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## Microhabitat associations and seedling bank dynamics in a neotropical forest

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**Abstract** We conducted a rigorous test of tropical tree seedling microhabitat differentiation by examining microhabitat associations, survival and growth of established seedlings of ten tropical tree species representing a four-factor gradient in seed size. Eight microhabitat variables describing soil and light conditions were measured directly adjacent to each of 588 seedlings within twelve 10×100 m belt transects at Paracou, French Guiana, and at 264 reference points along the transects. From these measurements, we defined three principal components describing soil richness, soil softness and canopy openness. Six of ten species (in 9 of 30 total cases) were distributed non-randomly with respect to microhabitat along at least one principal component. However, few species demonstrated clear microhabitat specialization. All shifts in distribution relative to reference points were in the same direction (richer, softer soil). Furthermore, of 135 pairwise comparisons among the species, only 7 were significantly different. More than three-fourths of all seedlings (75.3%) survived over the 2-year monitoring period, but survival rates varied widely among species. In no case was the probability of survival influenced by any microhabitat parameter. Relative height growth rates for the seedlings over 2 years varied from  $-0.031 \text{ cm cm}^{-1} \text{ year}^{-1}$  (*Dicorynia guianensis*, Caesalpiniaceae) to  $0.088 \text{ cm cm}^{-1} \text{ year}^{-1}$  (*Virola michelii*, Myristicaceae). In only 4 of 30 cases was height growth significantly associated with one of the three principal components. Because the conditions in this study were designed to maximize the chance of finding microhabitat differentiation among a group of species differing greatly in life

history traits, the lack of microhabitat specialization it uncovered suggests that microhabitat partitioning among tropical tree species at the established seedling stage is unlikely to contribute greatly to coexistence among these species.

**Keywords** French Guiana · Life history traits · Light availability · Regeneration niche · Soil nutrients

### Introduction

In many plant communities, species distributions are associated with landscape-scale habitat variables such as topography or elevation (Pregitzer et al. 1983; Gartlan et al. 1986; Barton 1993; Vazquez and Givnish 1998; Keating 1999), soil type (Newbery et al. 1986; Sabatier et al. 1997; Ribichich and Protomastro 1998) and climate conditions (Overpeck et al. 1990; Bongers et al. 1999). In species-rich communities such as tropical forests, these relationships have been purported to contribute to local patterns of species diversity (Ashton 1978), in accordance with theoretical models that predict coexistence in heterogeneous environments (Tilman and Pacala 1993). However, the large number of species that occur at small spatial scales, in some cases more than 280 species per hectare (Phillips et al. 1994), suggests that habitat partitioning at larger spatial scales alone is insufficient to explain local tree species diversity (Harms et al. 2001).

More compelling arguments for the role of habitat partitioning in controlling the distribution and diversity of tropical tree species have focused at smaller spatial scales, or microhabitats. These studies examine not the adult trees, but the seedling and sapling life history stages, where microhabitat heterogeneity has been suggested to play a more extensive role in determining species distributions (Grubb 1977; Ricklefs 1977). However, while the differential response of species to particular environmental gradients has been found in hundreds of *ex situ* experiments (many reviewed in Swaine 1996); in few cases have these results been related to actual differences

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in species distributions among microhabitat types (Svenning 1999). Only one group of tropical forest trees, the pioneer or early-successional species, has been clearly and consistently distinguished based on habitat association with disturbed areas such as large canopy openings (Whitmore 1989, 1996). These species are characterized by several life history attributes, including small seed size, high fecundity, and high growth rates (Swaine and Whitmore 1988). Yet, less than one-fourth of the species in most tropical forests would be placed in this guild (Grubb 1996) and these species share many life history characteristics with species outside the pioneer guild (Baraloto 2001). Among non-pioneer species, little evidence has been compiled to link any differences in individual-level response to environmental conditions to differences in distribution along environmental gradients. For example, Clark and Clark (1992) found that four of six non-pioneer species at La Selva, Costa Rica did not differ in sapling (<4 cm dbh) distribution with respect to canopy structure. A subsequent analysis of microsite light measurements for naturally occurring juveniles of 0.5–5 m height found no significant differences among any of these species, although differences between non-pioneers and two *Cecropia* spp. (pioneers) were detected (Clark et al. 1993). In a more comprehensive survey of saplings at Barro Colorado Island, Panama, Welden et al. (1991) found little evidence for interspecific differences in performance response to canopy height. Of the 68 tree species they studied, only 6 (8%) exhibited significantly higher performance in a particular canopy structure class (Welden et al. 1991). And, while Webb and Peart (2000) did find significant habitat associations for seedlings of five of 22 Indonesian tree species for a physiographic habitat index and 8 of 45 species for a light index, seedling associations were found to be even weaker than those of adults, with great variation in local abundance. Even researchers who once suggested that non-pioneers might partition microhabitats associated with canopy gaps (Brokaw 1985, 1987) or their size (Denslow 1980, 1987) have more recently acknowledged that little evidence exists for differences in the juvenile distribution of most mature forest tree species across gradients of canopy structure (Denslow et al. 1998; Brokaw and Busing 2000).

Still, the implication of these surveys, that species are distributed largely at random with respect to microenvironment within communities, can be challenged on several grounds. First, heterogeneity in environmental conditions that clearly influence seed and seedling survival, such as light, litter and soil moisture, has been shown to occur at spatial scales of less than 1 m (Molofsky and Augspurger 1992; Nicotra et al. 1999; Baraloto 2001). This suggests that the scale of most microhabitat surveys may be too coarse to detect the fine-scale microhabitat heterogeneity to which juveniles actually respond.

Second, tropical forest microhabitats are defined not by one type of environmental gradient, but rather by complex interactions among many conditions (Baraloto 2001). Seedling response to one environmental gradient may change depending on other factors. For example, Huante

et al. (1998) found that growth response to increased soil nutrient availability depended on light conditions. If optimal microhabitats differ for more than just large groups of species, then they are most likely to be detected along multivariate microhabitat gradients.

A third line of reasoning suggests that static surveys of association may fail to detect the influence of microhabitat on the important dynamics that occur in the seedling bank of most tropical trees. Many tropical tree seedlings can ‘sit and wait’ in the seedling bank for decades (Clark and Clark 1992), exhibiting little or no growth (Connell and Green 2000). As a result, the true influence of microhabitat on seedling bank dynamics may exert itself slowly over time, with seedlings surviving or growing only in the more favorable habitats. For example, Webb and Peart (2000) suggest that stronger associations among adults than seedlings in their survey might be the result of non-random mortality of seedlings in suboptimal habitats.

In this paper, we evaluate the influence of microhabitat characteristics on the seedling bank dynamics of ten mature forest tree species in French Guiana. To respond to some of the challenges posed to previous surveys, we maximized the potential to detect the influence of microhabitat in three ways. First, we measured microhabitat at the individual seedling level to account for fine-scale spatial heterogeneity that might not be detected in surveys at larger spatial scales. Second, we characterized microhabitat conditions at each site using multivariate measures including light and soil physical and chemical properties. Third, we followed marked individuals through time and evaluated growth and survival in relation to microhabitat. If microhabitat does play an important role in seedling community dynamics, we argue, then differences among species in occurrence, survival, or growth relative to microhabitat gradients are much more likely to be detected in this study than in previous studies.

To date, the community-level implications of studies of the relationships between tropical tree seedlings and microhabitat have been limited because they necessarily focus on a small proportion of the hundreds of species found in most forests (Whitmore 1996). However, results from such studies might be generalized to the community level if consistent relationships can be found between species’ traits and seedling performance or distributions in contrasting situations (Grubb 1996). Among tropical trees, seed size has emerged as a trait that appears to explain differential seedling performance under contrasting regimes of light (Foster and Janson 1985; Kelly and Purvis 1993; Osunkoya et al. 1994; Poorter 1999) and soil fertility (Hammond and Brown 1995; Huante et al. 1995). Thus, in this study we also examine the potential consequences of microhabitat associations for species’ distributions, using focal taxa that span the four-factor gradient in seed size common to many neotropical forests (Hammond and Brown 1995; Baraloto 2001). This wide variation in seed size among focal taxa also increases the likelihood that species differences in microhabitat response will be observed.

We thus addressed three sets of questions: (1) Do species' seedling distributions across microhabitat gradients differ from those of neighborhood reference points, and do they differ among species? (2) Does survival or growth in the seedling bank occur disproportionately in certain microhabitats, and do these "preferred" microhabitats differ among species? (3) If relationships to environmental conditions differ among species, can species' differences be understood in terms of seed size?

## Materials and methods

### Study site and species

This study was conducted at the Paracou Reserve, near Sinnamary, French Guiana (5°18'N, 52°55'W). The site is a lowland tropical rain forest receiving more than 60% of the annual 3,160 mm ±161SE of precipitation between April and June. Soil conditions are markedly heterogeneous at Paracou, and several studies have indicated that many soil physical and chemical properties are correlated with topographic position (Barthès 1991; Baraloto 2001). Ten species were chosen to represent a gradient of seed size and seedling morphology from the community of 221 species for which seedling morphology has been described (see Baraloto 2001), encompassing a four-factor gradient in seed size and initial seedling size (Table 1).

### Seedling survey

Established seedlings were surveyed along twelve 10×100 m transects (total area surveyed =1.2 ha), two within each of six 6.25 ha permanent plots at Paracou.

Transects were positioned using two criteria. First, to ensure that areas within the dispersal range of all of the focal species were represented, sites were chosen to maximize the number of focal species with adults adjacent to the transects. Second, transects were positioned to maximize the representation of microhabitat soil conditions by intersecting as many topographic situations as possible.

In February 1998, we tagged, mapped and measured the height of all *established seedlings* of the ten focal species along the transects. We defined these as individuals less than 2 m in height that were at least 1 year of age and for which all seed reserves were exhausted. All ten species have particular morphological characters that permit recently germinated seedlings to be distinguished from older, established seedlings of similar size. These individuals were subsequently surveyed every 6 months for survival and height growth; here we present the results from the most recent survey, 24 months after the initial survey.

### Environmental characterization

In March 1998, at the end of a short dry season and the onset of the major rainy season, we characterized the microhabitat of each seedling in the initial survey using environmental measures made directly adjacent to each individual. In addition, we characterized a set of reference sampling points along the transects to represent the potential range of microhabitats available for colonization by seedlings. These points were established every 10 m along the edge of each transect ( $n= 22$ /transect;  $n=264$  total). Environmental measures were made at each reference and seedling point as follows. Light energy,

**Table 1** Summary of traits for the focal species and results of the census. Species are listed in order of seed mass in this and subsequent tables

Species	Family	Dry seed mass (g) <sup>a</sup>	Seed shadow range (m) <sup>b</sup>	No. adults in range <sup>c</sup>	No. seedlings sampled	No. reference points <sup>d</sup>
<i>Goupia glabra</i>	Goupiaceae	0.0015	98 (65–114)	21	26	249
<i>Jacaranda copaia</i>	Bignoniaceae	0.028	36 (24–42)	12	18	134
<i>Qualea rosea</i>	Vochysiaceae	0.096	35 (26–43)	43	66	106
<i>Recordoxylon speciosum</i>	Caesalpinaceae	0.21	34 (26–52)	18	57	145
<i>Dicorynia guianensis</i>	Caesalpinaceae	0.35	26 (19–37)	14	65	111
<i>Sextonia rubra</i>	Lauraceae	1.18	78 (67–105)	11	26	210
<i>Virola michelii</i>	Myristicaceae	1.24	69 (62–83)	16	95	237
<i>Carapa procera</i>	Meliaceae	6.47	24 (11–41)	19	66	180
<i>Vouacapoua americana</i>	Caesalpinaceae	12.4	16 (12–33)	17	53	153
<i>Eperua grandiflora</i>	Caesalpinaceae	27.4	21 (14–37)	21	86	164

<sup>a</sup>Dry seed mass corresponds to the mean of 30–50 groups of seeds for small-seeded species (<0.1 g), and 30–50 seeds of other species

<sup>b</sup>A conservative estimate of the seed shadow range from mother trees, used to determine random sampling points for comparisons. Distances represent the distance within which 90% of germinating seedlings were found (with the 75 and 100% intervals in parentheses) in a 4.95 ha permanent plot at the Paracou site (Baraloto et al. unpublished data)

<sup>c</sup>Based on ArcInfo cross-referencing of transect coordinates and adult positions. For dioecious *V. michelii*, only trees known to be female were included

<sup>d</sup>Refers to the number of non-seedling sampling points from those located every 10 m along the twelve transects (264 maximum), that were within seed shadow range of identified adults

expressed as the percentage of energy transmitted from the canopy (percentage of full sun), was estimated using the diazo paper method (Friend 1961). Measurements were made in the field using diazo paper sensors attached to metal stakes at 50 cm height, directly adjacent to seedlings or at the non-seedling reference points. Papers were exposed for 72-h periods, with placement and removal occurring in the morning before dawn. Soil litter depth was estimated to the nearest 0.5 cm, as described in Molofsky and Augspurger (1992). Soil surface compaction was estimated using a pocket penetrometer (Forestry Suppliers, Jackson, Miss., USA) on surface soils from which litter had been removed. A 5-cm diameter soil core of 0–10 cm depth was collected 10 cm north of each seedling, from which gravimetric moisture content (mass of water per dry mass of soil) was determined after oven-drying to constant mass at 100°C. Approximately 100 g of soil was also sampled adjacent to the soil core for chemical analyses. Two fresh 10 g subsamples from these samples were used to determine soil pH in both distilled water and in 0.01 M CaCl<sub>2</sub> solution, using a 1:2 ratio of soil:solution. Because these measurements were strongly correlated (Pearson  $r=0.93$ ), we report only the distilled water measure here. A 50-g subsample of soil was dried to constant mass at 60°C, sieved to 2 mm and transported to the University of Michigan for chemical analyses. Extractable phosphorus was estimated colorimetrically using an ascorbic acid–molybdate complex in the orthophosphate procedure (880 nm) on an Alpkem Rapid Flow AutoAnalyzer (RFA 3550; OI Analytical, College Station, Tex., USA), following extraction of 5 g in 0.1 M NaHCO<sub>3</sub> as described in Olsen et al. (1954). Soil total carbon and total nitrogen were determined by gas chromatography following dry combustion at 700°C of a 50 mg subsample, using an automated elemental combustion system (NC2500, CE Instruments, Milan, Italy).

## Analyses

To reduce the number of variables necessary to define microhabitats, we first performed a principal components analysis on all environmental variables for the entire set of sampling points ( $n=822$ ). We then used the resulting multivariate factors in all subsequent analyses.

### *Microhabitat associations*

To determine whether the distribution of seedlings was not random with respect to microhabitat, we tested the null hypothesis that values at seedling sampling points did not differ from those of non-seedling sampling points within the range of seed shadows of all adult trees. To identify all potential mother trees, we inventoried all areas extending outside of the permanent plots that were within 100 m of any transect points. For the dioecious *V. michelii*, we limited the survey to only those adults that had been observed to produce fruit in previous years.

For each species, we defined a range of potential seed distribution around each adult tree near the transects based on calculations from a complementary dataset of juvenile and adult inventories between 1998 and 2002 in a 4.95 ha permanent plot at the Paracou site (C. Baraloto et al., unpublished data). We estimated seed shadow ranges from this dataset as the distances from nearest mother tree within which 75, 90% or all germinating seedlings have been found in that plot (Table 1).

We then used ArcMap 8.1 (ESRI, Redlands, Calif., USA) to eliminate the non-seedling reference points along all transects that did not fall within each of the three estimated seed shadows for each species. In cases where inventoried seedlings were found outside of these limited zones ( $n=12$ ), we added any reference points within 10 m of those seedlings. To determine the most appropriate seed shadow range, we compared the distribution of environmental variables for each species among the three ranges using two-sample Kolmogorov–Smirnov tests. For only one species (*E. grandiflora*) did we find any significant difference ( $P<0.05$ ) between the environmental distributions among these three ranges, and this occurred between the ranges defined using 75 and 90% of germinating seedlings. Here, we report results using reference points within the 90% range for all species as it is a conservative estimate that is most consistent with available literature on seed dispersal (Sabatier 1983; Forget 1988; Loubry 1993). The number of adult individuals identified and the number of reference points retained for each species are given in Table 1.

We compared the cumulative frequency distribution of each species along each environmental principal component to that of the species-specific set of reference points, using two-sample Kolmogorov–Smirnov tests. If seedlings were distributed non-randomly with respect to the range of available points to which we assumed that seeds could be dispersed, then these frequency distributions should differ. Similar distributions would suggest random seedling occurrence with respect to that microhabitat descriptor. We calculated the significance levels for the results of these tests using a Bonferroni correction.

This species-specific analysis might mistakenly identify a microhabitat association (a Type II error) for species whose seedlings were coincidentally clumped in locations characterized by non-random microhabitat conditions (Harms et al. 2001). However, two pieces of evidence suggest that this was not likely to be the case for most of the species in our survey. First, a lack of spatial autocorrelation for most of the microhabitat parameters measured in this survey was observed at the individual seedling scale (less than 50 cm; Baraloto 2001) in this same forest site, so clumping of conspecific seedlings would not necessarily result in a shared microhabitat. Second, for only one of the species (*E. grandiflora*) did we find significant differences between the frequency distributions of the species-specific reference points and that of all reference points combined; we thus felt confident that limiting our comparisons to the species-specific reference points did not introduce any bias.



To determine whether species differ in the range of microhabitats their seedlings occupy, we compared the distribution of each species along each principal component, to that of each other species. Here we also used Kolmogorov–Smirnov two-sample tests, with Bonferroni-corrected probability values.

To determine if any subset of microhabitats occupied by each species was related to seedling traits, we examined the relationship between seed size and a microhabitat deviation from reference points of each species. This microhabitat deviation was calculated as the difference in each microhabitat variable between each seedling site and the mean of all non-seedling sites within dispersal range for that species (Winn 1985; Barton 1993). Here we analyzed each microhabitat variable separately rather than the principal components, to facilitate interpretation of all results. We then calculated Spearman rank correlation coefficients among species between seed size and the mean microhabitat deviation, for each variable.

### Survival and microhabitat

To determine if the probability of seedling survival over 2 years for each species was associated with particular microhabitat conditions, we conducted binary logistic regressions, using the three principal components summarizing environmental conditions as independent variables. We used stepwise models with alpha to remove set at 0.15, and we used Wald's t-ratio to determine the significance of the contribution of each principal component to the binary independent variable, even if these variables were not retained in the final model (Hosmer and Lemeshow 1989).

### Seedling growth and microhabitat

We calculated the relative growth rate (RGR) of each surviving seedling as stem extension, determined after Hunt (1978) as

$$\text{RGR} = \frac{\ln(\text{Ht}_{24}) - \ln(\text{Ht}_0)}{2}$$

where the  $\text{Ht}_0$  and  $\text{Ht}_{24}$  are the height (in cm) at the initial and 24-month inventory, and time is measured in years (2), to permit comparison with other studies (Clark et al. 1993; Gavin and Peart 1997; Poorter 1998).

We examined the influence of microhabitat on the growth rate of each species using a backward stepwise multiple linear regression, with the principal components of microhabitat variables as independent variables, and RGR ( $\text{cm cm}^{-1} \text{ year}^{-1}$ ) as the dependent variable.

### Results

Overall, 558 seedlings were censused, with 18–95 seedlings per species (Table 1). Some species, such as *Q. rosea*, *D. guianensis*, and *V. americana*, while common at Paracou, exhibit patchy adult distributions (Collinet 1997). Seedlings of these species were found along most transects but were most abundant in transects adjacent to conspecific adults. Seedlings of *R. speciosum*, *C. procera* and *E. grandiflora* were limited to areas directly adjacent to conspecific adults, although adults were found along most transects. In contrast, seedlings of *G. glabra*, *J. copaia*, *S. rubra*, and *V. michelii* were widely dispersed along many different transects, although they differed in overall abundance (Table 1).

**Table 2** Microhabitat measures (mean, SE) for sampled seedlings of ten tropical tree species (sample sizes are given in Table 1) and 264 non-seedling reference points. Differences among species were

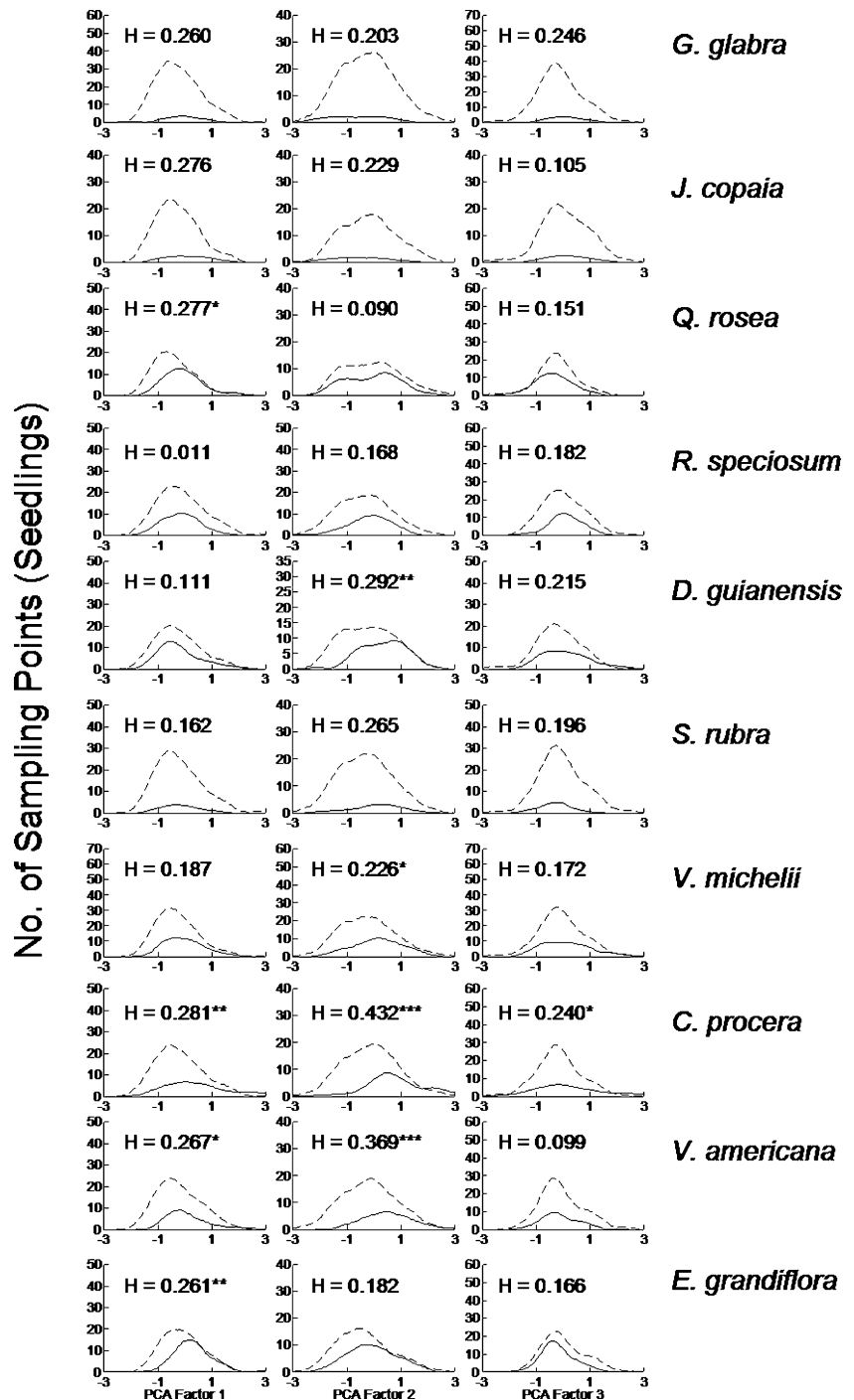
calculated based on frequency distributions rather than means, with results given in the text

Species	Light (% full sun)	Litter depth (cm)	Soil compaction (MPa)	Soil moisture (grav. %)	Soil total nitrogen ( $\text{cg g}^{-1}$ )	Soil total carbon ( $\text{cg g}^{-1}$ )	Soil $\text{PO}_4\text{-P}$ ( $\text{mg kg}^{-1}$ )	Soil pH $\text{dH}_2\text{O}$
<i>G. glabra</i>	1.27 (0.23)	1.95 (0.25)	0.13 (0.01)	19.02 (1.19)	0.28 (0.06)	4.15 (1.34)	4.85 (0.99)	4.25 (0.07)
<i>J. copaia</i>	1.28 (0.39)	1.85 (0.25)	0.13 (0.01)	19.46 (1.11)	0.24 (0.02)	3.07 (0.30)	5.97 (1.24)	4.27 (0.09)
<i>Q. rosea</i>	0.89 (0.10)	2.55 (0.15)	0.09 (0.01)	20.57 (0.59)	0.23 (0.01)	3.07 (0.16)	4.99 (0.38)	4.37 (0.04)
<i>R. speciosum</i>	1.21 (0.15)	2.70 (0.15)	0.11 (0.01)	19.45 (0.40)	0.22 (0.01)	2.92 (0.13)	3.88 (0.28)	4.24 (0.05)
<i>D. guianensis</i>	1.58 (0.21)	3.35 (0.15)	0.08 (0.01)	16.92 (0.78)	0.23 (0.01)	3.16 (0.15)	5.05 (0.39)	4.31 (0.05)
<i>S. rubra</i>	0.86 (0.11)	3.50 (0.30)	0.10 (0.01)	22.57 (0.55)	0.26 (0.04)	2.95 (0.17)	4.34 (0.61)	4.30 (0.07)
<i>V. michelii</i>	1.41 (0.15)	3.15 (0.15)	0.09 (0.01)	19.38 (0.50)	0.25 (0.01)	3.17 (0.11)	4.73 (0.31)	4.25 (0.03)
<i>C. procera</i>	2.07 (0.36)	4.50 (0.30)	0.06 (0.01)	23.00 (1.14)	0.30 (0.02)	4.80 (0.54)	5.31 (0.38)	4.19 (0.04)
<i>V. americana</i>	1.14 (0.14)	3.85 (0.30)	0.07 (0.01)	21.69 (0.78)	0.28 (0.03)	4.06 (0.61)	6.23 (0.78)	4.27 (0.05)
<i>E. grandiflora</i>	0.90 (0.09)	2.80 (0.15)	0.09 (0.01)	21.21 (0.42)	0.26 (0.01)	3.52 (0.12)	4.95 (0.42)	4.23 (0.03)
Reference sites	1.13 (0.08)	2.54 (0.09)	0.10 (0.01)	20.20 (0.29)	0.21 (0.01)	2.94 (0.09)	4.14 (0.20)	4.28 (0.02)

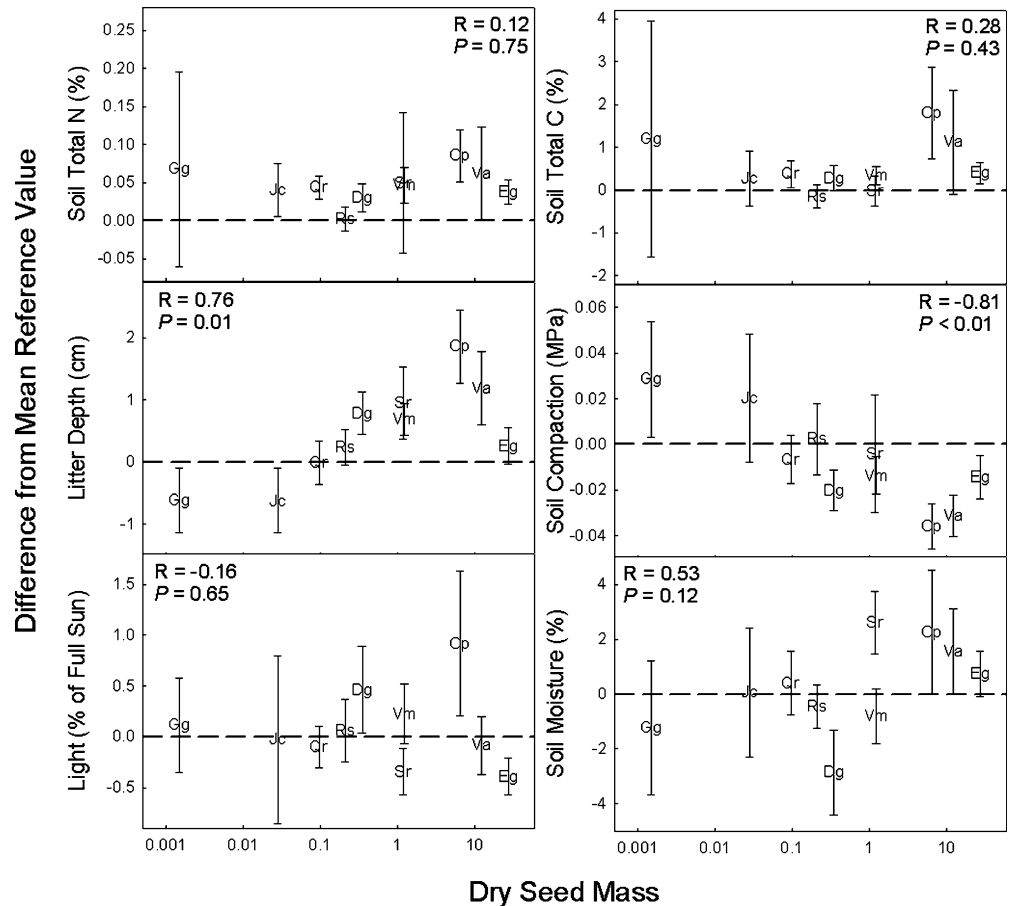
**Table 3** Loadings for the three principal components describing microhabitat conditions of seedlings along transects in tropical rain forest. Loadings of variables significantly correlated with a factor are shown in bold. Data ( $n=822$ ) are from 264 non-seedling sampling points every 10 m around the perimeter of twelve 10×100 m transects, and 558 seedling sampling points adjacent to seedlings of the ten focal species

Environmental variable	PCA factor 1	PCA factor 2	PCA factor 3
Light	0.052	-0.006	0.664
Litter depth	-0.191	0.811	0.090
Soil compaction	-0.111	-0.800	0.174
Soil moisture	0.272	0.157	-0.633
Soil total nitrogen	0.909	0.086	-0.015
Soil total carbon	0.916	0.141	0.043
Soil extractable phosphorus	0.281	0.416	0.020
Soil pH dH <sub>2</sub> O	-0.320	-0.124	-0.510
Percent of variance explained	24.2	19.2	14.3
Variate name	Soil richness	Soil softness	Canopy openness

**Fig. 1** Seedling distribution of ten tropical tree species along multivariate microhabitat gradients. Each plot includes the frequency distribution of tagged seedlings in 1998 (solid lines,  $n=18-95$ ) and the potential distribution based on reference sampling points within the seed shadow of all adult trees (dashed line,  $n=114-252$ ), along one of the principal components defining multivariate environmental conditions (Soil richness, Soil softness, Canopy openness; see Table 3). Test-statistics for two-sample Kolmogorov-Smirnov tests are indicated. \* $P<0.05$ , \*\* $P<0.01$ , \*\*\* $P<0.001$



**Fig. 2** Relationships between seed size and seedling microhabitat specialization along environmental gradients. Data are the mean for each species (with 5 and 95% confidence intervals) of the difference between each seedling sampling point (see Table 1 for sample sizes) and the mean value of all reference sampling points ( $n=114-252$ ) within the estimated seed shadow range of conspecific potential parents. Variables are arranged vertically as surrogates for the three principal components (Soil richness, Soil softness, Canopy openness; see Table 3). Symbols are the abbreviated epithet for each species. Spearman correlation coefficients ( $R$ ) between seed size and the mean microhabitat deviation for each species are shown within each panel, along with corresponding probability values



### Microhabitat associations

Mean values of all microhabitat measures for sampled seedlings of each species are given in Table 2. Correlations among all variables for these sampling sites in addition to all of the reference points were summarized by three principal components, which each contributed a significant proportion of the variation and together explained 57.7% of the variance in microhabitat conditions (Table 3). The first principal component clearly represents a gradient of conditions of soil organic material, defined primarily by positive loadings for soil carbon and nitrogen. This factor also included moderate positive loadings for soil moisture and soil  $\text{PO}_4\text{-P}$ , and a strong negative loading for soil pH. The second principal component was defined by the highly negative correlation between litter depth and soil compaction. Because soil  $\text{PO}_4\text{-P}$  was also more abundant in sites with deeper litter, it contributed a moderate positive loading to this 'soil softness' axis. The third principal component was defined by a strong positive loading for light availability and strong negative loadings for soil moisture and soil pH; we labeled this the canopy openness factor.

Of the 30 comparisons of frequency distributions between the occurrence of each species and that of reference points within seed shadow ranges, along each of the principal components, nine were significantly different after Bonferroni correction (Fig. 1). Six of the ten focal

species occupied microhabitats that differed in some way from that of reference points within seed shadow ranges of nearby adults. Seedlings of *Q. rosea*, *C. procera*, *V. americana*, and *E. grandiflora* were found in microhabitats characterized with higher total carbon and nitrogen content (i.e., higher values of PCA 1) than reference points. *D. guianensis*, *V. michelii*, *C. procera*, and *V. americana* all had more seedlings in 'softer' soils (increased values of PCA factor 2) relative to reference points. *C. procera* alone showed a skewed distribution toward higher values of PCA factor 3 (more open canopies) (Fig. 1).

Of the 135 possible comparisons among species pairs across the three principal components, only 7 were significantly different after Bonferroni correction. These cases all resulted from the skewed distributions of two species along an environmental gradient (Fig. 1). *C. procera* was found in soils with greater litter depth and less soil compaction relative to three other species (*J. copaia*, *R. speciosum* and *E. grandiflora*). *E. grandiflora* was found in soils with more organic material than four other species (*G. glabra*, *Q. rosea*, *D. guianensis*, and *V. michelii*).

To relate the microhabitat associations observed in the survey to traits of the species, we quantified the microhabitat associations as the deviation from the mean reference point values for the two variables most highly correlated with each of the three principal components

**Table 4** Effects of microhabitat on seedling survival of ten tropical tree species. Shown are the *t*-ratios for binary logistic regression coefficients of each of the three principal components describing

microhabitat, for the 2-year survival rates of the indicated number of seedlings. For no species was any PCA factor retained in the stepwise models with removal alpha =0.15

Species	<i>n</i> (percent survival)	PCA factor 1	PCA factor 2	PCA factor 3
<i>G. glabra</i>	25 (69.2)	0.53	-0.23	0.75
<i>J. copaia</i>	17 (72.2)	0.90	1.28	-0.08
<i>Q. rosea</i>	66 (86.4)	1.00	-0.56	-1.10
<i>R. speciosum</i>	57 (86.0)	0.38	-0.22	-0.92
<i>D. guianensis</i>	65 (52.2)	-1.01	-0.51	0.22
<i>S. rubra</i>	24 (88.0)	-1.08	-1.23	-0.64
<i>V. michelii</i>	94 (91.6)	-0.14	0.15	0.52
<i>C. procera</i>	66 (33.3)	0.98	0.04	0.73
<i>V. americana</i>	53 (81.1)	0.08	1.26	-0.43
<i>E. grandiflora</i>	85 (88.4)	-0.71	0.17	1.96

\* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$

describing microhabitats, and we examined relationships between seed size and these deviations (Fig. 2). The association between the large-seeded species *C. procera* and *V. americana* and 'softer' soils that was detected in the Kolmogorov–Smirnov tests can be seen more clearly in Fig. 2. Also apparent is a tendency for the smaller-seeded *G. glabra* and *J. copaia* to be found under the inverse conditions—that is, compacted soils with less litter. The juxtaposition of these two species pairs results in significant nonparametric relationships between seed size and seedling associations with conditions related to soil softness (Fig. 2). However, we note that the very large-seeded *E. grandiflora* did not exhibit any clear microhabitat preference along this gradient.

#### Microhabitat and seedling performance

Overall, three-fourths (75.3%) of the individuals sampled in the first inventory survived to the second inventory 2 years later; however, survival rates varied widely among

species (Table 4). In no case was the probability of survival over the 2-year period significantly explained by any of the principal components describing microhabitat (Table 4).

Among all species, the mean RGR was only 0.05 cm cm<sup>-1</sup> year<sup>-1</sup>. In other words, a 50 cm tall seedling grew, on average, only about 5 cm over 2 years. Species differed significantly in RGR ( $F_{9,410}=3.23$ ;  $P < 0.001$ ), with *D. guianensis* actually having a negative mean growth rate (Table 5). Low RGR was due in part to many cases of negative growth, in which seedlings were broken by branchfall or decapitated by grazing herbivores. Still, many seedlings that did not experience any damage did not grow at all over 2 years (Baraloto, personal observation). Interspecific variation for observed mean height RGR was not related to seed size ( $r^2=0.04$ ,  $P=0.79$ ;  $n=10$ ).

Microhabitat also exerted relatively little influence on seedling growth rates over the 2-year period. Significant regressions relating relative growth rate to the principal components of microhabitat conditions were observed for

**Table 5** Relative growth rate of seedlings of ten tropical tree species during the 2 years that seedlings were monitored. Data are the relative growth rates (SE) of seedlings tagged in 1998 over the subsequent 2-year period, with sample sizes of surviving seedlings

of each species as indicated. Also shown are the coefficients for multiple linear regressions of RGR versus the three principal components describing microhabitat

Species	<i>n</i>	RGR (cm cm <sup>-1</sup> year <sup>-1</sup> )	PCA factor 1	PCA factor 2	PCA factor 3
<i>G. glabra</i>	18	0.025 (0.049)	0.019 <sup>a</sup>	0.086	0.096*
<i>J. copaia</i>	13	0.049 (0.030)	0.014 <sup>a</sup>	0.009 <sup>a</sup>	-0.022 <sup>a</sup>
<i>Q. rosea</i>	57	0.073 (0.012)	-0.003 <sup>a</sup>	0.008 <sup>a</sup>	-0.021 <sup>a</sup>
<i>R. speciosum</i>	49	0.030 (0.016)	-0.015 <sup>a</sup>	0.008 <sup>a</sup>	0.018 <sup>a</sup>
<i>D. guianensis</i>	34	-0.031 (0.047)	0.083 <sup>a</sup>	0.019 <sup>a</sup>	0.054*
<i>S. rubra</i>	21	0.044 (0.007)	-0.002 <sup>a</sup>	0.003 <sup>a</sup>	0.016 <sup>a</sup>
<i>V. michelii</i>	87	0.088 (0.013)	0.025	0.009 <sup>a</sup>	0.026*
<i>C. procera</i>	22	0.031 (0.023)	-0.002 <sup>a</sup>	-0.057**	-0.012 <sup>a</sup>
<i>V. americana</i>	43	0.014 (0.018)	-0.011 <sup>a</sup>	0.011 <sup>a</sup>	-0.010 <sup>a</sup>
<i>E. grandiflora</i>	74	0.071 (0.011)	-0.007 <sup>a</sup>	-0.018 <sup>a</sup>	0.035

\* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$

<sup>a</sup>indicates that the independent variable was removed from the stepwise model ( $P > 0.15$ )



four species, but these relationships were relatively weak (Table 5). *G. glabra*, *D. guianensis* and *V. michelii* exhibited significantly increased RGR with increasing PCA factor 3 (canopy openness), although they did not exhibit any preferences in occurrence or survival along this microhabitat gradient (Fig. 1, Table 4). *C. procera* seedlings grew more slowly in microhabitats with softer soils (higher values of PCA factor 2), even though they occurred more frequently in these microhabitats (Fig. 1).

## Discussion

### Microhabitat associations

The most important and surprising result of this study was the lack of microhabitat partitioning observed among species differing in morphological and ecophysiological traits (Barigah et al. 1998; Bonal et al. 2000; Baraloto 2001). The survey was rigorous in terms of the number of parameters measured and the fine spatial scale at which they were measured; however, the tradeoff with this sampling intensity was a limited sample size for several of the species. To assess the strength of our conclusions, we estimated the statistical power of our sampling design using resampling techniques, as traditional power analyses assess parametric test statistics based on normal sampling distributions and thus are not applicable to the design we used here (Statsoft 2001). We compared two simulated species, for each of which we created natural populations of 1,000 seedlings whose distribution across environmental gradients was simulated by drawing values from all seedling-sampling points. We assumed that these two species did differ in their distribution to an extent that was biologically meaningful, and we simulated this by shifting the distribution of the second species by 20% of the median value along each PCA factor. We then simulated our design by randomly selecting from 10 to 100 seedlings of each species and comparing their distributions using Kolmogorov–Smirnov tests. These analyses demonstrate that the probability of committing a Type II error was greater than 20% when the number of seedlings sampled fell below 47. Thus, the conclusions for comparisons of at least three of the species we studied (*G. glabra*, *J. copaia* and *S. rubra*) must be interpreted with caution.

Still, we did detect non-random seedling distributions for six of ten species with respect to some multivariate microhabitat gradient (Fig. 1). However, all of these shifts in distribution occurred in similar directions relative to reference sampling points, a finding in direct contrast with the predictions of the regeneration niche hypothesis (Grubb 1977). A further challenge was posed by direct comparisons among species, in which only two of the ten species were found in distinct microhabitat types relative to the other species.

Experimental evidence supports the lack of causal relationships between seedling occurrence and microhabitat. A separate study showed that survival from seed for eight of these species was independent of microhabitat

conditions, including litter depth and soil compaction for *C. procera* and soil carbon and nitrogen for *E. grandiflora* (Baraloto 2001). And, in an experiment simulating the bare and compacted soils characteristic of skid trails in logged forest, neither *C. procera* nor *V. americana* exhibited reduced seed-seedling survival relative to treatments with litter and no compaction (Baraloto and Forget 2004).

Although the few correlations we did observe do not appear to be causal, they might reflect reverse causal relationships or effects of microhabitat on adult performance, either of which could contribute to microhabitat differentiation and coexistence (Grubb 1996). For example, seedlings might be separated in space or among potential microhabitats simply because of differences in patterns of seed distribution (seed shadow) in the forest (Augsburger and Kitajima 1992; Schupp 1995). While we did attempt to account for these influences at a large spatial scale by limiting the reference points to areas within a given species' estimated seed shadow, directed dispersal to particular microhabitats may operate at a smaller spatial scale than this correction. For example, within the 16–24 m seed shadow that we established around adults of *C. procera* and *V. americana*, many of the dispersed seeds were likely to have been placed underneath logs, near buttresses, or at the base of *Astrocaryum* spp. palms by scatter-hoarding rodents such as *Dasyproctus agouti* and *Agouti paca* (Forget 1994, 1996). Because these microsites tend to have more litter and less soil compaction than other sites, seedlings that result from dispersed seeds will certainly reflect this microhabitat association. Thus, the significant association of *C. procera* with softer soil microhabitats, which accounted for three of the seven differences among species, may be the result of directed dispersal to these microhabitats rather than differential germination or survival in these microhabitats. It is important to note that this pattern could be maintained without significant conspecific aggregation of seedlings at local (within transect) or regional (among transect) spatial scales, particularly for larger-seeded species that are dispersed as single seeds (Forget 1997). In fact, we observed a wide distribution of *C. procera* seedlings both within and among transects.

At a larger scale, the distribution of *E. grandiflora* seedlings in microhabitats with richer soils (accounting for the other four of seven differences among species) may in fact reflect the distribution of adult trees rather than germination and survival. Adults of *E. grandiflora* tend to occur on well-drained soils of higher topographic position in French Guiana (Barthès 1991; Sabatier et al. 1997), which tend to have higher concentrations of organic material and nitrogen (Baraloto 2001). In fact, the reference points within 21 m of adult trees of this species within this study ( $n=164$ ) were distributed non-randomly with respect to other reference points ( $n=122$ ) along the soil richness principal component (two-sample Kolmogorov–Smirnov test,  $H=0.334$ ,  $P<0.01$ ). This species also has extremely large seeds that are gravity-dispersed within 20 m of parent trees (Forget 1992). While we found *E.*

*grandiflora* seedlings in richer soils than the reference points within 21 m of parent trees, most seedlings tend to be aggregated within 5–15 m of parent trees (Baraloto 2001) because of substantial insect predation of seeds within 5 m of parent trees (Forget 1992). As a result, the non-random distribution of seedlings may reflect a poor estimation of the microhabitat effects on the viable seed shadow.

### Seedling bank dynamics

Clearly, our study presents only a snapshot of the physical environment at one instant in time. Temporal variability in several of the parameters we measured has been observed, particularly in seasonal tropical forests (Wright 1992; Roy and Singh 1995; Veenendaal et al. 1996). For example, litter that had begun to decompose at the time of this survey at the onset of the rainy season, may vary seasonally in a given site depending on inputs and decomposition rates, which also vary with precipitation (Puig et al. 1990). As a result, we must interpret the data on microhabitat associations with caution as our measurements characterize only the conditions that permit continued establishment rather than the environment of the seedling at establishment. A much stronger argument can be constructed using performance data that incorporates temporal variation, such as measures of seedling growth or survival that integrate several seasons. However, such an analysis presumes that the characterization of points in March 1998 was consistent across the 2 years during which performance was measured. We did repeat environmental measures in March of 1999 and 2000 for six points along each transect, from which PCA axes were constructed using the same weightings as those in 1998. We observed no significant change among years in any of the three PCA factors for these sampling points (repeated measures ANOVA  $P > 0.10$ ,  $df = 2.34$ ), suggesting that our protocol provided an adequate description of plot differences at a particular season for the 2 years during which we measured seedling performance.

The data on performance were consistent with the lack of microhabitat differentiation we observed among seedlings in the initial static survey. We found no effect of microhabitat on survival, suggesting that persistence in the seedling bank appears to be largely independent of microhabitat for these species. Given the low incidence of mortality relative to the number of individuals sampled, this result is not surprising. In contrast with our results, Clark and Clark (1992) did find significantly increased survival of saplings <1 cm dbh of four of six species with respect to crown illumination. However, the mean crown illumination of the surviving seedlings in their census corresponds to light conditions that were not encountered frequently in this census. Across a broader light gradient with many points receiving more than 50% of full sun, Kobe (1999) also found significant differences in patterns of mortality among four species of Cecropiaceae in Costa Rica. In light of this, our results should also be interpreted

with the understanding that the microhabitat gradients we measured represent a subset of the conditions in the forest that focus on understory conditions rather than gap contrasts. Among younger seedlings, significant effects of large canopy openings (>8% full sun) on survival have been observed for many of the species surveyed here (Baraloto 2001).

Although other studies have suggested a tradeoff between high maximum relative growth rates and high survival (Kitajima 1994; Pacala et al. 1994), we found no evidence for this pattern among these species during this study. The species with the highest maximum RGR (under conditions of unlimited resources) are *G. glabra* and *J. copaia* (Baraloto 2001); however, they exhibited intermediate survival rates here. Thus, even in the absence of high resources, especially light, these seedlings appear to adopt the ‘sit and wait’ strategy more often attributed to species with lower maximum RGR (see Walters and Reich 1996; Poorter 1999).

The most convincing evidence this survey provides for the absence of microhabitat differentiation among these species is based on the data for growth over 2 years. Again, we found little evidence for differential species growth along multivariate microhabitat gradients. Low growth rates such as those we observed are not uncommon in tropical forest tree seedling banks. In fact, Clark and Clark (1992) estimated that seedlings may require more than 25 years to attain 1 cm in diameter, and individuals of some species may require more than 180 years to reach the 10 cm dbh class. Connell and Green (2000) found several seedlings of one species that exhibited little or no growth over three decades in permanent plots in Australian rain forest.

Overall, these results further confirm that seedling growth rates once seed reserves have been exhausted may be independent of species traits such as seed size. In fact, among the ten species, the only significant differences in growth rate we observed were between *D. guianensis*, and three other species representing nearly the entire gradient of seed size sampled (*Q. rosea*, *V. michelii*, *E. grandiflora*). These results imply that the definition of functional groups among tropical trees will require not only an understanding of species traits related to initial seedling establishment, such as seed size and maximum RGR, but also long-term monitoring of many species throughout multiple size classes to determine how species grow in the forest understory (Clark and Clark 1999).

The consequences of seedling bank dynamics for population structure and growth will of course depend not only on mortality and growth in the seedling bank but also recruitment of new seedlings. For many species, particularly those with large seeds, recruitment events may be sporadic due to supra-annual fruiting events or low production years (DeSteven 1994; Condit et al. 1998; Connell and Green 2000). Such was the case for several of the species in this survey, and we thus did not measure new recruits into the seedling bank. A more comprehensive investigation of seedling bank dynamics will require

measurements of both mortality and recruitment over long time to interpret effects on population structure.

### Environmental specialization among rain forest trees

This study poses a serious challenge to the contribution of regeneration niches to tropical tree community structure. Among non-pioneer species differing widely in life history traits, we found few indications of differences in the microhabitat conditions permitting seedling bank establishment. Furthermore, neither survival nor growth of seedlings was related to microhabitat conditions measured at the individual seedling scale. These results thus concur with those from other studies that have found little evidence for microhabitat partitioning among non-pioneer tropical tree species (Welden et al. 1991; Clark and Clark 1992; Clark et al. 1993; Hubbell et al. 1999; Webb and Peart 2000; Harms et al. 2001). In concert, these studies provide further evidence that other mechanisms such as tradeoffs in life history strategies (Clark and Clark 1992), dispersal limitation (Silman 1996; Hubbell et al. 1999; Schupp et al. 2002), density-dependent mortality (Webb and Peart 1999; Harms et al. 2000), or even random fluctuations (Hubbell 1979) are responsible for the community structure of tropical forest trees.

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