions were estimated by the Kaplan-Meier method.

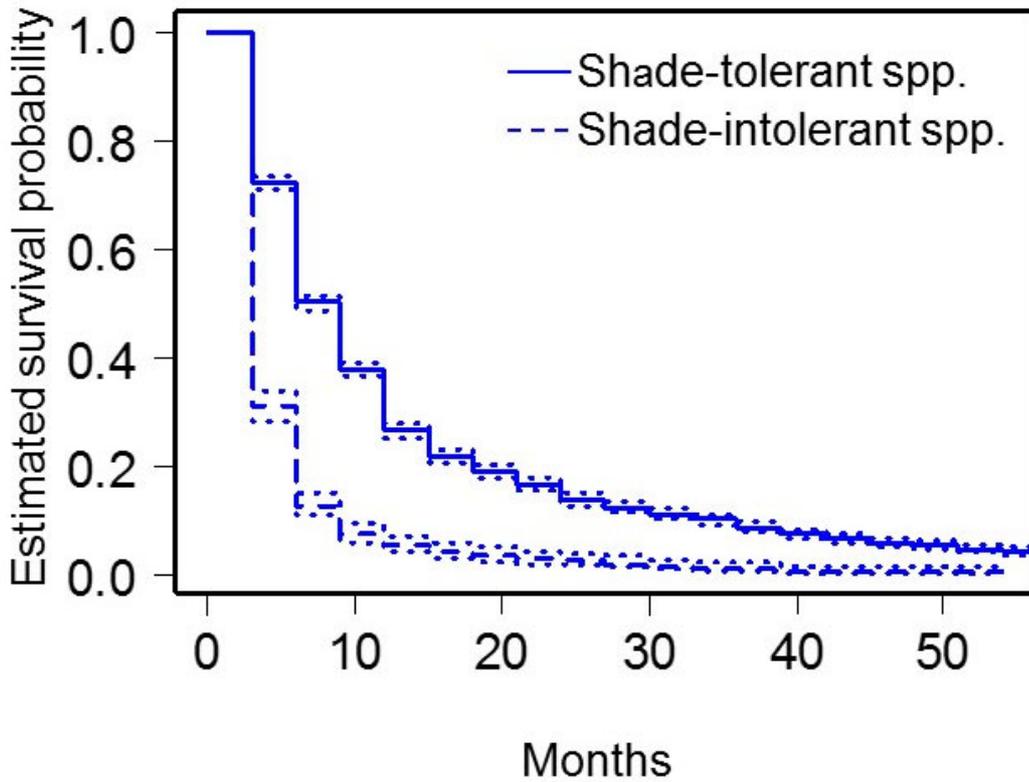


Fig. 3. Guild-specific survival functions defined by species' shade-tolerance in the Kenting Karst Forest Dynamics Plot. Estimated survival probabilities of shade-tolerant (solid lines) or -intolerant (dashed lines) species and their 95 % confidence intervals (dotted lines) are shown. Survival functions were estimated by the Kaplan-Meier method.