

Strong habitat preference of a tropical rain forest tree does not imply large differences in population dynamics across habitats

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Summary

1 Many tropical forest tree species show habitat preference, commonly revealed by differences in abundance among habitats. Very little is known about differences in individual performance and population dynamics across habitats.

2 We analysed habitat-specific performance and demography of *Scaphium borneense*, a tropical rain forest tree with strong habitat preference in a 52-ha plot at Lambir Hills, Malaysia. This species occurs at high densities on ridges with sandy soils ('preferred habitat'), at low densities in valleys on loamy soils ('non-preferred habitat') and at intermediate densities on slopes. We used 10-year demographic data to compare tree performance across habitats and constructed population matrix models to analyse population dynamics.

3 Tree performance was rather similar across habitats. Some vital rates (mortality) did not differ among habitats, while others were modestly (juvenile tree growth) to substantially higher (recruitment) in the non-preferred valley habitat, probably due to higher canopy openness.

4 Matrix models projected population sizes to remain stable in all habitats, thus maintaining abundance differences across habitats. This suggests that habitat preference of *Scaphium* is generated by (a)biotic differences among habitats and not by chance processes or disturbance history.

5 Population dynamics were also very similar among habitats. The distribution of elasticity values over categories and vital rates was almost equal for the three habitats. Life table response experiment (LTRE) analysis showed that habitat differences in vital rates had little effect on λ . Thus, *Scaphium* populations in the three habitats are maintained in a very similar way, despite differences in (a)biotic conditions and abundance.

6 We hypothesize that habitat preference of *Scaphium* is maintained because of a better performance in its preferred habitat relative to other species in that habitat, while the reverse may be true in non-preferred habitats. We suggest that such differences in performance may become apparent during periods of drought, creating windows of opportunity for maintaining density differences.

7 Strong habitat preference of rain forest tree species does not necessarily imply strong differences in tree performance, demography or population growth across habitats. The mechanisms that generate density differences across habitats remain to be unravelled.

Key-words: elasticity, habitat preference, life table response experiments, niche differentiation, population dynamics, population growth rate, matrix analysis, *Scaphium borneense*, tropical rain forest

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Introduction

Niche differentiation is commonly proposed to explain coexistence of species in diverse plant communities (Silvertown 2004). According to this hypothesis, plant species that are specialized for certain sets of environmental conditions can coexist because each is a slightly better competitor in its own niche, provided that there is sufficient environmental variation (in time and space). Tropical rain forests are particularly rich in species, and niche differentiation with respect to light availability, soil fertility and water availability has been put forward to explain their diversity. If niche differentiation occurs, species are expected to occur at higher density in areas with environmental conditions for which they are best adapted, while their density will be lower in 'niche margins', and may reach zero if conditions are (strongly) unfavourable. In tropical forests, numerous studies have reported density-differences for tree species across environmental gradients, e.g. with respect to understorey light conditions (Clark & Clark 1992; Poorter & Arets 2003; Yamada *et al.* 2006a), topography (Bunyavejchewin *et al.* 2003; Sri-Ngernyung *et al.* 2003; Yamada *et al.* 2006c), edaphic conditions (Baillie *et al.* 1987; Phillips *et al.* 2003; Palmiotto *et al.* 2004; Paoli *et al.* 2006) or their combination (Davies *et al.* 1998; Svenning 1999; Webb & Peart 2000; Harms *et al.* 2001; Itoh *et al.* 2003a). In some forest areas, a large share of the tree species exhibit density differences across habitats, e.g. in Lambir Hills National Park, Malaysia, 73% of 764 tree species were either positively or negatively associated with edaphic conditions (Davies *et al.* 2005). While the occurrence of niche differentiation implies that species show density variation along environmental gradients, not all density differences are necessarily the result of niche differentiation. Such variation can also

be generated by historical patterns of dispersal, colonization or disturbance history (Hubbell & Foster 1986; Harms *et al.* 2001; Baker *et al.* 2005).

Understanding how density differences between habitats are generated and maintained requires information on population dynamics in those habitats. Demographic comparisons across habitats have been made for plants in rather distinct habitats in temperate grasslands (e.g. Jongejans & de Kroon 2005; Angert 2006) and in successional stages of tropical forests (e.g. Alvarez-Buylla 1994; Horvitz & Schemske 1995; Martinez-Ramos & Samper 1998; Svenning 2002). However, such evaluations are lacking for the large group of non-pioneer canopy tree species in tropical forests that exhibit habitat preference with respect to topography or soil conditions.

Here we report on habitat-related variation in tree performance and demography of *Scaphium borneense* (Merr.) Kosterm., a non-pioneer canopy tree species in a Bornean tropical rain forest. Our study species is abundant in Lambir Hills National Park, Malaysia, and is strongly and positively associated with ridges on sandy soils, 'ridge habitat', negatively associated with valleys on loamy soils, 'valley habitat', and not with slopes, 'slope habitat' (Fig. 1; Yamada *et al.* 2006c). On ridges, *Scaphium* tree abundance (≥ 1 cm d.b.h., diameter at breast height) is almost 9 times higher than in the valley and 2.5 times higher than on slopes.

For a species with strong habitat preference, one would expect among-habitat differences in vital rates (growth, survival and recruitment) as a response to variation in abiotic conditions, forest structure and forest composition (Yamada *et al.* 2006c). Such differences may then generate variation in population dynamics among habitats. Using matrix models to analyse population dynamics, differences in dynamics across

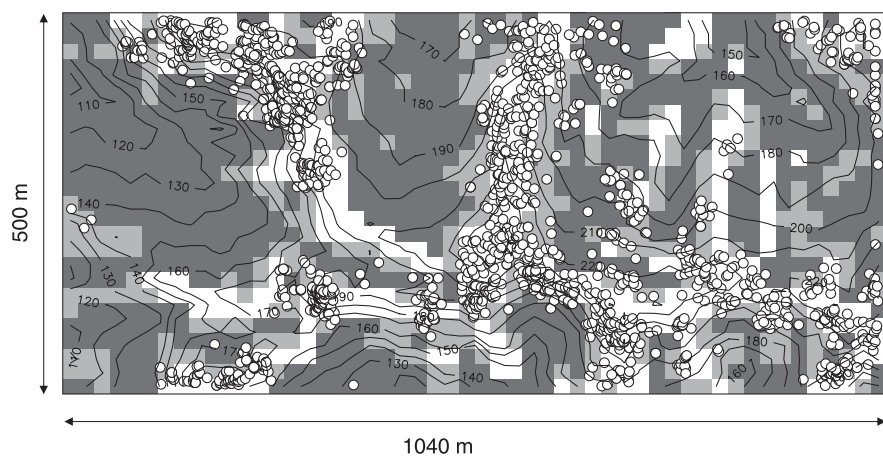


Fig. 1 Spatial distribution of *Scaphium borneense* and habitats in a 52-ha plot in Lambir Hills National Park. Each of the 1300, 20 × 20 m subquadrats of the plot were assigned to one of eight habitats by the combination of edaphic and topographic features and the association of *Scaphium borneense* with these habitats was analysed by using a torus-translation test. Dark, light grey and white squares show habitats with which *S. borneense* is negatively, neutrally and positively associated, which are termed 'valley habitat', 'slope habitat' and 'ridge habitat', respectively (Yamada *et al.* 2006c). Points show the position of all *S. borneense* trees of ≥ 1 cm d.b.h. in 1997. Isoclines are drawn for every 10 m in elevation above sea level.

habitats can be interpreted with LTRE analysis (life table response experiment, e.g. Angert 2006).

We address the following questions. (i) Do vital rates (survival, growth and recruitment) differ among habitats? (ii) Do population growth rates differ among habitats? (iii) Do population dynamics differ among habitats? To answer these questions, we used 10-year demographic data from a population of > 1200 trees in the Lambir Hills forest dynamics plot. Using these data we constructed habitat-specific population matrix models, calculated population growth rates and used prospective (elasticity) and retrospective (life table response experiments, LTRE) analyses to compare population dynamics across habitats.

Methods

STUDY SITE AND SPECIES

We performed our study in an equatorial rain forest in Lambir Hills National Park, East Malaysia (3°12' N, 114°00' E). Lambir Hills National Park is covered by about 7000 ha of primary dipterocarp forest. Annual rainfall averages around 3200 mm. The climate is largely aseasonal, but occasionally there are dry periods, e.g. in early 1998 when a very severe drought occurred (Potts 2003). Details of the climate, soils and vegetation are provided by Watson (1985).

Within the Lambir park, a 52-ha study plot has been established to monitor all trees ≥ 1 cm in d.b.h. (diameter at breast height, or 130 cm from the ground). The 52-ha plot was divided into 1300, 20 \times 20 m subquadrats. All trees ≥ 1 cm in d.b.h. were tagged, mapped, identified and their d.b.h. was measured to the nearest 1 mm in 1992. In 1997 and 2002, all trees inventoried in previous censuses were re-measured and newly recruited trees ≥ 1 cm in d.b.h. were censused.

The 52-ha plot is topographically (Yamakura *et al.* 1995), as well as edaphically (Palmiotto *et al.* 2004) heterogeneous and the spatial distribution of many woody species follows this variation (Davies *et al.* 1998; Itoh *et al.* 2003a). For example, Yamada *et al.* (2006c) divided the 1300 20-m by 20-m subquadrats into eight habitats by the combination of edaphic and topographic features and analysed the species–habitat associations of 10 Sterculiaceae species. Eight of these 10 species had statistically significant habitat associations. In the present study, we selected *Scaphium borneense*, a canopy species. This species was negatively associated with the valley habitat that is located on finer textural soils of high fertility, while the ridge habitat to which the species was positively associated is on coarse textured soils with low nutrient levels. The water-holding capacity of finer textural soils is probably larger than in coarse-textured soils. Finally, the topography of the ridge habitat leads to stronger soil water run-off and thus lower water availability, particularly during periods of water deficit. In the valley, water logging may lead to anoxic conditions for young roots during wet periods.

FOREST PHYSIOGNOMY

We calculated basal area (BA) and community-level tree density for each of 1300 subquadrats using census data from 1992 and 1997. To characterize the light climate of subquadrats, we calculated canopy closure index ($CCI_{community}$) (Lieberman *et al.* 1995) at four corners of subquadrats at a height of 1.99 m, which corresponds to the average height of *Scaphium borneense* at 1 cm d.b.h. The $CCI_{community}$ provides an estimate of the light climate based on the density and height of neighbouring trees within 10 m distance (Lieberman *et al.* 1995). Tree height was estimated using the community-wide allometry equation of Yamakura *et al.* (1996). For the calculation of $CCI_{community}$, only trees standing erectly with sound appearance were included. We excluded subquadrats along the border of the 52-ha plot.

VITAL RATES OF *SCAPHIUM BORNEENSE*

Growth, mortality and fecundity of *Scaphium borneense* were estimated based on the 1992, 1997 and 2002 census data of the 52-ha plot. Annual mortality rate was calculated for three size categories of small (d.b.h. < 5 cm), medium (5 cm \leq d.b.h. < 20 cm) and large (d.b.h. \geq 20 cm) following Sheil *et al.* (1995). These size categories were chosen to obtain an even distribution of sample sizes.

Annual d.b.h. growth was determined for all trees as the slope of a linear regression of d.b.h. against time and was averaged per size category. Period and habitat effects on d.b.h. growth were then analysed using a two-way ANOVA. We did not apply repeated measure ANOVA as trees that recruited or died would have been excluded, leading to bias in average growth.

To characterize light climate of each *Scaphium borneense* tree, the $CCI_{Scaphium}$ was calculated based on the 1992 and 1997 censuses. We estimated the *Scaphium borneense* height from d.b.h. following Yamada *et al.* (2006b). Again, trees within 10 m distance from the 52-ha plot margin were excluded.

POPULATION DYNAMICS OF *SCAPHIUM BORNEENSE*

Parameterization of matrix models

Size-classified projection matrices were used to project the size and structure of populations in time (Caswell 2001). We divided the population into nine d.b.h. categories of 5-cm width, except for the first category (1–5 cm d.b.h.). Matrix models have the basic form $n(t+1) = An(t)$, where A is a square matrix with transitions among size classes during 1 year, and n is the population vector containing densities of individuals in size classes. The dominant eigenvalue (λ) of matrix A is equivalent to the population growth rate. The stable population structure is the right eigenvector. We measured the distance between the stable population structure generated by the matrix and observed size structure by

Keyfitz's Δ (Caswell 2001). Six matrices were constructed for each combination of habitat and period.

In our size-classified matrix model, elements a_{ij} (with i denoting row number and j column number) of transition matrix A can be grouped into those representing stasis (P_j , the probability of surviving and remaining in size-class j over the time interval), progression (G_{ij} , the probability of surviving and growing from size-class j to i , $i = j + 1$), and fecundity (F_j , the number of sexual offspring produced by an individual in stage j). Matrix elements were built from underlying vital rates, which are survival (σ), growth (γ) and reproduction output (f), to which they are related by $P_j = \sigma_j \times (1 - \gamma_j/c_j)$, $G_{ij} = \sigma_j \times \gamma_j/c_j$ (of which c_j is category width), and $F_j = \sigma_j \times f_j$. The reproductive output (f_j) at a habitat was calculated as the quotient of abundance of newly recruited trees and the abundance of adult trees, both within the habitat. We assumed that reproduction starts when trees reach the canopy, at 20 cm d.b.h., and that the proportion of reproductive individuals increases linearly with tree height, and reaches 100% when trees attain the canopy at 37.5 cm d.b.h. (30 m height).

We first tested the difference in vital rates among habitats as well as between census periods. When no significant difference was found, variation between habitat and census period was ignored and the average of habitats or census periods was used to parameterize matrices. If case vital rates differed significantly among census periods or habitats, period- or habitat-specific values were used in the matrices.

Matrix analyses

We calculated the dominant eigenvalue (λ) of all six matrices and estimated the 95% confidential limit of λ using the series approximation approach (Caswell 2001). This method calculates the variance of λ by summing over all categories and vital rates, the product of variation in a vital rate and the squared sensitivity of that vital rate (see p. 218 in Caswell 2001; Zuidema & Franco 2001). As we lacked information on variation in fecundity, this variation was not included in the calculation, thus leading to a slight underestimation of the confidence interval.

To detect differences in population dynamics among habitats, we conducted elasticity analyses and life table response experiments (LTRE). Elasticity analysis considers the impact of a proportional change in a matrix element on proportional change in λ (de Kroon *et al.* 1986). This can also be calculated for vital rates by multiplying vital rate sensitivity (see p. 218 in Caswell 2001; Zuidema & Franco 2001) by x/λ , where x is the value of the vital rate under consideration. Note that unlike matrix element elasticities, vital rate elasticities do not sum to 1. Analysis of life table response experiments (Caswell 2001) quantifies the contribution of vital rates to the observed difference in population growth rate (λ) among habitats or between periods. In addition, in the case where differences in λ are very small or zero, LTRE

analysis may still reveal to what extent dynamics are different as in this case a positive contribution of one vital rate (e.g. due to higher growth in one habitat) may be outweighed by negative contributions of other vital rates (e.g. due to lower fecundity).

We applied a fixed-design LTRE as this allowed us to quantify the effects of habitat and period (Jongejans & de Kroon 2005). The LTRE model with two factors of habitat and period is:

$$\lambda^{(nm)} = \lambda^{(-)} + \alpha^{(m)} + \beta^{(n)} + (\alpha\beta)^{(nm)}$$

in which a given λ for habitat m and period n , $\lambda^{(nm)}$, is written as the sum of the dominant eigenvalue of the mean of all matrices, $\lambda^{(-)}$, the main effect of habitat m , $\alpha^{(m)}$, the main effect of period n , $\beta^{(n)}$, and the residual interaction effect $(\alpha\beta)^{(nm)}$ (Caswell 2001). In order to show the magnitude and direction (positive or negative) of the contributions of each vital rate, these effects were decomposed into contributions per vital rate, only for the main effects (Caswell 2001):

$$\alpha^{(m)} = \sum (x_j^{(m)} - x_j^{(-)}) \partial \lambda / \partial x_j |_{1/2(A^{(m)} + A^{(-)})}$$

$$\beta^{(n)} = \sum (x_j^{(n)} - x_j^{(-)}) \partial \lambda / \partial x_j |_{1/2(A^{(n)} + A^{(-)})}$$

in which differences between the value of a vital rate $x_j^{(m)}$ of the mean-habitat matrix $A^{(m)}$ or $x_j^{(n)}$ of the mean-period matrix $A^{(n)}$ and the overall mean vital rate $x_j^{(-)}$ of matrix $A^{(-)}$ are multiplied by the sensitivity of that vital rate calculated for a matrix midway between the matrix of interest and the overall mean matrix.

The results of our LTRE analysis only contain the contributions for those vital rates that were significantly different among habitats or periods. By testing for differences in vital rates between habitats and periods before constructing the transition matrices, we prevented LTRE contributions being caused by statistically non-significant differences in vital rates. This is relevant, as such small differences in vital rates with a high sensitivity may lead to a high LTRE contribution, thus obscuring the interpretation of LTRE analysis results.

Results

FOREST PHYSIOGNOMY

We found significant differences in basal area (BA), community-level tree density and canopy closure index ($CCI_{community}$) among habitats (ANOVA, $P < 0.05$). The ridge habitat had largest BA (mean \pm standard error = 53.4 ± 0.94 m² ha⁻¹ in 1992), community-level tree density (293.6 ± 3.70 per 400 m²) and $CCI_{community}$ (78.7 ± 0.93 , i.e. the most shaded light climate), whereas valley habitat had smallest BA (37.3 ± 0.66), community-level tree density (259.8 ± 2.60) and $CCI_{community}$ (62.0 ± 0.65). Values for the slope habitat were intermediate: BA (43.0 ± 0.93), community-level tree density (291.1 ± 3.64 in 1992) and $CCI_{community}$ (74.0 ± 0.90). Note that the 10% higher community-level tree density in the

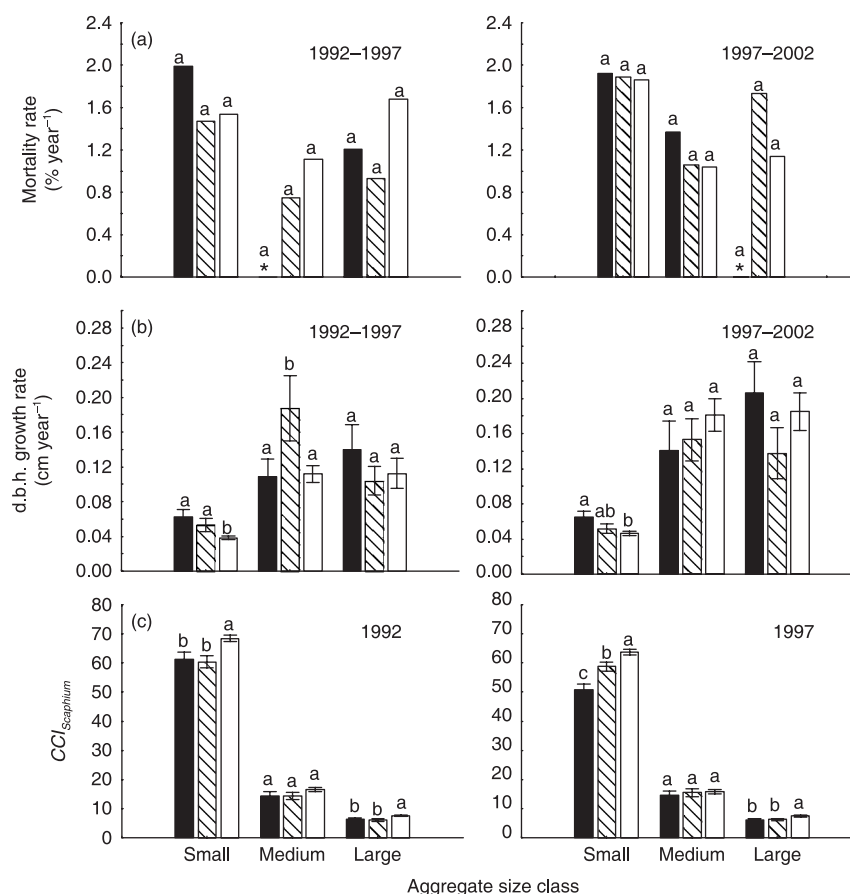


Fig. 2 Mortality rate (% year⁻¹) (a), d.b.h. growth rate (cm year⁻¹) (b) and canopy closure index, CCI_{Scaphium} (c) of *Scaphium borneense* in three aggregate size classes of small (d.b.h. < 5 cm), medium (d.b.h. 5–20 cm), and large (d.b.h. ≥ 20 cm) in valley (solid bars), slope (hatched bars), and ridge (open bars) habitats. Mean and SE (error bars) are shown. Different letters above the bars indicate significant differences among habitats but within size class (*G*-test for mortality rates and Fisher's LSD tests for d.b.h. growth rate and canopy closure index, *P* < 0.05). *No mortality observed.

ridge habitat was small compared with the nine-fold higher density of *S. borneense* in that habitat (Table 1). Differences for 1997 were similar.

VITAL RATES

The mortality rates for all aggregate size categories, habitats and census periods were highly similar (Fig. 2a) and we did not find significant differences among aggregate size categories, habitats or periods (*G*-test, *P* = 0.22). Still, mortality rate of small trees (< 5 cm d.b.h.) tended to be higher than that of larger trees in almost

all habitat and period combinations (Fig. 2a), in accordance with observations from this plot (Potts 2003) and long-term studies in other plots (e.g. Condit *et al.* 1995). Our limited sample size probably precluded finding statistical differences, but as we expect size-dependent survival in *S. borneense* to be similar to that found in overall community level, we parameterized our matrix models using a slightly lower annual survival rate for trees < 5 cm d.b.h. (0.982) than for the rest (0.990).

Two-way ANOVAS of d.b.h. growth showed significant effects for habitat, period and their interaction, for each of the three aggregate size categories (Table 2). Significant differences were found for small trees in 1992–97 (ridge < valley and slope) and in 1997–2002 (ridge < valley), and for medium-sized trees in 1992–97 (slope < ridge and valley, Fisher's LSD test; Fig. 2b). Diameter at breast height growth was faster in 1997–2002 than in 1992–97. Significant differences among all size categories were found in the ridge habitat.

Canopy closure index (CCI_{Scaphium}) was significantly influenced by habitat, period and their interaction (Table 2). Post-hoc tests (Fisher's LSD, Fig. 2c) revealed that light levels for small and large trees were generally lower in ridge habitat compared with the other two habitats.

Table 1 Observed changes in *Scaphium borneense* populations (individuals ≥ 1 cm d.b.h.) in three habitats over 10 years in a 52-ha plot in the Lambir Hills National Park

Habitat	Valley	Slope	Ridge	Total
Area (ha)	26.16	13.12	12.72	52.00
Abundance in 1992	176	301	757	1234
Density in 1992 (ha ⁻¹)	6.73	22.94	59.51	23.73
Mortality in 1992–97	14	19	54	87
Mortality in 1997–2002	13	23	55	91
Recruits in 1992–97	35	47	137	219
Recruits in 1997–2002	46	77	151	274

Table 2 Results of two-way ANOVAS of d.b.h. growth rate and canopy closure index, of which factors are habitat and census-period for three size categories of small (d.b.h. < 5 cm), medium (d.b.h. 5–20 cm) and large (d.b.h. ≥ 20 cm) of *Scaphium borneense*

Effect	d.f.	Dbh growth rate			Canopy closure index (CCI)		
		Small <i>F</i>	Medium <i>F</i>	Large <i>F</i>	Small <i>F</i>	Medium <i>F</i>	Large <i>F</i>
Habitat	1	11.6***	1	1.11	20.5***	1.6	8.5***
Census period	2	0.5	1	5.2*	14.4***	0	0
Census period × habitat	2	0.8	3*	0.28	2.35	0.6	0.1

Significance is denoted by asterisks, * $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$.

Tree recruitment (the number of newly recruited trees of > 1 cm d.b.h. per adult tree) was similar among habitats in 1992–97, but differed for 1997–2002. In 1992–97, 0.89, 0.80 and 0.65 new trees appeared per adult tree, in the valley, slope and ridge habitats, respectively (G -test, $P = 0.69$). In 1997–2002, these values were higher for the valley (1.17) and slope (1.32) habitat than for the ridge habitat (0.72, $P < 0.0001$). Overall, recruitment was significantly higher in the second census period ($P < 0.05$).

MATRIX ANALYSES

Our six transition matrices (Appendix 1) differed with respect to growth rate (both among habitats and periods) and recruitment rate (idem), but not with respect to survival (as no significant difference was found among habitats or periods). The stable size distributions resembled the observed size structure well, particularly in the ridge habitat. The minimum, maximum and average (\pm SD) Keyfitz's Δ were 0.046, 0.229, 0.124 (± 0.070), respectively, indicating that differences were small.

Population growth rates (λ) were slightly above unity for all six combinations of habitat and census period and hardly differed among habitats or periods. The 95% confidence interval of λ included the value of 1 in all cases (Fig. 3), suggesting that asymptotic population growth rates are not different from 1 and population sizes are maintained over time. The 95% confidence intervals also overlapped with each other, showing that population growth rates are not different among habitats or periods.

Differences in population dynamics among habitats and periods were assessed in two ways: by elasticity analysis and LTRE analysis. Elasticity analysis showed that survival had the largest influence on population growth rates, for all combinations of habitat and census period, while growth and fecundity had much lower importance (Fig. 4). The distribution of elasticity values over vital rates was very similar among habitats and between periods. Likewise, the size-dependent pattern of elasticities also showed strong resemblance among habitats and periods.

The results of the analysis of life table response experiments (LTRE) for two-way (habitat and period) decomposition of the variation in λ closely approached the differences in λ among the six matrix models: on average the observed change in λ differed by only

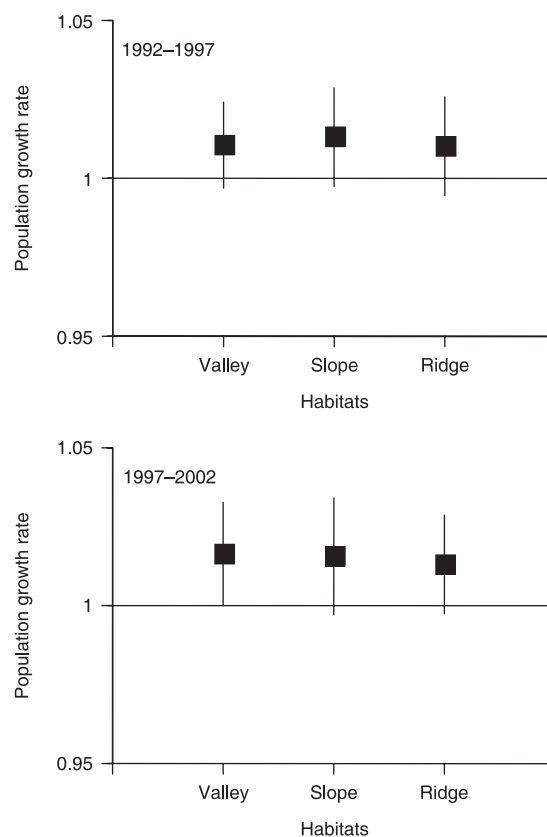


Fig. 3 Projection population growth rates (λ) of *Scaphium borneense* in valley, slope and ridge habitats in a 52-ha plot in Lambir Hills National Park. The vertical bars show 95% confidence intervals of λ .

0.87% from the summed LTRE contributions. This indicates that LTRE contributions provided a very accurate estimate of the effects on λ (Caswell 2001).

The LTRE analysis revealed that habitat and census period had small effects on λ , with an absolute maximum contribution of just 0.002 to the value of λ . The habitat and period effects were sometimes of different sign, indicating that certain periods or habitats would increase λ , while others decrease λ (Table 3). On average, the absolute period effect was somewhat larger than the habitat effect. Thus, the variation in population dynamics among periods was more important in determining the value of λ than the variation among habitats. The interaction effects of habitat and period were smaller than the main effects but were still relatively

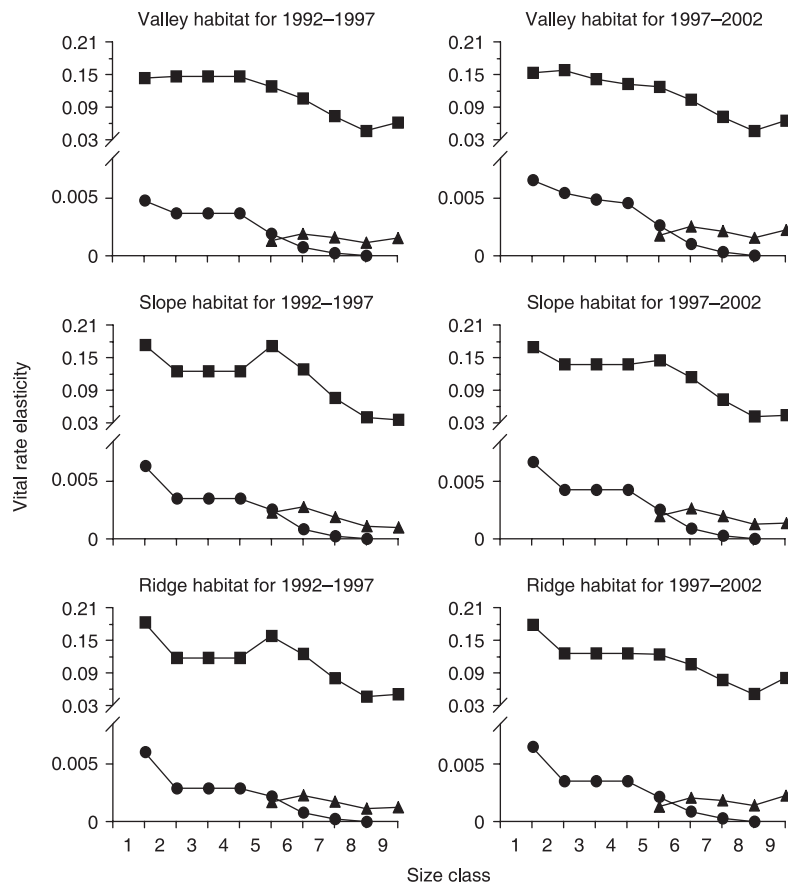


Fig. 4 Vital rate elasticity values for population projection matrices of *Scaphium borneense* in different habitats and periods in a 52-ha plot in Lambir Hills National Park. Shown are elasticity values for survival (squares), growth (circles) and fecundity (triangles). a, valley habitat for 1992–97; b, valley habitat for 1997–2002; c, slope habitat for 1992–97; d, slope habitat for 1997–2002; e, ridge habitat for 1992–97; f, ridge habitat for 1997–2002. Size classes are 5-cm d.b.h. categories (1–4 cm d.b.h., 5–10 cm d.b.h., etc.).

Table 3 Magnitude of the different effects in decomposition analysis (LTRE) of variation in population growth rate. The mean and standard deviation (SD) of the absolute values of all levels within a LTRE effect are also given

LTRE effect (×1000)	
Habitat	
Valley	−0.260
Slope	0.946
Ridge	−2.033
Mean ± SD of α^m	1.080 ± 0.894
Census-period	
1992–1997	−1.920
1997–2002	1.690
Mean ± SD of β^n	1.805 ± 0.162
Interaction between habitat and census period	
Valley 1992–97	−1.025
Valley 1997–2002	1.175
Slope 1992–97	0.315
Slope 1997–2002	−0.802
Ridge 1992–97	0.402
Ridge 1997–2002	−0.403
Mean ± SD of $\alpha\beta^{nm}$	0.687 ± 0.365

habitats were very small, with the maximum absolute contribution of a vital rate to λ amounting to just 0.0011 (Fig. 5). In the slope habitat, which had a positive habitat effect (Table 3), the contributions of almost all vital rates were positive, due to moderately higher values for the vital rates compared with the across-habitat average. For the other two habitats, contributions of vital rates were stronger, but also often differed in sign. For example, in the ridge habitat, the negative contributions of fecundity and growth of small trees (category 1; 1–5 cm d.b.h.) are partially offset by positive contributions of growth of larger trees (categories 2–4; 5–20 cm d.b.h.), resulting in a negative habitat effect. The opposite pattern of vital rate contributions was observed for the valley habitat: here, the negative contributions of growth in categories 2–4 were almost offset by positive contributions of fecundity and growth of category 1, still causing a slightly negative habitat effect.

Discussion

VITAL RATE DIFFERENCES AMONG HABITATS
Differences in soil, topography and understorey light among habitats have probably generated variation in

large, suggesting that the main period effect was not similar for all habitats, and vice versa.
When looking in more detail at the LTRE habitat effects, we can see that demographic differences among

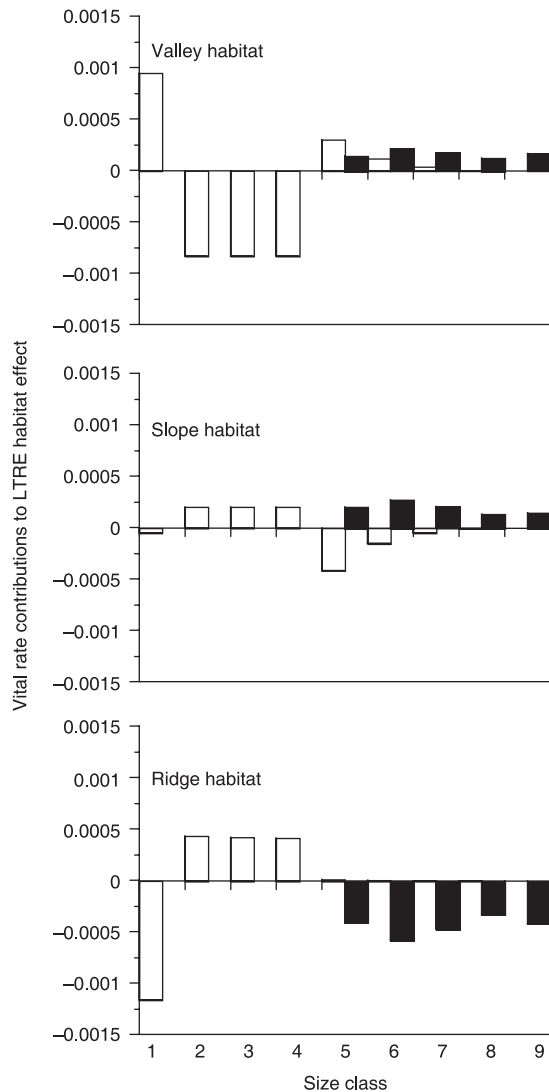


Fig. 5 Habitat effects in the decomposition of variation (LTRE) in population growth rate (λ) in *Scaphium borneense* in a 52-ha plot in Lambir Hills National Park. Shown are vital rate contributions for growth (open bars) and fecundity (solid bars). Size classes are 5-cm d.b.h. categories (1–4 cm d.b.h., 5–10 cm d.b.h., etc.).

diameter growth for *S. borneense*. Our data show that diameter growth of small trees was faster in the valley habitat, which can probably be explained by higher understorey light conditions and potentially by the supposed higher soil nutrient and moisture levels. This pattern corresponds with the results of Ashton & Hall (1992), who studied d.b.h. growth over 20 years in Lambir and two other Sarawak sites, and Russo *et al.* (2005), who reported soil-related differences in diameter growth in the same plot: trees on clay or fine loam soils had faster growth than those on sandy-loam soils, although this correlative relation does not imply that soil structure or fertility is causing the differences, as variation in soil types is associated with that in forest structure and composition. For larger trees, we did not find consistent differences in diameter growth among habitats. For example, trees of 5–20 cm d.b.h. in the slope habitat

had the fastest growth rate although the $CCI_{Scaphium}$ was not lowest (Fig. 2b,c).

Habitat-related differences in resource availability may affect the mortality rates of *S. borneense*, too. Because the ridge habitat probably has the lowest soil nutrients and levels of moisture, as well as the heaviest shaded forest understorey, one would expect the highest mortality there. However, no significant differences in mortality rate were found among habitats (Fig. 2a). In the study site, a very severe drought took place in 1998. Potts (2003) showed that during the drought (1997–98) community level mortality rate of trees > 1 cm d.b.h. (7.6% year⁻¹) was three times higher than that during the pre-drought period (2.4% year⁻¹). Mortality estimates over the 5-year period (1997–2002) including the drought, confirm this, showing a 0.5% higher annual mortality (T. Yamada, unpublished results). In contrast to this community-wide pattern, mortality of *S. borneense* trees was very similar in 1997–2002 (1.64% year⁻¹) compared with 1992–97 (1.45% year⁻¹) (Fig. 2). The reason for this may be that *S. borneense* is well adapted to lower water availability on sandy loam ridges (Ashton 1980) because, among other things, it has relatively deep roots (Yamada *et al.* 2005). Meteorological data suggest that drought events occur regularly in Lambir, clearly particularly affecting trees on ridges (Whitmore 1984; Potts 2003).

Recruitment rates differed among habitats in the second census period (1997–2002), which included the El Niño year: we found higher recruitment (expressed as new recruits per adult tree) in the slope and valley habitats. The lower recruitment on ridges contrasts with the results of other studies in Lambir, which generally found higher fruit production (Itoh *et al.* 2003b) and seedling establishment (Itoh 1995) in positively associated habitats. As our recruitment rates are for 1-cm d.b.h. trees, they also contain demographic processes after seedling establishment. The lower recruitment on ridges may be associated with lower growth in that habitat due to relative low light availability and negative density-dependence in growth and survival of seedlings in that habitat (e.g. Condit *et al.* 1994; Blundell & Peart 2004).

DIFFERENCES IN POPULATION DYNAMICS AMONG HABITATS

Scaphium borneense did not show significant differences in population growth rate (λ) among habitats. Populations are projected to maintain stable sizes in all habitats, as population growth rates (λ) are not distinguishable from 1. Observed dynamics over the 10-year observation period (Table 1) also do not show changes in the relative abundance among habitats. These results are in accordance with our expectation that population sizes in all habitats would remain stable in the case that habitat preference is maintained by environmental differences among habitats and their associated differences in forest structure or composition. If habitat preference had been generated by chance factors (Hubbell

& Foster 1986) or historical effects (Baker *et al.* 2005), one would have expected differential population growth rates and population structures among habitats. In that case, the habitat association would also not have been less consistent across the study area (Fig. 1). Thus, based on these results, we argue that habitat preference in *S. borneense* is likely to be caused by intrinsic differences among habitats.

In spite of the absence of habitat-dependent variation in population growth rate, population dynamics may still differ among habitats, as populations in different habitats may be maintained in different ways (e.g. Angert 2006). However, such variation was not observed in the analyses of elasticity and LTRE. First, elasticity values were highly similar among habitats, both in terms of distribution over vital rates and size-dependent patterns. For all combinations of habitat and period, elasticity distributions over vital rates were representative of those generally observed for long-lived woody species (Franco & Silvertown 2004). Secondly, LTRE analysis showed that population dynamics were only subtly different among habitats. The habitat effect was small, indicating that differences in habitat caused only small differences in population growth rate (Table 3). Similarly, the contributions of vital rates to the habitat effect are also small (Fig. 5), indicating that observed differences in vital rates between habitats have limited consequences for population growth. Combining the results from elasticity and LTRE analyses, we conclude that in spite of its very strong habitat preference, *S. borneense* shows very little variation in population dynamics among habitats.

A remarkable result of the LTRE analysis is that differences among habitats were less important for population growth than those in between census periods (Table 3). Most likely, the relatively strong period effect reflects differences in climatic conditions, gap formation and canopy openness between census periods. As the second period included a severe drought event leading to high community-wide tree mortality (Potts 2003), recruitment and seedling growth could have been favoured by increased gap formation following the drought. Indeed, population sizes in all habitats increased more in the second census period than in the first period (Table 1). The combination of continued low mortality rates, and higher growth rates in the second period, probably explains the small (though insignificant) increase in population growth. Similarly, increases in population size following dry El Niño periods were also found in Panama (Condit *et al.* 2004). Such dry periods may lead to increased relative abundance of drought-tolerant species such as *S. borneense*, in particular on ridges and sandy-loam soils where water availability is lowest.

Are subtle differences in tree performance and population dynamics among habitats to be generally expected for tree species with habitat preference in tropical rain forests? Some results for individual vital rates do point in this direction: a community level analysis of tree growth and mortality at our study site showed that species with optimal habitat in poor resource

conditions maintained slow growth and low mortality rates, even when growing on richer resource conditions (Russo *et al.* 2005). To the extent that these studies are representative, one may therefore expect to find similar subtle differences for other rain forest tree species. In general, subtle differences can be expected in highly diverse tropical forests such as Lambir, as variation in vital rates tends to be small in these forests (Condit *et al.* 2006). Nevertheless, our test for *S. borneense* requires wider application to other species and in other rain forest regions, to confirm this expectation.

HOW ARE ABUNDANCE DIFFERENCES AMONG HABITATS GENERATED AND MAINTAINED?

Our detailed analysis for *Scaphium borneense* shows that strong habitat preference does not necessarily imply strong differences in tree performance or population dynamics. Then, the question arises of how the observed large differences in density are generated and how they are maintained. Our results provide a cautious start to unravelling the mechanisms responsible for habitat associations, partly following the 'storage effect' hypothesis of Chesson (2000). First, differences in (a)biotic conditions across habitats may lead to differential performance of *S. borneense* trees relative to that of surrounding heterospecific trees. For instance, diameter growth of *S. borneense* on ridges may be higher than that of other species because of its better adaptation to water shortage (Yamada *et al.* 2005). In this way, *S. borneense* trees may have a competitive advantage in their preferred habitat. These relative differences may be increased periodically by rare events. For instance, survival of *S. borneense* trees on ridges was similar to that of heterospecifics in a period with normal rainfall (1992–97), but was 1% higher in the period including the El Niño drought (1997–2002), during which community-wide survival decreased (T. Yamada, unpublished results). This higher survival may lead to a small increase in recruitment and population size of *S. borneense* compared with other species. Such events may provide windows of opportunity for *S. borneense* to maintain its high abundance on ridges. In the non-preferred habitats, such windows of opportunity may be lacking in the case that higher survival during drier periods would be offset by a competitive disadvantage during periods with normal rainfall. In this way, differences in the impact of drought events among species and habitats could generate and maintain density differences across habitats.

A second mechanism that may act on top of the previous mechanism is negative density-dependence. If establishment, survival and growth of *S. borneense* seedlings are negatively affected by density as previously found for other rain forest trees (e.g. Condit *et al.* 1994; Blundell & Peart 2004), one would expect among-habitat differences in tree density to gradually disappear. But density dependence may also act to maintain density differences if the density of other species has an effect. If in the valley, density of other species has stronger

negative effects on vital rates than intraspecific density, while the reverse is true on ridges, then density dependence could cause subpopulations to become stable at different densities (cf. Chesson 2000).

Finally, a third mechanism, seed input from positive habitat, may be important for maintaining subpopulations in non-preferred habitats or 'niche margins' (cf. Guo *et al.* 2005). Harms *et al.* (2001) suggested that subpopulations of tropical forest trees in non-preferred habitats are sink subpopulations that depend on seed input from preferred habitats. This may also be the case for *S. borneense*, as a large proportion of the trees in the valley occurs at a short distance from the slope and ridge habitats (Fig. 1).

Clearly, a better understanding of the above mechanisms requires studies with a different approach. First, given that differences in (a)biotic conditions between habitats may generate differences in performance of all species, it is important that the performance of study species is related to that of other species in the community (e.g. Ashton *et al.* 2006) and that the relative impact of inter- and intraspecific density-dependence is understood. Secondly, the importance of seed input to maintain marginal populations requires demographic studies that incorporate seed exchange (e.g. Kaneko *et al.* 1999).

Our results suggest that habitat association of *Scaphium borneense* is predominantly caused by (a)biotic differences among habitats and not by chance processes or disturbance history. Nevertheless, the precise mechanisms that generate and maintain habitat associations remain poorly understood and need further exploration. We hypothesize that *S. borneense* and other habitat specialists may have slightly better performance in their preferred habitat relative to that of heterospecifics. Such differences may be confined to periods with unusual climatic conditions (e.g. drought), creating windows of opportunity for slight population increases. The repeated occurrence of such events over long time-spans, in combination with seed input to non-preferred habitats, is likely to generate and maintain strong habitat associations.

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Supplementary material

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Table S1 Six matrices used for this study.

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