BIOCHEMISTRY & PHYSIOLOGY - ORIGINAL ARTICLE

Light and dispersal strategies structure palm community along an elevation gradient in the Atlantic Forest

Sara Lucía Colmenares-Trejos[1] · Rita de Cássia Quitete Portela[2] · Alexandra Pires Fernandez[3] ·
Maria Isabel Guedes Braz[2] · Eduardo Arcoverde de Mattos[2]

Abstract

Light availability and seed dispersal can play a determinant role for plant growth and survival. The intricate interplay among these factors, coupled with pronounced topographic and elevational variation, may influence forest composition and structure. Despite the structural significance of palms within the Atlantic Forest, they are scarcely represented in both inventories and ecological studies. Additionally, functional trait variation among palm species is barely tested, and species are usually categorized into one or two functional types. We examined a palm community in terms of floristic composition and species replacement along an elevation gradient from 0 to 1400 m. Furthermore, we measured a set of morpho-physiological traits strongly associated with growth and survival strategies, such as photosynthetic capacity through Rapid Light Curves, leaf traits, height and fruit size and number. Our findings reveal highest richness from 300 to 800 m. Otherwise, palm density increased along elevation, peaking after 1200 m, mainly associated with *E. edulis* increase in density along elevation. Additionally, traits associated with enhanced light capture and dispersal capacity, i.e., higher photosynthetic capacity, height, and fruit number, were common among species widely distributed along the entire elevation gradient, such as *Euterpe edulis* M. and *Geonoma schottiana* M. In contrast, species with narrower distributions, exhibit the opposite traits. In conclusion, in our study area there is an integral role of light response and dispersal capacity in shaping the palm community structure in the Atlantic Forest along an elevation gradient from 0 to 1400 m.

Keywords Arecaceae · Dispersal patterns · Functional traits · Light response

1 Introduction

Species response to environment is one of the most fundamental drivers of community assembly (McGill et al. 2006; Hulshof et al. 2013; Hernández-Calderón et al. 2014; Luo et al. 2016). Shifts in plant functional traits across environmental gradients can be influenced by both deterministic and stochastic processes shaping community organization. Deterministic processes include environmental trait selection (habitat filtering) and species competition (niche differentiation) as outlined by Kraft et al. (2008), Andersen et al. (2012) and Pescador et al. (2015). However, it is crucial to also account for stochastic processes like convergent evolution, large disturbance events, or random niche dynamics, which can likewise mold species functional adaptation and engender diverse community responses to environmental alterations (Chase and Myers 2011). Trait-based approaches become useful during last years to understand how the environment may structure plant communities (Wright et al. 2004; Garnier and Navas 2012; Ames et al. 2016).

Environmental variation conveys filtering processes, which leads to changes in community trait composition due to the species turnover and abundance variation of coexisting species along gradients, and as well due to niche similarity/dissimilarity, phylogenetic relatedness, inner species

✉ Sara Lucía Colmenares-Trejos
slcolmenarest@gmail.com

1 Programa de Pós-Graduação em Ecologia, Departamento de Ecologia, Instituto de Biologia, Universidade Federal do Rio de Janeiro, Caixa Postal 68020, Rio de Janeiro CEP 21941-590, Brazil

2 Departamento de Ecologia, Instituto de Biologia, Universidade Federal do Rio de Janeiro (UFRJ), Rio de Janeiro, Brazil

3 Departamento de Ciências Ambientais, Instituto de Floresta, Universidade Federal Rural do Rio de Janeiro, (UFRRJ), Rio de Janeiro, Brazil

plasticity and genetic variation (Cornwell and Ackerly 2009; Andersen et al. 2011; Pescador et al. 2015). Conversely, biotic interactions play a role in reducing the overlap of similar traits among species exploiting similar niches and resources; this results in limiting similarity, which potentially leads to competitive exclusions that balance species dominance (2011(Andersen et al. 2012; Hulshof et al. 2013; le Roux et al. 2014). As elevation increases, the main environmental shifts are climatic, mainly related with temperature and rain regimes, along with soil conditions and fertility (Lomolino 2001; Körner 2007). These dual factors—environmental and biotic—jointly influence the traits that are favored or filtered out along an elevational gradient.

The consequent shifts in temperature and precipitation regimes could significantly influence physiological traits, such as metabolic rates, photosynthetic efficiency, and stress tolerance among species (Luo et al. 2016). Concurrently, variations in soil fertility along elevation drive morphological trait divergence like root depth, leaf size, and body size (Luo et al. 2016). On the dispersal front, species might employ divergent mechanisms to navigate through elevational gradients (Zheng et al. 2022). For example, for animal-dispersed seeds, dispersal capacity depends on the mobility of their dispersal agents; along with that dispersal endeavors could be hampered by physical barriers, adverse climatic conditions, and the paucity of suitable habitats, especially at higher elevations (Hulshof et al. 2013; Pescador et al. 2015; Zheng et al. 2022). Moreover, species competitive performance may depend on their dispersal capabilities, and those with superior dispersal mechanisms may swiftly colonize new elevational niches, potentially overshadowing less mobile species (Zheng et al. 2022).

Palms are characterized by presenting a high niche specialization (Balslev et al. 2011; Eiserhardt et al. 2011). The distribution of palms is restricted to regions where the interaction between temperature and humidity maintains a high vapor pressure level, or where temperature and moisture are relatively high and constant during the year (Eiserhardt et al. 2011; Renninger and Phillips 2016). Their dependence on such climatic conditions is associated with their morpho-physiological characteristics such as the presence of a single bud for the maintenance of the whole plant, their susceptibility to cavitation due to the absence of vascular cambium which makes them unable to replace vessels in their stem or leaves (Salm et al. 2007; Eiserhardt et al. 2011; Renninger and Phillips 2016) and, their inability to regulate bud dormancy which limits their capacity to tolerate low temperatures and frost (Salm et al. 2007; Renninger and Phillips 2016). Palm intolerance to low temperatures is probably their main ecophysiological limitation along elevation, together with the effect of variations in soil water availability and fertility (Balslev et al. 2011; Alvarado-Segura et al. 2012). Besides the

Amazonian forest, the Southeastern Brazilian Atlantic Forest constitutes a center of higher palm species diversity in Brazil (Salm et al. 2007), with around 60 species and 15 genera (Oliveira et al. 2014). The Atlantic forest is characterized by a high variation in topography and elevation (Eisenlohr et al. 2013; Sanchez et al. 2013), which presupposes a source of abiotic filtering for palms due to the high environmental heterogeneity associated with it (Alves et al. 2010).

Even though palms are recognized as being important structuring components of the Atlantic Forest (Joly et al. 2012; Hernández-Calderón et al. 2014; Benchimol et al. 2017), they are commonly underrepresented in inventories and ecological studies, especially the species with narrow distribution ranges and species with small stem diameters (i.e. less than 40 mm) (Portela et al. 2017). Previous research on palms in the Atlantic Forest covered aspects of population dynamics and structure (Portela and Santos 2011; Melito et al. 2014; Oliveira et al. 2014; Zucaratto and Pires 2015), ecophysiology (Gatti et al. 2008; Braz et al. 2012; Oda et al. 2016), dispersal syndromes and phenology (Genini et al. 2009; Galetti et al. 2013; Brancalion and Rodrigues 2014) and their conservation and management (Mengardo et al. 2012; Santos et al. 2015; Benchimol et al. 2017). Although results of these studies had been valuable, little information is available for morphological and physiological traits among non-cultivated palm species (see Göldel et al. 2015), and species are usually divided into one or two functional types based on the type of habitat they occur, or by their growth form (Santiago and Wright 2007; Ruiz-Jaen and Potvin 2010; Benchimol et al. 2017).

Additionally, most of the research has concentrated on soft traits, with only a handful exploring the inclusion of hard traits. Hard traits correspond to very precise measurements, mechanically linked to specific functions, which often entail more time, expertise, or financial resources to be accurately measured; examples include physiological traits like photosynthetic rate and stomatal conductance (Wright et al. 2004; Garnier et al. 2016). 'Soft traits' are usually morphological or anatomical characteristics that are easily measurable, albeit less directly related to specific functions (Wright et al. 2004; Garnier et al. 2016). Hard traits may provide clues on habitat preferences since they mediate direct and indirect effects of soft traits on habitat preferences (Belluau and Shipley 2018). More specifically, integrating physiological (hard) traits with biological (soft) traits can elucidate individuals' relative fitness, indicating their success in gene transmission to the next generation, and their survival ability in an environment, denoting their capacity to thrive amid habitat challenges. This combined examination provides a nuanced framework to understand adaptive strategies across individual to community levels in varying habitats, thereby enhancing our insight into species'

adaptation and survival mechanisms in diverse environmental contexts (Lavorel and Garnier 2002; Violle et al. 2007).

There is evidence on how elevation gradients impact species richness, community composition, and functional trait variations (Hulshof et al. 2013; Nettesheim et al. 2018). In many cases, a decrease in average temperature at higher altitudes leads to stronger environmental restrictions limiting species distribution by affecting their growth, survival, and dispersal capacity (Bjorholm et al. 2005; Hernández-Calderón et al. 2014; Pescador et al. 2015). Growth refers to the plant increase in size or biomass or its ability to exploit resources efficiently for survival and reproduction (Westoby 1998). As elevation increases, plant growth typically diminishes due to lower temperatures and oxygen levels, reduced atmospheric pressure, less favorable nutrient availability, more intense solar radiation, and water scarcity (Körner 2007; Defossez et al. 2018). Among key 'soft' traits associated to growth are height, specific leaf area, leaf dry matter content, and leaf area, which indicate relative growth rate, photosynthetic capacity, leaf lifespan, and leaf nitrogen content (Westoby 1998; Wright et al. 2004; Poorter and Bongers 2006). Moreover, hard traits such as chlorophyll content (ChT), maximum electron transport rate (ETR), alpha (α), and saturation light intensity (Ik) provide precise insights into photosynthetic capacities and light tolerance of species and are directly associated with growth and survival (Givnish 1988; Govindjee 2004; Schreiber 2004).

As growth and survival, the ability of movement of plant's seeds or spores away from the parent plant, i.e., dispersal capacity (Westoby 1998) can be facilitated by wind, water, or animals' movement, determining the potential for colonization of new areas (Westoby 1998; Cornelissen et al. 2003; Galetti et al. 2013). Key 'soft' traits related to dispersal capacity include fruit size, fruit number and height at maturity, which are also related with competitive position and seedling survival (Westoby 1998; Cornelissen et al. 2003; Galetti et al. 2013; Pérez-Harguindeguy et al. 2013, 2016). In this study, we explored floristic patterns and species turnover along an elevation gradient from 0 to 1400 m, anticipating signs of environmental filtering. We also utilized a broad range of morpho-physiological functional traits—both soft and hard—to enhance our understanding of the growth and dispersal strategies of species along the elevational gradient. We hypothesize that species richness will decrease at higher elevations and that species distribution will depend on palms with greater dispersal abilities and more efficient resource use as elevation increases.

2 Materials and methods

Study site Our study was carried out in a section of the Serra do Mar Mountain chain in Rio de Janeiro state, SE Brazil. The Serra do Mar Forests belongs to the Atlantic Forest domain, presenting high endemism and biodiversity (Cantidio and Souza 2019). This forest is exposed to the geological and topographic complexity of the Serra do Mar, placing it under extreme habitat and microclimate heterogeneous conditions (Alves et al. 2010). Data were collected along an elevational gradient from zero to 1400 m (Fig. 1). The sampling was performed within three long time protected areas in Rio de Janeiro state, where forests are in late successional stages, supporting a good status of conservation. We divided the whole gradient into five elevation belts based on elevation categories: 0–200 m (lowland forest), 300–500 m (submontane forest), 600–800 m (submontane forest), 900–1100 m (submontane-montane forest) and 1200–1400 m (montane forest). Lowland forest of Rio de Janeiro has annual precipitation of 2000 mm and average temperature of 25 °C (Lima et al. 2006), Submontane Forest has annual precipitation of 2000 mm and average temperature of 22 °C (Carvalho et al. 2009), Montane Forest has an annual precipitation of 3000 mm and temperature of 18 °C (Sattler et al. 2007). The area encompassing elevations from zero to 200 m and 500–800 m was established at the Três Picos State Park (PETP) (22° 19′ S/42° 41′ W), near Cachoeiras de Macacú city. This park holds the highest biodiversity index detected for the whole state representing one of the most prominent areas for conservation priorities of the Atlantic Forest (PESET). The region between 200 and 400 m was placed at a Brazilian non-profit non-governmental organization called Reserva Ecológica de Guapiaçú (REGUA) (22° 50′ S/42° 88′ W), which geographically borders the Três Picos State Park at 500 m, also near Cachoeiras de Macacú city. Thus, the area from 200 to 800 m belongs to the same area. The highest elevation belts were located at Serra dos Órgãos National Park (PARNASO) (22° 29′ S/43° 4′ W), at Teresópolis city. Climate below 1200 m is hot and wet, classified as tropical rainforest climate, *Af*, by the Köppen climate classification. Above 1200 m, climate is hot and humid in summer and cold and wet in winter, and it is classified as subtropical highland climate or Monsoon-influenced temperate oceanic climate, *Cwb*, by the Köppen climate classification.

Floristic composition and structure of the palm community We used a modified variable area method for palm sampling proposed by Portela et al. (2017). Only the first six adults in each transect ($10 \times T_{length}$ m transects) were sampled in the variable area method; in this case, transect length (T_{length}) was defined according to the distance of the sixth adult from the beginning of the transect. When fewer than six individuals were observed in each transect, transect length was extended up to 50 m to search for additional individuals. Palm species were identified based on Henderson's guides and experience from previous field expeditions in the Atlantic Forest (Pires 2006; Henderson 2011; Portela et al. 2016; Henderson et al.
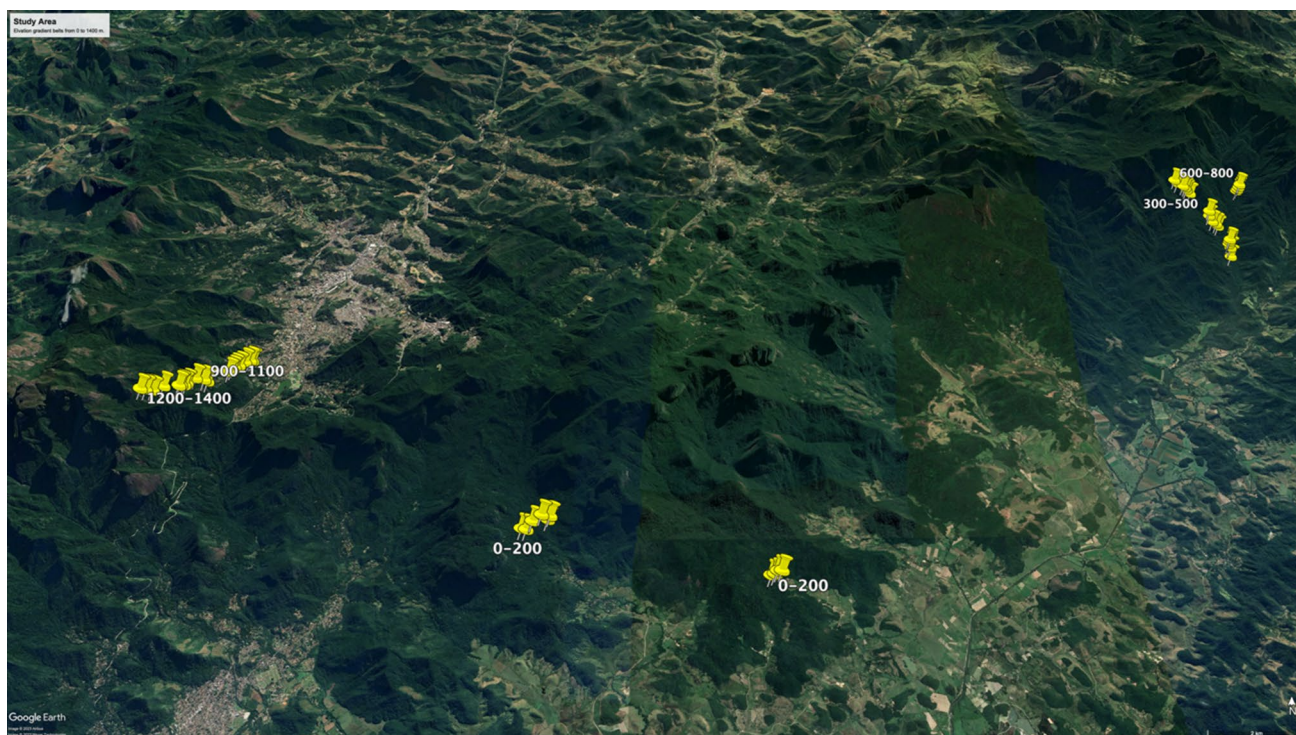
Fig. 1 Elevational gradient from zero to 1400 m. The gradient was divided into five elevation belts based on elevation categories: 0–200 m (lowland forest), 300–500 m (submontane forest), 600–800 m (submontane forest), 900–1100 m (submontane-montane forest) and 1200–1400 m (montane forest). Created with Google Earth (Lisle, 2006)

2019; Reflora 2019). We took measurements of basal diameter (BD) and height (H, length of stem) of every individual recorded in the census. To describe the community structure along elevation we calculated relative abundance, relative frequency, and relative dominance, as well as the importance value index (IVI, 300%) at species level. We also calculated the index of similarity (S) of Sorensen (Kent 2011).

Functional traits measurements We measured traits that are strongly associated with growth and survival strategies, which corresponded to structural traits, photosynthetic and biochemical traits and dispersal traits (Westoby 1998; Reich et al. 2003; Wright et al. 2004; Galetti et al. 2013) (Table 1). We collected the data during wet season mainly to avoid stress by drought. For each species, traits were measured on three to six adult individuals coming from different belts along the gradient. Data from species replicates were averaged to obtain a global mean trait value for each trait for each species (Carmona et al. 2015).

Structural traits

Sampled leaves corresponded to non-senescent, completely expanded and without self-shadow being the third or the fourth leaf of the crown counting from the spear (adapted from Colmenares-Trejos et al. 2011). Ten to 20 leaflets were selected from the second third section of the leaf to take lamina samples. Lamina samples were obtained from the second third section of each leaflet with a perforating tool of 121 mm^2, avoiding the central vein. LA was measured with a metric tape, taking the rachis length (b), without petiole, and the widest part of the leaf (a) to calculate the approximated leaf area based on ellipse area:

$$A = \pi \times a' \times b' \tag{1}$$

were a' corresponds to $a/2$ and b' corresponds to $b/2$.

For SLA, LDMC and TH, the lamina samples were water saturated in a humid camera for 12 h, at 4 ℃ and darkness (Pérez-Harguindeguy et al. 2013). Leaf fresh weight was measured from the saturated leaf with an Ohaus Scout Pro Portable balance. Lamina thickness was measured with a digital caliper (Mitutoyo absolute 500). After weighed, lamina samples were oven dried during 72 h to obtain dry weight. Specific leaf area and leaf dry matter content were calculated following Pérez-Harguindeguy et al. (2013). Stomatal density was calculated as the number of stomata per area. Stomatal counting was performed preparing an epidermal impression of the leaf sample on

Table 1 List of functional traits derived from measurements at field, from the literature, and from the Rio de Janeiro Botanical Garden Herbarium. Abb. = Abbreviation

Traits Type	Set	TRAIT	Unit	Abb.	Function or biological significance
Soft traits	Structural traits	Specific leaf area and Leaf dry matter content	mg/g m²/kg	LDMC SLA	An easily measured correlate of relative growth rate, photosynthetic capacity, leaf lifespan and leaf nitrogen content (Nicotra et al. 2010; Pérez-Harguindeguy et al. 2013; Westoby 1998). The interaction between these traits represents the fundamental trade-off between a rapid production of biomass, i.e. fast grow species, with high SLA and low LDMC species, and slow growing species which possess an efficient conservation of nutrients, represented by low SLA and high LDMC (Wright et al. 2004).
		Stomatal density	Ind/area	Stom	Control of water loss and CO_2 uptake (Hetherington & Woodward 2003). Presents changes in response to elevation (Kofidis & Bosabalidis 2008).
		Leaf size and leaf thickness	mm m²	TH LA	Crucial to growth and carbon balance (photosynthetic input of carbon versus loss of carbon through respiration). Crucial to defense against herbivory (Pérez-Harguindeguy et al. 2013).
	Dispersal traits	Fruit size and fruit number	cm number	FS FN	Dispersal capacity; seedling survival (Associated with seeds) (Pérez-Harguindeguy et al. (2013) Westoby 1998).
		Height at maturity	m	H	Competitive position in a stand, dispersal capacity.
Hard Traits	Photosynthetic and biochemical traits	Total Chlorophyll (ChT) and Chlorophyll a/b ratio (Cha/Chb)	mmol/g or mmol/mm² NA	ChT Cha/Chb	Allows differentiating light versus shade—grown leaves. Values of Cha/Chb above 2–2.5 are associated with light tolerance, while values below are associate with shade tolerant plants or leaves (Givnish 1988).
		Maximum electron transport rate	μmol e$-$/(m²·s)	ETR	Higher electron transport rates are related with greater capacity for photosynthesis. Potential indicators of palm responses to light.
		Alpha	electron/photon	α	Corresponds to the initial slope of a rapid light curve, related to maximum yield of photosynthesis.
		Saturation light intensity	μmol photons/(m²·s)	Ik	Photosynthetic Active Radiation (PAR) value of the point of inter section between a horizontal line ETR_{max} and the extrapolated initial slope.

a glass slide for microscopy using liquid transparent glue. After removing the leaf, the glass was placed under the microscope to count the number of stomata imprinted (adapted from Pérez-Harguindeguy et al. 2013).

Photosynthetic and biochemical traits

We included physiological and biochemical measurements as potential indicators of palm responses to light. These were rapid light response curves (RLC), total chlorophyll content (ChlT mmol $\times$ g^{-1}), and chlorophyll *a/b* ratio (Chlab). Rapid light response curves were measured at field using a PAM-2500 Portable Chlorophyll Fluorometer (Walz). The RLC comes as a default routine of the PamWin-3 software of the PAM 2500 fluorometer (Walz, Effeltrich, Germany, 2008). The curve provides three physiological key parameters that describe photosynthetic acclimation to light intensity: maximal relative electron transport rate (ETR, μmol e$^-$ (m$^2 \times$ s)$^{-1}$), the initial slope (alpha, electron/photon), and the saturation light intensity (Ik, μmol photons (m$^2 \times$ s)$^{-1}$). The measurement was made on three leaflets collected, from 10 a.m. to 14 p.m. during sunny days. The leaflet was disposed under dark conditions for acclimation to obscurity for 1 min approximately, and then submitted to the increasing intensities of actinic light provided by the fluorometer. A mean value was calculated for each plant measured.

Total chlorophyll and chlorophyll a/b ratio were measured at the laboratory. Chlorophyll was measured using dimethyl sulfoxide (DMSO) extraction method (Tait and Hik 2003). Lamina samples were immersed in one milliliter of DMSO and kept in the dark at field. Once at the laboratory, samples were placed in a water—bath maintained at 60 °C for one hour. After that, four to five repeated washings with DMSO were necessary to perform until total extraction. The chlorophyll extraction was diluted when necessary and transferred to a cuvette for spectrophotometer readings at 480, 649.1 and 665.1 nm (Spectrophotometer Shimadzu UV-1800, Kyoto, Japan). Chlorophyll concentration was calculated using the following equations for a UV spectrophotometer (Wellburn 1994):

$$C_a = 12.47A_{665.1} - 3.62A_{649.1} \tag{2}$$

$$C_b = 25.06A_{649.1} - 6.5A_{665.1} \tag{3}$$

$$C_{x+c} = \left(1000A_{480} - 1.29C_a - 53.78C_b\right)/220 \tag{4}$$

Once the formula was applied, final content was expressed in millimole (mmol) of chlorophyll per dry mass (g) and per area (mm^2). Chlorophyll a/b ratio was calculated by dividing Chla by Chlb.

*Dispersal traits*

Stem height *H* (m) was measured with a Nikon Forestry Pro Laser Rangefinder/Height Meter or with a metric tape depending on the species height. This trait was considered as both structural and dispersal trait. Fruit size (FS, diameter in cm) and fruit number (FN, fruits per bunch) were derived from literature and botanical garden herbarium collections (COPPETEC-UFRJ 2019). Material selection was made based on species occurrences reported at the studied areas. Fruit size was considered a surrogate for seed size, while these palms produce one seed per fruit and the fruit flesh is considerable thin around the seed. Fruit number was derived as categorical variable, from one to four, being one for species with less than 20–30 fruits per bunch, two between 50–100, three between 100–500 and four for species with more than 500 fruits per bunch.

Functional trait variation among species We measured species similarity using cluster analysis with significance testing. A matrix of similarity between observations (species *per* traits) was used. After a log transformation of trait data, we ran a bootstrap-version of cluster analysis to evaluate the consistency of the clusters by calculating *p*-values. Clusters with high "Approximately Unbiased *p*-value" (au > *p* = 0.90), were considered strongly supported by the data, meaning they really are very similar units that form a natural cluster. Whereas BP refers to raw "Bootstrap Probabilities" before statistical adjustments. For clustering, we used "ward.D2" = Ward's minimum variance method, and 10,000 boot-strapping replications were analyzed. Analysis was performed using the function "pvclust" in the package Pvclust (Suzuki and Shimodaira 2006, 2015) of the statistical software package "R" (R Core Team 2022). Rectangles around groups highly supported by the data were added using the function "pvrect" with alpha = 0.95.

Additionally, we applied a species' PCA using a species x traits matrix to identify the main patterns in how the traits vary together across species, and the combinations of traits that are most important in describing the differences between species and their strategies for growth and dispersion (Lebrija-Trejos 2010). Prior to PCA, we performed descriptive statistics, correlation matrix and scatter plot matrix. For each trait we calculated minimum, first quartile (*q*1), median, mean, third quartile (*q*3) and maximum for each trait. After a log transformation of trait data, a Pearson's correlation test was implemented for each pair of the 12 quantitative functional traits, and a scatter plot matrix showing the correlation coefficients between traits and the significance levels. Despite highly correlated variables ($r > 0.7$) they were not removed in the PCA. Principal component analyses were carried out on the standardized traits using the function PCA in R package FactoMineR (Lê et al. 2008). Finally, a biplot of variables (traits) and individuals (species) was performed.
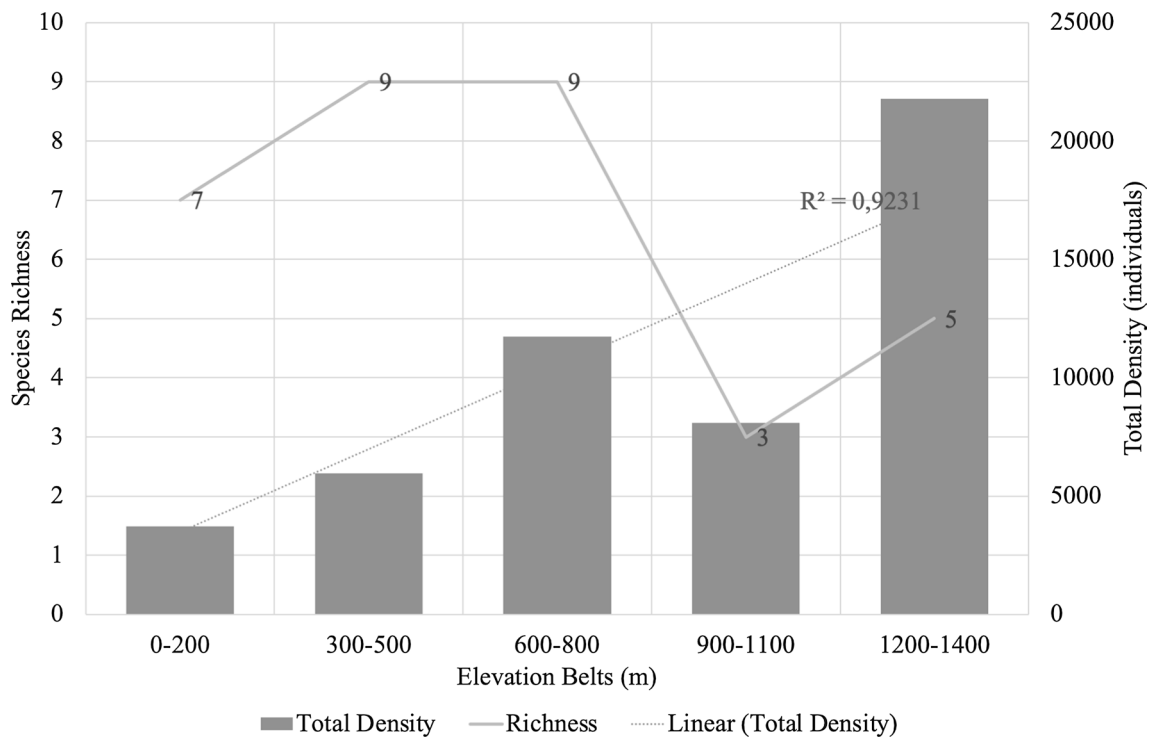
Fig. 2 Species Richness (S) and Density along Elevation. Species richness increased with elevation peaking from 300 to 800 m. Then, after 800 m it started to decline. Species density had a continuous increase along elevation, with the highest peak above 1200 m

Table 2 The Sorensen similarity index in the elevation gradient

Belt (m)	0–200	300–500	600–800	900–1100	1200–1400
0–200	7	6	6	2	3
300–500	0,75	9	8	3	3
600–800	0,75	0,89	9	3	4
900–1100	0,40	0,50	0,50	3	3
1200–1400	0,50	0,43	0,43	0,75	5

The gradient was divided into five elevation belts based on elevation categories: 0–200 m (lowland forest), 300–500 m (submontane forest), 600–800 m (submontane forest), 900–1100 m (submontane–montane forest) and 1200–1400 m (montane forest)

3 Results

Floristic composition and structure of the palm community A total of 1175 individuals belonging to five genera, and 12 species were sampled at the whole elevation gradient: *Astrocaryum aculeatissimum* (Schott) Burret (Aa), *Bactris caryotifolia* Mart. (Bc), *Bactris vulgaris* Barb. Rodr. (Bv), *Euterpe edulis* Mart. (Ee), *Geonoma elegans* Mart. (Ge), *Geonoma fiscellaria* Mart. ex Drude (Gf), *Geonoma kuhlmannii* Burret (Gk), *Geonoma pohliana* Mart. (Gp), *Geonoma schottiana* Mart. (Gs), *Geonoma trinervis* Drude and

H.Wendl. (Gt), *Geonoma wittigiana* Glaz. ex Drude (Gw), and *Syagrus weddelliana* (H.Wendl.) Becc. (Sw).

Species richness increased with elevation peaking from 300 to 800 m. Then, after 800 m it started to decline (Fig. 2). Index of similarity (*S*) of Sorensen among the altitudinal belts showed distinct patterns of species composition across varying altitudes. We found high similarity scores (0.75) between the lowest elevation belts (0–200 m and both 300–500 m and 600–800 m) which suggest these areas share many species. In contrast, lower scores (0.40 and 0.43) when comparing the lowest (0–200 m) and the highest (900–1100 m and 1200–1400 m) belts indicate differences in species compositions at these elevations. The moderate score (0.50) between the lowest (0–200 m) and the highest (1200–1400 m) belts points to some overlap in species. Notably, the high score (0.89) at mid-elevation belts, between the 300–500 m and 600–800 m, indicates very similar species composition. Lastly, the score (0.75) reflects a significant similarity between the two highest elevation belts (900–1100 m and 1200–1400 m) (Table 2). Regarding species density, we found a continuous increase along elevation, with the highest peak above 1200 m (Fig. 2). Moreover, patterns of density and distribution varied among species (Fig. 3), and phytosociological descriptors indicated a progressive loss of species with a low species turnover along elevation (Table 3). Considering the whole elevational gradient, *E. edulis*, *G. schottiana* and *A. aculeatissimum* (in bold
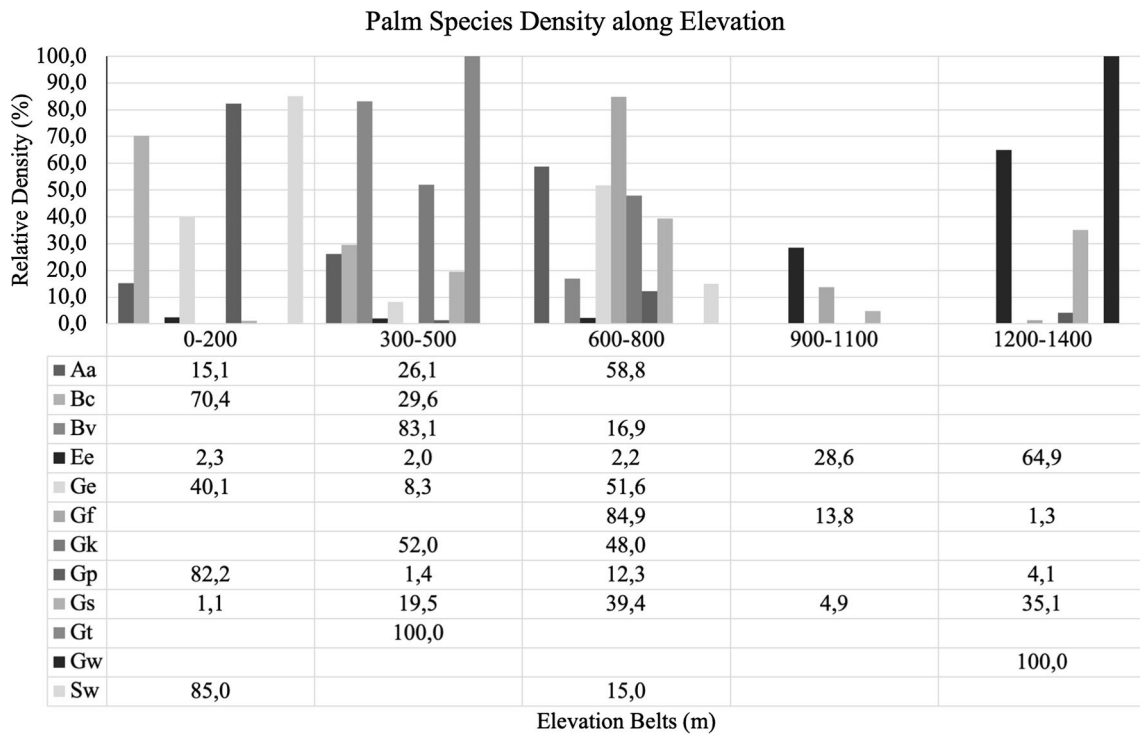
Fig. 3 Palm Species Density (relative) along Elevation. *Edulis edulis*, *G. schottiana* and *A. acculeatissimum* are the three species with the highest relative ecological importance in the community. *Astrocaryum aculeatissimum* (Schott) Burret (Aa), *Bactris caryotifolia* Mart. (Bc), *Bactris vulgaris* Barb. Rodr. (Bv), *Euterpe edulis* Mart. (Ee), *Geonoma elegans* Mart. (Ge), *Geonoma fiscellaria* Mart. ex Drude (Gf), *Geonoma kuhlmannii* Burret (Gk), *Geonoma pohliana* Mart. (Gp), *Geonoma schottiana* Mart. (Gs), *Geonoma trinervis* Drude & H.Wendl. (Gt), *Geonoma wittigiana* Glaz. ex Drude (Gw), and *Syagrus weddelliana* (H.Wendl.) Becc. (Sw)

Table 3 Phytosociological descriptors along elevation at species level. *Edulis edulis*, *G. schottiana* and *A. acculeatissimum,* in bold, are the three species with the highest relative ecological importance in the community

Species	Density ± SD (CV) (ha)	Relative abundance	Relative frequency	Relative dominance	IVI 300%
Ab	**26.5 ± 75.3 (2.8)**	**7.14**	**10.4**	**10.3**	**27.8**
Bc	6.3 ± 20.4 (3.1)	4.95	4.5	0.2	9.7
Bv	45.1 ± 150.6 (3.3)	3.43	3.2	0.3	6.9
Ee	**59.6 ± 99.2 (1.7)**	**24.59**	**25.8**	**78.6**	**128.9**
Ge	27.4 ± 67.8 (2.5)	8.24	4.5	0.3	13.1
Gf	136.1 ± 280.7 (2.1)	5.91	9.5	2.7	18.1
Gk	100.1 ± 308.5 (3.0)	1.37	1.4	0.1	2.8
Gp	18.5 ± 74.5 (4.0)	7.14	7.2	1.7	16.1
Gs	**455.1 ± 638.2 (1.4)**	**20.88**	**22.2**	**4.4**	**47.5**
Gt	12.9 ± 40.0 (3.1)	6.04	3.2	0.3	9.5
Gw	6,6 ± (4,8) (0,7)	5.22	3.2	0.1	8.5
Sw	34.09 ± 129.4 (3.8)	5.08	5	1.1	11.2

IVI (Importance value Index). *Astrocaryum aculeatissimum* (Schott) Burret (Aa), *Bactris caryotifolia* Mart. (Bc), *Bactris vulgaris* Barb. Rodr. (Bv), *Euterpe edulis* Mart. (Ee), *Geonoma elegans* Mart. (Ge), *Geonoma fiscellaria* Mart. ex Drude (Gf), *Geonoma kuhlmannii* Burret (Gk), *Geonoma pohliana* Mart. (Gp), *Geonoma schottiana* Mart. (Gs), *Geonoma trinervis* Drude & H.Wendl. (Gt), *Geonoma wittigiana* Glaz. ex Drude (Gw), and *Syagrus weddelliana* (H.Wendl.) Becc. (Sw)

at Table 3) presented the highest relative ecological importance among species, but only *E. edulis* and *G. schottiana* were present along the whole elevation gradient. *E. edulis* density increased progressively with elevation, *G. schottiana* peaked at mid elevation areas and followed a decline approaching higher elevation areas and *A. acculeatissimum*
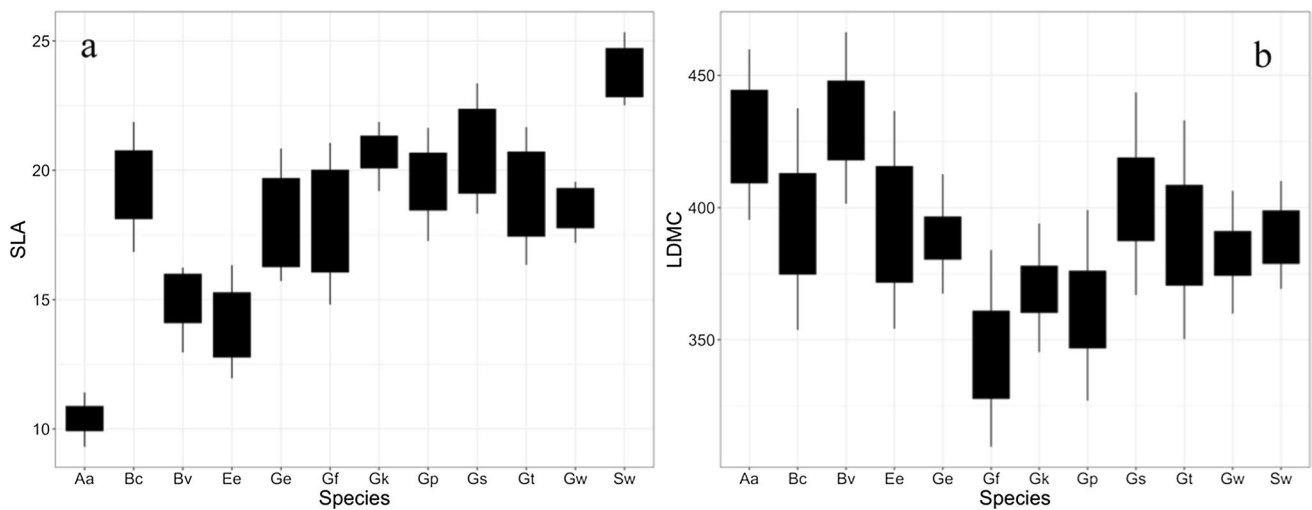
Fig. 4 Boxplot of structural traits of palm species found along the elevation gradient from zero to 1400m. a. Specific leaf area, SLA (m2/kg). b. Leaf dry matter content, LDMC (mg/g)

increased its density with elevation until 800 m. The rest of the species where commonly found at intermediate elevations (from 300–800 m.a.s.l) except for *G. wittigiana* which was found only above the 1200 m a.s.l.

Functional trait variation among species In general, we observed prominent variations in leaf form, leaf size as well as a wide variation in leaflet size, number, and distribution. The boxplot for SLA (Fig. 4a) and LDMC (Fig. 4b) shows *A. acculeatissimum* and *S. weddeliana* differ from the rest of the species in terms of their SLA values, each one being at the extremes, *A. acculeatissimum* with the lowest value and *S. weddelliana* with the highest value. As for LDMC, the extremes are between *B. vulgaris* and *A. acculeatissimu*m, with the highest values and *G. fiscellaria*, with the lowest value.

Regarding FS (Fig. 5a), *A. acculeatissimum* differs from all the other species by presenting the largest size, followed by *S. weddelliana* and *B. caryotifolia*; regarding FN (Fig. 5b), *E. edulis* differs from all the others with the highest value. In terms of height (*H*) (Fig. 5c), *E. edulis* and *A. acculeatissimum* are the highest species, and differentiate from all the other species, and between them, being *E. edulis* the tallest with values above 10 m. The rest of the palms are between zero and 5 m in height. In terms of LA (Fig. 5d), *E. edulis* and *A. acculeatissimum* have the largest leaf areas, above 4 m^2, while the rest of the species are below 2 m^2; in terms of stomatal density, Stom (Fig. 5e), *E. edulis* have the highest stomatal density of over 50 stomata per unit area, and *A. acculeatissimum*, *B. vulgaris* and *B. caryotifolia*, with the lowest stomatal density and the biggest sizes (data not shown). Finally, there is no prominent difference of leaf thickness (TH) between the species (Fig. f).

Regarding hard traits, the chlorophyll a/b ratio varied among species, with remarkable differences between *B. caryotifolia* and *B. vulgaris*, from the same genera. Also, among Geonoma genera, *G. elegans* presented a wide variation in Chla/Chlb ratio, compared with the rest of Geonomas (Fig. 6a). Regarding, being *G. fiscellaria* the species with the highest content of total chlorophyll (Fig. 6b). When looking at the components of the rapid light curves (ETR, Ik, alpha) these indicate that *E. edulis* and *A. acculeatissimum* are the species with highest photosynthetic rates and highest saturation points. The rest of the species, especially the smaller Geonomas, presented the lowest values (Fig. 6c–e). We also observed wide variation in basal diameter, height, fruit size and habit among species. *E. edulis* and *A. acculeatissimum* were the tallest species and presented the biggest stem diameter. *A. acculeatissimum*, *B. caryotifolia* and *B. vulgaris* presented high fiber density inside the tissues, high density of trichomes on the adaxial part of the leaf and spines along the leaf rachis and leaflets borders (Field observations).

The Pearson correlation analysis showed that ETR and Ik presented a positive and high correlation with height (*H*), 0.84[***] and 0.76[**] respectively. On the other hand, ChlT presented a negative correlation with *H*, − 0.78[**]. Among the soft traits, *H* was highly correlated with LA, 0.84[***], and with Th, 0.75[***]; finally, SLA was negatively correlated with Th, − 0.95[***].
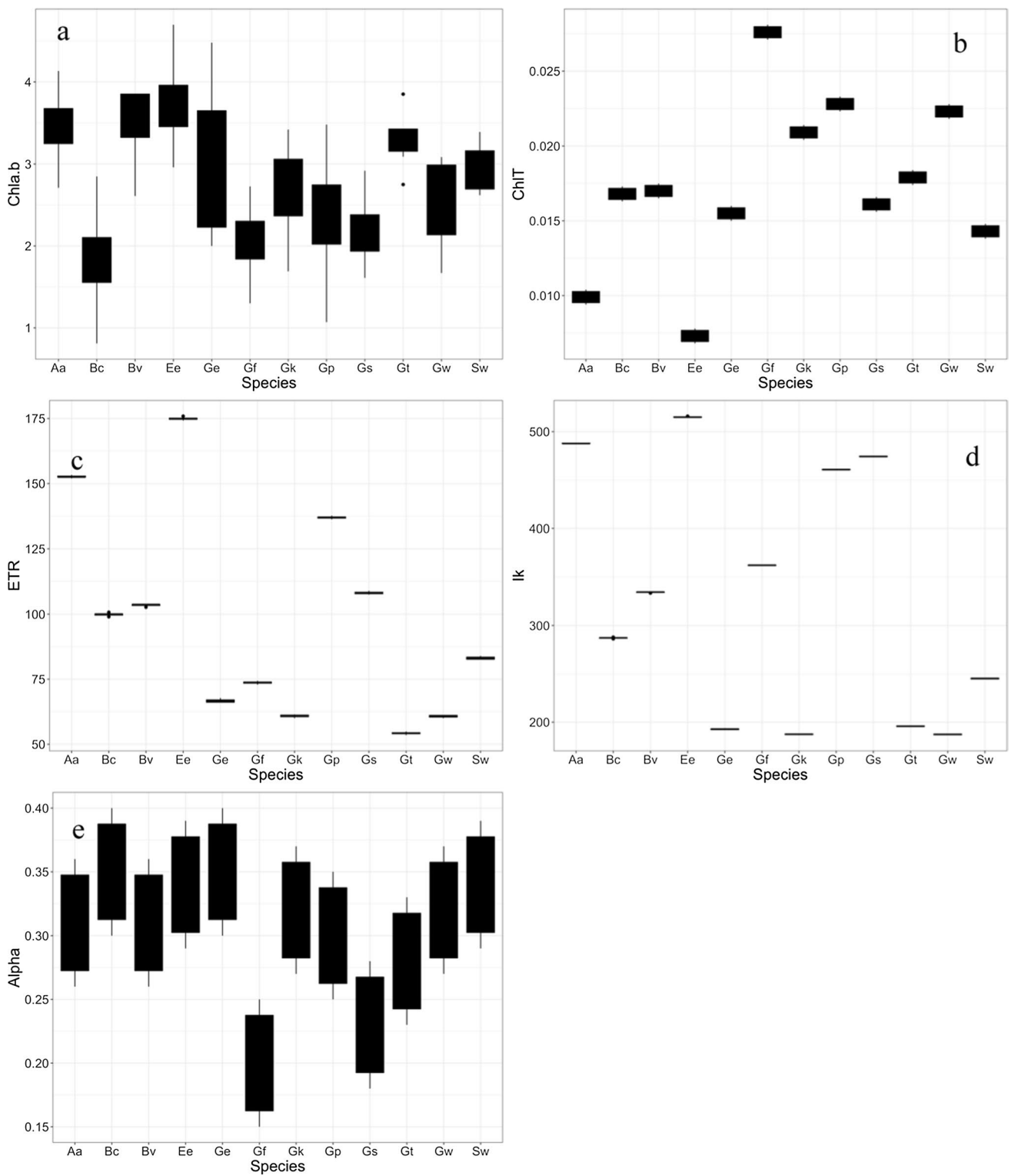
Cluster analysis with significance testing showed au *p-values > 0.90* (or 90%) for two general clusters: one conformed by *G. pohliana, G. schottiana, A. acculeatissimum* and *Euterpe edulis*, with 96% to occur; and a second
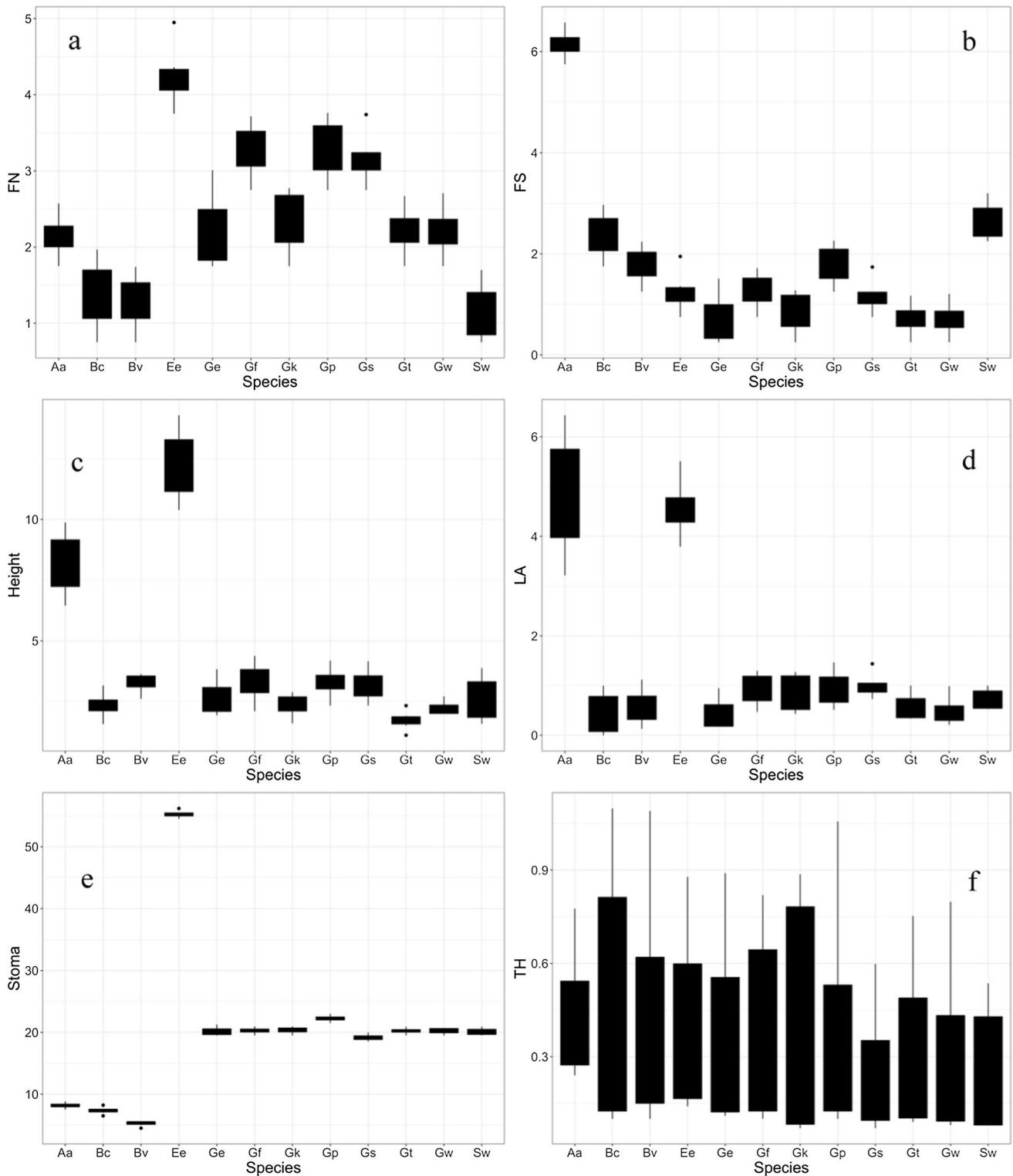
Fig. 5 Boxplot of dispersal and structural traits of palm species found along the elevation gradient from zero to 1400m. a. (Fruit size (FS). b. Fruit number (FN). c. Height. d. Leaf area (LA). e. Stomatal density (stoma). f. Leaf thickness (TH)

conformed by the rest of the species (96%). This second cluster had also sub-clusters with values above 90% to occur, one conformed by the *G. kuhlmannii*, *G. trinervis*, *G. elegans* and *G. wittigiana*, with 95%, and the other conformed by *G. fiscellaria*, *B. caryotifolia*, *B. vugaris* and *S. weddelliana*, with 94% (Fig. 7).

Fig. 6 Boxplot of photosynthetic and biochemical traits of palm species found along the elevation gradient from zero to 1400m. a. Chla/Chlb. b. CHlT. c. ETR. d. Ik. e. Alpha. Cluster analysis with significance testing to test species similarity. There are two general clusters (au > 0.95): one conformed by *G. pohliana*, *G. schottiana*, *A. aculeatissimum* and *E. edulis*; and a second conformed by the rest of the species. Abb: au = "Approximately Unbiased *p*-value"; bp = "Bootstrap Probabilities" before statistical adjustments

Fig. 7 Cluster analysis with significance testing to test species similarity. There are two general clusters (au>0,95): one conformed by *G. pohliana*, *G. schottiana*, *A. aculeatissimum* and *E. edulis*; and a second conformed by the rest of the species. Abb: au = "Approximately Unbiased p-value"; bp = "Bootstrap Probabilities" before statistical adjustments

Distance: euclidean
Cluster method: ward.D2
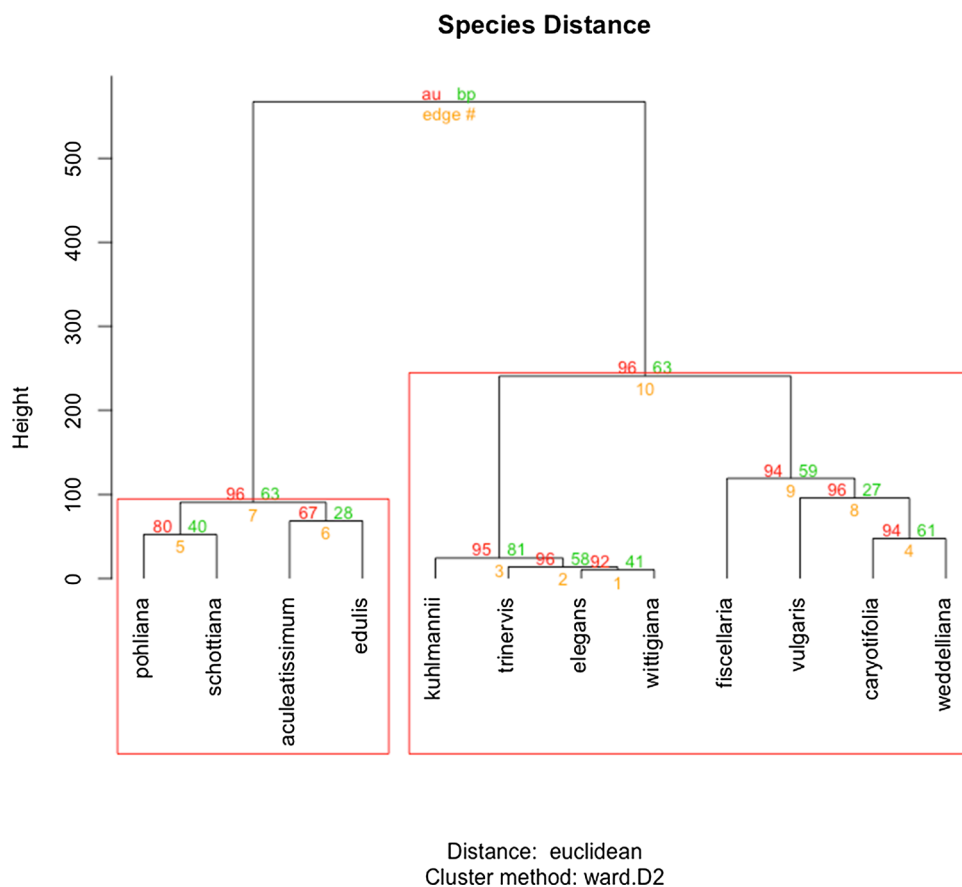
Finally, a general PCA was performed using the complete species *per* trait matrix to reveal the combined variation in their functional traits, which is an indication of the strategies used by plants. The two leading axes explained 69.2% of the total variation (Fig. 8). Species with high electron transport rate (ETR), saturation light intensity (Ik), height (H), leaf area (LA) correlated highly with the first PCA axis (scores > 0.5). In turn, *E. edulis* and *A. acculeatissimum* had high species scores on the first axis. Species extending towards the PCA's left side had increasing specific leaf area (SLA) and total chlorophyll content (ChlT) (absolute scores > 0.5). Species with high fruit number (FN) and stomatal density (Stom) correlated highly with the second PCA axis (scores > 0.5), while species with high electron/photon ratio (alpha) from the RLC (absolute scores > 0.5) were found on opposite side of the second PCA axis.

4 Discussion

Our study showed a clear altitudinal threshold after 800 m for palm species diversity and distribution. Species richness and community similarity declined steeply after 800 m, whereas species density presented its highest point at

1200 m. Along with this, the community presented the lowest basal area and height at mid elevation, with the highest concentration of shade tolerant—range restricted species like *G. elegans*, *G. trinervis*, *S. weddelliana* and *Bactris* species, a typical understory community. In addition, regarding trait results, contrasting palm species similarity groups and then their distribution along the functional trait space were an indicator of the occupancy of different environmental niches among species.

The higher species richness found between 300 and 800 m elevation can be explained, in part, as a response to the overlapping between range-restricted species and wide distributed species along the whole elevation gradient. This has been described for Neotropical areas, where palm richness patterns follow a complex spatial interaction of several range-restricted species with a relatively few wide range species (Kreft et al. 2005), where the variation in species range distribution is more related with ecophysiological responses, dispersal abilities and evolutionary history of the species (Svenning 2001; Kreft et al. 2005; Eiserhardt et al. 2011). The mid-peak richness followed by a decrease may appear as the result of shrinking in niche availability for forest interior species, such as shade-tolerant palm species, as has been reported in previous work done in the Atlantic forest that included palms (Joly

Fig. 8 Principal Components Analysis (PCA; first vs. second axes) of palm species characterized by functional traits. The PCA reveals thecombined variation in species functional traits indicating the strategies used by them
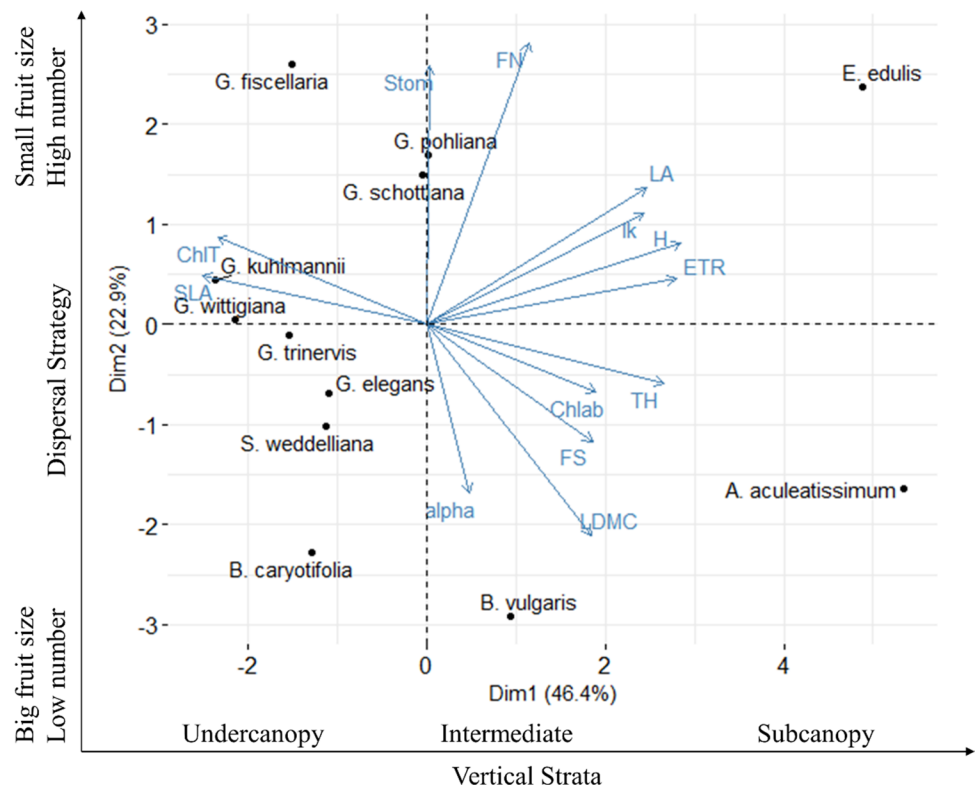
et al. 2012; Oliveira et al. 2014; Benchimol et al. 2017; Portela et al. 2021). This suggest a strong association with specific environmental conditions or dispersal limitation along elevation (Pires 2006; Braz et al. 2016; Cochrane et al. 2015; Oda et al. 2016).

Related to density, previous research at Atlantic Forest found that palm population densities increase with elevation, specially above 200 m, in response to increase in forest cover, shadow, humidity, and reduction of human exploitation (Joly et al. 2012; Oliveira et al. 2014). Similar patterns have been found in palms from Southeast Asia in response to the same factors, including topography (Stiegel et al. 2011). Our finding is influenced by the drastic increase in population density of the species *E. edulis* after 800 m, a pattern which was also observed in previous works (Joly et al. 2012).

The overall species strategies, reflected by the traits we measured, were associated principally to light response and dispersal capacity, giving us clues about their distribution. Despite palms analyzed in our study are considered shade-tolerant species (Arroyo-Rodríguez et al. 2007; Gatti et al. 2011), commonly present at ombrophilous forest, species varied in a continuum along the leaf economic spectrum, and we found two independent axes of trait variation in palms, one corresponding to light acquisition strategies and another to dispersal traits. The traits most closely aligned with PCA axis 1 are related to the fast–slow continuum (Reich 2014; Salguero-Gomez et al.

2016): Height, ETR, and SLA closely followed by LA and ChlT. However, the positive loading of Height, ETR, and LA onto PCA 1, opposite to the negative loadings by both SLA and ChlT, do not seem to follow completely the well-established fast-slow plant economic spectrum. High SLA is associated with fast resource acquisition strategy (high growth rates, low LDMC, low longevity leaves and higher photosynthetic rates) (Reich 2014). Our data suggest the opposite pattern, and species with higher SLA values did not present the highest photosynthetic performance and were not the larger ones.

Light environment is a factor of competition among coexisting species for light and may determine plant community structure and composition (Liu et al. 2010; Long et al. 2011). Several studies have suggested that SLA can be linked to light partitioning within communities on vertical gradients of light (Ackerly et al. 2002; Ackerly and Cornwell 2007; Markesteijn et al. 2007). Studies using tree height as a proxy for light availability, showed that SLA may decrease with height, likely reflecting responses to the degree of shading, arguing species with more light availability may achieve high growth rates by producing leaves with greater photosynthetic mass, i.e., low SLA (Liu et al. 2010; Long et al. 2011), as it was observed in our study for *A. acculeatissimum* and *E. edulis*.

We found palms were distributed in the functional trait space following the vertical strata, from understory to subcanopy species, supported by their structural, photosynthetic,

and biochemical attributes (Figs. 7, 8). In general, structural traits like specific leaf area (SLA), height (H), and stomatal density (Stom), as well as photosynthetic and biochemical traits were fundamental to distinguish shade-tolerant species (understory palms and species with small leaves) from more generalist species favored by their higher capacity to use higher light intensities (subcanopy palms). Thus, within a so-called shade-tolerant species functional group, we found three distinctive groups responding differently due to light response and dispersal capacity strategies: the larger and more widely distributed palms, associated with more luminous environments (*A. acculeatissimum, E. edulis, G. pohliana, a*nd *G. schottiana*); the small-leaved and small-seeded understory palms (*G. kuhlmannii, G. trinervis, G. elegans,* and *G. wittigiana*); and the small-leaved and large-seeded understory palms (*G. fiscellaria*, *B. vulgaris*, *B. caryotifolia*, and *S. weddelliana*), the last two groups associated with less luminous environments.

The possess of traits that conferred the ability to enhance light capture (high ETR, height and leaf area) and dispersal capacity (high fruit number and height) can be associated with a successful establishment along elevation. Species which such characteristics were *E. edulis*, and *G. schottiana*, the most ecologically important species along the whole altitudinal variation. The highest fruit number per bunch and the ability to germinate under wide-ranging environmental conditions of light and water availability of *E. edulis* and *G. schottiana* (Braz et al. 2014, 2016;; Mendes et al. 2019) seems to favor them to be amply distributed and also persistent at higher elevations. However, *G. schottiana* has been found to be more affected demographically by habitat reduction than *E. edulis*, and *A. acculeatissimum*, (Portela et al. 2021), where drought events may affect seedling survival rates (Braz et al. 2016; Portela et al. 2021). The species *A. acculeatissimum* also presented a high IVI and displayed an enhanced light capture capacity. However, it was present only until 800 m. By considering the large size of its fruits, dispersal constraints may be a reason for its absence at higher elevations, suggesting the lack of their natural disperser in those areas, as it has been found in studies with this species, where it is demonstrated the dependence of this palm to medium size dispersers such as agoutis for a successful dispersal, collapsing when they are not present (Donatti et al. 2009). However, there may be other restrictions related to the physiology of the plant that could be studied, such as seed germination or seedling survival at altitudes greater than 900 m.

Light is known as a limiting resource condition for growth and reproduction of palms (Gatti et al. 2011; Ma et al. 2015). An open canopy can act as a filtering factor for some of the understory palms especially during germination and recruitment events (Braz et al. 2014, 2016; Oda et al. 2016), while more generalist plants as *A. acculeatissimum* or

E. edulis can be favored by a higher light availability during germination and seedling establishment and growth (Cintra and Horna 1997; Fantini and Guries 2007; Kahn 2008; Gatti et al. 2011). Palms with small leaves, with lower stomatal density and low photosynthetic capacity have been shown vulnerable to stressful conditions associated with excess of light, drought, and soil nutrients (Svenning 2001; Chazdon 1986; Andersen et al. 2011; Camargo and Marenco 2011; Göldel et al. 2015). Such might be the case of *G. kulmanii*, *G. trinervis*, *G. elegans* and *G. wittigiana*, a group which traits evidenced their strongest association with low light environments and presented range-restricted distributions and low density along the whole elevation gradient. As found for other species of the same genus, such as *G. schottiana*, it is possible that these understory species are affected demographically by habitat reduction, reducing mainly the growth of juveniles by effect of increased light or water scarcity generated by habitat fragmentation (Benchimol et al. 2017; Portela et al. 2021).

The traits most closely aligned with PCA axis 2 are related to dispersal traits: fruit number, followed by structural traits stomatal density and LDMC. However, dispersal traits showed a great variability among palm species. Fruit size, fruit number and height are usually associated with species establishment capacity and dispersal (Westoby 1998; Galetti et al. 2013; Pérez-Harguindeguy et al. 2013). Animal-dispersed plants like palms depend on the type, foraging and movement of seed dispersers and predators, as well as on seed size and number, which also affect seed survival and dispersal (Moles and Westoby 2006; Galetti et al. 2013; Xiao et al. 2015). Big fruits and seeds need animals big enough to swallow or carry them for dispersal (Galetti et al. 2013; Göldel et al. 2015), affecting the dispersal distance capacity of the plant. With increase in elevation, we found that palms with large-seeded fruits were left behind at lower elevations, such as *G. fiscellaria*, *S. weddelliana*, *B. caryotifolia* and *B. vulgaris*. Shade-tolerant palms with large seeds are highly sensitive to habitat loss and fragmentation (Chazdon 1986; Genini et al. 2009; Benchimol et al. 2017), which is also related with animal – dispersion failure due to absent dispersers (Donatti et al. 2009). This overcomes into lower recruitment rates and increased difficulty to the maintenance and expansion of distribution areas (Santos 2005; Galetti et al. 2013). The species *S. weddelliana* and *B. caryotifolia* fall in this category. Regarding *B. vulgaris*, this species presented higher photosynthetic capacity, but it has very low fruit number, and it was usually found carrying bunches with unripe or spoiled fruits (field observations). Fruit malformation can be caused by various factors such as environmental stress, genetic factors, diseases or problems with pollination, as it has been found in cultivated species (Legros et al. 2009; Meléndez and Ponce 2016). *G. fiscellaria* is the species among the *Geonoma* genus with higher

fruit size, and is only present above 600 m, being highly abundant between 600 and 800 m and declining sharply from 900 to 1400 m, suggesting its dispersion is restricted to the mid elevation area.

Animal consumption of fruits may also produce negative effects on palms distribution. Fruits eaten by animals fall into the forest floor with an intact but exposed seed, making it susceptible to be predated by insects or pathogens (Andreazzi et al. 2009). Such is the case of *A. acculeatissimum* fruits, which are highly predated by insects in the forest floor (Pires 2006), or by mammals that bury the seed at unfavorable microsites for germination or recruitment (Donatti et al. 2009; Braz et al. 2014).

Unfortunately, it was not possible for us to test trait conservatism for phylogenetically related species due to the gap of molecular data for all the species, with the exception of *S. weddelliana* (Qian and Jin 2016). Similar trait values among species congeners from *Bactris* and *Geonoma* genera, may be an indication of a partially phylogenetic conservatism (De Bello et al. 2017). However, sympatric species from rich palm genera and species complexes, as *Bactris* and *Geonoma*, usually differ in traits that confer divergent light requirements or in traits that favor reproductive isolation favored by local environmental conditions (Svenning 2001). Trait differentiation offers the possibility to use every slight variation in the local environmental conditions by different species, as we found in this study. We suggest that, despite some similarities, the observed trait differentiation between species from *Bactris* and *Geonoma* genera may explain their close coexistence, as has been suggested for other palm species (Svenning 2001). However, experimental works are necessary to prove that.

We conclude that palm species distribution within the Atlantic Forest changes along elevation, with notable shifts in community structure, especially richness and composition above 800 m. In addition to this, we found wide distributed palms possess traits that optimize light capture and seed dispersal, indicating a strong link between these traits and species establishment, suggesting that niche occupancy is influenced by the interplay of light availability at the forest vertical gradient and dispersal constraints along elevation gradient. However, it is important to include a variety of environmental conditions in different mountainous regions. Soil characteristics, temperature fluctuations, and patterns of precipitation could all play pivotal roles in shaping these communities. Additionally, incorporating phylogenetic analyses, can unravel niche preferences and trait conservatism. Understanding these ecological and evolutionary dynamics is key to conserving these unique palm communities in the face of environmental change.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s40415-024-00982-4.

Declarations

References

Ackerly DD, Cornwell WK (2007) A trait-based approach to community assembly: partitioning of species trait values into within-and among-community components. Ecol Lett 10:135–145. https://doi.org/10.1111/j.1461-0248.2006.01006.x

Ackerly DD, Knight CA, Weiss SB, Barton K, Starmer KP (2002) Leaf Size, specific leaf area and microhabitat distribution of chaparral woody plants: contrasting patterns in species level and community level analyses. Oecologia 130:449–457

Alvarado-Segura AA, Calvo-Irabién LM, Duno de Stefano R, Balslev H (2012) Palm species richness, abundance and diversity in the Yucatan Peninsula, in a neotropical context. Nord J Bot 30:613–622. https://doi.org/10.1111/j.1756-1051.2012.01593.x

Alves LF, Vieira SA, Scaranello MA, Camargo PB, Santos FA, Joly CA, Martinelli LA (2010) Forest structure and live aboveground biomass variation along an elevational gradient of tropical Atlantic moist forest (Brazil). For Ecol Manag 260:679–691. https://doi.org/10.1016/j.foreco.2010.05.023

Ames GM, Anderson SM, Wright JP (2016) Multiple environmental drivers structure plant traits at the community level in a pyrogenic ecosystem. Funct Ecol 30:789–798

Andersen KM, Endara MJ, Turner BL, Dalling JW (2012) Trait-based community assembly of understory palms along a soil nutrient gradient in a lower montane tropical forest. Oecologia 168:519–531. https://doi.org/10.1007/s00442-011-2112-z

Andreazzi CS, Pires ADS, Fernandez FA (2009) Mamíferos e palmeiras neotropicais: interações em paisagens fragmentadas. Oecol Aust 13:554–574. https://doi.org/10.4257/oeco.2009.1304.02

Arroyo-Rodríguez V, Aguirre A, Benítez-Malvido J, Mandujano S. (2007) Impact of rain forest fragmentation on the population size of a structurally important palm species: Astrocaryum mexicanum at Los Tuxtlas, Mexico. Biol Cons Aug

1;138(1–2):198–206. https://doi.org/10.1016/j.biocon.2007.04.016

Balslev H, Kahn F, Millan B, Svenning JC, Kristiansen T, Borchsenius F, Pedersen D, Eiserhardt WL (2011) Species diversity and growth forms in tropical american palm communities. Bot Rev 77:381–425. https://doi.org/10.1007/s12229-011-9084-x

Belluau M, Shipley B (2018) Linking hard and soft traits: physiology, morphology and anatomy interact to determine habitat affinities to soil water availability in herbaceous dicots. PLoS ONE 13:e0193130. https://doi.org/10.1371/journal.pone.0193130

Benchimol M, Talora DC, Mariano-Neto E, Oliveira TL, Leal A, Mielke MS, Faria D (2017) Losing our palms: the influence of landscape-scale deforestation on Arecaceae diversity in the Atlantic forest. For Ecol Manag 384:314–322. https://doi.org/10.1016/j.foreco.2016.11.014

Bjorholm S, Svenning JC, Skov F, Balslev H (2005) Environmental and spatial controls of palm (Arecaceae) species richness across the Americas. Glob Ecol Biogeogr 14:423–429. https://doi.org/10.1111/j.1466-822x.2005.00167.x

Braz MIG, Portela RDCQ, Cosme LHM, Marques VGC, de Mattos EA (2014) Germination niche breadth differs in two co-occurring palms of the Atlantic Rainforest. Nat Conserv 12:124–128. https://doi.org/10.1016/j.ncon.2014.09.003

Braz MIG, Ferreira RDM, Portela RDCQ, Mattos EAD (2016) Ample germination ability under wide-ranging environmental conditions in a common understory tropical palm. Plant Species Biol 31:211–218. https://doi.org/10.1111/1442-1984.12104

Camargo MAB, Marenco RA (2011) Density, size and distribution of stomata in 35 rainforest tree species in Central Amazonia. Acta Amazon 41:205–212. https://doi.org/10.1590/S0044-59672011000200004

Cantidio LS, Souza AF (2019) Aridity, soil and biome stability influence plant ecoregions in the Atlantic Forest, a biodiversity hotspot in South America. Ecography 42:1887–1898. https://doi.org/10.1111/ecog.04564

Carvalho FA, Nascimento MT (2009) Diametric structure of a tree community and its main populations in a Sub-montane Atlantic Forest remnant (Silva Jardim-RJ, BraziL). Revista Árvore 33:327–337. https://doi.org/10.1590/S0100-67622009000200014

Carmona CP, Rota C, Azcárate FM, Peco B (2015) More for less: sampling strategies of plant functional traits across local environmental gradients. Funct Ecol 29:579–588. https://doi.org/10.1111/1365-2435.12366

Chase JM, Myers JA (2011) Disentangling the importance of ecological niches from stochastic processes across scales. Philos Trans R Soc 366:2351–2363. https://doi.org/10.1098/rstb.2011.0063

Chazdon RL (1986) Light variation and carbon gain in rain forest understorey palms. J Ecol 74:995–1012. https://doi.org/10.2307/2260229

Cintra R, Horna V (1997) Seed and seedling survival of the palm *Astrocaryum murumuru* and the legume tree Dipteryx micrantha in gaps in Amazonian Forest. J Trop Ecol 13(2):257–277

Cochrane A, Yates CJ, Hoyle GL, Nicotra AB (2015) Will among-population variation in seed traits improve the chance of species persistence under climate change? Glob Ecol Biogeogr 24:12–24. https://doi.org/10.1111/geb.12234

Colmenares-Trejos SL, Melgarejo LM, Romero AHM (2011) Ecophysiological studies of two Andean forest contrasting species *Abatia parviflora* and *Myrcianthes leucoxyla* under Bogotá conditions Colombia. Brazil J Plant Physiol 23:305–312. https://doi.org/10.1590/S1677-04202011000400008

COPPETEC-UFRJ (2019) Reflora—Brasil de Plantas: Rescate Histórico y Herbario Virtual para el Conocimiento y Conservación de la Flora de Brasil. . Accessed June 2019. https://flora

dobrasil.jbrj.gov.br/reflora/PrincipalUC/PrincipalUC.do?lingua=pt

Cornelissen JH, Lavorel S, Garnier E, Díaz S, Buchmann N, Gurvich DE, Reich PB, Ter-Steege H, Morgan HD, Van Der Heijden MGA, Pausas JG (2003) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. Aust J Bot 51:335–380. https://doi.org/10.1071/BT02124

Cornwell WK, Ackerly DD (2009) Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. Ecol Monogr 79:109–126. https://doi.org/10.1890/07-1134.1

de Bello F, Šmilauer P, Diniz-Filho JAF, Carmona CP, Lososová Z, Herben T, Götzenberger L (2017) Decoupling phylogenetic and functional diversity to reveal hidden signals in community assembly. Methods Ecol Evol 8:1200–1211. https://doi.org/10.1111/2041-210X.12735

Defossez E, Pellissier L, Rasmann S (2018) The unfolding of plant growth form-defence syndromes along elevation gradients. Ecol Lett 21:609–618. https://doi.org/10.1111/ele.12926

Donatti CI, Guimarães PR, Galetti M (2009) Seed dispersal and predation in the endemic Atlantic rainforest palm *Astrocaryum aculeatissimum* across a gradient of seed disperser abundance. Ecol Res 24:1187–1195. https://doi.org/10.1007/s11284-009-0601-x

Eisenlohr PV, Alves LF, Bernacci LC, Padgurschi MC, Torres RB, Prata EM, dos Santos FAM, Assis MA, Ramos E, Rochelle ALC, Martins FR (2013) Disturbances, elevation, topography and spatial proximity drive vegetation patterns along an altitudinal gradient of a top biodiversity hotspot. Biodivers Conserv 22:2767–2783. https://doi.org/10.1007/s10531-013-0553-x

Eiserhardt WL, Svenning JC, Kissling WD, Balslev H (2011) Geographical ecology of the palms (Arecaceae): determinants of diversity and distributions across spatial scales. Ann Bot 108(8):1391–1416. https://doi.org/10.1093/aob/mcr146

Fantini AC, Guries RP (2007) Forest structure and productivity of palmiteiro (*Euterpe edulis* Martius) in the Brazilian Mata Atlântica. For Ecol Manag 242:185–194. https://doi.org/10.1016/j.foreco.2007.01.005

Galetti M, Guevara R, Côrtes MC, Fadini R, Von Matter S, Leite AB, Labecca F, Ribeiro T, Carvalho CS, Collevatti RG, Pires MM (2013) Functional extinction of birds drives rapid evolutionary changes in seed size. Science 340:1086–1091. https://doi.org/10.1126/science.1233774

Garnier E, Navas ML (2012) A trait-based approach to comparative functional plant ecology: concepts, methods, and applications for agroecology. Rev Agron Sustain Dev 32:365–399. https://doi.org/10.1007/s13593-011-0036-y

Garnier E, Navas ML, Grigulis K (2016) Plant functional diversity: organism traits, community structure, and ecosystem properties. Oxford University Press

Gatti MG, Campanello PI, Montti LF, Goldstein G (2008) Frost resistance in the tropical palm Euterpe edulis and its pattern of distribution in the Atlantic Forest of Argentina. For Ecol Manag 256:633–640. https://doi.org/10.1016/j.foreco.2008.05.012

Gatti MG, Campanello PI, Goldstein G (2011) Growth and leaf production in the tropical palm *Euterpe edulis*: light conditions versus developmental constraints. Flora Morphol Distrib Funct Ecol 206(8):742–748. https://doi.org/10.1016/j.flora.2011.04.004

Genini J, Galetti M, Morellato LPC (2009) Fruiting phenology of palms and trees in an Atlantic rainforest land-bridge island. Flora Morphol Distrib Funct Ecol 204:131–145. https://doi.org/10.1016/j.flora.2008.01.002

Givnish TJ (1988) Adaptation to Sun and Shade: a whole-plant Perspective. Aust J Plant Physiol 15:63–92. https://doi.org/10.1071/PP9880063

Göldel B, Kissling WD, Svenning JC (2015) Geographical variation and environmental correlates of functional trait distributions

in palms (Arecaceae) across the New World. Bot J Linn Soc 179:602–617. https://doi.org/10.1111/boj.12349

Govindjee G (2004) Chlorophyll a fluorescence: a signature of photosynthesis. GC Papageorgiou (ed.). Springer, Dordrecht, 19, pp 1–42

Henderson A (2011) A revision of Geonoma (Arecaceae). Phytotaxa 17:1–271

Henderson A, Galeano G, Bernal R (2019) Field guide to the palms of the Americas, vol 5390. Princeton University Press, New Jersey

Hernández-Calderón E, Méndez-Alonzo R, Martínez-Cruz J, González-Rodríguez A, Oyama K (2014) Altitudinal changes in tree leaf and stem functional diversity in a semi-tropical mountain. J Veg Sci 25:955–966. https://doi.org/10.1111/jvs.12158

Hetherington AM, Woodward FI (2003) The role of stomata in sensing and driving environmental change. Nature 424:901–908. https://doi.org/10.1038/nature01843

Hulshof CM, Violle C, Spasojevic MJ, McGill B, Damschen E, Harrison S, Enquist BJ (2013) Intra-specific and inter-specific variation in specific leaf area reveal the importance of abiotic and biotic drivers of species diversity across elevation and latitude. J Veg Sci 24:921–931. https://doi.org/10.1111/jvs.12041

Joly CA, Assis MA, Bernacci LC, Tamashiro JY, Campos MCRD, Gomes JAMA, Lacerda MS, Santos FAMD, Pedroni F, Pereira LDS, Padgurschi MDCG (2012) Florística e fitossociologia em parcelas permanentes da Mata Atlântica do sudeste do Brasil ao longo de um gradiente altitudinal. Biota Neotrop 12:123–145. https://doi.org/10.1590/S1676-06032012000100012

Kahn F (2008) The genus Astrocaryum (Arecaceae). Rev Peru Biol 15:31–48

Kent M (2011) Vegetation description and data analysis: a practical approach. Wiley

Kofidis G, Bosabalidis AM (2008) Effects of altitude and season on glandular hairs and leaf structural traits of Nepeta nuda L. Bot Stud 49:363–372

Körner C (2007) The use of 'altitude'in ecological research. Trends Ecol Evol 22(11):569–574. https://doi.org/10.1016/j.tree.2007.09.006

Kraft NJB, Valencia R, Ackerly DD (2008) Functional traits and niche-based tree community assembly in an Amazonian Forest. Science 322:580–582. https://doi.org/10.1126/science.1160662

Kreft H, Sommer JH, Barthlott W (2005) The significance of geographic range size for spatial diversity patterns in Neotropical palms. Ecography 29:21–30. https://doi.org/10.1111/j.2005.0906-7590.04203.x

Lavorel S, Garnier É (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. Funct Ecol 16(5):545–556. https://doi.org/10.1046/j.1365-2435.2002.00664.x

Lê S, Josse J, Husson F (2008) FactoMineR: An R package for multivariate analysis. J Stat Softw 25:1–18

le Roux PC, Pellissier L, Wisz MS, Luoto M (2014) Incorporating dominant species as proxies for biotic interactions strengthens plant community models. J Ecol 102:767–775. https://doi.org/10.1111/1365-2745.12239

Lebrija-Trejos E, Pérez-García EA, Meave JA, Bongers F, Poorter L (2010) Functional traits and environmental filtering drive community assembly in a species-rich tropical system. Ecology 91:386–398. https://doi.org/10.1890/08-1449.1

Legros S, Mialet-Serra I, Caliman JP, Siregar FA, Clément-Vidal A, Dingkuhn M (2009) Phenology and growth adjustments of oil palm (Elaeis guineensis) to photoperiod and climate variability. Ann Bot 104:1171–1182. https://doi.org/10.1093/aob/mcp214

Lisle RJ (2006) Google Earth: a new geological resource. Geol Today 22:29–32. https://doi.org/10.1111/j.1365-2451.2006.00546.x

Liu F, Yang W, Wang Z, Xu Z, Liu H, Zhang M, Liu Y, An S, Sun S (2010) Plant size effects on the relationships among specific leaf area, leaf nutrient content, and photosynthetic capacity in tropical woody species. Acta Oecol 36:149–159. https://doi.org/10.1016/j.actao.2009.11.004

Lomolino MV (2001) Elevation gradients of species-density: historical and prospective views. Glob Ecol Biogeogr 10:3–13. https://doi.org/10.1046/j.1466-822x.2001.00229.x

Long W, Zang R, Schamp BS, Ding Y (2011) Within-and among-species variation in specific leaf area drive community assembly in a tropical cloud forest. Oecologia 167:1103–1113. https://doi.org/10.1007/s00442-011-2050-9

Luo YH, Liu J, Tan SL, Cadotte MW, Wang YH, Xu K, Li DZ, Gao LM (2016) Trait-based community assembly along an elevational gradient in subalpine forests: quantifying the roles of environmental factors in inter-and intraspecific variability. PLoS ONE 11:e0155749. https://doi.org/10.1371/journal.pone.0155749

Ma RY, Zhang JL, Cavaleri MA, Sterck F, Strijk JS, Cao KF (2015) Convergent evolution towards high net carbon gain efficiency contributes to the shade tolerance of palms (Arecaceae). PLoS ONE 10:e0140384. https://doi.org/10.1371/journal.pone.0140384

Markesteijn L, Poorter L, Bongers F (2007) Light-dependent leaf trait variation in 43 tropical dry forest tree species. Am J Bot 94:515–525. https://doi.org/10.3732/ajb.94.4.515

McGill BJ, Enquist BJ, Weiher E, Westoby M (2006) Rebuilding community ecology from functional traits. Trends Ecol Evol 21:178–185. https://doi.org/10.1016/j.tree.2006.02.002

Meléndez MR, Ponce WP (2016) Pollination in the oil palms Elaeis guineensis, E. oleifera and their hybrids (OxG), in tropical America 1. Pesqui Agropecu Trop 46:102–110. https://doi.org/10.1590/1983-40632016v4638196

Melito MO, Faria JC, Amorim AM, Cazetta E (2014) Demographic structure of a threatened palm (Euterpe edulis Mart.) in a fragmented landscape of Atlantic Forest in northeastern Brazil. Acta Bot Bras 28:249–258. https://doi.org/10.1590/S0102-33062014000200011

Mendes CN, Diniz ES, Terra MCNS, Jeannot KK, Fontes MAL (2019) Light conditions imposed by canopy: allometric strategies of an understory palm (Geonoma schottiana Mart.) in Atlantic Forest. J Trop for Sci 31(3):332–342

Mengardo AL, Figueiredo CL, Tambosi LR, Pivello VR (2012) Comparing the establishment of an invasive and an endemic palm species in the Atlantic rainforest. Plant Ecol Divers 5(3):345–354. https://doi.org/10.1080/17550874.2012.735271

Moles AT, Westoby M (2006) Seed size and plant strategy across the whole life cycle. Oikos 113(1):91–105. https://doi.org/10.1111/j.0030-1299.2006.14194.x

Nettesheim FC, Garbin ML, Pereira MG, de Araujo DSD, de Viveiros Grelle CE (2018) Local-scale elevation patterns of Atlantic Forest tree community variation and assembly drivers in a conservation hotspot in southeastern Brazil. Flora 248:61–69. https://doi.org/10.1016/j.flora.2018.08.016

Nicotra AB, Atkin OK, Bonser SP, Davidson AM, Finnegan EJ, Mathesius U, Poot P, Purugganan MD, Richards CL, Valladares F, van Kleunen M (2010) Plant phenotypic plasticity in a changing climate. Trends Plant Sci 15:684–692. https://doi.org/10.1016/j.tplants.2010.09.008

Oda GAM, Braz MIG, Portela RDCQ (2016) Does regenerative strategy vary between populations? A test using a narrowly distributed Atlantic Rainforest palm species. Plant Ecol 217:869–881. https://doi.org/10.1007/s11258-016-0612-y

Oliveira KFD, Fisch STV, Duarte JDS, Danelli MF, Martins LFDS, Joly CA (2014) Estrutura e distribuição espacial de populações de palmeiras em diferentes altitudes na Serra do Mar, Ubatuba,

São Paulo, Brasil. Rodriguésia 65:1043–1055. https://doi.org/10.1590/2175-7860201465414

Pérez-Harguindeguy N, Diaz S, Garnier E, Lavorel S, Poorter H, Jaureguiberry P, Bret-Harte MS, Cornwell WK, Craine JM, Gurvich DE, Urcelay C (2013) New handbook for standardised measurement of plant functional traits worldwide. Aust Bot 61, 167–234. Retrieved from the University of Minnesota Digital Conservancy, https://hdl.handle.net/11299/177647

Pérez-Harguindeguy N, Diaz S, Garnier E, Lavorel S, Poorter H, Jaureguiberry P, Bret-Harte MS, Cornwell WK, Craine JM, Gurvich DE, Urcelay C (2016) Corrigendum to: New handbook for standardised measurement of plant functional traits worldwide. Aust J Bot 64(8):715–716

Pescador DS, de Bello F, Valladares F, Escudero A (2015) Plant trait variation along an altitudinal gradient in Mediterranean high mountain grasslands: controlling the species turnover effect. PLoS ONE 10:e0118876. https://doi.org/10.1371/journal.pone.0118876

Pires ADS (2006) Perda de diversidade de palmeiras em fragmentos de mata atlântica: padrões e processos. 2006. xi, 108 f. Dissertation—Universidade Estadual Paulista, Instituto de Biociências. Available at: http://hdl.handle.net/11449/100678

Poorter L, Bongers F (2006) Leaf traits are good predictors of plant performance across 53 rain forest species. Ecology 87:1733–1743. https://doi.org/10.1890/0012-9658(2006)87[1733:LTAGPO]2.0.CO;2

Portela RDCQ, Santos FAMD (2011) Caracterização dos estádios ontogenéticos de três espécies de palmeiras: uma proposta de padronização para estudos de dinâmica populacional. Rev Bras Bot 34:523–535. https://doi.org/10.1590/S0100-84042011000400006

Portela RDCQ, Pires ADS, Braz MIG, de Mattos EA (2017) Species richness and density evaluation for plants with aggregated distributions: fixed versus variable area methods. J Plant Ecol 10:765–770. https://doi.org/10.1093/jpe/rtw085

Portela RDCQ, Colmenares-Trejos SL, de Mattos EA (2021) Linking plant functional traits to demography in a fragmented landscape. Front Glob Change 4:717406. https://doi.org/10.3389/ffgc.2021.717406

Qian H, Jin Y (2016) An updated megaphylogeny of plants, a tool for generating plant phylogenies and an analysis of phylogenetic community structure. J Plant Ecol 9:233–239. https://doi.org/10.1093/jpe/rtv047

R Core Team (2022) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Reflora (2019) Flora do Brasil. Retrieved from http://floradobrasil.jbrj.gov.br/

Reich PB (2014) The world-wide 'fast–slow' plant economics spectrum: a traits manifesto. J Ecol 102:275–301. https://doi.org/10.1111/1365-2745.12211

Reich PB, Wright IJ, Cavender-Bares J, Craine JM, Oleksyn J, Westoby M, Walters MB (2003) The evolution of plant functional variation: traits, spectra, and strategies. Int J Plant Sci 164:S143–S164. https://doi.org/10.1086/374368

Renninger, HJ, Phillips, NG (2016). Palm physiology and distribution in response to global environmental change. In: Goldstein, G., Santiago, L. (eds) Tropical Tree Physiology. Tree Physiology, vol 6. Springer, Cham. https://doi.org/10.1007/978-3-319-27422-5_4

Ruiz-Jaen MC, Potvin C (2010) Tree diversity explains variation in ecosystem function in a neotropical forest in Panama. Biotro 42(6):638–646.

Salguero-Gómez R, Jones OR, Jongejans E, Blomberg SP, Hodgson DJ, Mbeau-Ache C, Zuidema PA, De Kroon H, Buckley YM (2016) Fast–slow continuum and reproductive strategies structure plant life-history variation worldwide. Proc Natl Acad Sci USA 113:230–235. https://doi.org/10.1073/pnas.1506215112

Salm R, Salles NVD, Alonso WJ, Schuck-Paim C (2007) Cross-scale determinants of palm species distribution. Acta Amazon 37:17–25. https://doi.org/10.1590/S0044-59672007000100002

Santiago LS, Wright SJ (2007) Leaf functional traits of tropical forest plants in relation to growth form. Funct Ecol 21:19–27

Santos AS, Cazetta E, Morante Filho JC, Baumgarten J, Faria D, Gaiotto FA (2015) Lessons from a palm: genetic diversity and structure in anthropogenic landscapes from Atlantic Forest, Brazil. Conserv Genet 16:1295–1302. https://doi.org/10.1007/s10592-015-0740-2

Santos EF (2005) Ecologia da cutia Dasyprocta leporina (Linnaeus, 1758) em um fragmento florestal urbano em Campinas—SP (Rodentia: Dasyproctidae). 72 f. Dissertation—Universidade Estadual Paulista, Instituto de Biociências de Rio Claro. Available at: http://hdl.handle.net/11449/106597

Sattler D, Lindner A, Morawetz W (2007) A função da sazonalidade no levantamento estrutural da floresta montana tropical. In: Cronemberger C, Viveiros de Castro E (eds) Ciência e Conservação na Serra dos Órgãos. MMA-IBAMA, Brasilia, pp 105–116.

Schreiber U (2004) Pulse-amplitude-modulation (PAM) fluorometry and saturation pulse method: an overview. In: Papageorgiou GC (ed) Chlorophyll a fluorescence advances in photosynthesis and respiration, vol 19. Springer, Dordrecht

Stiegel S, Kessler M, Getto D, Thonhofer J, Siebert SF (2011) Elevational patterns of species richness and density of rattan palms (Arecaceae: Calamoideae) in Central Sulawesi, Indonesia. Biodivers Conserv 20:1987–2005. https://doi.org/10.1007/s10531-011-0070-8

Suzuki R, Shimodaira H (2015) pvclust: hierarchical clustering with P-values via multiscale bootstrap resampling. R package version, 2. Available at: http://stat.sys.i.kyoto-u.ac.jp/prog/pvclust/

Suzuki R, Shimodaira H (2006) Pvclust: an R package for assessing the uncertainty in hierarchical clustering. Bioinformatics 22:1540–1542

Svenning JC (2001) On the role of microenvironmental heterogeneity in the ecology and diversification of neotropical rain-forest palms (Arecaceae). Bot Rev 67:1–53. https://doi.org/10.1007/BF02857848

Tait MA, Hik DS (2003) Is dimethylsulfoxide a reliable solvent for extracting chlorophyll under field conditions? Photosynth Res 78:87–91. https://doi.org/10.1023/A:1026045624155

Violle C, Navas ML, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E (2007) Let the concept of trait be functional! Oikos 116:882–892. https://doi.org/10.1111/j.0030-1299.2007.15559.x

Wellburn AR (1994) The spectral determination of chlorophylls a and b, as well as total carotenoids, using various solvents with spectrophotometers of different resolution. J Plant Physiol 144:307–313. https://doi.org/10.1016/S0176-1617(11)81192-2

Westoby M (1998) A leaf-height-seed (LHS) plant ecology strategy scheme. Plant Soil 199:213–227. https://doi.org/10.1023/A:1004327224729

Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JH, Diemer M, Flexas J (2004) The worldwide leaf economics spectrum. Nature 428:821–827. https://doi.org/10.1038/nature02403

Xiao Z, Zhang Z, Krebs CJ (2015) Seed size and number make contrasting predictions on seed survival and dispersal dynamics: a case study from oil tea Camellia oleifera. For Ecol Manag 343:1–8. https://doi.org/10.1016/j.foreco.2015.01.019

Zheng J, Arif M, He X, Ding D, Zhang S, Ni X, Li C (2022) Plant community assembly is jointly shaped by environmental and

dispersal filtering along elevation gradients in a semiarid area. China Front Plant Sci 13:1041742. https://doi.org/10.3389/fpls.2022.1041742

Zucaratto R, Pires ADS (2015) Local extinction of an important seed disperser does not modify the spatial distribution of the endemic palm *Astrocaryum aculeatissimum* (Schott) Burret (Arecaceae). Acta Bot Bras 29:244–250. https://doi.org/10.1590/0102-33062015abb0008