

Divergence in functional traits in seven species of neotropical palms of different forest strata

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Research Article

Keywords: carbon stocks, carbon sequestration, environmental filtering, functional traits, niche divergence.

Posted Date: January 3rd, 2023

DOI: <https://doi.org/10.21203/rs.3.rs-2334225/v1>

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Version of Record: A version of this preprint was published at *Oecologia* on October 24th, 2023. See the published version at <https://doi.org/10.1007/s00442-023-05466-y>.

Abstract

Functional traits are morphological and physiological characteristics that determine growth, reproduction, and survival strategies. The leaf economics spectrum proposes two opposing life history strategies: species with an "acquisitive" strategy grow fast and exploit high-resource environments, while species with a "conservative" strategy emphasize survival and slow growth under low resource conditions. We analyzed interspecific variation in nine functional traits related to biomass allocation and tissue quality in seven Neotropical palm species from three forest strata (understory, subcanopy, and canopy). We expected that the level of resources of a stratum that a species typically exploits would determine the dominance of either the exploitative or conservative strategy, as well as the similarity in functional traits between species. If this is correct, then canopy and subcanopy species will show an acquisitive strategy emphasizing traits targeting a larger size, whereas understory species will show a conservative strategy with traits promoting efficient biomass allocation. Two principal components (57.22% of the variation) separated palm species into: a) canopy and subcanopy species whose traits were congruent with the acquisitive strategy and that emphasized large size (i.e., height, carbon content, and leaf area), and b) understory species whose traits were associated with efficient biomass allocation (i.e., dmf and tissue density). Since palms are one of the most abundant life forms in tropical forests, exploring the variation in functional traits within this group could significantly improve our understanding of plant adaptation to environmental gradients.

Introduction

Functional traits are morpho-physio-phenological characters that impact fitness through their effects on growth, reproduction, and survival (Violle et al. 2007). Variation in functional traits influence plant life history strategies, resource allocation for growth and defense (Coley et al. 1985), niche differentiation, and environmental filtering (Westoby et al. 2002; Poorter et al. 2008; Boukili and Chazdon 2017). Leaf economics spectrum theory has shown the existence of a universal trade-off between two opposing life history strategies (Wright et al. 2004). On one hand, species exhibiting an "acquisitive" strategy are characterized by high photosynthetic rates, thinner and low-cost leaves, with high nitrogen and phosphorus content and high specific leaf area (SLA) that exploit high-resource environments. On the other hand, species with "conservative" strategies have thicker, tougher, low SLA leaves, with low photosynthetic rates, high construction costs, low nitrogen content, and long lifespans, and exploit low-resource environments (Westoby et al. 2002; Wright et al. 2004). These strategies are consistent across biomes demonstrating the universality of this trade-off (Díaz et al. 2004, 2016).

Palms (Arecaceae) are one of the most diverse and widely distributed groups of plants in tropical and subtropical areas, with more than 2,600 species and 181 genera (Baker and Dransfield 2016) that dominate many tropical ecosystems (Mejia and Kahn 1990; Myers 2013). Palms are "hyperdominant" elements in the Amazon lowlands (ter Steege et al. 2013), with 6 out of the 10 most abundant species being palms. Although palms have a limited contribution to carbon stocks in diverse tropical rainforests (Fauset et. 2015), they influence forest function (Boukili and Chazdon 2017), play a crucial role in food

webs, provide habitat and food to a multitude of animal species (Zona and Henderson 1989; Howard et al. 2001; Onstein et al. 2017), and are invaluable to many human groups who use them as raw materials for construction, food, drink, clothing, fuel, medicine, and fibers (Jones 1995; Henderson 2002; Dransfield et al. 2008; Sylvester et al. 2012). To improve our understanding of the ecological role of palms of different forest strata and growth forms it is essential to improve the knowledge on their inter and intraspecific variation in functional traits (Westerband et al. 2021).

Many palm species start their lives as light-suppressed seedlings and juveniles in the understory, until they accumulate enough resources to develop appropriate mechanical support around the base of the stem to grow in height. Since light (Montgomery and Chazdon 2001; Sylvester and Avalos 2013) and nutrients (Wright et al. 2018; Wright 2019; Collins et al. 2022) can limit the survival of understory plants, the selective pressure to acquire and timely invest resources in growth are greater in the understory than in the canopy, or under higher light conditions. Species that spend their entire life cycle, or spend significant time in in the understory, have evolved to adapt to the shade (Avalos 2019). Understory palms produce long-lived fronds rich in structural defenses and increase their slenderness ratio (stem height divided by stem diameter) as they grow (Avalos and Fernández Otárola 2010; Otárola and Avalos 2014; Avalos 2022 in rev). Palm seedlings have thinner leaflets with high SLA to capture more light per unit of invested carbon (Avalos 2022, in rev). This trend reverses as the palms that start in the understory transition from small seedlings to adults and move to the canopy producing thicker, low SLA, long-lived leaves (Avalos 2019; Avalos 2022 in rev). Still little is known about the variation in functional traits in palms, and tropical plants in general, as they traverse different ontogenetic and successional stages (but see Hérault et al. 2011; Lasky 2015; Boukili and Chazdon 2017). Such research is fundamental to understand community organization specially in highly diverse tropical forests (Dayrell et al. 2018; Trujillo et al. 2022).

Palms have been excluded from most inventories of functional traits in tropical forests (DeWalt and Chave 2004; Chave et al. 2005; Lorenz and Lal 2010). As monocots, they have a different structure, allometry, and strategies of resource use relative to trees (Tomlinson 2006, 2011). With a few exceptions, palms are monopodial and lack aerial branching, have only one shoot meristem, and lack dormancy and secondary growth. In palm species where stem diameter and stem height show a significant relationship, diameter increases through sustained primary growth (i.e., through the division, lignification, and expansion of parenchyma cells, which also differentiate into fibers, Henderson 2002; Tomlinson 2011). In addition, leaf longevity and leaf construction costs are higher in palms than in dicotyledonous trees (Renninger and Phillips 2016), which have smaller leaves and could drop leaflets rather than the entire compound leaf to acclimate to new light conditions. Within the family Arecaceae there is considerable morphological variation which is reflected in niche differentiation and habitat filtering (Henderson 2002).

There is an incomplete inventory of functional traits for tropical plants, and especially for palms (Gödel et al. 2015). Functional traits such as tissue density (Rich 1986, 1987), dry mass fraction (dmf), slenderness ratio, leaf toughness, and SLA, and even stem height, as well as gas exchange parameters, are rarely documented for palms as a group, or are limited to a few species (i.e., Chazdon 1986a, 1986b;

Araus and Hogan 1994; da Silva et al. 2015; Renninger and Phillips 2016). Much less is known about how these traits vary with ontogenetic stage and palm size (but see Chazdon 1986a, 1986b). Tissue density, for instance, varied with position along the stem, since sclerotized tissue is denser closer to the base and periphery of the stem, and decreases in abundance close to the top of the stem (Niklas 1992). The functional trait databases (Perez-Harguindeguy et al. 2013) are still data-deficient for palms, and for tropical species in general, although Kissling et al. (2019) provide a very comprehensive compilation. Still, these databases are based on a few individuals (e.g., <http://db.worldagroforestry.org>), and often do not provide metadata. It is necessary to incorporate more species, a larger sample size per species, a greater range of sizes, and phylogenetic bias corrections.

Our main objective is to analyze the interspecific variation in nine functional traits related to biomass allocation and tissue quality (tissue density, dmf, slenderness ratio, carbon content, diameter, height, leaf area, and root:shoot ratios based on biomass and carbon content) in seven palm species from three forest strata (understory, subcanopy and canopy). We tested the hypothesis that the dominant light environment in each stratum (understory, subcanopy and canopy) that a palm species typically exploits, will determine the strategy of resource use, and thus, the degree of functional trait similarity among species. Therefore, palms that complete their life cycle in the understory will show a conservative resource-use strategy that emphasizes efficient biomass distribution (dominant traits in this strategy will be tissue density, slenderness ratio, root:shoot ratios, and dmf), in contrast to palms exploiting better lit environments (subcanopy and canopy species) that will show an acquisitive strategy, and therefore will be characterized by functional traits favoring large size and leaf area (i.e., diameter and height, total carbon content, leaf area). Augmenting our knowledge about the variation in palm functional traits is relevant not only to expand the database of functional traits in tropical plants, but also to understand how different resource allocation strategies regulate plant growth in contrasting light environments, and ontogenetic niche shifts in functional traits as the palm grows into the canopy, or within a given stratum (Dayrell et al. 2018; Westoby et al. 2022). Exploring the variation of functional traits within palms, one of the most abundant life forms in tropical forests, could significantly expand our understanding of how plants adapt to environmental gradients.

Materials And Methods

Study site

Palms were harvested from three tropical rain forest sites in the Caribbean lowlands of Costa Rica. The first two were La Selva Biological Station (10°26'N – 83°59'W, 30–150 masl, annual precipitation 4,162 mm) and Tirimbina Biological Reserve (10°24'N – 84°06'W, 180–220 masl, annual precipitation 3,833 mm), both situated in Sarapiquí, Heredia. The third site was the lowland forest of the agroecological farm El Progreso (10°30'35" N – 83°44'39" W, 45 masl, annual precipitation of 4,000 to 5,000 mm), located in Pococí, Limón. The three sites present an average daily temperature of 25°C and have a weak climatic seasonality, with November, December and February being the rainiest months (McDade et al. 1994).

Study species

We harvested 87 individuals of seven palm species belonging to three different forest strata, canopy, subcanopy, and understory (Fig. 1). The canopy species *Socratea exorrhiza* (S Nicaragua to Brazil, 0-750 masl) and *Iriartea deltoidea* (SE Nicaragua to Brazil, 0-800 masl) can reach 25 and 30 m of stem height, respectively, and are characteristic canopy components of mature forests (Grayum 2003). Both species have a cone of stilt roots, although roots in *I. deltoidea* are clustered at the base of the stem and grow up to 1.5 m above ground, whereas *S. exorrhiza* has a stilt root cone composed by well-separated roots, covered by spines, which can reach up to 4 m above the ground (Henderson et al. 1995). The subcanopy species *Euterpe precatorea* (Belize to Bolivia, 0-1150 masl) var *longevaginata* (Henderson 1995) is a single-stemmed palm that can reach 26 m in height and develops a stilt root cone that in extreme cases may reach over 2 m in height (Avalos and Schneider 2011). Understory species included *Prestoea decurrens*, *Chamaedorea tepejilote*, *Geonoma interrupta* and *Asterogyne martiana*. *Prestoea decurrens* (Nicaragua to Ecuador, 0-900 masl), is a clonal species reaching 10 m in height (Grayum 2003). *Chamaedorea tepejilote* (S Mexico to Colombia, 0-1600 masl) is a dioecious species which can grow up to 5 m (Grayum 2003; Castillo-Mont et al. 1994). *Geonoma interrupta* (S Mexico to Peru, 0-850 masl) has a solitary stem and may reach 6 m in height (and over 10 m in exceptional cases), being one of the tallest species in the genus (Grayum 2003). Finally, *Asterogyne martiana* (Belize to Ecuador, 0–1,000 masl) is an understory species with a decumbent stem often reaching 2 m in height, and with simple, bifid leaves.

Palm harvesting, morphological measurements, and estimation of carbon sequestration

Detailed harvesting methods are described in Avalos et al. (2022). In summary, harvesting took place from Sept 2013 to May 2015, with the goal of obtaining a representative sample with a wide range of size per species (Fig. 1). For canopy and subcanopy palms, this sample did not include individuals close to the maximum heights reported for the species due to the difficulty of obtaining permission to harvest very tall individuals. Stem diameter was measured at 1.3 m above the ground, at half the stem length in palms less than 1.3 m tall, or immediately above the stilt roots in palms with a root cone that surpassed 1.3 m in height. The harvested palms were separated into modules (stems, roots, and leaves) and the total fresh biomass of each module was measured in the field with a Pesola® Macro-Line Spring Balance (30 ± 0.25 kg). Then, these samples were dried in an oven at 65°C for 48 h or until constant weight. Carbon content was measured with an automated TruSpec CN analyzer, LECO Corporation, at the Laboratory of the Department of Systematic Botany of the University of Ulm, Germany, and an automatic analyzer for nitrogen and elemental carbon, VarioMacrocube, at the University of Costa Rica. The average carbon fraction for the palms analyzed here was $43.9\% \pm 1.28$ (Cambronero et al. 2018), but we used the average carbon fraction obtained for each species multiplied by the estimated total biomass per individual and module (root, shoots, leaves). Dry mass fraction or tissue moisture (dmf) was measured as the ratio of total dry over total fresh biomass per individual.

We measured the total length of the stem, or stem height, from the point of connection with the roots to the base of the petiole of the youngest leaf. This included the underground stem in *A. martiana*. Slenderness ratio was calculated as the ratio of stem height in m to diameter in cm (Niklas 1994; Niklas et al., 2006).

To measure stem tissue density (specific gravity, ρ , cm/mL) we used with a Haglof 2-wire incremental borer following the methods of Chave et al. (2005). We selected an entry point for the borer near the base of the stem, in the middle, and near the base of the crown. This tissue sample was placed in a test tube, sealed, and transferred to the laboratory for estimation of tissue density by volume displacement.

Estimation of total leaf area per palm

To determine the total leaf area, we followed the methods of Avalos and Sylvester (2010). We collected three leaves (one young, one intermediate, and one mature), cleaned them with a dry cloth, and measured leaf area with a LICOR LI-3100 C leaf area meter (LICOR, Lincoln, NE, USA). From these measurements we estimated the total leaf area per individual palm by averaging the leaf area of these three leaves and multiplying it by the total number of fronds.

Root:shoot ratios

We calculated root:shoot ratios as the dry biomass of roots over the dry biomass of above-ground parts (stems and leaves). This corresponded to the root:shoot ratio of dry biomass. In addition, we obtained the root:shoot ratio of the carbon fraction after calculating the carbon fraction of the above-ground and below-ground biomass (this was the root:shoot ratio based on the carbon fraction).

Analysis of the correlation structure of morphological traits of understory vs canopy palms

We used a principal component analysis (PCA) based on the correlation matrix of the Ln transformed values of nine morphological traits related to biomass allocation and tissue quality: the total amount of carbon content in kg per palm, diameter in cm (diam), total stem height from the base of the stem to the base of the leaf crown, dmf, stem tissue density, leaf area, slenderness ratio and root:shoot ratios (calculated based on the dry biomass, and carbon content levels). We used the scores of the first two components to inspect the distribution of palm species across forest strata in the multidimensional space defined by correlation structure of morphological traits.

Results

Palms showed a wide range of sizes with size and biomass increasing, from understory to canopy species (Fig. 1). *Prestoea decurrens* and *G. interrupta* included very large individuals and overlapped in height, leaf area, and diameter with canopy and subcanopy species (Fig. 1E, 1F). These species also showed overlap in the amount of sequestered carbon (Fig. 1I) with canopy and subcanopy species; the latter species did not include individuals with the maximum height reported in the literature (i.e.,

Henderson 2002). Except for *S. exorrhiza* and *A. martiana*, the species examined here differed little in root-to-shoot ratios, both at the total biomass ($F_{1,85} = 0.64$, $P = 0.42$) and total sequestered carbon levels ($F_{1,85} = 0.38$, $P = 0.53$, Fig. 1A, 1B).

Understory species showed higher values of dmf ($F_{1,85} = 83.97$, $P < 0.001$) and tissue density ($F_{1,85} = 56.64$, $P < 0.001$) than canopy and subcanopy species. Regarding slenderness ratio, understory species showed more variation than canopy and subcanopy species, and the latter tended to present lower values, but differences were not statistically significant between strata ($F_{1,85} = 1.66$, $P = 0.2$). Differences were not associated with strata, but were centered among species, with *E. precatorea*, *P. decurrens* and *G. interrupta* showing the highest values (Fig. 1H).

Correlation matrix of morphological traits

The highest correlations were found between diameter and total carbon (Pearson correlation coefficient = 0.89), diameter and total leaf area (0.79), height and leaf area, and tissue density and dmf (both with 0.74), and leaf area and total carbon (0.69, Fig. 2A). Root:shoot ratios showed little association with the rest of the variables. The correlogram distinguished two groups of traits with positive correlations. The first group included traits related to palm size (i.e., height, carbon content and leaf area), whereas the second group included traits associated to biomass distribution (i.e., dmf and tissue density, Fig. 2B). These two groups were negatively associated with each other.

Principal component analysis

We identified four principal components with an eigenvalue > 1 that explained 87.48% of the variation (Table 1). The first component (40.32%) showed a similar weight for variables related to palm size (e.g., diameter, total carbon content, leaf area, and height). The other three components had a similar weight. The second component (16.89%) had a similar contribution of tissue density and dmf. The third component (16.35%) had a dominant contribution of root:shoot ratio based on total dry biomass. Slenderness ratio and root:shoot ratio based on total carbon content dominated the fourth component (13.91%).

Table 1

Summary of principal component analysis applied to the Ln-transformed values of nine morphological traits in seven species of neotropical palms from Costa Rica (eigenvector coefficients of traits dominating each component in boldface).

		PC 1	PC 2	PC 3	PC 4
Eigenvalue		3.63	1.52	1.47	1.25
Percentage of variation		40.32	16.89	16.35	13.91
Percentage of cumulative variation		40.32	57.22	73.57	87.48
Trait	Abbreviation				
R:S biomass	RSbiom	0.02	0.07	0.77	-0.06
R:S carbon	RSCarb	0.08	-0.02	0.48	0.66
Tissue density	density	-0.21	0.69	-0.04	0.02
Stem diameter	diam	0.48	0.02	0.0001	-0.02
Stem height	H	0.38	0.31	0.14	-0.28
dmf	dmf	-0.32	0.55	0.06	-0.05
Total carbon Kg	Ckg	0.45	0.26	-0.08	0.16
Slenderness	slenderness	0.19	0.19	-0.35	0.59
Leaf area	Leafarea	0.45	0.09	0.008	-0.3

The distribution of palms in the multidimensional space defined by the first two components separated species according to forest strata and showed that understory species were more related to biomass distribution traits (tissue density and dmf), whereas subcanopy and canopy species were more associated to palm size traits (diameter, stem height, leaf area, total carbon content, Fig. 3), which confirms our hypothesis of functional trait segregation according to forest strata. Understory species showed a wider spread of the data reflecting the high structural diversity found in this group.

Discussion

Our results demonstrate that palm species partition the light resource following the “conservative” and “acquisitive” strategies of the leaf economic spectrum (Westoby et al. 2002; Wright et al. 2004). The classification of palms into forest strata revealed segregation in structure and strategy of resource use between understory, and subcanopy and canopy species, as deduced from the principal component analysis. While subcanopy and canopy species were linked to traits relevant to overall palm size, such as diameter, total height, and leaf area, understory species were associated to traits linked to biomass allocation, such as dmf and tissue density. These differences show general trends in resource partitioning to maximize survival in the shade or to invest in height growth to reach the canopy and were consistent

with our hypothesis that the dominant light environment in each stratum will determine the strategy of resource use, and thus, the degree of functional trait similarity.

However, shoot:root and slenderness ratios had a small influence segregating palms into forest strata contrary to our expectations. In some canopy species, such as *S. exorrhiza* and *E. precatorea*, slenderness ratio increases with stem height (Avalos et al. 2019), which is related to a greater investment in stature once sufficient mechanical support is achieved at the base of the stem. This in turn facilitates a greater biomass allocation to a larger crown formed by fronds with long life span. Slenderness ratio showed greater variation in understory species, which could reflect the greater light heterogeneity of this stratum relative to the canopy (Montgomery and Chazdon 2001). More specific studies are required to compare the ontogenetic development of this trait over time. Root:shoot ratios did not show a clear separation between palms of different strata and remained below the unity. We must not rule out the possibility that root biomass in palms, as in many other tropical species, could be underestimated due to the practical difficulties of measuring and extracting all the roots (Hairiah et al. 2001). In palms, there is a dearth of comparative data for root biomass, and thus, root:shoot ratios (but see Goodman et al. 2013; Avalos et al. 2022).

Conservative strategy of understory palms

Understory species were more associated to tissue density and dmf than subcanopy and canopy species. Tissue density is a leaf economics spectrum trait related to stem construction costs, plant architecture and stability, stem hydraulic conductance (Chave et al. 2006), as well as plant mortality (Kraft et al. 2010) and relative growth rate (Iida et al. 2016). Tissue density is a key predictor variable of carbon sequestration in the general model of Chave et al. (2014) to estimate the aboveground biomass of tropical forest species, which was not significantly different from the specific model for Arecaceae proposed by Avalos et al. (2022), which included only diameter at stem height. Likewise, dmf was part of the composite variable used to estimate the aerial biomass of Arecaceae in the study of Goodman et al. (2013). The latter model also converged with the models of Chave et al. (2014) and Avalos et al. (2022). However, the importance of tissue density and dmf needs to be further explored as very few palm species have been examined to date.

Many understory palms display their leaf area with a high degree of efficiency by reducing leaf overlap and increasing light interception (Takenaka et al. 2001; Alvarez-Clare and Avalos 2007). Efficiently allocating biomass resources in the shade has a higher selective value in understory, shade-adapted palms, as well as in palm species that start their life cycle in the understory (Westoby et al. 2002) than for canopy palms. Shade-adapted palms are positioned at the end of the resource conservative strategy and can complete their life cycle and reproduce in the understory (Chazdon 1986b; Sylvester and Avalos 2013; Avalos 2019). When light conditions improve, palms that start in the shade can opportunistically increase their leaf area (Sylvester and Avalos 2013) and augment height growth (Chazdon 1986a; Gatti et al. 2011). Canopy and subcanopy palms such as *S. exorrhiza* and *E. precatorea* increase their slenderness ratio with height as they escape the understory and expose their crown to better lit conditions (Avalos

2022 in rev). Once these palms cross a height threshold and have more access to light, they focus their allocation strategy in securing high resource acquisition by increasing in size and switching to the resource acquisitive strategy of sub-canopy and canopy species. The ample morphological variation shown in the space defined by the first two principal components demonstrates these general trends and illustrates the diversity of allometric strategies within understory and canopy species.

Acquisitive strategy of canopy and subcanopy palms

Canopy and subcanopy palms invest in increasing size, as reflected in larger height and diameter, higher slenderness ratios, larger crown area understory palms. During this transition the frond morphology and crown architecture also changes (Rich et al., 1995). For instance, small *I. deltoidea* and *S. exorrhiza* palms develop less stratified crowns whose fronds present wedge-shaped leaflets or fins with a similar angle orientation. At about 7–8 m in height the fronds produce narrow, longitudinal leaflets in between the fins and produce a multilayer crown. According to Rich et al. (1995), *I. deltoidea* and *S. exorrhiza* palms > 11–17 m produce more heterogeneous fronds with a variety of morphologically diverse leaflets resulting in a multilayered crown. The patterns of biomass allocation observed here are consistent with an acquisitive resource strategy as canopy and subcanopy palms showed a phenotype dominated by functional traits associated with achieving larger size and is consistent with trait growth theory (Westoby et al. 2022).

Complementary hypotheses to the leaf economics spectrum

Testing functional hypotheses to explain variation in niche partitioning requires the integration of more functional traits, especially those integrating whole-plant strategies in response to environmental gradients (Kraft et al. 2008). Key leaf economics spectrum traits, such as leaf area, SLA, maximum diameter, maximum height, leaf nitrogen content, and tissue density (Chave et al. 2006) have great potential as these traits integrate changes through ontogeny in response to environmental gradients (Westoby et al. 2002; Wright et al. 2010), as well as demographic and population processes such as density dependence (Umaña et al. 2018). There is a dearth of longitudinal studies examining functional traits in long-lived species (but see Wright et al. 2010; Boukili and Chazdon 2017), especially research linking functional traits and plant demography (Poorter et al. 2008; Worthy and Swenson 2019).

In addition to the economic spectrum, other hypotheses explaining differences in the trait distribution have received considerably less attention. For example, Westoby's (1998) leaf-height-seed (LHS) plant ecology strategy scheme proposes that traits related to leaf morphology (especially SLA), stem height, and leaf size seed (i.e., seed mass) could summarize plant responses to competition, stress, and disturbance. The current and historical effects of temperature and precipitation seasonality should also be considered since climatic factors have a strong effect on the distribution of functional traits such as SLA and maximum height (Göldel et al. 2015).

Trait growth ecology is another integrative attempt to scale individual and species variation in functional traits to ecosystem function. This theory has focused on body size as a driver of ecological, ecosystem,

and evolutionary processes. Implicit in this assumption is the importance of ontogenetic niche shifts, which are mediated through shifts in functional traits associated to plant size or stage (Westoby et al. 2022). These shifts are interpreted from an optimization approach, which is consistent with the leaf economics spectrum and with theories of leaf life span optimization (Kikuzawa 1995). Such efforts still require the integration of interspecific and intraspecific variation in functional traits, demography, and community and ecosystem ecology (Enquist et al. 2007, 2017).

These explanations are not mutually exclusive but are rather complementary to other hypotheses explaining community organization and diversity, such as the environmental filtering and niche differentiation hypotheses (Kraft et al. 2008), the growth mortality trade-off (Wright et al. 2010), as well as deterministic explanations involving species competition and plant-herbivore interactions (e.g., the differential mortality hypothesis, or the Janzen-Connell model, Janzen, 1970).

There are significant obstacles to achieving a synthesis that would integrate trait growth theory, the leaf economics spectrum, and other explanations to scale the variation in functional traits to community and ecosystem ecology. Monitoring the physiological performance of species of large size and long-life spans in highly diverse forests, as well as increasing the knowledge of functional trait variation in poorly known life forms, such as epiphytes, ferns, and palms, is still difficult. Functional ecology has the potential to identify resource use strategies using traits of universal importance that separate species according to their resource use strategy (Visser et al. 2016). This research becomes increasingly urgent as anthropogenic impacts intensify and make critical the capacity to predict the response of ecological systems to climate change.

Conclusions

Our classification of palm species into different forest strata reflected different strategies of segregation in resource use strategy among understory, subcanopy, and canopy species. Tissue density and dmf showed that understory species followed a "conservative" resource use strategy, while subcanopy and canopy palm species were associated to traits that reflected palm size and that conformed to the "acquisitive" strategy of resource use within the leaf economics spectrum (Westoby et al. 2002; Wright et al. 2004). These findings show general trends in resource partitioning to maximize survival in the shade or invest in height growth to reach the canopy. Our results demonstrate the need to include more palm species and to carry out longitudinal studies that would consider the species' ontogeny and population dynamics to understand the role of functional influencing plant responses to environmental gradients.

Declarations

Funding: This investigation was supported by a research grant from the International Palm Society to MC, and scholarships from the Organization for Tropical Studies (MC and CAV), the University of Costa Rica (MC), and Tirimbina Biological Reserve (CAV). The School for Field Studies provided logistic support.

Conflicts of interest/Competing interests: The authors declare that they have no conflict of interest.

Ethics approval: Not applicable.

Consent to participate: All patients included in this study gave written informed consent to participate in this research.

Consent for publication: All patients provided written informed consent to publish the data contained within this paper.

Availability of data and material: The data was deposited in Mendeley repository under the reference number Avalos, Gerardo; camb, mile; Alvarez-Vernagni, Carolina (2022), "Functional traits of 7 spp of tropical palms in Costa Rica", Mendeley Data, V1, doi: 10.17632/yw9tffmwjf.1.

Code availability: Not applicable.

Acknowledgements: Orlando Vargas facilitated field work at La Selva. Juan Manuel Ley facilitated field work at Tirimbina. Nutrient analyses were facilitated by Floria Bertsch at the Centro de Investigaciones Agronómicas, University of Costa Rica, and by Steven Jansen at the Department of Systematic Botany and Ecology, University of Ulm. The Alpízar Chaves family of El Progreso facilitated work in their property.

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Figures

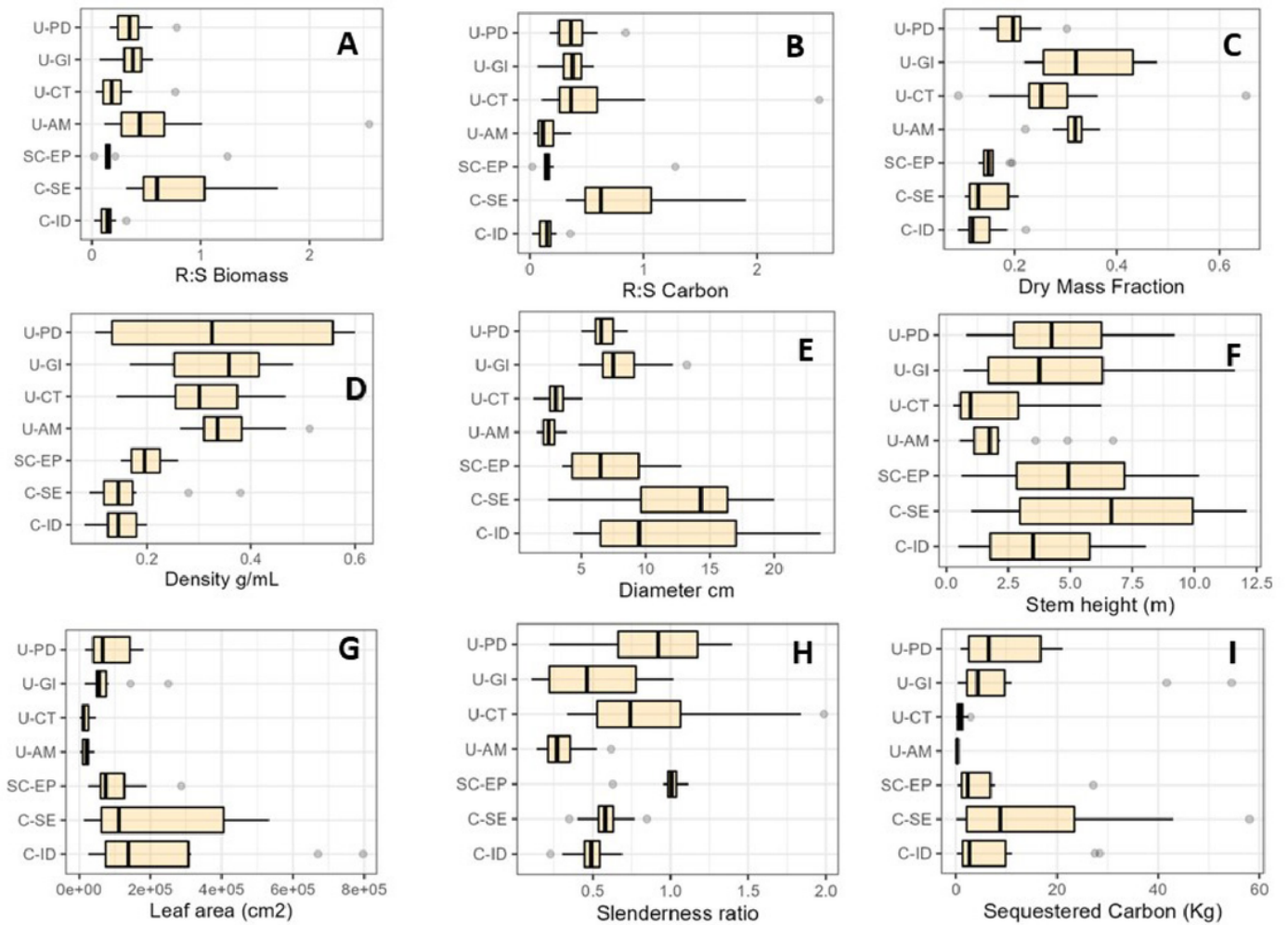


Figure 1

Variation in nine morphological traits in seven species of neotropical palms of different forest strata. Palm species are referred to by stratum (U = understory, SC = subcanopy, C = canopy) followed by the initial of the genus and species name.

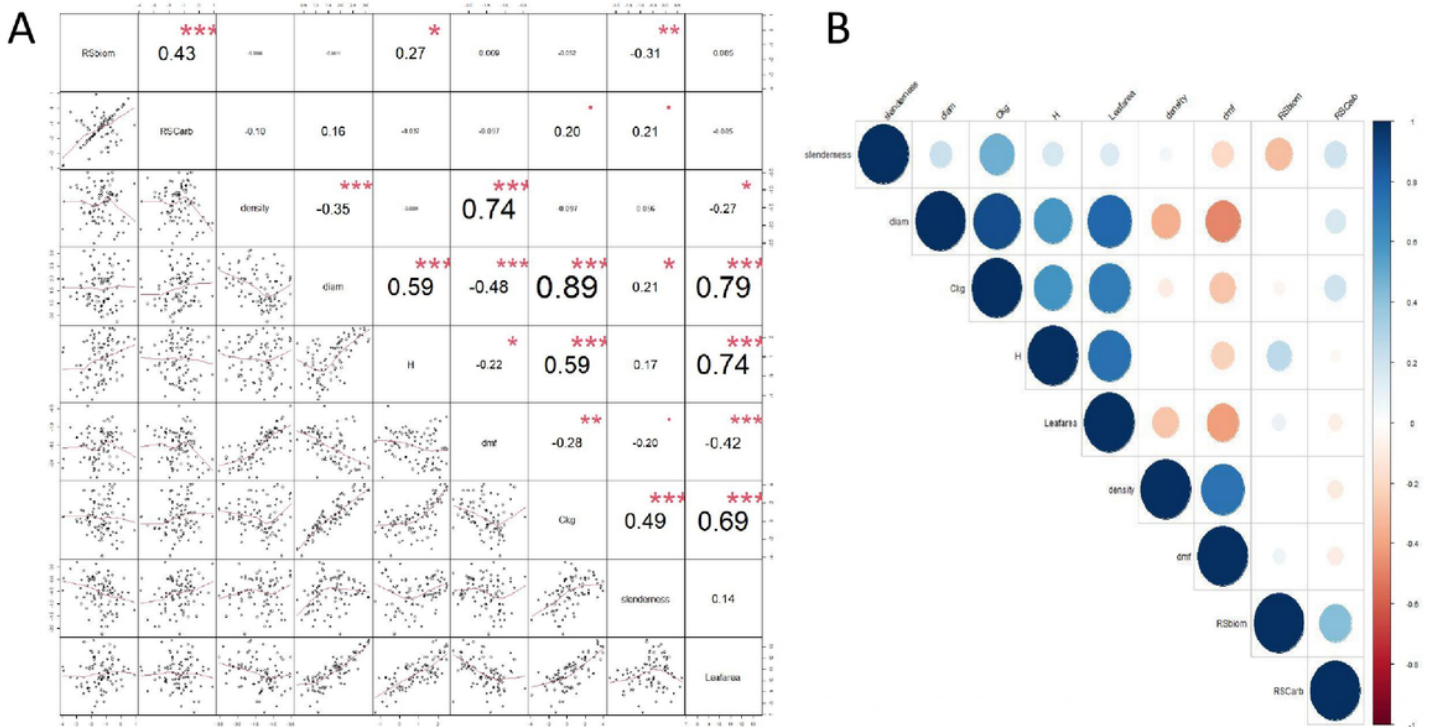


Figure 2

A. Correlation matrix of nine morphological traits in seven species of neotropical palms of different forest strata. Values indicate the magnitude of the Pearson Correlation Coefficient of the Ln-transformed values of morphological traits, and asterisks indicate the level of significance (p-values = 0, 0.001, 0.01, correspond to ***, **, *, respectively). B. Correlogram showing the direction and magnitude of Pearson correlation coefficients. Shades of blue indicate the magnitude of positive correlations and shades of orange indicate the magnitude of negative correlations. Trait abbreviations follow Table 1.

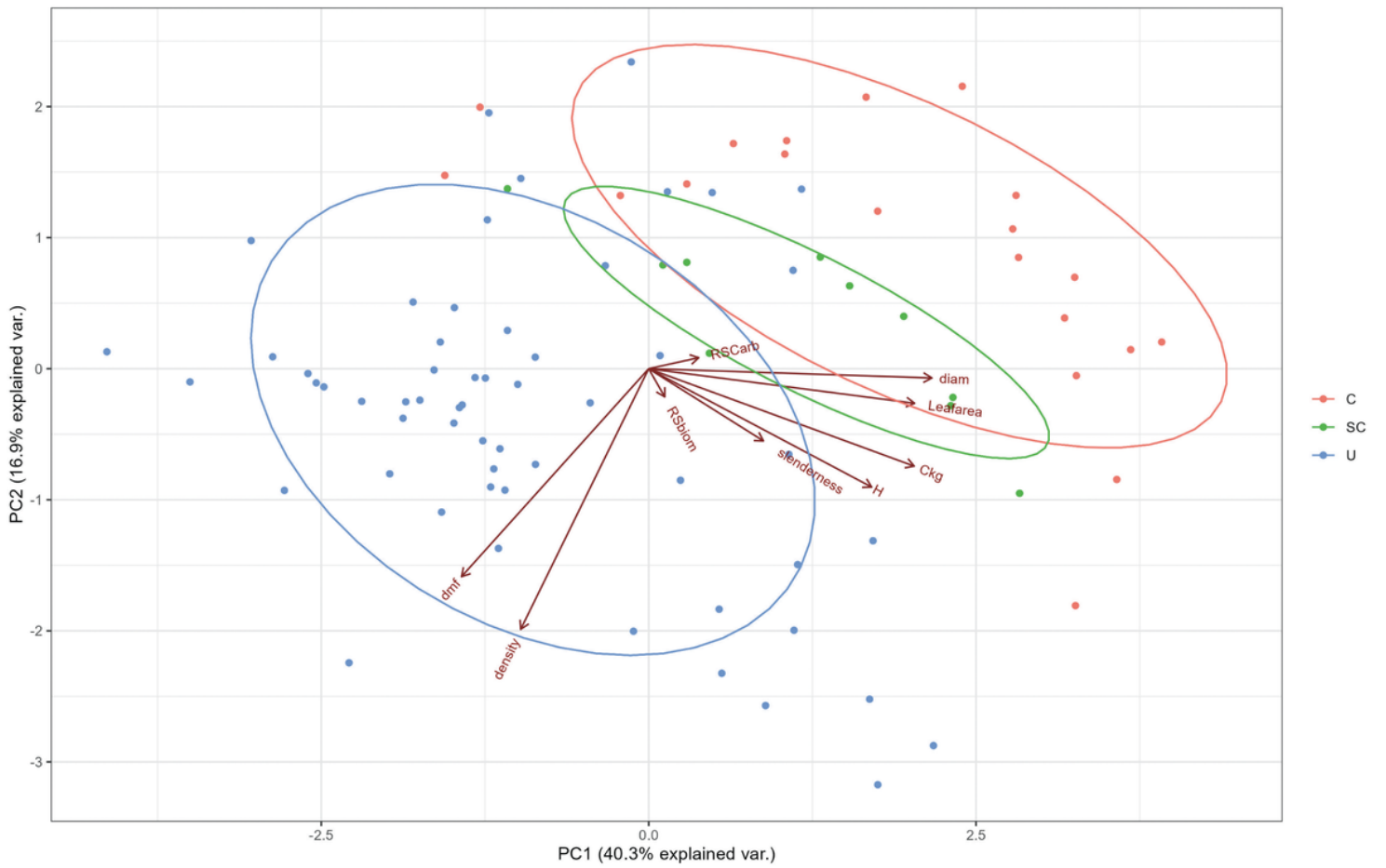


Figure 3

Spatial distribution of seven palm species of three forest strata in the space defined by the first two principal components of nine morphological traits. Trait abbreviations follow Table 1.