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Biotic and abiotic drivers of dipterocarp seedling survival following mast fruiting in Malaysian Borneo

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Abstract: South-East Asian tropical rain forests experience sporadic, but profuse, seed production after general flowering, leading to the synchronous emergence of various seedlings and subsequent seedling dynamics, which play a crucial role in determining species distribution and coexistence. We examined the relative importance of both biotic (initial height, conspecific seedling density) and abiotic (canopy openness, per cent sand, soil water content) drivers using survival data for 1842 seedlings of 12 dipterocarp species for 1.5 y following mast fruiting in an old-growth Bornean tropical rain forest. More than 30% of all dipterocarp seedlings survived 1.5 y after mast fruiting. When all species were analysed together, we found that initial seedling height, canopy openness and conspecific seedling density affected dipterocarp seedling survival. Negative density dependence indicated that predators were not satiated, but dipterocarp seedlings rather suffered from host-specific natural enemies or intraspecific competition. Species-level analyses of seven dipterocarp species showed large variation in response to biotic and abiotic factors. These results suggest that interspecific differences in the relative importance of biotic and abiotic effects on seedling survival might contribute to species coexistence.

Key Words: density dependence, Dipterocarpaceae, Janzen-Connell hypothesis, Lambir, masting, predator satiation hypothesis, seedling recruitment

INTRODUCTION

Masting, the synchronous and intermittent production of large seed crops, is a widespread phenomenon displayed by many plant species worldwide (Lamontagne & Boutin 2007, Norden *et al.* 2007, Norton & Kelly 1988, Shibata *et al.* 2002, Sork *et al.* 1993). In the South-East Asian humid tropics, masting at the community level, also termed ‘mast fruiting’ (MF), occurs at irregular intervals of one to several years (Appanah 1985, Ashton *et al.* 1988, Sakai 2002). Not only do the dominant dipterocarps bloom, but plants of diverse families bloom as well (Cannon *et al.* 2007, Sakai *et al.* 1999, 2006). After flowering, many fruits are produced and dispersed synchronously and the forest floor becomes covered with a carpet of various current-year seedlings (Curran & Leighton 2000).

One of the major hypotheses explaining the evolutionary cause of MF is the predator satiation hypothesis, in which seed survival is expected to be enhanced because a high density of seeds that all share the same seed predators can reduce the destructive impact of those predators (Janzen 1974, Sun *et al.* 2007, Visser *et al.* 2011). The mortality of dipterocarp seedlings has been reported to be high, and a major cause of initial seedling mortality is often predation by mammals (Curran & Webb 2000, Takeuchi & Nakashizuka 2007). Therefore, predator satiation at the seedling stage may also be important to the recruitment success of dipterocarp trees (Bagchi *et al.* 2011). Conversely, a high density of conspecific seedlings may attract host-specific predators or pathogens (Connell 1971, Janzen 1970), or may intensify intraspecific competition for resources, with a negative impact on seedling survival. A significant negative effect of conspecific seedling density on seedling survival has been reported in various tropical (Comita *et al.* 2009, 2010, Lin *et al.* 2012, Queenborough *et al.* 2007, Webb & Peart 1999) and other forests (Comita *et al.* 2014, Johnson *et al.* 2012).

Local abiotic factors also have significant effects on seedling dynamics in tropical forests (Comita *et al.* 2009,

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Queenborough *et al*. 2009). In a forest with a vertical gradient in irradiance, improved light conditions usually result in higher seedling survival (Brown & Whitmore 1992, Kobe 1999). Dipterocarp seedlings growing in canopy gaps often experience higher survival than those in the shade (Itoh 1995, Turner 1990). Tree seedling survival is also influenced by the availability of water and nutrients in the soil (Comita *et al*. 2009, Walker *et al*. 2003). Previous studies found that higher dipterocarp seedling mortality has been observed during periods of severe drought (Bebber *et al*. 2004, Delissio & Primack 2003). Furthermore, nutrient additions can enhance the growth of dipterocarp seedlings (Burslem *et al*. 1996), and therefore higher soil resource availability should impact dipterocarp seedling survival.

The relative importance of biotic and abiotic drivers for seedling survival may differ among dipterocarp species. Because the density of current-year dipterocarp seedlings from wingless (i.e. mainly gravity-dispersed) fruits tends to be higher than that of winged (i.e. wind-dispersed) fruits under the crown of mother trees, negative density dependence of dipterocarp seedlings may be more apparent in wingless than in winged fruits (Bai *et al*. 2012). The morphological traits of current-year seedlings also show high variation among dipterocarp species (Ng 1991). This variation in seedling morphology could alter responses to the light environment or soil conditions. However, few studies have investigated the relative importance of both biotic and abiotic drivers of dipterocarp seedling survival following a MF, which provides an excellent but relatively rare chance to improve our understanding of dipterocarp regeneration.

In this study, we assessed the effects of biotic and abiotic factors on dipterocarp seedling survival within 1.5 y following a MF, using data from 1842 seedlings of 12 dipterocarp species in an old-growth Bornean tropical rain forest. Specifically we explored (1) the relative importance of biotic and abiotic drivers in seedling survival following a MF, and (2) interspecific differences in the relative importance of these factors, to examine our hypotheses that abiotic factors are more apparent than biotic factor (i.e. density dependence) and that dipterocarp seedlings from wingless fruits are more sensitive to biotic factors than those from winged fruits.

METHODS

Study site

This study was carried out in and around an 8-ha Canopy Biology Plot (CBP; 200 m × 400 m) and a 4-ha Crane Plot (CP; 200 m × 200 m) in Lambir Hills National Park, Sarawak, Malaysia (LHNP; 4°12′N, 114°02′E, 20–150 m asl). The average annual rainfall and mean air temperature at LHNP from 2000 to 2009 were 2600 mm and 25.8 °C, respectively (Kume *et al*. 2011). The soils of LHNP contain sandstone-derived humult ultisols and shale-derived clay-rich udult ultisols (Lee *et al*. 2002). Soil nutrients vary according to the soil type and sandy loam is less fertile than clay (Davies *et al*. 2005, Ishizuka *et al*. 1998, Russo *et al*. 2005). In LHNP (about 7000 ha), which is dominated by an intact lowland dipterocarp forest, a major MF event occurred during 2009–2010 and many fruits were produced and dispersed (Nakagawa *et al*. 2012).

Seedling census

To explore dipterocarp seedling survival following the major 2009–2010 MF, we used three *Dipterocarpus* and nine *Shorea* species, which produced plentiful fruits at the study site (Table 1). In March 2010, a few weeks after mature fruits had been dispersed, three individual trees per species were selected and three seedling quadrats (1 × 1 m) were established under the crown of each individual tree (in total, 108 quadrats). Then all seedlings of the targeted dipterocarp species that recruited in the 2009–2010 MF in each quadrat were numbered and their height was measured. Seedling survival was monitored in June and September 2010 and in September 2011.

In total, 6–12 seedlings were harvested per individual tree in March 2010, except for one tree of *S. kunstleri* that had no extra sound seedlings. We quantified leaf area to the nearest 0.1 mm^2 using LIA software for Win32 (http://www.agr.nagoya-u.ac.jp/~shinkan/LIA32/). After oven-drying at 50 °C for 120 h, we measured the dry weights of leaves, roots and whole seedlings to the nearest 0.001 g, and calculated the root allocation (dry root weight/dry whole weight). We also calculated specific leaf area (SLA) by dividing the leaf area by the dry leaf weight.

Biotic and abiotic factors

To quantify the local biotic neighbourhood, we calculated the initial density of conspecific seedlings in each seedling quadrat. Because seedling quadrats were set under the crown of selected trees and most of the offspring recruited in seedling quadrats were of the targeted dipterocarp species, we did not include the density of heterospecific seedlings in this biotic factor. The distance of each seedling quadrat from the selected tree was also not included because most quadrats were placed within 10 m (mean ± SE, 4.9 ± 0.16 m). Although the importance of initial height for survival has been well-documented in tropical seedlings (Comita *et al*. 2009), we included the initial seedling height since the effect on the targeted dipterocarp species remains unclear.

Table 1. Dipterocarp species used in seedling census in Lambir Hills National Park. *N* is the initial number of seedlings. Diameter at breast height of selected trees (dbh, mean ± SD) is measured in 2009. Six trees selected around the plots were measured during 2001–2005. Mean dry weight (± SD) of dipterocarp fruits without wings (oven-dried at 50 °C for 120 h) was measured using mature, sound fruits collected in March 2010 under each selected tree (7–20 fruits per tree), with the exception of two *S. curtisii* trees.

Species	N	Tree dbh (cm)	Dry fruit weight (g)
Dipterocarpus globosus Vesque	34	85.9 ± 29.4	11.2 ± 3.08
Dipterocarpus pachyphyllus Meijer	70	116 ± 38.2	1.56 ± 0.38
Dipterocarpus tempehes Slooten	494	92.8 ± 26.8	5.39 ± 1.78
Shorea acuta P.S.Ashton	31	51.7 ± 1.0	2.64 ± 0.83
Shorea beccariana Burck	49	86.0 ± 7.2	4.96 ± 0.82
Shorea bullata P.S.Ashton	107	55.4 ± 20.9	1.24 ± 0.27
Shorea crassa P.S.Ashton	546	57.6 ± 21.6	1.48 ± 0.43
Shorea curtisii Dyer *ex* Brandis	154	82.3 ± 6.3	0.81 ± 0.14
Shorea exelliptica Meijer	61	72.7 ± 10.0	1.21 ± 0.20
Shorea kunstleri King	31	63.5 ± 26.0	1.34 ± 0.47
Shorea laxa Slooten	232	83.2 ± 17.3	6.39 ± 1.17
Shorea smithiana Symington	33	125 ± 26.0	2.14 ± 0.54
Total	1842		

We measured light conditions, soil water content and soil type as abiotic factors. To quantify the light conditions in each seedling quadrat, we measured per cent canopy openness using a digital camera with a fisheye lens (Cool Pix 950, Nikon). Images were taken at the centre of each seedling quadrat at a height of 30 cm in August 2010 and analysed using CanopOn 2 ver. 2.03c (http://takenaka-akio.org/etc/canopon2/). Soil water content was measured at five randomly selected points in each seedling quadrat using a sensor (SM200) and a Moisture Meter (Type HH2, Delta-T Devices Ltd). The sensor was placed into the soil at 10-cm depth. The measurements in all seedling quadrats were completed in a single day and conducted four times during the morning from September to October 2010, when monthly precipitation approximately averaged during the census period. We used the mean value of soil water content in each seedling quadrat. Soil samples from the centre of each seedling quadrat (5-cm in diameter and 15-cm depth) were air-dried and the per cent sand was measured using a Soil Texture Unit (LaMotte Company) in September 2010.

Statistical analyses

We modelled the probability of dipterocarp seedling surviving for 1.5 y as a function of the biotic and abiotic factors described above using generalized linear mixed models (GLMMs) with binomial errors (Bolker *et al.* 2009). First, to evaluate the effect of biotic and abiotic factors on dipterocarp seedling survival as a whole, we analysed the survival of all dipterocarp seedlings from March 2010 to September 2011 in a single community-level analysis. In this analysis, all dipterocarp species were pooled and tree individuals nested within species were included as random effects. All biotic and abiotic variables, plus log-transformed initial seedling height, were standardized using means and standard deviations across all seedlings and entered into the model as fixed effects. This allowed for a direct comparison between the relative importance of explanatory variables (Gelman & Hill 2006). Then the most appropriate model was determined by model selection based on Akaike's information criterion (AIC) (Anderson *et al.* 1998).

Second, we performed species-level (seven species with >60 initial seedlings) analyses for dipterocarp seedling survival over 1.5 y for each species. Tree individual was the only random effect included in the GLMMs of each focal species. All explanatory variables were again standardized using the mean and standard deviation of the seven dipterocarp species, which allowed us to compare the effects of factors across species. To test the effect of species on each dipterocarp seedling morphological trait (initial height, dry weight, SLA and root allocation), we used GLMMs with Gaussian distribution and tree individual as a random effect. To assess the statistical significance of species, we compared the change in deviance when a species was removed from the model with the *F*-distribution (Bolker *et al.* 2009). In post hoc comparisons, the family-wise error was adjusted based on Tukey's method at $P = 0.05$. Initial height, dry weight and SLA were log-transformed and root allocation was logit-transformed before analyses. All analyses were conducted in the software R version 3.0.2 (R development Core Team, http://www.r-project.org/), using the 'lme4' and 'multcomp' packages.

RESULTS

Current-year dipterocarp seedlings gradually decreased after MF (Figure 1), and overall, the mean (± SD)

Table 2. Morphological traits measured in March 2010 and seedling survival from March 2010 to September 2011 of 12 dipterocarp species in Lambir Hills National Park (mean ± SD). The survival was calculated for each selected individual (three individuals per species, 36 individuals for community-level mean survival). Different letters indicate significant differences among species in the results of multiple comparisons using Tukey's method at $P = 0.05$.

Species	Seedling height (cm)	Dry seedling weight (g)	SLA ($cm^2\ g^{-1}$)	Root allocation	Survival (%)
Dipterocarpus globosus	18.7 ± 4.3^{ab}	1.00 ± 0.31^{a}	170 ± 39.7^{efg}	0.492 ± 0.093^{cde}	59.5 ± 35.2
Dipterocarpus pachyphyllus	13.1 ± 3.0^{cde}	0.32 ± 0.07^{de}	201 ± 29.7^{cdef}	0.432 ± 0.057^{cde}	12.2 ± 10.9
Dipterocarpus tempehes	19.6 ± 7.1^{a}	0.71 ± 0.20^{b}	295 ± 63.0^{a}	0.365 ± 0.084^{e}	15.0 ± 21.7
Shorea acuta	12.9 ± 2.6^{cde}	0.62 ± 0.21^{bc}	146 ± 30.0^{g}	0.470 ± 0.080^{bcd}	16.0 ± 13.9
Shorea beccariana	19.2 ± 5.9^{ab}	1.13 ± 0.37^{a}	210 ± 133.4^{cdef}	0.475 ± 0.091^{bcd}	24.6 ± 22.1
Shorea bullata	14.2 ± 3.5^{cd}	0.27 ± 0.07^{ef}	245 ± 55.9^{abc}	0.479 ± 0.053^{bc}	26.2 ± 9.9
Shorea crassa	16.2 ± 5.2^{bcd}	0.35 ± 0.10^{de}	169 ± 46.6^{fg}	0.559 ± 0.077^{a}	48.6 ± 2.7
Shorea curtisii	17.3 ± 4.6^{abcd}	0.40 ± 0.13^{d}	191 ± 24.9^{def}	0.417 ± 0.069^{cde}	45.9 ± 17.2
Shorea exelliptica	12.0 ± 4.0^{e}	0.21 ± 0.09^{f}	221 ± 56.4^{abcd}	0.538 ± 0.086^{ab}	35.4 ± 19.0
Shorea kunstleri	17.9 ± 6.7^{abcd}	0.44 ± 0.10^{cd}	214 ± 26.5^{bcde}	0.450 ± 0.058^{bcd}	22.8 ± 22.2
Shorea laxa	18.4 ± 7.9^{ab}	1.16 ± 0.30^{a}	148 ± 26.1^{g}	0.480 ± 0.066^{bc}	50.6 ± 5.5
Shorea smithiana	18.3 ± 7.4^{abc}	0.58 ± 0.17^{bc}	245 ± 41.9^{ab}	0.402 ± 0.085^{cde}	38.0 ± 30.3
Total					32.9 ± 22.4

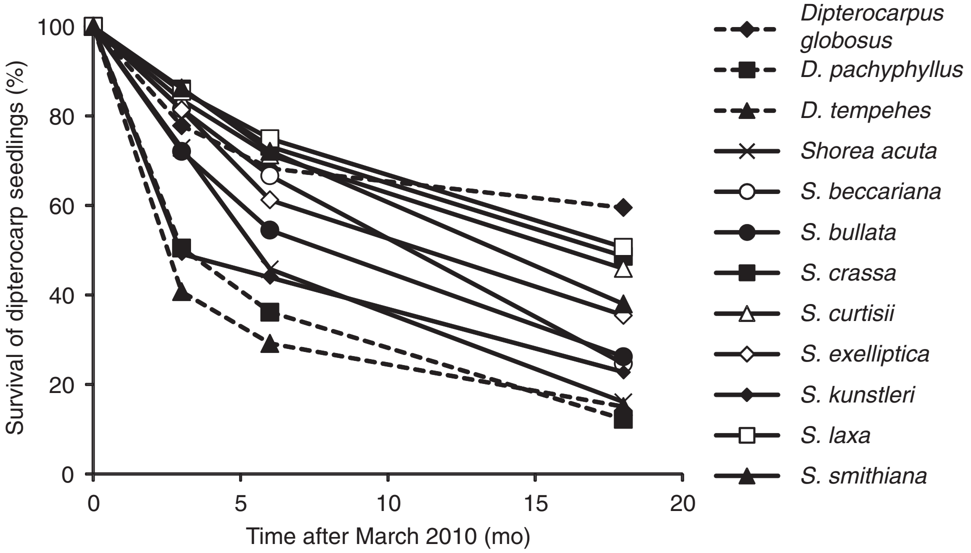

Figure 1. Seedling survival of 12 dipterocarp species from March 2010 to September 2011 in Lambir Hills National Park.

community-level seedling survival over 1.5 y was 32.9% ± 22.4% (Table 2). The mean survival of *D. globosus* and *S. laxa* was more than 50%, whereas that of *D. pachyphyllus*, *D. tempehes* and *S. acuta* was less than 20%. In the best-fit model of community-level dipterocarp seedling survival based on the AIC, one abiotic and two biotic drivers were included (Table 3). Initial height had the strongest impact on seedling survival, with larger seedlings having a higher probability of survival. Canopy openness was the second strongest factor, and dipterocarp seedlings growing under higher canopy openness had a higher probability of survival. Conspecific density had a negative impact on survival, wherein dipterocarp seedlings surrounded by higher density of conspecific seedlings showed lower survival.

All morphological traits of current-year seedlings significantly differed among dipterocarp species ($P < 0.01$). Dipterocarp species with larger fruit mass (*D. globosus*, *D. tempehes*, *S. beccariana* and *S. laxa*) had generally taller and larger-mass seedlings than those with smaller fruit mass (Table 1, 2). Mean SLA and root allocation were highest and lowest in *D. tempehes* seedlings, respectively. When examining dipterocarp seedling survival at the species level, biotic and abiotic factors were selected differently according to focal species. Although initial height positively affected the seedling survival of most dipterocarp species, conspecific density had negative effects on *D. tempehes*, *S. bullata*, *S. crassa* and *S. exelliptica* (Table 3). The effects of canopy openness and per cent sand were positive for *D. pachyphyllus* and

Table 3. Coefficients included in the best model for community-level and species-level analyses of dipterocarp seedling survival in Lambir Hills National Park.

Species	All species	*Dipterocarpus pachyphyllus*	*Dipterocarpus tempehes*	*Shorea bullata*	*Shorea crassa*	*Shorea curtisii*	*Shorea exelliptica*	*Shorea laxa*
(N)	(1842)	(70)	(494)	(107)	(546)	(154)	(61)	(232)
Log (height)	0.61	1.65	1.72	1.36	0.47	0.63		0.69
Canopy openness	0.42	4.07				1.63		
Conspecific density	− 0.40		− 2.37	− 9.25	− 0.25		− 9.01	
Per cent sand				1.17		2.89		
Soil water			2.66			− 0.73		0.34

S. curtisii seedlings, and for *S. bullata* and *S. curtisii* seedlings, respectively. The survival of *S. curtisii* seedlings decreased with increasing soil water content, whereas that of *D. tempehes* and *S. laxa* seedlings increased with soil water content.

DISCUSSION

Recruitment of dipterocarp seedlings after MF

Over 30% of dipterocarp seedlings survived 1.5 y after the 2009–2010 MF, in which the magnitude of fruit production was substantially larger than in other MF years at the study site (Nakagawa *et al.* 2012). By contrast, near-complete recruitment failure has been reported for Dipterocarpaceae in years of moderate and minor MF (Blundell & Peart 2004, Maycock *et al.* 2005). Once dipterocarp seedlings are established, various dipterocarp juveniles (height < 2.0 m) tend to show high survivorship (77–100% in a 1-year census; Aiba & Nakashizuka 2007). Therefore, the 2009–2010 MF appears to have been a relatively successful masting event in terms of seedling recruitment of dipterocarp species at the study site. On the other hand, higher seedling survival has been reported for several dipterocarp species (Brown *et al.* 1999, Delissio *et al.* 2002, Itoh *et al.* 1995). Long-term studies on the seedling survival of various dipterocarp species following MFs are essential for better understanding the relationships between the establishment success of the dipterocarp seedling community and the magnitude of flower and fruit production in MF.

Biotic and abiotic factors affecting dipterocarp seedling survival

We found that biotic and abiotic variables affected the survival of all dipterocarp species following MF. The importance of both biotic interactions and habitat environment for seedling dynamics has been reported in tropical and temperate forests (Bagchi *et al.* 2011, Bai *et al.* 2012, Shibata *et al.* 2010). With the exception of initial height, canopy openness had the strongest effect overall, increasing the survival of dipterocarp seedlings. Canopy openness has been observed to have similar positive effects on the survival of not only dipterocarp seedlings (Itoh 1995, Turner 1990), but also dipterocarp juveniles (Aiba & Nakashizuka 2007) and seedlings in other tropical and subtropical forests (Comita *et al.* 2009, Everham *et al.* 1996, Kobe & Vriesendorp 2011). In the present study, the canopy openness of each seedling quadrat ranged from 4.0% to 8.8% (mean ± SD, 6.0 ± 1.0 %), and we investigated only seedlings growing under closed canopy in a multi-layered forest. Under these conditions, slight increase in light level will generally result in increased dipterocarp seedling survival due to the better availability of photosynthetic assimilates. However, the effect on seedling survival of much higher light availability, such as in a gap, remains unclear.

The density of conspecific seedlings also affected the survival of dipterocarp seedlings. Assuming that predator satiation is effective for seedling establishment after MF, this relationship might be expected to be positive. However, the detected effect was negative, indicating that predator satiation did not affect the seedling stage during the 2009–2010 MF. Predator satiation might be more crucial at earlier reproductive stages such as the pre- or post-dispersal seed stages or during seedling establishment (Sun *et al.* 2007, Takeuchi & Nakashizuka 2007, Tokumoto *et al.* 2009). The negative conspecific density-dependent seedling survival found here is in agreement with previous studies in various tropical forests (Comita & Hubbell 2009, Comita *et al.* 2009, 2010; Harms *et al.* 2000, Kobe & Vriesendorp 2011, Lin *et al.* 2012, Queenborough *et al.* 2007). Negative density dependence is hypothesized to result from intraspecific competition for resources (Paine *et al.* 2008) and contribute to the maintenance of diversity in species-rich tropical forests via host-specific natural enemies, including herbivores and pathogens, which respond in a density- or distance-dependent manner (Bagchi *et al.* 2014, Connell 1971, Janzen 1970). Furthermore, the relative importance of biotic and abiotic factors changed over time after disturbance by a hurricane (Comita *et al.* 2009). As the overall density of dipterocarp seedlings dropped to about one-third of the initial density over 1.5 y after a MF, the effect of density dependence on dipterocarp seedling survival may change over time.

Variation in abiotic and biotic drivers among dipterocarp species

The results of species-level analyses showed a wider variation in responses to biotic and abiotic factors compared with the community-level analysis. Canopy openness had a significant effect on the seedling survival of only two dipterocarp species in our study. Dipterocarps are generally all late-successional species, although differences in shade tolerance and photosynthetic capacity have been suggested among species (Aiba & Nakashizuka 2005, 2007; Brown *et al.* 1999, Cao & Booth 2001). Philipson *et al.* (2012) reported that the response in 3-y-old seedling growth rate to experimentally controlled light conditions varied among dipterocarp species. Seedlings of *D. pachyphyllus* and *S. curtisii*, which in the present study showed positive relationships between survival and canopy openness, appear to be relatively light-demanding. However, these two dipterocarps showed not small but intermediate SLAs among studied species. Because SLA changes as seedlings develop (Ichie *et al.* 2001) and photosynthetic capacity is also influenced by other factors like leaf nitrogen content, further physiological measurements are needed to elucidate the relationship between seedling traits and the degree of sensitivity to light conditions.

Although a previous study at the same study site found that the survival of dipterocarp saplings with wingless fruits (*D. tempehes* and *S. laxa*) had no clear density dependence (Takeuchi *et al.* 2005), negative density dependence was observed in *D. tempehes* seedlings with wingless fruits as well as in seedlings of three winged-fruit *Shorea* species. In a temperate forest, Bai *et al.* (2012) reported that negative density dependence was more apparent in gravity-dispersed seedlings than in wind- or animal-dispersed ones, but that density dependence was detected only for younger seedlings (age 1–3 y). Further accumulation of empirical studies is necessary for identifying whether dispersal mode influences the occurrence and strength of negative density dependence (Bagchi *et al.* 2011).

The survival of tropical seedlings is often associated with habitat topology through species-specific habitat preferences or drought persistence (Chen *et al.* 2010, Comita & Engelbrecht 2009). Such a spatially variable effect of soil resource availability on seedling survival likely contributes to species distribution patterns and niche partitioning. Seedlings of *S. curtisii* had the advantage of higher survival at sites with a higher content of sand and lower soil moisture, which suggests a preference for habitats with dry, nutrient-poor soil. This is supported by previous studies, which found that *S. curtisii* trees are abundant on ridge crests (Whitmore 1984) and that those 30–130 cm tall can withstand water stress and nutrient shortages (Yagihashi *et al.* 2010). However, no clear trends appear to exist in the effects of soil environmental heterogeneity on seedling survival and seedling morphological traits. During the census period, every month had rainfall more than 100 mm, except for 68.2 mm in March 2010. Differences in seedling performance according to the morphological traits might emerge under more severe conditions (e.g. severe drought). Our species-level results indicate that the major drivers of dipterocarp seedling survival vary among species, which in turn may contribute to species coexistence. Future studies should focus on identifying the traits controlling species sensitivity to biotic and abiotic drivers of seedling survival.

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