Recruitment subsidies support tree subpopulations in non-preferred tropical forest habitats

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Summary

1. A large share of tree species in tropical forests exhibit preference for certain habitats, resulting in strong abundance differences across habitats. While the occurrence of such habitat preference is now documented for over a thousand species, little is known about the underlying mechanisms. How are subpopulations in non-preferred habitats able to survive? Theoretical studies have suggested that these subpopulations are maintained by source–sink dynamics – 'recruitment subsidies' from high-density to low-density subpopulations – but empirical tests are lacking.

2. Here, we evaluate the role of recruitment subsidies in maintaining subpopulations of a rainforest tree in non-preferred habitats. Our study species *Scaphium borneense* (Sterculiaceae) shows strong habitat preference for drier ridges at Lambir Hills, Malaysia, where it occurs at ninefold higher densities than in the wetter valleys. On slopes, *Scaphium* occurs at intermediate densities.

3. We estimated source–sink exchange between subpopulations in three habitats in a 52-ha plot, using nearest-neighbour analyses. We found evidence for strong recruitment subsidies to the non-preferred habitats: 83–91% of recruits (of 1 cm diameter) in the valley had likely mother trees in another habitat. For slope recruits this was 54–78%.

4. We then used 10-year demographic data to construct multi-state matrix models that included the dynamics within, and exchange of recruits between subpopulations. We found that blocking recruitment subsidies to valley and slope subpopulations led to strong reductions in subpopulation growth rates over 100 years (λ_{100}). By contrast, λ_{100} of the ridge population was hardly affected by blocking recruitment exchange.

5. Elasticity analysis confirmed the importance of recruitment subsidies for λ_{100} in valley and slope subpopulations: elasticity of recruitment subsidies to these subpopulations was three to five times larger than local recruitment. Again, the reverse pattern was found for the preferred habitat, where elasticity for recruitment from other habitats was very low.

6. *Synthesis.* Our results show that recruitment subsidies can be crucial for maintaining subpopulations of tropical tree species in non-preferred habitats. To the extent that such source–sink dynamics are common among tropical tree species, this mechanism may play a role in maintaining high tree diversity in tropical forests.

Key-words: elasticity analysis, habitat association, mass effect, matrix model, population growth, recruitment subsidy, source–sink dynamics, tree demography, tropical rain forest

Introduction

Plant species commonly show abundance variation in space, over resource gradients, across habitats or due to chance

effects. At the landscape level, this leads to heterogeneous spatial distributions with patches of high and low abundance, connected by seed exchange (Freckleton & Watkinson 2002). In tropical rainforests, many tree species show spatial variation in abundance at the landscape scale (e.g. Condit *et al.* 2000). Abundance differences very often reflect

associations of species to certain habitats (e.g. Harms *et al.* 2001; Yamada *et al.* 2006). Such habitat associations have now been found for over a thousand tree species in tropical forest regions worldwide (Ashton 1964; Davies *et al.* 1998; Clark, Palmer & Clark 1999; Harms *et al.* 2001; Bunyavejchewin *et al.* 2003; Sri-Ngernyuang *et al.* 2003; Palmiotto *et al.* 2004; Gunatilleke *et al.* 2006; Yamada *et al.* 2006; John *et al.* 2007). Although habitat associations could also be attributed to short dispersal distances, random-walk processes (Hubbell 2001; Zillio & Condit 2007) or disturbances (Bunyavejchewin *et al.* 2003), they likely reflect habitat preference in the majority of cases.

For species with habitat preference, the intriguing question arises how subpopulations in non-preferred habitats are able to persist (Pulliam 1988; Harms *et al.* 2001; Runge, Runge & Nichols 2006). Are they maintained at a different density because of variation across habitats in competitive strength, carrying capacity or density dependence (Harms *et al.* 2001)? Are subpopulations in non-preferred habitats unable to support themselves because reproduction is insufficient to balance local mortality (Pulliam 1988)? And should they therefore be considered as sink populations that are maintained by 'recruitment subsidies' from source populations (Pulliam 1988)? Are so-called mass effects at play: 'the dispersal of propagules from a population in a favourable environment to an unfavourable environment, where the species would not otherwise maintain itself' (Shmida & Ellner 1984)? These questions bear relevance to understanding how habitat associations are generated, but also to explaining spatial variation in diversity (Shmida & Ellner 1984; Svenning 1999; Leibold *et al.* 2004) and to practical conservation issues (Pulliam 1988).

Source–sink dynamics have been suggested to maintain subpopulations of tropical forest species in non-preferred habitats (e.g. Harms *et al.* 2001), but – in spite of the strong interest in detecting habitat associations – this has not been studied so far. Here, we test the hypothesis that subpopulations of a Bornean tree species in non-preferred habitats are strongly supported by recruitment subsidies from high-density habitat. We do so using multi-state matrix models, in which the dynamics within subpopulations and recruitment exchange between subpopulations is explicitly simulated. This approach allows blocking recruitment exchange between habitats and thus will reveal to what extent the growth of subpopulations in non-preferred habitats depends on recruitment subsidies from other habitats.

Our study species, *Scaphium borneense* (Merr.) Kosterm. (Sterculiaceae), shows strong habitat associations, occurring at ninefold higher densities on ridges compared to valleys in a 52-ha plot in Lambir Hills, Malaysia (Fig. 1a, Yamada *et al.* 2006). In a previous study at the same site we showed that *S. borneense* subpopulations on ridges, slopes and valleys only subtly differed in rates of tree growth and recruitment, leading to very similar subpopulation growth rates across habitats (Yamada *et al.* 2007).

Materials and methods

STUDY SITE AND SPECIES

We performed this study in an equatorial rain forest in Lambir Hills National Park, East Malaysia, located on the island of Borneo (3°12′N, 114°00′E; Lee *et al.* 2002). A 52-ha study plot was established in this park in 1992, divided into 1300 20 × 20 m subplots. All trees ≥ 1 cm d.b.h. (diameter at breast height, measured at 130 cm) in the plot were tagged, mapped, identified and their d.b.h. was measured to the nearest mm in 1992. In 1997 and 2002, all trees included in previous censuses were re-measured and newly recruited trees ≥ 1 cm in d.b.h. were counted and measured. Rates of growth, mortality and recruitment of *S. borneense* trees were calculated based on data of these three censuses (Yamada *et al.* 2007).

The 52-ha plot is topographically and edaphically heterogeneous and spatial distribution of many tree species is associated with this variation (Yamada *et al.* 2006). *Scaphium borneense* is a canopy species (maximum d.b.h. = 40.7 cm) with a strong habitat preference (Fig. 1a). The densities on ridges with coarse-textured soils and low nutrient levels are twice as high (59.5 ha^{-1}) as those on slopes with finer-textured soils (22.9 ha^{-1}) and nine times higher than in valleys on loamy soils (6.7 trees of > 1 cm d.b.h. ha^{-1}). In these valleys, the study species mainly occupies locations close to the lower slope (Fig. 1a). Significant positive associations exist with ridge habitat, negative associations with valley habitat and no association with slope habitat (Yamada *et al.* 2006).

Scaphium borneense is monoecious and shortly deciduous, flowering on bare twigs after leaf fall (Kochummen 1972). It produces wind-dispersed fruits with a 10-cm boat-shaped wing derived from a dehiscing follicle (Ashton 1988). All fruits contain one seed, which germinates within 1 month after dispersal. Fruits of *S. macropodum*, a close relative with similar fruits, are seldom dispersed > 40 m from the mother tree (Yamada & Suzuki 1997). A similar maximum dispersal distance is expected for our study species. There are no indications of secondary dispersal by animals for our study species and this kind of dispersal is unlikely to happen as seeds germinate almost instantaneously after the first rain (T. Yamada, *personal observations*).

Mean annual precipitation in the region is *c.* 3000 mm. During the second census interval (1997–2002) rainfall in the first months of 1998 was strongly reduced due to the 1997–98 El Niño event. In a previous study (Yamada *et al.* 2007), we found differences in demographic rates for our study species between intervals. All analyses here are therefore conducted for both census intervals.

SPATIAL DISTRIBUTION ANALYSIS

We evaluated the spatial relationship between adult trees (> 20 cm d.b.h.) and recruits (> 1 cm d.b.h.) that appeared in 1997 and 2002 following the approach of Hamill & Wright (1986). This analysis reveals whether recruits have a clumped, random or over-dispersed spatial distribution relative to adult trees. The method uses a null distribution that assumes a random spatial distribution of recruits around adults. Differences between observed and null distributions can then be tested by a Kolmogorov–Smirnov test. We performed this analysis three times, once for each habitat. In each analysis, we related recruits in a given habitat to nearest adults that could be either be present in the same or in a different habitat. Recruits within 40 m from the plot boundary were excluded from these analyses as their mother trees are likely located outside the plot.

If recruited trees are strongly clumped around adult trees at short distances, this is likely the result of limited seed dispersal distances. In
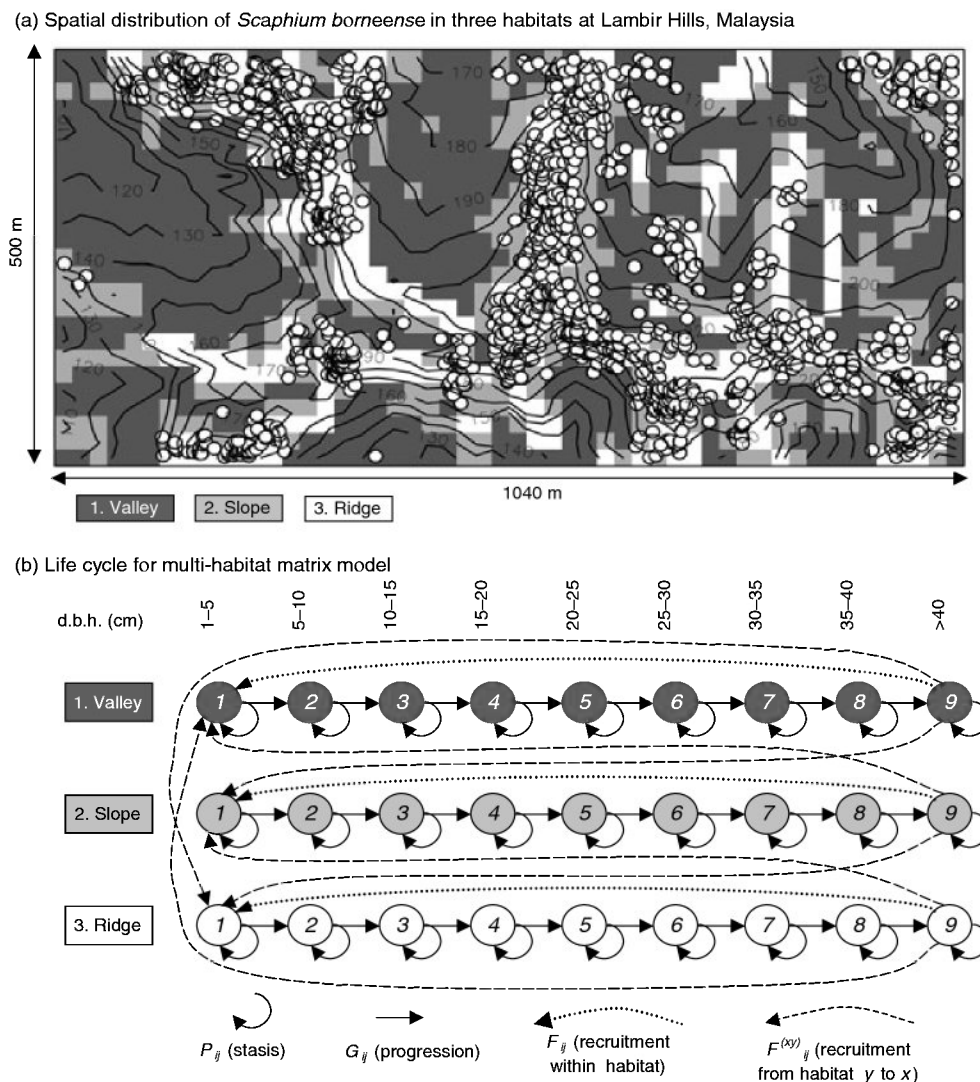
(a) Spatial distribution of *Scaphium borneense* in three habitats at Lambir Hills, Malaysia

(b) Life cycle for multi-habitat matrix model

Fig. 1. (a) Spatial distribution of trees > 1 cm diameter at breast height, d.b.h. and (b) life cycle of *Scaphium borneense* in Lambir Hills, Malaysia. Isoclines in (a) are in m above sea level. In (b), recruitment arrows have been omitted for categories 5–8 for the sake of clarity.

such cases, one may assume that the nearest adult tree is the mother of the recruited individual. In this way, we were able to identify whether the likely mother of each recruited tree is located in the same or a different habitat and then calculate the proportion of recruits with mothers in each of the habitats.

Clearly, the second- or third-nearest adult tree (and so on) can also be the mother of a recruit. Thus, treating the nearest adult tree to be the mother of a recruit probably (slightly) underestimates the true distance between recruits and adults. We therefore also calculated whether recruits are clumped around the *second*-nearest adult tree, using the same approach, and then calculated recruitment exchange under this second recruitment scenario. We compared the recruitment exchange of these two recruitment scenarios and implemented both scenarios in our demographic models (see below under Matrix model construction).

Note that the nearest-neighbour analyses reveal clumping of recruits *around* adult trees, not spatial clumping of recruits in general. Thus, if conditions for successful recruitment are clustered independent from adult location, no clustering around adult trees would be found (e.g. Zuidema & Boot 2002).

MATRIX MODEL CONSTRUCTION

We applied multi-state matrix models to simulate population dynamics of *S. borneense* within habitats and seed exchange (recruitment subsidies) between habitats (Pascarella & Horvitz 1998; Caswell 2001). Nine size categories were distinguished, based on tree diameter (1–5 cm d.b.h., 5–10 cm d.b.h., etc.; see Fig. 1b). The resulting transition matrix:

$$\mathbf{M} = \begin{pmatrix} \mathbf{A}^{(11)} & \mathbf{R}^{(12)} & \mathbf{R}^{(13)} \\ \mathbf{R}^{(21)} & \mathbf{A}^{(22)} & \mathbf{R}^{(23)} \\ \mathbf{R}^{(31)} & \mathbf{R}^{(32)} & \mathbf{A}^{(33)} \end{pmatrix}$$

contains three submatrices $\mathbf{A}^{(yy)}$ (dimension 9×9) that describe the dynamics within habitats (y = 1,2,3 for valley, slope and ridge, respectively) and six submatrices $\mathbf{R}^{(xy)}$ that quantify the recruitment subsidies from habitat y to x (x = 1,2,3). Thus, submatrices $\mathbf{A}^{(yy)}$ contain all probability transitions among life-cycle stages (from new recruits in category 1 to the largest trees in category 9) within habitat y, while submatrices $\mathbf{R}^{(xy)}$ only contain the number of recruiting trees of 1 cm d.b.h. that appear in habitat x

and were produced by adult trees in habitat y. For example, submatrix $\mathbf{R}^{(21)}$ contains recruitment exchange from valley ($y = 1$) to slope ($x = 2$). Transition matrices were constructed for two census intervals (1992–97 and 1997–2002) and are included in Tables S1 and S2 in Supporting Information.

Elements a_{ij} in submatrices $\mathbf{A}^{(yy)}$ can be grouped into stasis (P_{ij}; for $i = j$), progression (G_{ij} for $i = j + 1$), and recruitment into the 1-cm d.b.h. category (F_{ij} for $i = 1$ and $j > 4$). Their values were calculated from the underlying vital rates survival (σ), growth (γ), probability of being reproductive ($\Pr\{f\}_j$) and number of recruits of 1 cm d.b.h. produced by a reproductive tree (ρ, Zuidema & Boot 2002; Yamada *et al.* 2007). Progression was calculated as: $G_{ij} = \sigma_j \times \gamma_j = \sigma_j \times g_j / c_j$ (with g_j = d.b.h. growth rate, in cm year^{-1}; c_j = d.b.h. category width, in cm); stasis was calculated as $P_{ij} = \sigma_j \times (1-\gamma_j)$; and recruitment as $F_{ij} = \sigma_j \times \Pr\{f\}_j \times \rho^{(yy)}$. The values of these vital rates differ across diameter categories j. Size-dependent values for diameter growth (g_j), survival (σ_j) and $\Pr\{f\}_j$ were reported in Yamada *et al.* (2007), with diameter growth rates (g_j) differing across habitats. The value of $\rho^{(yy)}$ was calculated as the quotient of the rate at which new recruits (of 1 cm d.b.h.) with likely mother tree in habitat y appeared in that habitat (ha^{-1} y^{-1}), and the abundance of adult trees in habitat y (ha^{-1}).

Submatrices $\mathbf{R}^{(xy)}$ contain recruitment elements $F^{(xy)}_{ij}$ for $i = 1$ (recruit category) and $j > 4$ (adult categories). Recruitment from habitat y to habitat x was calculated in the same fashion as in $\mathbf{A}$: $F^{(xy)}_{ij} = \sigma^{(y)}_j \times \Pr\{f\}^{(y)}_j \times \rho^{(xy)}$. Per capita recruitment $\rho^{(xy)}$ was calculated as the quotient of the rate at which new recruits with likely mother tree in habitat y appeared in habitat x (ha^{-1} y^{-1}), and the abundance of adult trees in habitat y (ha^{-1}). The number of new recruits with likely mother trees in another habitat was based on information about the spatial distribution of recruits with respect to adult trees.

We constructed two types of models that represent different 'recruitment scenarios': a scenario in which $\rho^{(xy)}$ and $\rho^{(yy)}$ were determined by assigning recruits to the *nearest* neighbouring adult tree, and one that uses the *second*-nearest neighbour (see above, under 'Spatial distribution analysis').

MATRIX ANALYSES

Population dynamics were simulated as $\mathbf{n}(t + 1) = \mathbf{M}^*\mathbf{n}(t)$ (Caswell 2001), in which $\mathbf{n}$ is a vector containing the population structures in three habitats (order: valley, slope, ridge). We calculated asymptotic population growth rate λ_a (dominant eigenvalue) of the entire population, but were also interested in the growth rates of subpopulations per habitat. To obtain these rates, we projected the population for 100 years, obtained subpopulation sizes from $\mathbf{n}(t + 100)$ and calculated the annualized growth rate for subpopulation y, $\lambda^{(y)}_{100} = [\mathbf{n}(t + 100)/\mathbf{n}(t)]^{(1/100)}$.

We quantified the importance of recruitment subsidies for population growth in two ways: by calculating the changes in λ_a and λ_{100} after blocking recruitment exchange between habitats (i.e. $F^{(xy)}_{ij} = 0$) and by calculating elasticities for $\lambda^{(y)}_{100}$ and λ_a of changes in $F^{(xy)}_{ij}$. Although both are forms of perturbation analyses (Caswell 2001), they provide supplementary information: the former allows quantifying the full effect of blocking recruitment subsidies while the latter evaluates the effect of small (proportional) changes in recruitment subsidies. We calculated the elasticity of λ_a to changes in elements m_{ij} of matrix $\mathbf{M}$ analytically as $e_{ij} = \frac{\partial \lambda_a/\lambda_a}{\partial m_{ij}/m_{ij}} = \frac{m_{ij}}{\lambda} \frac{v_i w_j}{\langle \mathbf{w}, \mathbf{v} \rangle}$ where $\mathbf{v}$ and $\mathbf{w}$ are left and right eigenvectors of $\mathbf{M}$ and $<\mathbf{w}, \mathbf{v}>$ denotes their scalar product (Caswell 2001). We calculated the elasticity of the projected subpopulation growth rate $\lambda^{(y)}_{100}$ to changes in F_{ij} as $e^{*(y)}_{ij} = \frac{\Delta \lambda^{(y)}_{100}/\lambda^{(y)}_{100}}{0.01}$, in which $\Delta \lambda^{(y)}_{100}$ is the change in $\lambda^{(y)}_{100}$ resulting from the 1% increase in all F_{ij} values. (Applying a 1% decrease or larger increases and decreases yielded very similar results.)

Results

SPATIAL DISTRIBUTION AND EXCHANGE OF RECRUITS

Most recruited trees occurred at short distances from adult trees: 80–95% of the recruits were located at $<$ 40 m from the nearest adult (Fig. 2a–c). Clearly, clustering around *second*-nearest adults was less pronounced, but also in this case
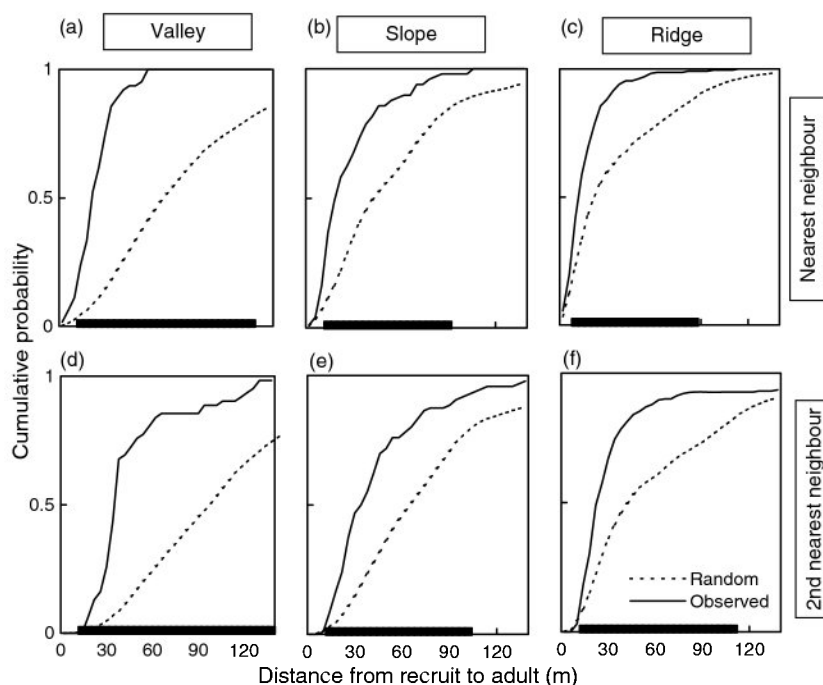

Fig. 2. Spatial clustering of *Scaphium borneense* recruits with respect to adults in three habitats in Lambir Hills, Malaysia. Recruits were assigned to adult trees in two ways (recruitment scenarios): using the nearest adult (upper panels) and the second-nearest adult (lower panels). The lines along the *x*-axes indicate distances at which recruits are significantly clumped (observed > null distribution) around adult trees (K-S tests, $P < 0.05$).

60–80% of the recruits appeared within 40 m of the second-nearest adult (Fig. 2d–f). Clustering occurred in similar fashion in all habitats.

The theoretical distribution of nearest-neighbour distances for random points differed between habitats, with lower probabilities in the valley compared to slope and ridge, due to lower adult density. Observed spatial distribution of recruits differed significantly and strongly from this theoretical distribution that assumes random placement of recruits with respect to adult trees. Significant clumping occurred at distances from 10–18 m and up to 86–126 in the case of nearest adult neighbour, and at distances from 14 m up to 102–138 m for the case of second-nearest neighbours (Fig. 2).

The exchange of recruits inferred from nearest and second-nearest neighbour analyses varied strongly among habitats (*G*-test, $P < 0.001$, for both periods and recruitment scenarios, Table 1). The vast majority (83–91%) of recruits in the valley had mother trees in other habitats, while this was just 13–24% for recruits on the ridge (Table 1). The slope habitat had intermediate values: 54–78% of the recruits there had a likely mother tree in other habitats. Thus, there is evidence for strong source–sink dynamics across habitats, with ridge subpopulations acting as recruitment sources and subpopulations in the valley and the slope as sinks. As expected, source–sink dynamics were stronger when the second-nearest adult was assumed to be the mother tree of recruits.

POPULATION STRUCTURES AND POPULATION GROWTH

Stable population structures (**w**) resembled observed population structures quite well (Fig. 3), with high correlation among them ($r^2 = 0.99$ for 1992–97 and 0.95 for 1997–2002). Keyfitz's Δ values, which quantify differences in two distributions (Caswell 2001), were also rather low: 0.20 for 1992–97 and 0.28 for 1997–2002. Annual population increment calculated from

a 10-year simulation that applied $\mathbf{M}_{1992–97}$ and $\mathbf{M}_{1997–2002}$ each for 5 years (1.018 year^{-1}), closely matched the observed changes in population size from 1992 to 2002 (1.022 year^{-1}, Yamada *et al.* 2007). The multi-habitat model thus realistically simulated dynamics and abundance differences across habitats.

Asymptotic (λ_a) and projected (λ_{100}) growth rates of the entire population were all slightly above 1 and very similar. For 1992–97, λ_a equalled 1.012, while λ_{100} was 1.013; for 1997–2002, $\lambda_a = 1.015$ and $\lambda_{100} = 1.016$. Values of λ_a and λ_{100} did not differ between recruitment scenarios.

At subpopulation level, projected growth rates $\lambda^{(y)}_{100}$ differed slightly across habitats and between periods, with a tendency for somewhat lower values for ridge subpopulations (filled symbols and continuous lines in Fig. 4). Subpopulation growth rates were the same for the two recruitment scenarios (lower and upper panels in Fig. 4).

RESPONSES OF POPULATION GROWTH TO CHANGES IN RECRUITMENT

Asymptotic (λ_a) and projected (λ_{100}) growth rates for the entire population were only slightly reduced when recruitment exchange across habitats was blocked. Stippled lines in Fig. 4 indicate λ_{100} values for the entire population, when the recruitment to the habitat along the *x*-axis was blocked. Changes ranged from -0.001 and -0.003 (corresponding changes in λ_a were smaller). Thus, at landscape level, recruitment exchange had little significance for maintaining populations.

A quite different response was observed for the growth of subpopulations. Blocking the recruitment subsidies to the valley and slope habitats had major impacts on projected growth of their subpopulations (Fig. 4a,b). For instance, using the 1992–97 data, $\lambda^{(y)}_{100}$ in the valley dropped from 1.015 to 0.997 when recruitment to that subpopulation was set to zero. By contrast, blocking recruitment subsidies to the ridge

Table 1. Recruitment rates and exchange of *Scaphium borneense* between habitats in a 52-ha plot in Lambir Hills, Malaysia. The percentage of recruits with a mother tree in the same (bold) or other habitats is shown, under the assumption that the nearest or the second-nearest adult tree is the recruit's mother

Mother tree is:	Period	Habitat of recruit	Habitat of most likely mother tree (%)			
			Valley	Slope	Ridge	Total (*n*)
Nearest adult	1992–97	Valley	**17**	34	49	100 (35)
		Slope	6	**41**	53	100 (47)
		Ridge	4	10	**86**	100 (137)
	1997–2002	Valley	**17**	24	59	100 (46)
		Slope	5	**46**	49	100 (77)
		Ridge	4	11	**85**	100 (151)
Second-nearest adult	1992–97	Valley	**11**	25	64	100 (28)
		Slope	2	**22**	76	100 (41)
		Ridge	0	13	**87**	100 (109)
	1997–2002	Valley	**9**	20	71	100 (35)
		Slope	0	**23**	77	100 (57)
		Ridge	2	22	**76**	100 (127)

Fig. 3. Population structures of *Scaphium borneense* in three habitats in Lambir Hills, Malaysia. Bars denote the observed structure in 1992, diamonds and triangles are stable stage distributions (**w**) of **M** for the two census intervals. Category boundaries are given in Fig. 1.
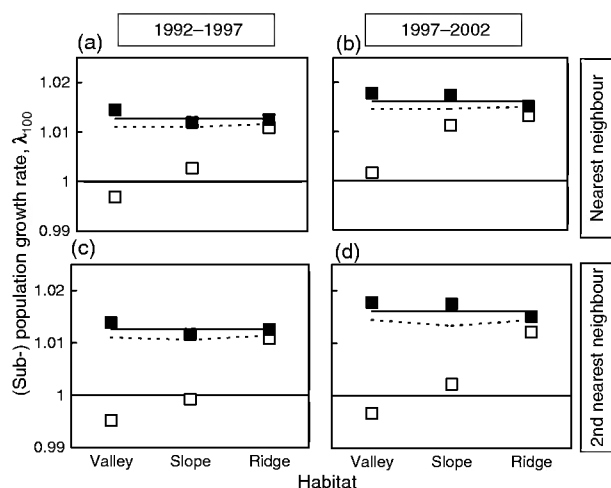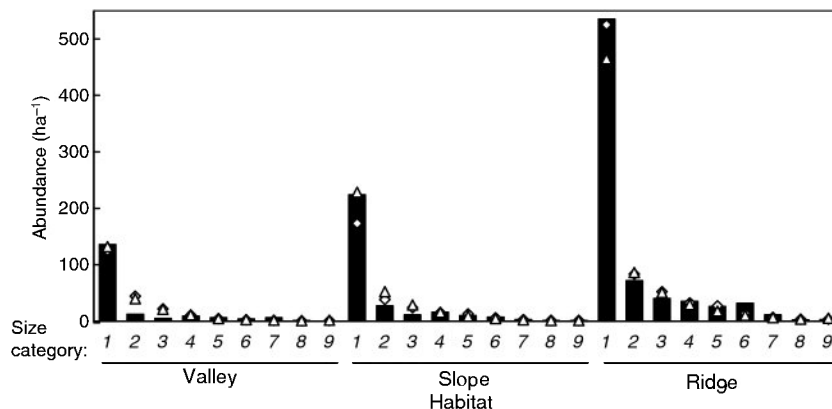

Fig. 4. Annual growth rates for populations (λ_{100}, lines) and subpopulations ($\lambda^{(y)}_{100}$, symbols) of *Scaphium borneense* in Lambir Hills, Malaysia. Filled symbols and continuous lines: full recruitment exchange between subpopulations; open symbols and dashed lines: no recruitment subsidies to indicated habitat. Results are for two periods (left and right panels) and two recruitment scenarios (upper and lower panels).

population hardly changed $\lambda^{(y)}_{100}$ of that subpopulation (1.012–1.011). On the slopes, reductions in $\lambda^{(y)}_{100}$ were also considerable. Again, these responses were consistent for both census intervals. To evaluate the magnitude of these changes, we calculated $\lambda^{(y)}_{100}$ values for a situation with no recruitment at all. For all three subpopulations and both periods, this population growth rate without recruitment equalled 0.987. Thus, the decrease in subpopulation growth due to blocked recruitment subsidies to the slope and valley habitats is large compared to this maximum change in $\lambda^{(y)}_{100}$ as a result of recruitment declines.

The models in which recruits were assigned to the *second*-nearest adult yielded similar patterns (Fig. 4c,d): strong reduction of $\lambda^{(y)}_{100}$ in the valley, no effect on the ridge and an intermediate effect on the slopes. There was a tendency for a somewhat larger impact on $\lambda^{(y)}_{100}$ in the slope habitat, as this second recruitment scenario resulted in a higher recruitment subsidy to this subpopulation (Table 1). In all, these results show that population growth was strongly influenced by recruitment subsidies in the valley and moderately so on slopes.

ELASTICITY ANALYSES

Elasticity values (e_{ij}) for the asymptotic growth rate of the entire population (λ_a) were very large (94–95%) for stasis elements (P_{ij}), and considerably smaller for progression (G_{ij}: 4.0–4.4%) and recruitment (F_{ij}: 0.7%; Fig. 5). There were also clear differences between subpopulations: the ridge subpopulation contributed seven to nine times more to λ_a than the valley subpopulation, and two times more than the slope subpopulation. These differences correspond with those in relative abundance of individuals over habitats in the stable size distribution (Fig. 3). When looking at the elasticities for recruitment (F_{ij}), an interesting pattern is observed: in the valley, the contribution of recruitment subsidies to population growth λ_a is larger than that of own recruits, while the reverse is true for the ridge habitat (Fig. 5). The two types of recruitment were equally important in the slope habitat.

As our prime interest was to quantify the contributions of recruitment subsidies at the level of subpopulations, we calculated elasticities $e^{*(y)}_{ij}$ of the habitat-specific population growth $\lambda^{(y)}_{100}$ for changes in recruitment elements (F_{ij}) in **A** and **R**. We found that recruitment subsidies were four to nine times more important for $\lambda^{(y)}_{100}$ in the valley than recruitment from the valley itself (Fig. 6). For the slope subpopulation, recruitment subsidies were up to four times more important than recruits from the own habitat. By contrast, $\lambda^{(y)}_{100}$ for the ridge was four
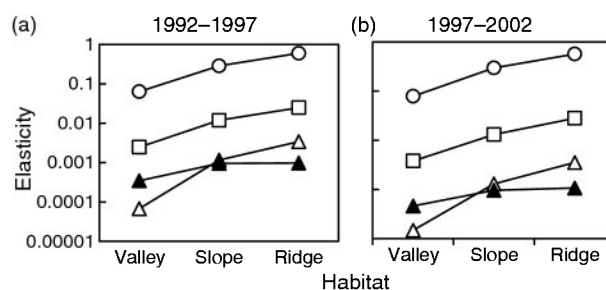

Fig. 5. Elasticity of asymptotic growth rate λ_a of the *Scaphium borneense* population in Lambir Hills, Malaysia, for two periods. Elasticity values for elements stasis (P_{ij}, circles), progression (G_{ij}, squares), recruitment to own habitat (F_{ij} elements in $\mathbf{A}^{(yy)}$, open triangles) and recruitment to other habitats (F_{ij} elements in $\mathbf{R}^{(xy)}$, filled triangles). Results are for the recruitment scenario with nearest adult trees.
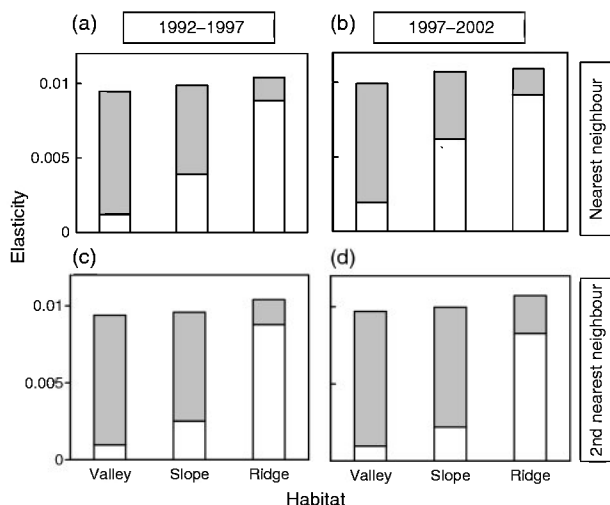
Fig. 6. Elasticity e^* of the 100-year growth rate, λ_{100}, of *Scaphium borneense* subpopulations for recruitment exchange ($F^{(xy)}_{ij}$; grey) and recruitment within own habitat ($F^{(yy)}_{ij}$; open). Results are for two periods (left and right panels) and two recruitment scenarios (upper and lower panels).

to five times more sensitive to changes in recruitment within the same habitat. These results were consistent for the two study periods. Thus, growth of subpopulations in valley and slope was sensitive to changes in recruitment subsidies.

As expected, the stronger source–sink dynamics that occurred in the scenario in which the *second*-nearest neighbour was assumed to be the mother tree led to higher elasticities of recruitment exchange for non-preferred valley and slope habitats (Fig. 6).

Discussion

SOURCE-SINK DYNAMICS

Scaphium borneense recruits were strongly clustered around potential mother trees. This clumped distribution is most likely caused by the short dispersal distances and the lack of secondary dispersal, as it is unlikely that germination, seedling establishment and growth to 1 cm d.b.h. would be positively density dependent. Clustering of recruits was similar across habitats, suggesting that seed dispersal distances did not differ between habitats.

Our nearest-neighbour analyses suggest that there is ample seed dispersal across habitats, leading to strong recruitment exchange. An estimated 35–49% of recruits appearing in the entire population had likely mother trees in another habitat. This proportion was much higher when considering just the recruits to the valley subpopulation (83–91%), or to the slope subpopulation (54–78%). The rugged terrain at Lambir causes strong habitat differences at relatively small spatial scales which may lead to a high incidence of recruitment exchange across habitats (Lee *et al.* 2002). This small-scale habitat heterogeneity is probably not specific to Lambir, as most of the 50-ha plots in tropical forests show clear habitat variation

within plot boundaries (Condit *et al.* 2000). Thus, recruit exchange across habitat boundaries may be common for rainforest tree species.

The two recruitment scenarios that we implemented yielded different estimates of recruitment exchange, with lower values when the nearest adult tree was assumed to be the likely mother, and higher values when the *second*-nearest adult was chosen. In the former case mother–recruit distances are almost certainly somewhat underestimated, while the second method likely overestimated these distances. In all, these two estimates appear to provide a fair estimate of the incidence of recruitment exchange across habitats. Clearly, genetic parentage analyses of recruits and mother trees (Hardesty, Hubbell & Bermingham 2006; Jones & Müller-Landau 2008) would yield precise and direct measurements of recruit-to-mother distances, but were not available during the observation period of this study.

We found evidence for strong source–sink dynamics, as the exchange of recruits was highly skewed. In the non-preferred valley habitat > 80% of recruited trees had a mother tree in one of the two other habitats. This percentage was lower for the slope habitat, in which *S. borneense* occurs at intermediate densities, but also there, over 50% of the recruits had a likely mother tree on the ridge. Other studies on recruitment in tree species with habitat associations showed similarly strong recruitment subsidies to unfavoured habitats (e.g. Kaneko, Takada & Kawano 1999; Kaneko & Kawano 2002). Our findings are in accordance with the predictions of the mass effect hypothesis (*sensu* Shmida & Ellner 1984), which stipulates that strong abundance differences generate recruitment subsidies from areas with a high density of adult individuals to one with a lower density. Such 'spill-over' is brought about by the larger production of seeds per unit area in the high-density area, causing a net influx of seeds – and thus recruits – into the low-density area. While such mass effects are likely common among the many tropical forest tree species that show habitat associations, this has hardly been quantified so far (Svenning 1999). Clearly, more research is required to evaluate mass effects and source–sink dynamics in tropical tree populations.

MAINTAINING POPULATIONS IN NON-PREFERRED HABITATS

The two types of perturbation analyses we performed showed that recruitment subsidies are important for maintaining subpopulations in non-preferred habitats (valley and slope). Blocking the recruitment subsidies to the valley subpopulation led to a projected population decline there. Similarly, if no recruits from other habitats would arrive in the slope subpopulation, its growth would be considerably reduced (Fig. 4). These results were confirmed by elasticity analyses: subpopulation growth in valley and slope was much more sensitive to recruitment subsidies from other habitats (mainly ridge) than to recruitment in the same habitat. In all perturbation analyses, results were consistent for the two recruitment scenarios that we applied. We should note that the importance of recruit subsidies for maintaining subpopulations in valley and slope may

change if survival rates differ across habitats (which they did not, Yamada *et al.* 2007), as tree survival is the vital rate that contributes most to population growth in tree species (Silvertown *et al.* 1993; Zuidema 2000). Thus, for our study system, recruitment subsidies from the ridge habitat play an important role in maintaining subpopulations in non-preferred habitats.

Another approach to identifying source and sink subpopulations was recently outlined by Runge, Runge & Nichols (2006). They proposed to identify sinks and sources in relation to their contribution to landscape-level population growth, and showed that this contribution can be assessed using reproductive values (v) from multi-habitat matrix models (appendix A in Runge, Runge & Nichols 2006). If reproductive values per habitat (standardized for relative abundance differences across habitats) are < 1, a subpopulation can be considered a sink, while a value of > 1 identifies a source subpopulation. Applying this approach to our multi-habitat models (for both periods and recruitment scenarios), we found that valley subpopulations were strong sinks (v ranges from 0.04 to 0.5), while subpopulations on the slope (0.8–1.3) and ridge (1.0–1.3) were moderate sources. These values are consistent with the results presented above.

HOW ARE HABITAT ASSOCIATIONS GENERATED AND MAINTAINED?

During the past decade, habitat association studies revealed that hundreds of tropical tree species are significantly associated with certain habitats (e.g. Harms *et al.* 2001; John *et al.* 2007). Now that habitat associations are extensively documented across continents and forest types, it is important to understand how such density differences across habitats are generated and maintained. A first step in this direction is to establish whether habitat associations for a given species are consistent across size categories. Recent work by Comita, Condit & Hubbell (2007) and Suzuki *et al.* (2009) showed that this is often not the case: habitat associations found for one size category may disappear at larger or smaller sizes. It is evident from these studies that habitat associations are probably maintained in a complex way, and that multiple size categories need to be included in future research. These studies also demonstrate the need to move from describing patterns to understanding the processes that generate density differences. Using data from large permanent plots, it is possible to monitor the performance of individual trees and compare this across habitats (e.g. Russo *et al.* 2008; Suzuki *et al.* 2009), with further analyses at population level (Kaneko & Kawano 2002; Yamada *et al.* 2007). A recent study by Russo *et al.* (2008) took such an approach to detect whether tree species in Lambir present differential performance across soil types. They found that species trade-off high growth on rich soils (corresponding roughly to the valley habitat used here) with low survival on poorer soils (i.e. on ridges). Although these trade-offs were not consistently found for groups of soil habitat specialists, the study of Russo *et al.* (2008) does reveal a mechanism by which tree species may be ecologically sorted across habitats. In the case of *S. borneense*, it is likely that the drought-adapted

seedlings and juvenile trees (Yamada *et al.* 2005) are strong competitors on the drier sandy-loam soils at the ridges, while being unable to compete on the wetter clay soils in the valley (cf. Ashton, Singhakumara & Gamage 2006; Engelbrecht *et al.* 2007). This may explain why the number of recruits (of 1 cm d.b.h.) produced per adult tree in the same habitat is higher for the drier ridge compared to the wetter valley (see Tables S1 and S2). Overall, it is likely that differences in competitive strength play a role in generating abundance differences across habitats.

Strong source–sink dynamics alone cannot generate and maintain density differences across habitats. This mechanism is crucial in keeping subpopulations alive in non-preferred habitats, but this in itself does not necessarily lead to lasting density differences across habitats. We therefore argue that source–sink dynamics act in tandem with differences in competitiveness across habitats to generate and maintain habitat associations (cf. Russo *et al.* 2008). Little is known about the respective roles of these two processes and there is an urgent need to include both source–sink dynamics and habitat-specific competitive ability into future studies on habitat associations. For our study species, this would imply a detailed study on competitiveness of seedlings and saplings in different habitats. The recent shift from describing patterns to analysing dynamics (Russo *et al.* 2008; Suzuki *et al.* 2009) is an important step in that direction.

CONSERVATION IMPLICATIONS

If source–sink dynamics as we observed in *S. borneense* are common among tropical forest tree species with habitat associations, then this implies that mass effects can be an important factor in maintaining high diversity in tropical forests. The role of mass effects in maintaining diversity has received quite some attention in theoretical work (e.g. Shmida & Ellner 1984; Hubbell 2001; Leibold *et al.* 2004) but much less so in empirical studies (Svenning 1999). If recruitment subsidies are maintaining subpopulations of many of the tree species in tropical forests, it follows that successful conservation of these species requires the protection of preferred habitats (cf. Pulliam 1988; Harms *et al.* 2001). This is particularly of relevance for reserves at the scale of hundreds of hectares, as this is the scale at which seed dispersal operates. The practical implications of source–sink dynamics for tropical tree conservation require more attention.

Acknowledgements

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Supporting Information

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

Table S1. Transition matrix **M** for 1992–1997.

Table S2. Transition matrix **M** for 1997–2002.

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