

Palm functional trait responses to local environmental factors in the Colombian Amazon

Research Article

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Abstract

Functional traits play a key role in driving plant community effects on ecosystem function. We examined nine functional traits in various palm (Arecaceae) species and their relationships with moisture, tree-fall gaps, slope, and forest type at 29 transects (500×5 m) in the northeastern region of the Colombian Amazon. Redundancy analysis of mean trait values of species within a plot weighted by their abundance and Pearson correlations were used to evaluate the relationships between traits and environmental factors. The community trait composition was correlated with local environmental factors, which explained 23% of the trait variance. We detected functional dominance of the tallest palms in soils with high moisture and in floodplain forests ($p \leq 0.05$). Palms with relatively long leaves were dominant in the flooded forests. Acaulescent and small palms were dominant on high slopes, and in *terra firme* forests, long-petioled palms were dominant in forest gaps. The number of seeds per fruit was not correlated with any environmental variable. Thus, hydrology is one of the main drivers of the functional composition of neotropical palm communities at the local scale, segregating tall palms with competitive and evasive strategies from small understory palms, which are mainly stress tolerant.

Introduction

Hydrology, topography, and the spatiotemporal dynamics of canopy gaps are among the main abiotic factors that determine the composition, structure, and richness of palm communities at both local and landscape scales (Eiserhardt et al. 2011). These factors strongly influence the functional response of the plants (Gratani 2014, Gross et al. 2008, Ishii & Asano 2010, Percy 2007, Salgado-Negret et al. 2015).

Hydrology determines the availability or amount of excess water in the soil. Elongation of shoots is a strategy to avoid anoxic stress by keeping the aerial parts of plants above the water level. This has been identified as a functional response of plants to survive in flooded areas (Blom & Voesenek 1996, Voesenek & Bailey-Serres 2015, Vormisto et al. 2004). There are few published works on the functional response of palms to flooding (Balslev et al. 2011). Compared with palms growing in well-drained soils, palms that grow in floodplain forests (FPs) have different tolerances and preferences (Clark et al. 1995); nevertheless, it is not clear how functional traits vary in response to these environmental traits. Palms may also be specific to particular microhabitats within these habitat types, and fine-scale palm distributions may depend on heterogeneity in terms of soil moisture and drainage (Svenning 1999, 2001).

The density and size of tree-fall gaps importantly affect forest dynamics because they generate variation in light availability and temperature (Kern et al. 2014). The gradient in light availability gives rise to increased richness (Muscolo et al. 2014) and causes physiological and morphological responses in some understory species (Gratani 2014, Ishii & Asano 2010, Percy 2007) depending on their tolerance to shade and the amount of increase in light after the formation of a gap. For palms, it has been suggested that large arborescent species depend on tree-fall gaps for recruitment (De Granville 1991, Kahn 1986). However, some species, such as *Euterpe edulis*, do not grow in open areas, such as large gaps; this phenomenon has been attributed to growth, survival and hydraulic traits, because photoinhibition and hydraulic limitations can affect growth rates (Gatti et al. 2014).

Topography is another environmental factor with important effects on plant growth and vegetation development (Den Dubbelden & Knops 1993). Soil on slopes experiences a relatively high degree of runoff, and such habitats favor species that evade wet and flooded areas (Méndez-Toribio et al. 2017). The local distributions of many palm species are significantly influenced by topography (Clark et al. 1995, Kahn 1986, Svenning 1999). However, palm species distribution

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patterns vary from one place to another because topography has no direct influence on itself but rather functions through its correlations with other environmental variables, such as drainage, formation of catenas, exposure of originally different sediment layers, and forest architecture (Vormisto et al. 2004).

The ecology and evolution of palms is strongly linked to inter-specific variation in the growth, reproduction, and morphology of stems, leaves, inflorescences, fruits, and seeds (Kissling et al. 2019). Moreover, the functional traits of the dominant species in a community determine ecosystem processes (Conti & Díaz 2013, Finegan et al. 2015, Hobbie 2015). Palms constitute a noticeable structural and functional component in the Amazon Forest (Gentry 1988); compared with other common species, they are well represented among trees and can reach very high population densities (Ter Steege et al. 2013), making them an ideal group for evaluating ecological responses because they are diverse, they are gregarious, and they are locally abundant (Terborgh & Andresen 1998).

This article investigates the relationships between local environmental variables and functional traits of palms in the Colombian Amazon, with the goal of contributing to the knowledge of the functional response and strategies of neotropical groups of high ecological importance, such as palms. The question asked is as follows: How are the functional composition of the palm community and the functional traits of palm species related to environmental characteristics (soil moisture, slope and gaps) in a locality in the northeastern region of the Colombian Amazon?

Methods

Study area

The study was performed along the Guaviare River in the eastern region of the Colombian Amazon in the departments of Guainía and Vichada (Figure 1), where three forest types are recognized. One type is *terra firme* forests, which are never flooded and generally have infertile and well-drained soils, with high local diversity. The second type is FPs, which are usually flooded annually. The third type is forests on terraces that are never or only very rarely flooded, and these include several ancient never-flooded terraces derived from rivers where they used to flow (Balslev et al. 2017, Villota 2005). The data collected along the Guaviare River form part of a larger dataset covering 546 transects in palm communities

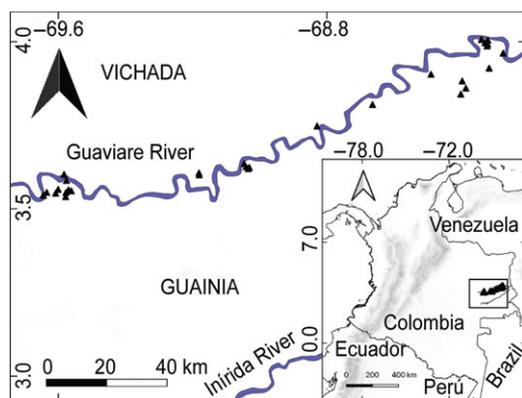


Figure 1. Study area along the Guaviare River in the Colombian Amazon. The triangles represent the position of 29 transects (500×5 m) in which all adult individuals of 25 species of palms were identified and counted.

covering the western region of the Amazon (Balslev et al. 2017, 2019).

Data collection

We established 29 transects of 500×5 m each, which were subdivided into 100 subunits of 5×5 m. The transects were established in the *terra firme* forests (11), in floodplains (14), and on terraces (4). In each transect, all adult palm individuals were registered, and on the basis of their size, it was determined whether they had reached the reproductive stage. The palm species were documented with voucher specimens under Rodrigo Bernal's numbers 4442–4541 deposited at the Colombian National Herbarium in Bogotá (COL), with duplicates at the Aarhus University Herbarium (AAU). The specimens can be seen on the Aarhus University Herbarium database (https://www.aubot.dk/search_form.php). Further details of the collection and census methodology can be found in the study of Balslev et al. (2010, 2019).

In each transect, the following environmental variables were recorded: (1) Presence/absence of gaps in each subunit of 5 × 5 m, with the subunits with gaps subsequently counted to obtain a value between 0 and 100 per transect; (2) moisture on the soil surface in subunits of 5×5 m within each transect, recorded as 0 or 1 for dry soil or muddy soil and/or stagnant water, respectively; with the subunits with values of 1 subsequently counted to obtain a value between 0 and 100 per transect; and (3) slope measured in degrees (0–90°) in each subunit of 5×5 m, which were averaged to obtain a single value per transect.

Palm functional traits were determined based on the literature (Galeano & Bernal 2010, Henderson 2011) and by examining specimens deposited in the Herbario Nacional Colombiano (COL). Nine functional traits were recorded for each palm species (Table 1): lifeform (LF; cespitose = ces, solitary = sol), growth form (GF; acaulescent = aca, erect = ere, climbing = cli), maximum stem height (StH), maximum leaf number (LN), maximum petiole length (PeL), maximum leaf rachis length (RL), maximum fruit diameter (FD), seed number per fruit (SN), and breeding system (BS, dioecious = dio, monoecious = mon) (Supplement 1).

Data analysis

The following continuous traits were categorized to show their distribution and frequencies among the forest types: maximum stem height (StH; short=0–8 m, medium=9–17 m, tall=18–25 m); maximum leaf number (LN; low=7–21, medium=22–35, high=36–50); maximum petiole length (PeL; short=45–120 cm, medium=121–225 cm; long=226–330 cm); maximum leaf rachis length (RL; short=0–263 cm, medium=264–526 cm, long=527–750 cm); maximum fruit diameter (FD; small=7–24 mm, medium=25–42 mm, large=43–60 mm); and seed number per fruit (SN; 1, 2 or 3 seeds). With the field data, three tables were constructed: matrix Q ($q \times m$) = 9 functional traits of 25 palm species (Table 1); matrix R ($n \times p$) = environmental variables of 29 transects; and matrix L ($n \times q$) = palm abundance in the 29 transects (Supplement 2).

The functional trait composition was calculated from the community-weighted means of traits (CWM) using the formula of Garnier et al. (2007). The CWM was obtained from the combination of the abundance (L) and trait (Q) matrices. The CWM calculates a trait value for each transect (Kleyer et al. 2012) from the mean trait value, weighted by the abundance of all the species present in that transect (for continuous traits), or the weighted proportion of species (for categorical traits). The CWM corresponds

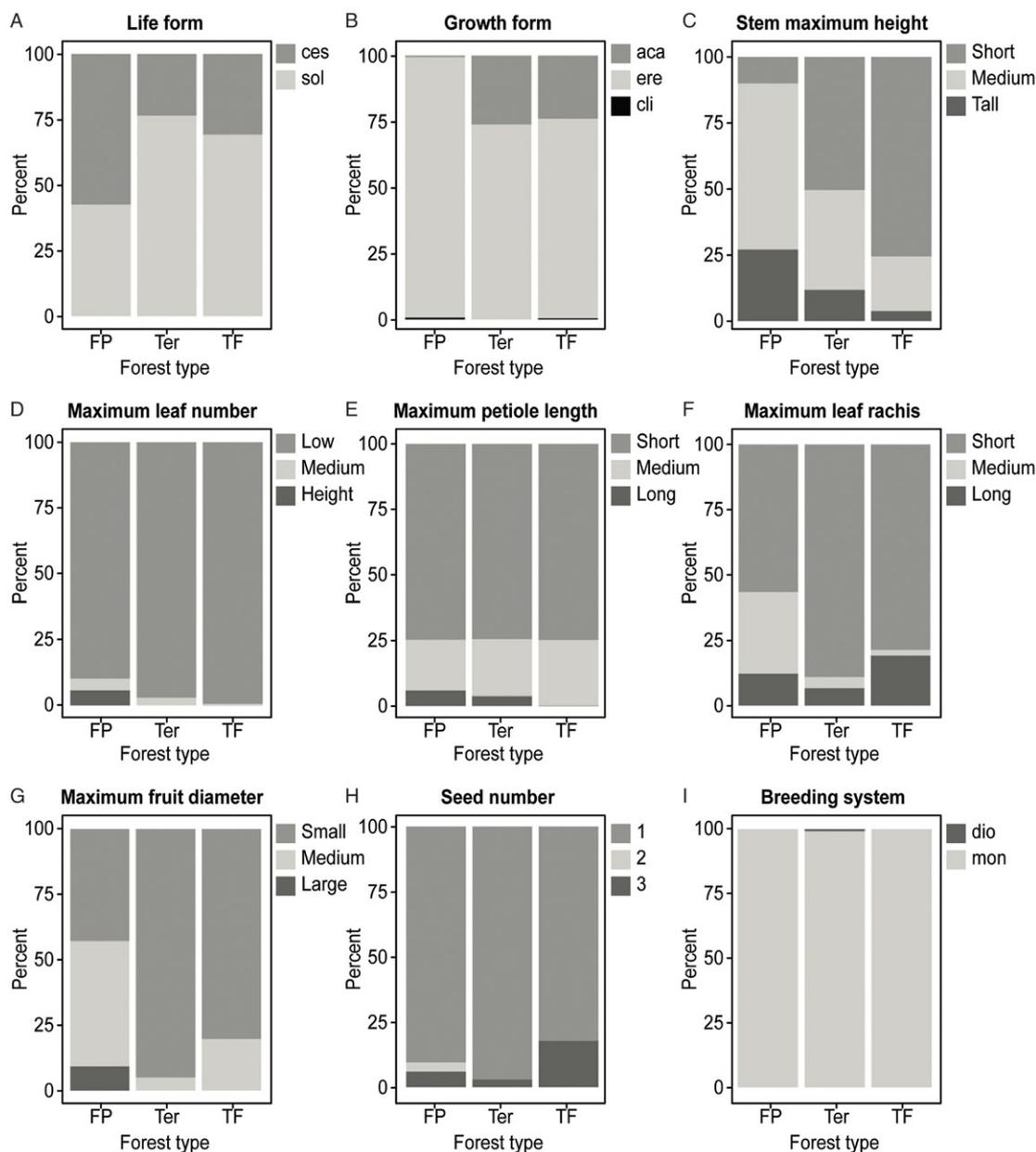


Figure 2. Relative frequency distribution of functional traits in a palm community in floodplain (FP), terrace (Ter), and *terra firme* forest types along the Guaviare River in the northeastern region of the Colombian Amazon.

to the weighted mean of the trait in the community (Díaz et al. 2007, Lavorel et al. 2008).

Redundancy analysis (CWM-RDA) was used to establish the relationships between functional composition (CWM) and environmental factors (Kleyer et al. 2012). The categorical variable 'forest type' was included in the analysis as a passive variable. Additionally, RLQ (Dolédéc et al. 1996), fourth corner (Dray et al. 2014), and Pearson correlation (Sokal & Rohlf 2000) analyses were used. All analyses were performed using R statistical software (R Core Team 2016) and the *Vegan* and *Ade-4* packages (Dray & Dufour 2007).

To test if the observed trait–environment relationships are potentially driven by phylogenetic covariation with other traits, we related our data to the most comprehensive palm phylogeny to date (Faurby et al. 2016), using the version of the phylogeny that includes full taxonomic constraints. We visually explored the

distribution of the traits across the phylogenetic tree, calculated phylogenetic signal, and statistically related mean trait values across communities to phylogenetic eigenvectors. These analyses were performed in R using the *phangorn* (Schliep 2011), *picante* (Kembel et al. 2010), and *PCPS* (Debastiani & Duarte 2014) packages.

Results

We recorded 3123 mature individuals from 25 palm species in the 29 transects that together encompassed a total of 7.25 ha (Table 1). The most diverse genus was *Bactris*, with seven species, followed by *Attalea*, *Desmoncus*, and *Geonoma*, each with three species. The most abundant species was *Iriartella setigera*, with 492 individuals, followed by *Geonoma deversa* and *Astrocaryum gynacanthum*, with 453 and 402 individuals, respectively. *Astrocaryum jauari*,

Table 1. Functional traits and abundances of 25 palm species registered in 29 transects, each covering 500×5 m, equalling 0.25 ha each or a total of 7.25 ha for all transects. The species names are according to the World Flora Online (worldfloraonline.org).

Species (Voucher Bernal#, COL)	Traits									Number of individual palms in each forest type			
	LF	GF	StH (m)	LN (#)	PeL (cm)	RL (cm)	FD (mm)	SN (#)	BS	FP	Ter	TF	Total
<i>Astrocaryum gynacanthum</i> Mart. (4521, 4537)	ces	ere	6	13	65	250	16	1	mon	14	0	388	402
<i>Attalea butyracea</i> (Mutis ex L.f.) Wess. Boer (4451, 4460, 4480 4513)	sol	ere	25	40	300	790	48	3	mon	55	0	0	55
<i>Attalea maripa</i> (Aubl.) Mart. (4474)	sol	ere	20	22	330	990	25	3	mon	2	7	3	12
<i>Attalea microcarpa</i> Mart. (4507, 4508, 4509)	sol	aca	0	16	205	600	30	3	mon	0	0	339	339
<i>Bactris acanthocarpa</i> Mart. (4447, 4471, 4499, 4503)	sol	aca	1.6	15	184	180	23	1	mon	3	43	116	162
<i>Bactris brongniartii</i> Mart. (4459, 4484, 4489)	ces	ere	9	7	140	390	15	1	mon	123	0	0	123
<i>Bactris corossilla</i> H. Karst. (4524, 4528, 4536)	ces	ere	6	8	70	152	20	1	mon	0	0	63	63
<i>Bactris hirta</i> Mart. (4468, 4470, 4473, 4496, 4506, 4525, 4530, 4535, 4538, 4539)	ces	ere	3	7	40	81	10	1	mon	3	9	68	80
<i>Bactris major</i> Jacq. (4453, 4454, 4455, 4456)	ces	ere	10	10	40	180	35	1	mon	383	0	0	383
<i>Bactris maraja</i> Mart. (4490, 4492, 4527)	ces	ere	7	10	59	140	17	1	mon	11	0	41	52
<i>Bactris simplicifrons</i> Mart. (4443, 4445, 4448, 4472, 4476, 4478, 4487, 4493, 4512)	ces	ere	2	9	40	25	10	1	mon	12	45	30	87
<i>Desmoncus giganteus</i> A.J.Hend. (4529, 4534)	sol	cli	25	50	30	200	25	1	mon	0	0	1	1
<i>Desmoncus mitis</i> Mart. (4461, 4517, 4531)	sol	cli	10	30	15	27	15	1	mon	2	0	6	8
<i>Desmoncus polyacanthos</i> Mart. (4495, 4510, 4522, 4523)	ces	cli	15	26	15	100	18	1	mon	5	0	1	6
<i>Euterpe precatória</i> Mart. (4475, 4494)	sol	ere	20	10	57	360	13	1	mon	129	7	22	158
<i>Geonoma deversa</i> (Poit.) Kunth (4466, 4477, 4491, 4498, 4500, 4501, 4502)	sol	ere	5	18	82	92	7	1	mon	46	4	403	453
<i>Geonoma macrostachys</i> Mart. (4444, 4485, 4511, 4526, 4532, 4541)	sol	aca	1	15	100	193	9.8	1	mon	2	19	6	27
<i>Geonoma maxima</i> (Poit.) Kunth (4446, 4458, 4467, 4481, 4482, 4483, 4488, 4497, 4505, 4516)	sol	ere	9	19	20	120	13	1	mon	15	19	10	44
<i>Hyospathe elegans</i> Mart. (4515)	sol	ere	7	20	41	125	8	1	mon	6	0	0	6
<i>Iriartella setigera</i> (Mart.) H. Wendl. (4462, 4479, 4504)	sol	ere	12	8	30	96	10	1	mon	41	71	380	492
<i>Manicaria saccifera</i> Gaertn. (4519)	sol	ere	10	25	130	700	60	2	mon	34	0	0	34
<i>Mauritiella armata</i> (Mart.) Burret (4469)	ces	ere	20	10	325	0	30	1	dio	0	2	0	2
<i>Oenocarpus bacaba</i> Mart. (4449, 4463, 4464, 4465, 4540)	sol	ere	25	17	160	600	22	1	mon	0	9	11	20
<i>Oenocarpus bataua</i> Mart. (4452, 4518)	sol	ere	20	16	155	900	25	1	mon	26	0	17	43
<i>Socratea exorrhiza</i> (Mart.) H.Wendl. (4442, 4457, 4486)	sol	ere	20	7	46	320	25	1	mon	48	3	20	71

Functional traits: LF=lifeform (cespitate=ces, solitary=sol), GF=growth form (acaulescent=aca, erect=ere, climbing=cli), StH= maximum stem height, LN= maximum leaf number, PeL= maximum petiole length, RL= maximum leaf rachis length, FD=maximum fruit diameter, SN=seed number, BS=breeding system (dioecious=dio, monoecious=mon). Forest type: TF=*terra firme*, FP=floodplain and Ter=terrace.

Bactris bidentula, and *Astrocaryum acaule* were identified and collected in the area, but they were not included in the analysis because they were collected only outside the transects.

Most individuals (62%) were solitary. The cespitate palms were evenly distributed between the floodplains and *terra firme* forests, while the solitary palms were more frequent in the *terra firme* forests (Figure 2A). Most individuals (83%) had erect growth forms. Notably, 99% of the acaulescent palms grew in the *terra firme* and terrace forests (Figure 2B).

The highest proportion of individuals had short stems (52%), particularly in the *terra firme* forests, whereas tall stems were more

frequent in the FPs (Figure 2C). Most individuals had few leaves (96%). The individuals with high and medium numbers of leaves were in the FP (Figure 2D). Of all individuals, 75% had short petioles (Figure 2E). Moreover, most individuals had short leaf rachises (73%); medium-rachis individuals and species were predominant in the FPs, and long-rachis individuals were better represented in the *terra firme* forests (Figure 2F).

Most individuals (70%) had small fruits, and all large-fruited palms grew in the FPs (Figure 2G). Most individuals (86%) had one seed in each fruit. Individuals with three seeds were best represented in the *terra firme* forests, while all individuals with two

seeds were in the FPs (Figure 2H). Most of the individuals palm were monoecious (99.9%); the only two dioecious individuals were in the terrace forests (Figure 2I).

Environmental variables and palm functional traits

Redundancy analysis (CWM-RDA) showed that the two first axes of the environmental variables (gaps, moisture, slope, and FT) explained 22% ($P = 0.002$) of the variation in the functional composition (Figure 3). Water in the soil surface (moisture) and the FPs were associated with positive values of axis 1, while the slope (slope) and *terra firme* forests (TF) were associated with the negative values of these axes. The presence of gaps (Gap) and terrace forests (Ter) were associated with positive values of axis 2 (Figure 3).

StH and FD were clearly associated with positive values of axis 1, while the number of seeds per fruit (SN) and the acaulescent growth form (GFaca) were related to negative values in the CWM-RDA. In general, the species with the relatively long petioles are present in greater numbers in sites with high numbers of forest gaps, while tall, large-leaved and climbing species occur mainly in sites with high moisture (Figure 3).

The RLQ analysis showed that species traits, environmental factors, and abundance were correlated ($P < 0.001$). Most of the variation was captured by the first axis of the RLQ (81%, Supplement 3). In the FP transects, the maximum height of the stem (StH) and the soil moisture were associated with positive values of this axis. Species of the *Socratea*, *Oenocarpus*, and *Euterpe* genera (all tall palms) were associated with axis 1, whereas *Attalea* and *Manicaria* species were associated with negative values of axis 2. Likewise, tree-fall gaps and terrace forests were associated with the positive values of axis 2, where mainly species of the genera *Geonoma* and *Bactris* were abundant (medium to low number of palms) (Supplement 3).

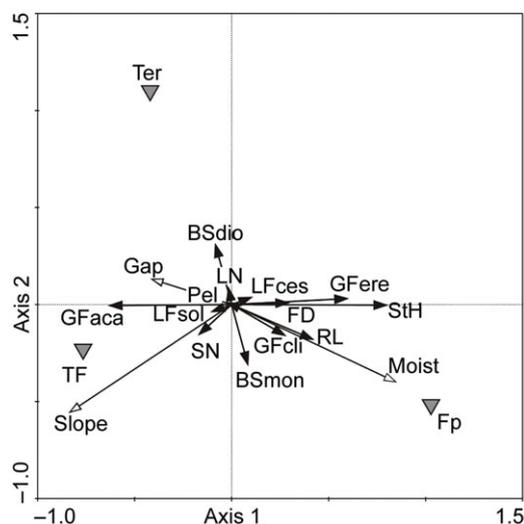


Figure 3. Ordination obtained by redundancy analysis (RDA) of the functional trait composition (CWM) in the palm community along the Guaviare River in the Colombian Amazon as a function of environmental variables. The white-tipped arrows represent environmental variables: Gap=presence of tree-fall gaps, Slope=inclination, Moist=soil moisture. The gray triangles are the forest types: TF=*terra firme* forests, Fp=floodplain forests and Ter=terrace forests. The black-tipped arrows represent traits: LF=lifeform (cespitose=ces, solitary=sol), GF=growth form (acaulescent=aca, erect=ere, climbing=cli), StH= maximum stem height, LN= maximum leaf number, RL= maximum leaf rachis length, Pel= maximum petiole length, FD=maximum fruit diameter, SN=seed number, BS=breeding system (dioecious=dio, monoecious=mon).

Individual trait-environment relationships

The acaulescent growth form was positively correlated with slope and *terra firme* forests and negatively correlated with moisture and FPs. The StH was positively correlated with soil moisture and FPs and negatively correlated with slope and *terra firme* forests. We found functional dominance of tall palms in FPs with high soil moisture and functional dominance of small palms in *terra firme* and sloping forests (Figure 4).

Leaf size was positively correlated with soil moisture and FPs and negatively correlated with terrace forests. The FD was strongly and positively correlated with FPs and negatively correlated with *terra firme* forests (Table 2). The seed number was not strongly correlated with any environmental variable measured.

Phylogenetic patterns

All traits except fruit diameter and acaulescent growth form showed phylogenetic signal significantly larger than random in a significant number of the phylogenies sampled from the posterior distribution of Faurby et al. (2016) (Supplement 4). Cespitose life form, climbing habit, seed number, and leaf dimensions (rachis and PeL) showed particularly strong phylogenetic signal. However, when testing for phylogenetic patterns in the distribution of traits across communities, only cespitose habit and – to a much lesser degree – PeL deviated from a phylogenetically random distribution (Supplement 4).

Discussion

Relationship between functional traits and environmental variables

Our results are in agreement with the plant ecology strategy scheme, which states that leaf morphology, stem height, and seed size (LHS) capture the main axes of plant responses to competition, stress, and disturbance (Westoby 1998). Tall and large-leaved palms were associated with moist and flooded areas, and small and acaulescent palms were associated with *terra firme* forests and sloping areas (Figure 3). This suggests that hydrology is the main environmental filter of functional composition, as has been documented in other studies of palm functional traits in the Amazonia region (Kristiansen et al. 2009, Pereira De Souza 2019). Hydrology segregates tall canopy palms with a competitive and avoidance strategy (Voisenek et al. 2004) from small understory palms, which are mainly stress tolerant (Grime 1974).

We found that slope was strongly correlated with acaulescent growth (Table 2). Previous studies of palms have shown that the effects of topography on the distribution and abundance of palms depend on species and varies between sites (Svenning 1999). It was suggested that topography has no direct influence on species but that slope is correlated with other environmental variables such as drainage, which does have an effect (Vormisto et al. 2004). This is the most plausible explanation of our results.

The strong correlation found between StH and flooded and moist environments (FP and moist) (Figure 4) suggests that being a tall palm is a functional response to prevent leaves and leaf buds from becoming submerged, making survival and growth in flooded zones possible. Therefore, it is an evasion strategy to avoid anoxic effects caused by water (Garssen et al. 2015, Gross et al. 2008, Mommer et al. 2006, Voisenek et al. 2004). Other studies have demonstrated strong dominance of tall palms in FPs and a low representation of medium and small palms in these environments (Balslev et al. 2011,

Kahn & De Castro 1985). On a local scale in Peru, the composition of species is determined by moisture at the soil surface (Normand et al. 2006); the results of this work show that these variables also determine the functional composition (Figure 4).

A proportional increase in petiole length with respect to leaf size reduces the overlap between leaves of adjacent *Geonoma cuneata* and *Asterogyne martiana* palms (Figure 3) (Chazdon 1985, 1986). Therefore, we interpret long petioles in the presence of gaps as the ability of the palms to compete for light, since the length of the petiole increases the diameter of the crown, allowing the palm to optimize the uptake of resources and grow rapidly. In this sense, it has been proposed that canopy palms can reach their adult state only in the presence of gaps because their light requirements increase with ontogeny (Kahn 1986, Salm et al. 2005), adapting to the opportunity for growth between disturbances through an acquisitive strategy (Reich et al. 2003). However, additional studies are needed to corroborate this relationship given the low statistical support we found (Table 1), and the finding that the distribution of petiole length across communities is phylogenetically structured (Supplement 4), indicating that the observed patterns may be driven by phylogenetic co-variation with other traits.

Long-leaved palm species are well represented in flooded habitats. This trait might represent an adaptation to floodplains to capture more light, as the canopy is more open in flooded environments (Kahn & De Castro 1985). However, the abundance of palms with long leaves may be due to the abundance of members of the genus *Astrocaryum* in FPs, and the correlation could be driven by a phylogenetic artifact (Kahn & De Castro 1985). On the other hand, leaf size may have an allometric correlation with plant size. Knowing the possible constraining effects of allometry, ontogeny, and phylogeny on leaf size may help us interpret the adaptive significance of this trait (Cornelissen 1999).

We found a clear relationship between FD and moist and flooded environments (Table 2). Generally, fruit diameter is related to the capability to colonize new habitats and to recruit in resource-limiting environments (Salgado-Negret & Paz 2016). Likewise, it has been documented that seed and fruit size determine the success of the establishment of plants because a relatively large seed mass increases the ability of seedlings to survive drought (Baskin & Baskin 2014). In particular, some studies in *varzea* and *igapo* forests in the central region of the Brazilian Amazonia have shown that large seeds are adapted to areas with high levels of flooding by promoting rapid seedling

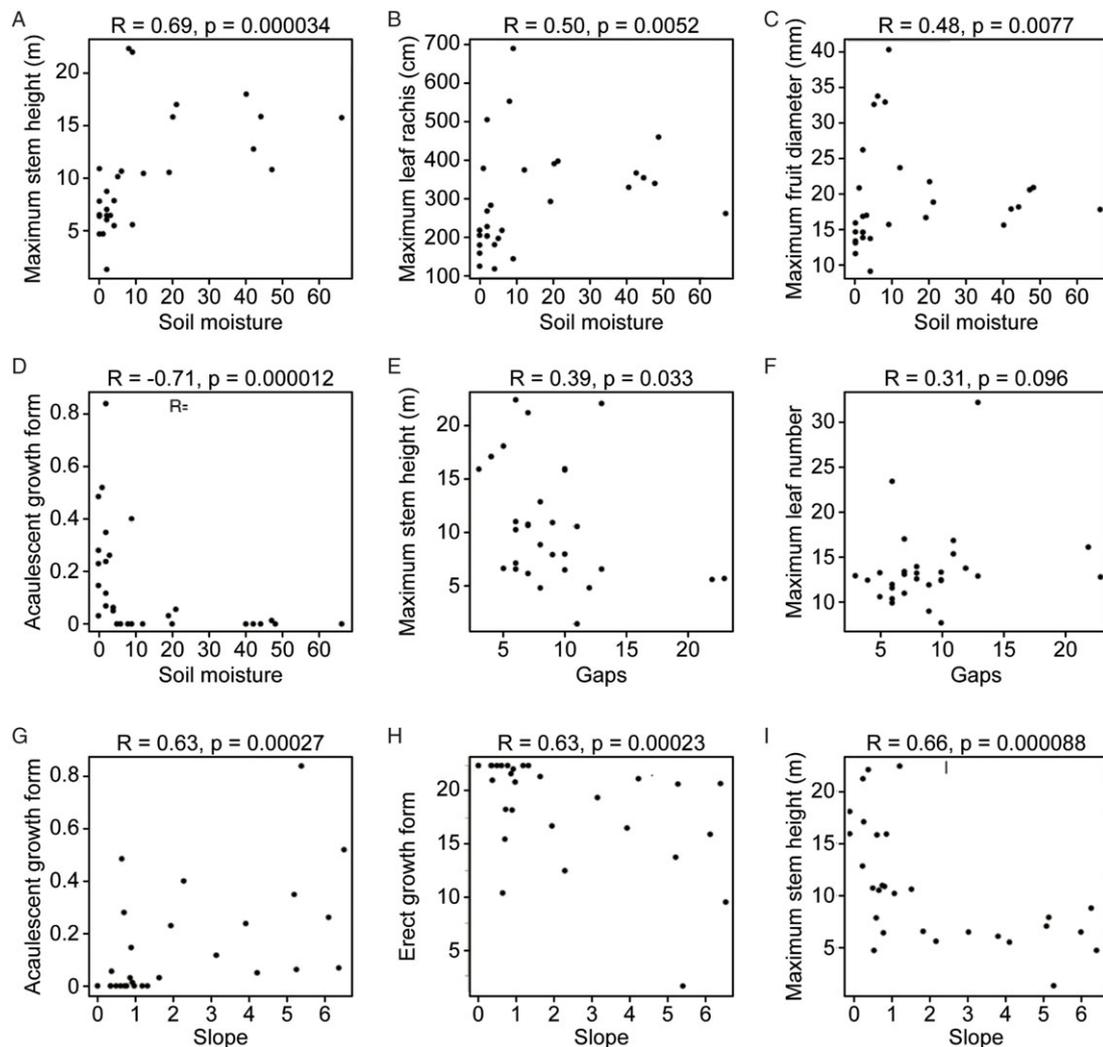


Figure 4. Scatter plots of palm functional traits and environmental variables that showed significant Spearman correlations in a palm community in the Amazon rainforest of Colombia, as studied in 29 transects of 500×5 m.

Table 2. Spearman's rank correlations between environmental variables and functional composition (CWM) of a palm community in the Colombian Amazon.

Traits	Moist	Gaps	Slopes	<i>Terra firme</i>	Floodplain	Terrace
LFces	0.020	0.060	-0.010	0.017	0.016	-0.048
LFsol	-0.013	-0.056	0.009	-0.017	-0.016	0.048
GFere	0.621***	-0.200	-0.632***	-0.573**	0.789***	-0.337
GFaca	-0.716***	0.219	0.627***	0.629***	-0.865***	0.369**
GFcli	0.114	0.079	0.090	0.084	0.058	-0.203
StH	0.690***	-0.396**	-0.663***	-0.671***	0.825***	-0.251
LN	0.071	0.314	0.099	0.068	0.066	-0.191
PeL	0.065	0.107	0.010	-0.034	0.041	-0.012
RL	0.504**	-0.114	-0.272	-0.280	0.586***	-0.454**
FD	0.484**	-0.038	-0.255	-0.408**	0.676**	-0.406**
SN	-0.009	-0.114	0.021	0.077	0.120	-0.281
BSdio	-0.272	-0.182	-0.068	-0.148	-0.183	0.472**
BSmon	-0.034	-0.093	-0.007	0.044	0.010	-0.076

N=29 transects. ***, $P < 0.001$; **, $P < 0.05$. Environmental variables: *moist*=soil moisture, *gaps*=presence of tree-fall gaps, *slope*=inclination; traits: LF=lifeform (cespitose=ces, solitary=sol), GF=growth form (acaulescent=aca, erect=ere, climbing=cli), StH= maximum stem height, LN= maximum leaf number, PeL= maximum petiole length, RL= maximum leaf rachis length, FD= maximum fruit diameter, SN=seed number, BS=breeding system (dioecious=dio, monoecious=mon).

establishment (Parolin et al. 2003). Seed size can affect germination by other means, but evidence that corroborates further relationships between large fruits and FPs is currently limited.

Conclusion

Soil moisture and flood regimes are the main environmental factors that affect the functional trait composition of this Amazonian rainforest palm community. Avoidance strategies allow palms to keep their aerial parts above the water level, preventing anoxic stress under waterlogged conditions. Acaulescence and small palm size are stress tolerance mechanisms on sloping and dry terrain (*terra firme*) under shady conditions, and palms with these traits do not tolerate flooded areas. Hydrology is one of the main determinants of the functional trait composition of neotropical palms on a local scale, and habitats with prolonged floods have communities of palms in which species are adapted to the stressful ecophysiological conditions that flooding creates.

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References

- Balslev H, Copete J, Pedersen D, Bernal R, Galeano G, Duque A, Berrio J and Sanchez M (2017) *Palm diversity and abundance in the Colombian Amazon*. In Myster R (ed.), *Forest Structure, Function and Dynamics in Western Amazonia*. New Jersey, NJ: John Wiley & Sons Ltd., pp. 101–123.
- Balslev H, Kahn F, Millan B, Svenning JC, Kristiansen T, Borchsenius F, Pedersen D and Eiserhardt WL (2011) Species diversity and growth forms in tropical American palm communities. *The Botanical Review* **77**, 381–425.
- Balslev H, Kristiansen SM and Muscarella R (2019) Palm community transects and soil properties in Western Amazonia. *Ecology* **100**, e02841.
- Balslev H, Navarrete H, Paniagua-Zambrana N, Pedersen D, Eiserhardt W and Kristiansen T (2010) El uso de transectos para el estudio de comunidades de palmas. *Ecología en Bolivia* **45**, 8–22.
- Baskin C and Baskin J (2014) *Seeds. Ecology, Biogeography, and Evolution of Dormancy and Germination*. Amsterdam: Elsevier.
- Blom C and Voeselek L (1996) Flooding: the survival strategies of plants. *Trends in Ecology & Evolution* **11**, 290–295.
- Chazdon RL (1985) Leaf display, canopy structure, and light interception of two understory palm species. *American Journal of Botany* **72**, 1493–1502.
- Chazdon RL (1986) The costs of leaf support in understory palms: economy versus safety. *The American Naturalist* **127**, 9–30.
- Clark DA, Clark DB, Sandoval RM and Castro MVC (1995) Edaphic and human effects on landscape-scale distributions of tropical rain forest palms. *Ecology* **76**, 2581–2594.
- Conti G and Díaz S (2013) Plant functional diversity and carbon storage—an empirical test in semi-arid forest ecosystems. *Journal of Ecology* **101**, 18–28.
- Cornelissen J (1999) A triangular relationship between leaf size and seed size among woody species: allometry, ontogeny, ecology and taxonomy. *Oecologia* **118**, 248–255.
- De Granville J (1991) Life forms and growth strategies of Guianan palms as related to their ecology. *Bulletin de l'Institut Français d'Études Andines* **21**, 533–548.
- Debastiani VJ and Duarte LdS (2014) PCPS – an R-package for exploring phylogenetic eigenvectors across metacommunities. *Frontiers of Biogeography* **6**, <https://doi.org/10.21425/F5FBG22943>.
- Den Dubbelden KC and Knops JM (1993) The effect of competition and slope inclination on aboveground biomass allocation of understory ferns in subtropical forest. *Oikos* **67**, 285–290.
- Díaz S, Lavorel S, De Bello F, Quétier F, Grigulis K and Robson TM (2007) Incorporating plant functional diversity effects in ecosystem service

- assessments. *Proceedings of the National Academy of Sciences of the United States of America* **104**, 20684–20689.
- Dolédéc S, Chessel D, Ter Braak CJ and Champely S** (1996) Matching species traits to environmental variables: a new three-table ordination method. *Environmental and Ecological Statistics* **3**, 143–166.
- Dray S and Dufour AB** (2007) The ade4 package: implementing the duality diagram for ecologists. *Journal of Statistical Software* **22**, 1–20.
- Dray S, Choler P, Dolédéc S, Peres-Neto PR, Thuiller W, Pavoine S and Ter Braak CJ** (2014) Combining the fourth-corner and the RLQ methods for assessing trait responses to environmental variation. *Ecology* **95**, 14–21.
- Eiserhardt WL, Svenning JC, Kissling WD and Balslev H** (2011) Geographical ecology of the palms (*Arecaceae*): determinants of diversity and distributions across spatial scales. *Annals of Botany* **108**, 1391–1416.
- Faurby S, Eiserhardt WL, Baker WJ and Svenning J-C** (2016) An all-evidence species-level supertree for the palms (*Arecaceae*). *Molecular Phylogenetics and Evolution* **100**, 57–69.
- Finegan B, Peña-Claros M, De Oliveira A, Ascarrunz N, Bret-Harte MS, Carreño-Rocabado G, Casanoves F, Díaz S, Eguiguren Velepucha P and Fernandez F** (2015) Does functional trait diversity predict above-ground biomass and productivity of tropical forests? Testing three alternative hypotheses. *Journal of Ecology* **103**, 191–201.
- Galeano G and Bernal R** (2010) *Palmas de Colombia: Guía de Campo*. Bogotá, D.C: Universidad Nacional de Colombia, Facultad de Ciencias, Instituto de Ciencias Naturales.
- Garnier E, Lavorel S, Ansquer P, Castro H, Cruz P, Dolezal J, Eriksson O, Fortunel C, Freitas H and Golodets C** (2007) Assessing the effects of land-use change on plant traits, communities and ecosystem functioning in grasslands: a standardized methodology and lessons from an application to 11 European sites. *Annals of Botany* **99**, 967–985.
- Garssen AG, Baattrup-Pedersen A, Voisenek LA, Verhoeven JT and Soons MB** (2015) Riparian plant community responses to increased flooding: a meta-analysis. *Global Change Biology* **21**, 2881–2890.
- Gatti MG, Campanello PI, Villagra M, Montti L and Goldstein G** (2014) Hydraulic architecture and photoinhibition influence spatial distribution of the arborescent palm *Euterpe edulis* in subtropical forests. *Tree Physiology* **34**, 630–639.
- Gentry AH** (1988) Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Annals of the Missouri Botanical Garden*, 1–34. <https://doi.org/10.2307/2399464>.
- Gratani L** (2014) Plant phenotypic plasticity in response to environmental factors. *Advances in Botany* **2014**, 1–17.
- Grime JP** (1974) Vegetation classification by reference to strategies. *Nature* **250**, 26–31.
- Gross N, Robson T, Lavorel S, Albert C, Le Bagousse-Pinguet Y and Guillemin R** (2008) Plant response traits mediate the effects of subalpine grasslands on soil moisture. *New Phytologist* **180**, 652–662.
- Henderson A** (2011) A revision of geonoma (*Arecaceae*). *Phytotaxa* **17**, 1–271.
- Hobbie SE** (2015) Plant species effects on nutrient cycling: revisiting litter feedbacks. *Trends in Ecology & Evolution* **30**, 357–363.
- Ishii H and Asano S** (2010) The role of crown architecture, leaf phenology and photosynthetic activity in promoting complementary use of light among coexisting species in temperate forests. *Ecological Research* **25**, 715–722.
- Kahn F** (1986) Life forms of Amazonian palms in relation to forest structure and dynamics. *Biotropica* **18**, 214–218.
- Kahn F and De Castro A** (1985) The palm community in a forest of Central Amazonia, Brazil. *Biotropica* **17**, 210–216.
- Kembel SW, Cowan PD, Helmus MR, Cornwell WK, Morlon H, Ackerly DD, Blomberg SP and Webb CO** (2010) Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* **26**, 1463–1464.
- Kern CC, Montgomery RA, Reich PB and Strong TF** (2014) Harvest-created canopy gaps increase species and functional trait diversity of the forest ground-layer community. *Forest Science* **60**, 335–344.
- Kissling WD, Balslev H, Baker WJ, Dransfield J, Gödel B, Lim JY, Onstein RE and Svenning JC** (2019) PalmTraits 1.0, a species-level functional trait database of palms worldwide. *Scientific Data* **6**, 178–191.
- Kleyer M, Dray S, Bello F, Lepš J, Pakeman RJ, Strauss B, Thuiller W and Lavorel S** (2012) Assessing species and community functional responses to environmental gradients: which multivariate methods? *Journal of Vegetation Science* **23**, 805–821.
- Kristiansen T, Svenning JC, Grández C, Salo J and Balslev H** (2009) Commonness of Amazonian palm (*Arecaceae*) species: cross-scale links and potential determinants. *Acta Oecologica* **35**, 554–562.
- Lavorel S, Grigulis K, McIntyre S, Williams NSG, Garden D, Dorrrough J, Berman S, Quéfier F, Thébault A and Bonis A** (2008) Assessing functional diversity in the field—methodology matters! *Functional Ecology* **22**, 134–147.
- Méndez-Toribio M, Ibarra-Manríquez G, Navarrete-Segueda A and Paz H** (2017) Topographic position, but not slope aspect, drives the dominance of functional strategies of tropical dry forest trees. *Environmental Research Letters* **12**, 085002.
- Mommer L, Lenssen JP, Huber H, Visser EJ and De Kroon H** (2006) Ecophysiological determinants of plant performance under flooding: a comparative study of seven plant families. *Journal of Ecology* **94**, 1117–1129.
- Muscolo A, Bagnato S, Sidari M and Mercurio R** (2014) A review of the roles of forest canopy gaps. *Journal of Forestry Research* **25**, 725–736.
- Normand S, Vormisto J, Svenning JC, Grández C and Balslev H** (2006) Geographical and environmental controls of palm beta diversity in paleo-riverine terrace forests in Amazonian Peru. *Plant Ecology* **186**, 161–176.
- Parolin P, Ferreira L and Junk W** (2003) Germination characteristics and establishment of trees from Central Amazonian flood plains. *Tropical Ecology* **44**, 155–168.
- Pearcy R** (2007) *Responses of plants to heterogeneous light environments*. In Pugnaire F and Valladares F (eds.), *Functional Plant Ecology*. New York, NY: Taylor & Francis Group, pp. 213–258.
- Pereira De Souza H** (2019) *Estrutura Funcional de uma Comunidade de Palmeiras (Arecaceae) ao Longo de Gradientes Ambientais em uma Floresta da Amazônia Central* (Masters' dissertation). Manaus: Instituto Nacional de Pesquisas da Amazônia.
- R Core Team** (2016) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna. <https://www.R-project.org/>
- Reich PB, Wright I, Cavender-Bares J, Craine J, Oleksyn J, Westoby M and Walters M** (2003) The evolution of plant functional variation: traits, spectra, and strategies. *International Journal of Plant Sciences* **164**, S143–S164.
- Salgado-Negret B and Paz H** (2016) *Escalando de los rasgos funcionales a procesos poblacionales, comunitarios y ecosistémicos*. In Salgado-Negret B (ed.), *La Ecología Funcional como Aproximación al Estudio, Manejo y Conservación de la Biodiversidad: Protocolos y Aplicaciones*. Bogotá, D.C: Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, pp. 12–35.
- Salgado-Negret B, Canessa R, Valladares F, Armesto JJ and Pérez F** (2015) Functional traits variation explains the distribution of *Aextoxicon punctatum* (*Aextoxicaceae*) in pronounced moisture gradients within fog-dependent forest fragments. *Frontiers in Plant Science* **6**, 511.
- Salm R, Jalles-Filho E and Schuck-Paim C** (2005) A model for the importance of large arborescent palms in the dynamics of seasonally-dry Amazonian forests. *Biota Neotropica* **5**, 151–156.
- Schliep KP** (2011) phangorn: phylogenetic analysis in R. *Bioinformatics* **27**, 592–593.
- Sokal R and Rohlf FJ** (2000) *Biometry. The Principles and Practice of Statistics in Biological Research*. New York, NY: W.H. Freeman and Company.
- Svenning JC** (1999) Microhabitat specialization in a species-rich palm community in Amazonian Ecuador. *Journal of Ecology* **87**, 55–65.
- Svenning JC** (2001) On the role of microenvironmental heterogeneity in the ecology and diversification of neotropical rain-forest palms (*Arecaceae*). *The Botanical Review* **67**, 1–53.
- Ter Steege H, Pitman NC, Sabatier D, Baraloto C, Salomão RP, Guevara JE, Phillips OL, Castilho CV, Magnusson WE and Molino JF** (2013) Hyperdominance in the Amazonian tree flora. *Science* **342**, 1243092.
- Terborgh J and Andresen E** (1998) The composition of Amazonian forests: patterns at local and regional scales. *Journal of Tropical Ecology* **14**, 645–664.
- Villota H** (2005) *Geomorfología Aplicada a Levantamientos Edafológicos y Zonificación Física de Tierras*. Bogotá: Instituto Geográfico Agustín Codazzi (IGAC).

- Voeselek I, Rijnders J, Peeters A, Van de Steeg H and De Kroon H** (2004) Plant hormones regulate fast shoot elongation under water: from genes to communities. *Ecology* **85**, 16–27.
- Voeselek LA and Bailey-Serres J** (2015) Flood adaptive traits and processes: an overview. *New Phytologist* **206**, 57–73.
- Vormisto J, Tuomisto H and Oksanen J** (2004) Palm distribution patterns in Amazonian rainforests: what is the role of topographic variation? *Journal of Vegetation Science* **15**, 485–494.
- Westoby M** (1998) A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil* **199**, 213–227.