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Seasonal differentiation in density-dependent seedling survival in a tropical rain forest

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Summary

1. Density-dependent survival is prevalent in tropical forests and is recognized as a potentially important mechanism for maintaining tree species diversity. However, there is little knowledge of how density dependence changes in fluctuating environments.

2. Across the 20-ha Xishuangbanna tropical seasonal rain forest dynamics plot in southwest China, which has distinct dry and wet seasons, we monitored seedling survival in 453 1-m^2 quadrats over 2 years. Density dependence was assessed using generalized linear mixed models with crossed random effects.

3. When pooling all species at the community level, there were strong negative effects of conspecific tree neighbours on seedling survival over the dry-season, wet-season and 2-year intervals. The proportion of conspecific seedling neighbours had a significant negative effect in the dry season, but not in the wet season.

4. At the species level, the effects of conspecific tree and seedling neighbours varied widely among species in the community and were significantly positively related to population basal area in the community over the dry-season interval. In contrast, over the wet-season interval, the effects of conspecific tree and seedling neighbours did not significantly vary among species in the community. Overall community- and species-level results suggest that local-scale negative density dependence (NDD) tends to be stronger in the dry than wet season in the Xishuangbanna tropical forest.

5. At the scale of the 20-ha plot, we found a community compensatory trend (CCT), in which rare species had relatively higher seedling survival than common species in both the wet and dry seasons. A positive association between potential NDD and population basal area suggests that the CCT results from local-scale NDD, specifically because of negative effects of conspecific tree neighbours.

6. *Synthesis*. Our results demonstrate that the strength of density-dependent seedling survival can vary between seasons and among species in tropical forests. Future research is needed to assess the underlying mechanisms of this temporal and interspecific variation in NDD and its consequences for species coexistence and community composition.

Key-words: compensatory trend, density dependence, Janzen–Connell hypothesis, mixed models, plant–plant interactions, tropical rain forest, water availability

Introduction

Negative density dependence (NDD) has been recognized as a driving mechanism that may underpin the maintenance of tree species diversity in tropical forests (Wills *et al.* 1997; Harms *et al.* 2000; Volkov *et al.* 2005; Freckleton & Lewis 2006). One explanation for patterns of NDD in tropical forests is the Janzen–Connell hypothesis, which predicts that species-specific natural enemies, such as pathogens and herbivores, can reduce survival, recruitment and growth at high local conspecific neighbour densities (LCD) (Janzen 1970; Connell 1971). In the past decades, many studies have provided evidence for the Janzen–Connell hypothesis by testing for density dependence (e.g. Augspurger & Kelly 1984; Hubbell, Condit & Foster 1990; Condit, Hubbell & Foster 1994; Wills *et al.* 1997; Webb & Peart 1999; Hille Ris Lambers, Clark & Beckage

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2002; Blundell & Peart 2004; Swamy *et al.* 2011). However, most of these studies have only included common species (Carson *et al.* 2008). When pooling all species at the community level, negative conspecific effects on survival have been documented at different developmental stages from seedlings to larger saplings and adults, especially in tropical tree communities (Hubbell *et al.* 2001; Peters 2003; Comita & Hubbell 2009; Metz, Sousa & Valencia 2010).

Density-dependent survival tends to be prevalent among species at the seedling stage (Harms *et al.* 2000; Hille Ris Lambers, Clark & Beckage 2002; Comita & Hubbell 2009; Chen *et al.* 2010; Comita *et al.* 2010). Seedlings may be more vulnerable to attack by natural enemies compared with adult trees, and seedlings also experience strong asymmetric resource competition with conspecific adults (Clark & Clark 1985; Wright 2002). The seedling stage therefore suffers high mortality and represents a significant bottleneck in the life cycle of trees (Harper 1977). According to the Janzen–Connell hypothesis, the negative effect of conspecific neighbours on seedling survival should be stronger than the effect of heterospecifics, a requirement for density-dependent survival to promote species diversity.

If local-scale NDD (species' sensitivity to conspecific neighbours) is similar among species in the community and common species have higher LCD, common species are expected to have higher overall seedling mortality. In this situation, local-scale NDD can result in a community compensatory trend (CCT; Connell, Tracey & Webb 1984) at larger spatial scales (Webb & Peart 1999; Queenborough *et al.* 2007; Chen *et al.* 2010), in which commoner species will have lower survival rates than rarer species, thereby promoting the maintenance of species diversity (Connell, Tracey & Webb 1984). In addition, species' sensitivity to conspecific neighbours has been found to vary among species (i.e. 'asymmetric density dependence') and to decrease with increased species abundance in a tropical tree community in central Panama, suggesting that local-scale NDD is a potential mechanism shaping species commonness and rarity (Comita *et al.* 2010). However, this negative association between the strength of local-scale NDD and species abundance appears to run counter to a CCT (Kobe & Vriesendorp 2011), because rare species could have higher mortality than common species if both have similar LCD or if rare species have higher LCD. However, a CCT could still result if LCD increased with species community abundance (Kobe & Vriesendorp 2011). Thus, to evaluate the role of local-scale NDD in generating a CCT, it is critical to consider two components to NDD that may vary across species: the per-neighbour negative effect of conspecifics (per-neighbour NDD) and the LCD that a species experiences (Kobe & Vriesendorp 2011).

Previous studies have typically examined NDD over a single time period. However, the two principal agents of density-dependent mortality, resource competition and host-specific natural enemies, are both subject to environmental fluctuations, and so the strength of NDD may vary substantially over time, particularly in variable environments. This is suggested, for example, by the finding of Comita *et al.* (2009) that the effect of conspecific neighbours varied over different census intervals following hurricane disturbance in Puerto Rico, likely due to changes in resource availability and the dynamics of natural enemies. Additional studies are needed to assess temporal variation in density dependence.

When the intensities of density-dependent agents increase, resulting in stronger local-scale NDD, a stronger CCT may also result, depressing survival rates of common species and providing opportunities for rare species. This would help prevent rare species from going extinct and hence promote the maintenance of species diversity. Therefore, examining changes in NDD in fluctuating environments can help deepen our understanding of its role in maintaining species diversity.

So far, studies examining the mechanisms responsible for NDD have focused on the role of host-specific natural enemies, rather than resource competition (Gilbert 2005; Freckleton & Lewis 2006). Tropical seasonal forests experience seasonal variation in water availability with distinct wet and dry seasons. Water availability may influence the strength of NDD in several ways. NDD may be stronger in the wet season because of increased abundance of pathogens and insect herbivores (Coley & Barone 1996). Alternatively, species are under stress during the dry season because of low water availability (Gerhardt 1996; Comita & Engelbrecht 2009) and therefore may be more likely to die from density-dependent agents. Furthermore, species may partition soil water resources differentially (e.g. through differences in rooting depth) (Jackson *et al.* 1995; Meinzer *et al.* 1999), which may increase intraspecific competition during periods of low water availability. On the other hand, under extremely stressful conditions, intraspecific competition may be weakened and facilitation may even occur (e.g. Fajardo & Mclntire 2011).

In this study, we examine temporal variations in the effects of local conspecific and heterospecific neighbours on seedling survival in a tropical seasonal rain forest in southwestern China. Using data on the survival of 7263 seedlings of 186 species in the 20-ha Xishuangbanna forest dynamics plot, we test for seasonal differentiation in density dependence and test whether local-scale NDD is related to community-level species abundance. Specifically, we answer the following questions: (i) Does the strength of density dependence differ between the dry season and the wet season? (ii) Does the strength of local-scale NDD vary significantly among species and relate to species commonness and rarity in this community? (iii) Is there evidence of a CCT in the Xishuangbanna tropical seasonal rain forest and does CCT (NDD at larger spatial scales) result from local-scale NDD?

Materials and methods

DATA COLLECTION

We conducted this study in the 20-ha Xishuangbanna tropical seasonal rain forest dynamics plot located in Mengla County, Yunnan province, southwest China (101°34′E, 21°36′N). The climate is strongly seasonal with distinct alternations between the dry season (November–April) and the wet season (May–October), as this area is situated in the north edge of tropics and has a typical monsoon climate. At the National Forest Ecosystem Research Station at

Xishuangbanna, annual precipitation averaged 1493 mm between 1959 and 1998, of which 1256 mm (84%) occurred in the wet season (Cao *et al.* 2006). During the study period, there were 273 and 131 mm of precipitation occurring in the first and second dry seasons, and 1525 and 1031 mm during the first and second wet seasons, respectively.

All free-standing tree stems ≥1 cm diameter at breast height (dbh) (henceforth referred to as trees) in the plot have been measured, mapped and identified to species between November 2006 and April 2007 (Lan *et al.* 2009). Trees in the Xishuangbanna forest exhibit masting behaviour, with masting occurring most recently in 2004 (Yan & Cao 2008) and 2007, based on field observations. We conducted the first seedling census in November 2007 (at the beginning of the dry season) after abundant post-masting germination and monitored seedling survival for the following two non-masting years. In the first census, we established 151 census stations in a stratified random design to monitor seed rain and seedling dynamics in the plot. Each station consisted of a 0.5-m^2 seed trap and three 1-m^2 seedling quadrats that were placed 2 m away from each of three sides of the seed trap. In each of 453 1-m^2 seedling quadrats, all free-standing tree seedlings and saplings < 1 cm dbh (hereafter referred to simply as seedlings) were tagged, measured and identified to species level. Unidentified seedlings (10.53% of all seedlings) were excluded before analysis. We re-censused each seedling quadrat every three months to assess survival and growth of previously tagged seedlings and recruitment of new individuals. Here we analyse seedling data collected in the first two years of the study (November 2007–November 2009).

DATA ANALYSES

We modelled the probability of seedling survival over a census interval as a function of local neighbourhood density variables, using generalized linear mixed models (GLMMs) with binomial errors (see Gelman & Hill 2006; Bolker *et al.* 2009). GLMMs provide a flexible approach for analysing the relationships between seedling survival (the binary response variable, survived vs. died) and local neighbourhood density variables (treated as fixed effects in GLMMs) with random effects, which included species identity, quadrat and station in this study. Quadrat-specific and station-specific random intercepts were used to characterize autocorrelation in survival of seedlings within the same quadrat and station (Chen *et al.* 2010). Species identity was included as a crossed random effect because seedlings of species with differing ecological strategies were expected to respond differently to local neighbourhood density variables. We tested for effects of several local neighbourhood density variables, including total, conspecific and heterospecific seedling density in 1-m^2 quadrats, as well as total, conspecific and heterospecific tree basal area of stems ≥1 cm dbh within 10 m of the station centre. We selected 10 m as the neighbourhood radius based on preliminary analyses comparing models with neighbourhood radii of 5, 10 and 20 m using Akaike's information criterion (AIC) (Burnham & Anderson 2002). Seedling survival was significantly related to seedling height, so we also included (log-transformed) initial seedling height as a covariate in the model.

We compared four classes of models (Table 1): (1) an unconditional model with no fixed effects, (2) a density-independent model including initial seedling height as a fixed effect, but no local neighbourhood density variables, (3) density-dependent models in which the effects of conspecific neighbours do not differ from those of heterospecific neighbours, and (4) density-dependent models in which the effects of conspecific neighbours differ from those of heterospecific neighbours. Models in the fourth category were consistent with the Janzen–Connell hypothesis only if conspecific neighbours had a stronger negative effect on the probability of seedling survival than heterospecific neighbours (Comita & Hubbell 2009). The best-fit model was selected as the one with the lowest AIC. However, models within 2 AIC units of the minimum are also considered to have strong support (Burnham & Anderson 2002). In addition, we analysed data separately for younger (seedlings ≤20 cm tall) and older cohorts (seedlings > 20 cm tall) over the dry-season, wet-season and 2-year intervals (see Tables S1 and S2 in Supporting Information), to test whether results differed with age and/or size class. Since the best-fit models for both the younger and older cohorts were not essentially different from the best-fit models when combining all seedlings together, we did not further analyse the models for the separate cohorts.

Seedling survival can appear to be positively related to overall seedling density because of habitat effects (Comita & Hubbell 2009), making it difficult to detect negative effects of conspecific seedling neighbours, therefore we also tried a model that included total

Table 1. Akaike's information criterion (AIC) values for generalized linear mixed models of seedling survival in the 20-ha Xishuangbanna tropical seasonal rain forest dynamics plot

		AIC		
Model type	Fixed effects*	Dry- season interval	Wet-season interval	2-year interval
Unconditional model (model 1)		9931.46	7541.91	6879.93
Density-independent (model 2)	Ht	9231.77	7058.27	6204.27
Density-dependent				
Effect of conspecific = effect of Heterospecific (model 3)	Ht + Tots	9232.35	7046.88	6205.84
	Ht + Totb	9231.42	7059.55	6205.17
	Ht + Tots + Totb	9231.34	7046.97	6206.99
Effect of conspecific ≠ effect of Heterospecific (model 4)	Ht + Cons + Hets	9223.69	7048.32	6193.47
	Ht + Cons + Hets + Totb	9221.79	7048.28	6194.04
	Ht + Conb + Hetb	9226.13	7059.24	6198.30
	Ht + Conb + Hetb + Tots	9224.69	**7045.08**	6200.30
	Ht + Cons + Hets + Conb + Hetb	**9219.04**	7046.97	**6193.13**

*Fixed effects include: Ht (initial seedling height), Tots (total seedling density), Cons (conspecific seedling density), Hets (heterospecific seedling density), Totb (total tree basal area), Conb (conspecific tree basal area) and Hetb (heterospecific tree basal area). Bold values denote the best-fit models based on the lowest AIC value; however, models within two AIC units of the minimum are also considered to have strong support.

seedling neighbour density and the proportion of conspecific seedling neighbours (instead of conspecific seedling neighbour density and heterospecific seedling neighbour density) (Chen *et al.* 2010).

Seedling survival was analysed over two census intervals, the dry-season interval and the wet-season interval. We combined observations of survival across two dry seasons in the analysis for the dry-season interval and across two wet seasons in the analysis for the wet-season interval. We also analysed survival over the entire 2-year interval for the seedlings present in the first census to look for density dependence over a longer period.

To quantify variation in density dependence among species in the community, we constructed a varying-slope model by adding species-specific random slopes to the coefficients of local neighbourhood density variables (Chen *et al.* 2010; Comita *et al.* 2010). To test the relationship between species-specific neighbourhood effects and population abundance (total number of conspecific tree stems ≥1 cm dbh on the 20-ha plot) or basal area (total basal area of conspecific tree stems ≥1 cm dbh on the 20-ha plot) in the community, we modelled these species-specific coefficients as a function of population abundance or basal area using linear regression.

To determine whether there was a CCT in the 20-ha plot, we used GLMMs to examine seedling survival rates over the dry-season, wet-season and 2-year intervals as a function of population abundance or basal area in the community, using the method of Chen *et al.* (2010). Kobe & Vriesendorp (2011) suggested 'potential NDD' (the maximum mortality attributable to density effects), which includes both per-neighbour NDD and maximum local conspecific neighbour densities (m_LCD), be used to evaluate whether CCTs result from local-scale NDD. If potential NDD increases with population abundance or basal area in the community, a CCT could result from local-scale NDD even if per-neighbour NDD decreases with increasing population abundance or basal area in the community (e.g. Comita *et al.* 2010). Potential NDD for species j is calculated as the per-neighbour NDD for species j multiplied by the maximum local conspecific density of species j.

In the CCTs and crossed random effects models, the values of all continuous explanatory variables were standardized by subtracting the mean value of the variable and dividing by 1 standard deviation before analyses (except when calculating per-neighbour NDD for the potential NDD analysis). All analyses were conducted in R 2.11.1 (R Development Core Team 2010). GLMMs were fitted by the lmer() function in the 'lme4' package with the Laplace approximation method (Bates, Maechler & Dai 2008). Likelihood ratio tests were used to assess the significance of random effects, and Wald Z tests were used to assess the significance of fixed effects (Bolker *et al.* 2009).

Results

SEEDLING DYNAMICS IN THE XISHUANGBANNA FOREST PLOT

A total of 7263 seedlings of 186 species were censused over the two years following the masting event in 2007. Of the initial seedling cohort (November 2007), 3722 out of 6628 seedlings (56%) had died by November 2009. Seedling survival rates varied widely among species, between dry and wet seasons and between years (see Table S3). Because of the masting in 2007, there were many more young seedlings at the start of the first dry season (November 2007) than in any other census (Fig. S1), which led to higher mortality during the first dry-season interval than other census intervals (Fig. S2). Although seedling recruitment occurred in both the dry and wet seasons (Fig S2), recruitment rates were always much lower than seedling mortality rates during the study period (Fig. S2), resulting in a continual decrease in total seedling abundance over time (Fig. S1). Conversely, average seedling height gradually increased through consecutive censuses (mean values of 20.0, 24.0, 26.3 and 28.0 cm). In summary, in the 2 years following the masting event, seedling survival and growth were more important drivers of seedling dynamics compared with recruitment.

LOCAL-SCALE DENSITY DEPENDENCE

Over the dry-season interval, the probability of seedling survival of all species combined was best described by the full density-dependent model in which the effect of conspecific neighbours was different from that of heterospecific neighbours, for both seedling and tree neighbours (Table 1). Conspecific tree neighbours had a strong negative effect on seedling survival, while the effect of heterospecific tree neighbours was near zero (Table 2). In contrast, heterospecific seedling neighbours were positively associated with seedling survival, while the effect of conspecific seedling neighbours was near zero (Table 2). In contrast, over the wet-season interval, the best-fit model included separate effects of conspecific and heterospecific tree neighbours, but not separate effects of

Table 2. Coefficients (and standard errors) estimated by the best-fit models of neighbourhood effects on seedling survival of all species combined for the dry-season interval, wet-season interval and 2-year interval

Independent variables	Dry-season interval	Wet-season interval	2-year interval
Intercept	−1.676 (0.231)***	−1.868 (0.282)***	−3.480 (0.293)***
Seedling height	1.461 (0.062)***	1.525 (0.078)***	1.609 (0.072)***
Total seedling density	–	0.015 (0.004)***	–
Conspecific seedling density	0.002 (0.003) NS	–	−0.005 (0.004) NS
Heterospecific seedling density	0.017 (0.005)**	–	0.012 (0.006)*
Total tree basal area	–	–	–
Conspecific tree basal area	−0.248 (0.084)**	−0.246 (0.104)*	−0.265 (0.128)*
Heterospecific tree basal area	−0.052 (0.067) NS	−0.040 (0.081) NS	−0.048 (0.098) NS

*P < 0.05; **P < 0.01; ***P < 0.001; NS, not significant.
– Means the term was not included in the best-fit model.

conspecific and heterospecific seedling neighbours (Table 1). However, the full density-dependent model had an AIC within two units of the minimum (Table 1), indicating it had similar support. Over the wet-season interval, the effects of conspecific and heterospecific tree neighbours were similar to those over the dry-season interval, while total seedling neighbours were positively associated with seedling survival (Table 2). Over the 2-year interval, the pattern of density dependence was similar to that over the dry-season interval (Table 2).

In the model that included total seedling neighbour density and the proportion of conspecific seedling neighbours (instead of conspecific seedling neighbour density and heterospecific seedling neighbour density), total seedling neighbour density had a positive effect on seedling survival over both the dry-season and wet-season intervals, but was not different from zero over the 2-year interval (Table 3). The proportion of conspecific seedling neighbours had a strong negative effect on seedling survival over the dry-season and 2-year intervals, but a much weaker effect over the wet-season interval. The negative effect of the proportion of conspecific seedling neighbours was significantly stronger over the dry-season interval than over the wet-season interval (Table 3).

VARIATION AMONG SPECIES IN THE STRENGTH OF DENSITY DEPENDENCE

Over the dry-season interval, there was significant variation among species in the effects of conspecific tree and seedling neighbours on survival, as indicated by a likelihood ratio test comparing models with and without variation among species in neighbour effects (Table 4). Despite the wide variation, conspecific tree and seedling neighbour densities showed negative effects on seedling survival for nearly all species (Fig. 1a,b, Table S4). The effect of heterospecific tree neighbours on seedling survival was also negative for all species in the community, but values varied little across species (Fig. S3a). Similarly, the relationship between heterospecific seedling neighbours and seedling survival varied little across species (Fig. S3b).

Over the wet-season interval, the effects of both conspecific and heterospecific tree neighbours were negative for all species, but, unlike in the dry season, values did not vary significantly among species (Table 4, Fig. 1c and Fig. S3c). In contrast, both conspecific and heterospecific seedling neighbours showed a positive relationship with seedling survival for most species, with little variation among species (Table 4, Fig. 1d and Fig. S3d).

Over the 2-year interval, there was significant variation in the effect of conspecific tree and seedling neighbours among species, with survival being negatively related to conspecific tree neighbours for some species and positively related for others, and being negatively related to conspecific seedling neighbours for nearly all species (Fig. 1e,f, Table S5). The effect of heterospecific tree neighbours did not vary significantly among species (Table 4) and values approached zero for most species (Fig. S3e). Heterospecific seedling neighbours did have variable effects among species (Table 4), although, in contrast to conspecific seedling neighbour effects, the relationship with survival was positive for most species (Fig. S3f, Table S5).

The effects of conspecific tree and seedling neighbours on survival were both significantly positively correlated with population basal area over the dry-season interval (Table 4). In other words, rarer species experienced stronger local-scale NDD than commoner species. We did not test this relationship over the wet-season interval since there was not significant variation in the effects of conspecific tree and seedling neighbours among species during that period. Over the 2-year interval, we found no relationship between the effect of conspecific tree neighbours and population basal area, but did find a significant positive relationship between the effects of conspecific seedling neighbours and population basal area, again indicating that rarer species experienced stronger local-scale NDD than did commoner species over the 2-year interval (Table 4). We did not find a significant relationship between neighbourhood effects and population abundance (Table 4).

COMMUNITY-LEVEL COMPENSATORY TRENDS

Seedling survival rates were significantly negatively related to population basal area in the 20-ha plot over both the dry-season and wet-season intervals. Over the 2-year interval, this relationship was marginally significant (Table 5). This result indicates a significant CCT in the 20-ha Xishuangbanna tropical seasonal rain forest dynamics plot. When using population abundance, no CCT was detected in any interval. Based on AIC values, the models using population basal area were better than those for population abundance (Table 5).

Over the dry-season, wet-season and 2-year interval, the m_LCD for both tree and seedling neighbours significantly increased with population basal area (Table S6). When multiplying m_LCD by per-neighbour NDD to calculate potential NDD, we found mixed results in terms of the relationship between potential NDD and population basal area. Over the

Table 3. Coefficients (and standard errors) estimated by the models of neighbourhood effects with total seedling density and the proportion of conspecific seedling on seedling survival of all species combined for the dry-season interval, wet-season interval and 2-year interval

Independent variables	Dry-season interval	Wet-season interval	2-year interval
Intercept	−1.407 (0.205)***	−1.849 (0.253)***	−3.120 (0.247)***
Seedling height	1.444 (0.062)***	1.515 (0.078)***	1.598 (0.072)***
Total seedling density	0.006 (0.002)*	0.015 (0.004)***	0.001 (0.004) NS
Proportion of conspecific seedling	−0.835 (0.166)***	−0.316 (0.186)#	−1.225 (0.206)***

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; #$P < 0.1$; NS, not significant.

Table 4. Results of linear regression models used to test for a relationship between neighbourhood effects† and population abundance (conspecific tree abundance‡, model 1) or basal area (conspecific tree basal area§, model 2) in the community. The tests were only performed when the neighbourhood effects were found to vary significantly among species, based on likelihood ratio tests. Values of abundance and basal area were standardized by subtracting the mean value and dividing by 1 standard deviation before analyses

Census intervals	Neighbourhood effects	Likelihood ratio test	Model	Intercept	Population abundance or basal area
Dry-season interval	Conspecific tree	***	1	−0.271***	0.001 NS
			2	−0.271***	0.013*
	Heterospecific tree	NS	–	–	–
	Conspecific seedling	**	1	−0.268***	0.012#
			2	−0.268***	0.037***
	Heterospecific seedling	NS	–	–	–
Wet-season interval	Conspecific tree	NS	–	–	–
	Heterospecific tree	NS	–	–	–
	Conspecific seedling	NS	–	–	–
	Heterospecific seedling	NS	–	–	–
2-year interval	Conspecific tree	***	1	−0.025***	−0.005 NS
			2	−0.025***	−0.009 NS
	Heterospecific tree	NS	–	–	–
	Conspecific seedling	*	1	−0.330***	0.011#
			2	−0.330***	0.026***
	Heterospecific seedling	**	1	0.132***	−0.006 NS
			2	0.132***	0.015***

†Only includes those neighbourhood effects in the best-fit models.

‡Total number of conspecific tree stems ≥1 cm dbh on the 20-ha plot.

§total basal area (m^2) of conspecific tree stems ≥1 cm dbh on the 20-ha plot. *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; #$P < 0.1$; NS, not significant.

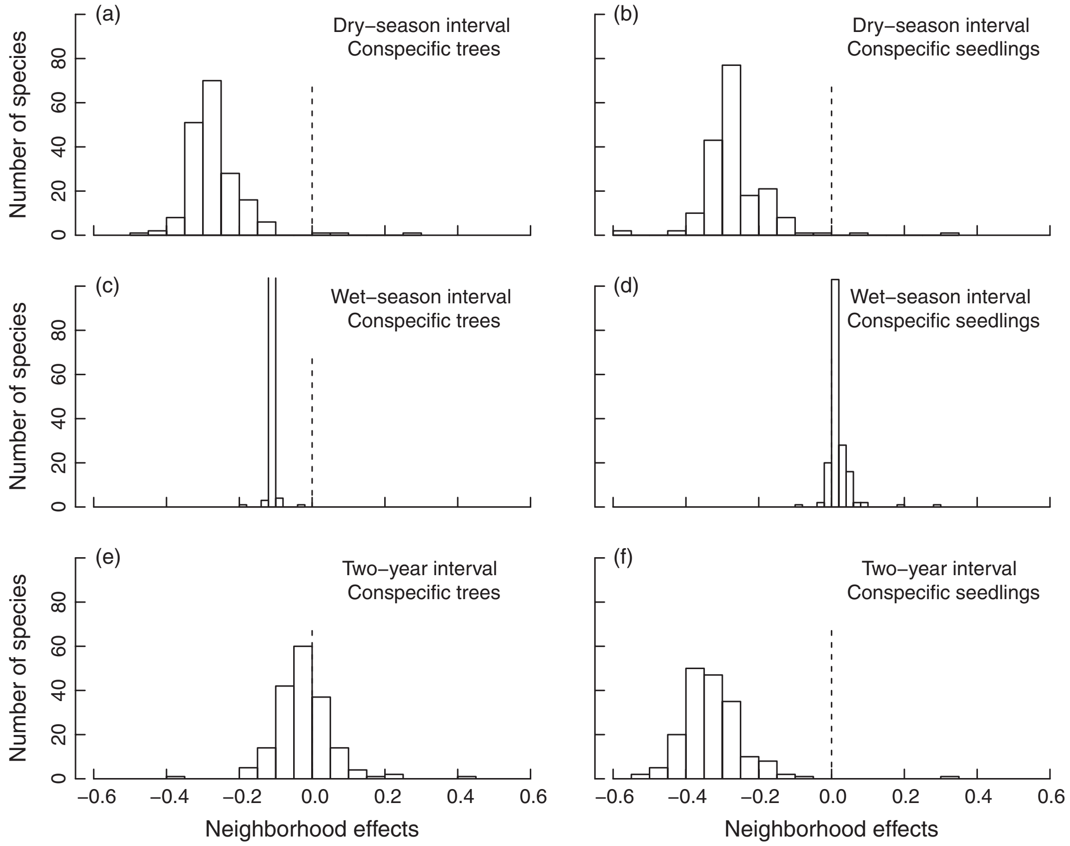

Fig. 1. Distribution of the neighbourhood effects on seedling survival. Histogram bars are based on coefficients of neighbourhood density variables. Bars to the left of the dashed zero line indicate species whose survival is reduced by increasing neighbour density.

Table 5. Coefficients (and standard errors) estimated in generalized linear mixed models used to test for a relationship between seedling survival and population abundance (conspecific tree abundance†, model 1) or basal area (conspecific tree basal area‡, model 2) in the community, that is, a community compensatory trend. Akaike's information criterion (AIC) values of the models are also given

Census interval	Model	Seedling height	Population abundance or basal area	AIC
Dry-season interval	Model 1	1.007 (0.042)***	−0.095 (0.184) NS	9233.512
	Model 2	1.007 (0.042)***	−0.556 (0.271)*	9229.869
Wet-season interval	Model 1	1.013 (0.052)***	−0.167 (0.196) NS	7059.555
	Model 2	1.012 (0.052)***	−0.638 (0.251)***	7054.541
2-year interval	Model 1	1.100 (0.049)***	−0.081 (0.223) NS	6206.139
	Model 2	1.097 (0.049)***	−0.708 (0.377)#	6202.947

†Total number of conspecific tree stems ≥1 cm dbh on the 20-ha plot.

‡Total basal area (m^2) of conspecific tree stems ≥1 cm dbh on the 20-ha plot. *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; #$P < 0.1$; NS, not significant.

dry-season and wet-season interval, potential NDD of conspecific tree neighbours was significantly positively correlated with population basal area, indicating that more common species suffered more from NDD because of their higher conspecific tree densities. In contrast, potential NDD of conspecific seedling neighbours showed a significant negative correlation with population basal area (Table S7). This suggests that the CCTs resulted from local-scale NDD of conspecific tree neighbours, but not conspecific seedling neighbours. Over the 2-year interval, the relationship between potential NDD and population basal area was not significant for seedling neighbours and only marginally significant for tree neighbours (Table S7).

Discussion

In this study, community- and species-level results suggest that local-scale NDD tends to be stronger in the dry than wet season in the Xishuangbanna tropical forest. In addition, we found significant variation among species in the strength of neighbour effects, with rarer species suffering stronger negative effects of conspecifics (on a per-neighbour basis). However, individuals of common species experienced higher local conspecific densities. As a result, at the community-level, seedling survival rates declined with population basal area, consistent with a CCT. We expand on these findings below.

SEASONAL DIFFERENCES IN NDD AT THE COMMUNITY LEVEL

Negative density dependence appears to be stronger in the dry season compared with the wet season in the Xishuangbanna forest. While conspecific tree neighbours had a strong negative effect on seedling survival in both seasons, conspecific seedling neighbours had a stronger impact in the dry compared with the wet season. This was most evident in analysis that examined the effect of the proportion of conspecific seedling neighbours on seedling survival and found a significantly stronger negative effect in the dry season (Table 3). This result is in contrast to the findings of Bunker & Carson (2005), who found that NDD was stronger in plots that had been irrigated compared with control plots in seasonal forest in Panama, suggesting that increased soil moisture promotes stronger NDD.

Why might conspecific seedling neighbours have a stronger negative effect in the dry season? Seedlings may be weakened in the dry season because of drought stress, and as a result, be more susceptible to, or likely to die from, attack by pathogens or herbivores. The low water availability during the dry season may also lead species to compete with conspecifics more than heterospecifics because species may partition soil water resources differentially (Jackson *et al.* 1995; Meinzer *et al.* 1999). Therefore, stronger NDD may result from stronger intraspecific competition during the dry season. This runs contrary to the stress gradient hypothesis, which proposes that facilitative interactions among plants become more dominant than competitive interactions with increasing physical harshness of the environment (e.g. Maestre *et al.* 2009; Fajardo & Mclntire 2011). However, this phenomena is unlikely to occur at our study site, where plants experience only moderate drought stress, due in part to fog water that serves as an important source of moisture (Liu *et al.* 2004, 2005) and can be used by seedlings in the dry season (Liu *et al.* 2010). In addition, other studies have demonstrated that the stress gradient hypothesis does not apply in all circumstances (Tielbörger & Kadmon 2000; Maestre, Valladares & Reynolds 2005).

In contrast to effects of conspecific seedling neighbours, conspecific tree neighbours had similar negative effects on seedling survival in the dry and wet seasons. Species-specific natural enemies tend to be more numerous near mature trees (Janzen 1970; Connell 1971), which could be the potential mechanism that underpins negative effects of conspecific tree neighbours. As mentioned earlier, under drought stress in the dry season, seedlings may be more likely to die from natural enemy attack. However, pathogens and insect herbivores tend to be more abundant in the wet season (Coley & Barone 1996). Thus, increased negative effects of conspecific tree neighbours because of drought stress in the dry season may be balanced by increased natural enemy attack in the wet season.

In contrast to conspecific neighbours, effects of heterospecific and total seedling neighbours on survival tended to be positive. The species herd protection hypothesis (Wills & Green 1995) predicts that increased heterospecific crowding results in fewer encounters between a host and its host-specific natural enemies, which thereby increases host survival (Peters 2003). In this study, the pervasive positive effects of heterospecific seedling neighbours (Table 2) support the idea that heterospecific neighbours can enhance protection from natural enemies. However, there may be another cause for the positive effects of heterospecific seedling neighbours: habitats that are beneficial for seedlings (e.g. small light gaps) will lead to both high seedling densities and high seedling survival (Comita & Hubbell 2009). This would result in a spurious positive relationship between heterospecific or total seedling neighbours and seedling survival.

SEASONAL DIFFERENCES IN NDD AT THE SPECIES LEVEL

In this study, we found wide variation among species in the strength of NDD over the dry-season interval (Fig. 1a,b), but not over the wet-season interval (Fig. 1c,d). This indicates that seasonal differentiation in NDD can be more easily detected at the species level than the community level. In the dry season, if drought stress strengthens NDD, species-specific variation in the strength of NDD may result from the differences in species sensitivities to drought. In that case, species-specific NDD in the wet season, when drought stress is minimal or non-existent, would converge on the same level, as shown by our results (Fig. 1c,d). Over the 2-year interval of the study, species also varied significantly in the strength of NDD. However, in contrast to the dry season where nearly all species were negatively affected by conspecific neighbours, a number of species showed positive effects of conspecific neighbours (i.e. positive density dependence) over the 2-year interval (Fig. 1). This may be attributed to habitat filtering becoming a stronger driver of seedling survival over longer time intervals.

At this point, however, we can only speculate about the underlying mechanisms driving the patterns of NDD observed at our site. There have been several experimental studies at other sites confirming that pathogens play a key role in negative effects of conspecific neighbours (Augspurger & Kelly 1984; Bell, Freckleton & Lewis 2006; Bagchi *et al.* 2010; Mangan, Herre & Bever 2010; McCarthy-Neumann & Kobe 2010). There have also been several experiments examining seedling competition in tropical forests (Gerhardt 1996; Massey *et al.* 2006; Paine *et al.* 2008). However, further experimental investigations are needed to determine the relative importance of natural enemies and resource competition for the patterns of NDD observed here (e.g. Kobe & Vriesendorp 2011).

ASYMMETRIC DENSITY DEPENDENCE AND POPULATION BASAL AREA

Over the dry-season and 2-year intervals, the strength of negative conspecific effects decreased with increasing population basal area in the community (Table 4). This means that rarer species were more negatively affected by conspecifics than commoner species, on a per-neighbour basis. Rarer species could therefore be prevented from increasing their abundance because of the stronger local-scale NDD they experience when their local abundance increases. In other words, less common species cannot achieve dominance in the community under stronger local-scale NDD. This kind of species-asymmetric density-dependent seedling survival might be an underlying mechanism maintaining patterns of species commonness and rarity in the community, as suggested by Comita *et al.* (2010) and Mangan *et al.* (2010). If species-asymmetric density dependence is related to differential drought sensitivity among species at our study site, we would predict that common species should have lower drought sensitivity than rare species. In future studies, the differentiation in NDD between drought-sensitive species and drought-tolerant species needs to be investigated further, to examine the mechanisms governing the relationship between NDD and species abundance in the community.

COMMUNITY COMPENSATORY TRENDS

Previous studies have found mixed evidence for the existence of CCTs in tropical forests (e.g. Connell, Tracey & Webb 1984; Welden *et al.* 1991; He, Legendre & LaFrankie 1997; Webb & Peart 1999; Queenborough *et al.* 2007; Comita & Hubbell 2009; Chen *et al.* 2010). In the Xishuangbanna forest, we did find a compensatory trend at the 20-ha scale during both the wet and dry seasons, in which seedling survival increased with decreasing population basal area in the community. Under CCTs, rarer species have a greater per capita probability of survival than commoner species in the community. The conventional interpretation of a CCT is that per-neighbour NDD is similar among species in the community and individuals of rarer species are less likely to be surrounded by conspecifics at local scales. Indeed, the m_LCD significantly increased with population basal area (Table S6). However, per-neighbour NDD showed a wide variation among species (Fig. 1) and was negatively correlated with population basal area (as discussed earlier). This would tend to offset a CCT, unless potential NDD (per-neighbour NDD × m_LCD) increases correspondingly with species community abundance (Kobe & Vriesendorp 2011). Our analysis of the relationship between potential NDD and population basal area suggest that over both the dry-season and wet-season interval, CCTs may have resulted from local-scale NDD of conspecific tree neighbours, but not conspecific seedling neighbours.

Under CCTs, mortality should be disproportionately low for rarer species, which could offset any disadvantage of drought stress for rarer species in the dry season (or other stresses, such as pathogen attack, in the wet season) and could promote the persistence of rarer species. Thus, CCTs induced by local-scale NDD prevailing in both the dry season and the wet season may promote the maintenance of rare species in fluctuating environments. However, the CCT was only marginally significant over the 2-year interval (Table 5). This may be because, over longer intervals, factors such as species' habitat preferences or shade tolerance strongly influence seedling survival rates and may obscure the relationship between population basal area and seedling survival (Queenborough *et al.* 2007; Comita & Hubbell 2009; Chen *et al.* 2010).

Conclusions

Our results suggest that local-scale NDD tends to be stronger in the dry than wet season in the Xishuangbanna tropical forest. This study provides further evidence that the density and identity of neighbouring individuals influence juvenile survival at both local and larger spatial scales in forest communities, and lends support to the idea that NDD influences the diversity and abundances of tropical tree species. In addition, our results highlight the fact that simple models of NDD, in which the strength of conspecific neighbour effects is consistent over time and across species, do not capture the variation observed in real-world communities. Nonetheless, few empirical or theoretical studies have examined this variation, the underlying mechanisms or the consequences of such variation for community structure (but see Chisholm & Muller-Landau 2011). Thus, further empirical research is needed to better characterize patterns and drivers of variation in density dependence, coupled with theoretical efforts to explore how temporal and interspecific variation in the strength of NDD influences species coexistence and abundance in diverse communities.

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References

Augspurger, C.K. & Kelly, C.K. (1984) Pathogen mortality of tropical tree seedlings: experimental studies of the effects of dispersal distance, seedling density, and light conditions. *Oecologia*, **61**, 211–217.

Bagchi, R., Swinfield, T., Gallery, R.E., Lewis, O.T., Gripenberg, S., Narayan, L. & Freckleton, R.P. (2010) Testing the Janzen-Connell mechanism: pathogens cause overcompensating density dependence in a tropical tree. *Ecology Letters*, **13**, 1262–1269.

Bates, D., Maechler, M. & Dai, B. (2008) lme4: Linear Mixed-Effects Models Using S4 Classes. R Package Version 0.999375-28. Available at: http://lme4.r-forge.r-project.org/.

Bell, T., Freckleton, R.P. & Lewis, O.T. (2006) Plant pathogens drive density-dependent seedling mortality in a tropical tree. *Ecology Letters*, **9**, 569–574.

Blundell, A.G. & Peart, D.R. (2004) Density-dependent population dynamics of a dominant rain forest canopy tree. *Ecology*, **2004**, 704–715.

Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H. & White, J.S. (2009) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution*, **24**, 127–135.

Bunker, D.E. & Carson, W.P. (2005) Drought stress and tropical forest woody seedlings: effect on community structure and composition. *Journal of Ecology*, **93**, 794–806.

Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multimodel Inference: A Practical Information-theoretic Approach*, 2nd edn. Springer, New York.

Cao, M., Zou, X., Warren, M. & Zhu, H. (2006) Tropical forests of Xishuangbanna, China. *Biotropica*, **38**, 306–309.

Carson, W.P., Anderson, J.T., Leigh Jr, E.G. & Schnitzer, S.A. (2008) Challenges associated with testing and falsifying the Janzen-Connell hypothesis: a review and critique. *Tropical Forest Community Ecology* (eds W.P. Carson & S.A. Schnitzer), pp. 210–241. Wiley-Blackwell, Oxford.

Chen, L., Mi, X., Comita, L.S., Zhang, L., Ren, H. & Ma, K. (2010) Community-level consequences of density dependence and habit association in a subtropical broad-leaved forest. *Ecology Letters*, **13**, 695–704.

Chisholm, R.A. & Muller-Landau, H.C. (2011) A theoretical model linking interspecific variation in density dependence to species abundances. *Theoretical Ecology*, **4**, 241–253.

Clark, D.B. & Clark, D.A. (1985) Seedling dynamics of a tropical tree: impacts of herbivory and meristem damage. *Ecology*, **66**, 1884–1892.

Coley, P.D. & Barone, J.A. (1996) Herbivory and plant defenses in tropical forests. *Annual Review of Ecology and Systematics*, **27**, 305–335.

Comita, L.S. & Engelbrecht, B.M.J. (2009) Seasonal and spatial variation in water availability drive habitat associations in a tropical forest. *Ecology*, **90**, 2755–2765.

Comita, L.S. & Hubbell, S.P. (2009) Local neighborhood and species' shade tolerance influence survival in a diverse seedling bank. *Ecology*, **90**, 328–334.

Comita, L.S., Uriarte, M., Thompson, J., Jonckheere, I., Canham, C.D. & Zimmerman, J.K. (2009) Abiotic and biotic drivers of seedling survival in a hurricane-impacted tropical forest. *Journal of Ecology*, **97**, 1346–1359.

Comita, L.S., Muller-Landau, H.C., Aguilar, S. & Hubbell, S.P. (2010) Asymmetric density dependence shapes species abundances in a tropical tree community. *Science*, **329**, 330–332.

Condit, R., Hubbell, S.P. & Foster, R.B. (1994) Density dependence in two understory tree species in a neotropical forest. *Ecology*, **75**, 671–680.

Connell, J.H. (1971) On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. *Dynamics of Numbers in Populations* (eds P.J. den Boer & G. Gradwell), pp. 298–312. Center for Agricultural Publication and Documentation, Wageningen.

Connell, J.H., Tracey, J.G. & Webb, L.J. (1984) Compensatory recruitment, growth, and mortality as factors maintaining rain forest tree diversity. *Ecological Monograph*, **54**, 141–164.

Fajardo, A. & Mclntire, E.J.B. (2011) Under strong niche overlap conspecifics do not compete but help each other to survive: facilitation at the intraspecific level. *Journal of Ecology*, **99**, 642–650.

Freckleton, R.P. & Lewis, O.T. (2006) Pathogens, density dependence and the coexistence of tropical trees. *Proceedings of Royal Society B*, **273**, 2909–2916.

Gelman, A. & Hill, J. (2006) *Data Analysis Using Regression and Multilevel/hierarchical Models*. Cambridge University Press, Cambridge.

Gerhardt, K. (1996) Effects of root competition and canopy openness on survival and growth of tree seedlings in a tropical seasonal dry forest. *Forest Ecology and Management*, **82**, 33–48.

Gilbert, G.S. (2005) Dimensions of plant disease in tropical forests. *Biotic Interactions in the Tropics: Their Role in the Maintenance of Species Diversity* (eds D.F.R.P. Burslem, M.A. Pinard & S.E. Hartley), pp. 141–164. Cambridge University Press, Cambridge.

Harms, K.E., Wright, S.J., Calderon, O., Hernandez, A. & Herre, E.A. (2000) Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature*, **404**, 493–495.

Harper, J.L. (1977) *Population Biology of Plants*. Academic Press, London.

He, F., Legendre, P. & LaFrankie, J.V. (1997) Distribution patterns of tree species in a Malaysian tropical rain forest. *Journal of Vegetation Science*, **8**, 105–114.

Hille Ris Lambers, J., Clark, J.S. & Beckage, B. (2002) Density-dependent mortality and the latitudinal gradient in species diversity. *Nature*, **417**, 732–735.

Hubbell, S.P., Condit, R. & Foster, R.B. (1990) Presence and absence of density dependence in a neotropical tree community. *Philosophical Transactions of the Royal Society B*, **330**, 269–281.

Hubbell, S.P., Ahumada, J.A., Condit, R. & Foster, R.B. (2001) Local neighbourhood effects on long-term survival of individual trees in a neotropical forest. *Ecological Research*, **16**, 859–875.

Jackson, P.C., Cavelier, J., Goldstein, G., Meinzer, F.C. & Holbrook, N.M. (1995) Partitioning of water resources among plants of a lowland tropical forest. *Oecologia*, **101**, 197–203.

Janzen, D.H. (1970) Herbivores and the number of tree species in tropical forests. *The American Naturalist*, **104**, 501–528.

Kobe, R.K. & Vriesendorp, C.F. (2011) Conspecific density dependence in seedlings varies with species shade tolerance in a wet tropical forest. *Ecology Letters*, **14**, 503–510.

Lan, G., Zhu, H., Cao, M., Hu, Y., Wang, H., Deng, X. *et al*. (2009) Spatial dispersion patterns of trees in a tropical rainforest in Xishuangbanna, southwest China. *Ecological Research*, **24**, 1117–1124.

Liu, W.J., Meng, F.R., Zhang, Y.P., Liu, Y.H. & Li, H.M. (2004) Water input from fog drip in the tropical seasonal rainforest of Xishuangbanna, SW China. *Journal of Tropical Ecology*, **20**, 517–524.

Liu, W.J., Zhang, Y.P., Li, H.M. & Liu, Y.H. (2005) Fog drip and its relation to groundwater in the tropical seasonal rainforest of Xishuangbanna, SW China: a preliminary study. *Water Research*, **39**, 787–794.

Liu, W.J., Liu, W.Y., Li, P.J., Duan, W.P. & Li, H.M. (2010) Dry season water uptake by two dominant canopy tree species in a tropical seasonal rainforest of Xishuangbanna, SW China. *Agriculture and Forest Meteorology*, **150**, 380–388.

Maestre, F.T., Valladares, F. & Reynolds, J.F. (2005) Is the change of plant-plant interactions with abiotic stress predictable? A meta-analysis of field results in arid environments. *Journal of Ecology*, **93**, 748–757.

Maestre, F.T., Callaway, R.M., Valladares, F. & Lortie, C.J. (2009) Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *Journal of Ecology*, **97**, 199–205.

Mangan, S.A., Herre, E.A. & Bever, J.D. (2010) Specificity between Neotropical tree seedlings and their fungal mutualists leads to plant-soil feedback. *Ecology*, **91**, 2594–2603.

Mangan, S.A., Schnitzer, S.A., Herre, E.A., Mack, K.M.L., Valencia, M.C., Sanchez, E.I. & Bever, J.D. (2010) Negative plant-soil feedback predicts tree-species relative abundance in a tropical forest. *Nature*, **466**, 752–756.

Massey, F.P., Massey, K., Press, M.C. & Hartley, S.E. (2006) Neighbourhood composition determines growth, architecture and herbivory in tropical rain forest tree seedlings. *Journal of Ecology*, **94**, 646–655.

McCarthy-Neumann, S. & Kobe, R.K. (2010) Conspecific plant-soil feedbacks reduce survivorship and growth of tropical tree seedlings. *Journal of Ecology*, **98**, 396–407.

Meinzer, F.C., Andrade, J.L., Goldstein, G., Holbrook, N.M., Cavelier, J. & Wright, S.J. (1999) Partitioning of soil water among canopy trees in a seasonally dry tropical forest. *Oecologia*, **121**, 293–301.

Metz, M.R., Sousa, W.P. & Valencia, R. (2010) Widespread density-dependent seedling mortality promotes species coexistence in a highly diverse Amazonian rain forest. *Ecology*, **91**, 3675–3685.

Paine, C.E.T., Harms, K.E., Schnitzer, S.A. & Carson, W.P. (2008) Weak competition among tropical tree seedlings: implications for species coexistence. *Biotropica*, **40**, 432–440.

Peters, H.A. (2003) Neighbour-regulated mortality: the influence of positive and negative density dependence on tree populations in species-rich tropical forests. *Ecology Letters*, **6**, 757–765.

Queenborough, S.A., Burslem, D.F.R.P., Garwood, N.C. & Valencia, R. (2007) Neighborhood and community interactions determine the spatial pattern of tropical tree seedling survival. *Ecology*, **88**, 2248–2258.

R Development Core Team (2010) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Swamy, V., Terborgh, J., Dexter, K.G., Best, B.D., Alvarez, P. & Cornejo, F. (2011) Are all seeds equal? Spatially explicit comparisons of seed fall and sapling recruitment in a tropical forest. *Ecology Letters*, **14**, 195–201.

Tielbörger, K. & Kadmon, R. (2000) Temporal environmental variation tips the balance between facilitation and interference in desert plants. *Ecology*, **81**, 1544–1553.

Volkov, I., Banavar, J.R., He, F.L., Hubbell, S.P. & Maritan, A. (2005) Density dependence explains tree species abundance and diversity in tropical forests. *Nature*, **438**, 658–661.

Webb, C.O. & Peart, D.R. (1999) Seedling density dependence promotes coexistence of Bornean rain forest trees. *Ecology*, **80**, 2006–2017.

Welden, C.W., Hewett, S.W., Hubbell, S.P. & Foster, R.B. (1991) Sapling survival, growth, and recruitment: relationship to canopy height in a neotropical forest. *Ecology*, **72**, 35–50.

Wills, C. & Green, D.R. (1995) A genetic herd-immunity model for the maintenance of MHC polymorphism. *Immunological Reviews*, **143**, 263–292.

Wills, C., Condit, R., Foster, R.B. & Hubbell, S.P. (1997) Strong density- and diversity-related effects help to maintain tree species diversity in a neotropical forest. *Proceedings of the National Academy of Sciences of the United States of America*, **94**, 1252–1257.

Wright, S.J. (2002) Plant diversity in tropical forests: a review of mechanisms of species coexistence. *Oecologia*, **130**, 1–14.

Yan, X.F. & Cao, M. (2008) Seedling growth and survival of the endangered tree species *Shorea wantianshuea* after a mast-fruiting event. *Journal of Plant Ecology (Chinese Version)*, **32**, 55–64.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Figure S1. Total number of living seedlings, including younger and older seedling cohorts, in the 453 1 m × 1 m quadrats in each of the five censuses.

Figure S2. Seedling recruitment rates and mortality in all 453 1 m × 1 m quadrats over the dry-season and wet-season intervals.

Figure S3. Distribution of the neighbourhood effects on seedling survival for heterospecific tree and seedling neighbours.

Table S1. Akaike's information criterion (AIC) values for generalized linear mixed models for survival of the younger seedling cohort in the 20-ha Xishuangbanna tropical seasonal rain forest dynamics plot.

Table S2. Akaike's information criterion (AIC) values for generalized linear mixed models for survival of the older seedling cohort in the 20-ha Xishuangbanna tropical seasonal rain forest dynamics plot.

Table S3. Seedling survival rates of 186 species in the 453 1 m × 1 m quadrats over each dry-season, wet-season and one-year interval and the 2-year interval.

Table S4. The species-specific effects of conspecific tree and seedling neighbours on seedling survival over the dry-season interval in generalized linear mixed models with crossed random effects.

Table S5. The species-specific effects of conspecific tree and seedling neighbours and heterospecific seedling neighbours on seedling survival over the 2-year interval in generalized linear mixed models with crossed random effects.

Table S6. Parameter estimates in linear regression models used to test for the relationship between the maximum local conspecific neighbour densities and population basal area in the community.

Table S7. Parameter estimates in linear regression models used to test for the relationship between the potential NDD and population basal area in the community.