

Interspecific variation in seedling responses to seed limitation and habitat conditions for 14 Neotropical woody species

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Summary

1. We assessed the relative importance of dispersal and niche processes in structuring plant populations at the seedling stage for 14 woody plant species (12 trees and 2 lianas) in an old-growth tropical forest of French Guiana.
2. We combined long-term data from a network of 160 stations, each comprising a seed trap and two to three neighbouring seedling plots, with fine-scale quantification of environmental variables.
3. For each species, we quantified seed limitation as the proportion of seed traps that were not reached by seeds, and establishment limitation as the proportion of stations where seeds arrived but where seedlings did not occur. All species showed strong seed limitation, whereas only one species showed significant establishment limitation.
4. We determined the proportion of variance in local seedling density explained by either seed density or environmental factors, and we assessed the effect of environment on seedling survival.
5. Although seeds showed considerable spatial clumping in all species, seed density explained a significant fraction of the variance in seedling density for only five species. Habitat preferences explained a significant fraction of the variance in seedling density for six species. Of the remaining species, four showed no significant relationship with either seed arrival or habitat conditions.
6. Environmental effects on local seedling abundance were weakly related to those on seedling survival. When seedling density was significantly correlated with a given environmental factor, survival was usually not correlated with that factor. Habitat association patterns might change over time, as environmental filtering operates.
7. *Synthesis.* Our results show that both seed arrival and habitat preferences contribute to explaining the abundance of tropical woody species at the seedling stage, but their relative importance showed important interspecific differences. Although our study was limited to a subset of woody species, they accounted for 27% of the individuals composing the seedling layer. Thus, our findings are likely to have important consequences in the structuring of the seedling community.

Key-words: environmental heterogeneity, French Guiana, habitat preferences, seed limitation, seedling regeneration, spatial distribution, survival

Introduction

Predicting the ecological processes that determine the structure of species-rich plant communities across life-history changes remains one of the major challenges in plant ecology (Tilman 1982; Hubbell & Foster 1986; Weiher & Keddy 1995; Hubbell 2001). Recently, a number of studies have examined

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the relative roles of environment and geographical distance in explaining variation of floristic diversity in tropical tree communities at different spatial scales (Potts *et al.* 2002; Tuomisto *et al.* 2003; Potts *et al.* 2004; Svenning *et al.* 2004; Chust *et al.* 2006; Jones *et al.* 2006). These approaches have relied upon the assumption that in the absence of competition or habitat partitioning, floristic similarity among plant communities should decrease with increased geographical distance as a consequence of dispersal limitation (Hubbell 2001; Chave & Leigh 2002). However, spatial variation in adult plant communities should also reflect species filtering events occurring throughout plant ontogeny (Grubb 1977; Nathan & Muller-Landau 2000), and it is unclear how these local processes scale-up spatially.

At local scales, the successful establishment of a plant necessitates overcoming two consecutive ecological filters, seed limitation, the absence of recruitment because of limited seed supply, and establishment limitation, the absence of recruitment because of limited availability of suitable microsites (Muller-Landau *et al.* 2002). Both processes have critical implications for species coexistence. Seed limitation allows inferior competitors to reach sites where better competitors fail to arrive, thereby slowing competitive exclusion and favouring chance events (Tilman 1994; Hurtt & Pacala 1995). Establishment limitation is expected to favour species coexistence if species have evolved in the habitats in which they are found, developing adaptations that may enable them to out-compete the other species in these habitats.

The respective roles of seed limitation and establishment limitation in fostering diversity during the regeneration phase have been studied in detail for several tropical tree species. Previous studies found that both rates of seed arrival (Dalling *et al.* 1998, 2002; Makana & Thomas 2004; Svenning & Wright 2005) and of seed dispersal (Stevenson 2000; Webb & Peart 2001; Hardesty *et al.* 2006) play a critical role in seedling recruitment. Another set of empirical studies has explored the role of environmental variables on the performance of selected species. Limited light availability (Nicotra *et al.* 1999; Montgomery & Chazdon 2002), soil fertility (Hall *et al.* 2003; Fine *et al.* 2004; Palmiotto *et al.* 2004), drought (Engelbrecht *et al.* 2002), and litter depth (Molofsky & Augspurger 1992) were all found to be limiting factors during the establishment of the studied tree species.

Despite the importance of these two processes, studies evaluating simultaneously the role of seed dispersal and of habitat specialization in structuring tropical plant communities during early stages remain scarce. Muller-Landau *et al.* (2002) used long-term seedfall data from seed traps and neighbouring seedling plots on Barro Colorado Island (BCI, Panama), to evaluate the importance of both seed arrival and establishment limitation for four tree species. They quantified the intensity of establishment limitation by the failure of seedlings to establish at a given microsite when seed arrival was not limiting, not by directly measuring habitat variables. Uriarte *et al.* (2005) used levels of light availability to predict the spatial variation of seedling recruitment in a tropical forest of Puerto Rico, but they used local trees as a proxy of seed sources, and did not directly quantify seed arrival. In a

previous study, we assessed the influence of seed arrival and of several environmental factors on seedling dynamics at the community level in a tropical forest of French Guiana (Norden *et al.* 2007). We showed that, irrespective of species identity, community-wide seedling dynamics were driven both by inter-annual variation in seedfall and by environmental filtering. Yet, it remains unclear whether this pattern is uniform among species or whether species show differential responses to seed supply and to environmental factors.

In this study, we investigated the role of seed limitation and establishment limitation on the abundance and survival of 14 woody seedling species displaying a wide variety of life-history traits in an old-growth tropical forest of French Guiana. We quantified seed limitation using long-term seedfall data from seed traps, and we evaluated establishment limitation by monitoring seedling plots adjacent to the seed traps, in which several environmental variables were measured (light availability, soil fertility, topography and litter depth). The spatial distribution of seedlings may follow one of two patterns depending on the relative importance of dispersal- and niche-based processes. If the main predictor of seedling recruitment is seed arrival, then we predict spatial concordance between seedfall and seedling abundance. The more seed-limited a species is, the more dependent on seed arrival seedling spatial patterns should be (Nathan & Muller-Landau 2000). However, if seedlings are filtered by the habitat, differential survival among habitat conditions should lead to niche-based distributional biases in the spatial distribution of seedlings (Grubb 1977). Specifically, we address the following questions: (i) What is the relative strength of seed limitation and of establishment limitation during seedling regeneration? (ii) To what extent does spatial variation in seedling density reflect seed limitation and further environmental filtering? (iii) Are the differences in species abundance among habitats generated by differential survival across environmental conditions?

Methods

STUDY SITE

This study was conducted at the Nouragues Biological Station, in a pristine tropical rainforest of French Guiana (4°05'N, 52°40'W; Bongers *et al.* 2001). Average annual rainfall is 2990 mm with a 2–3 month dry season, from September to November. The study area consists of two permanent sampling sites of tropical rain forest covering 82 ha in total. One of the sites, henceforth called Grand Plateau (GP), is 70-ha in area and it is on clay soil with a metamorphic volcanic substrate. The other site, Petit Plateau (PP), is 12-ha and its soil is a granitic-derived sandy-clay mixture. Fruiting phenology in the area shows marked seasonal patterns. The species richness and biomass of ripe fruits, especially of animal-dispersed ones, peaks in April–May and is minimal in August–September (Sabatier 1985; P.-M. Forget, N. Norden and P. Châtelet unpublished data).

SEED AND SEEDLING CENSUSES

Beginning in February 2001, we established a network of 160 seed traps, each 0.5-m² in size, and placed at 1.5 m above-ground to avoid

disturbance by large mammals. Twenty traps were set up along each of five parallel trails in the GP (totalling 100 traps), and fifteen along each of four parallel trails in the PP (totalling 60 traps; Norden *et al.* 2007). Seeds and fruits were collected twice monthly since the establishment of the network. This study presents results based on data until July 2006. Viable seeds (with undamaged endosperm or tegument) were counted and identified to species or morpho-species using a reference seed collection, but also using van Roosmalen (1985), and examining vouchers at the Herbar de Guyane (Cayenne, CAY). When a sample could not be given a species name, it was given a morpho-species name (see Appendix S1 in Supporting Information).

In February 2004, we established three 1-m² seedling plots around 50 seed traps within the GP, and two 1-m² seedling plots around the remaining 110 traps; totalling 370 plots (250 plots in the GP and 120 plots in the PP). Seedling plots were established 1.5 m from the edge of the trap in the directions that do not face the trail. We henceforth call a 'station' the seed trap plus the seedling plots around the trap. Between February and March 2004, all woody seedlings in the plots were tagged with a unique number, mapped, and were measured for height to the apical bud. Here, we focus our analyses on seedlings < 100 cm in height. Subsequent censuses took place twice a year, in October 2004, March 2005, October 2005, and July 2006. During each census, newly recruited seedlings were tagged, mapped and measured, and missing seedlings were recorded as 'dead'. Surviving seedlings were measured once a year. Seedlings were identified to morpho-species by comparing them to digital photographs of a reference collection of seedling specimens growing in the vicinity of the plots. Vouchers were compared to botanical specimens at the Herbar de Guyane. When vouchers could not be matched reliably to botanical specimens, they were given morpho-species name (see Appendix S1).

ENVIRONMENTAL VARIABLES

In October 2004, we took hemispherical photographs above each seedling plot using a Nikon Coolpix 2300 camera with a Nikon FC-8 fisheye lens. Photographs were taken at 1.30 m above the ground, early in the morning (6:30–8:00 am) or late in the afternoon (4:40–6:30 pm) to avoid over-exposure by direct sunrays (Montgomery & Chazdon 2002). Because light intensity varies considerably

during sunset and sunrise, the pictures were taken at different exposure times (1/60, 1/125 and 1/250) to ensure the same level of contrast between canopy openings and the surrounding vegetation. Digital photographs were analyzed using the software Gap Light Analyzer (GLA Version 2.0; Frazer *et al.* 1999). Photographs with the best contrast and the least over-exposure were selected for analysis so that all had approximately the same level of contrast.

In October 2004, we collected soil samples near each seed trap to characterize the soil chemical composition. Around each trap 1 kg of topsoil (0–10 cm depth) was collected, by bulking four soil samples. Superficial leaf litter and the humus layer were removed before soil sampling. Soil samples were dried in the field at *c.* 60 °C during 24-h and then stored in dried conditions until laboratory analysis. In the laboratory, the samples were re-dried at 50 °C during 3 days, and then filtered with a 2-mm mesh sieve. After crushing the fine fraction (< 2 mm), total concentration of five major elements (Ca, Mg, K, Al, Fe) was measured with an ICP-OES (Inductively Coupled Plasma-Optical Emission Spectrometry, Thermo Jarrell Ash® Iris Advantage). Carbon and Nitrogen concentrations were measured using a CHN analyzer (NA 2100 Protein, CE Instruments®). Soil pH was measured in a standard solution made of one volume of soil diluted into three volumes of water.

For each plot, mean leaf litter depth was measured to the nearest 0.5 cm from five random points using a ruler. Because leaf litter fall is strongly seasonal, it was measured at each census. Mean values over time were computed at every station from all values obtained for each census. Finally, we measured the slope at each station with a laser telemeter (LaserAce® 300), and we defined the local topography as a categorical variable with three levels: flat (1–7°), low slope (8–14°), and steep slope (15–31°).

STUDY SPECIES

Fourteen taxa were present in sufficient number both as seeds and seedlings to be included in the analyses (Table 1). For 10 species (nine trees and one liana), identification was reliable to the species-level. Two additional trees (*Qualea* sp. 1 and *Licania* sp. 1) could not be confidently matched to specimens at the Herbar de Cayenne. However these trees were unambiguously identified to the morpho-species level both at the seed and seedling stage and thus were also

Table 1. Species, life forms, dispersal syndromes, seed masses and sample sizes. Life forms are tree (T), liana (L). Life histories are shade-tolerant (ST) and light-demanding (LD). Life forms and life histories are from Mori *et al.* (2002). Dispersal mode is from van Roosmalen (1985). Seed mass is the mean diaspore mass estimated from 10 dried seeds

Species	Family	Life form	Life history	Dispersal mode	Seed mass (g)	Number of seeds	Number of recruits
<i>Bauhinia</i> spp.	Fabaceae	L	ST	Ballistic	0.27	101	289
<i>Chrysophyllum lucentifolium</i> Cronquist	Sapotaceae	T	ST	Animal	1.08	41	110
<i>Dicorynia guianensis</i> Amshoff	Fabaceae	T	LD	Wind	0.32	396	29
<i>Eperua falcata</i> Aubl.	Fabaceae	T	ST	Ballistic	3.52	37	65
<i>Hippocratea volubilis</i> L.	Celastraceae	L	LD	Wind	0.07	272	563
<i>Licania membranacea</i> Laness.	Chrysobalanaceae	T	ST	Animal	0.37	1083	141
<i>Licania</i> sp. 1	Chrysobalanaceae	T	ST	Animal	0.61	418	136
<i>Pourouma</i> spp.	Urticaceae	T	LD	Animal	0.44	525	182
<i>Pseudopiptadenia suaveolens</i> (Miq.) J. W. Grimes	Fabaceae	T	LD	Wind	0.05	374	121
<i>Qualea</i> sp. 1	Vochysiaceae	T	LD	Wind	0.02	312	46
<i>Quararibea duckei</i> Huber	Malvaceae	T	ST	Animal	0.45	94	212
<i>Sterculia pruriens</i> (Aubl.) K. Schum.	Malvaceae	T	ST	Animal	1.71	56	160
<i>Tetragastris altissima</i> (Aubl.) Swart	Burseraceae	T	ST	Animal	0.49	33	132
<i>Virola michelii</i> Heckel	Myristicaceae	T	ST	Animal	1.62	55	59

included in the analyses (see Appendix S1). We also included two taxa that contain more than one species. *Bauhinia* spp. is a species-rich liana genus, but in the study area it potentially contains only two species: *Bauhinia guianensis* Aubl. (abundant) and *Bauhinia siqueirae* Ducke (rare), plus other taxa often considered as synonymous to *B. guianensis* (Boggan *et al.* 1997; Mori *et al.* 2002). Their distinction, based on the secondary venation of the leaf blades, is difficult since seedlings show an important heterophylly, and the seeds look very similar. *Pourouma* spp. may comprise up to seven species in the study area (Mori *et al.* 2002). While seeds and seedlings are easily identified to genus, species-level identifications are difficult to make, with the exception of one species, *Pourouma minor*. In our analysis, *Pourouma* spp. denoted all species in the genus *Pourouma*, except for the shade-tolerant strategist *P. minor*. Throughout the paper, we loosely refer to all taxa with the term 'species', and for brevity, we refer to them by their generic names, except for *Licania*. A detailed description for each species, comprising pictures of seeds and seedlings, is provided in Appendix S1. The selected species are scattered across the angiosperm phylogeny, thus we do not expect any phylogenetic bias in our results.

STATISTICAL ANALYSES

Seed and establishment limitation

To assess the relative strength of seed limitation, we measured the proportion of stations that were not reached by seeds ('fundamental seed limitation' *sensu* Muller-Landau *et al.* 2002). This measure was defined as follows:

$$\text{Seed limitation} = 1 - \frac{a}{n} \quad \text{eqn 1}$$

where a is the number of stations receiving seeds throughout the study period, and n is the total number of stations. To quantify the strength of establishment limitation, we measured the proportion of stations where seeds arrived but where seedlings did not occur ('realized establishment limitation' *sensu* Muller-Landau *et al.* 2002).

$$\text{Establishment limitation} = 1 - \frac{r}{a} \quad \text{eqn 2}$$

where r is the number of stations where both seeds and seedlings occurred. This calculation gives information on establishment, once seeds have successfully reached a site.

Because abundant species tend to reach more sites than rare species, these measures are biased by sample size. We thus compared observed seed and establishment limitation measures with those obtained from simulations using a null model in which seeds and seedlings occurred randomly in the stations, according to a Poisson distribution. One thousand random replications were generated using the observed number of seeds and seedlings of each species. For each replication, we first calculated the number of stations reached randomly by seeds, then the number of stations where seeds had already been found, also reached by seedlings. We then compared observed values with 95% confidence limits of the simulated ones. To compare the strength of seed and establishment limitation among species by accounting for differences in seed abundance, we calculated δ_{seed} and δ_{seedling} , the relative difference between the observed and expected seed and establishment limitation, respectively. This measure varies between -1 and 1: the more positive δ is, the more limited the species is, and vice-versa. Finally, to test the influence of each of seed size, dispersal syndrome and life history on δ , we performed a one-way ANOVA followed by a *post hoc* Tukey HSD test. Seed mass

was transformed to a 3-level factor distinguishing small size (< 0.1 g), medium size (0.1–1 g) and large size seeds (> 1 g).

Linear modelling of seedling density

For each species, we used linear regression models to evaluate the extent to which local seedling abundance reflected seed arrival and environmental filtering. We modelled the ln-transformed values of seedling density (number of seedlings m⁻²) at each station against the ln-transformed values of seed density (number of seeds m⁻²) at each trap. We added 1 before the ln-transformations because seed or seedling densities were equal to zero in several stations. We used seedling density rather than the total number of seedlings at each station because the number of seedling plots per station was uneven across stations. Since seedlings censused in the initial census represent a multiple-aged cohort, and it was impossible to date the fruiting events from which they were recruited, we distinguished the initially sampled seedlings from seedlings recruited in the subsequent censuses. We thus separately related (i) seedlings censused in the initial census (March 2004) with seeds censused from February 2001 to February 2004 (period henceforth called 'c0'); and (ii) seedlings recruited in subsequent censuses (October 2004 to July 2006) with seeds censused from April 2004 to June 2006 (period henceforth called 'recruits'). Species were excluded from a particular analysis if they had < 20 recorded seeds or seedlings, to avoid bias due to lack of statistical power. Because seedlings were unevenly distributed across stations, we restricted this analysis to the stations where the presence of either seeds or seedlings was reported. Hence, we tested the existence of a correlation between seed and seedling densities only within the restricted range of potential seed distribution in the study area.

Since establishment limitation operates after seed limitation, we assessed the effect of habitat conditions after seed deposition by modelling the residuals from the seed-seedling regression model against environmental variables. To reduce the number of variables describing soil factors, we performed a principal components analysis (PCA) on physical and chemical soil variables for the entire set of sampling stations. Of the 160 stations, three were excluded because of technical difficulties during the chemical analyses, hence reducing our sampling size to 157 stations. In all subsequent correlative analyses, we used the scores of the two principal components describing variation in soil environmental conditions. The first PCA axis distinguished GP from PP stations, highlighting geological differences between these two plots (Fig. 1). The second PCA axis represented a gradient of conditions in soil fertility. This axis was positively related with soil organic matter and it was negatively related with pH. Together, these axes explained 69.6% of the variance in soil conditions. Henceforth, we refer to the first PCA axis as 'soil PC1' and to the second as 'soil PC2'. Because several measures were taken to describe light availability (canopy openness, percentage of diffuse and direct transmitted radiation), we also performed a PCA on light variables and used the first PCA axis, which explained 99.3% of the variance in light conditions. Our full set of environmental variables therefore included five variables: the two PC variables describing soil conditions, the PC variable describing light conditions ('light'), litter depth, and slope.

Linear modelling of seedling survival

To analyse seedling survival, we performed an individual-based analysis for each species. We predicted the demographic status of the individual (alive = 1, dead = 0) at the last census date by logistic regressions. The dependent variables were (i) the environmental

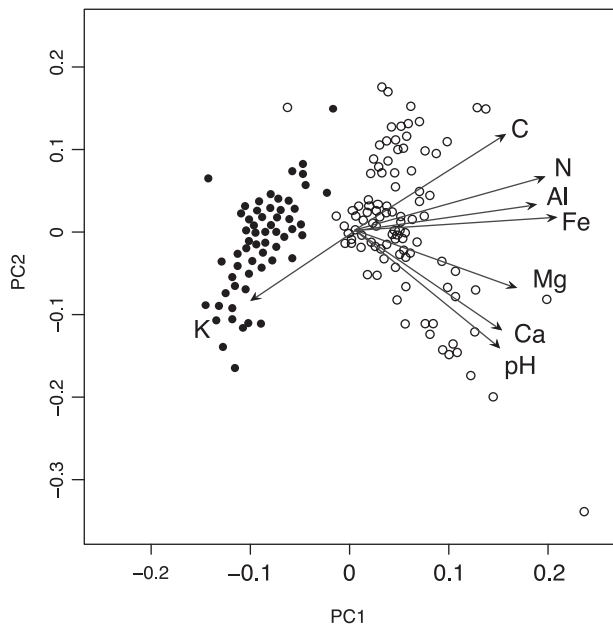


Fig. 1. Principal component analysis of the soil variables in 157 stations. Black circles illustrate Petit Plateau's stations and open circles illustrate Grand Plateau's stations.

variables, (ii) the ln-transformed total counts of seeds in each seed trap throughout the study period, (iii) the mean conspecific density of seedlings in each station during the life span of the individual, (iv) the initial height and (v) a 2-level factor indicating whether seedlings were recruited in the initial census ('c0') or subsequently ('recruits'). We included total seedfall and conspecific seedling density in the analysis because these factors are likely to influence seedling survival. Typically, most seeds fall close to parent trees, thus seedfall has greater chances to occur in the vicinity of a parent tree (Janzen 1970). Seed input is therefore an informative factor in terms of habitat association if seedling survival is higher in the habitat with which adults are associated. Likewise, the density of conspecifics is informative in terms of habitat association if seedling survival is enhanced in sites where conspecifics are abundant, suggesting that the site is of good quality for the target species. Also, initial seedling size confers many advantages to seedlings since large seedlings are more likely to withstand environmental hazards than small ones (Leishman *et al.* 2000). Initial height could therefore be an important predictor of seedling survival.

To test the influence of seed size, dispersal syndrome and life history on seedling recruitment patterns, we used a linear model including all the species to predict the ln-transformed values of seedling density against (i) ln-transformed values of seed density, (ii) species, (iii) seed size class, (iv) dispersal syndrome, and (v) life form. We also performed a logistic regression to predict the demographic status of the individual at the last census against the species term and the traits considered.

For both density and survival models, we performed a step-wise procedure to select the best statistical model based on the Akaike Information Criterion (AIC). The step-wise model selection method performs a random search through the space of possible combinations of predictor variables, dropping and adding predictors sequentially until the model with the lowest AIC is found. This procedure minimizes the risk of multi-collinearity, while maximizing the explanatory power of the data set (Burnham & Anderson 2002).

All statistical analyses were performed using the R statistical package (R Development Core Team 2006, version 2.4.1).

Results

SEED AND ESTABLISHMENT LIMITATION

A total of 18 561 undamaged seeds were collected in the 160 seed traps between 14 February 2001 and 14 July 2006 (65 months). Of these seeds, 3797 belonged to the 14 study species (21%). The 370 seedling plots included 8449 seedlings, of which 2245 belonged to the study species (27%). The most abundant species at the seedling stage were *Hippocratea*, *Quararibea*, and *Licania membranacea* (Table 1).

Overall, seed limitation was higher than establishment limitation (Table 2). For all species, observed seed limitation was higher than expected under a null model of random dispersal (Table 2, Fig. 2). In contrast, establishment limitation was higher than expected under a null model for only one species, lower for six, and not significantly different from a null model for seven (Table 2, Fig. 2). Seed size class had a nearly significant effect on seed limitation (δ_{seed} ; see Appendix S2), with small-seeded species showing marginally higher seed limitation than large-seeded species (Tukey HDS, $P = 0.07$). Establishment limitation ($\delta_{\text{establishment}}$) was not related with any of the traits considered (see Appendix S2).

RELATION OF SEEDLING DENSITY WITH SEED DENSITY AND ENVIRONMENTAL VARIABLES

The relationship between seed and seedling densities exhibited much variation among species and between census periods (Table 3). The deviance in seedling density data explained by seed density varied between 0% and 39%. For the already established seedlings in the initial census, seedling density was positively related to seed density for four species (*Bauhinia*, *Hippocratea*, *Pourouma* and *Sterculia*; Fig. 3), and negatively so for three species (*Qualea*, *Quararibea* and *Virola*; Fig. 3). For the seedlings recruited in subsequent censuses, this relationship was positive for two species (*Hippocratea* and *Pseudopiptadenia*) and negative for another two (*Quararibea* and *Virola*). The six remaining species did not show any relationship between seed and seedling densities.

The relationship between seedling density and environmental variables is summarized in Table 4. The deviance explained by environment varied between 0% and 18%. For nine species, environmental factors had a significant or a nearly significant effect on seedling density for seedlings either censused initially or recruited subsequently (*Bauhinia*, *Chrysophyllum*, *Dicorynia*, *Hippocratea*, *Pseudopiptadenia*, *Qualea*, *Quararibea*, *Tetragastris* and *Virola*). Among the five light-demanding species, two showed significantly positive associations with light availability (*Dicorynia* and *Qualea*). Two shade-tolerant species, *Quararibea* and *Virola*, were positively associated with light, and another two, *Bauhinia* and *Tetragastris* were negatively so. The influence of light availability was more conspicuous on already established seedlings than on newly recruited ones. Soil conditions and topography influenced local seedling density for six species (*Bauhinia*, *Chrysophyllum*, *Hippocratea*, *Quararibea*, *Tetragastris* and *Virola*). Newly

Table 2. Number of stations where the presence of seeds and/or seedling have been reported over the 160 stations, observed seed- and establishment-limitation measures, and mean of the randomized seed- and establishment-limitation measures for each species. Confidence intervals of the randomized measures (obtained from 1000 replications) are given in parentheses. Significant observed values of seed and establishment limitation are indicated in bold. A sign (+) or (-) indicates whether limitation is higher or lower than expected under a null model, respectively

Species	Number stations receiving seeds	Number stations with seedlings	Seed limitation	Randomized seed limitation	Establishment limitation	Randomized establishment limitation
<i>Bauhinia</i> spp.	28	52	0.83 (+)	0.53 (0.49–0.57)	0.11	0.16 (0.08–0.24)
<i>Chrysophyllum lucentifolium</i>	13	32	0.92 (+)	0.77 (0.75–0.80)	0.23 (-)	0.50 (0.36–0.65)
<i>Dicorynia guianensis</i>	46	20	0.71 (+)	0.08 (0.05–0.12)	0.67 (-)	0.83 (0.81–0.86)
<i>Eperua falcata</i>	14	17	0.91 (+)	0.79 (0.78–0.81)	0.36 (-)	0.66 (0.52–0.79)
<i>Hippocratea volubilis</i>	55	78	0.66 (+)	0.18 (0.14–0.23)	0.16 (+)	0.03 (0.01–0.06)
<i>Licania membranacea</i>	31	70	0.81 (+)	10 ⁻³ (10 ⁻⁴ –10 ⁻³)	0.32 (-)	0.41 (0.37–0.46)
<i>Licania</i> sp. 1	55	68	0.66 (+)	0.07 (0.04–0.11)	0.42	0.43 (0.37–0.47)
<i>Pourouma</i> spp.	46	77	0.71 (+)	0.04 (0.01–0.07)	0.33	0.32 (0.27–0.37)
<i>Pseudopiptadenia suaveolens</i>	43	35	0.73 (+)	0.10 (0.06–0.14)	0.47	0.47 (0.42–0.52)
<i>Qualea</i> sp. 1	22	27	0.86 (+)	0.14 (0.10–0.18)	0.50 (-)	0.75 (0.71–0.79)
<i>Quararibea duckei</i>	44	70	0.73 (+)	0.55 (0.51–0.59)	0.20	0.27 (0.17–0.36)
<i>Sterculia pruriens</i>	14	35	0.91 (+)	0.70 (0.68–0.73)	0.36	0.37 (0.24–0.49)
<i>Tetragastris altissima</i>	18	43	0.89 (+)	0.81 (0.79–0.83)	0.39	0.44 (0.27–0.60)
<i>Virola michelii</i>	33	40	0.79 (+)	0.71 (0.68–0.74)	0.45 (-)	0.69 (0.58–0.80)

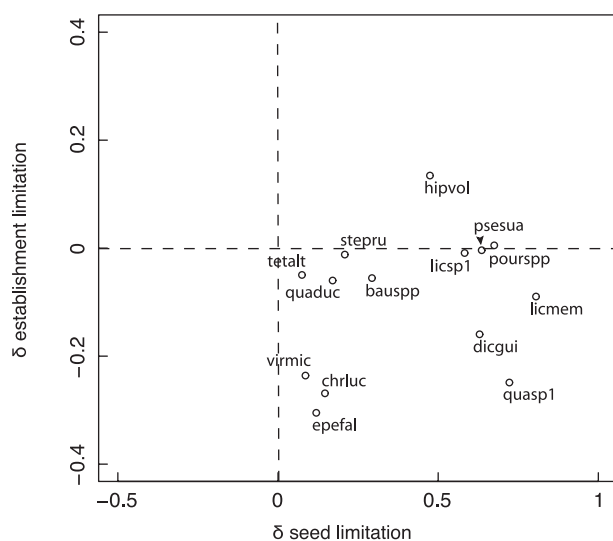


Fig. 2. Seed and establishment limitation for the 14 studied species, calculated as δ , the difference between the observed values of seed and establishment limitation and the mean of the expected seed and establishment limitation under a null model, respectively. Species abbreviations correspond to the first three letters of the genus and species.

recruited seedlings of *Pseudopiptadenia* were negatively influenced by litter depth.

All species combined, none of the traits considered (seed size, dispersal syndrome and life history) was selected in the step-wise procedure. Only the term 'species' had a significant effect on seedling density ($P < 0.005$).

RELATION OF SEEDLING SURVIVAL WITH ENVIRONMENTAL VARIABLES

The relationship between seedling survival and independent variables is summarized in Table 5. Survival of *Chrysophyllum*,

Licania sp. 1 and *Sterculia*, all shade-tolerant, was negatively associated with light availability. Soil variables and topography also had a significant or a nearly significant effect on survival for seven species (*Bauhinia*, *Dicorynia*, *Eperua*, *Pseudopiptadenia*, *Quararibea*, *Sterculia* and *Virola*). Litter depth had a significantly negative effect on the survival of *Bauhinia*. Overall, these findings were not consistent with environmental effects on seedling density (see Discussion).

Although we expected seedling height to be a strong predictor of seedling survival, only six species showed a positive relationship between seedling survival and initial seedling height (*Bauhinia*, *Chrysophyllum*, *Hippocratea*, *Licania membranacea*, *Licania* sp. 1 and *Quararibea*). The census period was a significant predictor of seedling survival for only one species, *Virola*, which showed higher survival for newly recruited seedlings.

Seedling survival showed a variety of species-specific responses to conspecific seed and seedling densities. Seedling survival of *Bauhinia* and *Sterculia* was lower in stations with high seedling density but higher in stations receiving higher seed densities. In contrast, seed density suppressed survival significantly in *Tetragastris* and marginally in *Hippocratea*.

All species combined, none of the traits considered was selected in the step-wise procedure. Only the term 'species' had a significant effect on seedling survival ($P < 0.005$).

Discussion

SEEDLING RESPONSES TO SEED LIMITATION AND TO ENVIRONMENTAL FILTERING

Many studies have shown that in tropical plant communities, seed limitation plays an important role in seedling recruitment (Hubbell *et al.* 1999; Nathan & Muller-Landau 2000; Muller-Landau *et al.* 2002; Svenning & Wright 2005). The spatial

Table 3. Estimates from the linear model predicting the ln-transformed values of seedling density as a function of the ln-transformed values of seed density, at each station. Estimates in bold are significant or marginally significant ($***P \leq 0.001$, $**P \leq 0.01$, $*P \leq 0.05$, $\dagger P \leq 0.1$). Also reported are the R^2 , numbers of seeds in 160 seed traps; numbers of seedlings in 370 1-m² seedling plots over periods 'c0' and 'recruits'. NA denoted species excluded from a particular analysis

Species ln(seedling density + 1)	ln(seeddensity + 1)		R^2		Number of seeds		Number of seedlings	
	c0	recruits	c0	recruits	c0	recruits	c0	recruits
<i>Bauhinia</i> spp.	0.28**	-0.10	0.22	0.01	63	38	197	92
<i>Chrysophyllum lucentifolium</i>	0.12	0.12	0.06	0.02	24	17	47	63
<i>Dicorynia guianensis</i>	-0.02	NA	0.01	NA	169	227	23	6
<i>Eperua falcata</i>	0.01	-0.17	0	0.03	24	13	47	18
<i>Hippocratea volubilis</i>	0.15**	0.51***	0.14	0.37	191	81	128	435
<i>Licania membranacea</i>	0.01	NA	0	NA	1067	16	130	11
<i>Licania</i> sp. 1	-0.01	NA	0	NA	386	32	124	12
<i>Pououma</i> spp.	0.08*	0.02	0.08	0	352	173	57	124
<i>Pseudoptadenia suaveolens</i>	NA	0.20***	NA	0.20	32	342	13	108
<i>Qualea</i> sp. 1	-0.07†	-0.05	0.11	0.05	88	42	26	20
<i>Quararibea duckei</i>	-0.10†	-0.11†	0.05	0.06	52	42	114	98
<i>Sterculia pruriens</i>	0.27**	NA	0.23	NA	54	2	109	51
<i>Tetragastris altissima</i>	-0.08	-0.10	0	0	31	2	72	60
<i>Virola michelii</i>	-0.21**	-0.21***	0.22	0.39	39	16	35	24

Table 4. Estimates from the linear model predicting the residuals from the seed-seedling regression as a function of environmental measures. Estimates in bold are significant or marginally significant ($***P \leq 0.001$, $**P \leq 0.01$, $*P \leq 0.05$, $\dagger P \leq 0.1$). Also reported is the R^2_{adj} . If the predictor was not selected in the step-wise procedure, the cell is empty (-). NA denoted species excluded from a particular analysis

Species	Soil PC1		Soil PC2		Light		Slope		Litter depth		R^2_{adj}	
	c0	recruits	c0	recruits	c0	recruits	c0	recruits	c0	recruits	c0	recruits
<i>Bauhinia</i> spp.	-	-	0.15†	-	-	-0.09*	0.44***†	-	-	-	0.18	0.09
<i>Chrysophyllum lucentifolium</i>	-0.18*	-0.21	-	0.22	-	-	-	0.81*†	-	0.50	0.18	0.23
<i>Dicorynia guianensis</i>	-	NA	-	NA	0.06**	NA	-	NA	-	NA	0.16	NA
<i>Eperua falcata</i>	-	-	-	-	-	-	-	-	-	-	0	0
<i>Hippocratea volubilis</i>	-	0.08†	-	-	-	-	-0.32**	-	-	-	0.12	0.03
<i>Licania membranacea</i>	-0.03	NA	-	NA	-	NA	-	NA	-	NA	0.02	NA
<i>Licania</i> sp.1	-	NA	-	NA	-	NA	-	NA	-	NA	0	NA
<i>Pououma</i> spp.	-	-	-	-	-	-	0.13	-	-	-	0.03	0
<i>Pseudoptadenia suaveolens</i>	NA	-	NA	-	NA	-	NA	-	NA	-0.08†	NA	0.04
<i>Qualea</i> sp. 1	-	-	-	-	0.11**	0.06*	-	-	0.05	-	0.31	0.15
<i>Quararibea duckei</i>	-	0.06†	-	-	0.07**	-0.03	0.17*†	-	-	-	0.14	0.06
<i>Sterculia pruriens</i>	-	NA	-	NA	-	NA	-	NA	-	NA	0	NA
<i>Tetragastris altissima</i>	0.08	-	-	-	-	-	-0.26†‡	-	-	-	0.05	0
<i>Virola michelii</i>	-0.06	-0.02	-	-	-	-	0.17†‡	-	-	-	0.08	0.05

‡Denoted association to flat slope.

distribution of seed-limited species is thus expected to correlate with that of seed arrival. However, our findings based on the null model approach were not consistent with those based on the correlative approach. While all the study species showed considerable seed limitation, only five out of 14 species showed a positive relationship between seed and seedling densities at any of the two periods of time considered. A possible explanation for the discrepancy between these two approaches is that they embrace different aspects of seed limitation. In the null model, seed limitation is measured as the failure of seeds to arrive at a given site (Muller-Landau *et al.* 2002), while in the correlative approach seed limitation is measured as the strength of the dependency of seedling establishment on seed

arrival (Turnbull *et al.* 2000; Svenning & Wright 2005). Seed limitation involves manifold processes affecting various stages over the seed to seedling transition (Nathan & Muller-Landau 2000). Here, by dissecting seed limitation into two different aspects, we address important processes explaining the spatial pattern of woody species at the seedling stage.

A remarkable example for the discrepancy between the null model approach and the correlative approach is given by the most seed-limited species, *L. membranacea* (Fig. 2), for which its initial seedling cohort was unrelated to the seed arrival recorded during the three previous years. This species fruited massively in 2002 (Table 2), and seedfall showed a strongly aggregated pattern, with over 90% of the seeds reaching only

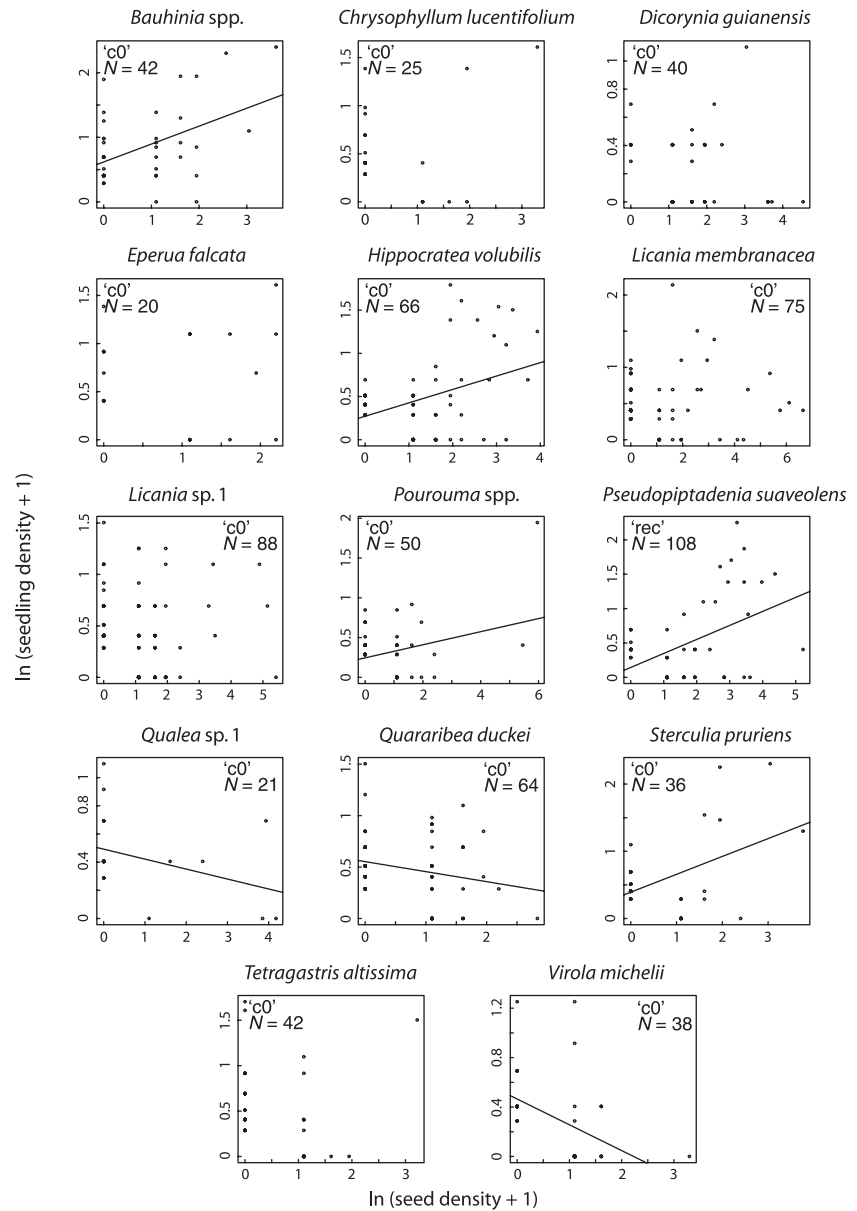


Fig. 3. Relationships between the \ln -transformed values of seed and seedling density for the 14 studied species in one of the two periods studied. We report N , the number of stations, and the census period. Note that points overlap in some cases.

six traps out of 160 (see Appendix S3). In contrast, seedlings were widely distributed across the study area. Six further species also exhibited a lack of relationship between seed and seedling densities over this period. Such patterns might be due to the fact that seedlings from the initial cohort arose from fruiting events occurring before the initiation of the seed censuses. These findings suggest that temporal variation in spatial patterns in seedfall mitigate seed limitation over time (Nathan & Muller-Landau 2000; Muller-Landau *et al.* 2002).

Yet, temporal inconsistencies between fruiting events and seedling recruitment were not the only cause for the absence of relationship between seed and seedling spatial distributions. When focusing on subsequent cohorts, among the 10 species included in the analyses, six did not show any relationship between seed and seedling spatial distributions. Two further species showed a negative relationship between seeds and seedling densities throughout the study period. Environmental

filtering might have uncoupled the spatial concordance between seeds and seedlings subsequently to seed deposition (Nathan & Muller-Landau 2000; Wang & Smith 2002). However, among the nine species showing no positive response to seed arrival, only four were significantly influenced by some of the environmental factors studied. We were unable to determine whether these observed habitat associations were directly responsible for the lack of relationship between seed and seedling densities. Thus, we did not find direct evidence that habitat partitioning following seed deposition was responsible for such patterns. Reciprocal transplantations should bring further light to this hypothesis (e.g. Fine *et al.* 2004).

Overall, many species showed significant habitat preferences. Soil-driven biases in seedling abundance were observed in six species and light had a significant influence in the spatial patterns of four species. In addition, five species (*Chrysophyllum*, *Hippocratea*, *Quararibea* and *Virola*) were widely distributed

Table 5. Estimates from the logistic model predicting seedling survival as a function of environmental variables, height, conspecific seed and seedling densities and census period. Estimates in bold are significant or marginally significant ($***P \leq 0.001$, $**P \leq 0.01$, $*P \leq 0.05$, $\dagger P \leq 0.1$). Also reported is the R_{adj}^2 . If the predictor was not selected in the step-wise procedure, the cell is empty (–)

Species	Height	Soil PC1	Soil PC2	Light	Slope	Litter depth	ln(cons. dens. +1)	ln(seed dens. +1)	Census	R_{adj}^2
<i>Bauhinia</i> spp.	0.02 [†]	–	0.46 *	–	–	–0.23 *	–0.32 ***	0.63 **	–	0.06
<i>Chrysophyllum lucentifolium</i>	0.14 [†]	0.77	–	–0.36 [†]	–1.47	–	–	–	–	0.14
<i>Dicorynia guianensis</i>	0.16	–	1.13 [†]	–	–	–	–	–0.65	–	0.26
<i>Eperua falcata</i>	–	0.37	–	–	–2.41 * [‡]	–	–0.47	–	–	0.03
<i>Hippocratea volubilis</i>	0.14 *	–	–	–	–	–	–	–0.21 [†]	–	0.04
<i>Licania membranacea</i>	0.04 **	–	–	–	–	–	–	–	–	0.04
<i>Licania</i> sp. 1	0.07 *	–	–	–0.27 *	–	–	–	–	–	0.07
<i>Pourouma</i> spp.	0.02	–0.21	–	–	–	–	–0.26	–	0.71	0.09
<i>Pseudoptadenia suaveolens</i>	0.13	–	–1.14 *	–	–1.43	–	–	–	–	0.15
<i>Qualea</i> sp. 1	–	–	–	–	–	–	–	–	–1.07	0.02
<i>Quararibea duckei</i>	0.07 *	–	0.35 *	–	–	–	–	–	–	0.07
<i>Sterculia pruriens</i>	–	–	0.55 *	–0.53 **	–1.80 *	–	–0.27 *	0.82 **	–	0.06
<i>Tetragastris altissima</i>	–	–	0.37	0.23	–	–	–	–0.70 *	–	0.08
<i>Virola michelii</i>	–	–0.30 *	–	–	–	0.43	–	–	1.78 *	0.07

[‡]Denoted association to low slope.

within the GP plot, whereas they were absent in the PP as both seeds and seedlings (and trees). Since both GP and the PP occur on distinctive soil types with well-defined boundaries, habitat heterogeneity is probably responsible for these distributional biases (Poncy *et al.* 2001). Because we restricted our analysis to stations where either seeds or seedlings occurred, this result is not highlighted in the regression analyses.

For four species, the fraction of variance explained by either seedfall or habitat conditions was < 5%. These species were abundant in the seedling layer, suggesting that our results do not reflect a lack of statistical power. Several studies have suggested that seed dispersal is an important source of stochasticity in seed deposition patterns (Feer *et al.* 2001; Poulsen *et al.* 2002; Russo 2005). If an important proportion of the established seedlings arose from isolated dispersal events (Stevenson 2000; Webb & Peart 2001) or from secondary dispersal (Forget 1996; Jansen *et al.* 2004), the large proportion of unexplained variance in local seedling density could be due to the difficulty to sample both rare dispersal events and their subsequent seedling recruitment when using seed traps. In addition, we did not monitor all possible environmental factors, such as water availability (Engelbrecht *et al.* 2007), and this might explain the small predictive power of the model. However, our study did encompass a broad array of finely measured environmental descriptors, and it is unlikely that a large fraction of the variance would be accounted for by unmeasured variables.

HOW ARE DISTRIBUTION BIASES GENERATED IN THE SPATIAL DISTRIBUTION OF SEEDLINGS?

For species showing habitat partitioning, one would expect consistent differences in survival rates across habitats. However, the factors that influenced seedling abundance appeared to be unrelated to the factors influencing seedling

survival. An illustration is provided by the legume tree species *Dicorynia guianensis*. Light availability was an important predictor for the spatial distribution of *Dicorynia* seedlings of the initial cohort, confirming its light-demanding status (van der Meer *et al.* 1998; Rijkers *et al.* 2000). However, *Dicorynia*'s survival was only affected by soil fertility. This result suggests that seedlings undergo a strong filter driven by light conditions early on during establishment, so that the spatial distribution of established seedlings shows biases towards high light environments. The influence of soil factors on seedling survival may occur subsequently, mostly for seedlings with a well-developed root system. Many other species showed inconsistencies in habitat preferences between seedling spatial patterns and seedling survival. This pattern may be the result of different habitat associations through subsequent stages of recruitment (Schupp 1995). During germination and early establishment, seedlings require particular environmental conditions that may become either neutral or antagonistic for seedling persistence. For example, a recent study showed that many trees of Barro Colorado Island exhibit different habitat associations across life stages (Comita *et al.* 2007). Our results suggest that such changes may also occur at a finer level, within the same developmental stage.

Conspecific seed and seedling densities did not correlate simply with seedling survival. Only two species survived better in stations with high seed densities, suggesting positive interactions between seedlings and neighbouring conspecific adults. This could reflect the fact that seedlings survive better near parents because they show consistent habitat preferences across life-history stages (Webb & Peart 2000). At the same time, the stations with high seedling density of these species also showed higher mortality, suggesting a density-dependent regulation on population size at the seedling stage (Webb & Peart 1999). Thus, at least for some species, seedlings interact both negatively with conspecific neighbouring seedlings

(see also Queenborough *et al.* 2007), and positively with conspecific neighbouring adults, a pattern that could blur species habitat preferences.

COMPARING SPECIES RESPONSES TO SEED LIMITATION AND NICHE PARTITIONING

We found that seedling abundances depended in a species-specific manner on seed arrival and environmental heterogeneity. We expected this interspecific variation to be related with life-history traits (Westoby *et al.* 2002), and particularly with seed size. Large-seeded species are usually more dispersal-limited than small-seeded species (Foster & Janson 1985), and therefore spatial aggregation could be related to seed size. Seidler & Plotkin (2006) showed that conspecific spatial aggregation in tropical adult trees is significantly correlated with seed size and seed dispersal syndrome. In our study, however, we found that the three small-seeded species (*Hippocratea*, *Pseudopiptadenia* and *Qualea*) showed higher seed limitation than the four large-seeded species (*Chrysophyllum*, *Eperua*, *Sterculia* and *Virola*). These findings might be the result of large-seeded species having more seed sources near traps than small-seeded species. Indeed, these large-seeded species are abundant trees in the study area. Yet, we do not have extensive data on tree distribution for these species that could bring support to this assumption.

The species showing a significant relationship between seed and seedling abundances displayed a variety of life-history traits, being either trees or lianas, shade-tolerant or light-demanding and dispersed by animals, wind or gravity. This suggests that the relation between seed arrival and seedling spatial distribution is independent of these life-history traits. However, this could be also explained by the fact that our study is limited to a finite subset of species. Also, we expected that light-demanding species would show a different response to light availability than shade-tolerant species. Surprisingly, only two of the five species reported as light-demanding were more abundant in high light environments. The three remaining light-demanding species did not show any positive response to higher light availability. Environmental filtering may require more time to operate (Webb & Peart 2000; Paoli *et al.* 2006).

CONCLUSIONS

Our study provides evidence that woody species show a variety of ecological responses to biotic and abiotic factors at the seedling stage. Both seed arrival and environmental filtering appeared to substantially explain seedling abundance of several plant populations, but their relative importance showed notable interspecific differences. Dispersal processes appeared to play a critical role in limiting the local abundance of some species, and habitat specialization was detected for others. Thus, community assembly emerges from the interaction of different mechanisms involving both dispersal- and niche-based processes. Understanding which ecological processes determine the structure of woody plant communities will

require a synthetic theory integrating diverse mechanisms of species coexistence (Chave 2008).

Many seedling populations appear to adopt the 'sit and wait' strategy (Baraloto & Goldberg 2004), therefore increasing the range of occupied sites and the opportunity to be at the right place at the right time for growth to adult stages. Contradictory patterns in habitat preferences at the seedling stage suggest that habitat associations observed in adult trees are not the result of clear niche differences during regeneration, but rather build up as the plant grows (Webb & Peart 2000; Comita *et al.* 2007). Linking the importance of dispersal and niche processes with life-history traits in multiple species and in different forests will provide valuable insights into better understanding the spatial distribution of tropical woody species in a changing environment.

Acknowledgements

Authors thank Maily Gonzalez, Ludovic Lagrange, Emilie Morin, Flore Moser, Diego Navarrete, Jean-Phillipe Orts, and Thomas Samel for their help during the seedling censuses. David Coomes, Robin Chazdon, Bettina Engelbrecht, Kyle Harms, Franck Jabot, Simon Queenborough, and Cam Webb, provided insightful comments on the manuscript. This work has been funded through a grant Action Concertée Incitative Jeunes Chercheurs of the French Research Ministry to JC, by the CNRS and the MNHN to PMF.

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Received 21 January 2008; accepted 9 September 2008
 Handling Editor: Bettina Engelbrecht

Supporting Information

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

Appendix S1. Plates illustrating the study species.

Appendix S2. One-way ANOVA for the effect of species, seed size, dispersal syndrome and life history on seed and establishment limitation.

Appendix S3. Figure illustrating the mean number of seeds per trap (\pm SD) for each species.

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