100 YEARS Journal of Ecology British Ecological Society

Journal of Ecology 2012, **100**, 643–651 doi: 10.1111/j.1365-2745.2011.01937.x

Soil resource availability shapes community trait structure in a species-rich dipterocarp forest

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Summary

1. Habitat filtering and limiting similarity have been proposed as two opposing forces structuring community memberships. Community assembly theory proposes habitat filtering as a mechanism restricting community membership according to the ecological strategies of species in a given environment. Limiting similarity posits that some species exclude others that are ecologically similar.

2. We quantified nine ecophysiological and life-history traits for 80 dipterocarp species in the 52-ha Lambir Forest Dynamics Plot (FDP; Lambir Hills National Park, Sarawak, Malaysia). We studied forests on four soil types differing in fertility and moisture, focusing on soil resource availabilities as environmental determinants of habitat filtering processes. We used a null-model approach to detect the strengths of habitat filtering and limiting similarity. We quantified the relative contributions of soil resources (nutrients and water) to habitat filtering by comparing the strength of habitat filtering processes (i.e. effect sizes) at the overall plot scale and at the individual soil-type scale. We also compared the strengths of assembly processes among soil types.

3. Compared to a null model at microscale (20 × 20 m), trait range and variance were reduced for seven of nine functional traits, suggesting the importance of habitat filtering in the dipterocarp community. We also found a broader distribution of five traits, and more even spacing for seven traits (20 × 20 m), which is consistent with the concept of limiting similarity. Randomizations that swapped species occurrences within soil types (i.e. null models removing soil effects in assembly processes) were much closer to observed values, and there were no phylogenetic constraints on habitat association. Hence, soil resource availability acted as a habitat filtering mechanism in the FDP; relative contributions to habitat filtering ranged from 35% for seed mass to 77% for relative growth rate. Furthermore, soil types apparently affected the strengths of habitat filtering and limiting similarity.

4. *Synthesis*. We demonstrate that soil resource availability is a crucial determinant of habitat filtering in this species-rich tropical rain forest; the strengths of assembly processes differed among soil types. Variation in soil resource availability can shape the distribution of traits through community assembly processes, promoting trait diversification and species coexistence.

Key-words: determinants of plant community diversity and structure, functional traits, habitat filtering, Lambir, limiting similarity, null models, soil nutrients, tropical forest dynamics plot

Introduction

A central goal of community ecology studies is to understand how ecological communities are assembled from species pools (Weiher & Keddy 1995; McGill *et al.* 2006). Habitat filtering and limiting similarity have been proposed as two opposing forces for community assembly processes (MacArthur & Levins 1967; Weiher & Keddy 1995). The habitat filtering concept proposes that species succeed or fail in a given environmental condition according to their functional traits. If conditions restrict the range of viable strategies, this leads to more restricted trait values within communities than expected by chance. Limiting similarity posits that some species exclude others that are ecologically similar, leading to a more even distribution of trait values than expected. A wide range of empirical studies show that habitat filtering acts as a strong

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determinant at local scales in many communities including tropical tree communities (Kraft, Valencia & Ackerly 2008; Swenson & Enquist 2009; Kraft & Ackerly 2010) where stochasticity is thought to act as a strong determinant of species composition (Hubbell 2001; Kembel & Hubbell 2006). However, the roles of environmental parameters in filtering processes remain unclear. Identifying environmental parameters that restrict suitable traits in a community or quantifying the relative contributions of these factors in habitat filtering processes will lend further support to the importance of the trait-based approach in community ecology (McGill *et al.* 2006).

Tropical tree species have non-random distributions in relation to environmental gradients (Davies *et al.* 1998, 2005; Valencia *et al.* 2004; Engelbrecht *et al.* 2007; John *et al.* 2007). For example, individuals of 11 different tropical tree species were shown to have distributions closely related to light requirements (Davies *et al.* 1998). The aggregation of tropical tree species in specific soil resource types is perhaps the clearest evidence for habitat filtering (Valencia *et al.* 2004; Davies *et al.* 2005). Ordoñez *et al.* (2009) have provided a global quantification of the trade-off between traits associated with fast growth and those associated with resource conservation 'strategies' in relation to soil resource availability. Furthermore, the strength of a trade-off between growth and mortality rates can vary as a function of below-ground resource availabilities (Russo *et al.* 2008). Hence, variation in soil moisture and nutrients may be critical in habitat filtering processes, and the strengths of assembly processes may vary along soil resource gradients in tropical rain forests.

The 52-ha Lambir Forest Dynamics Plot (FDP; Lambir Hills National Park, Sarawak, Malaysia) contains possibly the richest local diversity of tree species in the Old World (Lee *et al.* 2002). Analyses of soil and topographic variation have detected four soil types. Ranked in descending order of fertility and moisture, these are clay (C), fine loam (FL), loam (L) and sandy loam (SL) (Davies *et al.* 2005; Russo *et al.* 2005). Spatial variation in tree species composition in the FDP is significantly correlated with variation in soil resource availability (Davies *et al.* 2005). The forest is dominated by a single family of angiosperms, the Dipterocarpaceae (*c.* 40% of plot total basal area). Dipterocarp species have spatially aggregated dispersions and habitat preferences in the FDP (Palmiotto *et al.* 2004; Davies *et al.* 2005). Members of the family are generally late-successional species (Ashton 1988). There is a very large taxonomic diversity within the Dipterocarpaceae (80 species within the FDP) and a large variation in morphological and physiological traits (Aiba & Nakashizuka 2005). These taxonomic and functional diversities provide an ideal system for identifying and quantifying (i) environmental factors that restrict trait values and (ii) changes in trait-based assembly processes along soil resource gradients. In addition, as tropical rain forests can be characterized by diverse species within a single large genus and/or family, assembly processes among close relatives are particularly important to address the coexistence of tropical tree species.

We analyse trait distribution patterns of a dipterocarp community in the FDP to investigate the importance of soil resource availability in assembly processes within this diverse tropical rain forest. First, we expect that trait values of the local dipterocarp community are simultaneously restricted and evenly spaced as predicted by assembly rules and an early morphological study (Aiba & Nakashizuka 2005). We use a null-model approach to determine trait distribution values. Second, we expect that soil resource availability contributes a considerable proportion of habit filtering. Finally, we quantify changes in the trait mean values and the strength of assembly processes along a soil resource gradient. We predict that fast-growing species and their related traits [e.g. high specific leaf area (SLA) and high foliar N] tend to be sorted to fertile, moist soil (Ordoñez *et al.* 2009). We further predict that in infertile, dry soil, the shortage of below-ground resources will limit the range and variance of traits.

Methods

STUDY SITE AND SPECIES

The study was conducted in the 52-ha (FDP; altitude, 104–224 m) in Lambir Hills National Park (Lambir), Sarawak Malaysia (4°11′N, 114°01′E). This mixed dipterocarp lowland forest receives 2700 mm of rain each year, with no distinct dry season; the mean annual temperature is 26 °C (Nakagawa *et al.* 2000). The FDP contains more than 350 000 mapped trees [≥1 cm diameter at breast height (d.b.h.)] belonging to 1195 species. Repeated censuses have been conducted at 5-year intervals since 1991. Our analysis is based on the third census, which was conducted in the period 2002–03, and focuses on 80 dipterocarp tree species.

TRAIT SELECTION

Nine functional plant traits were included in the analysis: (SLA, leaf area per unit mass), leaf size, leaf nitrogen content (N_{mass}, nitrogen per unit leaf mass), leaf succulence (leaf water content per unit area), leaf toughness (leaf fracture resistance), seed mass, wood specific gravity (WSG, dry mass per green volume), the 95th quantile of d.b.h. distribution among all trees with d.b.h. values >10% of the maximum for the species in question ($D95_{0.1}$, used as a proxy for maximum height) and growth rates under favourable conditions, i.e. the 95th quantile of relative growth rates (RGR_{95}). Leaf size is related to environmental nutrient stresses and disturbances (Cornelissen *et al.* 2003). SLA, N_{mass} and leaf succulence are regarded as components of the leaf economics spectrum (Garnier & Laurent 1994; Wright *et al.* 2004), which represents a trade-off between strategic allocations to low construction costs, high photosynthetic rates and short leaf life spans vs. high construction costs, low photosynthetic rates and long leaf life spans. N_{mass} reflects mass-based photosynthetic capacity while SLA and leaf succulence reflect area-based light capture potential and the balance between carbon gain and water loss through transpiration (Wright *et al.* 2004). Leaf toughness strongly influences leaf life span, plant–herbivore interactions, litter decomposition and nutrient cycling (Onoda *et al.* 2011). WSG represents a trade-off between mortality and growth rates (Swenson & Enquist 2007; Wright *et al.* 2010). Seed mass is an important trait for regeneration; it represents a trade-off between colonization and competition (Moles & Westoby 2006). Diameter is allometrically related to height (Thomas 1996). Consequently, $D95_{0.1}$ is independent of species abundance and highly correlated with maximum plant height (King, Davies & Noor 2006), which is related to successional status and light niche (Aiba & Kohyama 1997). RGR_{95} is correlated with mortality rate of the slowest growing individuals (Wright *et al.* 2010) and is a direct indicator of growth strategies.

TRAIT MEASUREMENT

Although mean values of leaf traits change during transitions from sapling to adult, ranks of species by leaf traits tend to be consistent across ontogenetic stages (Kitajima & Poorter 2010). Therefore, we used leaf trait measures on saplings to calculate representative mean trait values for species. During September 2009, we randomly collected mature leaf samples from outer canopy leaves of saplings in the 1–5 cm d.b.h. size class growing under closed canopy in the plot. Following established criteria (Cornelissen *et al.* 2003), we excluded individuals with signs of severe herbivory damage. Two to 20 leaves were sampled from 1 to 8 individuals belonging to 76 of the 80 dipterocarp species (Table S1). Fresh leaf sizes (cm^2) were measured on scanned images using IMAGEJ (http://rsbweb.nih.gov/ij/). Leaf mass was recorded before and after drying at 60 °C to constant weight. SLA ($cm^2\ g^{-1}$) was calculated as the ratio of fresh leaf size to dry mass. Leaf succulence ($g\ H_2O\ cm^{-2}$) was calculated by subtracting leaf dry mass from leaf fresh mass and dividing by leaf fresh size. Leaf toughness (leaf fracture resistance; $kN\ m^{-1}$) was estimated as the mean of three punch tests per unit fracture length performed with a digital penetrometer (3.0 mm diameter, model RX-1; Aikoh, Osaka, Japan) on two fresh leaves from each individual. N_{mass} (%) values were determined from ground leaf samples using an NC analyser (Vario EL III; Elementar Analysensysteme, Hanau, Germany).

Wood specific gravities were obtained for 46 of the 80 dipterocarp species in the plot from literature on tropical timber properties (Soerjanegara & Lemmens 1994). We used WSG ($g\ cm^{-3}$: dry mass by fresh volume) values for the analyses. When literature reports provided only wood densities at 10–18% moisture content rather than basic wood densities, we multiplied available values by 0.861 for conversion to WSG (Chave *et al.* 2006; Swenson & Enquist 2007).

Seed masses [weight (mg) of 1000 seeds] were obtained for 17 of the 80 dipterocarp species in the plot from the Royal Botanic Gardens Kew Seed Information Database (http://data.kew.org/sid). Seed volumes (mm^3) were obtained for 71 of the 80 species (including the 17 whose seed mass statistics were extracted from the Kew data base) from the literature on dipterocarps (Newman, Burgess & Whitmore 1998). As seed mass and volume were well correlated (seed mass = 1.02 × seed volume; $r^2 = 0.91$; $n = 17$ species), we used the regression equation to convert seed volumes to seed masses.

$D95_{0.1}$ is known to highly correlated with maximum height and was calculated as the 95th quantile of the diameter distribution for all trees that had reached > 10% of the maximum diameter for the species (King, Davies & Noor 2006). This method cannot be used on rare species; therefore, we used maximum d.b.h. for species represented by < 20 individuals in the plot.

Relative diameter growth rates (RGR; % $year^{-1}$) and RGR_{95} were based on tree censuses in the FDP in 1997 and 2003 and calculated as $RGR = \ln(DBH_f/DBH_i)/[(t_f - t_i)/365]$, where DBH_f and DBH_i are d.b.h. values at the 1997 (t_f) and 2003 (t_i) censuses, respectively. RGR_{95} represents growth under favourable conditions and was calculated as the 95th quantile of RGR.

Specific leaf area, leaf size, N_{mass}, leaf toughness, leaf succulence and seed mass were $\log_{10}$-transformed to meet the assumption of normality in the data.

PLOT-WIDE HABITAT FILTERING AND LIMITING SIMILARITY

We tested for non-random patterns of community assembly using randomly generated null communities for all dipterocarp trees ≥1 cm d.b.h. The entire plot was divided into one thousand three hundred 20 × 20 m quadrats; we considered each quadrat as a local community. To determine whether observed trait distribution patterns for each quadrat deviated from those expected by chance, we generated 999 random communities for each quadrat using the independent swap algorithm (Gotelli 2000) implemented in the R software package 'picante' (Kembel *et al.* 2010). This independent swap algorithm constrains the row and column sums of the quadrat/species occurrence matrix to the original matrix while swapping species among quadrats using chequerboard submatrices. This null model constrained the occurrence frequency for each species in the null community to a value equal to the actual frequency in the plot; therefore, the model considered a dispersal-limited assembly mechanism. There were 20 000 swaps for each run.

We used four metrics [i.e. variance, range, kurtosis and SDNDr (see definition later in this paragraph)] to quantify trait distributions within quadrats. Habitat filtering is expected to restrict the range of trait values and reduce the variance of trait values within a community (Cornwell, Schwilk & Ackerly 2006; Kraft, Valencia & Ackerly 2008). To test for habitat filtering, we determined whether the variance or range of traits in each quadrat was less than the null prediction for individual quadrats. As the range of trait values is likely to be affected by extreme trait values, we used both variance and range as metrics for habitat filters. Limiting similarity is expected to space the trait distribution evenly and lead to a platykurtic distribution (Kraft, Valencia & Ackerly 2008; Cornwell & Ackerly 2009). To test for limiting similarity, we sorted species by their trait values within each quadrat and calculated all neighbour distances as the difference in trait values between two species of adjacent trait-value ranks. We then quantified the standard deviation of neighbour distance divided by the range of traits present (SDNDr) (Stubbs & Wilson 2004; Ingram & Shurin 2009). We determined whether the kurtosis or SDNDr of traits in each quadrat was less than the null prediction for individual quadrats. Kurtosis and SDNDr are the most powerful metrics to detect limiting similarity (Kraft & Ackerly 2010). As lower kurtosis indicates that trait distributions are flatter and broader and lower SDNDr indicates that trait distributions are more evenly spaced than expected by chance, one measure may be more prone to statistical bias. Therefore, we used both metrics.

We used a standardized effect size (SES) to assess the significance of non-random patterns of trait distribution. We calculated an SES for each metric: $SES = (Metric_{obs} - Metric_{null})/Metric_{SD}$, where $Metric_{obs}$ is the value of the observed metric in the quadrats, $Metric_{null}$ is the mean value of the metric for quadrats in 999 null communities and $Metric_{SD}$ is the standard deviation of the metric for quadrats in 999 null communities (Gotelli & Graves 1996). We subsequently used a one-tailed Wilcoxon test to determine whether mean values of SES were significantly different from zero among all quadrats in the plot.

As trait distribution patterns were positively spatially autocorrelated, which may lead to misinterpretation of environmental effects on trait distribution, we transformed all SES and quadrat trait means and removed spatial autocorrelation from the residuals. To do this, we used a simultaneous spatial autoregressive model (SAR) (Kembel & Hubbell 2006) with the generalized least-square model based on a first-order queens case spatial connectivity; calculations were made with the R software package 'spdep' (http://www.r-project.org/). These were intercept-only models with metrics as response variables. Transformed metrics were used for all analyses.

ASSEMBLY PROCESSES ALONG A SOIL RESOURCE GRADIENT

In a previous study (Davies *et al.* 2005), four soil types in the FDP were distinguished by variation in nutrient concentrations (total C, N and P; pH; and extractable K, Ca and Mg) and elevation on a 20 × 20-m scale. Ranked in descending order of fertility and moisture, these soil types are referred to as C, FL, L and SL (Russo *et al.* 2005). Davies *et al.* (2005) identified tree species in the FDP with spatial distribution patterns biased with respect to these four soil types using a Poisson cluster model (Plotkin *et al.* 2000). Among the 764 species tested, 73% had distributions significantly associated with one or two soil types, suggesting that species identity might be a critical factor for habitat filtering processes. To test the importance of soil resource availability as a habitat filtering process, we compared SES values of variance and range obtained from a plot-wide null model with those from a null model restricted by soil type. This was performed with an independent swap algorithm for each soil type. In this null model, species were swapped only within soil types, which allowed us to detect non-random trait distribution patterns in individual soil types. We calculated percentage reduction in the absolute values of mean SES of variance and range when the restricted null model was implemented. The significance of SES reduction was assessed with a one-tailed Wilcoxon test. The amount of reduction was considered as the relative contribution of soil resource availability to habitat filtering. Additionally, we looked for evidence of habitat filtering and limiting similarity within soil types. The Wilcoxon test was also used to assess statistical significance following SAR transformation.

A recent study suggested the detection of community assembly rules dependent on the pool of samples considered (de Bello 2011). To determine whether observed reduction of SES arises from the restricted species pool itself, rather than the distribution of species and traits related to soil resource availability, we tested whether soil types reduced SES more than expected by 100 random divisions of the plot into four classes. This was performed with an independent swap algorithm for each class.

To test whether mean trait values, and strengths of habitat filtering and limiting similarity differed among soil types, we compared metrics among soil types with one-way ANOVA followed by Bonferroni correction for multiple pairwise tests at $P = 0.05$.

Lastly, to investigate whether there were phylogenetic constraints on species distributions, we performed a likelihood ratio test to determine whether genera were positively or negatively associated with any of the four soil types. Soil type preferences of each species (Davies *et al.* 2005) are listed in Table S1. The species has a positive (1), negative (−1) or neutral (0) association with a given soil type.

All statistical tests were performed using R version 2.10 software (R Development Core Team 2009).

Results

PLOT-WIDE HABITAT FILTERING AND LIMITING SIMILARITY

Dipterocarp community structure had consistently non-random trait distribution patterns (Table 1). Relative to the null expectation, trait ranges and variances were significantly reduced for SLA, leaf size, N_{mass}, leaf toughness, leaf succulence, seed mass and RGR_{95}. Trait kurtosis was significantly reduced for SLA, leaf size, N_{mass}, seed mass, WSG and RGR_{95}. Trait SDNDr was significantly reduced for N_{mass}, leaf toughness, leaf succulence, WSG, $D95_{0.1}$ and RGR_{95}.

ASSEMBLY PROCESSES ALONG A SOIL RESOURCE GRADIENT

A null model restricted to each soil type significantly reduced the effect sizes of trait distributions (Table 2). Both the

Table 1. Plot-wide trait-based dipterocarp community structure in the 52-ha Lambir Forest Dynamics Plot, Lambir Hills National Park, Sarawak, Malaysia

	Habitat filtering				Limiting similarity			
	Variance		Range		Kurtosis		SDNDr	
	Mean SES	*P*	Mean SES	*P*	Mean SES	*P*	Mean SES	*P*
SLA	−0.305	< **0.001**	−0.302	< **0.001**	−0.124	**< 0.001**	0.817	1.000
Leaf size	−0.014	< **0.001**	−0.059	< **0.001**	−0.073	< **0.001**	0.224	1.000
N_{mass}	−0.143	< **0.001**	−0.185	< **0.001**	−0.219	< **0.001**	−0.011	**0.005**
Leaf toughness	−0.261	< **0.001**	−0.169	< **0.001**	0.340	1.000	−0.464	< **0.001**
Leaf succulence	−0.303	< **0.001**	−0.244	< **0.001**	0.238	1.000	−0.515	< **0.001**
Seed mass	−0.074	< **0.001**	−0.075	< **0.001**	−0.050	< **0.001**	0.825	1.000
WSG	0.035	1.000	0.069	1.000	−0.032	< **0.001**	−0.344	< **0.001**
$D95_{0.1}$	0.038	0.059	0.049	0.709	0.083	1.000	−0.514	< **0.001**
RGR_{95}	−0.074	< **0.001**	−0.096	< **0.001**	−0.084	< **0.001**	−0.061	< **0.001**

Habitat filtering leads to more restricted range and variance of trait values, whereas limiting similarity leads to broader and more evenly spaced distribution of trait values than expected (See Introduction and Methods for description). Negative mean standardized effect sizes (SES) indicate that metrics in a quadrat are smaller than expected by chance. SES was estimated with a simultaneous spatial autoregressive model. *P*-values in bold typeface indicate significant reductions in metrics compared to a null expectation (one-tailed Wilcoxon test). $D95_{0.1}$, the 95th quantile of d.b.h. distribution among all trees with d.b.h. values > 10% of the maximum for the species; N_{mass}, nitrogen per unit leaf mass; RGR_{95}, the 95th quantile of relative growth rates; SDNDr, standard deviation of neighbour distance divided by the range; SLA, specific leaf area; WSG, wood specific gravity.

Table 2. Contributions of soil resource availability to habitat filtering

	Habitat filtering					
	Variance			Range		
	ΔSES	Percentage reduction	*P*	ΔSES	Percentage reduction	*P*
SLA	0.197	64.62	**< 0.001**	0.184	60.79	**< 0.001**
Leaf size	−0.009	–	1.000	0.007	11.10	0.310
N_{mass}	0.091	64.08	**< 0.001**	0.127	68.48	**< 0.001**
Leaf toughness	0.190	72.95	**< 0.001**	0.129	75.94	**< 0.001**
Leaf succulence	0.214	70.62	**< 0.001**	0.167	68.39	**< 0.001**
Seed mass	0.026	35.29	**0.043**	0.013	17.39	0.806
WSG	–	–	–	–	–	–
$D95_{0.1}$	–	–	–	–	–	–
RGR_{95}	0.046	62.58	**< 0.001**	0.074	77.09	**< 0.001**

ΔSES and percentage reduction values indicate reductions in metrics obtained from a plot-wide null model compared to a restricted null model. *P*-values in bold typeface indicate significant reductions in SES (one-tailed Wilcoxon test). See Table 1 footnote for description of the abbreviations.

ranges and variances of SLA, N_{mass}, leaf toughness, leaf succulence and RGR_{95} and the range of seed mass shifted significantly towards random patterns in the restricted null model relative to the plot-wide null model. The distribution patterns of these traits also showed reduced SES more than expected by a random division of the plot into four classes (Table S2). The relative contributions of soil resource availability to habitat filtering ranged from 35% for seed mass to 77% for RGR_{95}.

Dipterocarp community structure also had non-random trait distribution patterns within each soil type (Table S3). Trait ranges and variances within soil types were significantly reduced for SLA, leaf size, N_{mass}, leaf toughness, leaf succulence, seed mass, WSG, $D95_{0.1}$ and RGR_{95} in any one of the

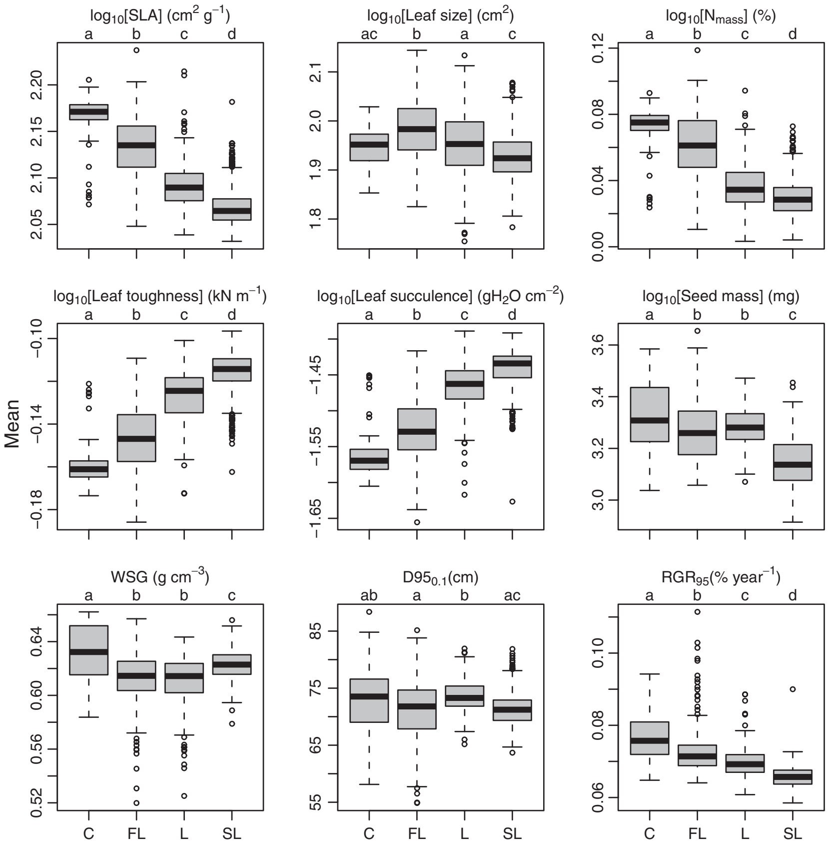

Fig. 1. Box and whisker plots comparing quadrat mean trait values among four soil types in the 52-ha Lambir Forest Dynamics Plot, Lambir Hills National Park, Sarawak, Malaysia. The centre line in each box indicates the median, and upper and lower box sides indicate the interquartile range. The whiskers extend to a maximum of 1.5 times the interquartile range. The trait mean of each metric was estimated using a simultaneous spatial autoregressive model. Trait means were compared among soil types using one-way ANOVA, followed by Bonferroni correction for multiple pairwise testing. Effects sharing the same letters are not significantly different at $P < 0.05$ level. C, clay; FL, fine loam; L, loam; SL, sandy loam; ranked in descending order of fertility and moisture. The trait abbreviations are specific leaf area (SLA), nitrogen per unit leaf mass (N_{mass}), wood specific gravity (WSG), the 95th quantile of d.b.h. distribution among all trees with d.b.h. values > 10% of the maximum for the species ($D95_{0.1}$) and the 95th quantile of relative growth rates (RGR_{95}).

four soil types. Trait kurtosis values were significantly reduced for SLA, leaf size, N_{mass}, WSG and RGR_{95} in each of the four soil types. Trait SDNDr values were significantly reduced for WSG and RGR_{95} in each of the four soil types.

Trait means weighted by presence/absence were significantly different among soil types for all traits studied (ANOVA; SLA, $F_{3,1292} = 751.3$, $P < 0.001$; leaf size, $F_{3,1292} = 85.23$, $P < 0.001$; N_{mass}, $F_{3,1292} = 474.9$, $P < 0.001$; leaf toughness, $F_{3,1292} = 747.3$, $P < 0.001$; leaf succulence, $F_{3,1292} = 745.4$, $P < 0.001$; seed mass, $F_{3,1292} = 207.6$, $P < 0.001$; WSG, $F_{3,1283} = 72.26$, $P < 0.001$; $D95_{0.1}$, $F_{3,1292} = 22.23$, $P < 0.001$; RGR_{95}, $F_{3,1292} = 315.5$ $P < 0.001$; Fig. 1). Trait means for SLA, N_{mass}, seed mass and RGR_{95} declined significantly as soil resources declined. Conversely, trait means for leaf toughness and leaf succulence increased significantly as soil resources declined. Trait means for leaf size, WSG and $D95_{0.1}$ differed significantly among soil types, but there were no consistent trends.

Standardized effect size values of metrics across traits also differed significantly among soil types (Fig. S1 in Supporting information). Variances and ranges of N_{mass} and $D95_{0.1}$ decreased in step with the decline in soil resource availability (Figs 2 and S1). The kurtosis values of SLA and leaf toughness increased with declining soil resources; kurtosis of RGR_{95} tracked a reverse trend. The SDNDr of N_{mass} increased with declining soil resources availability (Fig. S1).

There are eight genera in the FDP: *Anisoptera*, *Cotylelobium*, *Dipterocarpus*, *Dryobalanops*, *Hopea*, *Parashorea*, *Shorea* and *Vatica*. Genera did not have higher than expected numbers of species aggregated on any particular soil type ($P > 0.2$).

Discussion

PLOT-WIDE HABITAT FILTERING AND LIMITING SIMILARITY

Trait distributions of the dipterocarp tree community in the lowland tropical rain forest in Lambir were non-random. Restricted ranges and reduced variances of SLA, leaf size, N_{mass}, leaf toughness, leaf succulence and RGR_{95}, which relate to resource economics strategies (Westoby *et al.* 2002; Wright *et al.* 2004), are consistent with patterns of habitat filtering. As communities are more finely defined taxonomically, limiting similarity is more common (Swenson *et al.* 2007). Despite the very restricted subset of the phylogeny in our study (within one family only), we found evidence of habitat filtering and this result is similar to patterns observed at diverse taxonomic scales in the Neotropical rain forest of the Yasuni region in eastern Ecuador (Kraft, Valencia & Ackerly 2008) and the Neotropical dry forest in San Emilo, Costa Rica (Swenson & Enquist 2009). Closely related tropical species have been found to occupy different habitats within sites (Valencia *et al.* 2004), and variation in ecological traits among close relatives may be an important mechanism enabling species coexistence in tropical rain forests (Davies *et al.* 1998; Aiba & Nakashizuka 2005). Our results add further support to these concepts.

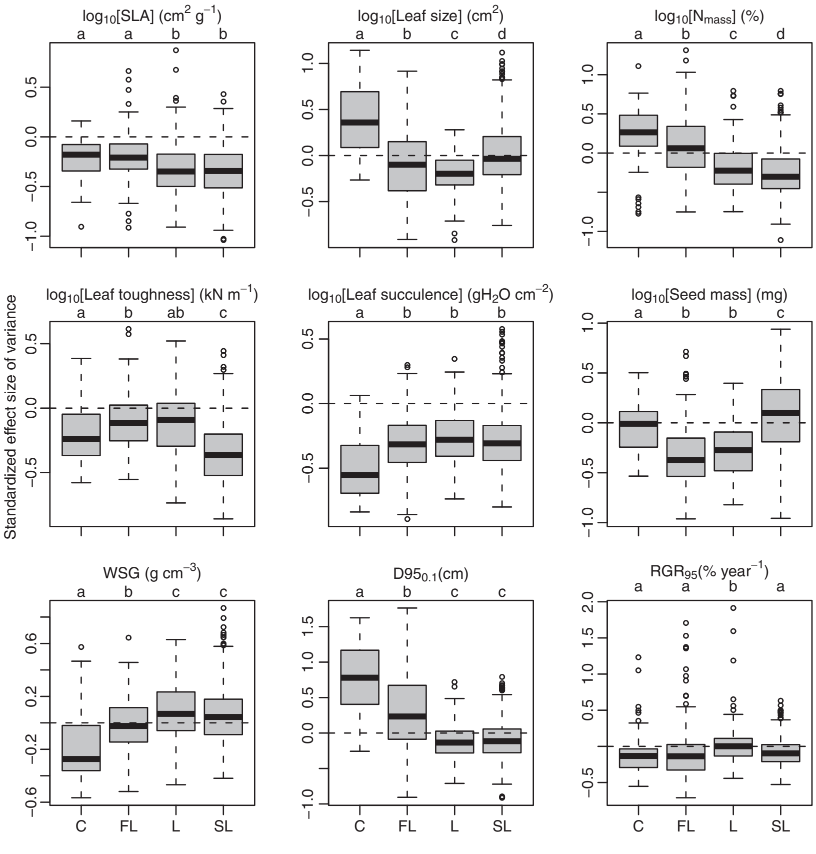

Fig. 2. Box and whisker plots comparing standardized effect size (SES) of variances among four soil types in the 52-ha Lambir Forest Dynamics Plot, Lambir Hills National Park, Sarawak, Malaysia. The centre line in each box indicates the median, and upper and lower box sides indicate the interquartile range. The whiskers extend to a maximum of 1.5 times the interquartile range. The SES of each metric was estimated using a simultaneous spatial autoregressive model and compared among soil types by one-way ANOVA, followed by Bonferroni correction for multiple pairwise testing. Effects sharing the same letters are not significantly different at $P < 0.05$ level. See Fig. 1 legend for description of the abbreviations.

In addition to habitat filtering, we also found broader distributions of SLA, leaf size, N_{mass}, seed mass, WSG and RGR_{95}, and more evenly spaced N_{mass}, leaf toughness, leaf succulence, WSG, $D95_{0.1}$ and RGR_{95} than expected from a null model within 20 m by 20 m quadrats. Even spacing of these traits, which are related to resource economics strategies, is also consistent with a concept of limiting similarity driven by niche partitioning (MacArthur & Levins 1967; May 1973). Previous studies have suggested that maximum height, which is highly correlated with $D95_{0.1}$, may be important in promoting species coexistence in forest ecosystems through light niche differentiation (Aiba & Kohyama 1997; King, Wright & Connell 2006); differentiation of regeneration niches is likely to promote species coexistence at local scales (Grime 2006; Swenson & Enquist 2009; Kraft & Ackerly 2010). Dipterocarp species are abundant in canopy layers and are considered to be late-successional species (Ashton 1988); accordingly, they span a relatively restricted light and regeneration niche space in the forest we studied. Our results also suggest that niche differentiation between relatively functionally similar species promotes species coexistence.

SOIL RESOURCE AVAILABILITY AS A HABITAT FILTERING MECHANISM

Randomizations restricted to each soil type were much closer to observed trait ranges and variances than expected from both the plot-wide null model and the randomly restricted null model, suggesting that soil resource availability acts as a habitat filter. Additionally, soil resource availability accounted for a considerable proportion of habit filtering (e.g. 73% for variance of leaf toughness and 64% for variance of SLA). We used only mean species trait values; however, incorporation of intraspecific variation improves statistical power for the detection of non-random trait patterns (Jung *et al.* 2010). Hence, we may have underestimated habitat filtering in our analysis. Previous studies demonstrated that individuals of tropical tree species tend to aggregate on soils with specific resource availabilities (Davies *et al.* 2005; John *et al.* 2007). We clearly showed that soil resource availability strongly restricted trait values and community membership in the dipterocarp component of this tropical rain forest. A previous study conducted at our site found that 73% of species distributions were restricted in most cases to one or two soil types (Davies *et al.* 2005). This finding, in combination with our results, indicates that habitat filtering in the Lambir rain forest operates on individual species according to their traits, which in turn strongly promotes differentiation of trait-value distribution among soil types. There is large variation in soil nutrients within the FDP (Lee *et al.* 2002) that may importantly shape trait-based community structure and increase diversification of dipterocarp species. Alternatively, the observed role of soil resource availability in habitat filtering processes may be maintained by phylogenetic constraints (Schreeg *et al.* 2010). That is, functionally similar species in the FDP may be very close congeneric relatives that can be distinguished by reproductive traits. However, introgressive hybridization is common among dipterocarp species (Kamiya *et al.* 2005). Moreover, genera did not have higher than expected numbers of species aggregated on any particular soil type, suggesting that close relatives belonging to the same genera were functionally diversified in the FDP.

We also found restricted ranges and reduced variances of trait values within soil types, suggesting that habitat filtering also works within the same soil types. Therefore, habitat filtering processes in the FDP cannot be explained by soil preferences alone (Davies *et al.* 2005). Microscale environmental variation within soil types may be responsible for the additional habitat filtering effects. Disturbance regime may also shape trait distribution patterns within soil types (Grime 2001). Therefore, incorporating within-habitat environmental variables and disturbance regime that determine the trait-based structure of this tropical tree community is crucially important for improved understanding of assembly processes. Additionally, our detection of limiting similarity using a restricted null model suggests that dipterocarp species diversity may be maintained by differentiation of strategies within a habitat.

ASSEMBLY PROCESSES ALONG A SOIL RESOURCE GRADIENT

All trait means differed at the quadrat scale among soil types. On fertile, moist soils, species tended to have higher SLA, N_{mass}, seed mass and RGR_{95} values and lower measures of leaf toughness and leaf succulence. Soil resources, especially nitrogen availability, are known to affect leaf nitrogen content (Ordoñez *et al.* 2009). Species with high N_{mass} tend to have high SLA (Wright *et al.* 2004), which leads to elevated growth rates (Poorter & Bongers 2006; Wright *et al.* 2010) on fertile, moist sites in the FDP. Higher SLA also decreases the leaf structural resistance (Onoda *et al.* 2011). Tough and dense leaves may be important to support long leaf life span to optimize carbon gain per unit leaf nutrient in infertile, dry sites. Seed mass represents a trade-off between colonization and competition (Moles & Westoby 2006) and was positively correlated with RGR_{95} (Table S4). Thus, species with large seed mass are competitive and may be favoured on fertile, moist sites where fast-growing dipterocarp species tend to be distributed. Habitat may restrict trait values to narrow ranges, causing shifts in mean values along the soil resource gradient. We demonstrated that habitat filtering may simultaneously restrict trait ranges within tree communities and among different soil types.

Most of the trait values indicated that strengths of habitat filtering and limiting similarity differed among soil types (Fig. S1). Leaf traits were correlated with one another at the species level (Table S4). Hence, we expected similar trends in habitat filtering strengths across the soil resource gradient among these correlated traits. However, we detected two types of change in the strength of habitat filtering that restrict trait values. First, infertile, dry soil strongly restricted trait values, but other soil types did not. For example, $D95_{0.1}$, which was highly correlated with maximum height and N_{mass}, had a more restricted range and reduced variance on infertile, dry sites than on fertile, moist sites. Hence, species in fertile, moist sites are able to select from among a broad range of ecological strategies made available to them by the abundance of belowground resources. Second, all soil types restricted trait values to a moderate extent. For example, trait values of SLA and leaf toughness were restricted on all soil types.

We also found that the strength of limiting similarity varied among soil types. The breadth of distributions of SLA, leaf toughness and N_{mass} was greater at the higher end of the soil resource gradient; RGR_{95} tracked a reverse trend. Although there was no evidence of shifts in assembly processes that matched patterns in the distributions of traits associated with growth and resource conservation strategies, the relative importance of habitat filtering and limiting similarity across different traits may nevertheless vary along the soil resource gradient.

Conclusions

Habitat filtering can be thought of as a match between ecological strategies and particular environmental conditions, but this concept has seldom been explored quantitatively. We demonstrated that soil resource availability restricts and largely reduces the range and variance of trait values, contributing to a considerable proportion of habitat filtering processes within a Malaysian tropical rain forest. Variation in soil resource availability between soil types may sort species into different habitats. Within soil types, both environmental filtering and limiting similarity mechanisms operated simultaneously, but the strengths of these assembly processes differed between fertile and infertile soil types. Together, these mechanisms operating at different scales between and within soil types promote trait diversification and coexistence among dipterocarp trees in the FDP. Lastly, while our study is based on a single family, the strength of assembly processes may differ among taxa, which may play an important role in speciation. An important next step is to extend our analysis to embrace the complete community with all other plant taxa and ecological strategies also represented. The phylogenetic structure of the community will help to link the assembly of the community to its evolutionary history (Cavender-Bares *et al.* 2009).

Acknowledgements

We thank the Forest Department of Sarawak and Sarawak Forest Research Corporation for their kind permission to conduct research in Lambir Hills National Park. We also thank many people who contributed to the 52-ha Long-Term Ecological Research Project. The 52-ha Long-Term Ecological Research Project is a collaborative project of the Forest Department of Sarawak, Malaysia, Harvard University, USA (under NSF awards DEB-9107247 and DEB-9629601 to P.S. Ashton), and Osaka City University, Japan (under Monbusho grant 06041094 to T. Yamakura, 08NP0901 to S. Tamura and 09NP0901 to S. Sasaki). We are also grateful to Douglas and Rose for their assistance in the field, to N. Swenson for helpful advice on the analyses, to M. Aiba, P. Bellingham, W. Cornwell, H. Cornelissen, K. Kitajima and one anonymous referee for constructive comments on an early draft of the manuscript. This study was supported by Grant-in-Aid for JSPS Fellows to M.K and partly supported by Grant-in-Aid for Scientific Research (B) (2337007) and the Environment Research and Technology Development Fund (S-9-3) of the Ministry of the Environment, Japan.

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Received 12 May 2011; accepted 9 November 2011
Handling Editor: Hans Cornelissen

Supporting Information

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

Table S1. Trait and habitat preference data for each species.

Table S2. Contributions of soil resource availability to habitat filtering obtained from a randomly restricted null model compared to a restricted null model.

Table S3. Within soil types trait-based dipterocarp community structure in the FDP.

Table S4. Pairwise Pearson's product-moment correlations (r) between the nine functional traits used in this study.

Figure S1. Box and whisker plots comparing standardized effect sizes (SES) of (a) range, (b) kurtosis and (c) SDNDr among four soil types in the FDP.