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Species Diversity and Growth Forms in Tropical American Palm Communities

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Abstract To advance our understanding of the processes that govern the assembly of palm communities and the local coexistence of numerous palm species, we here synthesize available information in the literature on species diversity and growth-form composition in palm communities across the Americas. American palm communities surveyed had 4–48 (median 16) species in study plots covering 0.09–7.2 ha. Climate, soils, hydrology, and topography are the main factors determining palm community species richness. Tropical lowland *terra firme* rain forests are the most species-rich whereas forests that are inundated or grow on sandy soils or in areas with seasonal climate have much fewer species. Palm communities in the central-western Amazon and in Central America are significantly richer than the average region and those in the Caribbean significantly poorer in species. As for branching, the 789 species of tropical American palms belong to Corner's model (solitary, 268 species, 33%), Tomlinsons model (cespitose, 521 species, 66%) and Schoute's model (dichotomous branching, three species, <1%). We assigned the species to eight different growth forms: (*i*) Large tall-stemmed Palms (102 spp), (*ii*) Large-leaved medium–short-stemmed Palms (31 spp), (*iii*) Medium-sized Palms (95 spp), (*iv*) Medium/Small Palms with Stout Stem (42 spp), (*v*) Small Palms (423 spp), (*vi*) Large acaulescent Palms (28 spp), (*vii*) Small acaulescent Palms (56 spp), and (*viii*) Climbing Palms (12 spp). The eight growth forms are differently represented in the palm communities, and the categories Small Palms and Large tall-stemmed Palms dominate the communities both in terms of species richness and in number of individuals.

Keywords Amazon · Arecaceae · Functional Diversity · Habitat Specialization · Palmae · Species Richness · Tropical Forest · Tropical Trees

Introduction

The palm family (Arecaceae) is a diverse and distinctive element of all tropical and subtropical regions, with more than 2,400 species worldwide (Govaerts & Dransfield, 2005; Dransfield et al., 2008b). The Americas harbour some 789 species of palms in 67 genera, of which only two genera (*Raphia*, *Elaeis*) and one species (*Raphia taedigera*) are shared with the Old World (Dransfield et al., 2008b). Palms are often key functional components of ecosystems, and form complex assemblages of different, co-existing growth forms ranging from small shrubs to tall trees (up to 60 m in *Ceroxylon quindiuense*) and lianas in *Desmoncus* and *Chamaedorea elatior*. Some plant communities are dominated by single palm species, such as the *Sabal palmetto* woodlands in southeastern Mexico (López & Dirzo, 2007), the *morichales* swamps in the Amazon basin where *Mauritia flexuosa* is the monodominant canopy species (Kahn & de Granville, 1992), or some Amazonian forests on old river terraces where *Lepidocaryum tenue* forms enormous clonal stands in the understory (Kahn & Mejía, 1987; Balslev et al., 2010a). On the other hand, dozens of palm species may co-occur locally, many of them with the same growth form. In particular, understory palms in tropical rainforests can reach high local diversity (e.g., Svenning, 1999; Andersen et al., 2010), often including numerous rare species (Balslev et al., 2010a). The local co-existence of palm species (in 'palm communities') and the mechanisms underlying the assembly and maintenance of this diversity has been the subject of some studies, especially in the Americas (Svenning, 1999, 2001a; Eiserhardt et al., 2011), but much remains to be researched. Other studies have looked at broad-scale palm diversity patterns across the Americas (Bjorholm et al., 2005, 2006, 2008; Svenning et al., 2008). To further our understanding of the processes that govern the assembly of palm communities and sometimes allow the local coexistence of numerous palm species, we here synthesize available information on species diversity and growth-form composition in local palm communities across the Americas. To this end, we establish a growth-form typology for all palm species native to the Americas, analyze the growth-form composition of tropical American palm communities described in the literature, and discuss these patterns in relation to species richness and composition of these communities.

Understanding palm communities is not only of scientific relevance. Local human populations throughout the tropics rely heavily on palm products for their livelihoods (FAO, 1998; de la Torre et al., 2009), and the diversity of palm uses, particularly in rural subsistence societies, is overwhelming (Byg & Balslev, 2006; Byg et al., 2007; de la Torre et al., 2009; Macía et al., 2011) and such uses involve virtually all parts of palms (Balslev & Barfod, 1987; Balslev et al., 2010b). However, only a few palm species have been truly domesticated (in the Americas only *Bactris gasipaes*), in sharp contrast to other major groups of useful plants such as Poaceae (Glemin & Bataillon, 2009), and where cultivation occurs it is often extensive and supplements product extraction from the wild (Byg & Balslev, 2006). Consequently, the palm communities harboured in tropical forests are of great importance to humans and their livelihoods. Knowing the spatial structure of palm richness and palm community composition is therefore of direct interest to socio-economic stakeholders, and political decision-makers, enabling them to appraise the amount of palm products potentially available to rural populations or for extraction (Millennium Ecosystem Assessment, 2006). Moreover palm communities are likely to change, both as a consequence of extraction, land-use change and global warming and studying determinants of palm community structure and diversity is therefore far more than an academic exercise (Blach-Overgaard et al., 2009).

Methods

For our review of tropical American palm community structure we gathered published and unpublished accounts of palm communities in the Americas that included a species list based on a census of all palm individuals within one or more plots of known size (Fig. 1). We tabulated a number of descriptive statistics related to the geographic and environmental context (location, biogeographic region, habitat), sampling design (area, extent) and the palm community itself. Based on the locality descriptions, we assigned each study to one of seven broad habitat categories (Table 1). Surveyed area was calculated as the cumulative area of the inventory plots. Study extent was calculated as the maximum distance between two plots, or for studies containing just one plot as $(2\times\text{area})^{0.5}$, i.e., assuming quadratic plot shape. Number of individuals ha^{-1}, number of species, number of genera, and number of tribes (following the taxonomy of Dransfield et al., 2008b) was taken from the original articles or extracted from the species lists. Fisher's α (Fisher et al., 1943) was calculated from the abundance data given in the original publications using the

Fig. 1 Locations of the palm community studies reviewed in this article. Numbers refer to Table 2. The regions indicated are those suggested in Henderson et al. (1995)

Table 1 Habitat Classification Used for the Present Review

Number	Short name	Definition
1	*Terra firme* forest	Non-inundated lowland tropical evergreen forest
2	Floodplain forest	Floodplain in lowland tropical evergreen forest (incl. *restinga* in Peru)
3	Swamp forest	Swamp in lowland tropical evergreen forest (seasonal and aseasonal)
4	White sand forest	Lowland tropical evergreen forest on white sands
5	Deciduous forest	Lowland tropical deciduous forest
6	Lower montane forest	Tropical evergreen forest 500–1,000 ma.s.l.
7	Upper montane forest	Tropical evergreen forest >1,000 ma.s.l.

function *fisher.alpha* of the package *vegan* 1.17-2 (Oksanen et al., 2010) in R 2.10.1 (R Development Core Team, 2010). To test the relationship between palm species richness, area, extent, and the region where the study, we used Standard Least Squares regression analysis in JMP 8.0.1 (SAS institutes) including only main effects. For our review of tropical American palms' branching patterns and growth forms we reviewed the available literature (e.g., Corner, 1966; Dransfield, 1978; Kahn, 1986; de Granville, 1992; Kahn & de Granville, 1992; Borchsenius et al., 1998; Dransfield et al., 2008b; Balslev et al., 2010a) and combined that with the authors' field experience. We also computed the number of species in each growth-form category, percent cespitose species, and number of species with palmate or costapalmate leaves from the species lists.

Species Composition and Turnover

The 789 palm species occurring in the Americas vary substantially in their geographic commonness on continental, regional and local scales (Henderson et al., 1995; Kristiansen et al., 2009), with numerous species being range-restricted. Strong turnover in species composition has been observed at broad scales, i.e., between palm assemblages in 1 × 1° grid cells (Bjorholm et al., 2008). At these scales, dispersal limitation and, to a lesser extent climate, have been shown to determine compositional turnover (Bjorholm et al., 2008). As the mechanisms that determine species distributions and compositional turnover are highly dependent on geographic scale of investigation, including both extent and grain size (Whittaker et al., 2001; Pearson & Dawson, 2003; Eiserhardt et al., 2011), the relevant mechanisms for the species composition of local palm communities are not necessarily the same as those for larger geographic scales. However, explaining compositional turnover has been the focus of various community studies identifying a variety of determinants, including soil, topography, hydrology, forest structure, dispersal limitation, and historical factors.

Palm species composition has been found to depend on local topography in many settings (Kahn, 1987; Svenning, 1999; Svenning et al., 2009), but not (Vormisto et al., 2004a) or only weakly in other settings (Normand et al., 2006). Relative topographic position can be a good predictor of species composition on a local scale (e.g., Svenning, 1999: extent≈1 km), probably subsuming the effects of a range of more proximal environmental variables, while being of little predictive value on larger scales (e.g., Vormisto et al., 2004b). Interestingly, the topographic preferences of individual species (e.g., for valley bottoms or hill tops), which are directly related to any correlations between species composition and topographical position, appear to vary in geographic space (Vormisto et al., 2004b; Montufar & Pintaud, 2006). This could confirm locality-specific relations between topography and other environmental factors (Vormisto et al., 2004b). On the other hand, it could also reflect regional differences in a species' fundamental or realized niche (Montufar & Pintaud, 2006), due to genetic variation or variation in competition regime. To disentangle these possibilities, and to obtain models of more general predictive ability, future studies should use environmental variables of more proximate (functional) importance rather than indirectly capturing their effects by topographic proxies (Guisan & Zimmermann, 2000). Altitude and aspect influenced the distribution of individual palm species in a lower montane wet forest on the eastern slopes of the Andes in Ecuador (Svenning, 2001b). These findings imply that these variables impact palm community composition, probably by locally modulating climate (topoclimate), i.e., precipitation, temperature and irradiation (Svenning, 2001b).

There is some evidence that soil physicochemical properties may affect palm communities. Differences in chemical and physical soil characteristics have been shown to explain compositional variation on the regional scale (study extent=0.5–550 km) in *terra firme* rainforest in the western Amazon (Vormisto et al., 2004a). However, a similar study located in palaeo-riverine terraces in the western Amazon (extent= 0.3–143 km) found only a weak and insignificant correlation between soil chemistry and palm community composition (Normand et al., 2006).

Hydrology is an important determinant of plant community structure (Silvertown et al., 1999), and also affects palm communities. On a local scale (extent=5–500 m) analysis of palm communities in palaeo-riverine terrace forests in Peru (Normand et al., 2006), soil moisture explained more compositional variation than any other measured environmental variable. It must be noted that only 10–13% of the total compositional variation could be explained in this study, leaving a large fraction to hypothetical unmeasured variables or stochasticity. However, a high turnover of palm community composition along a local scale inundation gradient has also been described from other settings (e.g., Kahn & de Castro, 1985). Soil moisture can vary over short distances between complete water logging and relatively dry conditions (Kahn & de Castro, 1985), depending on topographic position relative to the ground water table, soil drainage qualities, and flooding regime. Moreover, inundation can be either constant (swamp) or seasonal (river flood plains), and when seasonal it can occur at more or less regular intervals. Palm species composition can show a zonation along topographic-hydrological gradients (Kahn & de Castro, 1985), implying that different parts of the inundation gradient provide qualitatively different conditions for palms. Plots situated on non-inundated terraces, and on geographically close floodplains, respectively, were shown to separate clearly in an ordination of compositional similarity (Normand et al., 2006). This is not surprising as plants that occur in seasonally flooded areas have been shown to possess a number of highly specialized adaptations to this habitat (Parolin, 2009).

Composition of palm communities may also depend on forest structure and dynamics. Weak but significant correlations of palm community composition with canopy height (Svenning, 1999) and canopy openness (Normand et al., 2006) have been found on a local scale (extent<1 km). Density and demographic structure of palm populations were shown to be sensitive to disturbance, at least in the form of forest edge conditions (Baez & Balslev, 2007). In that study, disturbance appeared to reduce palm density and the proportion of adult individuals, likely mediated by changes in the overall forest structure. The effects of disturbance were found to differ between species, but none seemed to benefit from forest-edge conditions in that specific setting in forest fragments in lowland western Ecuador (Baez & Balslev, 2007). However, it is known that some palms such as *Desmoncus* spp. (Henderson et al., 1995) or *Chamaedorea* spp. (Svenning, 1998) grow preferentially at forest edges and in disturbed areas. Topography may influence canopy conditions, e.g., via its hydrological effects, and topographic effects on palm species distributions and community composition may also reflect these effects (Svenning, 2001a).

In a study of 21 plots in the western Amazon (extent≈0.5–550 km), Vormisto et al. (2004a) found a strong, logarithmic decay of floristic similarity with geographic distance. Even when environmental variables, including soil and topography, were taken into account, pure spatial distance explained as much as 40% of the compositional variation. Qualitatively similar findings exist for palaeo-riverine terrace forests (extent=0.3–143 km) in the Pastaza fan (Normand et al., 2006). The high pure spatial fraction of explained variation in compositional similarity recovered in these studies is consistent with a prominent role of dispersal limitation (Vormisto et al., 2004a; Normand et al., 2006) on the local to regional scale. It must be noted, however, that spatially auto-correlated environmental factors that are not included in the analysis are always an alternative explanation for this kind of result (e.g., Svenning et al., 2009). Svenning et al. (2009) likewise found apparently non-environmental site effects on palm composition when comparing three sites (extent≈ 350–1,000 m) in a montane forest area. Although the influence of unmeasured ecological determinants could not be ruled out the authors suggest local dispersal limitation as an explanation. This conclusion is supported by the observations that strongly clumped palm species tend to have large-fruits, and that clumping also applies to seedlings. These results support an earlier study showing that palm populations can be strongly clumped (Svenning, 2001b). Palm distributions have also been observed to be limited by rivers (Montufar & Pintaud, 2006). On the other hand, river-aided dispersal processes have been suggested to explain floristic similarities at a regional scale (Normand et al., 2006). It appears that characteristics of dispersal and recruitment play a role on all scales, while being more predictable on larger scales (high correlations between compositional similarity and geographic distance) and increasingly stochastic on smaller scales (much unexplained variation). Interestingly, compositional similarity on the regional scale seems generally to be better explained by environmental factors when based on species presence/absence rather than abundance (e.g., Vormisto et al., 2004b), perhaps indicating mass effects (Kessler, 2000; Svenning, 2001a). If high propagule pressure allows species to grow with low abundances on environmentally sub-optimal sites, floristic differentiation along environmental gradients will be much less pronounced if species presence, rather than abundance, is analysed.

Historical legacies, such as a major vicariance event resulting from the formation of the Iquitos Arch and other geological features in the western Amazon, have been suggested as an explanation for compositional changes between the lower Ucayali region (Peru) and Yasuní (Ecuador) (Montufar & Pintaud, 2006). However, this has neither been tested formally nor favoured over alternative explanations, e.g., differences in soil fertility (Montufar & Pintaud, 2006).

Species Richness

In those palm communities where systematic inventories have been performed (Fig. 1, Table 2), species richness varies strongly (Fig. 2). The lowest species richness (4 spp. in 4 ha) was found in a deciduous forest on the Yucatán peninsula, Mexico (Alvarado and Balslev, unpublished data), and the highest richness (48 spp in 2.8 ha) in the Iquitos-Pebas region, Peru (Vormisto et al., 2004a). Fisher's α varied between 0.39 and 7.77 among the palm communities included in Table 2. This index jointly estimates species richness and equitability (Kempton & Wedderburn, 1978). In our case, Fisher's α correlated strongly with species richness ($r=0.9$), suggesting that differences in diversity were not driven by differences in the abundance distribution, meaning that the amount of rare species increased proportionally with species richness. Thus, we focus the following discussion on species richness.

Sampling area and extent is not equal for the studies reviewed here, providing a potential explanation for the differences in species richness (Fig. 2). The area surveyed (cumulative area of inventory plots) varied by two orders of magnitude, from 0.09 to 7.2 ha (median 0.86). Standard Least Squares analysis of the effects of log(area), log(extent) and study region on recorded species richness ($n=50$ as 15 of 65 studies in Table 1 have no recorded study extent; adj. $r^2=0.59$) showed significant positive effects of area ($P<0.05$) and extent ($P<0.01$). Species richness was significantly higher than average in the Western Amazon ($P<0.001$) and Central Amazon ($P<0.05$) regions, but significantly lower than average in the Caribbean region ($P<0.001$). If extent was removed from analysis in order to maximize sample size ($n=65$; adj. $r^2=0.47$) significant effects were additionally found for location in Central America (positive, $P<0.05$), and the Eastern Amazon (negative; $P<0.05$). An effect of area on species richness is expected because larger areas allow sampling of more individuals, increasing the probability of capturing rare species. Moreover, larger areas can encompass more environmental heterogeneity, leading to higher species richness per se. For the same reasons the geographic extent of the study is expected to have a positive impact on species richness. The geographic extent covered by the evaluated studies varied by three orders of magnitude, ranging from 0.05 to 245 km (median 1.2). At the largest scale a biogeographical effect may even enter onto the study. The impact of extent on species richness is stronger than the impact of area. To ascertain that our results are not confounded by area or extent, we performed a multiple regression of species richness on area and extent (all variables $\log_{10}$-transformed), and used the back-transformed residuals instead of species richness in all below analyses. In all cases this lead to the same patterns, so we discuss results for raw species richness only (Fig. 3).

The abiotic environment is thought to be an important determinant of species richness in general and also specifically for palm communities, with different factors being relevant at different spatial scales (Willis & Whittaker, 2002; Eiserhardt et al.,

Table 2 Diversity and Life form Composition of Tropical American Palm Communities. Density = no. individuals ha^{-1}. Percent Palmate-leaved Species Includes Species with Costapalmate Leaves

#	Locality	Habitat as given in reference	Habitat-type (Table 1)	Study extent [km]	Area surveyed [ha]	Density	No. species	No. genera	No. tribes	Fisher's α	% cespitose spp.	% palmate spp.	Life forms		
													Number of species		
													Large	Large/ Medium	Medium
	Central American Region														
1	San Juan Biological Corridor, Costa Rica	Lowland wet forest (fragments)	1	67	0.4	5,173	26	15	8	–	63	4	3	1	3
2	Fortuna Forest Reserve, Chiriqui Province, Panama	Lower montane forest	7	13	0.4	8,466	24	7	4	3.7	45	0	0	0	0
3	Western Ecuador	Tropical moist forest	1	166	0.5	1,644	17	13	7	3.03	35	0	5	1	3
4	Bosque Protector La Perla, Western Ecuador (79°25′W, 00°01′S)	Evergreen lowland rainforest (fragments)	1	2	1	6,371	12	11	6	1.42	13	0	5	1	2
5	Tutunendo, Western Colombia (76°32′24,4″W, 05°44′41.7″N)	Tropical lowland rainforest	1	–	1.5	2,545	29	18	6	4.27	54	3	4	0	2
6	Angostura, Western Colombia (76°26”0.73”W, 05°17′26″N)	Tropical lowland rainforest	1	–	1	1,429	23	15	5	3.89	45	0	4	0	2
	Caribbean Region														
7	Quintana Roo, Yucatán peninsula, Mexico	Deciduous forest	5	27	4	278	4	4	4	0.39	50	75	1	0	0
8		Semi-evergreen rainforest	5	42	3.8	2,267	5	5	4	0.51	40	80	1	0	1
9		Evergreen rainforest	1	43	4	7,396	9	7	4	0.86	33	33	2	0	2
	Amazon Region (Guyana Shield)														

10	French Guyana, Piste de St. Elie (5°N, 53°W)	Poorly drained *terra firme*	1	0.07	0.3	1,728	13	6	3	2.52	64	0	3	1	0
11		Floodplain	2	0.07	0.3	956	15	7	4	3.59	63	0	5	1	0
12		Well drained *terra firme*	1	0.1	0.5	1,432	14	6	3	2.47	54	0	5	1	0
13		Swamp	3	0.07	0.2	3,338	11	6	3	1.8	70	0	2	1	0
14	Galbao Mts., French Guyana (53°18′W, 03°35′S)	*Terra firme* rainforest	1	1.3	1.3	686	10	6	4	1.59	70	0	2	0	0
15	Waki River valley, French Guyana (53°40′W, 03°19′N)	*Terra firme* rainforest	1	0.06	0.2	2,094	9	6	3	1.66	56	0	3	0	1
16	Surumoni, Venezuela (65°40′19″ W, 03°10′27″N)	*Terra firme*	1	0.14	1	–	7	5	4	–	71	0	2	0	0
17		Flooded forest	2	0.14	1	–	10	7	5	–	70	10	3	0	0
	Amazon Region (eastern)														
18	Pará, Brazil (51°57′W, 07°46′S)	Seasonally dry forest in bottomlands	5	0.23	0.6	798	9	8	4	1.42	44	0	5	0	0
19		Seasonally dry forest in uplands	5	0.15	0.6	187	8	6	4	1.7	50	0	4	0	0
20		Seasonally dry forest in hills	5	0.4	0.6	164	6	5	3	1.22	33	0	4	0	0
21	Pará, Brazil (50°42′W, 06°00′S)	Seasonal swamp forest	3	–	1	3,975	8	7	4	0.96	50	0	5	0	0
22	Lower Tocatins, Pará, Brazil	Seasonal swamp	3	–	0.5	1,875	8	7	4	1.21	50	0	5	0	0
23	Tucuruí, Pará, Brazil	*Terra firme* rainforest	1	–	3.8	897	12	8	4	–	67	0	4	0	1
	Amazon Region (central)														
24	Reserva Ducke, Amazonas, Brazil (60°04′W, 03°08′S)	*Terra firme* rainforest	1	1.4	2	357	26	11	5	5.3	62	4	5	2	2
25	Reserva Ducke, Amazonas, Brazil (59°59′W, 02°55′S)	*Terra firme* rainforest	1	11	7.2	2,358	38	13	5	–	63	5	6	1	1
26	Reserva Ducke, Manaus, Brazil (59°59′W, 02°55′S)	*Terra firme* rainforest	1	–	0.6	668	16	10	5	3.33	43	0	4	1	1
27	Reserva Km 41, Amazonas,	*Terra firme*	1	–	0.3	809	25	10	4	4.25	68	0	5	1	2

Table 2 (continued)

#	Locality	Habitat as given in reference	Habitat-type (Table 1)	Study extent [km]	Area surveyed [ha]	Density	No. species	No. genera	No. tribes	Fisher's α	% cespitose spp.	% palmate spp.	Life forms		
													Number of species		
													Large	Large/ Medium	Medium
	Brazil (60°W, 02°30′S)	rainforest													
28	Reserva Km 41, Amazonas, Brazil	*Terra firme* rainforest	1	–	0.5	102	25	11	4	5.68	72	0	4	1	1
29	Reserva Km 41, Amazonas, Brazil (60°W, 02°30′S)	Stream margins	2	–	0.6	672	26	10	4	6.29	73	0	4	1	1
30	Reserva Km 41, Amazonas, Brazil (59°52′W, 02°24′S)	*Terra firme* rainforest	1	–	0.1	461	22	9	5	3	65	0	4	1	1
31	Reserva Km 41, Amazonas, Brazil (60°W, 02°30′S)	*Terra firme* rainforest	1	–	0.2	–	29	11	5	–	70	0	4	1	1
32	BDFFP plots, Amazonas, Brazil (59°50′W, 02°24′S)	Lowland rainforest fragments	1	–	4.4	5,278	32	11	5	–	71	3	5	1	1
33	Amazonas, Brazil (60° 60.156 W, 02°20.307S)	*Terra firme* rainforest	1	–	0.1	245	27	11	4	7.77	73	0	5	1	1
34	Lower Rio Negro, Amazonas, Brazil	Seasonal swamp	3	0.07	0.2	10,512	7	7	5	0.88	29	14	3	2	0
35	Amazonas, Brazil (60°00′-60°20′W, 02°35′-02°40′S)	*Terra firme*	1	6	0.7	3,231	26	9	4	–	–	0	3	0	1
36		Transitional	1	6	0.2	4,667	10	9	5	–	–	10	3	0	0
37		Floodplain	3	6	0.2	10,513	7	7	5	–	–	14	3	1	0
38	Amazonas, Brazil (04.7877°S, 60.66515°W)	*Terra firme* rainforest	1	131	2.6	–	38	13	6	4.36	66	11	9	1	1
	Amazon Region (western)														
39	Cuyabeno, Ecuador (76°12′W, 00°00′S)	*Terra firme* rainforest	1	0.14	1	5,745	23	14	5	3.2	57	4	7	0	2

40	Yasuní, eastern Ecuador (76°23′W, 00°40′S)	*Terra firme* rainforest	1	1.2	4.7	–	30	16	7	–	57	3	7	2	2
41	Yasuní, eastern Ecuador	*Terra firme* rainforest	1	12	2.5	5,012	33	18	6	4.54	59	0	7	4	2
42	Lower Ucayali river, Peru (73°40′W, 04°55′S)	Floodplain	2	0.09	0.4	703	10	9	5	1.3	50	0	3	2	1
43		Swamp	3	0.14	1	1,184	10	9	5	1.5	50	10	4	1	1
44		‘Bosque de quebrada’	3	0.14	1	238	18	10	5	2.65	67	11	4	1	1
45	Lower Ucayali river, Peru (73°45′W, 04°58′S)	*Terra firme* rainforest	1	–	2	501	47	19	8	7.19	58	6	7	2	3
46	Lower Ucayali river, Peru	Dry white sand forest	4	0.06	0.2	1,585	6	5	5	1.05	83	17	1	0	1
47		Waterlogged white sand forest	4	0.07	0.3	873	23	12	5	3.54	61	9	4	1	1
48	Lower Ucayali river, Peru (73°40′W, 04°55′S)	*Terra firme* rainforest	1	17	1.2	896	43	19	8	5.69	64	5	9	2	2
49	Pastaza river, Peru (76°25′, 03°45′S)	*Restinga* forest	2	7	0.5	3,838	26	16	7	4.25	32	4	7	3	2
50		Floodplain	2	0.5	0.3	10,252	11	8	5	1.45	40	0	5	2	1
51	Urituyacu river, Peru (75°38′-75°49′W, 04°22′-04°44′S)	*Restinga* forest	2	90	2	6,976	27	16	8	3.09	42	7	7	4	1
52		Floodplain	2	0.5	0.3	478	14	12	7	2.32	50	7	4	3	1
53	Upper Huallaga river, Peru (76°26′W, 08°17′S)	Seasonal swamp	3	0.18	1.6	1,716	14	11	6	1.93	57	7	5	1	1
54		Floodplain	2	0.09	0.4	2,938	14	12	8	2.23	38	14	5	2	1
55	Tigre river, Peru (74°45′W, 03°27′S)	*Terra firme* rainforest	1	–	1.5	5,752	38	15	6	5.69	74	3	5	0	2
56	Iquitos-Pebas, Peru	*Terra firme* rainforest	1	220	2.8	4,456	48	19	8	7.27	70	4	7	3	3
57	Upper Ucayali river, Peru	Andean hills	1	113	2	1,622	32	16	7	6.3	63	3	8	2	2
58		*Terra firme* rainforest	1	0.5	0.3	42	18	9	6	2.41	56	6	5	0	2

Table 2 (continued)

#	Locality	Habitat as given in reference	Habitat-type (Table 1)	Study extent [km]	Area surveyed [ha]	Density	No. species	No. genera	No. tribes	Fisher's α	% cespitose spp.	% palmate spp.	Life forms		
													Number of species		
													Large	Large/ Medium	Medium
59		Terrace forest	1	150	3.3	6,756	42	19	8	6.31	64	7	8	2	2
60		Floodplain	2	245	3.3	146	18	10	7	2.89	61	6	5	2	1
	Andean Region														
61	Pereira, Risaralda, Western Colombia	Montane forest	7	0.05	0.1	268	10	6	6	2.05	50	0	1	0	2
62	Western Ecuador	Premontane wet to pluvial forest	6	86	0.2	3,755	15	12	5	2.87	53	0	3	0	1
63	Zamora-Chinchipe, Eastern Equador (79°04′W, 03°58′S)	Montane forest	7	1	1	12,081	7	6	4	0.72	20	0	2	0	3
64	Nangaritza river, SE Ecuador	Lower montane rainforest	6	21	4.8	4,137	25	14	6	2.83	44	0	5	1	4
65	Apolo, Bolivia	Mountain forest	7	40.5	3.8	2,567	16	12	6	1.87	31	0	7	0	3

#	Life forms												
	Number of species					Percentage of individuals							
	Medium Stout Trunks	Small	Acaul. Large	Acaul. Small	Climbing	Large	Large/Medium	Medium	Medium Stout Trunks	Small	Acaul. Large	Acaul. Small	Climbing
1	0	16	0	1	0								
2	0	20	0	0	0								
3	0	8	0	0	0	18	2	22	0	58	0	0	0

4	0	4	0	0	0	36	0	43	0	21	0	0	0
5	0	18	1	1	1	20	0	51	0	28	0	1	0
6	0	14	1	1	0	14	0	37	0	47	1	2	0
7	0	3	0	0	0	19	0	0	0	81	0	0	0
8	0	3	0	0	0	5	0	30	0	66	0	0	0
9	0	4	0	0	1	2	0	6	0	90	0	0	3
10	0	6	1	1	0	51	34	0	0	14	1	0	0
11	0	6	1	1	0	30	7	0	0	13	50	1	0
12	0	5	1	1	0	33	34	0	0	28	3	2	0
13	0	6	1	0	0	58	1	0	0	39	2	0	0
14	0	6	1	1	0	25	0	0	0	47	6	22	0
15	0	3	1	1	0	9	0	0	0	16	68	7	0
16	0	5	0	0	0								
17	0	7	0	0	0								
18	0	3	0	0	1	33	0	0	0	67	0	0	0
19	0	4	0	0	0	43	0	0	0	57	0	0	0
20	0	2	0	0	0	57	0	0	0	43	0	0	0
21	0	2	0	0	0	76	0	0	0	24	0	0	0
22	0	3	0	0	0	92	0	0	0	8	0	0	0
23	0	6	0	0	0	22	0	2	0	76	0	0	0
24	0	14	1	1	1	13	28	3	0	42	12	2	0
25	0	19	4	2	1								
26	0	5	2	0	1	55	21	2	0	11	11	0	0
27	0	14	1	1	1	75	6	2	0	13	3	1	0
28	0	16	1	1	1	10	32	1	0	30	20	6	1
29	0	17	1	1	1	3	32	2	0	53	7	3	1
30	0	11	1	1	1	34	24	5	0	29	6	2	1

Table 2 (continued)

#	Life forms												
	Number of species					Percentage of individuals							
	Medium Stout Trunks	Small	Acaul. Large	Acaul. Small	Climbing	Large	Large/Medium	Medium	Medium Stout Trunks	Small	Acaul. Large	Acaul. Small	Climbing
31	0	14	1	1	1								
32	0	20	2	1	1								
33	0	16	1	1	1	37	22	6	0	30	3	1	0
34	0	2	1	0	0	96	0	0	0	3	1	0	0
35	0	20	2	0	0								
36	0	5	2	0	0								
37	0	2	1	0	0								
38	0	19	2	2	1	26	4	0	0	68	1	1	0
39	0	12	0	1	1	49	0	0	0	47	0	3	0
40	0	12	1	1	3								
41	0	15	1	1	3	48	7	2	0	29	0	15	0
42	0	2	0	1	1	17	68	0	0	10	0	4	0
43	0	2	0	1	1	59	0	10	0	7	0	21	2
44	0	9	1	1	0	43	1	2	0	44	0	10	0
45	0	26	2	1	3	36	3	1	0	53	3	4	0
46	0	3	0	1	0	21	0	5	0	74	0	0	0
47	0	15	1	1	0	39	0	0	0	54	0	6	0
48	0	27	1	1	1	6	0	0	0	90	0	4	0
49	0	11	0	2	1	22	29	8	0	34	0	7	1
50	0	2	0	1	0	43	46	0	0	11	0	0	0
51	0	10	0	1	2	30	54	0	0	13	0	1	0

52	0	5	0	1	0	25	43	5	0	20	0	7	0
53	0	4	0	1	1	50	12	0	0	25	0	12	0
54	0	3	0	1	0	26	54	11	0	3	0	5	0
55	0	23	2	2	4	23	0	2	0	67	2	6	0
56	0	32	0	1	3	33	12	1	0	43	0	10	0
57	0	17	0	1	3	18	1	6	0	73	0	1	1
58	0	10	0	1	0	11	0	3	0	80	0	6	0
59	0	25	0	1	4	10	4	1	0	81	0	4	0
60	0	8	0	1	1	10	23	0	0	66	0	0	1
61	0	7	0	0	0	9	0	29	0	62	0	0	0
62	0	11	0	0	0	35	0	11	0	54	0	0	0
63	0	5	0	0	0	5	0	22	0	73	0	0	0
64	0	13	0	1	1	15	0	46	0	40	0	0	0
65	0	7	0	0	0	73	0	1	0	27	0	0	0

References: **1)** Wang 2008 [two species were only encountered as seedlings and not named. Thus they are omitted in genus/tribe/life form count]; **2)** Andersen et al. 2010 [only understory species surveyed]; **3)** Borchsenius 1997 [seedlings not included]; **4)** Baez and Balslev 2007; **5–6)** Ramírez-Moreno and Galeano 2011; **7–9)** Alvarado & Balslev, unpublished data; **10–13)** Sist 1989b; **14–15)** Kahn and de Granville 1992; **16–17)** Listabarth 1999 [only fertile individuals surveyed]; **18–20)** Salm et al. 2007 [only individuals with visible stem counted for abundance. only dbh >5 cm in *Euterpe precatoria*, *Socratea exorrhiza*; only reproductive genets in *Geonoma baculifera*]; **21)** Scariot et al. 1989; **22)** Kahn and de Granville 1992; **23)** Kahn 1987; Kahn and de Granville 1992; **24)** Cintra et al. 2005 [only fertile individuals surveyed]; **25)** Costa et al. 2009 [only individuals >1 m tall surveyed]; **26)** De Castilho et al. 1998; **27)** Rodrigues 2004; **28)** Ribeiro 2007; **29)** Munari 2005 [only adults surveyed—no further definition of “adult”]; **30)** De Castilho 1998; **31)** De Castilho et al. 1998; **32)** Scariot 1999; **33)** A. De La Torre et al. 2003 [only individuals >0.5 m tall surveyed]; **34)** Kahn and de Granville 1992; **35–37)** Kahn and de Castro 1985; **38)** De Sousa 2007 [only individuals >0.2 m tall surveyed]; **39)** Poulsen et al. 2006; **40)** Svenning 1999 [only individuals with stems >0.1 m and/or leaves >0.5 m surveyed]; **41)** Vormisto et al. 2004a; **42–44)** Kahn and Mejía 1990 [43 and 44: only individuals >1 m tall surveyed]; **45)** Montufar and Pintaud 2006; **46–47)** Kahn and de Granville 1992; **48)** Kahn and Mejía 1991; **49–52)** Normand et al. 2006; **53–54)** Kahn and Mejía 1990; **55)** Montufar and Pintaud 2006; **56)** Vormisto et al. 2004a; **57–60)** Balslev et al. 2010a; **61)** Correa-Gómez and Vargas-Ríos 2009; **62)** Borchsenius 1997 [seedlings not included]; **63)** Svenning et al. 2009; **64)** Byg et al. 2006; **65)** H. Balslev, unpublished data.

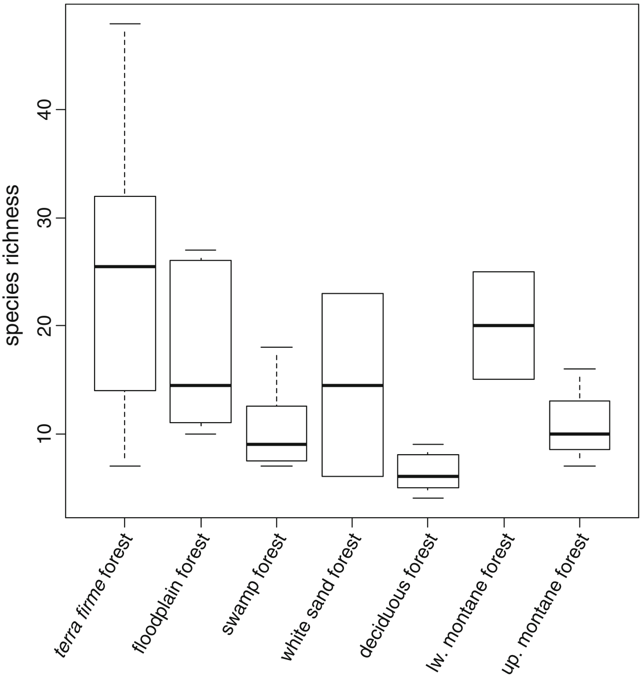

Fig. 2 Palm species richness in eight different habitat types throughout tropical America (Habitat types from Table 1, data from Table 2)

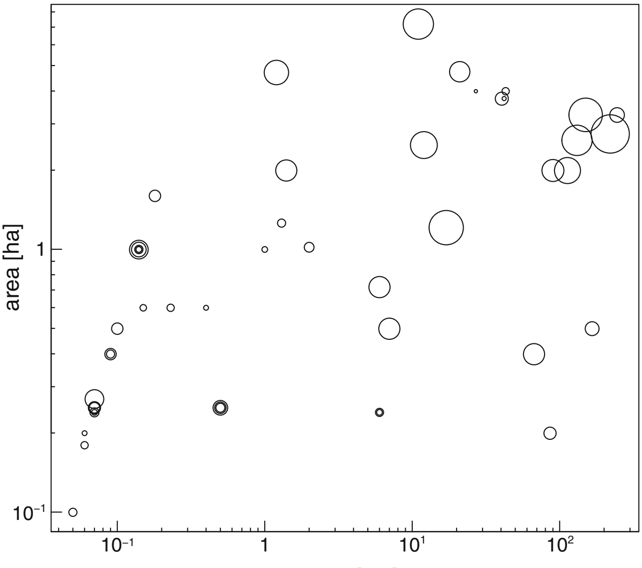

Fig. 3 Species richness of American palms as a function of the two measures of spatial coverage of the study, namely the cumulative area of the inventory plots and the extent covered, i.e., the largest distance between two sample points included in the study (extent). Circle size is proportional to species richness

2011). In palms, four environmental determinants have been shown to be particularly important: climate, soils, hydrology, and topography. All four factors are represented in our definition of habitat. Standard Least Squares analysis including habitat, log (area) and log(extent) as explanatory variables showed that palm species richness in *terra firme* forest was significantly above average ($p<0.05$) whereas deciduous forest had fewer than average species ($p<0.01$).

Continental-scale studies have found water-energy availability to be the most important determinant of palm species richness (Bjorholm et al., 2005, 2006, 2008; Kreft et al., 2006; Svenning et al., 2008). The highest numbers of palms were found in warm and humid climates, confirming the traditional view of the palm family as a wet-tropical element (e.g., Corner, 1966). However, these studies were performed at a coarse spatial resolution ($1\times1°$ grid cells), preventing direct conclusions at the scale of local communities. Species richness in local communities is consistently lower than in the corresponding square degree cell (Fig. 4), indicating that turnover between local communities is an important component of regional richness. Our finding of low richness in deciduous forests indicates that the effect of climate, in particular seasonality, on palm species richness is also relevant at the level of local communities. A high sensitivity of palms to seasonal climate is plausible given their inability to undergo dormancy (Tomlinson, 2006) and their supposed vulnerability to climate extremes because of their single apical meristem (Salm et al., 2007).

To explore the effect of climate on palm communities in more detail, we obtained four climatic variables from the WorldClim global climate database (Hijmans et al., 2005): Mean annual temperature (MAT), minimum temperature of coldest month (MTCM), annual precipitation (AP) and precipitation of the driest month (PDM). Climate values were extracted from the 30 arc second resolution climate layers based on the coordinates of the community studies. This approach is a rough approximation, as coordinates are often derived from coarse locality descriptions, and studies with a large geographic extent are represented by a single point locality. However, the WorldClim dataset is also interpolated, especially in the Amazon (Hijmans et al., 2005), so that better geo-referencing is unlikely to improve the data much; and broad-scale climatic trends should be captured anyway. A model including the four climatic variables, log (area) and log(extent) as explanatory variables showed significant positive effects on species richness of MTCM and PDM ($p<0.01$). These effects have the expected direction, with higher palm richness in warm, wet a-seasonal climates. A possible explanation is that climate does not only impact the number of species co-existing locally, but also the turnover between communities within regions. Svenning et al. (2008) explained the high regional richness of palms at low latitudes with an elevated diversification rate in warm, wet and long-term stable climates. If this diversification involves an increasing habitat specialisation of species, it might impact regional richness independently of local, within-habitat richness.

Soil fertility has been found to be the second most important determinant of regional palm species richness across the Americas, with more species in regions with richer soils (Bjorholm et al., 2006). This factor has also been discussed as a determinant of richness within regions; differences in regional and mean local palm diversity between the Iquitos-Pebas and Yasuní regions (Western Amazon) have been related to differences in overall soil fertility and diversity of soil types (Vormisto et al., 2004a; Montufar & Pintaud, 2006): Species richness is highest in the region with the poorer soils (Iquitos-Pebas), but this region also has a wider variety of soil types (Vormisto et al., 2004a). Within regions, species richness appears likewise to be negatively related to soil fertility (Clark et al., 1995; Vormisto et al., 2004b). On the first glance, this is at odds with the general notion that palms are most species-rich on fertile soils (Svenning, 2001a and references therein; Bjorholm et al., 2006). This discrepancy might be due to differences in spatial and environmental scale, the latter studies referring to a broad inter-habitat scale, while Vormisto et al. (2004a,b) and Clark et al. (1995) analysed differences within the *terra firme* habitat. The relationship between palm richness and soil chemistry clearly deserves further investigation (Eiserhardt et al., 2011).

Hydrology has featured prominently in explanations of species richness differences between palm communities (Kahn & de Granville, 1992). Especially when comparing inundated habitats (floodplains, permanent and seasonal swamps) to non-inundated habitats (*terra firme*) in the Amazon, large richness differences have been observed, with inundated habitats consistently being less species-rich (Kahn & de Castro, 1985; Balslev et al., 1987; Kahn & Mejía, 1990, 1991; Normand et al., 2006). It appears that many palm species are not able to tolerate flooding (Losos, 1995; Pacheco, 2001; cf. Eiserhardt et al., 2011), providing a potential explanation for these differences; however, inundation regime often co-varies with other factors such as soil fertility and disturbance. As expected, non-inundated lowland tropical evergreen forest (*terra firme*) had the highest average richness in our dataset, with a mean of 25.0±11.6 SD (n=34). Highest richness is also reached in this habitat (Vormisto et al., 2004a). In comparison, we found that inundated tropical lowland forest habitats were less diverse, with floodplains having 17.1 species on average (±6.8 SD, n=10) and swamps having a mean species richness of 10.4±3.9 SD (n=8).

Topography does not itself influence species performance and distributions; it rather modulates soil conditions, hydrology, wind exposure, temperature, fog frequency, biotic interactions as well as forest structure and dynamics (Vormisto et al., 2004a; Svenning, 1999, 2001b; Svenning et al., 2009). Thus, it can serve as an indirect predictor subsuming the influence of those environmental factors on palm species richness. How exactly these factors co-vary with relative topographical position might, however, depend on particularities of the place (Vormisto et al., 2004a), making generalizations difficult. Along a similar vein, the relationship between topography and palm species richness might be scale dependent (Eiserhardt et al., 2011). A negative relationship between palm richness and altitude has been shown on a regional scale (Lieberman et al., 1996), while palm richness was found to be positively related to elevation on a local scale (Poulsen et al., 2006). The very low number of montane palm communities in our dataset precluded a sensible analysis of topography relationships; montane palm communities appear to be of intermediate diversity (Fig. 2), but more data is needed to substantiate this idea.

Community-level species richness is thought to depend not only on the local environment, but also on the number of species present in the region (species pool hypothesis; Zobel, 1997). This effect appears to be influential in American palms: local species richness is low in regions with low species richness and local species richness is low or high in regions with high species richness, i.e. there is a triangular rather than a linear relationship between local and regional species richness (Fig. 4). On average, the communities analysed here included 41% of the species present in

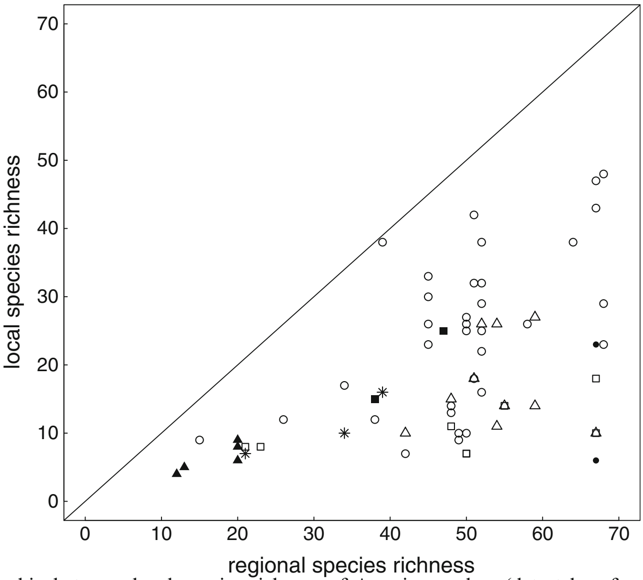

Fig. 4 Relationship between local species richness of American palms (data taken from Table 2) and regional species richness, i.e., the number of species in the 1° grid grid square in which the study site is located (following Bjorholm et al., 2005). Symbols indicate habitat type (Table 1): open circle, *terra firme* forest; open triangle, floodplain forest; open square, swamp forest; solid circle, white sand forest; solid triangle, deciduous forest; solid square, lower montane forest; asterisk, upper montane forest

the corresponding 1 × 1° grid cell (data from Bjorholm et al., 2005). The degree to which local communities sample the regional species pool ranged from 9% to 97%. Values as high as the latter may be due to extremely low regional species pool consisting of a few widespread species or it could be a taxonomic artefact if the species list of the local study uses different taxonomic circumscription than the regional study. The triangular relationship between regional and local species richness (Fig. 4), showing that higher regional richness allows for higher local richness, but does not preclude very species poor communities. Part of this variation can possibly be explained by differences between habitats. Only palm communities in *terra firme* forests attain a high sampling of the regional species pool, while wet habitats (floodplain, swamp) consistently contain a smaller proportion of the species present in the region (Kruskal-Wallis test $P<0.001$). This might reflect either that relatively few palm species are adapted to wet habitats, or that fewer species can coexist under these ecological conditions. However, within each habitat type (disregarding the types represented by <5 community studies) a positive relationship between local and regional species richness can be observed (Fig. 4), indicating a species pool effect. It appears that large-scale biogeographic and evolutionary processes (Bjorholm et al., 2006, 2008; Svenning et al., 2008) affect local palm richness through the regional species pool, while the degree of sampling of this pool is related to habitat differences. As a consequence, the number of species even in the richest palm communities included in this review does not exceed 6% of the total palm flora of the Americas.

Branching Patterns

Only three growth models (sensu Hallé et al., 1978) are found in palms out the total of 23 models that have been described for higher plants. All three models are represented in the American palm flora: Corner's model, in which basal axillary branching is absent, Tomlinson's model, in which basal axillary buds develop into new axes, and Schoute's model, in which the stem branches dichotomously. Upper axillary buds always produce inflorescences (Henderson, 2002); hapaxanthy is absent in American palm genera, except in *Raphia* that is represented by only one species (*R. taedigera*) in tropical America. While Corner's and Tomlinson's models are common in American palms, Schoute's model is only found in few cases, namely *Allagoptera*, *Manicaria*, and *Chamaedorea cataractarum* (Fisher & Zona, 2006; Dransfield et al., 2008b). Another dichotomously branching palm, *Nypa fruticans* (Tomlinson, 1971), is today restricted to the mangroves of Southeast Asia although it was present in the early Tertiary of the Americas (Gee, 2001; Gómez-Navarro et al., 2009). Recently, it has been introduced to West Africa and tropical America where it now grows in some estuaries along the Atlantic coast of Central America (Duke, 1991) and in French Guiana.

We use the term "solitary" to describe species that do not branch basally, and we use the term "cespitose" in a broad sense to describe species that do branch basally. Basal branching produces a number of reproductive axes in space and time. In some species, axes separate by rooting and fragmentation (e.g., *Geonoma baculifera*). The ability to branch basally is differently expressed from one species to another. A cespitose species will produce either a multistemmed palm (e.g., *Astrocaryum jauari, Euterpe oleracea, Oenocarpus mapora, Syagrus stratincola*), or a single stemmed palm with several basal suckers (e.g., *Astrocaryum ulei, Bactris simplicifrons, Oenocarpus minor, Wettinia augusta*), or a single stemmed palm without apparent branching at the base (e.g., *Geonoma brongniartii*, *G. macrostachys*, *Phytelephas macrocarpa*). In the latter case the palm maintains its ability to branch basally. Several stoloniferous species branch profusely at the base and form clumps of many axes (e.g., *Bactris barronis, B. bidentula, B. brongniartii, B. coloniata, B. concinna, B. guineensis, B. hatschbachii, B. major, B. martiana, B. riparia, Geonoma baculifera, Lepidocaryum tenue*). Among tropical American palms about two thirds are solitary and one third of the species are cespitose and less than 1% branch dichotomously (Table 3). The cespitose habit may be dominant or variable among the species in a genus (Table 4). In a given cespitose species, a variable proportion of individuals may nevertheless be solitary (Table 5).

Growth Forms

Growth form is the morphological and physiological response of a plant species to ecological constraints (Corner, 1966; Dransfield, 1978; de Granville, 1992; Kahn & de Granville, 1992; Henderson, 2002). Below we describe eight growth forms found in tropical American palms, and we assign the 789 native American palm species in 67 genera to them. Of the species 494 are from South-America and 361 from Central America, the Caribbean and North America (Henderson et al., 1995; Govaerts & Dransfield, 2005; Pintaud et al., 2008; Galeano & Bernal, 2010; Lorenzi et al., 2010). Within each growth form, the species are classified as either solitary or cespitose. Further divisions are largely based on the maximun size of the leaves, absence or presence of an aerial stem, and length and diameter of the aerial stem. While we emphasize maximum values for this classification, we note that several species reach different maximum sizes in different parts of their geographic range. For instance, *Socratea exorrhiza*, *Oenocarpus bacaba* and *Astrocaryum rodriguesii* are usually larger in the eastern Amazon basin and the Guianas than they are in the central Amazon basin, and *Iriartea deltoidea* is usually larger in the western Amazon lowlands than it is in the Andean foothills. In open areas, Large tall-stemmed Palms usually produce shorter stems than they do in closed forest. Similar variation is found in palms with medium-sized leaves and stems; in open areas on poor soils they grow as small stemmed palms, while they may reach larger size in adjacent forest. An example of this is *Mauritiella armata* in the Amazon basin and *Ceroxylon vogelianum* in wet parts of the central Andes in Peru. The opposite may also be true when small stemmed species such as *Astrocaryum huaimi* and small species of *Mauritiella* grow into medium-sized palms under favorable conditions. The assignment of the American palms to growth form is based on data extracted from a number of publications (Rizzini, 1963; Medeiros-Costa & Panizza, 1983; Zona, 1990; Galeano, 1992; Kahn & de Granville, 1992; Henderson, 1995; Henderson et al., 1995; Borchsenius et al., 1998; Henderson, 2002; Moraes 2004; Borchsenius & Moraes, 2006; Moraes 2007; Pintaud et al., 2008; Galeano & Bernal, 2010; Lorenzi et al., 2010) and several original descriptions recently published of *Butia*, *Calyptrogyne, Chamaedorea*, *Geonoma*, *Lytocaryum* and *Syagrus*. We have had personal communications from L. R. Noblick, J.-C. Pintaud and F. W. Stauffer, and many of the designations are based on the authors' observations in the field. We would like to note, however, that the classification should be seen as preliminary since the morphological variation of many species remains poorly known. We therefore foresee some modifications in the delimitation of the growth forms, and also that a few species may shift to a different growth form when their attributes become better known.

Large Tall-Stemmed Palms

These have tall stems 20–35 m long, and 20–100 cm in diameter and include 102 species in 19 genera (Table 6). *Large tall-stemmed Palms* are mainly defined by their height and stem diameter. Their leaf size varies greatly from one group to another. They occur in all tropical forest ecosystems, in Andean vegetation at high elevation,

Table 3 Number of Solitary and Cespitose Palm Species in Tropical America. Dichotomous Branching was Observed in Rare Cases in the Three Species

Species	% Species	Branching
521	66	Solitary
268	34	Cespitose
3	>1	Dichotomous
789	789	**Total**

Table 4 The Tropical American Palm Genera Divided According to their Branching Patterns and Prevalence of Cespitose Species Compared to Total Number of Species

Genera in which all species are solitary	*Acrocomia* 6, *Aphandra* 1, *Asterogyne* 5, *Attalea* 64, *Barcella* 1, *Calyptrogyne* 16, *Calyptronema* 3, *Ceroxylon* 12, *Coccothrinax* 50, *Colpothrinax* 3, *Copernicia* 21, *Elaeis* 1, *Gastrococcos* 1, *Gaussia* 5, *Hemithrinax* 3, *Hexopetion* 2, *Iriartea* 1, *Itaya* 1, *Jubaea* 1, *Leucothrinax* 1, *Lytocaryum* 4, *Mauritia* 2, *Neonicholsonia* 1, *Parajubaea* 3, *Pseudophoenix* 4, *Roystonea* 10, *Sabal* 16, *Schippia* 1, *Thrinax* 3, *Washingtonia* 2, *Welfia* 1
Genera with varying number of cespitose species (cespitose/total)	*Aiphanes* 11/30, *Allagoptera* 1/5, *Astrocaryum* 13/40, *Brahea* 3/10, *Butia* 2/17, *Chamaedorea* 20/108, *Chelyocarpus* 1/4, *Cryosophila* 2/10, *Dictyocaryum* 1/3, *Euterpe* 5/7, *Geonoma* 56/82, *Hyospathe* 4/6, *Leopoldinia* 2/3, *Manicaria* 1/2, *Oenocarpus* 3/9, *Pholidostachys* 1/4, *Phytelephas* 1/5, *Prestoea* 9/10, *Reinhardtia* 4/6, *Socratea* 1/4, *Syagrus* 17/51, *Synechanthus* 1/2, *Trithrinax* 3/4, *Wettinia* 4/21
Monotypic cespitose genera	*Acoelorrhaphe*, *Ammandra, Lepidocaryum, Raphia, Rhapidophyllum, Serenoa, Wendlandiella, Zombia*
Genera with mostly cespitose species	*Bactris* 76, *Desmoncus* 12, *Iriartella* 2, *Mauritiella* 4

and in savannas and open areas. In lowland *terra firme* forest, adult individuals of large palms are commonly found in low density, while the number of seedlings and juveniles is high in the understory. *Large tall-stemmed Palms* juveniles represented 18% of the palm individuals in the 1–10 m stratum in an eastern Amazonian forest, 13% in a central Amazonian forest, and 4% and 18% in two western Amazonian forests; seedlings of large palms represented 13–55% of all palm seedlings in the 0–1 m stratum in the same forests (Kahn & de Granville, 1992). The most common

Table 5 Frequency of Cespitose Individuals in a Number of Palm Species in the Amazon Basin. In those Species, Clumps of 2–4 Axes are the Most Frequent (87%) (Based on Kahn & de Granville, 1992)

Species (synonym)	% cespitose individuals
Astrocaryum carnosum	43
Astrocaryum gynacanthum	38
Bactris elegans	79
Bactris humilis (=*B. acanthocarpa*)	19
Bactris sphaeocarpa	71
Bactris monticola (=*B. maraja*)	40
Geonoma deversa	81
Geonoma maxima	81
Geonoma piscicauda (=*G. stricta*)	29
Oenocarpus mapora	49
Oenocarpus minor	21
Wettinia augusta	26

species of *Large tall-stemmed Palms* are *Attalea maripa, Astrocaryum chambira, Iriartea deltoidea*, *Oenocarpus bacaba* and *O. bataua*. *Socratea exorrhiza* is a *Large tall-stemmed Palm* species that is usually found in gaps between large trees and may behave as a pioneer species. However, this species is associated with old-growth forest in some places (Svenning et al., 2004). On patches of poorly-drained sandy soils (podzol) found on *terra firme* slopes and plateaus, the density of *Large tall-stemmed Palms* is higher than on well-drained clay soils; the common species is *Oenocarpus bataua*. Large cespitose palms are usually in low density in *terra firme* forests.

The canopy of swamp forests is mainly composed of *Large tall-stemmed Palms*. The cespitose *Euterpe oleracea* forms dense stands in coastal swamps under tidal influence in the Amazon estuary (Anderson, 1988) as well as in the Orinoco delta (González Boscán, 1987). *Mauritia flexuosa* is the dominant species in permanent swampy vegetation in the western Amazon basin (Gonzáles Rivadeneyra, 1971; Salazar & Roessl, 1977; Urrego Giraldo, 1987; Kahn & de Granville, 1992). In seasonal swamps in the eastern Amazon basin the *Large tall-stemmed Palms* are *Attalea maripa*, *A. speciosa* (babassu), *Oenocarpus distichus*, *Socratea exorrhiza* (Scariot et al., 1989; Kahn & de Granville, 1992), and *Euterpe oleracea* is also frequent (Oldeman, 1969; Ricci, 1990); in the central and western Amazon basin, several *Large Palm* species grow together, such as *Mauritia flexuosa, Oenocarpus bataua*, and *Euterpe precatoria* (Kahn, 1988a; de Castro, 1993; Miranda et al., 2008). Juveniles of *Large tall-stemmed Palms* represented almost 40% of the palm community in the 1–10 m stratum in seasonal swamp forests, and 51% in a permanently flooded swamp forest (Kahn & de Granville, 1992).

Large tall-stemmed Palms are also found in forests on alluvial soils subject to annual flooding; the most frequent species there are *Attalea phalerata*, *Euterpe precatoria* and *Socratea exorrhiza*.

Astrocaryum jauari, a cespitose *Large tall-stemmed Palm* is found throughout the Amazon and Orinoco basins in riparian forests that are flooded several months each year; here, it may form dense stands along black-water rivers (Rio Negro in Brazil and Venezuela, Río Nanay in Peru).

Large tall-stemmed Palms are frequent in the canopy of cloud forests on Andean slopes and form dense stands on steep and sharp ridges (*Dictyocaryum lamarckianum, Iriartea deltoidea*). In the Andean vegetatio*n*. *Large tall-stemmed Palms* are present at high elevation (1,800–3,000 m), represented by two genera, *Ceroxylon* and *Parajubaea*.

In all humid tropical regions, there are *Large tall-stemmed Palms* that colonize open areas. They may behave as invaders, where deforestation is very intensive such as in the case of babassu, *Attalea speciosa*, and inajá, *A. maripa*, in the Amazon basin in Brazil. Some economically important *Large tall-stemmed Palms* may become very abundant locally when they are protected by humans, such as in the case of *Astrocaryum aculeatum* and *Euterpe oleracea* in Manaus and Belem, respectively (Anderson, 1988; Moussa & Kahn, 1997) or *Parajubaea cocoides* in Quito (Moraes & Henderson, 1990).

In savannas at the periphery of the Amazon basin, several Amazonian *Large tall-stemmed Palms* dominate the landscape, for instance several species of *Attalea* on drained soils and *Mauritia flexuosa* along streams. *Mauritia carana* is a large palm

Table 6 Growth forms in South American palm genera and species

Acoelorrhaphe (*CNAm*)—**Small Palms:** *A. wrightii (c)*

Acrocomia**—Large tall-stemmed Palms:** *SAm/CNAm—A. aculeata, A. totai*; **Medium/Small Palms with Stout Stems:** *SAm—A. intumescens*; *CNAm—A. crispa;* **Small Palms:** *SAm—A. glaucescens* (sometimes found as Medium-sized palms); **Small acaulescent Palms:** *SAm—Acrocomia emensis, A. hassleri.*

Aiphanes—**Medium-sized Palms:** *SAm—A. grandis, A. leiostachys (c), A. linearis (c), A. pilaris, A. verrucosa*; *CNAm—A. minima*; **Small Palms:** *SAm—A. bicornis, A. buenaventurae*, *A. chiribogensis, A. concinna (c)*, *A. deltoidea (c), A. duquei, A. eggersii (c), A. erinacea (c), A. gelatinosa (c), A. graminifolia (c), A. horrida, A. killipii, A. lindeniana, A. macroloba (c), A. multiplex, A. parvifolia, A. simplex (c), A. stergiosii, A. tricuspidata, A. ulei*, *A. weberbaueri*; *SAm/CNAM—A. hirsuta (c)*; **Small acaulescent Palms:** *SAm—A. acaulis, A. spicata.*

Allagoptera (*SAm*)—**Small Palms:** *A. arenaria (c, p), A. caudescens, A. leucocalyx*; **Small acaulescent Palms:** *A. brevicalyx, A. campestris.*

Ammandra (*SAm*)—**Large-leaved medium–short-stemmed Palms:** *A. decasperma (c, p).*

Aphandra (*SAm*)—**Large-leaved medium–short-stemmed Palms:** *A. natalia.*

Asterogyne—**Small Palms:** *SAm—A. guianensis, A. ramosa, A. spicata, A. yaracuyense*; *SAm/CNAm—A. martiana (p).*

Astrocaryum—**Large tall-stemmed Palms:** *SAm—A. aculeatum, A. chambira, A. jauari (c), A. rodriguesii*; *SAm/CNAm—A. standleyanum*; *CNAm—A. confertum*; **Large-leaved medium–short-stemmed Palms:** *SAm—A aculeatissimum (c), A. carnosum (c), A. chonta, A. cuatrecasanum, A. faranae (c), A. farinosum, A. ferrugineum, A. giganteum, A. gratum, A. huicungo (c), A. javarense, A. macrocalyx, A. murumuru (c), A. perangustatum, A. sciophilum, A. scopatum (c), A. vulgare (c), A. triandrum, A. ulei (c), A. urostachys (c)*; **Small Palms:** *SAm—A. echinatum, A. gynacanthum (c), A. huaimi (c), A. minus*; **Large acaulescent Palms:** *SAm—A. acaule, A. ciliatum, A malybo, A. paramaca, A. sociale*; **Small acaulescent Palms:** *SAm—A. arenarium, A. campestre (c), A. kewense, A. pygmaeum, A. weddellii.*

Attalea—**Large tall-stemmed Palms:** *SAm—A. anisitsiana, A. apoda, A. bassleriana, A. brasiliensis, A. brejinhoensis, A. burretiana, A. butyracea, A. cephalotes, A. colenda, A. compta, A. dahlgreniana, A. dubia, A. eichleri, A. funifera, A. kewensis, A. macrocarpa, A. macrolepis, A. maracaibensis, A. maripa, A. moorei, A. oleifera, A. peruviana, A. phalerata, A. pindobassu, A. plowmanii, A. princeps, A. salazarii, A. seabrensis, A. salvadorensis, A. septuagenata, A. speciosa, A. tessmannii, A. weberbaueri, A. wesselsboeri*; *SAm/ CNAm—A. cohune, A. osmantha*; *CNAm—A. guacuyule, A. crassispatha, A. liebmannii, A. lundellii, A. rostrata*; **Large acaulescent Palms:** *SAm—A. amygdalina, A. attaleoides, A. barreirensis, A. camopiensis, A. cuatrecasana, A. degranvillei, A. exigua, A. ferruginea, A. geraensis, A. guianensis, A. guaranatica, A. humilis, A. insignis, A. luetzelburgii, A. maripensis, A. microcarpa, A. nucifera, A. polysticha, A. sagotii, A. spectabilis, A. vitrivir*; *SAm/CNAm—A. allenii*; *CNAm—A. iguadummat.*

Bactris—**Medium-sized Palms:** *Sam/CNAm—B. gasipaes (c)*; **Small Palms:** *SAm—B. acanthocarpa (c), B. acanthocarpoides (c), B. aubletiana (c), B. bahiensis (c), B. balanophora (c), B. bidentula (c), B. bifida (c), B. brongniartii (c), B. campestris (c), B. caryotifolia (c), B. chaveziae (c), B. concinna (c), B. constanciae (c), B. corossilla (c), B. cuspidata (c), B. elegans (c), B. faucium (c), B. ferruginea (c), B. fissifrons (c), B. glassmanii (c), B. glaucescens (c), B. halmoorei (c), B. hatschbachii (c), B. hirta (c), B. horridispatha (c), B. killipii (c)*, *B. macroacantha (c), B. martiana (c), B. nancibaensis (c), B. oligocarpa (c). B. oligoclada (c), B. pickelii (c), B. pliniana (c), B. ptariana (c), B. raphidacantha (c), B. riparia (c), B. rostrata (c), B. schultesii (c), B. setiflora (c), B. setosa (c), B. setulosa (c)*, *B. simplicifrons (c), B. soeiroana (c), B. sphaerocarpa (c), B. syagroides (c), B. tefensis (c), B. timbuiensis (c), B. tomentosa (c), B. turbinocarpa (c), B. vulgaris (c)*; *SAm/CNAm—B. barronis (c), B. coloniata (c), B. coloradonis (c), B. glandulosa (c), B. guineensis (c), B. hondurensis (c), B. major (c), B. maraja (c), B. pilosa (c)*; *CNAm—B. ana-juliae (c), B. caudata (c), B. charnleyae (c), B. cubensis (c), B. dianeura (c), B. gracilior (c), B. grayumi (c), B. herrerana (c), B. jamaicana (c), B. kunorum (c), B. longiseta (c), B. mexicana (c), B, militaris (c), B. panamensis (c), B. plumeriana (c)*; **Small acaulescent Palms:** *SAm—B. gastoniana (c).*

Barcella (*SAm*)—**Small acaulescent Palms:** *B. odora.*

Brahea (*CNAm*)—**Medium-sized Palms** (sometimes, small stemmed palms): *B. aculeatea, B. decumbens (c, p), B. dulcis (c), B. calcarea (c), B. pimo, B. sarukhanii*; **Medium/Small Palms with Stout Stems:—**

Table 6 (continued)

B. armata, B. brandegeei, B. edulis, B. moorei.

Butia (*SAm*)—**Medium/Small Palms with Stout Stems:** *B. archeri, B. capitata, B. catinarensis, B. eriospatha, B. lallemantii (c)*, *B. lepidotispatha, B. matogrossensis, B. odorata, B. paraguayensis, B. pubispatha, B. purpurascens, B. yatay*; **Small acaulescent Palms:** *B. campicola (c), B. exospadix, B. leptospatha, B. marmorii, B. microspadix.*

Calyptrogyne—**Small Palms:** *SAm—C. baudensis*; *SAm/CNAm—C. costatifrons*; *CNAm—C. allenii, C. anomala (p), C. deneversii*, *C. kunorum (p), C. sanblasensis*, *C. osensis, C. tutensis*; **Small acaulescent Palms:** *CNAm—C. coloradensis*, *C. condensata, C. ghiesbreghtiana, C. herrerae, C. panamensis*, *C. pubescens, C. trichostachys.*

Calyptronema (*CNAm*)—**Medium-sized Palms:** *C. occidentalis, C. plumeriana, C. rivalis.*

Ceroxylon (*SAm*)—**Large tall-stemmed Palms:** *C. alpinum, C. amazonicum, C. ceriferum, C. echinulatum, C. quindiuense, C. sasaimae, C. ventricosum*; **Medium-sized Palms:** *C. parvifrons, C. parvum, C. vogelianum*, C. weberbaueri.* (**C. vogelianum* also grows as a small palm with slender stem).

Chamaedorea—**Small Palms:**. *SAm—C. angustisecta, C. christinae, C. fragrans (c), C. linearis (p), C. pauciflora, C. ricardoi*; *SAm/CNAm—C. allenii (p), C. deneversiana (p), C. pinnatifrons (p), C. pygmaea, C. sullivaniorum (p), C. tepejilote (c), C. warscewiczii (p), C. woodsoniana*; *CNAm—C. adscendens, C. alternans (c, p), C. amabilis, C. anemophila, C. arenbergiana (p), C. atrovirens (c), C. benziei (p), C. binderi, C. brachyclada (p), C. brachypoda (c), C. carchensis (p), C. castillo-montii (p), C. cataractarum (c), C. chazdoniae (p), C. correae (p), C. costaricana (c), C. crucensis, C. dammeriana (p), C. deckeriana (p), C. elegans, C. ernesti-augustii, C. falcifera, C. foveata, C. frondosa, C. geonomiformis, C. glaucifolia, C. graminifolia (c), C. guntheriana (p), C. hodelii, C. hooperiana (c), C. ibarrae, C. incrustata, C. keelerorum, C. klotzschiana, C. lehmannii, C. liebmannii, C. lucidifrons, C. macrospadix (p), C. matae (p), C. metallica, C. microphylla, C. microspadix (c), C. minima (p), C. moliniana, C. murriensis (c), C. nationsiana, C. neurochlamys, C. nubium (c), C. oblongata (p), C. oreophila, C. pachecoana (p), C. palmeriana, C. parvifolia, C. parvisecta, C. pedunculata (p), C. piscifolia, C. pittieri, C. plumosa, C. pochutlensis (c), C. ponderosa, C. pumila (p), C. queroana (p), C. quezalteca (c), C. radicalis, C. recurvata, C. rhizomatosa (c), C. rigida (p), C. robertii (p), C. rojasiana, C. rosibeliae, C. rossteniorum, C. sartorii, C. scheryi (p), C. schiedeana, C. schippii (c), C. seifrizii (c), C. serpens, C. simplex (p), C. skutchii (c), C. stenocarpa (p), C. stolonifera (c, p), C. stricta, C. subjectifolia, C. tenella, C. tenerrima (p), C. thuerckheimii (p), C. undatifolia (p), C. verapazensis, C. verecunda (p), C. volcanensis, C. vulgata, C. whitelockiana, C. zamorae*; **Climbing Palms:** *CNAm—C. elatior (c).*

Chelyocarpus (*SAm*)—**Small Palms:** *C. chuco (c), C. dianeurus*, *C. repens (p), C. ulei.*

Coccothrinax (*CNAm**)—**Medium-sized Palms (sometimes, Small Palms):** *C. argentata, C. barbadensis, C. borhidiana, C camagueyana, C. clarensis, C. crinita, C. fragrans, C. garciana, C. gracilis, C. guantanamensis, C. gundlachii, C. hiorami, C. jamaicensis, C. littoralis, C. microphylla, C. muricata, C. pauciramosa, C. proctorii, C. pseudorigida, C. readii*; **Medium/Small Palms with Stout Stems:** *C. spissa*; **Small Palms:** *C. acunana, C. alexandri, C. argentea, C. baracoensis, C. bermudezii, C. boschiana, C. concolor, C. cupularis, C. ekmanii, C. elegans, C. fagildei, C. inaguensis, C. leonis, C. macroglossa, C. miraguama, C. moaensis, C. montana, C. munizii, C. nipensis, C. orientalis, C. pumila, C. rigida, C. salvatoris, C. saxicola, C. scoparia, C. trinitensis, C. victorini, C. yuquensis, C. yuraguana. (*C. barbadensis is also present in Trinidad).*

Colpothrinax (*CNAm*)—**Large tall-stemmed Palms:** *C. cookii*; **Medium/Small Palms with Stout Stems:** C. *aphanopetala, C. wrightii.*

Copernicia—**Large tall-stemmed Palms:** *SAm—C. alba; CNAm—C. baileyana, C. fallaensis, C. gigas, C. longiglossa, C. rigida*; **Medium-sized Palms:** *SAm—C. prunifera, C. tectorum*; *CNAm—C. berteronea, C. brittonorum, C. cowellii, C. ekmanii, C. glabrescens, C. macroglossa*; **Medium/Small Palms with Stout Stems:** *CNAm—C. hospita, C. curbeloi, C. curtissii, C. humicola, C. molineti, C. roigii, C. yarey.*

Cryosophila—**Medium-sized Palms:** *CNAm—C. cookii, C. warscewiczii*; **Small Palms:** *SAm—C. macrocarpa*; *SAm/CNAm—C. kalbreyeri*; *CNAm—C. bartletii (c), C. grayumii (c), C. guagara, C. nana, C. stauracantha, C. williamsii.*

Desmoncus—**Climbing Palms:** *SAm—D. cirrhiferus (c), D. giganteus (c), D. mitis (c), D. phoenicocarpus (c), D. polyacanthos (c)*; *SAm/CNAm—D. orthacanthos (c)*; *CNAm—D. anomalus (c), D. chinantlensis (c), D. costaricensis (c), D. isthmius (c), D. schippii (c).* **Small palms:** *D. stans (c).*

Table 6 (continued)

Dictyocaryum (*SAm*)—**Large tall-stemmed Palms:** *D. fuscum, D. lamarckianum, D. ptarianum (c).*

Elaeis (*SAm/CNAm*)—**Large-leaved medium–short-stemmed Palms:** *E. oleifera (p).*

Euterpe—**Large tall-stemmed Palms:** *SAm—E. oleracea (c)*; *SAm/CNAm—E. precatoria*; **Medium-sized Palms:** *SAm—E. catinga (c), E. edulis, E. longebracteata (c)*; *CNAm*—E. broadwayi (c)*; **Small Palms:** *SAm—E. luminosa (c). (*E, broadwayi is also present in Trinidad).*

***Gastrococcus (CNAm)*—Medium/Small Palms with Stout Stems:** *G. crispa.*

Gaussia (*CNAm*)—**Medium-sized Palms:** *G. attenuata, G. gomez-pompae, G. maya, G. princeps, G. spirituana.*

Geonoma—**Small Palms:** *SAm—G. appuniana (c), G. aspidiifolia (c), G. awensis (c), G. baculifera (c), G. blanchetiana (c), G. bondariana, G. brevispatha (c), G. brongniartii (c), G. calyptrogynoidea (c), G. camana, G. chlamydostachys, G. conduruensis (c), G. ecuadorensis, G. elegans (c), G. euspatha (c), G. frontinensis, G. fusca (c), G. gamiova (c), G. gastoniana, G. hollinensis (c), G. irena (c, p), G. lanata (c), laxiflora (c), G. leptospadix (c), G. linearis (c), G. littoralis, G. longepedunculata (p), G. maxima (c), G. meridonialis (c), G. megalospatha, G. multisecta, G. occidentalis (c), G. oldemanii (c), G. oligoclona (c), G. paradoxa, G. paraguanensis (p), G. pauciflora (c), G. pinnatifrons, G. platybothros (c), G. poeppigiana, G. pohliana (c), G. procumbens (c), G. pulcherrima (c), G. pycnostachys (c), G. ramosissima (c), G. rivalis (c), G. rubescens, G. santanderensis (c), G. schottiana (c), G. simplicifrons (c), G. skovii, G. spinescens (c), G. stricta (c), G. supracostata, G. telesana (c), G. tenuissima (c), G. triglochin (c, p), G. trigona, G. umbraculiformis, G. vaga (c), G. wilsonii (c)*; *SAm/CNAm—G. chococola, G. concinna (c), G. cuneata (c), G. deversa (c), G. divisa (c), G. ferruginea (c), G. interrupta (c), G. longivaginata (c), G. orbignyana (c, p), G. triandra (c), G. undata*; *CNAm—G. congesta (c), G. epetiolata, G. hugonis (c, p), G. jussieuana, G. monospatha (c), G. mooreana (c), G. scoparia, G. talamancana*; **Small acaulescent Palms:** *SAm—G. atrovirens, G. macrostachys (c).*

Hemithrinax (*CNAm*)—**Medium/Small Palms with Stout Stems:** *H. compacta*; **Small Palms:** *H. ekmaniana, H. rivularis.*

Hexopetion (*CNAm*)—**Small Palms:** *H. alatum, H. mexicanum.*

Hyospathe—**Small Palms:** *SAm—H. frontinensis, H. macrorhachis (p), H. peruviana (c), H. pittieri (c), H. wendlandiana (c)*; *SAm/CNAm—H. elegans (c).*

Iriartea (*SAm/CNAm*)—**Large tall-stemmed Palms:** *I. deltoidea.*

Iriartella (*SAm*)—**Small Palms:** *I. setigera (c), I. stenocarpa (c).*

Itaya (*SAm*)—**Small Palms:** *I. amicorum.*

Jubaea (*SAm*)—**Large tall-stemmed Palms:** *J. chilensis.*

Leopoldinia (*SAm*)—**Small Palms:** *L. major (c), L. piassaba, L. pulchra (c).*

Lepidocaryum (*SAm*)—**Small Palms:** *L. tenue (c).*

Leucothrinax (*CNAm*)—**Medium-sized Palms:** *L. morrisii.*

Lytocaryum (*SAm*)—**Small Palms:** *L. hoehnei, L. insigne, L. weddellianum*; **Small acaulescent Palms:** *SAm—L. itapebiensis.*

Manicaria (*SAm/CNAm*)—**Large-leaved medium–short-stemmed Palms:** *M. martiana (c), M. saccifera.*

Mauritia (*SAm*)—**Large tall-stemmed Palms:** *M. carana, M. flexuosa.*

Mauritiella (*SAm*)—**Medium-sized Palms:** *M. armata (c)*; **Small Palms:** *M. aculeatea (c), M. macroclada (c), M. pumila (c).*

Neonicholsonia (*CNAm*)—**Small acaulescent Palms:** *N. watsonii.*

Oenocarpus—**Large tall-stemmed Palms:** *SAm—O. bacaba, O. distichus*; *SAm/CNAm—O. bataua*; **Medium-sized Palms:** *SAm—O. balickii*; *SAm/CNAm—*O. *mapora (c)*; **Small Palms:** *SAm—O. circumtextus, O. makeru, O. minor (c), O. simplex (c).*

Parajubaea (*SAm*)—**Large tall-stemmed Palms:** *P. cocoides, P.sunkha, P. torallyi.*

Pholidostachys—**Small Palms:** *SAm—P. synanthera*; *SAm/CNAm—P. dactyloides, P. kalbreyeri, P. pulchra (c).*

Phytelephas—**Large-leaved medium–short-stemmed Palms:** *SAm—P. aequatorialis, P. schottii (p), P. tenuicaulis (c), P. tumacana*; *SAm/CNAm—P. macrocarpa (p).*

Table 6 (continued)

Prestoea**—Medium-sized Palms (sometimes Small Palms):** *SAm—P. tenuiramosa (c)*; *SAm/CNAm—P. acuminata (c)*; **Small Palms:** *SAm—P. carderi (c, p), P. pubigera, P. schultzeana (c), P. simplicifolia (c)*; *SAm/CNAm—P. decurrens (c), P. ensiformis (c), P. longepetiolata (c), P. pubens (c),*

Pseudophoenix (*CNAm*)—**Large tall-stemmed Palms:** *P. lediniana, P. vinifera*; **Medium/Small Palms with Stout Stems:** *P. ekmanii, P, sargentii.*

Raphia (*SAm/CNAm*)—**Large-leaved medium–short-stemmed Palms:** *R. taedigera (c).*

Reinhardtia**—Medium-sized Palms (sometimes Small Palms):** *CNAm—R. paiewonsckiana*; **Small Palms:** *SAm/CNAm—R. gracilis (c), R. koschnyana (c), R. simplex (c)*; *CNAm—R. elegans, R. latisecta (c).*

Rhapidophyllum (*CNAm*)—**Small Palms:** *R. hystrix (c, p).*

Roystonea**—Large tall-stemmed Palms:** *SAm/CNAm—R. oleracea*; *CNAm—R. altissima, R. borinquena, R. dunlapiana, R. lenis, R. maisiana, R. princeps, R. regia, R. stellata, R. violacea.*

Sabal**—Large tall-stemmed Palms:** *CNAm—S. guatemalensis, S. maritima, S. mexicana, S. uresana*, *S. yapa*; **Medium-sized Palms:** *SAm/CNAm—Sabal mauritiiformis*; **Medium/Small Palms with Stout Stem:** *CNAm—S. bermudana, S. causiarum, S. domingensis, S. gretherae, S. palmetto, S. pumos, S. rosei*; **Small acaulescent Palms:** *CNAm—S. etonia (p), S. miamiensis, S. minor.*

Schippia (*CNAm*)—**Small Palms:** *S. concolor.*

Serenoa (*CNAm*)—**Small Palms:** *S. repens (c, p).*

Socratea**—Large tall-stemmed Palms:** *SAm—S. hecatonandra, S. rostrata*; *SAm/CNAm—Socratea exorrhiza**; **Medium-sized Palms:** *SAm—S. salazarii* (c)*. (**S. exorrhiza* also grows as a medium-sized palm, *S. salazarii* as a small slender palm).

Syagrus**—Large tall-stemmed Palms:** *SAm—S. romanzoffiana, S. sancona*; **Medium-sized Palms:** *SAm—S. botryophora, S. cearensis (c), S. coronata, S. glaucescens, S. inajai, S. kellyana, S. macrocarpa, S. oleracea, S. picrophylla, S. pseudococos, S. vermicularis*; *CNAm—S. amara*; **Small Palms:** *SAm—S. campylospatha (c), S. cocoides, S. comosa, S. deflexa (c), S. flexuosa (c), S. lorenzoniorum, S. orinocensis (c), S. ruschiana (c), S. schizophylla (c), S. smithii, S. stenopetala, S. stratincola (c), S. yungasensis*; **Small acaulescent Palms:** *SAm—S. allagopteroides, S. angustifolia (c), S. caerulescens, S. cardenasii (c), S. cerqueirana (c), S. duartei, S. evansiana, S. graminifolia, S. gouveiana, S. harleyi (c), S. itacambirana (c), S. lilliputiana, S. loefgrenii, S. longipedunculata, S. microphylla (c), S. mendanhensis, S. minor, S. petraea (c), S. pleioclada, S. pleiocladoides, S. procumbens, S. rupicola, S. vagans (c), S. werdermannii (c).*

Synechanthus**—Small Palms:** *SAm/CNAm—S. warscewiczianus (c)*; *CNAm—S. fibrosus.*

Thrinax (*CNAm*)—**Medium-sized Palms:** *T. excelsa, T. parviflora, T. radiata***.**

Trithrinax (*SAm*)—**Medium/Small Palms with Stout Stems:** *T. acanthocoma, T. brasiliensis (c), T. campestris (c)*; **Medium-sized Palms:** *T. schizophylla (c).*

Washingtonia (*CNAm*)—**Large tall-stemmed Palms:** *W. filifera, W. robusta.*

Welfia (*SAm/CNAm*)—**Medium-sized Palms:** *W. regia.*

Wendlandiella (*SAm*)—**Small Palms:** *W. gracilis (c).*

Wettinia**—Medium-sized Palms:** *SAm—W. anomala, W. castanea, W. disticha, W. fascicularis, W. kalbreyeri (c), W. maynensis, W. microcarpa, W. oxycarpa, W. praemorsa (c), W. quinaria, W. verruculosa*; **Small Palms:** *SAm—W. aequatorialis, W. augusta (c), W. drudei (c), W. hirsuta, W. lanata, W. longipetala, W. minima*; *SAm/CNAm—W. aequalis, W. radiata*; *CNAm—W. panamensis.*

Zombia (*CNAm*)—**Small Palms:** *Z. antillarum (c).*

(c) = cespitose species (see text); solitary species (name not followed with c); *(p)* = prostrate stem; SAm = South American palms (Trinidad included); CNAm = Central, Caribbean and North American palms

in the savannas on waterlogged white sandy soils in the northern Amazon basin. Long narrow stands of *Mauritia flexuosa* follow the streams that drain the Roraima savanna in northern central Brazil and the coastal savanna in the Guianas. The palm flora of the Venezuelan llanos includes several *Large tall-stemmed Palms* such as *Acrocomia aculeatea, Attalea butyracea*, *A. maripa* and *Mauritia flexuosa* (Stauffer, 2007). *Large tall-stemmed Palms* are also found in gallery forests in Brazilian cerrado (*Attalea anisitsiana*, *A. phalerata*, *Syagrus sancona*). In the Pantanal of Brazil and Bolivia *Large tall-stemmed Palms* are found in dry places (*Acrocomia totai, Attalea phalerata, A. eichleri*) whereas *Copernicia alba* grows in wet places; the two latter species also grow in the Chaco of southern Bolivia, northwestern Paraguay, Mato Grosso in Brazil and northern Argentina.

Jubaea chilensis is found in valleys and slopes of Andean foothills at low elevation in seasonally dry regions (Henderson et al., 1995).

Large tall-stemmed Palms in the Central American rain forest belong to the genera *Astrocaryum* (*A. confertum*, *A. standleyanum*) and *Colpothrinax* (*C. cookii*); several species of *Attalea* (e.g., *A. cohune*) are less frequent in forest but common in disturbed places northwards to Mexico. Other large species of *Sabal* and *Washingtonia* are found in Mexico and southern USA (*Sabal guatemalensis, S. mexicanum* in dry lowlands, *S. uresana* in thorn forest and oak forest, *Washingtonia filifera* in desert, *W. robusta* in wet places, near the sea). In the Caribbean Islands *Large tall-stemmed Palms* are represented by *Attalea crassispatha*, a very rare species in Haiti, and *Sabal maritima*, which grows in shrubby vegetation in Cuba and Jamaica.

Large-Leaved Medium–Short-Stemmed Palms

These have stems 1–20 m tall, usually 15–25 cm in diameter*;* when short-stemmed they may be subacaulescent with the stem no more than 1 m long and entirely covered with the sheaths of dead leaves. Their leaves are 4–10 m long in adult palms. This growth form is developed by 31 species in seven genera (Table 6). *Ammandra decasperma* is often acaulescent, but can develop a prostrate stem. Some species are gregarious and form dense and extended patches in non-inundated tropical rain forest understory, such as *Astrocaryum sciophilum* in French Guiana (Sist, 1989a) and Surinam (Van der Steege, 1983), *A. farinosum* in Guyana and northern central Brazil, *Aphandra natalia* in the western Amazon basin in Brazil (Acre), Ecuador and Peru (Borgtoft Pedersen & Balslev, 1990; Boll et al., 2005; Kronborg et al., 2008). *Manicaria saccifera* and several species of *Astrocaryum* grow in seasonal swamp forests, *M. martiana* on waterlogged sandy soils, *Raphia taedigera* occurs only in Atlantic coastal swamps. *Large-leaved medium–short-stemmed Palms* are also well represented in the understory of forests on periodically flooded alluvial soils. For instance, there were 352 individuals of *Astrocaryum carnosum* and 34 of *Phytelephas macrocarpa* (=*P. tenuicaulis*) in the 1–10 m stratum in a 0.4 ha plot in the upper Huallaga valley, Peru (Kahn & Mejía, 1990). In northern Peru and adjacent Ecuador *Aphandra natalia* populations had densities of 44–692 individuals ha^{-1}, and of these 4–17% were adults (Kronborg et al., 2008). Several species of *Large-leaved medium–short-stemmed Palms* (*Aphandra*, most species of *Astrocaryum*) tolerate deforestation and some of them may colonize pastures and open areas (Borgtoft Pedersen & Balslev, 1990; Johnson, 1996). Only one species of *Large-leaved medium–short-stemmed Palms* occurs in Central America (*Phytelephas macrocarpa*) and none is found in the Caribbean islands and North America.

Medium-Sized Palms

These palms have stems 8–15 m long and 12–15 cm in diameter and their leaves are 2–4 m long. *Medium sized Palms* include 95 species in 21 genera (Table 6) and are represented in most ecosystems. In tropical rain forests on *terra firme*, *Medium-sized Palms* occupy intermediate strata (*Oenocarpus balickii*, *Syagrus inajai, Wettinia maynensis*). They are frequently found in Amazonian forests on alluvial soils (*Oenocarpus mapora*), in dry forests (*Syagrus sancona*), in Andean cloud forests (*Euterpe longebracteata*, *Prestoea acuminata*, *P. tenuiramosa*, various species of *Wettinia*), and in the Brazilian coastal forest (*Euterpe edulis*). *Bactris gasipaes* is an example of a cultivated species belonging here. *Medium-sized Palms* also include *Copernicia tectorum* in periodically flooded savannas in Colombia and in the Venezuelan llanos, *Sabal mauritiiformis* in Colombian savannas, *Syagrus coronata* and *S. glaucescens* and *Thrithrinax schizophylla* in Brazilian cerrado, and *Coccothrinax barbadensis* in dry coastal vegetation in Margarita Island and on the Paria Peninsula of Venezuela.

Caribbean and North American *Medium-sized Palms* are found in dry areas (*Brahea aculeatea, B. decumbens*), on coastal sandy soils and open places near the sea (*Coccothrinax borhidiana, C. gracilis, Thrinax radiata*), in woodlands (*Coccothrinax argentata, C. gundlachii, Copernicia brittonorum, Thrinax parviflora*), in dry, deciduous lowlands and open vegetation (*Leucothrinax morrisii*) in rocky places (*Gaussia gomez-pompae, G. maya, Copernicia ekmanii, Thrinax excelsa*), in savannas (*Coccothrinax crinita, C. pauciracemosa, Gaussia princeps, G. spirituana, Copernicia cowelii, C. glabrescens, C. macroglossa*), in wet places (*Calyptronoma occidentalis, C. plumeriana, C. rivalis*), under strong seasonal rain fall (*Gaussia attenuata, G. princeps*), in premontane forest (*Reinhardtia paiewonsckiana*), in pine-oak forest (*Brahea calcarea, B. pimo, B. sarukhanii*), and in somewhat seasonal tropical moist forest (*Cryosophila warscewiczii*).

Medium/Small Palms with Stout Stems

These palms have stems with diameter of 30–60 cm or with the stem diameter significantly enlarged by persistent skirt of dead leaves. *Medium/Small Palms with Stout Stems* include 42 species in 12 genera (Table 6). *Medium/Small Palms with Stout Stems* are found in open vegetation. In South America, *Acrocomia intumescens* grows in the northern region of the Brazilian Atlantic forest on floodplains, and species of *Butia* grow in open cerrado and pampa in southern Brazil, and in Paraguay, Argentina, and Uruguay. Several species of *Butia* develop a very short aerial stout stem (*B. lallemantii, B. lepidotispatha, B. matogrossensis, B. pubispatha*); *Butia lallemantii* forms semi-hemispherical domes about 1 m high in subtropical pampas of Brazil and Uruguay.

Medium/Small Palms with Stout Stems are well-represented in the Caribbean and North American palm floras with species growing in open savannas, sandy and marshy habitats (*Coccothrinax spissa, Colpothrinax wrightii, Copernicia* spp., *Sabal bermudana, S. causiarum, S. gretherae*), on limestone cliffs on rocky outcrops (*Hemithrinax compacta*), on coastal dunes (*Sabal palmetto*), near the sea (*Pseudophoenix sargentii*), in secondary vegetation (*Sabal domingensis*), on dry open hillsides on calcareous soils (*Pseudophoenix ekmanii*), and in desert-like vegetation (*Brahea armata, B. brandegeei*, and *B. edulis*). *Brahea moorei* and *Sabal pumos* are found in the understory of oak woods. *Colpothrinax aphanopetala* grows in wet forest on Caribbean and Pacific slopes in Central America.

Small Palms

These palms have stems 0.1–8 m long and 0.4–12 cm in diameter. *Small Palms* include 423 species in 36 genera (Table 6). They are present in most tropical American ecosystems. In tropical *terra firme* rain forest understory *Small Palms* are particularly frequent with many species in a few genera (*Bactris, Geonoma* and *Hyospathe*), which are found throughout the Amazon basin. The genera *Chelyocarpus, Pholidostachys, Wendlandiella* and some small species of *Syagrus* (*S. smithii*) and *Wettinia* (*W. maynensis*, *W. drudei*) are limited to the western Amazon basin. The genera *Iriartella* and *Oenocarpus* occur in the central (*I. setigera, O. minor*) and western Amazon basin (*I. stenocarpa*, *O. makeru, O. simplex).*

Small Palms include several cespitose species that dominate the understory, e.g., the cespitose *Lepidocaryum tenue* and *Bactris sphaerocarpa*. In a 0.7 ha plot in the lower Ucayali River valley, Peru there are 3,801 stems of the former and 1,237 stems of the latter representing 54% and 18% of the density of the palm community, respectively (Kahn & Mejía, 1991). Along the upper Ucayali river *Lepidocaryum tenue* is superabundant on old terraces where it may have >4,000 ind ha^{-1} (Balslev et al., 2010a). The crowns of small (<6.5 m) palms represent 60–70% of the total cover in those forests (Marmillod, 1982). Understory palms do not tolerate deforestation and disappear with the forest. Small stemmed species of *Bactris* are less diversified in swamp forests and periodically flooded forests on alluvial soils (*B. bifida* forms dense large colonies on these soils), and in forests that are periodically flooded by black waters (*B. maraja* and *B. riparia* are very frequent). *Mauritiella aculeatea*, *M. macroclada, M. pumila* and several species of *Bactris* are found in savannas on waterlogged sandy soils. Species of *Chamaedorea*, *Geonoma*, *Euterpe* (*E. luminosa*), *Prestoea*, and *Wettinia* (*W. augusta*) grow in Andean cloud forest understory. Andean vegetation to 3,000 m includes *Geonoma megalospatha*, *G. orbignyana* and *G. undata* (Borchsenius & Moraes, 2006). In wet forests in the coastal range in Venezuela or in the Andes in Colombia, *Small Palms* belong to the genera *Asterogyne* (*A. racemosa*, *A. spicata*) and *Geonoma* (*G. paraguanensis, G. platybothros, G. simplicifrons* and *G. spinescens*). In the Brazilian coastal forest, *Small Palms* include *Butia eriospatha, Lytocaryum weddellianum*, 11 species of *Bactris* and eight species of *Geonoma*; in the forest of the Pacific slopes of the Andes *Small Palms* include species of *Aiphanes*, *Bactris, Chamaedorea* and *Geonoma*. In periodically flooded savannas in the Amazon, and along the basins southern periphery, *Small Palms* are represented by *Astrocaryum huaimi*, *Bactris campestris, B. glaucescens, Geonoma brevispatha*; in dry forests by *Chamaedorea angustisecta* and *Geonoma occidentalis*; in Venezuelan llanos by *B. campestris*, *B. guineensis*, *B. major* where they grow in open areas (Stauffer, 2007); and finally in cerrado vegetation of central Brazil and bordering countries *Small Palms* include *Astrocaryum echinatum*, *Bactris glaucescens*, and *Geonoma brevispatha*.

Small Palms are well represented in rain forest understory of Central America and Mexico by *Chamaedorea*, which is the most species rich genus in the Americas, *Calyptrogyne, Cryosophila, Hexopetion*, *Reinhardtia* and *Schippia*. *Desmoncus stans*, a small, slightly creeping, often erect palm, grows in rain forest understory in Costa Rica. *Hemithrinax rivularis* grows in wet coastal savannas in Cuba. *Small Palms* of the genus *Coccothrinax*, *Thrinax ekmaniana,* and *Zombia antillarum* are found in dry savannas and in open woods in the Bahamas, Cuba and Hispaniola. Outside the tropics, *Serenoa repens* is found in sandy pine-oak wood understory and *Rhapidophyllum hystrix* grows on calcareous soils in wet areas in deciduous woods in south-eastern USA.

Large Acaulescent Palms

These palms have 4–8 m long leaves and a subterranean stem that never grows above ground. The palm's leaf sheaths and bases of petioles and inflorescence peduncles emerge from the ground (Henderson, 2002). *Large acaulescent Palms* include 28 species in two genera (Table 6) and are commonly found in the Amazon basin. Some species form dense patches on well-drained soils, such as *Astrocaryum paramaca* and various species of *Attalea* in the Guianas. In a forest in the central Amazon basin a total of 674 individuals (1–10 m high) of *Astrocaryum sociale* (444) and *Attalea attaleoides* (232) were counted in a 0.7 ha plot (Kahn & de Granville, 1992). In this region, *Astrocaryum acaule* and *Attalea spectabilis* reach high densities on poorly drained sandy soils. *Astrocaryum malybo* grows in forest west of the Andes in Colombia. Funnel-like crowns of large leaves collect litter falling from trees (de Granville, 1977); they also shelter a diversified fauna in *Astrocaryum paramaca* in French Guiana (Gasc, 1986). A relationship between these *Large acaulescent Palms* with subterranean stems and Amazonian forest structure and dynamics was proposed (Kahn, 1986). *Large acaulescent Palms* (*Attalea barreirensis*) are also found in gallery forests in dry regions of eastern central Brazil. In Central America *Large acaulescent Palms* are represented by two species: *Attalea allenii* grows in lowland rain forests from northwestern Colombia to the Atlantic slope of Panama where *A. inguadummat* also occurs. There are no acaulescent palms with large leaves in Caribbean islands and North America.

Small Acaulescent Palms

In *Small acaulescent Palms* the stem is apparently absent and subterranean or too short to be conspicuous and the leaves are less than 2 m long. *Small acaulescent Palms* include 56 species in 13 genera (Table 6). These palms are found in the understory of lowland *terra firme* forest on clay soils (species of *Aiphanes*, *Bactris, Geonoma, Lytocaryum, Neonicholsonia*) and in periodically flooded forests on alluvial soils (*Geonoma macrostachys*). Acaulescence is frequent in grassland, savanna, and shrub land (Henderson, 2002). *Barcella odora* grows in campina vegetation on waterlogged sandy soils. In open cerrado vegetation in central Brazil there are small acaulescent palms in the genera *Allagoptera* (*A. campestris*, *A. leucocalyx*), *Acrocomia* (*A. emensis, A. hassleri*), *Astrocaryum* (*A. arenarium*, *A. campestris*, *A. kewense*, *A. pygmaeum*, *A. weddellii*), and *Syagrus* (e.g., *S. duartei*, *S. harleyi*, *S. microphylla*, *S. pleioclada*). *Small acaulescent Palms* are also found in *Butia* species in *cerrado* and grasslands, often on sandy soils in southern Brazil and northern Paraguay. Such palms are also present in coastal vegetation of the southern Atlantic coast of Brazil (*Allagoptera arenaria*, *A. brevicalyx*). *Small acaulescent Palms* are adapted to dry conditions (Rawitscher & Rachid, 1946). Outside the tropics, *Sabal etonia* is found on sandy soils in pine-oak wood understory, *Sabal minor* grows on rich alluvial soils in the southern part of the USA. *Sabal miamiensis*, a probably extinct species of this growth form (Zona, 1990), was found on outcrops of oolithic limestone near sea level in southern Florida.

Climbing Palms

These palms have stems unable to grow vertically without support, except in the seedling and juvenile stages. In the Americas *Climbing Palms* include 12 species in two genera (Table 6). Scandence is common in lowland moist forests (Henderson, 2002). The leaf rachis in climbing *Desmoncus* (11 of the 12 species)is prolonged into a cirrus, except in *Desmoncus stans*, which is a small, slightly creeping, often erect palm, interpreted as a neotenic species. *Desmoncus cirrhiferus* is found in the coastal lowlands of Colombia and Ecuador up to 800 m above sea level. The other species of *Desmoncus* are either exclusively Amazonian (*D. giganteus, D. mitis, D. phoenicocarpus*) or widely distributed in tropical America (*D. orthacanthos* and *D. polyacanthos*); the latter species extend from the Brazilian coastal forest to the eastern Andean slopes where they may occur up to elevations of 1,000 m. *Desmoncus costaricensis, D. isthmius*, and *D. chinantlensis* grow in Central America and southeastern Mexico. *Chamaedorea elatior,* the only climbing species in the genus, is found in rain forest on the Atlantic and the Pacific slopes in Mexico, Guatemala and Honduras. *Desmoncus polyacanthos* and *D. orthacanthos* grow in the Brazilian Atlantic forest.

Functional Diversity

The eight palm growth forms described above are differently represented in palm communities, both in terms of species and individuals.

Across all communities, *Small Palms* contribute most species, followed by *Large tall-stemmed Palms*, while the other growth forms are only represented by few species (Fig. 5). The species growth form spectrum (percentage of species in each growth form) is similar to the one found by Balslev et al. (2010a) for palm communities in both inundated and *terra firme* evergreen lowland tropical forest in the upper Ucayali basin, Peru. The species growth-form spectrum within communities clearly reflects the species growth-form spectrum measured across all American palms (Fig. 5, red dots), indicating that geographic commonness does not differ strongly between growth forms. Thus, the species growth-form spectrum of each community can to a certain degree be explained by a random sampling of species from the palm flora of the Americas. However, there are some striking, non-random patterns in the growth-form spectra across all communities and within certain habitats.

Across all communities (Fig. 5a), *Large tall-stemmed Palms* are clearly over-represented (Wilcoxon Signed Rank Test: $P<0.001$), supporting earlier findings that large palms have a comparatively broad range size and ecological niche (Ruokolainen & Vormisto, 2000; Kristiansen et al., 2009). Conversely, *Medium Sized Palms* are clearly under-represented in all habitat types ($P<0.001$), indicating that these palms are either relatively range-restricted or occur preferentially in habitat types that are not well-covered by the community studies analysed here. *Medium/Small Palms with Stout Stems* have not been found in any of the community surveys reviewed here. Interestingly, palms of this growth form are found close to the latitudinal extremes of the distribution of the New World palms, possibly reflecting adaptation to dry-seasonal climates. While the percentage of *Small Palms* species is not different from the percentage in the overall species growth-form spectrum, *Small acaulescent Palms* are under-represented ($P<0.001$). An obvious explanation for the under-representation of medium sized and small acaulescent palms may involve that most of the palm community surveys are from fairly closed tall forest, where these

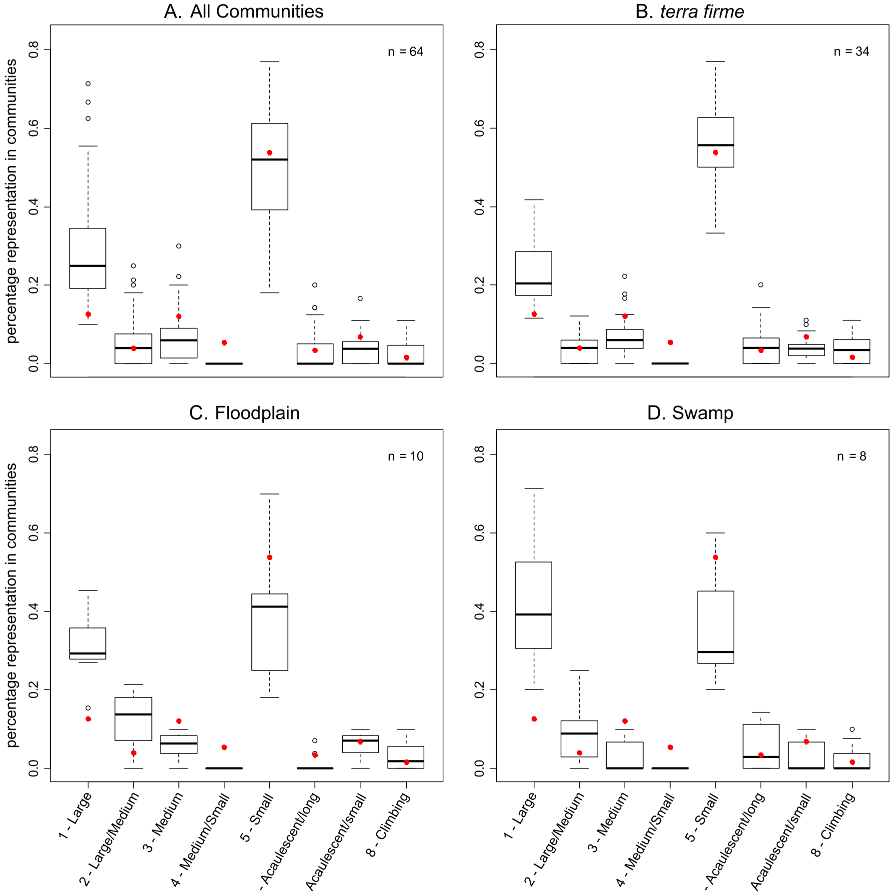

Fig. 5 Percentage of species in American palm communities belonging to each growth form, overall and in different habitats. Box and-whiskers plots correspond to the median (*thick line*), the distributional quartiles (*box*), the range of the distribution excluding outliers (*whiskers*), and outliers (*circles*). Numbers 1–8 refer to the growth form categories described in more detail in the text. Red dots indicate the values expected from proportional sampling of the American palm flora

growth forms may have problems harvesting enough light for growth and reproduction: smaller palms require less light for these processes, while *Large tall-stemmed Palms* escape light limitation by growing up into less dark, higher parts of the forest canopy (Chazdon, 1986a,b; de Granville, 1992).

In addition, there are habitat-specific deviations from the overall growth-form spectrum. The three habitats represented by >5 communities in our dataset (*terra firme,* floodplains and swamps in lowland tropical evergreen forest) separate clearly in a PCA performed on the number of species in each growth form (excluding *Medium/Small Palms with Stout Stems*) (Fig. 6). *Terra firme* communities display a growth form distribution very similar to the one measured across all communities (Fig. 5). The two wetland habitats (floodplain and swamp), however, show characteristically different patterns. In these communities, the over-representation of *Large tall-stemmed Palms* is especially pronounced (cf. Kahn & de Castro, 1985), suggesting that this growth form has an ecological advantage in inundated habitats, possibly due to the more open canopy structure associated with flooding (cf. Svenning et al., 2000). In floodplain forest, *Large-leaved medium–short-stemmed Palms*—which are under-represented on *terra firme*—occur more frequently than expected from a random assembly process ($P<0.01$). Conversely, *Medium Sized Palms* and *Small Palms* are under-represented ($P<0.001$ and $P<0.05$, respectively). This pattern might reflect that the understory especially on floodplains is a stressful environment, due to both flooding per se (anaerobic stress, shading) and disturbance and possibly also to the light limitation during flooding. onsequently the ability to stay emersed during floods could favour tall growth forms.

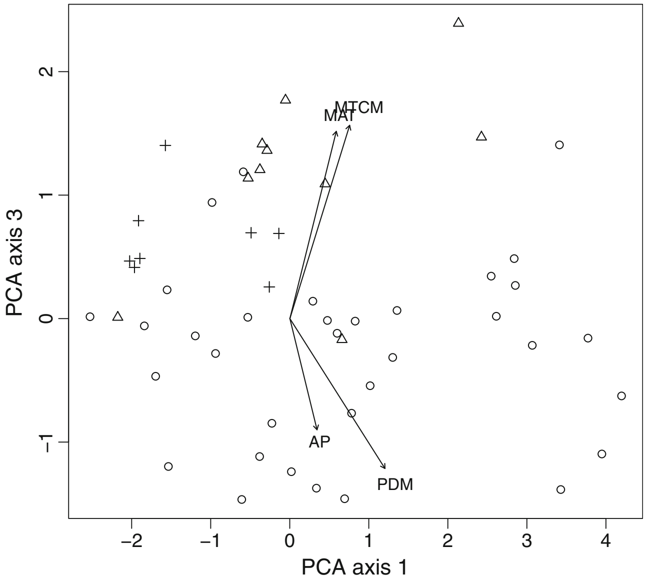

Fig. 6 Principal Components Analysis of the number of tropical American palm species in each growth form per community. Only communities in *terra firme* forest [circles], floodplain forest [triangles] and swamp forest [+] displayed. Arrows show the correlation of four environmental factors (Mean Annual Temperature, Mean Temperature of Coldest Month, Annual Precipitation, and Precipitation of Driest Month) with the PCA axes

The individual based growth-form spectrum (percentage of individuals in each growth form) within palm communities (Fig. 7a) shows a pattern somewhat similar to the species based growth-form spectrum, with *Small Palms* having the highest relative abundance, followed by *Tall Palms*. However, there are some deviations indicating that abundance differences might be related to growth form. In particular, *Medium-Sized Palms* and *Small Palms* ($P>0.01$) and *Small acaulescent Palms* ($P<0.001$) are less numerous than expected under the assumption of equal abundances per species (blue dots in Fig. 7).

Within particular habitats (Fig. 7b–d), the individual growth-form spectrum is different from the overall pattern (Fig. 7a, red dots in Fig. 7b–d). On *terra firme* (Fig. 7b), *Tall large-stemmed Palms* tend to be less abundant, and *Small Palms* tend to be more abundant (not significant). Conversely, *Small Palms* are under-represented on floodplains (Fig. 8c; $P<0.001$), but the upper tail of the distribution

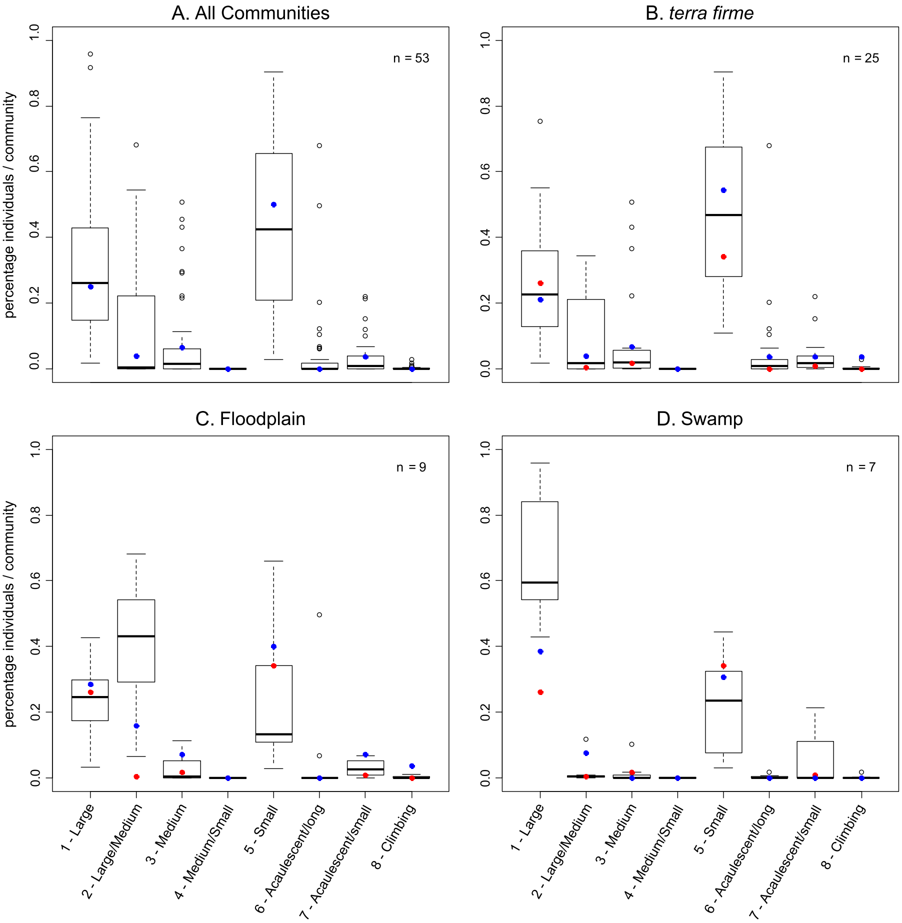

Fig. 7 Percentage of individuals in tropical American palm communities belonging to each of the eight growth forms described, overall and in different habitats. Numbers 1–8 refer to growth form categories. Box-and-whiskers plots correspond to the median (*thick line*), the distributional quartiles (*box*), the range of the distribution excluding outliers (*whiskers*), and outliers (*circles*). Blue dots show the median percentage of species in each growth form (i.e., not considering their number of individuals). Red dots correspond to the median for all communities

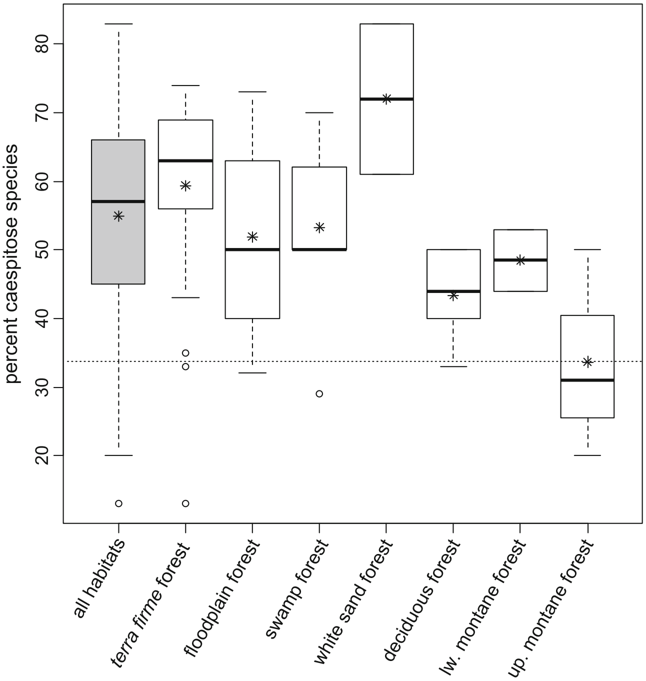

Fig. 8 Percentage of cespitose species in tropical American palm communities, overall and in each habitat type. Box-and-whiskers plots correspond to the median (*thick line*), the distributional quartiles (*box*), the range of the distribution excluding outliers (whiskers), and outliers (*circles*). Asterisks indicate the distributional mean. The dashed line indicates the percentage of cespitose species in the entire American palm flora

is long, probably due to the dominance of some understory species (genus *Bactris*) in some floodplain communities. Most strikingly, species of *Large-leaved medium–short-stemmed Palms* are strongly overrepresented ($P>0.01$). This growth form might represent an adaptation to this habitat; because the canopy is more open in flooded situations (Kahn & de Castro, 1985; Scariot et al., 1989), the development of a tall stem might not be necessary for receiving sufficient light. However, *Large tall-stemmed Palms* are present and not strongly underrepresented on floodplains. In fact, the overrepresentation of *Large-leaved medium–short-stemmed Palms* is almost certainly due to the genus *Astrocaryum being* abundant on floodplains. The pattern might also be a phylogenetic artefact, with *Astrocaryum* having this growth form as a conserved characteristic, and at the same being time well-adapted to inundation for other reasons. In swamps, *Large tall-stemmed Palms* are hyper-abundant (Fig. 7d). This supports the general notion of swamps being dominated by single species of canopy palms (“palm swamps”, Kahn & de Granville, 1992). In swamps all other growth forms tend to be under-represented.

Like growth form, the representation of species with different branching patterns appears to be related to habitat (Fig. 8). The percentage of cespitose species was significantly different between habitats in an ANOVA ($P<0.01$). Across all habitat types, the percentage of cespitose species is significantly larger than the percentage of cespitose species in the American palm flora as a whole (*t*-test: $P<0.001$). This indicates that cespitose species might have larger ecological amplitude or larger range sizes; indeed, the ability to form additional shoots should reduce the vulnerability to environmental extremes because the palm does not have to rely on a single apical meristem (Salm et al., 2007). Moreover, cespitose palms are less dependent on sexual reproduction and might therefore be able to establish more efficiently from small initial populations, rendering them good colonists. Although for most cespitose species clonality is more a growth strategy than a reproductive strategy (cf. Svenning, 2000), it may still favor them by reducing their mortality rate (as they have more than one apical meristem). Most habitats mirror the general trend of over-representation of cespitose species, with the exception of upper montane forest where the percentage of cespitose species is indistinguishable from a random sampling (Fig. 8). Cespitose palms have been hypothesised to cope better with cold, dry or seasonal climate than solitary ones (Salm et al., 2007), as palms with a single apical meristem are thought to be particularly vulnerable to climatic extremes (Salm et al., 2007). This suggests that deciduous forest should be particularly dominated by cespitose species, which is not the case in the communities analysed here. However, the percentage of cespitose species was not significantly lower in deciduous than in evergreen forest (Kruskal-Wallis test: $P>0.1$). The number of communities in deciduous forests is too low to test this hypothesis with confidence; however, correlations with climate variables also indicate that the proportion of clustering species is higher in warmer, wetter, and less seasonal environments (Spearman's ρ: 0.30–0.45). Interestingly, cespitose palms are relatively species-poor in upper montane forest. Taken together, this tentative evidence indicates that the cespitose habit might not be advantageous in extreme climates, but rather in the climates most favourable to palms. Further analyses are clearly required to investigate this hypothesis.

A morphological feature with a strikingly non-random distribution in American palm communities is leaf shape (Table 2). The percentage of (costa-)palmate species is generally very low with the exception of the communities in the Yucatán peninsula (Alvarado and Balslev, unpublished data). In these communities, 63% (±26% SD) of all palm species are palmate-leaved, versus 3.5%±4.6% SD in all other communities (Fig. 9). This huge difference is clearly attributable to an interaction of macroevolutionary and broad-scale biogeographic processes. Leaf shape is phylogenetically strongly conserved in palms; with variation expressed mostly at the subfamily level (only three tribes or subtribes have a different leaf shape than the rest of the corresponding subfamily, i.e., Coryphoideae-Phoeniceae, Coryphoideae-Caryoteae, and Calamoideae-Mauritiinae). Palm communities in South America and parts of Central America are strongly dominated by the pinnate-leaved subfamily Arecoideae, having a long history in the New World (Bjorholm et al., 2006). The palmate-leaved Coryphoideae are thought to have reached the New World during the Paleocene/Eocene on a northern hemisphere route (boreotropic invasion; Bjorholm et al., 2006 and references therein). Reflecting this history, coryphoid palms are still most diversified in North America, parts of Central America and the Caribbean, leading to a high representation of palmate-leaved species in the communities of these regions. The contemporary northern hemisphere bias of Coryphoideae is probably due to a combination of dispersal limitation and phylogenetic niche conservatism; many of these palms are adapted to seasonally-dry climates, so their southward dispersal might be hindered by the extensive evergreen lowland rainforests of northern South America.

Fig. 9 Proportions of species that are cespitose (clustering, *grey column*) and that have palmate leaves (*black column*) in each of the study sites (*black dots*) reviewed in this paper

The palmate-leaved species found in South American palm communities belong either to the few coryphoid lineages that have colonised this continent (*Chelyocarpus*, *Copernicia*, *Itaya*, *Trithrinax*) or species of the calamoid subtribe Mauritiinae.

Conclusion

American palm communities include as many as 48 co-existing species in equatorial warm and humid regions without seasonality in temperature and precipitation. In the other extreme we find species-poor palm communities where the conditions are less favourable, i.e., in colder, drier, or seasonal regions. Soil fertility, precipitation, seasonality, topography, and soil-water conditions all influence the composition and species richness of the palm communities. All these factors, however, interact and are strongly scale-dependent (as is also generally found for species richness; Whittaker et al., 2001). Palms generally appear to favor nutrient-rich soils, but at a regional scale an area with soils that are on the average nutrient-poor may have more species than a more nutrient-rich area if the former has higher soil type heterogeneity. This was demonstrated by the comparison of the Yasuni (Ecuador) and Iquitos (Peru) areas, where the higher diversity of the latter in part reflects that it contains species that occur only in its special very nutrient-poor white sand areas (Vormisto et al., 2004a). On a large scale, increasing elevation is accompanied with fewer species, but on a local scale slopes and hills may have more palm species than adjacent valleys (Montufar & Pintaud, 2006). Soil-water conditions strongly influence both species richness and composition in palm communities, and the number of species generally decrease with increased flooding and the parts of the floodplains that sustain the longest flooding have palm communities with specialized species, adapted to the stressful eco-physiological conditions that flooding implies. In addition to these ecological drivers there are other factors that influence palm community composition and richness. Dispersal limitation, reflected in distance-related dissimilarities in the communities, has been shown to function on both rather limited scales of less than 150 km and also on larger scales up to 500 km (Normand et al., 2006; Vormisto et al., 2004a). The species present in a community obviously must be a subset of the regional pool of species, and we did not find a linearly increasing trend for local species richness against regional species richness. Rather we found a triangular relationship in which species poor regions have species poor communities, and species rich regions may have both very rich and very poor communities due to local variation in habitats within a region. This is in contrast to, at least some, other findings, in which local richness was strongly related to regional species richness, for example in mangrove ecosystems (Ellison, 2002).

We provide new insight into palm community assembly by considering the functional ecology of their constituent species. Eight growth forms of palms, defined on the basis of their leaf and stem size and on whether they have aerial or subterranean stems, have different representation in palm communities in different habitat types. *Small palms* (<8 m tall, <12 cm stem diam.) make up the majority (53%) of American palms and they are the most common in all habitat types and proportionally represented both in terms of species and in terms of individuals. *Large tall-stemmed Palms* (<35 m tall, 20–40 cm diam.) are the second in terms of species (13%) and overrepresented in terms of species present in local communities which coincides with the hypothesis that large palms have broad ecological niches and are widespread (Ruokolainen & Vormisto, 2000; Kristiansen et al., 2009). Cespitose palms are overrepresented relative to a random draw of all American palms, in all communities examined in this study, except in the upper montane forests. This discards the idea that the cespitose habit should be an adaptation to extreme conditions, in which case one would have expected a differentiation with higher prevalence of cespitose species in habitats with more unfavourable communities. In contrast, cespitose palms appear to be particularly successful in the warm, wet environments most favourable to palms. The underlying functional relationship remains elusive at this point. A strong non-random pattern was the high incidence of species and individuals with (costa-)palmate leaves in the Central American palm communities compared to the South American communities. This pattern is related to very strong historical drivers that shaped the palm flora of the two regions; Central America was populated by a boreo-tropical flora that encompassed much of the northern hemisphere and where the mostly palmate-leaved subfamily Coryphoideae was abundant, whereas the South American continent, which was relatively isolated from Central America until 2–3 million years ago, was the evolutionary play ground for another palm-subfamily, the Arecoideae, in which the leaves are pinnate. Given that these leaf morphologies may not necessarily have identical functionality, palms here exemplify that there may be deep-time historical legacies not just in species diversity patterns (Ricklefs, 1987), but also in community functional diversity and functioning.

Overall, tropical American palm communities are shaped, both in terms of species richness, species composition and diversity in growth forms, by a series of ecological drivers in addition to historical ones, notably dispersal limitation and geological processes, such as the separation of the North/Central American and South American land areas until recent geological times. Importantly, all drivers of palm community assembly are strongly scale-dependant, some working with different strength at different geographic- and time scales, others working in opposite directions at different scales.

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