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Interspecific Demographic Trade-Offs and Soil-Related Habitat Associations of Tree Species along Resource Gradients

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Summary

1. Interspecific relationships between fundamental demographic rates, often called demographic trade-offs, emerge from constraints within individuals related to morphology, physiology and resource allocation. Plant species that grow fast in high light usually have high mortality in shade, and this well-established relationship in part defines a species' successional niche. More generally, this relationship represents a trade-off between a species' ability to grow quickly to exploit abundant resources vs. avoiding mortality when resources are less plentiful, but few studies have described this demographic trade-off with respect to environmental factors other than light.
2. Using demographic data from 960 tree species in Bornean rain forest, we examined the evidence for an interspecific demographic trade-off between fast growth and low mortality and its variation among habitats defined by variation in soil fertility and moisture. Such a trade-off could contribute to sorting of tree species among habitats and partly explain the striking patterns of species' edaphic associations in this and other forests.
3. We found strong evidence for this demographic trade-off, both within the same habitat and when growth on edaphically rich habitats was compared with mortality on a habitat with lower below-ground resource availability.
4. The slope of the growth-mortality relationship varied among habitats, being steepest on the habitat lowest in below-ground resources. For species with the fastest potential growth rates, mortality was higher on this habitat than at comparable growth rates on the three more edaphically rich habitats, providing a possible mechanism by which fast-growing species may be eliminated from the poorest habitat. Adaptations for fast growth may entail a greater mortality risk, if inherently fast-growing species fail to maintain a positive C-balance when below-ground resources are scarce.
5. Conversely, for species with the slowest potential growth rates, the highest species' mortality rates occurred on the habitats with greatest below-ground resource availability, implying that slow-growing species may have a competitive disadvantage in resource-rich environments.
6. Synthesis. Differences among habitats in the steepness of this trade-off may sort species into different habitats along this edaphic gradient, whereas on the same soil, this demographic trade-off could facilitate coexistence of at least some species in this forest. Thus, by generating emergent demographic trade-offs that vary along resource gradients, plant life-history strategies can influence species diversity and distribution.

Keywords: Borneo, Edaphic gradient, Growth rate, Life-history trade-offs, Mixed dipterocarp forest, Mortality rate, Soil resources, Tree demography, Tropical rain forest

Introduction

Life-history trade-offs underlie much ecological theory explaining species' coexistence, distribution and abundance in plant communities (Levins & Culver 1971; Tilman 1982; Rees et al. 2001). Such trade-offs may be manifested at multiple levels of organization (Suding et al. 2003) and on multiple axes of environmental variation (Purves & Pacala 2005). Fundamentally, they arise from functional design and genetic constraints within the individual related to morphology, physiology and allocation (Stearns 1992). The aggregate of individual responses in a population produces emergent patterns, not only in functional trait variation among species (Reich et al. 2003; Westoby & Wright 2006), but also in species' demographic responses (Poorter & Garnier 1999; Suding et al. 2003; Condit et al. 2006). Thus, it is through covariation in fundamental demographic rates, such as species' growth, mortality and

recruitment, along environmental resource gradients that plant functional trait variation can ultimately influence species diversity and distribution.

Among trees, the interspecific demographic trade-off between a species' ability to grow quickly in high light vs. its ability to avoid mortality in shade explains successional dynamics (Kobe et al. 1995; Pacala et al. 1996; Walters & Reich 1996; Kobe 1999; Bloor & Grubb 2003; Gratzer et al. 2004) and the distributions of tree species in different light environments (Kobe 1996; Davies 2000; Pearson et al. 2003). Even though light is only one of the resources affecting plant performance, fewer studies examining trade-offs have accounted for the effects of soil resources on demographic rates (Coomes & Grubb 2000). As such, this demographic trade-off can be seen more broadly in terms of adaptations allowing species to survive in environments low in resources vs. those promoting competitive ability when resources are more abundant (Grime 1979; Pierce et al. 2005). Below-ground resources, such as soil moisture and mineral nutrients, would therefore also represent important axes for demographic trade-offs to arise. Nevertheless, above- and below-ground resource gradients often covary: more fertile, moister soils generally have greater canopy density and, consequently, reduced light penetration through the canopy (Ashton 1964; Coomes & Grubb 2000), and soil characteristics and topography influence disturbance regimes (Ohkubo et al. 2006). Interspecific demographic trade-offs may therefore operate on multiple axes of environmental variation within a habitat and would contribute to ecological sorting of tree species on edaphic gradients, as well as successional gradients in light.

Distributions of tree species that are correlated with environmental variation along topographic, moisture and fertility gradients (Clark et al. 1998; Silvertown et al. 1999; Caspersen & Kobe 2001; Davies et al. 2005; John et al. 2007) support the idea that species are sorted among habitats, especially when species' functional traits also covary along these gradients (Turner et al. 2000; Wright et al. 2001; Santiago et al. 2004; Baltzer et al. 2005; Paoli 2006). As with light, species associated with soils having low resource availability characteristically have traits promoting resource conservation, such as tougher, long-lasting tissues and higher nutrient- and water-use efficiencies, but typically lack the traits that engender greater responsiveness to increases in resource availability, such as elevated photosynthetic capacity often seen in specialists of more fertile, moist soils (Chapin 1980; Chapin et al. 1993). Although such patterns are well documented with respect to light, fewer studies address the demographic mechanisms that are required to sort species among edaphic habitats and that are necessary to link trait variation and species' distributions.

If an interspecific trade-off between fast growth and low mortality rates exists, variation in its steepness among soil-related habitats may be a mechanism by which species are sorted along edaphic gradients. This would be the case if traits enabling fast growth cause a plant to be incapable of maintaining consistent internal resource supplies (C, mineral nutrients) in environments low in below-ground resources, but also provide a competitive advantage when resources are more plentiful (Chapin et al. 1993; Pierce et al. 2005). Alternatively, species' growth and mortality rates may not covary if tree death is entirely stochastic and unrelated to species' traits (Hubbell 2001) or if individual responses to environmental variation are highly variable (Clark et al. 2003). Here, we examine the evidence for an interspecific demographic trade-off between fast growth and low mortality and its variation along an edaphic gradient among tree species in a species-rich Bornean rain forest.

In north-west Borneo, the floristic composition of mixed dipterocarp rain forest varies along gradients of topography and soil moisture and fertility (Ashton 1964; Baillie et al. 1987; Yamakura et al. 1996; Potts et al. 2002). Within a forest dynamics plot in this region at Lambir Hills National Park (hereafter, Lambir), most tree species have distributions that are significantly aggregated on one of four habitat types defined on a gradient of increasing soil mineral nutrients and moisture (Lee et al. 2002; Davies et al. 2005). Although this gradient varies continuously at different spatial scales in terms of above- and below-ground resources, these habitat types, particularly those at the edaphic extremes (sandy loam and clay), are quite discrete in terms of both their pedological origins (Baillie et al. 2006) and their tree species composition (Palmiotto et al. 2004; Davies et al. 2005). A benefit of large-scale forest dynamics plots is that the effects of environmental variation at multiple spatial scales can be analysed. Here, we focus on possible mechanisms acting at the between-habitat scale that might explain the soil-related habitat associations of tree species in the Lambir plot. These associations arise partly due to sorting of species among soil-related habitats as trees age (Russo et al. 2005). Although species may be present in the sapling community, with time they are lost non-randomly from habitats on which they do not achieve high abundance. As a result, species composition on a habitat becomes increasingly comprised of home-habitat specialists. Here, we explore a possible trade-off based mechanism for this sorting process.

If an interspecific trade-off between fast growth and low mortality contributes to sorting of tree species along this edaphic gradient, then species with fast growth rates, generally specialists of the three habitats highest in fertility and moisture (Table 2 in Russo et al.

2005), may have high mortality rates and may be progressively eliminated from the habitat lowest in soil fertility and moisture. Conversely, specialists of the habitat with the poorest soil, which generally have the lowest growth and mortality rates (Table 2 in Russo et al. 2005), may be unable to compete with the faster growing specialists on the three richer habitats, causing them to be over-topped before reaching reproductive maturity. We therefore predicted that: (i) across all habitats, the relationship between species' growth and mortality rates would be positive, reflecting an interspecific demographic trade-off, and (ii) the slope of the trade-off would vary among habitats, such that, at a given species' growth rate, the population-level mortality rate would be higher on a habitat with lower below-ground resource availability than on one with greater resource availability. We further predicted: (iii) that the relationship between growth on habitats with more abundant below-ground resources vs. mortality on habitat with the poorest soil would not only be positive, again reflecting the interspecific growth-mortality trade-off, but (iv) that it would also vary among groups of habitat-specialists, reflecting the disparity in the life-history strategies of species adapted to different below-ground resource availabilities. Lambir is particularly well suited to this question because its high species richness provides ample power to detect interspecific trade-off relationships.

Methods

STUDY SITE

Lambir Hills National Park, Sarawak, Malaysia (4°11' N, 114°01' E), encompasses 6,800 ha of lowland mixed dipterocarp forest with the highest tree species richness recorded in the Palaeotropics (Ashton & Hall 1992; Lee et al. 2002). Rainfall is c. 3,000 mm year-1, with all months averaging > 100 mm (Watson 1985). In 1991, a 52-ha plot (Lambir) was established in the Park to monitor all trees = 1 cm in diameter at breast height (diameter), following methods used in similar studies by the Center for Tropical Forest Science (Condit 1998). All trees = 1 cm in diameter, excluding palms, were tagged, mapped, identified, and their diameters measured to the nearest 1 mm. In 1997, all trees from the first (1992) census were re-censused to estimate growth and mortality rates for the c. 1,200 species in the plot.

Floristic composition, stand structure, soils and geomorphology of Lambir are described in Lee et al. (2002). Soils range from coarse loams that are sandstone-derived, leached, nutrient-depleted and well drained, with substantial raw humus (named humult in previous studies), to clays that are shale-derived, less nutrient-depleted and less well-drained, with little raw humus (previously named udult; Lee et al. 2002; Baillie et al. 2006). The sandstone-derived loam is located on an extensive elevated dipslope in the north and west of the plot, and the shale-derived clay is located on a lower and less extensive dipslope on shale in the south. Intergrading the two is a complex of steep and unstable scarp slopes and streambeds on mixed lithology in the east and south (Figure 1; Baillie et al. 2006). Relative to other tropical soils, the shale-derived soils at Lambir (clay and fine loam) have low to very low Ca- and P-fertility, but are moderately fertile for K and Mg, although the latter are not in immediately accessible forms. The sandstone-derived soils are less fertile than the shale-derived ones for all nutrients. The Lambir soils are similar in fertility to soils on Peninsular Malaysia at Pasoh Forest Reserve, but substantially less fertile than soils in tropical forest in Northern Thailand (Huai Kha Khaeng

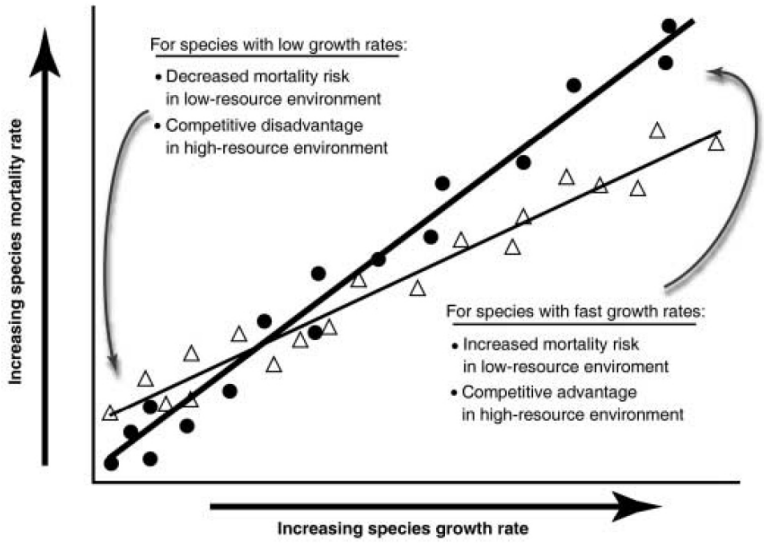

Figure 1. A schematic illustration of the predicted positive interspecific relationship between species' growth and mortality rates, demonstrating a trade-off varying among environments with differing resource availability. Each point represents a species' growth and mortality rate in two different environments at opposite ends of a gradient of below-ground resource availability (high resources, open triangles, fine line; low resources, closed circles, heavy line).

Table 1. Posterior mean parameter estimates ($\bar{x}$) and 95% credibility intervals (CI) for the relationship between tree species' growth and mortality rates on each of four habitats in a Bornean rain forest. Habitats are listed in order of increasing fertility and moisture. β is the habitat-specific slope parameter relating species' growth and mortality rates, and α is the habitat-specific intercept. Details of the model (Equation 1) and fitting are in the Methods and Appendix S1

	Habitat							
	Sandy loam		Loam		Fine loam		Clay	
	α	β	α	β	α	β	α	β
$\bar{x}$	1.45	-4.11	0.94	-3.45	0.58	-3.16	0.55	-3.06
CI	1.38-1.52	-4.15-4.06	0.87-1.02	-3.52-3.38	0.54-0.61	-3.21-3.11	0.45-0.65	-3.15-2.95

Wildlife Sanctuary), Panama (Barro Colorado Island Nature Monument) and Costa Rica (La Selva Biological Station) (I.C. Baillie, personal communication).

Davies et al. (2005) identified four habitats in Lambir based on variation in nutrients (total C, N and P and exchangeable K, Ca and Mg) and elevation at a 20 × 20 m scale. Ranked in ascending order of fertility and moisture, these soil-defined habitats are: sandy loam, loam, fine loam and clay, which correspond to habitats A, B, C and D, respectively, in Davies et al. (2005). Means of total nitrogen, total phosphorus, pH, exchangeable magnesium and calcium, and elevation for each of the four habitats are reported in Russo et al. (2005; Table 1). Means for exchangeable and reserve nutrients, total exchangeable bases, cation exchange capacity, and base saturation for the sandy loam and clay habitats are reported in Baillie et al. (2006; Table 1).

Here we focus on the effects on demography of the edaphic component of environmental variability among these different soil-defined habitats at Lambir, but topography, disturbance and light covary with soil fertility and moisture among these habitats, as well as at finer spatial scales (Ashton 1964; Baillie et al. 2006; Ohkubo et al. 2006). Although there exist no quantitative data on variation in light among habitats at Lambir, visual impressions indicate that average understorey light levels are lowest on the two richer soils (clay and fine loam), moderate on the poorest soil (sandy loam), and highest on loam (S.E. Russo, personal observation; P.S. Ashton, personal communication). The habitat ranks in insolation therefore do not appear to parallel directly the ranks in soil fertility and moisture. This variation in insolation is likely to be due to the facts: (i) that the clay habitat tends to occur at lower elevations in valleys, whereas the sandy loam habitat tends to be on higher-elevation dipslopes, and the loam habitat tends to be on steeper slopes with a more easterly aspect (Baillie et al. 2006), and (ii) that higher soil fertility and moisture on clay and fine loam support greater canopy density and thereby create deeper shade than on the less fertile soils (Ashton 1964).

Tree species in Lambir show spatial distribution patterns strongly biased with respect to these four soil-defined habitats (Davies et al. 2005). Among the 764 species tested, 73% had distributions significantly aggregated on one or two habitats (specialists), and 13% had a completely neutral distribution with respect to habitat (generalists). For simplicity, for species that were found to be aggregated on two habitats (11% of all species; Davies et al. 2005), we designated the habitat with greater tree density as that of aggregation. Thus, species were categorized into five possible habitat specialization patterns: specialists of sandy loam (285 species), loam (66 species), fine loam (152 species), or clay (57 species), and generalists (100 species), and we focused on these 660 species that had either aggregated or neutral distribution patterns with respect to these four habitats.

MODELING APPROACH

First, we compared the interspecific trade-off between growth and mortality among soil types at Lambir using data from juvenile trees (defined as being 1-10 cm in diameter at breast height in the 1992 census) for all species with $n \geq 10$ juveniles on a habitat (960 species out of a possible 1,171 species with $n \geq 10$ juveniles on the entire plot). We chose to model habitats using a categorical predictor because the patterns of species' distribution on the different habitats in this forest that we sought to explain are quite discrete. Thus, while continuous variation in edaphic resources is present in this forest, there are also discontinuous transitions that have geomorphological origins, as described above, and our model reflects these transitions.

Expected species' habitat-specific counts of tree deaths from 1992 to 1997 were modelled as a binomial process (Condit et al. 2006) with, $m_{jk} \sim \text{Binomial}(N_{jk}, pjk)$. Here, N_{jk} is the number of individual trees observed alive in 1992, and mjk is the observed number of trees dead by 1997 for species j on habitat k, and p_{jk} is the expected probability of an individual from species j on habitat k dying. Based on exploratory analyses, we modelled the logit-transformed species mortality probability on a habitat as a linear function of its habitat-specific annual growth rate, with

$$\log\left(\frac{p_{jk}}{1-p_{jk}}\right) = \beta_k g_{jk} + \alpha_k \quad \text{(Equation 1)}$$

Here, g_{jk} is the observed mean annual growth rate of species j growing on habitat k from 1992 to 1997, β_k is the habitat-specific slope parameter relating species mean growth to mortality probability p_{jk}, and α_k is a habitat-specific intercept parameter. Because there

were four habitats, habitat-level parameters (β_k and α_k) were treated as fixed effects. Note that not every species is present on every habitat, which is a consequence of the floristic variation among habitats at Lambir (Davies et al. 2005). Differences among habitats in species composition simply reflect the biotic environment in which demographic trade-offs may arise. The logit transformation bounds each species' mortality probability between zero and one, even though 20% of species had no tree deaths from 1992 to 1997, reflecting the generally low mortality rates in this forest (Russo et al. 2005), although mortality rates increase during drought events (Potts 2003). Thus, β_k estimates the strength of the interspecific growth-mortality trade-off on each habitat and represents the change in the chance of dying with a 1-mm year-1 increase in species' growth rate (the log odds ratio).

Secondly, a set of three separate models analogous to Equation 1 evaluated species' mortality probabilities on the habitat with the lowest soil fertility and moisture (sandy loam) as a function of growth on each of the three habitats with greater below-ground resources (loam, fine loam, and clay). Writing M_{jl} and z_{jl} for the total number of individuals and deaths on sandy loam, respectively, for species j with habitat specialization l, we have $z_{jl} \sim \text{Binomial}(M_{jl}, q_{jl})$, with

$$\log\left(\frac{q_{jl}}{1-q_{jl}}\right) = \delta_l g_{jl} + \gamma_l \quad \text{(Equation 2)}$$

For these three models, qjl is the mortality probability on sandy loam for species j with habitat specialization l. Note that the slope and intercept parameters (δ_l and γ_l) are different for each of the five habitat specialization groups. The model is applied three times, and for each of the habitats, loam, fine loam and clay, the growth rate g_{jl} for the species is estimated on that habitat type and the parameters re-estimated. In parallel with studies of growth as a function of shade tolerance and based on previous estimates at Lambir (Russo et al. 2005), we assumed that a species' mean growth rate would be highest on habitats with greater below-ground resources. These three models thus test the trade-off between fast growth when below-ground resources are relatively abundant vs. low mortality when below-ground resources are less available. In each model the strength of this interspecific trade-off was compared among the five species' habitat specialization groups based on the growth slope term (δ_l). Note that in order for a species to be included in this analysis, it had to have $n \geq 10$ stems of 1-10 cm diameter on sandy loam and one of the other three habitats (sample sizes for each habitat were: 454, 444 and 224 species on loam, fine loam and clay, respectively). The most specialized species, those with few or no stems on non-home habitat types, are thus not included.

Bayesian inference with Markov Chain Monte Carlo (MCMC) simulation (Gelman et al. 2004) was used to estimate parameters and test for significance. We chose

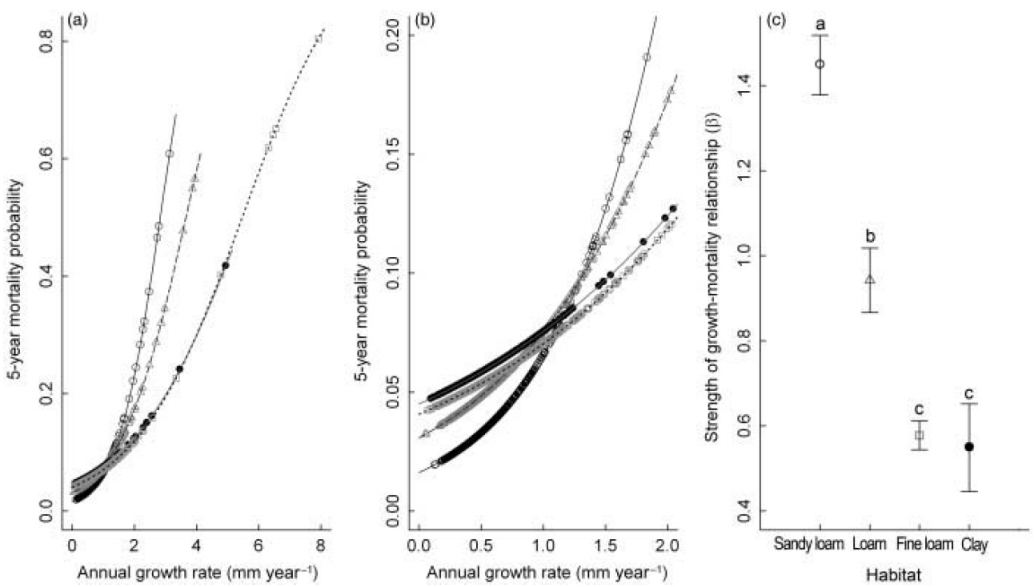

Figure 2. (a) and (b) The relationship between observed annual growth (mm year^{-1}) and predicted mortality rates (probability of mortality in 5 years) of tree species on four habitats in a Bornean rain forest. Points represent species, and lines represent fitted relationships. For the points, growth rates are from data, and mortality rates are estimated by the model, which is why they fall along the fitted line. (a) depicts the full extent of data; (b) is a detail from (a) showing differences among habitats at slow growth rates. (c) Posterior means and 95% credibility intervals for the habitat-specific slope parameters (β_k in Equation 1 in text) describing the relationship between species' growth and mortality on four different habitats, as shown in (a) and (b). Habitats are coded with symbols and lines: sandy loam, open black circles and solid black line; loam, grey triangles and long dashed line; fine loam, grey squares and dotted line; clay, closed circles and solid grey line. In (c) lower case letters indicate significant differences among habitats based on 95% credibility intervals. Parameter estimates are in Table 1.

Table 2. Increase in an individual's odds of mortality resulting from a 1 mm year^{-1} increase in species' mean growth rate, for each habitat relative to all other habitats. The estimated log odds ratio for each habitat (β_k, Equation 1) was exponentiated and divided by that for every other habitat

Odds of dying on ...	Relative to ...		
	Loam	Fine loam	Clay
Sandy loam	1.63	2.39	2.46
Loam	-	1.43	1.48
Fine loam	-	-	1.03

non-informative, proper prior distributions for all parameters (normal distributions with large variance; see Appendix S1 in Supplementary Material), allowing the observed data to dominate inferences. We fit our models using the software WinBUGS v. 1.4.1 (Spiegelhalter et al. 2003) run through the statistical package R v. 2.3.1 (The R Core Development Team 2006) using the contributed package, R2WinBUGS (Sturtz et al. 2005). For each model, we ran 50,000 iterations and discarded the early iterations ('burn-in,' generally the first 20,000). After burn-in, chains were thinned by retaining only every 10th sample, decreasing the dependence of samples in the Markov chain (Gelman et al. 2004). We ran three chains to monitor convergence based on variance components of multiple sequences using the potential scale reduction factor for each parameter, ‰ (Gelman et al. 2004). Convergence was also assessed by visual inspection and using diagnostics in the R contributed package, coda (Plummer et al. 2005).

Parameter estimates (means) and their 95% credibility intervals were obtained from each parameter's posterior distribution. Posterior distributions were generated from combining samples from multiple Markov chains after burn-in and thinning. Parameters (e.g. β_1 and β_2) were compared among habitats or habitat specialization groups using posterior means and 95% credibility intervals. The joint posterior distribution of model parameters and further details on Bayesian model fitting, prior distributions and convergence assessment are in Appendix S1.

Results

INTERSPECIFIC GROWTH-MORTALITY TRADE-OFF ON EACH HABITAT

The relationship between tree species' growth and mortality (Equation 1) was positive (Figure 2). Species with faster growth rates had higher mortality rates, providing evidence for a trade-off between a species' ability to grow quickly and its ability to maintain a low mortality rate. Most species' growth and mortality rates were concentrated in a narrow range at the low end of the spectrum of rates (Figure 2; Figure S1). On average, species' growth and mortality rates were lowest on sandy loam and higher on the three habitats with greater fertility and moisture (Table 1; Figure S1).

The slope of the interspecific growth-mortality relationship differed significantly among all pairs of habitats except between fine loam and clay (Table 1; Figure 2). The slope was steepest on the habitat with the lowest fertility and moisture (sandy loam) and decreased with increasing soil fertility and moisture. Hence, as species' growth rate increased, mortality rate increased fastest on sandy loam relative to the other three soil types (loam, fine loam and clay), and this rate of increase declined with increasing below-ground resources. On average, with an increase in growth rate of 1 mm year^{-1}, trees on sandy loam had a 1.63-2.46 times greater chance of dying than when growing on any of the three habitats richer in below-ground resources (Table 2). As a result, at the fastest growth rates, species' mortality is predicted on average to be the highest on the sandy loam, followed by loam soil, relative to what it would be on fine loam and clay at the same growth rate (Figure 2a). Conversely, for species with the slowest growth rates, their lowest average mortality rates occurred on sandy loam, followed by loam, with the highest mortality rates at low growth being on fine loam and clay (Figure 2b).

We assessed the variability among habitats of the interspecific growth-mortality relationship by calculating, for each growth rate in the observed range, the proportion of MCMC simulations for which each habitat

Table 3. Posterior mean parameter estimates ($\bar{x}$) and 95% credibility intervals (CI) for the relationship between tree species' growth rates on habitats with more available below-ground resources (loam, fine loam and clay) and mortality rates on edaphically poor habitat (sandy loam) in a Bornean rain forest for five habitat specialization groups. For each habitat specialist group, β and α are the slope and intercept, respectively, relating species' growth and mortality rates. Details of the model (Equation 2) and fitting are in the Methods and Appendix S1

	Habitat specialization group									
	Sandy loam		Loam		Fine loam		Clay		Generalist	
	α	β	α	β	α	β	α	β	α	β
Model: Growth on loam, mortality on sandy loam										
$\bar{x}$	0.81	-3.99	0.82	-3.66	0.80	-3.89	0.19	-3.77	1.28	-4.28
CI	0.66-0.96	-4.07-3.90	0.68-0.97	-3.81-3.52	0.62-0.98	-4.07-3.72	-0.86-1.16	-4.38-3.19	1.19-1.38	-4.41-4.16
Model: Growth on fine loam, mortality on sandy loam										
$\bar{x}$	0.70	-3.92	1.02	-3.96	0.46	-3.63	0.14	-3.69	0.74	-4.01
CI	0.53-0.86	-4.01-3.83	0.84-1.20	-4.16-3.77	0.37-0.55	-3.76-3.50	-0.74-0.90	-4.23-3.17	0.68-0.79	-4.12-3.91
Model: Growth on clay, mortality on sandy loam										
$\bar{x}$	-0.14	-3.59	1.35	-4.15	0.38	-3.64	0.08	-3.67	0.68	-4.02
CI	-0.37-0.09	-3.72-3.46	0.91-1.79	-4.50-3.82	0.27-0.49	-3.78-3.50	-0.85-0.88	-4.21-3.11	0.25-1.13	-4.33-3.72

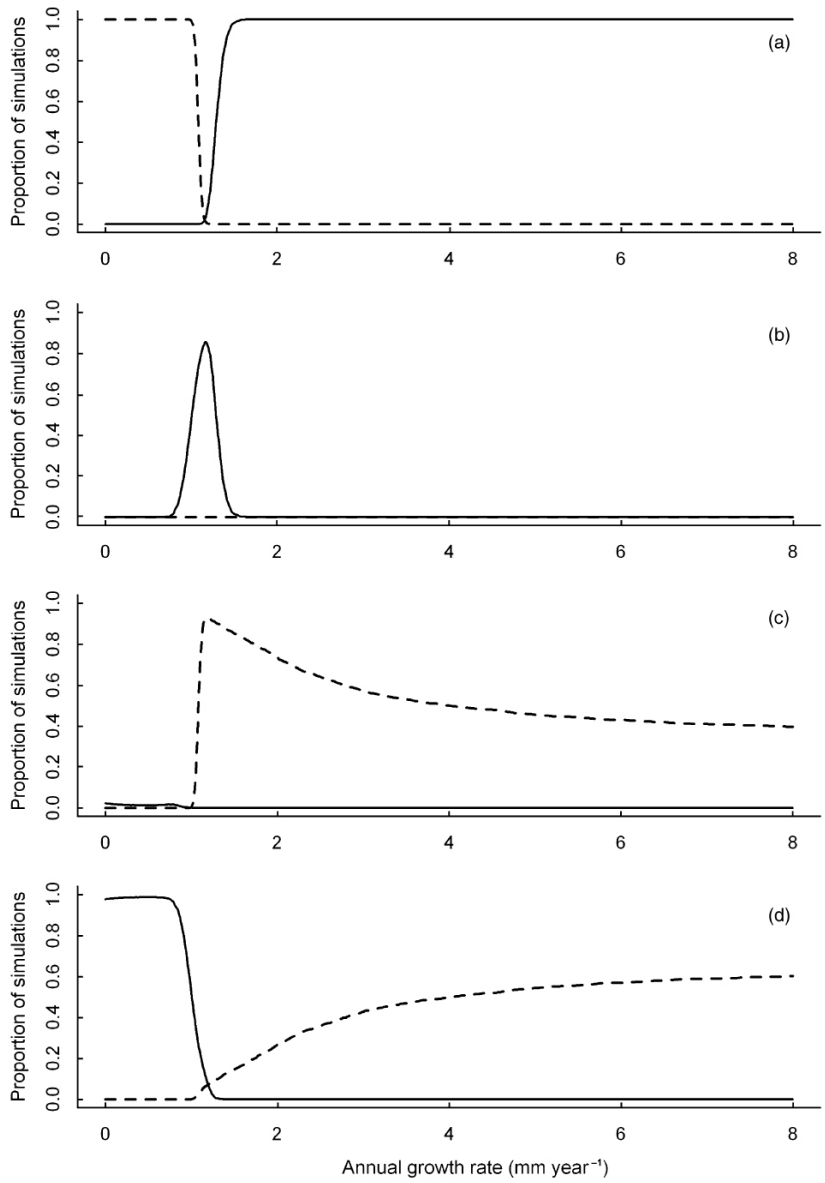

Figure 3. Proportions of Markov Chain Monte Carlo simulations with either the highest (solid line) or lowest (dashed line) predicted tree species mortality rate at a given species' growth rate for four habitats, (a) sandy loam, (b) loam, (c) fine loam and (d) clay, in Bornean rain forest.

had the highest or lowest mortality rate (Figure 3). Below a species growth rate of c. 1.0 mm year^{-1}, the lowest species mortality rates were found on sandy loam (the habitat with least below-ground resources; Figure 3a), whereas at these slow growth rates, the highest species mortality rates were found predominantly on clay (the habitat with greatest below-ground resources; Figure 3d). On the other hand, above a species growth rate of c. 1.8 mm year^{-1}, the highest species mortality rates always occurred on sandy loam (Figure 3a). Above c. 1.0 mm year^{-1}, the lowest mortality rates occurred in relatively similar proportions on the two habitats with greatest below-ground resources, the fine loam and clay (Figure 3c,d). The loam habitat never supported the lowest mortality rates, and only for a narrow window of relatively slow growth rates did it sometimes support the highest mortality rates (Figure 3b).

INTERSPECIFIC TRADE-OFFS BETWEEN GROWTH ON EDAPHICALLY RICH HABITATS VS. MORTALITY ON THE POOREST HABITAT

In each model relating species' growth rates on each of the three habitats richer in mineral nutrients and moisture (loam, fine loam and clay) to its mortality rate on the habitat lowest in below-ground resources (sandy loam), there was a positive relationship (Table 3), indicating that species trade off the ability to grow quickly on resource-rich soils vs. the ability to maintain a low mortality rate when below-ground resources are relatively scarce.

For growth on loam, habitat specialists did not differ dramatically in the strength of the growth-mortality relationship, although generalists had a significantly steeper slope. This may result from the fact that among the different habitats, sandy loam is most sim-

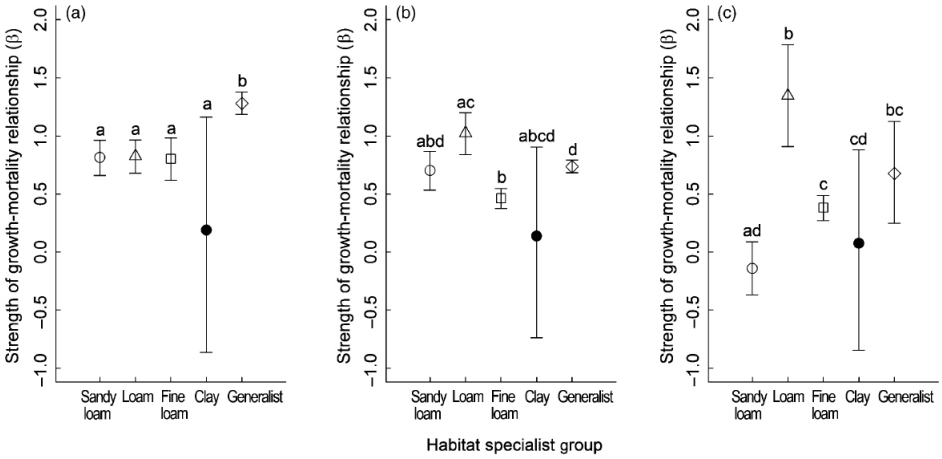

Figure 4. Posterior means and 95% credibility intervals for the slope parameter of each habitat specialist group (β_l in Equation 2) for the interspecific relationship between tree mortality probability on sandy loam soil and growth rate on (a) loam, (b) fine loam and (c) clay habitats in Bornean rain forest. Lower case letters indicate significant differences among habitat specialist groups, based on 95% credibility intervals. Symbols correspond to those in Figure 2. Parameter estimates are in Table 3.

ilar to loam in terms of texture, moisture and mineral nutrient concentrations (Lee et al. 2002; I.C. Baillie, personal communication). However, differences among the five groups of habitat specialists and generalists in the slope of the relationship between species growth on the edaphically richer habitats and mortality on the edaphically poorest habitat became more pronounced as below-ground resources increased (Figure 4). Because there were relatively few species with sufficient sample size on both clay and sandy loam to be included in this analysis, credibility intervals of the slope parameter for clay specialists are too wide to allow comparison. We will therefore focus on interpreting results for the other three habitat specialists and the generalists. For sandy loam specialists, the strength of the growth-mortality trade-off declined with increasing below-ground resources, so that increasing growth rates on clay resulted in no significant change in mortality probability (slope not different from zero; Figure 4). Hence, sandy loam specialists maintain low mortality rates even on edaphically rich sites. Similarly, for fine loam specialists and generalists, the strength of the growth-mortality relationship also declined with increasing below-ground resources, but this decline was less dramatic than for sandy loam specialists. In contrast, for loam specialists, the relationship steepened with increasing edaphic resources.

Discussion

Our results revealed a positive relationship between tree species' growth and mortality rates in this Bornean rain forest. This was the case when these demographic parameters were compared on the same habitat (Equation 1) and when growth on habitats with greater availability of below-ground resources was compared with mortality on a habitat with far lower below-ground resource availability (Equation 2). Our results support the hypothesis that species in this forest trade off the ability to be an effective exploitative competitor, that is, to grow quickly and thereby usurp relatively more available resources, with the ability to avoid mortality when resources are less plentiful (Grime 1979). Although this demographic trade-off is well-documented with respect to light, we show that it also shifts in steepness along gradients in soil resource availability and may provide a mechanism for the ecological sorting of species that is observed among soil-related habitats in this forest (Russo et al. 2005), corroborating studies in temperate forests (Schreeg et al. 2005; Kobe 2006). In addition to ecological sorting among habitats, this demographic trade-off may also have consequences for species coexistence on the same habitat. This would be true to the extent that it promotes the storage effect or produces non-linearities in species' responses to environmental variation at multiple spatial and temporal scales (Chesson 2000; Dalling & Burslem 2005). In addition, if it equalizes species' relative fitness, this demographic trade-off has the potential to reduce the magnitude of stabilizing coexistence mechanisms required for multispecies coexistence (Chesson 2000; Dalling & Burslem 2005).

DIFFERENCES AMONG HABITATS

The slope of the interspecific growth-mortality relationship was steepest on sandy loam and declined with increasing below-ground resource availability, suggesting that this trade-off is strongest on the habitat lowest in below-ground resources. At the fastest growth rates, tree species' mortality was higher on this habitat than at comparable growth rates on the three more edaphically rich habitats, which provides a possible mechanism by which fast-growing species may

be eliminated from the sandy loam habitat: adaptations for fast growth, such as leaves that are thin, short-lived, and low in mineral nutrients and defensive compounds, and wood that is low in density and high in hydraulic conductance, may entail a greater mortality risk on a soil with reduced below-ground resource availability relative to more resource-rich soils (Loehle 1988; Chapin et al. 1993; Poorter & Garnier 1999; Engelbrecht & Kursar 2003; King et al. 2006). Species with inherently fast growth rates may fail to maintain nutrient- or C-balance in low-resource habitats, particularly if there is greater allocation to traits promoting fast growth rather than to carbohydrate reserves (Kobe 1997; Canham et al. 1999; Pierce et al. 2005). Conversely, at the slowest species' growth rates, the highest species' mortality rates occurred on the habitats with greater resource availability, implying that slow-growing species may be at a competitive disadvantage in edaphically rich environments (Grime & Hunt 1975; Poorter & Garnier 1999; Schreeg et al. 2005). Thus, consistent with studies from temperate systems (Latham 1992; Lusk & Matus 2000; Cornwell et al. 2006), variation among soil-defined habitats in this demographic trade-off may be a possible mechanism for trait-based ecological sorting of species among edaphic environments.

DIFFERENCES AMONG HABITAT SPECIALIST GROUPS

The models comparing growth on habitats with greater below-ground resources with mortality on the most edaphically poor habitat demonstrated that this demographic relationship varies among habitat specialist groups. The differences among habitat specialist groups became more pronounced as the disparity in below-ground resource availability between the two habitats being compared increased. The divergent trade-off axes among groups are likely to reflect the different adaptive strategies of their constituent species, as well as those of the particular set of species that were sufficiently abundant on both soils to be included in the analyses.

We would expect the slope of the trade-off to become steeper as the disparity in below-ground resources between the habitats being compared increased. This was the case for loam specialists, for which the severity of this demographic trade-off tended to increase. This pattern may result from the fact that, among specialist groups, loam specialists have the greatest proportion of light-demanding, early successional species (Russo et al. 2005). On average for trees of all diameters across all habitats, loam specialists have the highest growth rates (Table 2 in Russo et al. 2005). They also have the highest growth rates on their home habitat (loam), which appears to have the greatest average insolation. Growth of loam specialists declines sharply on clay (Figure 4 in Russo et al. 2005), even though it has the highest below-ground resource availability, as it is the habitat on which understorey light levels appear lowest. Together, this variation produces the increase in the slope of the interspecific growth-mortality relationship with increasing edaphic resource availability of the growth environment that we found (Figure 4a vs. 3c). Hence, variation in light contributes to the demographic patterns of loam specialists.

Other specialist groups, however, responded differently. Specialists of sandy loam maintained low mortality rates despite increasing edaphic resources, such that for the comparison with growth on clay, there was no significant trade-off relationship with mortality on sandy loam. This result is consistent with the hypothesis that these species have conservative demographic strategies that are less responsive to increases in below-ground resources. The severity of the growth-mortality trade-off for specialists of fine loam and generalists tended to decrease slightly with increasing edaphic resources. Nonetheless, these two groups still showed evidence of a significant fast growth-low mortality trade-off.

THE ROLE OF MULTIPLE SOURCES OF ENVIRONMENTAL VARIATION

We have focused on the effects of edaphic resource availability on this interspecific demographic trade-off, because soil-related variation is an important basis from which light and disturbance also vary among these habitats at Lambir (see 'Study site'). Furthermore, in many tropical forests, tree species show strong associations with soil nutrient distributions (John et al. 2007) and moisture (Engelbrecht & Kursar 2003), and nutrient limitation appears to have been an important selection pressure on plant stress responses (Chapin et al. 1993; Pierce et al. 2005). Nonetheless, the variation among habitats that we found in this trade-off is likely to be an emergent property resulting from covarying functional traits influencing plant performance in an environment that is heterogeneous in many characteristics. As noted above, visual impressions indicate that understorey light levels reach their lowest on clay and fine loam, are moderate on sandy loam, and are highest on loam (see 'Study site'). Covariation between above- and below-ground resources is likely to influence the variation in this trade-off among habitats that we observed, and this was particularly clear for loam specialists. Because the gradient in understorey light levels at Lambir does not appear to correspond directly with that of below-ground resources, it is unlikely that the variation we observed among soil types in the fast growth-low mortality trade-off can be explained by light alone. For example, contrasting responses of

seedlings of clay specialists vs. sandy loam specialists to reciprocal transplantation at Lambir suggested a trade-off between traits related to efficient resource capture (high relative growth rate, specific leaf area, leaf area ratio, and plasticity) vs. survival (Palmiotto et al. 2004), results that are corroborated on a similar edaphic gradient in Sabah, Malaysian Borneo (Baltzer et al. 2005). In both studies, differences between edaphic specialists became more pronounced in high light.

While adaptations for fast growth can provide a competitive advantage by way of rapid exploitation of resources when they are relatively abundant, an inability to acclimate to reduced resource availability could increase mortality risk. For example, higher hydraulic conductance and lower leaf water potential during dry periods may limit tree species to moister soils (Gibbons & Newbery 2003; Santiago et al. 2004) and elevate mortality on well-drained soils (Nakagawa 2000; Engelbrecht & Kursar 2003; Potts 2003). In addition, woody plant species associated with fertile soils often have higher leaf photosynthetic rates (Wright et al. 2001; Baltzer et al. 2005), which would result in greater potential C-gain and faster growth (Poorter & Garnier 1999), but the associated elevated respiration rates could increase mortality risk when soil resources are lacking. Plant traits are likely to be under countervailing selection pressures to maximize growth capacity while minimizing respiratory and other losses. Many plant traits show coordinated variation (Reich et al. 2003), but multiple trait strategies almost certainly lead to similar demographic outcomes in an environment, particularly viewed from a whole-plant perspective (Marks & Lechowicz 2006).

It is an open question whether ecological sorting based on functional trait variation is strongest as a result of relatively small differences in performance that are iterated over the long time periods for adult tree recruitment or as a result of catastrophic performance failures due to, for example, climatic extremes. Although there was a clear positive relationship between species' growth and mortality rates at Lambir, many species were clustered at the lower end of the range of demographic rates, as observed in other species-rich tropical forests (Hubbell 2001; Condit et al. 2006). This probably reflects the dominance of shaded nutrient-poor soil environments in tropical forests. In addition, within-species variation in demographic rates is often high among tree species (Clark et al. 2003). Hence, the time scales necessary for ecological sorting to produce the habitat-specialization patterns at Lambir may be quite long. However, catastrophic events are also likely to play an important role. At Lambir, El Niño drought increases mortality rates dramatically, most strongly on sandstone-derived soils (Nakagawa 2000; Potts 2003). Furthermore, a detailed demographic analysis of *Scaphium borneense* at Lambir (Sterculiaceae; Yamada et al. 2007) found that demographic differences among habitats were less important for population growth than were differences due to census period. They concluded that an El Niño extreme dry period favoured the drought-tolerant *S. borneense*, particularly in habitats with the lowest soil water availability (the sandstone-derived soils). Even more frequent, but moderate, droughts could select for drought tolerance (Engelbrecht et al. 2006). Because the Lambir 1992-97 census did not span a severe drought, our present analyses are unable to detect the effects of catastrophic drought, but future models will account for this possibility.

THE ROLE OF SEED DISPERSAL

Alternatively, edaphic specialization may be maintained by chance establishment on a particular habitat, followed by strong seed dispersal limitation restricting a tree population to that habitat over long time periods (Shmida & Wilson 1985; Cottenie 2005). Dispersal limitation may therefore predispose species to evolve habitat specialization or may generate 'apparent' habitat specialization through mass-effects. In an analysis of 196 species representing 11 genera at Lambir, Potts (2001) found evidence that more dispersal-limited species had greater associations with particular habitats than did better-dispersed species. However, this result was not strong, and for genera with species specialized to at least two habitats, there was no clear relationship between habitat association and dispersal mode. On the other hand, in a comparative phylogenetic analysis of 308 species (119 genera) at Lambir, Russo et al. (2007) found no association between habitat specialization, dispersal mode or seed size. Whether ecological sorting mediated by performance trade-offs is more important than dispersal-related mass-effects in determining the spatial and demographic structure of ecological communities remains an open question.

Conclusions

Here, we have demonstrated that the strength of a trade-off between tree species' growth and mortality rates varies with respect to below-ground resources in a Bornean rain forest. Light-based demographic trade-offs are commonly considered a dominant determinant of forest community structure. Our findings suggest that demographic trade-offs may also arise along edaphic gradients and that they may contribute to species sorting among soil-related habitats. An important next step is to incorporate into our models species' responses to both above- and below-ground resource availability to identify how they jointly affect demographic trade-offs, and ultimately, species distributions and diversity.

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Supplementary material

The following supplementary material is available for this article:

Appendix S1 Details of model fitting.

Figure S1 Distributions of tree species' mean annual growth rates and annual mortality probabilities on four habitat types in a Bornean rain forest.

This material is available as a part of the online article from the University of Nebraska-Lincoln Digital Commons as well as: http://www.blackwell-synergy.com/doi/abs/10.1111/j.1365-2745.2007.01330.x