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Comparison of seedling recruitment under arborescent palms in two Neotropical forests

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Abstract Certain overlying strata in forests may disproportionately reduce seedling density and species richness. For eight arborescent palm species, we quantified the relative restriction of seedling recruitment under individual palms versus non-palm sites and extended to the landscape scale by quantifying the total area covered by arborescent palms at Barro Colorado Island (BCI), Panama and La Selva Biological Station, Costa Rica. We also examined whether differences among palm species in restricting seedling recruitment were associated with differences in crown architecture, litter depth, and light availability. Woody seedlings had lower mean density/m^2 and mean number of species/m^2 under individual palms than at non-palm sites for all four palm species at BCI, but for none at La Selva. Estimated species richness for woody seedlings, derived via rarefaction, was lower under palm than non-palm microsites at both BCI and La Selva, but not for non-woody seedlings. Differences in seedling density corresponded to some key architectural characters that differed among the palm species. Light availability was lower under palm than non-palm microsites at both BCI and La Selva, but only estimated species richness of woody seedlings at BCI was strongly correlated with % canopy openness. The coverage of arborescent palms was much lower at BCI than La Selva. Therefore, at BCI, the relative restriction of woody seedling recruitment under individual palms does not accumulate greatly at the landscape scale. At La Selva, for woody seedlings, only estimated species richness was relatively limited under palms, and non-woody seedlings had relatively lower mean density/m^2 and mean number of species/m^2 under only one palm species. Therefore, the relative restriction of seedling recruitment by arborescent palms at La Selva is limited at both individual and landscape scales.

Keywords Crown architecture · Landscape scale · Light availability · Rarefied species richness · Seedling density

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Introduction

Forest understory species may restrict seedling recruitment if they act as mechanical barriers to seed arrival or biological inhibitors to seedling establishment (George and Bazzaz 1999). Understory dwarf palms reduce seedling recruitment under individual palms relative to non-palm sites in the forest at La Selva, Costa Rica (Wang and Augspurger 2004). Furthermore, since dwarf palms are so abundant there, their restriction of seedlings has a big impact on the forest as a whole. Arborescent palms may have a similar negative impact on seedling recruitment, both because of similar and additional mechanisms acting under individual palms, as well as their prominence in some tropical forests.

Multiple mechanisms may cause the restriction under individual arborescent palms. Their umbrella-like crown architecture may prevent seed arrival or cast particularly deep shade (Denslow et al. 1991). Their large leaves can cause heavy damage to seedlings when they fall (Clark and Clark 1989; Clark and Clark 1991; Peters et al. 2004). Their thick leaves may be slow to decay and accumulate as deep leaf litter that may hinder seed germination, seedling emergence, and root penetration. Seed predators may hide within the stems of clonal palms. Arborescent palm species have varying growth forms and crown architecture and may present varying strengths of suppression and may act by different mechanisms. For example, clonal palms accumulate thick leaf litter and greatly limit light near the crown center, while canopy palms drop heavy leaves and affect a large area of seedlings. Species with a large crown area, large number and size of leaves and leaflets, and tight spacing between leaflets may limit light availability and impact recruitment more than the species lacking these traits.

For arborescent palms to have a significant impact on seedling recruitment in the forest as a whole, they require not only that these mechanisms act under individual palms, but also that a forest has a large number of palms. In some Neotropical forests, arborescent palms have great density and coverage in both canopy and subcanopy strata (Svenning 2001).Therefore, this important component of many tropical forests may both create habitat heterogeneity for seedling recruitment at the local scale and reduce seedling recruitment overall at the landscape scale.

Prior studies have demonstrated that arborescent palms can reduce seedling recruitment at the local scale. Areas with greater arborescent palm density in an old-growth forest on Barro Colorado Island (BCI), Panama, had lower seedling density (Denslow and Guzman 2000). Also at BCI, plots under the subcanopy clonal palm species, *Oenocarpus mapora*, had lower seedling density and lower estimated number of species of seedlings than plots without the palm (Lopez-Farris et al. 2004). Furthermore, seedlings under *O. mapora* were of larger-seeded species than seedlings that were not under the palm. Between all the plots, seedling density was positively correlated with light availability and negatively correlated with leaf litter depth. The generality of these findings for other species of arborescent palms and in other tropical forests is unknown. Also these studies do not scale their results to the landscape scale to summarize the overall impact of these palms on seedling recruitment.

This study extends the prior work by quantifying relative seedling recruitment at under-palm versus non-palm microsites for eight arborescent palm species in two Neotropical rainforests, and expands these results to the landscape scale. The specific objectives were: (1) to quantify the relative extent to which individual arborescent palms of eight species restrict seedling density and estimated species richness; (2) to examine whether variation in restriction of seedling recruitment among arborescent palms corresponds to differences in crown architecture, litter accumulation, and light availability; (3) to evaluate the importance of any restriction at the landscape scale by quantifying the density and total area covered by arborescent palms; and (4) to compare the restriction on seedling recruitment by arborescent palms in one seasonal and one aseasonal Neotropical forest.

Methods

Study sites

One 300-ha study area was in the old-growth aseasonal forest on the northeastern side of La Selva biological station in the Atlantic lowlands of Costa Rica (10°26'N, 84°00'W; elevation 37–150 m). La Selva is classified as a tropical wet forest in the Holdridge life zone system. It has a mean annual rainfall of 3,962 mm, with no monthly rainfall < 100 mm, and a mean temperature of 26°C (Sanford et al. 1994). The flora consists of 339 tree species (McDade et al. 1994) and 31 palm species (Chazdon 1985). Arborescent palms have an importance value comparable to the dominant woody species, *Pentaclethra macroloba* (Willd.) Kuntze (Hartshorn and Hammel 1994).

The second 300-ha study area was in the old-growth seasonal forest on the central and western sides of BCI in the Panama Canal (9°09'N, 79°51'W; elevation 25–137 m). BCI is classified as tropical semideciduous forest due to its distinct seasonality in rainfall. It has a mean annual rainfall of 2,600 mm, but 90% occurs during the rainy season from May to December. The mean annual temperature is 27°C (Dietrich et al. 1996). The flora consists of 211 tree species > 10 m tall and 18 palm species (Croat 1978).

Seedling recruitment under individual palms

In this study we define arborescent palms as tall, single-stemmed, and medium-sized, multiple-stemmed palm species (Kahn and de Granville 1992). We include both canopy and subcanopy palm species. Identical methods were applied to studies at BCI and La Selva. At BCI, 15 of each of the four arborescent palm species (*Astrocaryum standleyanum* L. H. Bailey, *Attalea butyracea* (Mutis ex L.f.) Wess. Boer, *Oenocarpus mapora* H. Karst., *and Socratea durissima* (Oerst.) H. Wendl.) were haphazardly chosen: seven of each species were in kaolinitic and eight were in montmorillonitic soils, the two dominant soil types at BCI (Dietrich et al. 1996). Focal palms were a minimum of 100 m apart and minimally 10 m away from the trail. At La Selva, 16 of each of the four arborescent palm species (*Geonoma congesta* H. Wendl. ex Spruce, *Iriartea deltoidea* Ruiz & Pav., *Prestoea decurrens* (H. Wendl. ex Burret) H. E. Moore, and *Welfia regia* H. Wendl. ex André) were haphazardly chosen. Four of each species were in each of the four habitats that differ in soil type and topography: old alluvium terrace, residual soil flat area, residual soil slope (> 6° angle), and swampy areas (Clark et al. 1999). In selecting focal species, we aimed to incorporate a range of growth forms that were representative of the guild of arborescent palms. We also required that the palms be abundant and widespread among the habitats at each study site. Individual palms were of reproductive size. The minimum size of the clones was at least ten ramets. We roughly paired the focal species by growth forms between the two study sites: *Attalea* and *Welfia* (large subcanopy species); *Astrocaryum* and *Prestoea* (medium-sized subcanopy species); *Socratea* and *Iriartea* (canopy/subcanopy species with stilt roots); and *Oenocarpus* and *Geonoma* (medium-sized clonal species). *Geonoma* is shorter than the other species, but its crown area is within the range of the other species (see below). Therefore, we consider it to be closer to an arborescent than a dwarf palm. Subsequent analysis of their crown architectural characteristics confirmed the general similarity within the pairs (see below).

Seedling censuses were conducted in 2002 at BCI and in 2003 at La Selva. Seedlings were compared in circular areas projected by the palm crowns versus those in an immediately adjacent non-palm microsite of equivalent size as the focal palm crown, but without any dwarf or arborescent palms. The non-palm microsite was selected in a random direction from the focal palm trunk, and its edge abutted the palm microsite. Only half of the area under the palm crown and in the non-palm microsite was sampled for seedlings; the half was based on a randomly chosen direction. Seedling zones were delimited as 1-m annuli from the palm trunk to the edge of the crown. For clonal species, the first seedling zone began from the center of the clump. The number of seedling zones ranged from 3–6, depending on crown size of each focal palm.

Within each seedling zone, one 1×1 m quadrat was chosen in a random direction for the seedling census. Litter depth was measured in the center of each quadrat. In each quadrat, post-cotyledonous seedlings (<100 cm in height) of two growth forms were counted and identified to species or morphospecies: (1) woody species and (2) non-woody species (i.e., Araceae, Arecaceae, Costaceae, Cyclanthaceae, Heliconiaceae, Marantaceae, Zingiberaceae, grasses, ferns, and *Selaginella*). Clonal non-woody species were quantified using the number of ramets.

Crown architectural characters

The crown architecture of each focal palm was characterized in order to determine if variation in any traits corresponded to variation in seedling recruitment under different palm species. DBH, trunk height, and crown diameter were measured. For palms with stilt roots, DBH was measured immediately above the stilt roots. Trunk height was visually estimated. Crown diameter was based on two perpendicular measurements. The number of leaves and number of intact fallen leaves were counted. For clonal species (*Oenocarpus* and *Geonoma*), total crown area and the number of leaves per ramet were used. For one freshly fallen leaf at each focal palm, total length, petiole length, length and width of the leaf area, total number of leaflets, maximum length and width of a leaflet, and distance between leaflets at distal, middle, and basal portions of the leaf were measured.

Light availability

One hemispherical photo was taken immediately adjacent to the trunk of each focal palm and in the center of each non-palm microsite. A Nikon Coolpix 990 digital camera with a Nikon FC-E8 fisheye converter was set on a tripod 25 cm above ground level. The magnetic north direction was indicated with a white tag attached to the lens. The camera was leveled horizontally with a bubble level. The self-timer was used for the photographer to hide behind the vegetation. The autofocus, exposure mode and compensation, and *f* stop were manually set to infinity, aperture priority −0.7 eV, and *f*/2.6, respectively (Frazer et al. 2001). The images were saved in the XGA (1024×768 pixels) mode with NORMAL (medium compression) quality, and then analyzed in the Gap Light Analyzer (GLA) version 2.0 (Frazer et al. 1999). From the output of the analysis of hemispheric photos, percent canopy openness was used to compare light environments.

Arborescent palms at the landscape scale

The density and coverage of the arborescent palm community were quantified in order to estimate the extent of restriction on seedling recruitment by arborescent palms at the landscape scale. Identical methods were applied at BCI and La Selva. Fifteen 10×10 m plots in each of three habitats at BCI (kaolinite flat, montmorillinite flat, and kaolinite/montmorillinite slopes) (45 plots in total) and in each of the four habitats at La Selva (old alluvium terrace, residual soil flat area, residual soil slope ($>6°$ angle), and swampy areas) (60 plots in total) were censused in old-growth forest. We first selected random points among trail markers and then established plots >10 m from that point into the forest. The plots were a minimum of 100 m apart. Within each plot, all arborescent palms with DBH >1 cm were counted and measured for DBH. For clonal palms, number of ramets was counted. Area of each juvenile arborescent palm was determined from two perpendicular measurements of crown diameter. In addition, total coverage of arborescent palms was estimated in each plot by using cover classes of 0–10%, 10–25%, 25–50%, 50–75%, and 75–100%.

Data quantification and analysis

Species richness is highly dependent on the number of individuals sampled. Number of seedlings varied between palm and non-palm microsites and among palm species. Therefore, estimates of species richness were made using rarefaction methods. There was a low number of seedlings per quadrat (2.1/quadrat at BCI; 1/quadrat at La Selva). Therefore, we combined all quadrats at a given palm or non-palm microsite. There was also a high frequency of a low number (<5) of individuals of a given species under a given palm or non-palm microsite. Therefore, we pooled all palm or non-palm microsites of a given palm species. Fifteen palm or non-palm microsites were pooled for BCI and 16 for La Selva for each palm species (Chazdon et al. 1998).

The software EstimateS 7.5 (Colwell and Coddington 1995) was used to compute the means of species richness estimates, based upon species abundance matrices and 100 randomized orders of palm or non-palm microsites of a given species (Colwell and Coddington 1995). All seedlings were assumed to have a random spatial distribution. We examined eight non-parametric species richness estimates: abundance-based coverage estimator (ACE) (Chao et al. 2000), incidence-based coverage estimator (ICE) (Chao et al. 2000), abundance-based Chao 1 (Chao 1984), incidence-based Chao 2 (Chao 1987), first-order incidence-based Jackknife 1 (Heltshe and Forrester 1983), second-order incidence-based Jackknife 2 (Palmer 1991), incidence-based Bootstrap (Smith and van Belle 1984), and Michaelis–Menten richness estimator (Colwell et al. 2004).

The relative performance of these eight species estimates was evaluated by comparing species accumulation curves derived from estimated versus observed species richness (Coleman et al. 1982). The criteria used to select the best performing estimators were stability throughout the curve, the extent to which the curve reached an asymptote, and the smallest number of microsites at which an asymptote was reached. The two best estimators were selected separately for woody and for non-woody seedlings. We then used ANOVA to compare the differences in mean estimated species richness between palm versus non-palm microsites for woody or non-woody seedlings at BCI or La Selva. This analysis only compared palm versus non-palm microsites irrespective of palm species identity. Therefore, in addition, we analyzed the total number of species/m^2 as an individual-based measure in order to compare among palm species.

In preliminary analyses the effect of microsite (palm vs. non-palm), study site (BCI vs. La Selva), and seedling growth form (woody vs. non-woody) on mean seedling density/m^2 and number of species/m^2 were examined in mixed linear models. The unit of replication was the focal palm or the non-palm microsite. These analyses found significant main effects of the study site, seedling growth form, and microsite (palm vs. non-palm) on seedling density and number of species. Subsequently, we analyzed the two major growth forms (woody and non-woody seedlings) separately in each of the two study sites separately. Within each study site the effect of palm species per se could then be examined. Only the second set of analyses is reported below.

To determine whether variation in seedling recruitment under the eight palm species corresponded to their contrasting architectural characters, principal component analysis (PCA) was conducted first to eliminate unimportant architectural characters. Fourteen architectural characters were initially included in the PCA (Appendix 1). Based upon the correlation matrix of these original variables, PCA generated principal components, i.e., linear combinations of the original variables that represented a gradient of maximum variation. Four principal components had eigen values >1, and they accounted for 73% of the total variance (data not shown). PCA then generated principal component loadings, i.e, the correlations between variables and principal components, which represented the relative importance of the original variables. The greater the correlation, the greater the variation of the variables (McGarigal et al. 2000). Comparisons of correlations between the characters versus the first two principal components after a varimax rotation indicated that the following nine characters had relatively high positive or negative correlations with principal components one and two: the number of leaves, crown diameters, leaf length and width, petiole length, and three distances between leaflets. These nine variables were then condensed into four characters based on the high correlations between or among them: the number of leaves, crown area (mean crown radius^2 × π), leaf area (leaf width × leaf blade length), and an average of the three distances between leaflets.

The remaining four characters from this exploratory analysis were then used to classify palm species into separate groups by a discriminate function analysis (DFA) in order to examine whether palm species differed in their crown architecture in univariate and multivariate dimensions. The eight palm species differed significantly in each of the four architectural characters and in multivariate space (Table 1). The architectural characters demonstrated varying strengths of discrimination among the palm species on canonical axes one and two. The number of leaves and leaf area had the greatest influence on axis one, whereas crown area had the greatest influence on axis two (data not shown). The DFA on architectural characters confirmed the similarity of paired palms from BCI and La Selva (data not shown). Large subcanopy species (*Attalea* and *Welfia)*, medium-sized subcanopy species (*Astrocaryum* and *Prestoea*), and species with stilt roots (*Iriartea* and *Socratea*) were similar to each other. The clonal species, *Geonoma* and *Oenocarpus*, however, were less similar to each other, especially on axis two. For the eight focal palm species, the effects of the four architectural characters on mean seedling density/m^2, mean number of species/m^2, and estimated species richness at palm microsites were then examined in mixed linear models.

To evaluate the effects of light environments, we first compared differences in percent canopy openness between palm versus non-palm microsites and among palm species in a mixed linear model. Then, the effects of the percent canopy openness, palm versus non-palm microsites, and palm species on mean seedling density/m^2,

Table 1 Univariate and multivariate analyses in DFA discriminating different palm species based on their crown architectural characters

Variable	*R* Square	*F*
Univariate statistics		
Number of leaves	0.79	33.14***
Crown area	0.73	24.39***
Leaf area	0.61	13.74***
Average distance between leaflets	0.54	10.50***

Statistics	*df*	Value	*F*
Multivariate statistics			
Wilk's lambda	28	0.019	15.26***

***$P < 0.0001$

mean number of species/m^2, and estimated species were examined in the mixed linear models. Correlations between percent canopy openness and these three seedling variables were calculated separately for BCI and La Selva.

The main effects and only two-way interactions were examined in the mixed linear models using SAS 8.02, SAS Inc. Least square means were used for post-hoc tests after finding significant main and interaction effects.

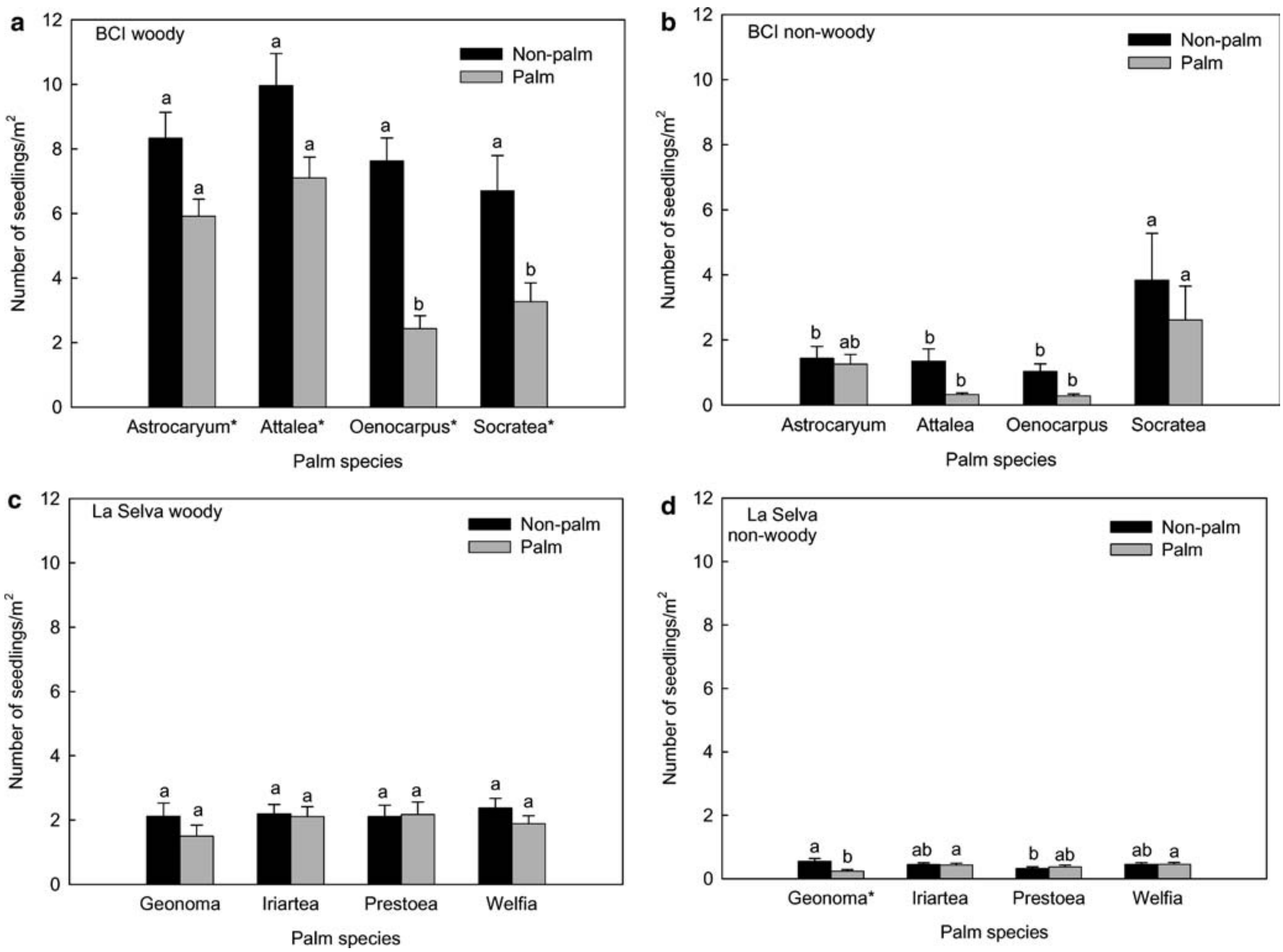

Fig. 1 Mean (+1 SE) seedling density/m^2 of woody and non-woody seedlings at BCI (**a**, **b**) and La Selva (**c**, **d**) in microsites of focal palm species versus adjacent non-palm microsites. Different lowercase letters above bars indicate significant differences among focal palm species within either non-palm or palm microsite ($P < 0.05$ by least-square means). *Asterisk* indicates significant differences between non-palm versus palm microsites of a given focal palm species ($P < 0.05$)

Results

Overall census

Barro Colorado Island and La Selva differed in overall number of seedlings and overall number of species of seedlings. At BCI, among a total of 5,576 seedlings censused in 60 pairs of plots, the numbers of identifiable species were split between growth forms as follows: woody (54), fern (5), large monocot/aroid (5), palm (5), grass (5), and *Selaginella* (1). Woody seedlings represented 52% of all seedlings at BCI. In comparison, among a total of 1,472 seedlings censused in 64 pairs of plots at La Selva, numbers of identifiable species were split as follows: woody (137), fern (11), large monocot (14), aroid (14), and palm (14). Woody seedlings represented 50% of all seedlings at La Selva. Therefore, in the total census, BCI had four times as many seedlings as La Selva, while La Selva had a much greater number of species in each growth form. Both density/m^2 and number of species/m^2, however, were greater at BCI than at La Selva (Fig. 1, 2). At BCI woody seedlings were 5.6 times denser than non-woody seedlings (Fig. 1a vs. 1b), whereas at La Selva woody seedlings were 5.5 times denser than non-woody seedlings (Fig. 1c vs. 1d). At BCI there were 16.8 times more species/m^2 of woody seedlings than non-woody seedlings (Fig. 2a vs. 2b), whereas at La Selva they were 5.6 times more species/m^2 of woody seedlings than non-woody seedlings (Fig. 2c vs. 2d).

Restriction on seedling recruitment under individual palms

Seedling density

At BCI mean density/m^2 of woody seedlings differed significantly between microsites and among palm species

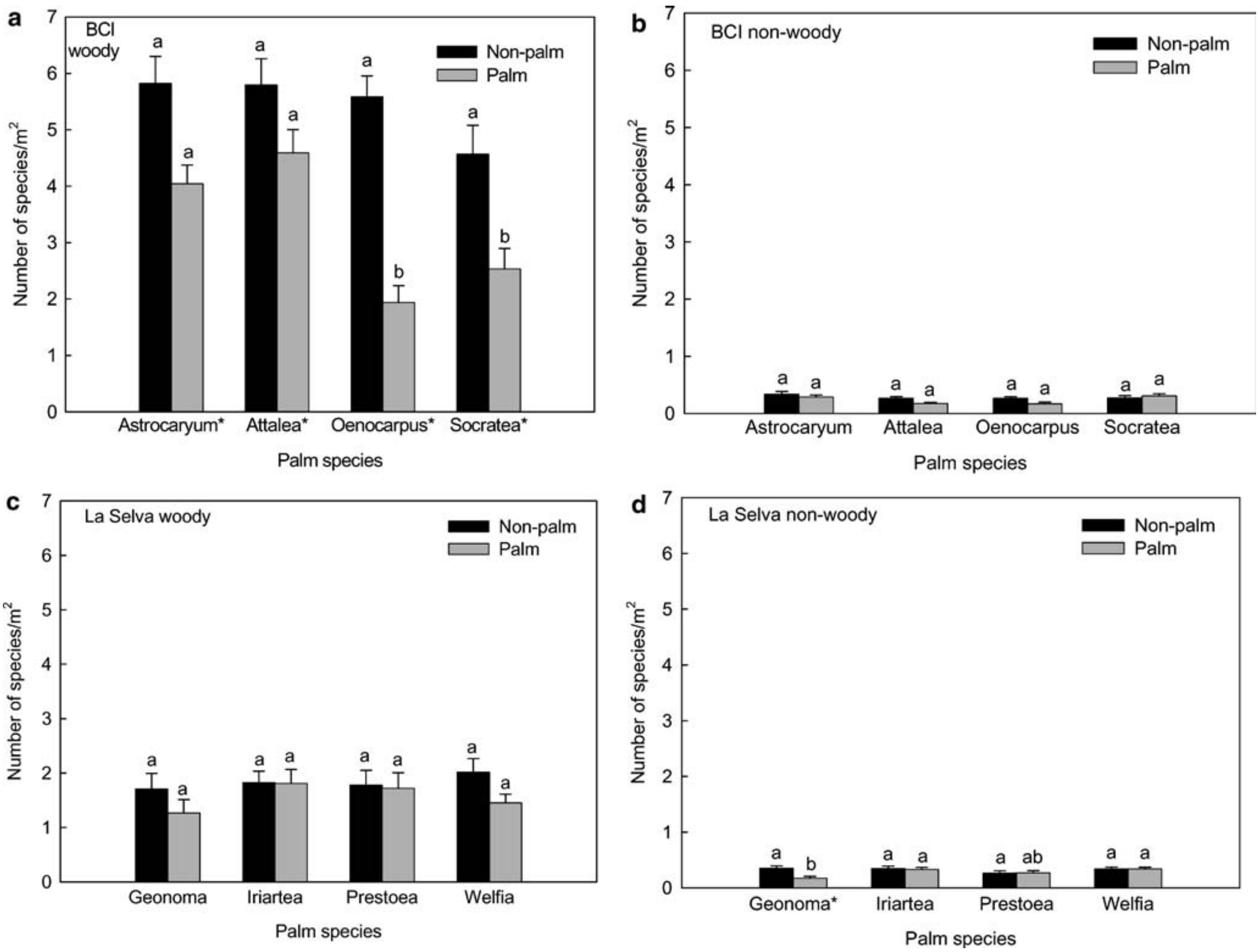

Fig. 2 Mean (+1 SE) number of species/m^2 of woody and non-woody seedlings at BCI (**a**, **b**) and La Selva (**c**, **d**) in microsites of focal palm species versus adjacent non-palm microsites. *Different lowercase letters above bars* indicate significant differences among focal palm species within either non-palm or palm microsite ($P < 0.05$ by least-square means). *Asterisk* indicates significant differences between non-palm versus palm microsites under a given focal palm species ($P < 0.05$)

Table 2 Differences in mean seedling density/m^2 and mean number of species/m^2 between palm versus non-palm microsites and under different palm species for woody and non-woody seedlings separately

Seedling growth form	Effect	*DF*	*F* for BCI density	*F* for La Selva density	*F* for BCI richness	*F* for La Selva richness
Woody seedlings	Microsite	1	38.38***	1.75	49.55***	2.55
	Palm species	3	2.82*	0.2	2.35	0.26
	Palm species × Microsite	3	1.44	0.44	3.60*	0.65
Non-woody seedlings	Microsite	1	4.71*	2.15	2.05	2.89
	Palm species	3	3.17*	0.55	1.74	1.11
	Palm species × Microsite	3	0.34	2.74*	0.6	2.32

The mixed linear model analysis was conducted separately for BCI and La Selva. Only significant interactions are listed
*$P < 0.05$, ***$P < 0.0001$

(Table 2). Overall, mean density/m^2 was 42% lower at palm than at non-palm microsites. More specifically, for each of the four palm species on BCI, density was significantly lower at palm than at non-palm microsites (Fig. 1a). Among the four palm species, the clonal *Oenocarpus* had the lowest density at palm microsites, and the greatest difference between palm versus non-palm microsites.

In contrast, at La Selva mean density/m^2 of woody seedlings did not differ significantly between microsites or among palm species (Table 2). Furthermore, for each of the four palm species at La Selva, density did not differ between palm versus non-palm microsites (Fig. 1c).

Similar to woody seedlings, mean density/m^2 of non-woody seedlings at BCI differed significantly between microsites and among palm species (Table 2). Their density was 58% lower at palm than at non-palm microsites. However, no significant differences in density between palm and non-palm microsites were found for individual palm species (Fig. 1b).

At La Selva, mean density/m^2 of non-woody seedlings showed no significant difference between microsites or among palm species (Table 2). A significant microsite × palm species interaction arose, however, because density under only *Geonoma* was significantly lower at palm than at non-palm sites (Table 2; Fig. 1d).

Estimated species richness

For woody seedlings at both BCI and La Selva, species richness estimates of ACE and Jackknife 2 performed best on the species accumulation curve, and therefore were used in subsequent analyses. At both sites estimated species richness of woody seedlings differed significantly between palm versus non-palm microsites. At BCI, estimated species richness under palms was 23% (ACE: $df = 1$, $F = 10.92$, $P < 0.05$) to 27% (Jackknife 2: $df = 1$, $F = 7.72$, $P < 0.05$) lower than at non-palm microsites (Table 3). At La Selva, estimated species richness of woody seedlings under palms was 24% (Jackknife 2: $df = 1$, $F = 6.15$, $P < 0.05$) to 30% (ACE: $df = 1$, $F = 5.92$, $P < 0.05$) lower than at non-palm microsites (Table 3).

In contrast, for non-woody seedlings at BCI, Bootstrap and Jackknife 1 estimates of species richness did not differ between palm versus non-palm microsites ($P > 0.05$; Appendix 2). Likewise, for non-woody seedlings at La Selva, Bootstrap and Jackknife 2 estimates of

Table 3 Total number of seedlings, observed number of species, and estimated species richness for woody seedlings at palm versus non-palm microsites

Palm species	Microsite	Number of seedlings	Number of species	ACE species richness estimate	Jackknife 2 species richness estimate
A. BCI					
Astrocaryum	Non-palm	316	52	63	81.98
	Palm	225	41	44.29	49.76
Attalea	Non-palm	666	65	76.25	90.96
	Palm	476	56	65.01	77.47
Oenocarpus	Non-palm	418	58	74.8	84.15
	Palm	151	43	64	61.41
Socratea	Non-palm	163	48	78	75.99
	Palm	83	34	50.89	55.95
B. La Selva					
Geonoma	Non-palm	121	40	72.55	79.48
	Palm	80	34	66.58	63.1
Iriartea	Non-palm	139	56	111.91	119.16
	Palm	116	49	78.55	85.88
Prestoea	Non-palm	90	50	134.14	102.64
	Palm	89	43	78.2	81.87
Welfia	Non-palm	185	66	112.67	124.08
	Palm	121	47	79.55	82.45

species richness did not differ between palm versus non-palm microsites ($P > 0.05$; Appendix 2).

Number of species/m^2

At BCI mean number of species/m^2 of woody seedlings differed significantly between microsites (Table 2). Overall, it was 39% lower at palm than at non-palm microsites. More specifically, for each of the four palm species on BCI, number of species/m^2 was significantly lower at palm than non-palm microsites (Fig. 2a). Number of species/m^2 did not differ significantly among palm species, but there was a significant interaction between palm species and microsites because the difference between microsites was greater for some species than others (Table 2). Microsites under clonal *Oenocarpus* had the lowest number of species/m^2 among the four palm species, and had the greatest difference between palm versus non-palm microsites (Fig. 2a). In contrast, at La Selva number of species/m^2 did not differ significantly between microsites or among palm species (Table 2; Fig. 2c).

Unlike woody seedlings at BCI, number of species/m^2 of non-woody seedlings at BCI did not differ significantly between microsites or among palm species. (Table 2; Fig. 2b). Similar to woody species at La Selva, number of species/m^2 of non-woody species at La Selva did not differ significantly between microsites or among palm species (Table 2). Number of species/m^2 under only *Geonoma* was significantly lower at palm than at non-palm sites (Fig. 2d).

Is restriction of seedling recruitment under palms associated with palm crown architecture?

On the whole, for woody and non-woody seedlings combined, seedling density/m^2 corresponded to palm architectural characters ($P < 0.05$). Moreover, significant interactions between palm species and each of the four palm architectural characters were found ($P < 0.05$), indicating that the effect of each architectural character on density differed among palm species. In contrast, the number of species/m^2 did not correspond to either architectural characters ($P > 0.05$) or palm species of varying architectural characters ($P > 0.05$). When woody species were analyzed separately, significant main effects of architectural characters and their interactions with palm species were not found for density/m^2 or the number of species/m^2. However, the species richness estimate (ACE) responded to three palm architectural characters: the number of leaves, leaf area, and distance between leaflets ($P < 0.05$).

The number of leaves, leaf area, and crown area were the major architectural characters that discriminated among palm species (see above). However, none of these characters alone demonstrated a linear relationship with seedling density/m^2, estimated species richness, or the number of species/m^2.

Table 4 Differences in percent canopy openness between palm versus non-palm microsites under different palm species and at BCI and La Selva from the mixed linear model analysis

Site	Effect	*df*	*F*
BCI	Microsite	1	71.13***
	Palm species	3	1.05
	Palm species × Microsite	3	7.12**
La Selva	Microsite	1	46.14***
	Palm species	3	0.98
	Palm species × Microsite	3	4.12*

*$P < 0.05$, **$P < 0.001$, ***$P < 0.0001$

Does limitation in light availability affect seedling recruitment?

We anticipated the architectural characters of palms to decrease light availability that, in turn, would restrict seedling recruitment. Hemispheric photos indicated significant differences in percent canopy openness between palm versus non-palm microsites at both BCI and La Selva (Table 4). Percent canopy openness was 3.6% at palm microsites versus 4.2% at non-palm microsites at BCI, and 3.2% at palm microsites versus 3.7% at non-palm microsites at La Selva. Significant interactions between microsite and palm species were found in percent canopy openness at both BCI and La Selva (Table 4). However, linear or polynomial relationships between number of leaves, leaf area, or crown area of palms and the light environment did not exist ($P > 0.05$).

Percent canopy openness at palm microsites decreased in this order at both sites: large subcanopy palms, medium-sized subcanopy palms, clonal palms, and palms with stilt roots (Appendix 1). Palms in all growth forms at BCI showed higher percent canopy openness than their counterparts at La Selva. The values for palms with stilt roots are lowest due, in part, to the effect of the roots in reducing light levels. Percent canopy openness did not differ between palm versus non-palm microsites when the large subcanopy palms, *Attalea* at BCI and *Welfia* at La Selva, were the focal species ($P > 0.05$), but did for other species pairs ($P < 0.05$).

Overall, for woody and non-woody seedlings combined, mean seedling density/m^2 corresponded positively to percent canopy openness ($df = 1$, $F = 4.59$, $P < 0.05$). For woody seedlings alone, a significant interaction between microsites and percent canopy openness occurred for density/m^2 ($df = 1$, $F = 4.17$, $P < 0.05$) at BCI, but not La Selva. Density responded more to changes in percent canopy openness at non-palm than at palm microsites. Weak correlations existed between percent canopy openness and seedling density/m^2 (Pearson's $r = 0.065$, $P < 0.05$), and the number of species/m^2 (Pearson's $r = 0.321, P < 0.05$) at BCI, but not at La Selva.

For woody seedlings at BCI, a strong positive correlation existed between percent canopy openness and estimated species richness (Jackknife 2) (Pearson's $r = 0.763$, $P < 0.05$). For non-woody seedlings there was no significant correlation between percent canopy openness and estimated species richness at either BCI or La Selva ($P > 0.05$).

Arborescent palms at the landscape scale

Arborescent palms are much more abundant at La Selva than at BCI. Mean stem density/ha of non-clonal arborescent palms (>10 cm DBH) and clonal palms combined was 3.2 times greater at La Selva than at BCI (Appendix 3). Likewise, mean percent crown cover/plot by arborescent palms was much greater at La Selva (43%) than at BCI (13%) (Appendix 3). The total number of species of arborescent palms in all plots combined also was greater at La Selva (11) than at BCI (5) (Appendix 4).

Discussion

Do individual arborescent palms restrict seedling recruitment?

The restriction of seedlings under individual palms relative to non-palm sites was not uniform. Overall, there was variation among palm species, between study sites, and between woody and non-woody species in the relative restriction of seedlings by individual arborescent palms. Mean woody seedling density/m^2 and mean number of woody species/m^2 were lower under palm than in non-palm sites for all four species at BCI, but for none at La Selva. However, the estimated species richness of woody seedlings was lower under palm than in non-palm sites at both BCI and La Selva. Non-woody seedlings were restricted by only one palm species at La Selva, but by no species at BCI. In the study design, study site and palm species were not independent. Focal palm species were unique to each site. Therefore, it is impossible to separate the independent effect explained by differences in study site versus differences in palm species. As both sites were censused in only 1 year, it is also impossible to separate the effects of year-to-year variation in seed production and species-specific dispersal and recruitment, both of which may have affected the results.

Although La Selva had no relative difference in mean seedling density/m^2 or number of species/m^2 between palm versus non-palm sites, the differences in estimated species richness indicated some relative impact on seedling recruitment. Moreover, arborescent palms at La Selva may have an absolute impact on seedling density as well. La Selva has a dense understory, including saplings and large, herbaceous monocots at non-palm sites, although not often under arborescent palms (Y.H.Wang and C.K.Augspurger, personal observation). Arborescent palms may restrict seedlings to a similar extent as the understorey vegetation, thus leading to no difference in density under palm versus non-palm sites. Alternatively, the canopy trees, upper subcanopy trees, or epiphytes may have caused the key reduction in light or some unmeasured variable may have caused the reduction in seedlings at La Selva. In these two latter scenarios, palms would not necessarily have an additional effect. Given the experimental design, it is not possible to conclude that arborescent palms alone have a strong absolute impact. Arborescent palms, or some factor associated with them, along with the understorey plants, cause seedling density overall to be lower at La Selva than BCI. In contrast, the more open understory at non-palm sites at BCI (Y.H.Wang and C.K.Augspurger, personal observation) may restrict seedlings less than at La Selva. Consequently, a large relative difference between palm versus non-palm sites arose under arborescent palms at BCI but not at La Selva.

What is the mechanism restricting seedlings?

This study explored three mechanisms that may act to restrict seedlings, viz. litter, light, and architecture. There was no or only weak evidence that any of them may be important. Density/m^2 and the number of species/m^2 of the study's post-cotyledonous seedlings were not affected by litter depth. This result contrasts with the earlier report that seedling density was negatively correlated with litter depth under *Oenocarpus* (Farris-Lopez et al. 2004). Litter would have its main effect on the earlier life stages of seedling emergence and small cotyledonous seedlings (Molofsky and Augspurger 1992; Vazquez-Yanes and Orozco-Segovia 1992).

Alternatively, the difference in palm effects between BCI and La Selva may be due to differences in crown architecture and/or light environment of the focal palm species. We attempted to minimize the differences between the two palm groups. Nevertheless, measurements of architectural characters revealed that *Astrocaryum, Attalea*, and *Oenocarpus* at BCI each had greater height, larger crowns and leaves, and a more complete umbrella-like architecture than their counterparts, *Prestoea*, *Welfia*, and *Geonoma* at La Selva. These larger architectural features at BCI, however, did not correspond to lower light. The absolute amount of light under palms was consistently lower at La Selva than at BCI between each pair of species. The lower light at La Selva may contribute to its overall lower seedling density.

Differences among the four species at BCI in their relative restriction of woody seedlings may be related to differences in their architecture and light. Both clonal *Oenocarpus* and stilt-rooted *Socratea* had lower light availability than *Astrocaryum* and *Attalea*. *Oenocarpus* limits light via a high density of ramets with overlapping crowns. *Socratea's* wide stilt root structure blocks light near the crown center, although its crown has only a few leaves and an incomplete umbrella. Both species had lower mean seedling density/m^2 and mean number of species/m^2 at their palm sites than *Astrocaryum* and *Attalea*. The low recruitment under *Oenocarpus* is consistent with the earlier study of Farris-Lopez et al. (2004). Alternatively, architecture may not be important, because mean seedling density/m^2 and estimated species richness, but not number of species/ m^2, corresponded weakly to the varying architectural characters of the different palm species. Likewise, the correlations between mean seedling density/m^2 and mean number of species/m^2 and the light environment were weak, and only woody seedling density at BCI corresponded to percentage canopy openness. Similar weak correspondence has been described in other studies (Nicotra et al. 1999; Montgomery and Chazdon 2001).

The difference in restriction between woody and non-woody seedlings may be related to their response to light. At BCI, only woody seedling density at non-palm sites corresponded to changes in percent canopy openness more than at palm sites, and the estimated species richness of only woody seedlings was positively correlated to percent canopy openness. This suggests that the woody seedlings at BCI have a wider range of shade tolerance than non-woody seedlings, including species that do not adapt to under-palm environments. In contrast, at La Selva, the difference in restriction between woody and non-woody seedlings showed no clear relationship to percent canopy openness.

This study did not test whether palms are selective filters (Denslow et al. 1991; George and Bazzaz 1999) among species with contrasting shade tolerance and life history traits. Farris-Lopez et al. (2004) demonstrated at BCI that *Oenocarpus* lowered survival, especially of small-seeded and shade-intolerant species. Therefore, at least at BCI, one species of arborescent palms may selectively favor certain groups of species during seedling establishment.

What is the extent of restriction on seedling recruitment at the landscape scale?

Density and cover by arborescent palms are greater at La Selva than at BCI. Similarly, Clark et al. (1995) found non-clonal arborescent palms to have a wide distribution and high abundance at La Selva. Arborescent palms at La Selva had a negative impact on only estimated species richness of woody seedlings, but not mean density/m^2 and mean number of species/m^2. The estimates were based on pooled data from all individual palms, while the other two variables were based on individual palms. Therefore, arborescent palms at La Selva appear to play a role in affecting woody seedling species richness only at some scale larger than the individual level. If they have a large negative impact on the absolute number of seedlings, as proposed above, then, coupled with their great abundance, they may play a role at the landscape scale in causing the overall low seedling recruitment at La Selva.

In contrast, at BCI, individual arborescent palms lowered mean seedling density/m^2, estimated species richness (woody seedlings only), and mean number of species/m^2 relative to non-palm sites. This differential impact is not extended to the landscape scale, however, because of the relative scarcity of arborescent palms there. Therefore, while habitat heterogeneity for seedling recruitment occurs, given the differences between palm versus non-palm microsites, arborescent palms at BCI do not significantly affect seedling recruitment at the landscape scale.

At the individual palm level, dwarf palms at La Selva are comparable to arborescent palms at BCI in their negative impact on seedling recruitment. At the individual dwarf palm level, seedling growth, survival, density, and number of species were 30–50% lower at dwarf palm than non-palm microsites at La Selva (Wang and Augspurger 2004). Furthermore, dwarf palms have great density and coverage at La Selva, covering 21% of the landscape. Therefore, at both individual and landscape scales at La Selva, dwarf palms play a more prominent role than arborescent palms in differentially restricting seedling recruitment. In contrast, at BCI, dwarf palms are rare, while arborescent palms have somewhat low coverage. Neither group of palms at BCI, therefore, has a large landscape-scale impact on seedling recruitment.

This study demonstrates that tropical forests differ both in the extent to which individual arborescent palms impact seedling recruitment and in their overall abundance in the landscape. Tropical forests differ in the species composition of arborescent palms, as well as palm density and cover (Kahn 1987; Sist 1989; Kahn and de Granville 1992; Kahn and Mejia 1990, 1991). Therefore, the role of arborescent palms in affecting seedling recruitment is expected to vary greatly among forests.

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Appendix 1

Mean (±1SE) crown architectural characters and percent canopy openness of the eight focal palm species

	BCI palms				La Selva palms			
	Astrocaryum	*Attalea*	*Oenocarpus*	*Socratea*	*Geonoma*	*Iriartea*	*Prestoea*	*Welfia*
Crown architectural characters								
Trunk height (m)	12.2 ± 0.8	14.56 ± 1.1	11.4 ± 0.4	16.9 ± 0.9	5.1 ± 0.1	15.8 ± 0.8	9.6 ± 1.1	10.4 ± 0.4
Number of leaves[a]	14.2 ± 0.9	17.5 ± 1.3	5.8 ± 0.2	6.1 ± 0.3	9.0 ± 0.2	6.1 ± 0.2	7.7 ± 0.5	15.9 ± 1.0
Number of fallen leaves on the ground[b]	2.3 ± 0.4	3.5 ± 0.9	8.1 ± 0.9	2.1 ± 0.3	11.0 ± 0.7	1.3 ± 0.2	1.5 ± 0.2	2.1 ± 0.2
Crown diameter 1 (m)[b]	6.1 ± 0.4	10.3 ± 0.5	8.4 ± 0.3	3.8 ± 0.1	5.4 ± 0.2	5.8 ± 0.2	4.3 ± 0.2	7.6 ± 0.4
Crown diameter 2 (m)[b]	6.2 ± 0.3	10.5 ± 0.6	8.8 ± 0.2	3.8 ± 0.2	5.1 ± 0.1	5.6 ± 0.2	4.5 ± 0.2	7.6 ± 0.2
Leaf length (cm) (including petiole)	329.6 ± 19	524.4 ± 48.3	282.5 ± 11.8	231.6 ± 11.4	114.4 ± 6.5	312.4 ± 91.8	301.4 ± 41	387.9 ± 44.7
Leaf width (cm)	137.2 ± 6.9	146.2 ± 11.7	137 ± 10.2	116.1 ± 5.6	41.2 ± 1.7	162.8 ± 41.8	96.4 ± 11.8	133.1 ± 15.4
Petiole length (cm)	138.2 ± 10.1	51.1 ± 15.1	126.5 ± 8.4	152.7 ± 6.8	45.6 ± 2.4	153.6 ± 38.4	120 ± 20.1	96.3 ± 11.1
Number of pairs of leaflets per leaf	71.0 ± 6.4	73.1 ± 9.7	53.1 ± 1.5	18.4 ± 0.9	3.2 ± 0.2	21.0 ± 2.4	58.4 ± 8.2	49.9 ± 1.9
Leaflet length (cm)	88.3 ± 5.9	73.1 ± 9.7	76.9 ± 4.3	66.1 ± 2.9	43.9 ± 1.7	115.6 ± 12.6	66 ± 4.6	91.7 ± 7.9
Leaflet width (cm)	3.5 ± 0.3	7.2 ± 2.9	5.3 ± 0.3	13.4 ± 2.2	11.1 ± 0.5	23.8 ± 5.2	4.6 ± 0.4	6.3 ± 0.6
Distance between leaflets (distal) (cm)	2.7 ± 0.6	2.6 ± 0.3	2.9 ± 0.3	4.0 ± 0.5	3.6 ± 0.7	7.2 ± 1.6	3.6 ± 0.2	5.4 ± 0.4
Distance between leaflets (middle) (cm)	5.9 ± 1.7	4.7 ± 0.6	6.6 ± 0.4	10.1 ± 0.9	1.1 ± 0.6	12.4 ± 1.3	4.9 ± 0.3	8.0 ± 0.6
Distance between leaflets (basal) (cm)	5.9 ± 1.3	8.0 ± 0.9	7.1 ± 0.6	8.8 ± 0.9	4.2 ± 0.7	14.8 ± 1.1	5.3 ± 0.3	10.3 ± 0.6
Litter depth (cm)	6.6 ± 0.4	4.9 ± 0.2	4.2 ± 0.2	4 ± 0.3	1.2 ± 0.1	1.3 ± 0.1	1.8 ± 0.1	2.1 ± 0.1
Light environment								
Percent canopy openness	3.8 ± 0.1	3.9 ± 0.2	3.4 ± 0.2	3.3 ± 0.1	3.1 ± 0.1	2.9 ± 0.1	3.2 ± 0.1	3.6 ± 0.2

[a]Number of leaves per ramet for clonal species
[b]Values are for entire clone for clonal species

Appendix 2

Total number of seedlings, observed number of species, and estimated species richness for non-woody seedlings at palm versus non-palm microsites at BCI (A) and La Selva (B)

Palm species	Microsite	Number of seedlings	Number of species	Bootstrap species richness estimate	Jackknife 1 species richness estimate
A. BCI					
Astrocaryum	Non-palm	307	11	11.96	13.8
	Palm	222	10	10.92	11.87
Attalea	Non-palm	530	17	20.03	23.53
	Palm	121	12	13.6	15.73
Oenocarpus	Non-palm	354	13	14.11	15.8
	Palm	66	14	16.57	22.4
Socratea	Non-palm	599	10	11.42	12.8
	Palm	440	10	10.87	10.93
B. La Selva					
Geonoma	Non-palm	109	22	34.24	35.19
	Palm	66	19	23.2	33.04
Iriartea	Non-palm	139	26	30.56	42.67
	Palm	145	28	33.14	44.85
Prestoea	Non-palm	84	24	39.92	29.44
	Palm	92	24	35.25	41.37
Welfia	Non-palm	181	31	35.55	43.19
	Palm	183	30	34.22	46.85

Appendix 3

Comparison between BCI and La Selva of arborescent palm communities

	Site		La Selva habitats				BCI habitats		
	La Selva	BCI	A	RF	RS	S	KF	MF	KMS
Number of species									
Arborescent palms	11	5	8	9	10	7	4	5	3
Density (stem number/ha)									
Non-clonal palms (> 10 cm dbh)	142	47	100	160	213	93	20	60	60
Non-clonal palms (> 1– < 10 cm dbh)	803	32	844	574	913	880	13	14	67
Clonal palm ramets	1,485	454	1,625	774	1,934	1,607	547	467	347
Juveniles (> 1 m leaf length)	200	11	281	80	293	147	1	13	20
Percent cover (mean/plot)(from cover class estimates)									
Non-clonal palms	18	3	16	16	23	18	2	6	2
Clonal palms	22	8	22	26	24	15	10	9	6
Juveniles (from crown measurements)	2.9	2.1	4.5	2.8	1.4	2.7	1.7	3.2	1.3
Basal area (m^2 /ha)									
Arborescent palms (> 1 cm dbh)	3.7	1.1	3.2	3.7	5.2	2.8	0.3	2.1	1.1
Habitat area									
Percent of 300 ha study site	100	100	20	25	37	18	24	67	9
Percent of study site covered by non-clonal palms	19	5	3	3	9	3	0.5	4	0.1
Percent of study site covered by clonal palms	23	9	4	7	9	3	2	6	0.5
Percent of study site covered by juveniles	3	3	1	1	1	1	0.4	2	0.1

Values of mean per 10×10 m plot were standardized to values per hectare
A old alluvium terrace, *RF* residual flat area, *RS* residual slope, *S* swamp, *KF* kaolinitic flat soil, *MF* montmorillonitic flat soil, *KMS* both soil types on slopes combined

Appendix 4

Total number of each arborescent palm species in the 15 plots of each habitat at BCI and 16 plots of each habitat at La Selva

Species	La Selva habitats				BCI habitats			
	Alluvium	Residual flat	Residual slope	Swamp	Kaolinitic flat	Montmorillonitic flat	Slope	Total
Astrocaryum alatum	0	0	1	7	0	0	0	8
Astrocaryum confertum	0	1	0	0	0	0	0	1
Astrocaryum standleyanum[a]	0	0	0	0	3	7	0	10
Attalea butyracea[a]	0	0	0	0	2	13	4	19
Bactris coloradensis	0	3	3	4	0	0	0	10
Crysophila warscewiczii	13	15	12	24	0	0	0	64
Elaeis oleifera	0	0	0	0	0	1	0	1
Euterpe precatoria	1	4	2	0	0	0	0	7
Geonoma congesta[a]	40	48	49	26	0	0	0	163
Iriartea deltoidea[a]	7	2	9	0	0	0	0	18
Oenocarpus mapora[a]	0	0	0	0	29	70	31	130
Pholidostachys pulchra	1	0	6	0	0	0	0	7
Prestoea decurrens[a]	27	15	13	58	0	0	0	113
Socratea durissima[a]	18	57	42	10	5	2	17	151
Welfia regia[a]	65	56	40	13	0	0	0	174
Total	172	201	177	142	39	93	52	876

Nomenclature follows McDade et al. (1994) and Croat (1977)
[a]indicates focal study species used for palm microsites

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