Long-term Seedling Dynamics of Tree Species in a Subtropical Rain Forest, Taiwan

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ABSTRACT: Knowledge of demographical rates at seedling stage is critical for understanding forest composition and dynamics. We monitored the seedling dynamics of tree species in a subtropical rain forest in Fushan, northern Taiwan (24°45' N, 121°35' E) during an 8-yr period (2003–2010). There were great temporal fluctuations in the seedling density, which might be largely driven by the pulses of seedling recruitment. Interspecific variation in the seedling abundance, however, was not related to the reproductive adult abundance. Previous studies showed that frequent typhoon disturbances contributed to the high canopy openness and high understory light availability at Fushan, which might benefit tree regeneration. But our results do not support this idea. Most of the newly recruited seedlings died within six months and only grew 1.55 ± 0.20 cm per year, which might be suppressed by the dense understory vegetation. Our results suggested that the majority of tree species in Fushan were recruitment limited, which might have important consequences for species coexistence. High temporal variability in recruitment density and low growth rates of seedlings emphasize the importance of long-term studies to our understandings of forest dynamics.

KEY WORDS: Fushan Forest Dynamics Plot, linear mixed-effects model, masting, recruitment limitation, regeneration, seedling growth, seedling survival.

INTRODUCTION

In forest ecosystems, recruitment processes such as seed production of parent trees, together with factors that influence seedling establishment, play important roles in determining local abundance and diversity of adult trees (Tilman, 1994; Hurtt and Pacala, 1995; Dalling et al., 1998; Harms et al., 2000). Quantifying the demography at seedling stage is therefore essential for understanding the forest composition and dynamics. The ecological processes that affect changes in population abundance cannot be revealed, nor can management plans to preserve rare species to be made, without demographic knowledge of this stage. However, understory seedling densities were highly variable over time at both population and community levels in many forests (Connell and Green, 2000; Norden et al., 2007; Metz et al., 2008). For instance, many tropical tree species reproduce at irregular supra-annual intervals (Ashton et al., 1988; Newstrom et al., 1994; Sakai, 2002). Accurate estimations of demographic rates can be obtained only with long-term observations made at adequate intervals (Connell and Green, 2000).

A species' abundance in the seedling layer is largely determined by three demographics rates: recruitment into seedling layer, mortality of seedlings, and growth out of the seedling layer into large size classes. All demographic parameters exhibit variation within and among species and over space and time. Interspecific variation in recruitment may result from differences in seed production of reproductive adults in the community. Species abundance in the seedling layer would be linearly correlated with the reproductive adult abundance if the number of recruits per adult is constant (Comita et al., 2007). However, temporal fluctuations in recruitment success of some tree species may obscure this relationship. Many studies have consistently found large inter-annual fluctuations in seed production in many plant species (Kelly and Sork, 2002). Nevertheless, long-term studies would alleviate the impact of this temporal variability because better estimates of seedling recruitment could be obtained with long-term data (Clark et al., 1999).

Seedling growth and survival may be regulated by interactions between overstory and understory (Beckage et al., 2000; Beckage and Clark, 2003). Canopy cover influences levels of light, soil moisture, and nutrients in forest understory, all of which are limiting factors for seedling performance (Augspurger, 1984; Denslow et al., 1990; Pacala et al., 1994). Understory vegetation further modifies resource heterogeneity beneath canopies, and affects seedling performance in canopy gaps (Veblen, 1989; George and Bazzaz, 1999a, 1999b).

Strong tropical cyclones, or typhoons, affect forest structure, composition, and dynamics in both tropical and temperate forests (Sousa, 1984; Boose et al., 1994; Lin et al., 2011). However, the effect of tropical storms on tree seedling recruitment remains one of the least

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understood aspects of forest dynamics. Fushan (24°45' N, 121°35' E) has forests experiencing the most frequent typhoon disturbances in the world (Lin et al., 2011). Previous studies showed that the understory light level at Fushan was much higher than that in many temperate and tropical forests due to frequent typhoon disturbances, and suggested that the understory light environment was suitable for both shade-tolerant and shade-intolerant species regeneration (Lin et al., 2003; Lin et al., 2011). In this study, we monitored the seedling demography of all tree species in Fushan for eight years (2003–2010). Specifically we asked: (1) Did the interspecific variation in recruitment reflect the difference in the reproductive adult abundance? (2) What was the major driver of the temporal variation of the seedling density: recruitment, mortality, or growth? (3) How was the seedling performance in the Fushan forests?

MATERIALS AND METHODS

Study site

This study was conducted in the 25-ha Fushan Forest Dynamics Plot (FDP; 24°45′ N, 121°35′ E; 600–733 m asl) in northeastern Taiwan. The Fushan FDP is situated in an old-growth subtropical rain forest. The vegetation type of Fushan forest is a submontane evergreen broadleaf forest in the *Machilus-Castanopsis* zone (Su, 1984). Dominant families include Fagaceae, Lauraceae, Theaceae, Sabiaceae, Cyatheaceae, Proteaceae, and Julandaceae. A detailed plot description can be found in Su et al. (2007) and Su et al.(2010). The climate of the study site is very moist and strongly seasonal (Lu et al., 2000; Lu et al., 2009). Between 1990 and 2010, the annual precipitation ranged from 2740 to 7440 mm, with a mean of 4100 mm. The relative humidity is > 90 percent throughout the year. The mean annual temperature is 18.3°C, ranging from 11.9°C in January to 24.5°C in July.

Seedling census

Eighty-seven seed traps were established within the Fushan FDP for the study of phenology (Chang-Yang et al., In press). To monitor seedling dynamics in the Fushan FDP, we placed three 1-m^2 seedling plots 2 m away from each of three sides of each seed trap (Fig. 1) according to the protocol which had been used in the FDP on Barro Corolado Island, Panama (Harms et al., 2000). The trap and its surrounding plots comprise a census station. Distances between the nearest stations are 18.2 ± 2.5 m (mean ± SD). In November 2002, all seedlings of tree species <1 cm DBH (Diameter at Breast Height) within the plots were marked with a unique tag number, measured for height to the apical bud, and identified to species. In subsequent censuses, surviving seedlings were measured and recruits were tagged, measured and identified to species. We have recensused seedling plots every three months since February 2003. In this study, we used the data from February 2003 to November 2010, a total of 30 censuses were included. Censuses of May 2004 and August 2010 were skipped due to a lack of manpower. Seedlings of *Machilus zuihoensis* and its variety *Machilus zuihoensis* var. *mushaensis* were treated as the same taxa and referred as *Machilus zuihoensis* because of difficulty of distinguishing these two taxonomic groups. Nomenclature follows Flora of Taiwan edition II (Huang and Editorial Committee of the Flora of Taiwan, 1993–2003).

Seedling recruitment

We examined interspecific variation in newly recruited seedlings among 28 tree species with at least one newly recruited seedlings and one reproductive-size adult in the seedling and tree censuses, respectively. We investigated the relationship between recruit abundance and reproductive adult abundance. The reproductive adult abundance is the total number or total basal area (m^2) of reproductive-sized adults within the 20 m from the center of the seedling plots. We defined the reproductive size of each species as one third of the maximal DBH of that species based on our field observation. We used the 0.999 quantile as the maximal DBH for each species.

Seedling survival

We analyzed the seedling survival data using the survival function *S(t)* because our seedling survival data were right-censored (i.e., there were seedlings alive at the last census). *S(t)* is the probability that an individual survives beyond time *t*, i.e. Pr (*T* > *t*), where *T* represents the time at death. We calculated nonparametric survival functions that do not require any distributional assumptions. We used an algorithm based on Turnbull (1976) to estimate nonparametric survival functions. The algorithm iteratively estimates the survival function using the Kaplan-Meier product-limit estimator:

$$\hat{S}(t) = \begin{cases} \prod_{t_i < t} 1 - \frac{d_i}{r_i} & t_i < t \text{ or} \\ 1 & t < t_i \end{cases} \quad (1)$$

where d_i is the number of deaths that occur in the interval t_i, and r_i is the number of seedlings at risk, that is, alive at the beginning of the interval t_i. The median times at death were estimated for all species together and for each sampled species based on the survival functions.

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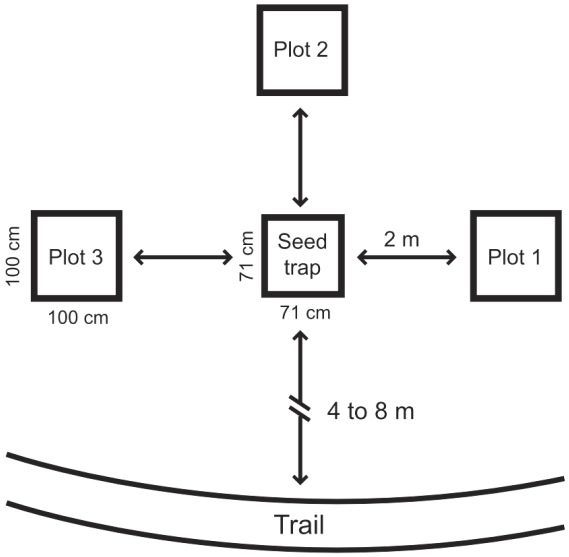


Fig. 1. Census station layout.

Seedling growth

We used the linear mixed-effects model (LMM) to estimate the annual growth rate for seedling height at community level. We modelled the temporal variation of the seedling height as a function of the time since the seedling was first tagged. We constructed a varying-slope model by adding by-species random slopes to the coefficient of independent variable. The species specific growth rate can be estimated even for the rarest species by taking advantage of the borrowed strength from other species in the analysis (Gelman and Pardoe, 2006). Because we had multiple observations of some individuals that survived several censuses, we also included seedling individual as a random effect to account for the serial dependence. The LMM with random slope and random intercept can be specified as:

$$H_{ij} = [\beta_0 + \beta_1 x_{ij}]_{\text{fixed_part}} + [\gamma_{\text{species}} x_{ij} + \mu_{\text{species}} + \mu_i]_{\text{random_part}} \quad (2)$$

where H_{ij} was the height for seedling i at census j, and x_{ij} was the time interval since seedling i was tagged. The first set of brackets in equation 2 includes the fixed effects of the model, where β_0 represents the community-level seedling height at time zero (initial height), and β_1 represents the height increment per unit time, that is, annual growth rate, at community level. The second set of brackets includes the random effects of the model, where γ_{species} denotes the random slope term for each species (i.e. variation among species in the coefficient β_1), and μ_{species} and μ_i refer to species-specific and individual-specific random intercepts, respectively, which characterize the variation among species and individuals.

Only the newly recruited seedlings were included in the analysis of seedling survival and growth because their age could be approximated by the time since they were tagged. All analyses were performed using the statistical programming language R, version 2.15.1 (R Development Core Team, 2012). The survival analysis was computed based on the 'survival' library (Therneau, 2012). The linear mixed-effects model was fitted by the 'lmer' function of the 'lme4' library with the recommended Laplace method (Bolker et al., 2009; Bates et al., 2012).

RESULTS

We found a total of 11,127 seedlings representing 36 tree species in the 261 seedling plots in 30 censuses between 2003 and 2010. Among them, 97.5% were newly recruited seedlings, comprising 28 species (35% of the tree species found in the FDP). The most abundant species was *Myrsine seguinii*, with 6888 recruits (63% of the total), followed by *Schefflera octophylla* (1161 recruits) and *Glochidion acuminatum* (976 recruits). Only ten species had more than 50 recruits during the study period. Interestingly, neither the abundance nor the total basal area (BA) of the neighboring reproductive-sized adults could explain the interspecific variation in recruitment (Fig. 2; Spearman's rank correlation, adults' abundance vs. recruit: ρ = 0.266, P = 0.171; adults' BA vs. recruit: ρ = 0.367, P = 0.055). The most abundant tree species in the plot, *Helicia formosana*, only had 15 recruits during the 8-yr study period (Appendix).

There were great inter-annual fluctuations in the seedling density, ranging from 1.5 seedlings m^{-2} in February 2003 to 12.7 seedlings m^{-2} in August 2003. The seedling density peaked in 2003, 2005, and 2007, and was highly correlated with the density of recruitment (Fig. 3). The peak of seedling mortality lagged three to six months behind the large recruitment events (Fig. 3). The density of transition (growth out of < 1-cm DBH category) contributed almost nothing to the temporal variations in seedling density. Only three seedlings grew out of the < 1-cm DBH category during the study period (not shown in Fig. 3).

The survival analysis showed that most of the newly recruited seedlings died within one year (Fig. 4). The time that 50% of the individuals died (median time at death) was 0.52 year. Only 2% of the newly recruited seedlings could survive more than five years. There were considerable variations in the median times at death among the 28 sampled species with newly recruited seedlings (Fig. 5). The median times at death were less than one year for 16 species. In contrast,

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Helicia formosana had the highest median time at death (3.2 years).

From 2003 to 2010, only four newly recruited seedlings grew >50 cm in height. Individual-based mixed model with by-species random effects was utilized to quantify the temporal variation of seedling heights. With all 28 species combined, the seedling height increment was 1.55 ± 0.20 (± 1SE) cm per year, while the estimated initial height was 6.84 ± 0.77 (± 1SE) cm. A large proportion of variation in seedling heights was explained by the variation among species ($\sigma^2_{\text{species (intercept)}} = 15.39$, $\sigma^2_{\text{species (slope)}} = 0.90$, $\sigma^2_{\text{individual}} = 4.15$, $\sigma^2_{\text{residual}} = 2.86$). Most of the explained variation was contributed by the differences in the initial height among species, whereas the annual height increment was similar among the 28 sampled species (Fig. 6).

DISCUSSION

We found large temporal variation in the understory seedling density in the Fushan subtropical rain forest, which appeared to be largely driven by pulses in seedling recruitment. Mortality peaked after the major recruitment episodes with a 6-month lag, as also revealed by the estimated median age to death. The seedlings in Fushan grew 1.5 cm per year and only three seedlings grew out of the < 1-cm DBH seedling class, which had little impact on the inter-annual difference of the seedling density.

The interspecific variation in recruitment was not related to the difference of reproductive-sized adult abundance among species. Several dominant tree species in Fushan only had less than 20 recruits during the 8-yr study period (Appendix). Seedling dynamics observed in the eight years could hardly explain the current structure and species composition of the forests. The seed trap data suggested that seed limitation might be the major driver of this pattern. Most species with few seedlings produced few seeds during this period (Chang-Yang, unpublished data). Since the long life spans of tree species allow them to persist through years with low recruitment (Chesson and Warner, 1981; Warner and Chesson, 1985), tree species in Fushan may take advantage of rare events (such as extremely strong storms or masting) that happen in low frequency to regenerate.

Previous studies showed that, because of frequent typhoon disturbances, the understory light level in the Fushan forest was much higher than that in temperate and tropical forests, and suggested that this light environment might be favorable for tree regeneration (Lin et al., 2003; Lin et al., 2011). However, our results do not support this idea. In fact, we observed high mortality and low growth rates in the newly recruited

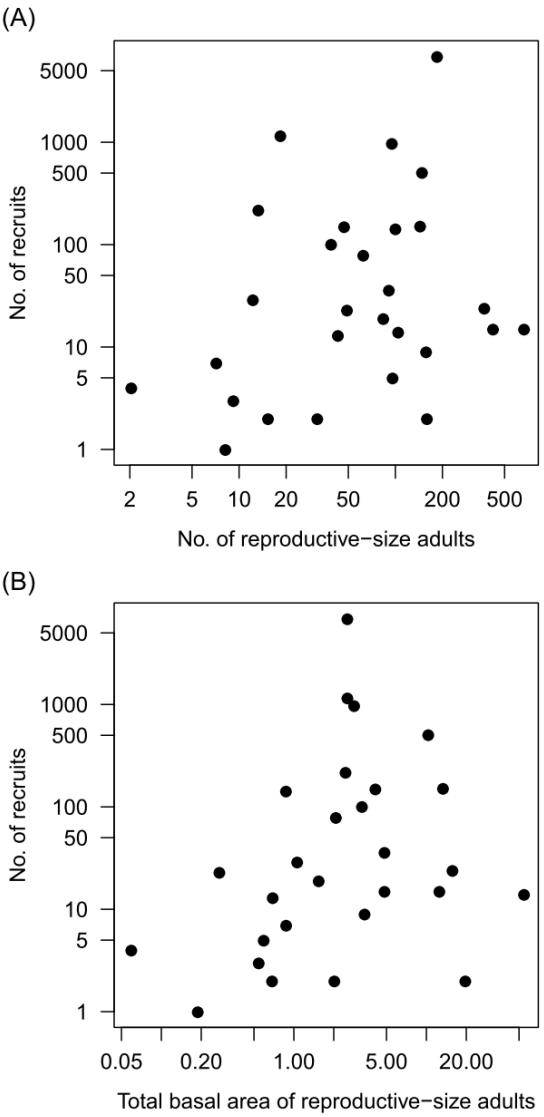


Fig. 2. Relationships between recruitment for all the sample years and reproductive-sized adult abundance (A) and total basal area (m^2) (B) for the 28 tree species in the Fushan subtropical rain forest. Note both axes are in log scale.

seedlings. One possible explanation for this pattern is that the level of light in the understory may reduce if there were few typhoons during the study period. But this is unlikely to be true because the number of typhoon in the vicinity of Taiwan increased abruptly from 3.3 per year before 2000 to 5.7 per year after 2000 (Tu et al., 2009). The dense understory vegetation in the Fushan forests provides another possible explanation for our results (Lu, 2004). Many forests support dense understory vegetation that may compete with tree seedlings for resource such as light, diminishing the effects of canopy gaps on promoting seedling recruitment (Yamamoto et al., 1995; Beckage et al., 2000; Hille Ris Lambers and Clark, 2003).

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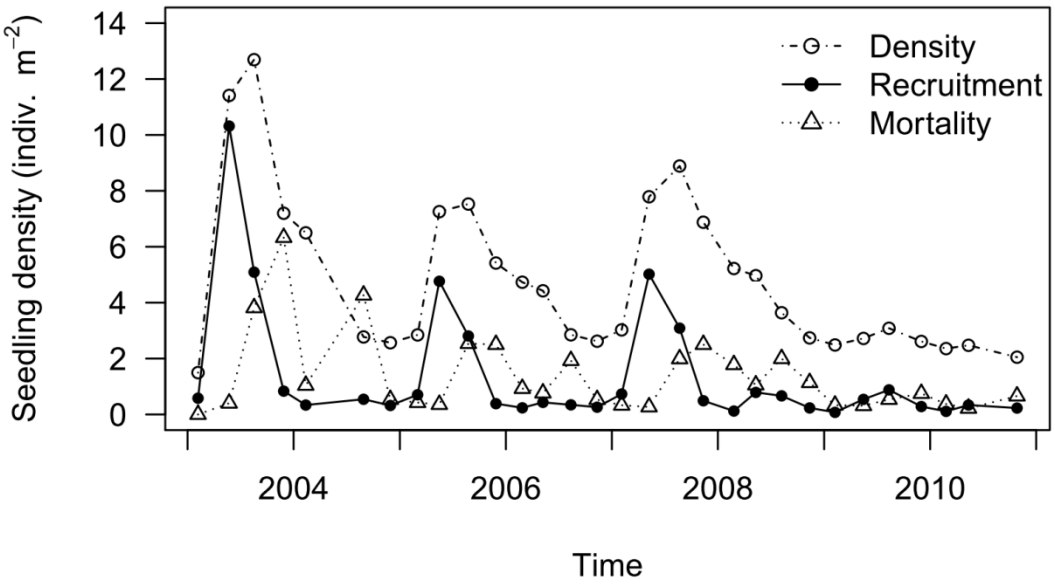


Fig. 3. Temporal variation in seedling demography (2003–2010) in the Fushan subtropical rain forest. Points represent the density of individuals in any census of all seedlings < 1 cm DBH (Density), seedlings that newly recruited over the census interval (Recruitment), and seedlings that died over the census interval (Mortality).

Despite there were more than 11,000 seedlings found during the study period, most of them died within six months and very few seedlings could survive more than five years. In the last census, the seedling density was only two individuals per square meter. These results, together with the fact that many dominant species had very few individuals in the seedling layer, suggested that the majority of species in the Fushan forest were recruitment limited. Because of the low seedling density, few species will be competing at the local scale (Comita et al., 2007). Community-wide recruitment limitation was also observed in both tropical and temperate forests (Ribbens et al., 1994; Clark et al., 1998; Hubbell et al., 1999; Norden et al., 2007). Theoretical studies have shown that recruitment limitation can maintain local species coexistence by allowing competitively inferior species to persist in the community by occupying the sites where superior species are absent (Tilman, 1994; Hurtt and Pacala, 1995; Chave et al., 2002).

The observed temporal variations in seedling density may have little impact on the density of individuals in large size classes because only few seedlings grew out of the < 1-cm DBH seedling class. Nevertheless, temporal fluctuations in recruitment may have important consequences for species coexistence. Large inter-annual variations in recruitment processes may foster species coexistence by allowing diverse tree species to establish in years different from the masting years of best competitor (Warner and Chesson, 1985; Kelly and Bowler, 2002). Our results highlighted the importance of long-term studies to our understanding of forest dynamics. Continuing monitoring seedling dynamics will allow us to get physical evidence for the influence of recruitment on forest dynamics.

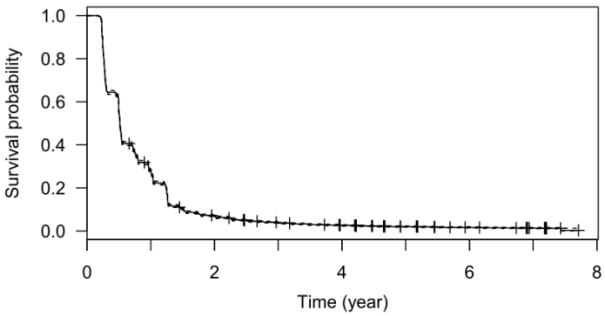


Fig. 4. Seedling survival of 10,851 newly recruited seedlings in the Fushan subtropical rain forest. The survival function is the non-parametric Kaplan-Meier estimate. The dash lines represent the 95% confidence interval. The pluses denote the censoring data.

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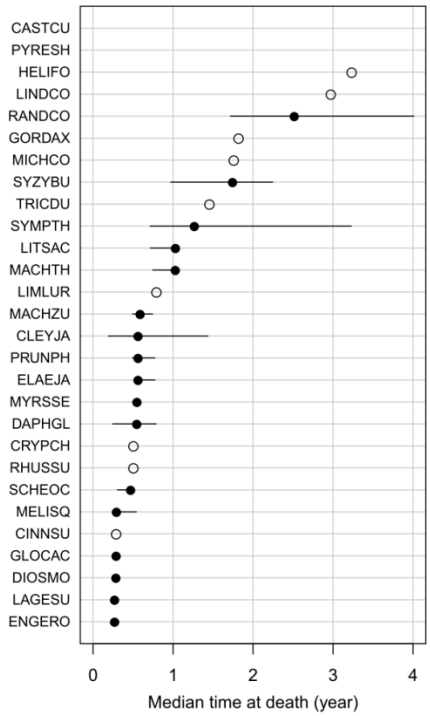


Fig. 5. Estimated median time at death with 95% confidence interval of newly recruited seedlings for the 28 tree species in the Fushan subtropical rain forest. The 95% confidence interval can not be estimated for the species with limited sample size, as indicate by open circles. Note that the median time at death can not be estimated for two species because >50% of the seedlings survived at the end of the study. Species abbreviations see Appendix.

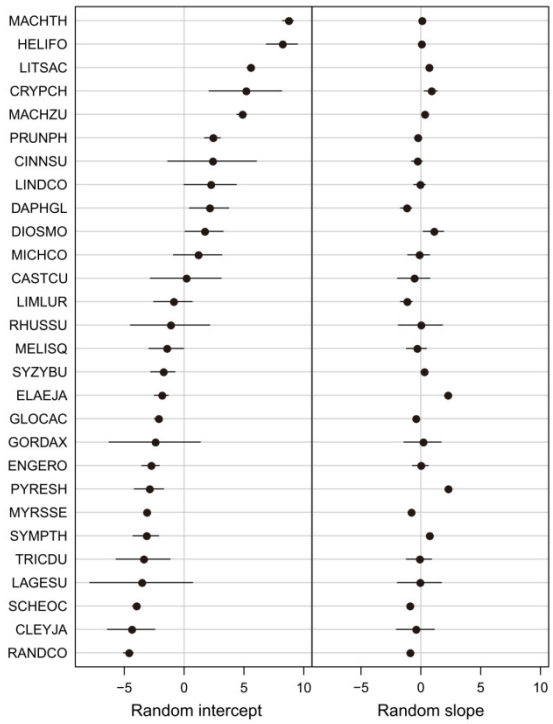


Fig. 6. Estimated random intercepts and random slopes with 95% prediction intervals of the linear mixed-effects model of seedling growth for the 28 tree species in the Fushan subtropical rain forest. Species abbreviations see Appendix.

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台灣亞熱帶雨林喬木小苗之長期動態

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摘要：關於植物小苗新增、成活表現的研究對於了解森林的組成與動態，扮演著極為重要的角色。本研究於台灣北部的福山亞熱帶雨林（24°45’ N, 121° 35’ E）長期監測喬木小苗的動態（2003至2010年），發現森林地被層中的小苗密度有著很大的年間變化，而此現象主要是受到研究期間每年小苗新增數量不同的影響，此外，研究期間各樹種新增苗數量上的差異與其母樹數量無關。福山地區先前的研究認為頻繁的颱風干擾導致森林冠層破碎、林下光線充足，應該有利於樹種的更新，然而我們的研究結果並不支持此一論述：絕大多數的新增小苗會在6個月內死亡，且新增小苗平均每年僅生長1.55 ± 0.20 cm，推測可能是受到福山濃密的地被壓抑所致。研究結果顯示大多數福山的樹種都有明顯的更新限制，此一機制可能對於福山地區樹種的共存有很大的影響。小苗新增有著很大的年間變化，加上小苗的生長緩慢，這些現象再再突顯長期研究對於了解森林動態的重要性。

關鍵詞：福山森林動態樣區、線性混合效應模式、豐年、更新限制、森林更新、小苗生長、小苗存活。

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Appendix. Species code, mean initial height of the newly recruited seedlings, number of recruits, and reproductive-sized adult abundance of the 28 tree species in the Fushan subtropical rain forest.

Species	Family	Species code	Initial height (cm)	No. of recruits	Reproductive-sized adult abundance	
					No. of individuals	Total basal area (m^2)
Castanopsis cuspidata* var. *carlesii	Fagaceae	CASTCU	8.0	2	156	19.19
Cinnamomum subavenium	Lauraceae	CINNSU	8.8	2	15	0.67
Cleyera japonica	Theaceae	CLEYJA	2.2	9	154	3.33
Cryptocarya chinensis	Lauraceae	CRYPCH	9.1	2	31	1.97
Daphniphyllum glaucescens* ssp. *oldhamii	Daphniphyllaceae	DAPHGL	7.5	13	42	0.68
Diospyros morrisiana	Ebenaceae	DIOSMO	6.8	36	89	4.71
Elaeocarpus japonicus	Elaeocarpaceae	ELAEJA	5.3	101	38	3.19
Engelhardtia roxburghiana	Juglandaceae	ENGERO	4.7	150	46	4.02
Glochidion acuminatum	Euphorbiaceae	GLOCAC	3.4	976	93	2.78
Gordonia axillaris	Theaceae	GORDAX	2.0	1	8	0.18
Helicia formosana	Proteaceae	HELIFO	15.9	15	652	4.71
Lagerstroemia subcostata	Lythraceae	LAGESU	1.8	29	12	1.03
Limlia uraiana	Fagaceae	LIMLUR	7.3	14	102	53.21
Lindera communis	Lauraceae	LINDCO	9.0	4	2	0.06
Litsea acuminata	Lauraceae	LITSAC	11.9	508	145	10.07
Machilus thunbergii	Lauraceae	MACHTH	14.8	152	141	13.02
Machilus zuihoensis	Lauraceae	MACHZU	11.3	218	13	2.39
Meliosma squamulata	Sabiaceae	MELISQ	5.5	24	363	15.34
Michelia compressa	Magnoliaceae	MICHCO	8.0	7	7	0.85
Myrsine seguinii	Myrsinaceae	MYRSSE	1.0	6888	181	2.47
Prunus phaeosticta	Rosaceae	PRUNPH	8.3	79	61	2.02
Pyrenaria shinkoensis	Theaceae	PYRESH	4.9	15	413	12.22
Randia cochinchinensis	Rubiaceae	RANDCO	1.8	143	98	0.85
Rhus succedanea	Anacardiaceae	RHUSSU	5.0	3	9	0.53
Schefflera octophylla	Araliaceae	SCHEOC	2.2	1161	18	2.47
Symplocos theophrastifolia	Symplocaceae	SYMPTH	4.3	19	82	1.50
Syzygium buxifolium	Myrtaceae	SYZYBU	5.2	23	48	0.27
Tricalysia dubia	Rubiaceae	TRICDU	3.6	5	94	0.58

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