Differing Life History Characteristics Support Coexistence of Tree Soil Generalist and Specialist Species in Tropical Rain Forests

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ABSTRACT

Niche differentiation is a prominent mechanism for explaining tree species coexistence in tropical rain forests. Theory predicts that species that are specialized on a set of environmental conditions should competitively exclude generalists in those conditions, and that environmental heterogeneity allows the coexistence of many different species based on niche specialization. Yet, many tropical tree species of the family Dipterocarpaceae have broadly similar habitat preferences, with some occurring widely across several soil types. These soil generalists clearly persist despite the presence of other dipterocarp species that show clear soil specialization. We evaluate comparative seedling performance (growth and survival) of six *Shorea* species (Dipterocarpaceae) which differ in their adult tree habitat associations within the Sepilok Forest Reserve (Borneo, Malaysia). We tested the hypothesis that seedlings of species associated with a particular soil type perform better on that soil type than seedlings of soil generalist species, with generalists in turn performing better than specialists on a different soil type. We conducted a reciprocal transplant experiment including two soil types (alluvial and mudstone) and two light treatments (gap and understory). The soils differed in soil acidity, Al and P concentration. Observed species-specific differences in seedling responses to soil, light, and occasional flooding events could partially explain observed adult distribution, although not all species could be fully differentiated along these axes. Other trade-offs, such as investment in defense against herbivores and tolerance to soil waterlogging, may play additional roles in explaining coexistence of these species.

Abstract in Malay is available in the online version of this article.

Key words: Dipterocarpaceae; life history characteristics; niche theory; relative growth rate; *Shorea*; survival; topography; tropical rain forest.

IN MANY TROPICAL RAIN FORESTS TREE RICHNESS EXCEEDS 200 SPECIES PER HECTARE (Davies & Becker 1996, De Oliveira & Mori 1999, Lee *et al.* 2002). This exceptionally high species richness is unlikely to be explained by any single mechanism, and instead several causes likely contribute to patterns of species number and distribution observed in rain forests (Wright 2002, Leigh *et al.* 2004, Ghazoul & Sheil 2010). Prominent among such mechanisms are negative density-dependence that provides a rare-species advantage (Blundell & Peart 2004; Bagchi *et al.* 2010, 2011) and niche partitioning along any number of environmental and biotic axes (Barker *et al.* 1997, Russo *et al.* 2005, Paoli *et al.* 2006). The niche-assembly hypothesis (Grubb 1977, Denslow 1987, Wright 2002, Silvertown 2004) focuses on the importance of environmental heterogeneity, where species coexist through specialization and resource partitioning. Species are effectively specialists that respond differentially to variation in abiotic and biotic conditions. Recently, these mechanisms have been challenged by suggestions that species coexistence can, to a large degree, be explained by neutral models that assume functional

equivalence of species and in which coexistence is maintained by dispersal limitation (Hubbell *et al.* 1999, Hubbell 2006). While these mechanisms undoubtedly contribute to local dynamics underlying coexistence, their relative contributions remain uncertain.

Moreover, density dependence and neutral theories can, at least at local scales, only explain alpha diversity (see Chave & Leigh 2002 for application of neutral theory to beta diversity at very large forest scales). It is evident, however, that even on fine scales many species cluster according to any number of environmental variables, most obvious of which are soil and topography (Harms *et al.* 2001, Potts *et al.* 2002, Paoli *et al.* 2006, Sukri *et al.* 2012). The degree of this presumed niche-specialization allows for increased species packing in heterogeneous environments. This assumes that specialization based on adaptive trade-offs in plant life history traits prevents the spread of one competitively dominant species at the expense of others (Kneitel & Chase 2004, Silvertown 2004). One of the most prominent trade-offs is between growth rate and survival which purportedly defines species-specific responses to environmental conditions, and particularly light (Condit *et al.* 2006, Wright *et al.* 2010). Plant species with rapid growth rates under high light conditions generally have poor seedling survival under low light conditions, and vice versa.

Trade-offs in themselves do not counter neutral theory, but neutral theory is undermined if such trade-offs underlie spatially explicit and predictable species differentiation.

Light is considered the primary limiting resource for growth and survival of seedlings and saplings in tropical rain forests (Denslow 1987, Burslem *et al.* 2005, Maharjan *et al.* 2011, Philipson *et al.* 2012, reviewed in Ghazoul & Sheil 2010). Many empirical studies have investigated the response of tropical trees to differing amounts of irradiance; however, a clear segregation of individual species along light axes is difficult to resolve (Whitmore & Brown 1996, Brokaw & Busing 2000, Aiba & Nakashizuka 2007, Queenborough *et al.* 2007). Many tropical tree studies have also emphasized specialization to particular soil environments as being an important contributing factor to species coexistence (John *et al.* 2007). Even fine-scale soil nutrient heterogeneity can lead to resource partitioning and thus niche specialization, especially during the seedling establishment phase (Grubb 1977). A consistent association of many tropical tree species to specific soil types has, however, proven difficult to demonstrate (Sollins 1998), but there is increasing support for segregation in relation to soil drainage, topography, and the availability of soil nutrients such as P (Phillips *et al.* 2003, Baltzer *et al.* 2005, Paoli *et al.* 2006, Comita & Engelbrecht 2009).

A further challenge to niche theory for explaining tropical species coexistence is the presence of tree species that are apparent generalists in their environmental preferences. By definition, generalist species are able to tolerate a wide variety of environmental conditions, but in a particular environment they should be at a selective disadvantage compared to specialist species adapted to that environment. Consequently, specialist species should competitively exclude generalists, particularly in relatively stable environments free from recurrent disturbance (Wright 2002, Silvertown 2004). Yet, the persistence of common soil generalist tree species in many tropical regions suggests that this is not the case (Pitman *et al.* 1999, Webb & Peart 2000, Chuyong *et al.* 2011). Thus, niche differentiation based on partitioning of the forest soil environment can only be a partial explanation for tropical forest tree diversity. One possibility is that other species traits and trade-offs might have been underestimated or are unaccounted. Recent work has shown that sensitivity to flooding (Lopez & Kursar 2003, Baraloto *et al.* 2007), herbivory (Fine *et al.* 2004, Bagchi *et al.* 2010), drought (Gibbons & Newbery 2002, Comita & Engelbrecht 2009), or competition for pollinators (Ng *et al.* 2006, Kettle *et al.* 2011) can render apparent generalists as specialists once these additional niche dimensions are included.

The objective of this study was to empirically assess, using a reciprocal seedling transplant experiment, the performance of co-generic and co-occurring tree species that differ in the extent of their edaphic specialization on different soil types. We focus on partitioning of the regeneration niche, that is, the differential performance of seedlings, which is thought to be particularly important in shaping the structure of forest communities (Grubb 1977, Poorter 2007), and where competition and selection among individuals is considered to be most severe. We test the hypothesis that on any particular soil type, seedling growth rates, and survival of apparent specialists on that soil type will exceed that of apparent generalists, which in turn will exceed that of specialists of an alternative soil type. We further explore how light regime might interact with soil conditions in terms of differential species growth and survival responses.

METHODS

STUDY SITE AND SPECIES.—The study was conducted for two years starting in October 2006 at Sepilok Forest Reserve (SFR) in Sabah, Malaysia (5°51′ N, 117°56′ E). Annual rainfall is about 3000 mm, and mean annual temperature is in the range of 26.7–27.7 °C (Nilus 2004). The wettest months are November to February and during this time flooding events lasting a few days frequently occur in the flat lower areas in SFR. SFR comprises evergreen lowland dipterocarp forest (0–170 m asl), which is representative of lowland rain forests in northeast Sabah (Fox 1983). The overall forest topography is flat with gently undulating low mudstone hills, interspersed with narrow sandstone ridges (Fox 1973).

Within SFR our research was conducted on the alluvial flats and adjacent low mudstone hills. The forest canopy is characterized by large Dipterocarpaceae trees (canopy heights of 45–60 m), which form the dominant floristic element of Southeast Asian forests, with a center of diversity in Borneo (Ashton 1988, Newman *et al.* 1996). The mudstone hills reach maximum amplitude of around 15 m (being 15–30 m asl) and, unlike the alluvial flat areas, are not inundated during the wet season. Alluvial flat and mudstone hill areas can be clearly differentiated and mapped, as mudstone hills rise abruptly from the alluvial flats. Tree community composition differs between alluvial flat and mudstone hill habitat with some dipterocarp species being largely confined to one or other of these habitats, while others are found more or less equally on both (Fig. 1).

We selected six *Shorea* species (Dipterocarpaceae) that vary in their degree of local habitat association in SFR, based on surveys of adult trees within a 68-ha plot (Fig. 1; Table 1). At SFR, *Shorea johorensis* Foxw. and *S. leprosula* Miq. are predominantly found on alluvial flats and are referred in this study as alluvial specialists. *Shorea macroptera* Dyer and *S. argentifolia* Symington are mainly found on mudstone hills in SFR, and henceforth are considered mudstone specialists. Finally, *Shorea xanthophylla* Symington and *S. parvifolia* Ashton are more or less equally common on both alluvial flats and mudstone hills in SFR and are termed 'generalist' in the context of this study, although at larger spatial scales that encompass other edaphic formations both these species appear as soil specialists as they are restricted to alluvial/mudstone sedimentary deposits (Ashton 2004). These species-soil associations have been confirmed through the application of a torus translation procedure (following Harms *et al.* 2001) by Margrove (2013; see Table S1).

EXPERIMENTAL DESIGN.—We established a reciprocal transplant experiment on alluvial flats and mudstone hills in forest gaps and in shaded understory to examine the importance of soil type and
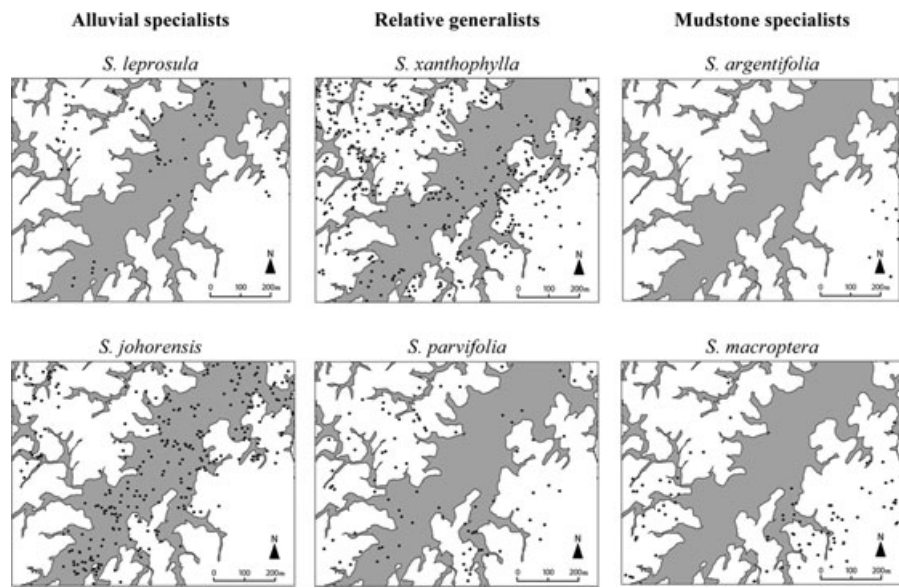
FIGURE 1. Distribution maps of adult *Shorea* trees of the six study species on a 68-ha plot in Sepilok Forest Reserve. The flat alluvial habitat is shaded gray and the mudstone hill habitat is white.

TABLE 1. *Counts of adult* Shorea *trees in an area of 24.5-ha alluvial flat soil (AL) and 43.5-ha mudstone hill soil (MU) according to the distribution maps in Fig. 1. The percentage of individuals found on mudstone soil is corrected for area. Species distributions are indicated as predominantly alluvial (AL), generalist (GEN) or mudstone (MU).*

Species	No of adults AL	No of adults MU	AL density (No/ha)	MU density (No/ha)	% trees on MU
S. johorensis (AL)	198	97	8.1	2.2	21.6
S. leprosula (AL)	41	32	1.7	0.7	30.5
S. parvifolia (GEN)	27	57	1.1	1.3	54.3
S. xanthophylla (GEN)	101	279	4.1	6.4	60.9
S. macroptera (MU)	14	68	0.6	1.6	73.2
S. argentifolia (MU)	0	9	0.0	0.2	100.0

light environment on the comparative survival and growth of the six *Shorea* species. A nested two by two factorial design of soil types and light treatments was replicated using four blocks with paired (gap and understory) plots on each soil type, giving a total of eight blocks with 16 plots. The blocks were widely separated (by several hundred meters) within the primary forest at SFR. At each location, the gap plot was established in an existing canopy gap (small gaps *ca* 200 m^2) which was cleared of small stems (*i.e.,* < 10 cm diam at breast height). Shade plots were established in the adjacent understory which was similarly cleared of small stems. Light environment at each plot was quantified using hemispherical photography (see Table S2, S3 and Appendix S1 for details).

To describe differences between alluvial and mudstone soils, we conducted chemical and physical soil analyses of the experimental plots. Five points in each plot were randomly selected for soil sampling. Top soil was auger-sampled at 0–15 cm depth in May 2007 and these five soil cores were thoroughly mixed by hand. Soil analyses were conducted on the mixed soil samples. For nitrate and ammonium two randomly assigned auger-samples per plot were taken and individually analysed within 24 h. The average of the two samples per plot was used for the analysis. Full details of soil analytical methods and results are included in Appendix S2.

Seedlings of all species except *S. xanthophylla* were obtained from the Innoprise-FACE Foundation project nursery (INFAP-RO Danum Valley). These seedlings had been grown in polyethylene bags (200 ml, clay-rich Danum forest soil) under nursery conditions (around 11% full sunlight). The seeds had been sourced from wild fruiting trees in Ulu Segama Forest Reserve (150 km south of SFR). We acknowledge that seed sourced from another forest reserve might not have the same genetic make-up as seed sourced from SFR, but given the similar climate and soil environments of the two forest areas and the fact that they belong to the same floristic region on Borneo (Slik *et al.* 2003), we assume that these differences will not bias the outcome of the experiment. The nursery seedlings were of equal age (*ca* 8 mo), and equal size within species, though mean heights among species ranged from 27 to 79 cm. The seedlings were transferred to a temporary nursery in the SFR understory (around 5% full-light conditions) for acclimatization to forest conditions for 1 mo before planting. They were watered regularly during this time.

Shorea xanthophylla seedlings were collected as wildings from SFR. These seedlings are all almost certainly derived from the previous *S. xanthophylla* flowering event at the end of 2005,

making them around 10-mo old at the start of the experiment. Seedlings were collected in randomly selected locations in both alluvial and mudstone areas and planted in polyethylene bags using the soil of origin and also allowed to acclimatize with the other seedlings.

In September 2006, 12 seedlings of each of the six species were planted in each of the 16 plots in a random arrangement with respect to species identity (total of 1152 seedlings). They were planted in an 8 × 9 grid with 0.75 m spacing between each plant. All dead or dying seedlings were replaced during the first month after planting. Flooding in December 2006 (3 mo after planting) affected the plots in flat alluvial environments, and on this occasion dead seedlings (mostly *S. argentifolia, S. parvifolia,* and *S. xanthophylla*) were replaced in January and April 2007. In total, species seedling mortality across all plots up to April 2007 ranged between 2 to 14 percent of seedlings, except for *S. argentifolia* (a mudstone specialist) which had 31 percent seedling mortality (80 percent of which was in the flooded alluvial plots). After April 2007, there were no further replacements of seedlings.

SEEDLING GROWTH ANALYSIS.—Seedling performance was characterized by stem height growth rate (HeiGR) and total stem length including branches (HbGR). Stem height was measured from the soil surface to the highest living apical bud, and branches from node to growing tip. Measurements of seedlings were made every 6 mo from October 2006 (January 2007 or April 2007 for seedlings replaced after the flood) to October 2008. HeiGR and HbGR was calculated including all seedlings alive in October 2008 as $(W2 - W1)/(t2 - t1)$, where $W2$ is 'height' or 'height and branches' in October 2008, and $W1$ is the 'height' or 'height and branches' at the first measurement, while t is the respective growing period in months.

We calculated both relative growth rates and absolute growth rates, but as the conclusions derived from these metrics did not differ we report only absolute growth measurements. Twenty-one seedlings for HeiGR and 47 seedlings for HbGR with negative growth were removed from the data set, because they had been damaged by animals or fallen debris and were therefore not instructive for growth measures.

STATISTICAL ANALYSES.—All statistical analyses were performed with R 2.10.1 (R Development Core Team 2009) and followed the methods recommended by Crawley (2009). The experimental treatment effects of soil and light were separately analyzed for HeiGR and HbGR using ANOVA. The experimental setup was a split:plot design, where paired light treatment plots were grouped and nested within blocks (four blocks on each soil type). The effect of soil type was tested on the block level (error structure one), whereas the effect of light treatment and the effect of the soil:light interaction was tested on the soil:light:block interaction (error structure two), which corresponded to the plot level. The effect of species, the light:species, the soil:species, and the soil:light:species interactions were tested on the residuals (error structure three). Tukey's honest significant difference range test (Tukey HSD) was applied to the full model to perform pair-wise compari-

sons among the species on the two soil types if species were significantly different in the ANOVA. HeiGR and HbGR variables were transformed if necessary to fulfill requirements of the model.

Seedling survival was recorded on five occasions: January, April, and October 2007, and April and October 2008. Only seedlings planted in October 2006 were used for the survival analysis. Individuals that survived beyond the end of the experiment were coded with '0'. Seedlings with no leaves were recorded as dead and coded with '1'. Seedlings destroyed by monkeys or pigs during the experiment (13 individuals from five species) were censored and thus coded with '0', which allows them to be informatively included in the analysis while alive. All survival analyses were conducted using the library 'survival'. To compare timing of seedling mortality across species and treatments we used Kaplan–Meier survival curves. To compare species contrasts at the end of the experiment, we used the parametric survival analysis function 'survReg' by fitting a Weibull distribution model (implying a non-constant hazard with the risk of seedling death being dependent on seedling age). To calculate instantaneous risk of death, non-parametric cox proportional hazard (which calculates immediate risk of a seedling dying under a certain treatment by assuming constant hazard ratio over time) was calculated using the 'coxph' function (Crawley 2009). Parametric and non-parametric survival analyses used soil (alluvial and mudstone), light (gap and under-story shade), species (all six *Shorea* species), and their two-way interactions as fixed factors, while plot was included with the 'frailty' function as a random effect. Three-way interactions were omitted in order to avoid over-fitting the model.

RESULTS

SOIL AFFINITIES OF ADULT TREES.—Tree distributions showed differential segregation by habitat type across species based on the results of the torus translation analysis (Fig. 1; Table S1). *Shorea johorensis* and *S. leprosula* were predominantly associated with the flat alluvial habitat where more than two thirds of their individuals (corrected for area) occurred (Table 1). *Shorea macroptera* and *S. argentifolia* were associated with the mudstone hill habitat (although the sample size for *S. argentifolia* is limited). The two remaining species *S. xanthophylla* and *S. parvifolia* occurred more or less equally on both mudstone hill and alluvial habitats.

SEEDLING GROWTH.—Over two years, seedling height growth rate (HeiGR) and seedling total growth rate including height and branches (HbGR) were 16 and 35 times greater in gaps than understory (HeiGR $P < 0.001$; HbGR $P < 0.001$; Tables 2 and 3; Fig. 2). In gaps (Table 2), species mean HeiGR ranged from 1.4 cm/mo (*S. xanthophylla* in mudstone) to 8.6 cm/mo (*S. leprosula* in alluvial), while in shade they were between 0.2 cm/mo (*S. xanthophylla* and *S. macroptera* both in alluvial) and 0.6 cm/mo (*S. leprosula* in mudstone).

For HbGR in gaps (Table 2) growth was between 2.7 cm/mo (*S. xanthophylla* in mudstone) and 89.0 cm/mo (*S. parvifolia* in alluvial), while in shade they were between 0.3 cm/mo (*S. xanthophylla* in alluvial and mudstone) and 2.3 cm/mo (*S. parvifolia*

TABLE 2. *Mean and standard error of* Shorea *seedling height growth rate (HeiGR), and height and branches growth rate (HbGR). Measures were taken in gap (Gap) and understory shade (Shade) on alluvial (AL) and mudstone (MU) soils. All measures are in cm per mo.*

| | HeiGR | | | | HbGR | | | |
| | Gap AL | | Gap MU | | Gap AL | | Gap MU | |
Species	Mean	SE	Mean	SE	Mean	SE	Mean	SE
S. argentifolia	6.45	0.61	5.70	0.49	63.45	8.27	57.98	6.43
S. johorensis	6.40	0.59	3.73	0.48	53.62	6.50	24.32	3.34
S. leprosula	8.58	0.44	5.04	0.47	71.69	5.72	35.68	4.89
S. macroptera	4.65	0.35	2.66	0.24	23.82	2.20	12.03	1.27
S. parvifolia	7.34	0.53	5.58	0.47	89.04	10.88	58.25	7.66
S. xanthophylla	1.97	0.24	1.35	0.16	4.42	0.71	2.68	0.28

| | Shade AL | | Shade MU | | Shade AL | | Shade MU | |
Species	Mean	SE	Mean	SE	Mean	SE	Mean	SE
S. argentifolia	0.24	0.04	0.43	0.05	1.46	0.48	2.00	0.27
S. johorensis	0.19	0.02	0.21	0.04	0.90	0.09	1.58	0.28
S. leprosula	0.57	0.10	0.59	0.08	1.33	0.18	1.98	0.30
S. macroptera	0.17	0.02	0.27	0.03	0.36	0.06	0.70	0.16
S. parvifolia	0.26	0.04	0.45	0.01	0.96	0.13	2.25	0.58
S. xanthophylla	0.17	0.02	0.20	0.02	0.27	0.03	0.27	0.03

mudstone). Species differed significantly in their HeiGR ($P < 0.001$; Table 3; Fig. 2) and HbGR ($P < 0.001$; Table 3; Fig. 2). The significant light:species interaction effect for both HeiGR and HbGR (both $P < 0.001$; Table 3) suggests different growth responses among species in response to different light conditions. These results appear to be driven mainly by *S. xanthophylla,* which had clearly lower HeiGR and HbGR values than other species in gap conditions, but was not different to these species under shade (Fig. 2). When grown under gap conditions, *S. leprosula* (alluvial associated), *S. johorensis* (alluvial associated), and *S. macroptera* (mudstone associated) revealed stronger HeiGR

($P < 0.001$; Table 3) and HbGR ($P = 0.002$; Table 3) on alluvial soils compared to mudstone soils (Figs. 2A and C). In understory shade, soil had no effect on seedling growth (Figs. 2B and D). The three-way interaction soil:light:species was significant for HbGR ($P = 0.01$; Table 3), indicating differences among species in how they respond to the combination of light and soil conditions. The other tested factors, which included overall soil effect and soil:light interaction showed no effect on seedling growth rate. The two error terms block (HeiGR and HbGR $P < 0.001$) and soil:light:block (HeiGR and HbGR $P < 0.001$) were highly significant.

Pair-wise species comparisons in gaps showed that *S. xanthophylla* (soil generalist) had substantially lower HeiGR and HbGR than the five other species (Figs. 2A and C). HeiGR differences across the other five species are not clear in alluvial gaps, although when HbGR is considered *S. macroptera* (mudstone associate) has lower values than the other four species. In mudstone gaps *S. parvifolia*, *S. argentifolia,* and *S. leprosula* had higher growth rates than *S. johorensis* and *S. macroptera*, while *S. xanthophylla* had lowest growth rate.

There was some separation among species in the understory shade treatments, although species ranks were not consistent between soil types. Ranks also changed depending on whether HeiGR or HbGR was the measure of interest (Figs. 2B and D). Species with rapid height growth rates in the understory are *S. leprosula*, *S. parvifolia,* and *S. argentifolia*. When lateral growth was included (*i.e.,* HbGR), *S. macroptera* and *S. xanthophylla* separate from the other species by having lower rates.

SURVIVAL ANALYSIS.—Survival curves of seedlings growing in gaps showed no clear separation of species except for higher mortality of *S. xanthophylla* in both habitats, and of *S. argentifolia* on alluvial soils (Figs. 3A and C). In the shade treatments, however, *S. argentifolia*, *S. parvifolia* and *S. leprosula* seedlings had far higher mortality in both habitats (Figs. 3B and D). *Shorea parvifolia* (generalist) and *S. argentifolia* (mudstone) had particularly high mortality in alluvial shade plots, and the timing of mortality was linked to the onset of high rainfall events at Sepilok (arrows in Fig. 3).

TABLE 3. *ANOVA table of seedling height growth rate (HeiGR), and total seedling height and branches growth rate (HbGR) over two years, as a function of soil (alluvial and mudstone), block (four paired gap and understory plots), light (gap and understory), and their interactions.*

| | df | | Mean Sq | | F | | P | |
	HeiGR	HbGR	HeiGR	HbGR	HeiGR	HbGR	HeiGR	HbGR
Soil	1	1	5.89	10.54	0.47	0.45	0.517	0.525
Error 1 (= block)	6	6	12.41	23.19	29.16	35.29	<0.001	<0.001
Light	1	1	1700.29	2773.25	176.95	252.68	<0.001	<0.001
soil:light	1	1	21.11	21.37	2.20	1.95	0.189	0.212
Error 2 (= soil:light:block)	6	6	9.61	10.98	22.59	16.70	<0.001	<0.001
Species	5	5	29.30	127.17	68.86	193.53	<0.001	<0.001
light:species	5	5	5.85	12.51	13.75	19.04	<0.001	<0.001
soil:species	5	5	2.42	2.58	5.68	3.93	<0.001	0.002
soil:light:species		5		1.99		3.03		0.010
Error 3 (= residuals)	915	881	0.43	0.66				
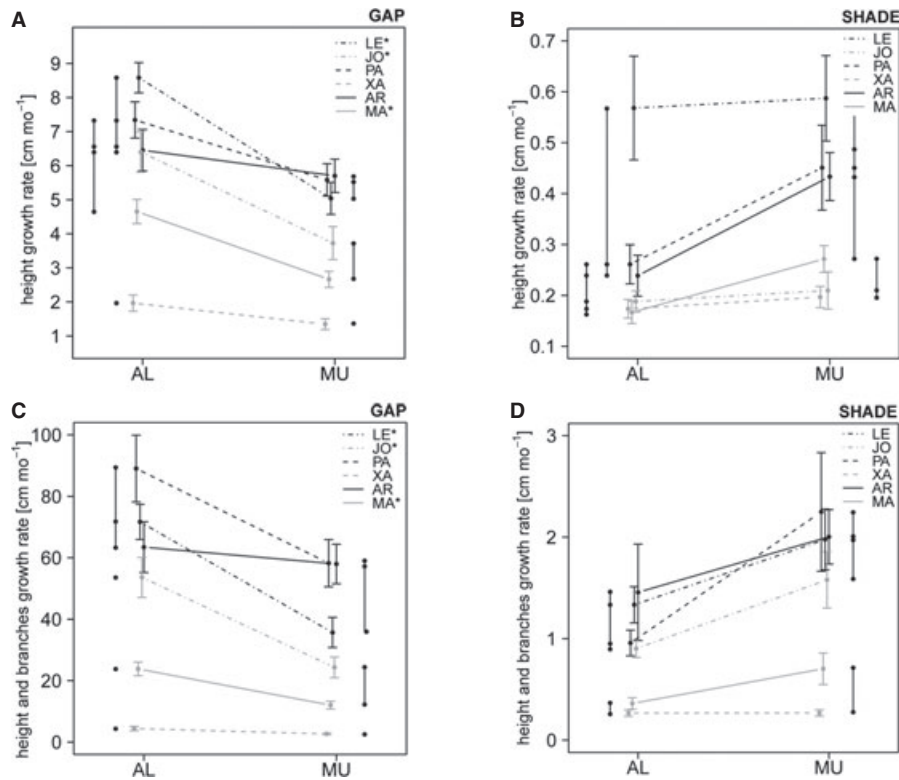
FIGURE 2. Mean and standard error of (A) stem height growth rate (cm per mo) in gap and (B) understory shade, as well as (C) height and branches growth rate (cm per mo) in gap and d) understory shade of six *Shorea* species seedlings grown on alluvial (AL) and mudstone (MU) soil. Significant differences (Tukey HSD) within soil type are indicated with non-connected dots on the side and with stars in the legends for among soil type within species comparisons. AR = *S. argentifolia*, JO = *S. johorensis*, LE = *S. leprosula*, MA = *S. macroptera*, PA = *S. parvifolia*, XA = *S. xanthophylla*.

The cox proportional hazard represents the immediate risk of a seedling dying under a certain treatment by assuming constant hazard ratio over time. Since hazard normally decreases with seedling age, cox proportional hazards are strictly speaking overestimated. Since overestimation is the same for all treatments and species, cox proportional hazards remain useful for comparisons of species among treatments. Cox proportional hazard numbers vary greatly among species (Table S4). Particularly high numbers are obtained for *S. argentifolia*, *S. parvifolia*, and *S. leprosula* in both alluvial and mudstone shade conditions. Cox proportional hazard values were lower in gap environments, with *S. argentifolia* being particularly severely affected in alluvial conditions, while *S. xanthophylla* had relatively high mortality in both alluvial and mudstone gap conditions. The cox proportional hazard analysis for overall treatment effects (Table S5) revealed that soil, light, species, and plot have a significant effect on seedling survival (all effects $P < 0.001$). The significant soil:species and light:species interactions (both $P < 0.001$) suggest differential seedling survival among species in response to different light and soil conditions.

DISCUSSION

SEEDLING RESPONSES TO SOIL AND LIGHT DIFFERENCES.—The expectation that seedlings would perform best on the soil type with which their adults are associated is not well supported by our results (Fig. 2). In shaded understory, there was little obvious differentiation in growth rates and little growth overall across all species and treatments (Figs. 2B and D). In gap conditions, three species, *S. leprosula*, *S. johorensis,* and *S. macroptera*, had higher growth on alluvial soil compared to mudstone, perhaps reflecting more favorable soil conditions for plant growth. Nevertheless, differences among species within particular treatments were not well resolved, and rank growth rates remained broadly similar across treatments. While this suggests little niche differentiation across light and soil axes, there are subtle differences in species responses which, together with differential survival, might shape community structure (see further discussion below).

The main difference between the two soil types was acidity and P availability (Table S6). On average, mudstone soils were more acidic in both active (pH) and exchangable acidity. The consequence for plant growth is that high acidity limits cation exchange (H^+ blocks base cation sites). This is also reflected in the different base saturation measures between the two soil types. The proportion of cation exchange sites in the soil occupied by base cations was only 14 percent on mudstone soils, compared to 40 percent in alluvial soils. Furthermore, exchangeable acidity of both mudstone and alluvial soils was below pH 5, the threshold below which Al hydrolyzes in solution and becomes toxic for plants (Delhaize & Ryan 1995). The significantly higher exchange-
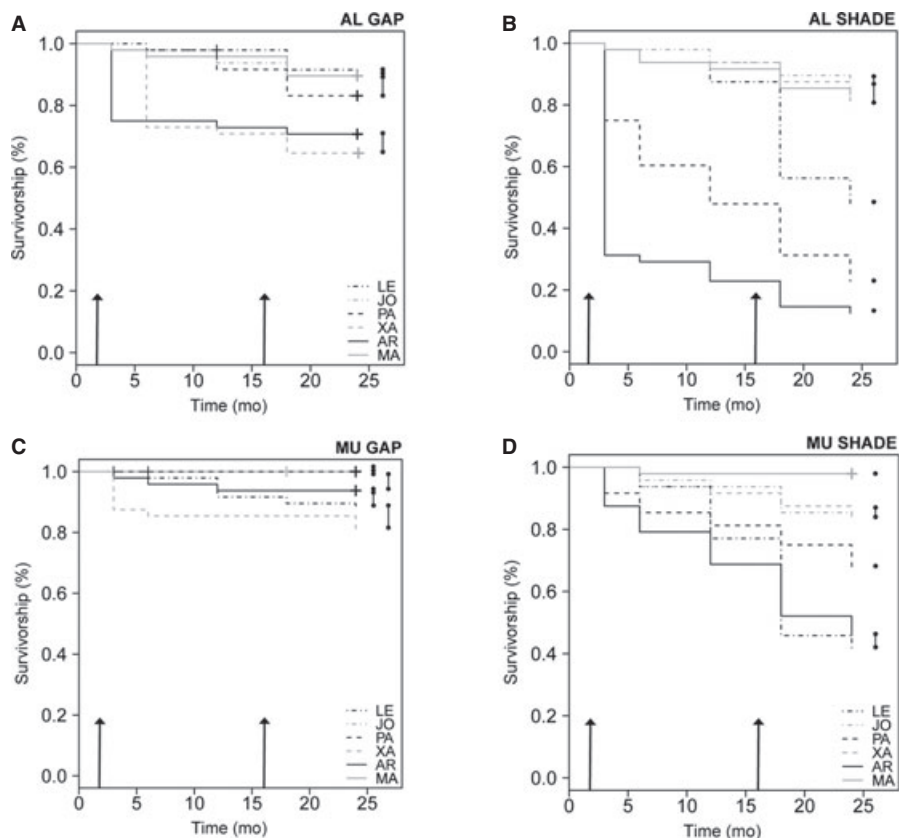
FIGURE 3. Kaplan–Meier survival curves of *Shorea* seedlings growing in (A) alluvial (AL) gaps and (B) alluvial understory shade, and (C) mudstone (MU) gaps and (D) mudstone understory shade. The occurrence of censored individuals are shown by a+ at the end of each curve in the graphs. Significant differences among species (obtained with parametric survival analysis) are indicated with non-connected dots on the side. Arrows indicate start of the wetter season in Sepilok Forest Reserve, where flooding events are likely to occur.

able Al concentration of mudstone soils (4.5 versus 2.6 m.e. per 100 g) can influence plant growth under such acidic conditions (Robson 1989), mainly by affecting root growth and function (Sollins 1998). Furthermore, Al in acidic soils can form insoluble compounds with inorganic phosphate and reduce its availability for plants. Higher growth rates on alluvial soils might thus also be attributed to higher P concentrations (7.92 μg/g in alluvial soils versus 5.18 μg/g on mudstone soils). Several dipterocarp studies in Borneo have highlighted the importance of P for species habitat associations (Palmiotto *et al.* 2004; Paoli *et al.* 2005, 2006, 2008; Russo *et al.* 2005).

We also expected that species associated with a particular soil type (as reflected by adult distributions) would have higher seedling survival when grown on that soil type. Mortality under gap conditions was generally low, with little species differentiation (Figs. 3A and C). In the understory, however, mortality was particularly high for *S. argentifolia* and *S. parvifolia* (Figs. 3B & D). *Shorea argentifolia* (mudstone) mortality was highest in alluvial sites, particularly following the first flooding event: about 25 percent of seedlings died in gap alluvial plots (Fig. 3A) and 70 percent died in shaded alluvial plots (Fig. 3B), compared to less than five and ten percent, respectively, in (non-flooded) mudstone sites

(Figs. 3C & D). *Shorea parvifolia* (generalist) also suffered seedling loss associated with flooding in alluvial flats, especially in shade conditions.

This suggests that there is differential tolerance among the six *Shorea* species to short duration flooding and soil waterlogging events, and such ephemeral events might shape the distribution of species in the low-lying alluvial areas. *Shorea argentifolia* might, for example, become largely restricted to mudstone habitats on account of sensitivity to occasional flooding, while *S. parvifolia* might become restricted to alluvial gap sites where the species seems to suffer lower mortality, or to microsites in the alluvial flats where soil waterlogging and flooding are less severe. Indeed, *S. parvifolia* is relatively uncommon in the alluvial flats, and where it does occur it has a rather clumped distribution (Fig. 1). Previous dipterocarp research has paid little attention to the effect of ephemeral floods and waterlogging on seedling survival and growth. Neotropical studies are beginning to show that soil moisture differences can determine species distributions on relatively small scales of tens of meters (Lopez & Kursar 2003, Parolin *et al.* 2004, Sedio *et al.* 2012).

High mortality under shade conditions was also found for *S. leprosula* on both soil types, but particularly on mudstone soils

(cox proportional hazard on mudstone 224 compared to alluvial 151; Table S4). This does not seem to be driven by vulnerability to flooding events (Figs. 3B and D) as mortality was not correlated with such. Alternatively, light availability might not have been sufficient to maintain light requirements to sustain its rapid growth and survival. On alluvial soils, the alluvial specialist *S. leprosula* has a seven times higher cox proportional hazard under shade compared to gap, while the slower growing alluvial specialist *S. johorensis* has only three times the hazard value (Table S4). There are also large differences among mudstone specialists on mudstone soils: the fast growing *S. argentifolia* has far higher hazard values than *S. macroptera*, particularly under shade conditions (Table S4). This might explain why *S. argentifolia* is relatively rare in Sepilok.

That there are differences in shade tolerance and growth rates among dipterocarp species in response to light regime is already widely known (Aiba & Nakashizuka 2005, Russo *et al.* 2008, Baltzer & Thomas 2010, Philipson *et al.* 2012), but the importance of these traits for niche differentiation along light gradients has been questioned (Brown & Whitmore 1992, Whitmore & Brown 1996, Barker *et al.* 1997). Our study provides evidence that localized adult distributions of six cogeneric dipterocarp species can be partially explained by soil–light interactions, but that other traits including tolerance to waterlogging also need to be considered.

EVIDENCE FOR NICHE PARTITIONING AMONG SIX *SHOREA* SPECIES.—We expected that specialist species would perform better on their home soil compared to generalists and specialists of the alternative soil type. In alluvial gaps, the alluvial specialist *S. leprosula* is indeed the fastest growing species, but its growth rate in alluvial gaps is not significantly different to that of the mudstone specialist *S. argentifolia* or the generalist *S. parvifolia*, and hence clear indications of niche partitioning are not obvious. *Shorea argentifolia* might be excluded from alluvial areas by its vulnerability to flooding events. *Shorea johorensis* is the more shade tolerant of the two alluvial specialists (Fig. 3B), and this might allow it to coexist with the light-demanding *S. leprosula* in alluvial areas.

Explaining the distribution of species on mudstone habitats is even more difficult. High survival and better growth rates of the mudstone specialist *S. macroptera* on alluvial soils was unexpected, and it also appears resilient to flooding. While *S. macroptera* growth rates are similar to or lower than the alluvial-associated species *S. johorensis* and *S. leprosula* in either mudstone or alluvial gaps, *S. macroptera* still grows faster on alluvial than mudstone soils, a result that does not tally with expectation based on its adult distribution. *Shorea macroptera* appears to persist on mudstone soils on account of very high seedling survival in both light and shade conditions (unlike *S. leprosula* and, to a lesser extent, *S. johorensis*), and is presumably outcompeted on alluvial soils by the faster growing alluvial specialists. *Shorea argentifolia* grows well on the mudstone soils with which its adult distribution is associated, but its growth here cannot be separated from that of *S. parvifolia* (generalist) or *S. leprosula* (alluvial). It remains unclear how alluvial specialist *S. leprosula* is displaced from mudstone gaps based on its growth rates, but intolerance to shade

clearly excludes it from shaded mudstone conditions (Fig. 3D). The growth of *S. johorensis* is significantly lower than that of *S. argentifolia, S. leprosula,* and *S. parvifolia* in mudstone gaps, but it has higher survival, particularly under shade. Yet, *S. johorensis* adults are comparatively rare on mudstone soils, and we presume that subsequent exclusion of *S. johorensis* continues beyond the early seedling and sapling stages. Even so, we recognize that despite strong negative associations of *S. johorensis* and *S. leprosula* to mudstone habitats (and strong positive associations to alluvial habitats; Table S1), both these species remain common in absolute terms in mudstone habitats, and indeed *S. johorensis* is more common than both the putative mudstone specialists on mudstone soils. Clearly, there are other factors that determine absolute abundances in addition to habitat preferences, the evaluation of which lies beyond the scope of this study.

The two generalist species reveal contrasting life history strategies. *Shorea parvifolia* has high growth under gap conditions on both soil types but suffers high mortality under shade (Figs. 3B and D), particularly on alluvial soils after flooding. The regeneration of this species is therefore expected to be favoured in mudstone and alluvial gaps, but in the latter only when it can escape flooding. *Shorea xanthophylla*, the second generalist species, grows slowly both in gaps and under shade regardless of soil type, but has high survival under shade, and indeed is the only species that has lower hazard numbers under shade compared to gaps (Table S4). Shade tolerance and continued slow growth under shade conditions might allow this species to persist in the forest understory in areas that are too dark for the other species examined in this study. This strategy corresponds with other traits, including its subcanopy status as an adult, and poor dispersal of its wingless fruit that drop beneath the canopy of the mother tree (pers. obs.). Such traits suggest that *S. xanthophylla* adopts a strategy of maintaining continued occupancy of a site once established.

An alternative null-model to niche-based explanations for the distributions of these two species is to assume functional equivalence of species, with species' distributions dictated by random dispersal and mortality (Hubbell 2001). It is likely that such processes contribute to shaping species distributions, but it is also clear that the assumption of functional equivalence is problematic (especially comparing *S. xanthophylla* and *S. parvifolia*) and that differences in growth and mortality responses to soil, light, and flooding are relevant to community assembly of these species and the wider suite of dipterocarp species. A recent analysis of tree species community structure at eight pantropical 50 ha plots concluded that all measured environmental variables (principally soil resources and topography) account for 13–39 percent of compositional variation (Baldeck *et al.* 2013). A similar fraction (19–37%) of spatially structured variation remained unexplained, suggesting a role for dispersal processes, but some fraction of this unexplained variance might equally be attributable to unmeasured environmental variables (Baldeck *et al.* 2013).

This study has shown that adult distributions might, in part, be explained by differential growth and mortality among species at seedling and sapling stages across different soil, light, and drainage regimes. While there is no clear signal of fine-scale niche

differentiation for any one factor in isolation, interactions among these factors suggest that the distributions of some species are shaped by the combination of growth rate and vulnerability to ephemeral flooding events that affect alluvial areas. The high mortality experienced by some species in alluvial areas immediately after flooding suggests that soil water relations might play a significant role in differential survival of *Shorea* seedlings and saplings. Thus, the relative abundance of adults of these six species on low-lying alluvial soils can be partially explained by their seedlings responding to a combination of susceptibility to flooding (*S. argentifolia* and *S. parvifolia*), high growth in gap conditions (*S. parvifolia, S. johorensis,* and *S. leprosula*), and high survival under shade (*S. xanthophylla* and *S. johorensis*). We recognize that adult distributions are unlikely to be shaped only by factors acting on seedlings and saplings, and such effects on pole and other juvenile stages remain poorly understood. Nevertheless, substantial mortality at early growth stages might set the template on which subsequent filtering at later life history stages takes place.

A longer experimental period might reveal changes in the height ranking order of the species (Whitmore & Brown 1996), and ontogenetic trade-offs that span different life history stages in combination with microhabitat trade-offs could also contribute to species coexistence and adult distributions (Baraloto *et al.* 2005). We have evidence that there is also some differential herbivory across species, with *S. leprosula* being particularly vulnerable, while vulnerability of the other species varied according to light regime (Born 2011). Consequently, the inclusion of other niche axes, including vulnerability to herbivory (Bagchi *et al.* 2010, Eichhorn *et al.* 2010) or interactions with drought (Newbery *et al.* 1999, Gibbons & Newbery 2002) might be instructive in further explaining species segregation.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

APPENDIX S1. Plot light environment.
APPENDIX S2. Soil analytical methods.
TABLE S1. *Habitat associations of the six* Shorea *species included in the study within the 160 ha Sepilok plot based on analysis using a torus translation procedure (following Harms* et al. 2001).
TABLE S2. *Canopy openness measured with 13 hemispherical photography readings in each gap and understory shade plot on alluvial and mudstone soil.*
TABLE S3. *ANOVA summary table of canopy openness in the experimental design, as a function of soil, block, light, and their interactions.*
TABLE S4. *Cox proportional hazard (risk of a seedling dying under a certain treatment) numbers.*
TABLE S5. *ANOVA table for cox proportional hazard analysis (risk of a seedling dying under a certain treatment) with fixed factors being soil, light, species and their two-way interactions, and plot as random factor.*
TABLE S6. *ANOVA results of the effects of soil and light on soil chemical and physical properties.*

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