Palms and Palm Communities in the Upper Ucayali River Valley – a Little-Known Region in the Amazon Basin

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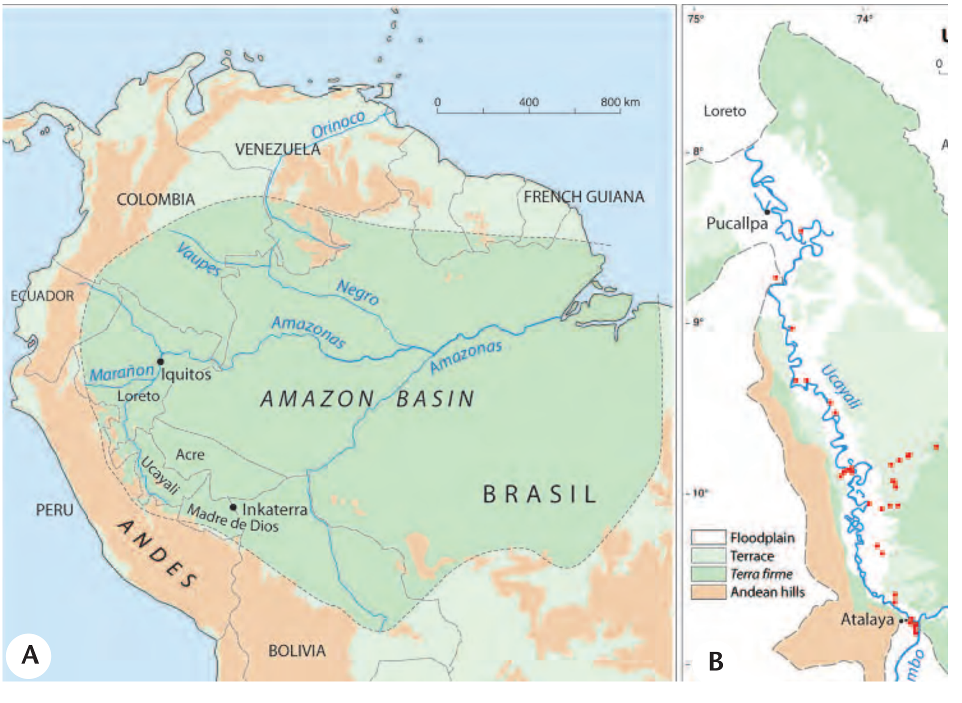
The Amazon region and its palms are inseparable. Palms make up such an important part of the rain forest ecosystem that it is impossible to imagine the Amazon basin without them. Palms are visible in the canopy and often fill up the forest understory. Palms – because of their edible fruits – are cornerstone species for the survival of many animals, and palms contribute substantially to forest inventories in which they are often among the ten most important families. Still, the palms and palm communities of some parts of the Amazon basin remain poorly studied and little known. We travelled to a little-explored corner of the western Amazon basin, the upper Ucayali river valley. There, we encountered 56 different palms, 18 of which had not been registered for the region previously, and 21 of them were found 150–400 km beyond their previously known limits.

The importance of palms in the Amazon basin attracted the attention of early European travellers in the region. When Alexander von Humboldt (1769–1859) explored the Americas from 1799 to 1804 he was impressed with the role of palms in the lives of the people he met. He was particularly impressed with the majestic *Mauritia flexuosa,* which he observed when navigating the rivers along the northern fringe of the Amazon basin along the Orinoco and its tributaries (Humboldt 1850). Carl Friedrich Philip von Martius (1794–1868) was sent to Brazil from 1817–21 by the king of Bavaria to explore the plant richness of that remote region. He travelled extensively along the Amazon river and its tributaries and became fascinated with the palms – so fascinated that upon his return to Europe he immersed himself in the study of the palm family – and a few years later published the first volume of what was to become the most complete monograph of any plant family, the famous *Historia Naturalis Palmarum* (3. vols. 1823–1853). Thirty years later, between 1848 and 1852, the young naturalist Alfred Russel Wallace (1823–1913) travelled along the Amazon, Rio Negro and Vaupes in search of birds and butterflies but – as with earlier travellers – palms impressed themselves so much upon him that he took special notes and made a series of pencil sketches of them. Although Wallace lost most of his collections in a shipwreck on his way back to Europe he managed to save his drawings and later published the *Palm Trees of the Amazon and Their Uses* (Wallace 1853), a handsome little book that underscores the importance of palms to people in the Amazon. The great explorer of the Amazon and the Andes, Richard Spruce (1817–1893) spent 13 years in the region (1849–1862) and again – even if his purpose was different – he developed a special liking for the palms of the region and published a detailed account of his findings under the title *Palmae Amazonicae* (Spruce 1871). The Brazilian government, duly impressed with the results of the palm explorations, particularly those of Martius, contracted João Barbosa Rodriguez (1842–1909) to continue the exploration of the region's palm resources. Barbosa Rodrigues efforts produced two important references for Amazon palm botany, *Enumeratio Palmarum Novarum* (Barbosa Rodrigues 1875) and *Sertum Palmarum Brasiliensium* (Barbosa Rodrigues 1903). On one of his travels Barbosa Rodrigues was accompanied by the physician James Trail (1851–1919) who, fascinated with palms, went on to study and make botanical collections of them, and upon his return to Europe published his results in the *Journal of Botany* with descriptions of 72 new palm taxa from the Amazon (Trail 1876, 1877). More recently Andrew Henderson compiled and critically evaluated all information and collections of Amazon palms and published the monograph

1. A. Northern South America with indication of the position of the Ucayali region in the Peruvian Amazon and other localities mentioned in the text. B. The Ucayali region with indication of the Ucayali river valley and the landforms that characterize the region (floodplain, terraces, *terra firme,* and Andean hills. The positions of the 35 transects are indicated with red squares.



2. A. The crew of boatmen and "macheteros" who cut and marked our transects. In the background the riverboat *El Delfincito,* which was our home and laboratory for the five weeks on the upper Ucayali river. B. The team at work identifying palms along the transect, and collecting and photographing them. C. Pressing a *Socratea salazarii* on the boat deck. D. Walking through cultivated land to reach tall forest.

The Palms of the Amazon (Henderson 1995) in which he accepted 151 palm species. Apart from its wealth of information about the Amazon palms, Henderson's treatment clearly demonstrates that many parts of the Amazon basin remain unexplored or under-explored as far as palms are concerned. One such region is the upper Ucayali river valley in the western part of the Amazon basin, right at the foot of the great Andean cordillera in central Peru (Fig. 1A). This paper is an account of the palm flora of the upper Ucayali river valley, based on five weeks of exploration in 2008.

The Ucayali Region

The Ucayali region forms a narrow band on the western edge of the Amazon basin between the great cordillera of the Andes and the vast flat plain of the mighty Amazon river and its tributaries (Fig. 1A). Politically Ucayali is a part of the Peruvian Amazon, inserted between the Loreto and Madre de Dios regions and the

Brazilian state of Acre. The region's main coherence is due to the Ucayali river (Fig. 1B) that flows northwards and continues into the Loreto region, where it discharges into the Marañon that eventually becomes the Amazon river. In the northern part of Ucayali lies Pucallpa, the region's capital and largest city with close to 200,000 inhabitants, and towards the South lies Attalaya, a small town with maybe 30–40,000 inhabitants. The Ucayali river originates near Attalaya at the confluence of the Urubamba and Tambo rivers, both of which originate high in the Andes. The Ucayali river is up to one kilometer wide and flows in a very flat valley, where it meanders through a 20–100 km wide floodplain.

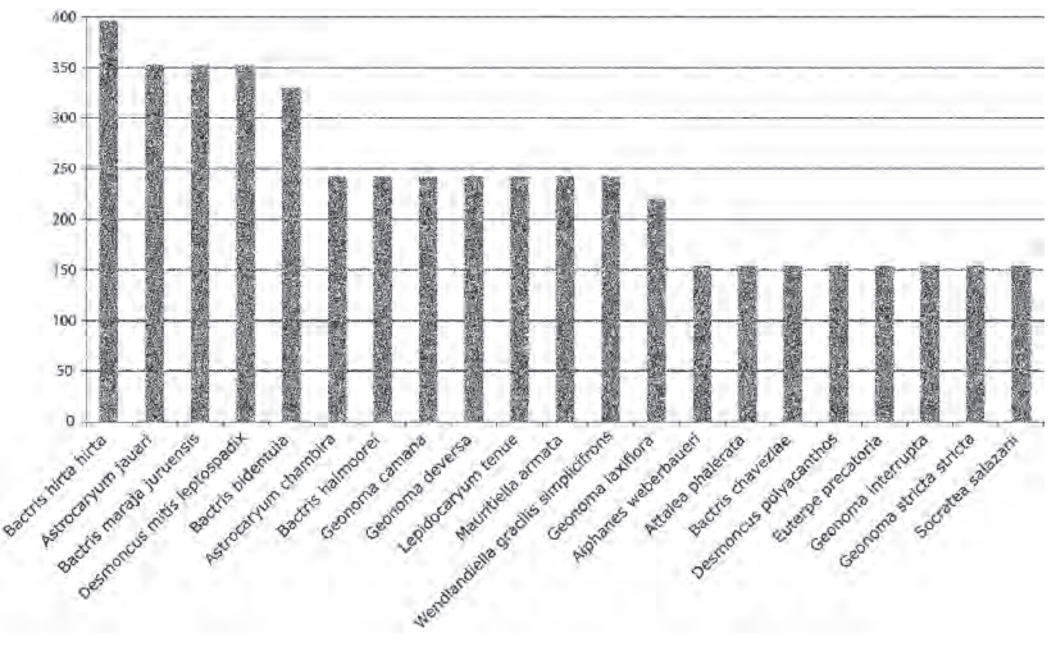
Fieldwork

During five weeks (22 September to 26 October, 2008) we travelled on the riverboat *El Delfincito* (Fig. 2A) along the Ucayali river between Pucallpa and Attalaya, stopping whenever convenient to explore the palm flora and the palm communities ashore. We made special efforts to explore as many different habitats as was practically possible, collecting herbarium specimens of palms and collecting data about their abundance in transects.

We collected 334 numbers of herbarium specimens (Fig. 2C), each one with a duplicate for the herbarium of the Universidad Nacional Amazonense de Peru in Iquitos (AMAZ), and one for the herbarium at Aarhus University (AAU). The collections represent all stages of the palms from seedlings over juveniles to adults. This may be unusual, since most herbaria accept only fertile material of mature individuals. Because the purpose of our research is also ecological it has become an important part of our field protocol to be able to identify palms in all stages of development. Consequently we collect specimens that represent the juvenile and seedling phases, which are valuable in our subsequent analysis of the ecological data, and in our elaboration of identification keys that help us putting names on individuals representing all stages of the palms.

To determine the abundance of individual species of palms and other ecological parameters, we made 35 transects (location on Fig. 1B) each one five meters wide and 500 meters long. In subunits of 5 × 5 meters we counted and identified all palm individuals, from the smallest seedlings to the largest adults and we noted the developmental stage of the individual as seedling, juvenile, subadult or adult. In total we counted and identified close to 31,000 palm individuals. The transects were laid out so that they would represent the variation in vegetation types as we could see them on satellite images that we brought along. After selecting a site we would approach its position as closely as we could on the river and then reach it overland using GPS (Fig. 2D). Once at the site our three *macheteros* would

3. Range extensions of 150–400 km for 21 species of palms encountered in the upper Ucayali river valley.



4. Floodplain and floodplain palms. **A**. Dicot tree in the flood plain with mud marks about 3.5 m above the ground, indicating the level of the most recent flooding episode. **B**. *Attalea phalerata,* a common large tree palm on the flood plain. **C**. *Bactris bifida,* a locally abundant, colonial, understory palm on the floodplain. D. Stand of colonial *Bactris brongniartii*. **E**. Fresh leaves of *Bactris brongniartii,* showing the very characteristic large yellow spines.

cut a straight trail, avoiding any damage to the palms along the trail, and placing sticks for every five meters and marking each stick with a pre-printed paper label with the transect number and subunit number (Fig. 2B). Then followed a team of three consisting of the person identifying the palms (HB), one person filling in the numbers of individuals on a pre-printed list of all species expected in the region (DP), and one person who measured ecological variables along the transect such as light penetration through the canopy, inclinations of the ground, etc. (CG). The tail of our team included a plant collector (WE) who was assisted by two students and a photographer. With this menagerie of 13 people we could

Table 1. The upper Ucayali river valley palm community with indication of name, literature reference, collecting number, number of individual encountered in 35 5x500m transects (total 8.75 hectares), and the average number of individuals/species in each of four habitat types (floodplain, terrace, terra firme and Andean hills).

Species name	New to Ucayali (•) or previo-usly reported reference	Collected HB-number	Seen and not collected	Not seen	Number of individuals counted in 35 transects	Individuals per hectare: Andean hills (8 transects)	*Terra firme* (1 transect)	Terrace (13 transects)	Floodplain (13 transects)	pal architecture	Growth form	Leaf architecture
Lepidocaryum tenue Mart. var. *tenue*	•	7605			13823		2384	4070		Col	MsT	pal
Geonoma brongniartii Mart.	1,3,4	7552			2580	131	640	434	230	Sol	Shr	pin
Astrocaryum chonta Mart.	4	7658			1803	15		226	320	Sol	LaT	pin
Bactris brongniartii Mart.	2,4	7542			1486			3	454	Col	MsT	pin
Oenocarpus bataua Mart. var. *bataua*	4	7606			1377	31	44	401	1	Sol	LaT	pin
Iriartella stenocarpa Burret	1,4	7562			1233	259		220		Ces	MsT	pin
Wettinia augusta Poepp. ex Endl.	4	7550			1015	247	84	154		Ces	LaT	pin
Geonoma macrostachys var. *acaulis* (Mart.)Skov	1,4	7590			883	9	12	264	1	Sol	Aca	pin
Geonoma stricta var. *trailii* (Burret) Henderson	1	7869			739	55	112	186		Ces	Shr	pin
Geonoma maxima var. *chelidonura* (Spruce) Henderson	3	7626			580	214		47		Ces	MsT	pin
Bactris bifida Mart.	2,4	7875			574				177	Col	Shr	pin
Iriartea deltoidea Ruiz & Pav.	1,4	7723			548	149	372	48		Sol	LaT	pin
Attalea phalerata Mart. ex Spreng	1	7752			459	3		25	115	Sol	LaT	pin
Euterpe precatoria Mart.	4	7569			431	9	32	121	4	Sol	LaT	pin
Oenocarpus mapora H.Karst.	1,4	7563			280	26	16	69		Ces	LaT	pin
Bactris maraja Mart. var. *maraja*	2,4	7596			194	8		75	4	Ces	MsT	pin
Bactris concinna Mart.	2,4	7780			246				76	Col	MsT	pin
Socratea salazarii H.E.Moore	1,4	7594			237	72	132	19		Sol	LaT	pin
Socratea exorrhiza (Mart.) H. Wendl.	1,4		•		230	73	28	23	1	Sol	LaT	pin
Bactris hirta Mart. var. *hirta*	•	7603			187	75		21		Ces	Shr	pin
Hyospathe elegans Mart.	4	7574			210	74	4	19		Ces	MsT	pin
Attalea maripa (Aubl.) Mart.	1,4		•		137	17		32		Sol	LaT	pin
Geonoma deversa (Poit.) Kunth	4	7641			127		136	29		Ces	MsT	pin
Bactris maraja var. *trichospatha* (Trail) Henderson	2	7835			265	9		33		Ces	MsT	pin
Bactris simplicifrons Mart.	2,4	7591			94	21		16		Ces	Shr	pin
Phytelephas macrocarpa Ruiz & Pav.	1,4		•		91	5		7	18	Ces	MsT	pin
Bactris halmoorei Henderson	•	7595			81	1		25		Ces	MsT	pin
Astrocaryum jauari Mart.	•	7778			71				22	Ces	LaT	pin
Wendlandiella gracilis var. *gracilis* Dammer	4	7570			71			22		Col	Shr	pin
Bactris maraja var. *juruensis* (Trail) Henderson	•		•		2	34				Ces	MsT	pin
Chamaedorea pauciflora Mart.	1,4	7694			68	8	148	5		Sol	Shr	pin

The growth form of each species is indicated as MsT (=Medium sized tree, Shr(=shrub), LaT (=large tree), Aca (=acaulescent), Lia (=liana), and the palm architecture is given as Col(=colonial), Sol (=solitary), Ces (=cespitose), and the leaf architecture is given as pal (palmate), pin (=pinnate) and cop (=costapalmate).

Chelyocarpus ulei Dammer	1,4	7623			65	10		14		Sol	MsT	pal
Bactris chaveziae Henderson	•	7749			63	4		2	15	Ces	MsT	pin
Desmoncus polyacanthos Mart. var. *polyacanthos*	4	7776			65	2		3	15	Ces	Lia	pin
Geonoma stricta (Poit.) Kunth var. *stricta*	4	7583			55	5		14		Ces	Shr	pin
Wendlandiella gracilis var. *simplicifrons* (Burret) Henderson	•	7747			40	20				Col	Shr	pin
Desmoncus mitis var. *leptospadix* (Mart.) Henderson	•	7579			36	1		10		Ces	Lia	pin
Astrocaryum chambira Burret	•	7621			35		12	10		Sol	LaT	pin
Geonoma arundinacea Mart.	4	7858			37			11		Ces	Shr	pin
Bactris acanthocarpa Mart.	•	7604			3	2		10		Ces	MsT	pin
Desmoncus giganteus Henderson	•	7708			20	5		5		Ces	Lia	pin
Geonoma interrupta (Ruiz & Pav.) Mart. var. *interrupta*	3,4	7669			24	12				Sol	MsT	pin
Geonoma macrostachys Mart. var. *macrostachys*	1,4	7665			24	12				Sol	Aca	pin
Mauritia flexuosa L.f.	1,4		•		24			7		Sol	LaT	cop
Bactris bidentula Spruce	•	7546			22				6	Ces	MsT	pin
Chamaedorea pinnatifrons (Jacq.) Oerst.	1,4	7649			20	6	8	2		Sol	Shr	pin
Geonoma camana Trail	4	7592			19	1	8	5		Sol	MsT	pin
Geonoma leptospadix Trail	1,3,4	7632			16			5		Sol	Shr	pin
Bactris corossilla H.Karst.	2,4	7575			9			3		Ces	Shr	pin
Geonoma laxiflora Mart.	•	7847			7				2	Ces	Shr	pin
Geonoma triglochin Burret	•	7827			7		28			Sol	MsT	pin
Aiphanes weberbaueri Burret	•	7648			6			2		Sol	Aca	pin
Bactris macroacantha Mart.	2,4	7601			5			2		Ces	MsT	pin
Desmoncus orthacantos Mart.	•	7820			5			2		Ces	Lia	pin
Mauritiella armata (Mart.) Burret	•	7834			1				1	Ces	LaT	cop
Aiphanes aculeata Willd.	•	7663								Sol	MsT	pin
Aphandra natalia (Balslev&Henderson) Barfod	1			•						Sol	LaT	pin
Attalea butyracea (Mutis ex L.f.) Wess.Boer	1		•							Sol	LaT	pin
Attalea tessmannii Burret	1,4			•						Sol	LaT	pin
Bactris gasipaes Kunth var. *gasipaes*	2		•							Ces	LaT	pin
Bactris riparia Mart.	2			•						Col	MsT	pin
Chamaedorea angustisecta Burret	1,4		•							Sol	MsT	pin
Chamaedorea linearis (Ruiz & Pav.) Mart.	4			•						Sol	MsT	pin
Geonoma stricta var. *piscicauda* (Dammer) Henderson	4			•						Ces	Shr	pin
Syagrus sancona H. Karst.	1,4		•							Sol	LaT	pin
Syagrus smithii (H.E.Moore) Glassman	1,4			•						Sol	MsT	pin
Total number of pal individuals					30730	3244	1050	21956	4746			
Number of pal individuals per hectare					3512	1622	4200	6756	1460			
Number of species in each habitat type:					55	36	18	44	18			

References: 1. Henderson(1995); 2. Henderson (2000); 3. Henderson personal information (*Geonoma* database); 4.Kahn and Moussa 1994a; • reported here

5. Floodplain palms in the upper Ucayali river valley. **A.** *Astrocaryum jauari,* a large tree palm, which is characteristic along river margins and low laying floodplains. **B**. Petiole of *Astrocaryum jauari,* showing the characteristic red-brown colour which helps in the identification of seedlings and juveniles. **C**. Colony of *Bactris concinna,* a medium sized tree palm that forms large colonies on the floodplain. **D**. Infructescence of *Bactris concinna.*

locate, mark and collect data in one or two transects on a good day, assuming that we had access to suitable places which was, however, not always the case, giving an average of about one transect per day over the five weeks of fieldwork. The data that goes with each of the 334 herbarium specimens and 750 cross-referenced photos are uploaded on the Aarhus University Herbarium webpage and can be viewed at: http://herb42.bio.au.dk/aau_herb/search_form.php (enter collector "Balslev" and number range "7542-7876")

6. Terrace forest in the upper Ucayali river valley. **A**. View along old logging trail showing the tall dicot trees and the dense understory of medium sized tree palms. **B**. *Lepidocaryum tenue* var. *tenue,* a dense colony of this medium sized tree palm; note transect stick with mark in center. **C**. *Oenocarpus bataua,* old infructescence; note horse-tail shape. **D**. *Chelyocarpus ulei,* the only palm of subfamily Coryphoideae in our area; note palmate leaves with white undersurface.

The size of the Ucayali palm flora

We collected 51 taxa of palms including five varieties (Tab. 1). In addition we encountered five species in the transects for which we did not make voucher collections because they were very common and well-known species. Finally we saw *Bactris gasipaes, Chamaedorea angustisecta* and *Attalea butyracea* along the river and *Syagrus sancona* near Attalaya, but not where we made collections or transects. Consequently we observed 60 taxa of palms during our fieldwork. In his *Palms of the Amazon* and his monograph of *Bactris,* Henderson (1995, 2000) cited 34 taxa for the

Ucayali region. Of these we did not see four (*Aphandra natalia, Syagrus smithii, Attalea tessmannii, Bactris riparia*). In addition Kahn and Moussa (1994a) reported *Chamaedorea linearis* and *Geonoma stricta* var. *piscicauda* from Ucayali. All this taken together, the upper Ucayali river valley palm flora includes 60 documented species (in 21 genera) and six additional varieties or a total of 66 taxa. Of the 66 taxa, 18 are here reported for the first time from the Ucayali region (Tab. 1). These 66 taxa correspond to over one-third of the entire Amazon basin palm flora and 40–50% of the entire Peruvian palm flora. Compared to other areas in which Ucayali is not nested, the region harbors over two-thirds as many species as found in the 10 times larger area of Bolivia. Such richness of species is not unheard of. Ecuador, for instance, which has only one quarter of the area of Bolivia, has 130 palm taxa, and the one degree square (111 × 111 km) where the Peruvian Amazon's capital Iquitos is located has 71 palm species. The accumulation of many species in small areas is a general feature of tropical rainforests, and although this local richness in species is variable, the Ucayali palm flora is no exception to that general pattern (Tab. 2).

Range extensions

Many of the taxa we encountered as new to the Ucayali region represented extensions of their known ranges. In other cases our recording of taxa new to the Ucayali region were simply filling of gaps. We measured the distance that these known range extensions represented by calculating the distance from the center of the one degree square in which we found the taxon to the center of the nearest one degree square in which it was reported to occur according to the dots maps reproduced in Henderson's book *Palms of the Amazon* (Henderson 1995). In this way we could demonstrate that 21 species had been recorded anywhere from 150–400 kilometers from their nearest previously known occurrence (Fig. 3). The most impressive thing about these range extensions is not the distance from the previously known occurrence and the newly documented occurrence, but rather the fact that about one-third of the recorded species were found outside their previously known ranges. This testifies to the patchy nature of the present state of knowledge of Amazon palms.

The palm communities

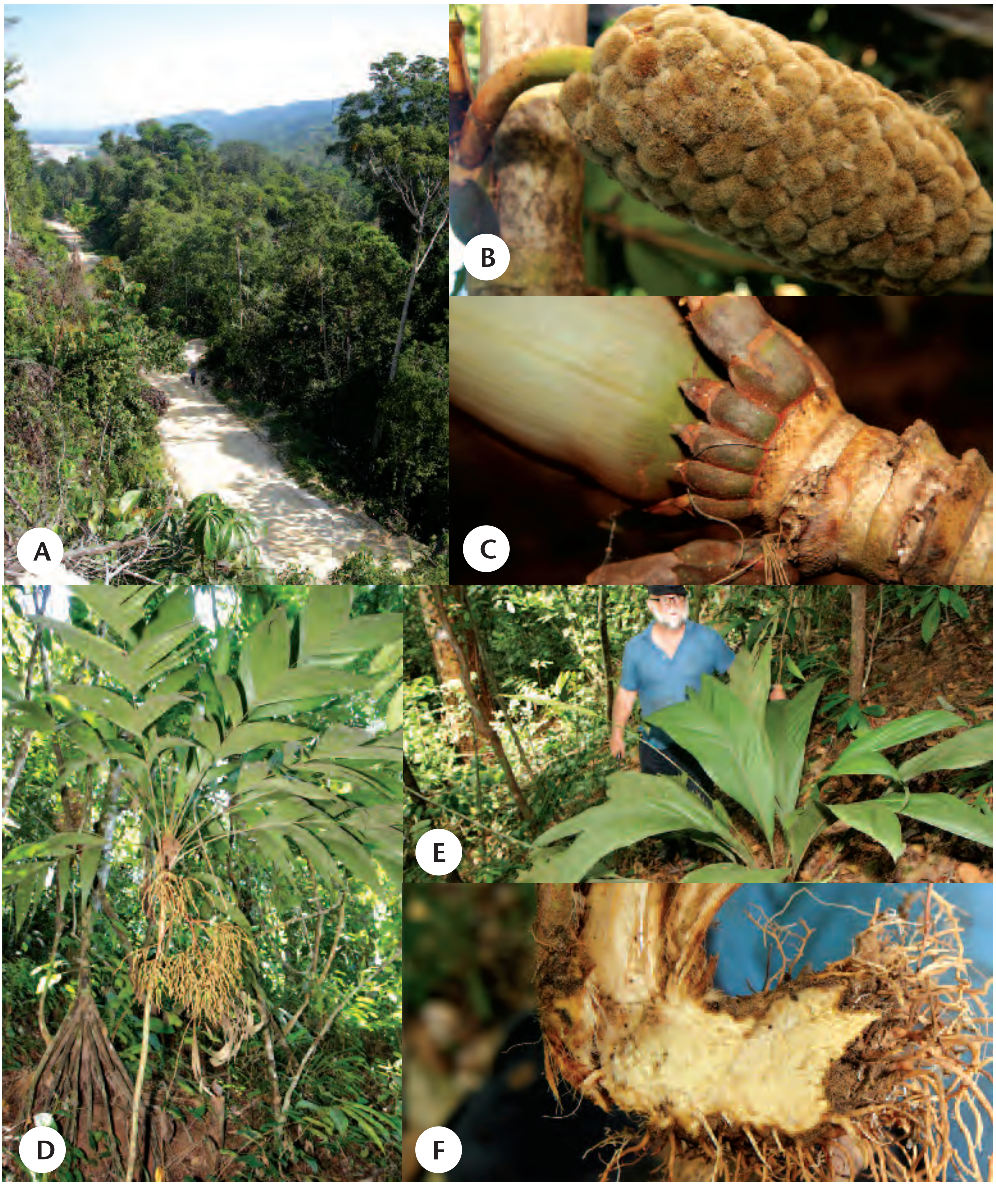
Palm communities in different habitats – The upper Ucayali river valley includes a series of habitats with different conditions for the growth and development of palm communities.

Close to the river and sometimes stretching for tens of kilometers beyond the river channel, the floodplain (Fig. 1B) forms a very flat and gently sloping plain which is subject to flooding during the rising and falling cycles of the river. The parts of the floodplain closest to the river would be flooded annually at high water whereas more distant parts of the plain are flooded only during extreme events of high water (Fig. 4A). This transition from annually flooded to rarely flooded parts of the plain is mirrored in a gradient of plant communities, generally from communities with few species to ones with a species richness that approaches what is found on the never-flooded *terra firme*. We placed 13 of our transects in such floodplain sites. The density of palms in the floodplains was 1460 individuals per hectare, and we encountered a total of 18 species in them (Tab. 1; Figs. 4 & 5). The most abundant floodplain palms were *Bactris brongniartii* (Figs. 4D & E), *Astrocaryum chonta, Geonoma brongniartii, Bactris bifida* (Fig. 4C) and *Attalea phalerata* (Fig. 4B). These were all restricted to, or occurring primarily on, the floodplain, except for *Geonoma brongniartii,* which appears to be a generalist species that happens to be very abundant on the floodplain. Less abundant but certainly conspicuous in the floodplain palm community were *Bactris concinna* (Figs. 5C & D) and *Astrocaryum jauari* (Figs. 5A & B), which are both habitat specialists on the floodplain and along river margins.

The floodplain is bordered by a system of terraces (Fig. 1B) formed by prehistoric floodplains over the past two million years or more. These old terraces are flat and, although they are built of fluvial sediments, they are never flooded by the river in its current cycles of high and low water levels. These terraces have become "lifted" above the active flood plain through tectonic movements or erosion of the river channel. Terraces therefore share some features with flood plains such as flat topography (Fig. 6A) and alluvial sediments, but they differ in never being flooded. We placed 13 transects on terraces and we measured an average density of 6756 palm individuals per hectare. We encountered a total of 44 species in the terrace palm community (Tab. 1; Fig. 6). The most abundant of these were *Lepidocaryum tenue* (Fig. 6B), which was

7. *Terra firme* forest palms in the upper Ucayali river valley. **A**. *Geonoma triglochin,* a disjunct and range restricted species that we encountered in a single transect. **B**. Inflorescence of *G. triglochin* in pistillate flower. **C**. *Socratea salazarii,* leaf, note entire pinnae which distinguishes this species from the related and sympatric *S. exorrhiza*. **D**. *Geonoma brongniartii,* an unusually large individual of this very variable palm.

super-abundant, *Geonoma brongniartii* and *Oenocarpus bataua* (Fig. 6C), all of which were also found in other habitats. The Coryphoid *Chelyocarpus ulei* (Fig. 6D) was also conspicuous on the terraces. More interesting may be a series of taxa found in the terrace palm



8. Andean hills and their palms. **A**. Landscape south of Atalaya. **B**. *Wettinia augusta,* mature infructescence. **C**. *W. augusta,* multiple inflorescence buds at the node just below the crownshaft. **D**. *Geonoma interrupta,* a medium sized tree. **E**. *Geonoma macrostachys* var. *macrostachys,* one of the very few acaulescent rosette palms in the upper Ucayali river valley forest. **F**. *G. macrostachys* var. *macrostachys,* longitudinal section of the below-ground stem.

community but not in other habitats (*Wendlandiella gracilis* var. *gracilis, Geonoma arundinacea, Mauritia flexuosa, Geonoma leptospadix, Bactris corosilla, Aiphanes weberbaueri, Bactris macroacantha, Desmoncus orthacanthos*). These species appear to be habitat specialist, but each of them would need to be evaluated individually, including an assessment of the habitats in which they have been found outside of our study area to determine their status. In any case the tail of less abundant and possible habitat specialists is much longer in these terrace palm communities, contributing to making them the most species rich community in the upper Ucayali river valley.

East of the Ucayali floodplain and in a few places towards the Andes, the terraces give way to upland *terra firme* (Fig. 1B). This landform is shaped by old geological deposits dating back to Miocene and Oligocene some 20–30 million years ago. These old sediments have subsequently been transposed, lifted, tilted, etc. through tectonic movements and then eroded from the top through climatic processes. Consequently, they form a landscape of rolling hills with valleys that have been carved out by creeks and streams. The soils on the upland *terra firme* are typically red clay soils which are nutrient poor because they have been subject to millions of years of leaching; in the erosion creeks, however, deposits of alluvium may create small patches of nutrient rich soils. The rain forest on this *terra firme* is typically very tall and often has enormous local species richness. During our field work we were able to reach such *terra firme* forest only at a single locality. We therefore have only one transect representing this habitat type and our data are clearly insufficient to represent fully the palm communities found in it. Based on a single transect (0.25 ha) we calculated a density of 4200 palms per hectare. We found 18 species of palms in our single transect (Tab. 1). The most abundant species were *Lepidocaryum tenue*, *Geonoma brongniartii* (Fig. 7D) and *Iriartea deltoidea; Socratea salazarii* (Fig. 7C) and *Geonoma deversa* were also common in this habitat. The only species restricted to this habitat type was *Geonoma triglochin* (Figs. 7A & B), which is a range-restricted species that occurs disjunctly in a relatively small area in the Ucayali river valley. Much more data about this habitat type in the Ucayali river valley is needed to truly assess its palm communities; the 18 species reported here surely represent only a fraction of the entire palm community.

To the west the terraces are bordered by Andean hills (Figs. 1B, 8A) resulting from the immense folding of the South American continental plate where is collides with the Pacific Nazca plate. The hills rise rather steeply from the lowland Amazon plain, and the folding exposes deep rocks, and the slopes therefore are rocky, often with shallow soils and cliff outcrops. The soils are loamy and appear to be rich in nutrients. Like the flat plain below, they are covered with dense, tall broadleaf forest with high diversity of trees, shrubs, epiphytes, herbs and also some lianas. We were able to place eight transects in the Andean hills. The density of palms was 1622 palm individuals per hectare, and the community was made up of 36 species (Tab. 1). The most abundant species on the Andean hills were *Iriartella stenocarpa* and *Wettinia augusta* (Figs. 8B & C), and *Geonoma interrupta* (Fig. 8C) also grew here. Species found on the hills but not in any of the other habitats were *Bactris maraja* var. *juruensis, Geonoma macrostachys* var. *macrostachys* (Fig. 8D & E) and *Wendlandiella gracilis* var. *simplicifrons* (Fig. 8). Elsewhere these are typical *terra firme* species but not necessarily limited to Andean premontane forests.

The four habitats shared five taxa (*Geonoma brongniartii, Oenocarpus bataua, Geonoma macrostachys* var. *acaulis, Euterpe precatoria, Socratea exorrhiza*), but more characteristically they were dominated by different sets of abundant species, and of the 55 taxa encountered in the transects 19 were restricted to one of the four habitats (Tab. 1). The floodplain forests palm communities were not very dense with an average of 1460 individuals per hectare, and the number of species growing in the flood plain forest was 18, which was

9. Abundances of species in the upper Ucayali river valley palm communities. The number along the vertical axis is the total number of individuals encountered of each species in 35 transects of 5 × 500 m, i.e., 8.75 hectares in total.

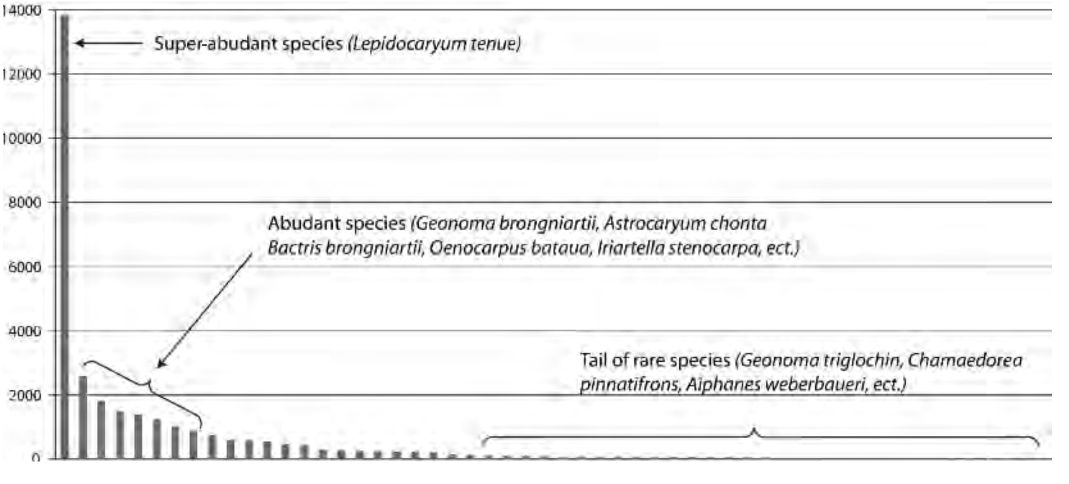


Table 2. Number of palm species encountered in nine Neotropical areas of variable extent.

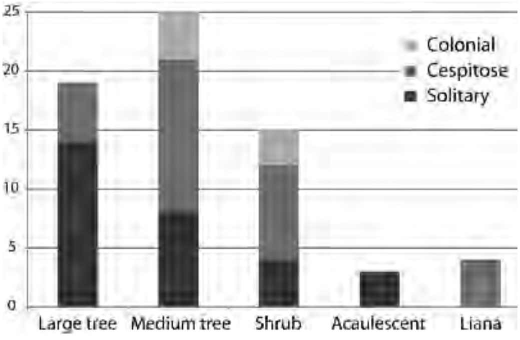
Place	area (x1000 km^2)	Species	Reference
Inkaterra	0.0001	20	Valenzuela et al. 1992
Central French Guiana	0.0013	34	Mori et al. 1997
Iquitos 1 degree square	12	71	Bjorholm et al. 2005
Ucayali	102	59	this study
Ecuador	256	120	Borchsenius et al. 1998
Bolivia	1098	80	Moraes 2004
Peru	1285	140	Kahn and Moussa 1994b
Peru	1285	105	Henderson et al. 1995
Amazon basin	8235	151	Henderson 1995

low compared to the other habitats (disregarding *terra firme* on hills where we made only one transect); the Andean hills were intermediate in species richness and palm abundance (36 species; 1622 individuals/ha) and the terrace palm transects were by far the most dense and species rich palm community in the Ucayali river valley with 6756 individuals per hectare and 44 palm taxa in the transects. These differences between the palm communities show that the diversity of the Ucayali palm flora is driven also by high between-habitat turnover of species, the so-called beta-diversity. Understanding the Ucayali palm community beta-diversity would, however, require further and more detailed sampling.

The four habitats we have defined here separate very coarsely defined types, and within each of them there are much finer divisions that contribute to structuring the palm community. The flood plains have zones with different length and depth of flooding, oxbow lakes, back swamps and several other habitat types. The terraces are rather uniform, but have a fine topographic variation depending on proximity to the creeks that traverses the terraces. The *terra firme* hills have crests, slopes and valley bottoms with differences in the palms occurring in them. Finally the Andean hills have similar divisions depending on slope, humidity, etc., that need more sampling to be described and understood.

Rare and common species – A general feature of ecosystems is that some species (usually a few) are abundant and others (usually many) are rare and scarce. This is also true in the Ucayali palm communities (Tab. 1, Fig. 9). *Lepidocaryum tenue* is by far the most abundant species making up almost 45% of all individuals found in the 8.75 hectares covered by our 35 transects. This super-abundant species had more than five times as many individuals as the second most abundant species, *Geonoma brongniartii*. The reason why some species are very abundant may vary. Some abundant species have wide ecological niches and tolerate great variation in growth conditions; they may be able to grow on both wet and dry soils, on both flat and sloping terrain and in both shade and light exposed places. Others are abundant because they are able to produce very large numbers of individuals when they occur in their favorite habitats. *Lepidocaryum tenue* belongs to this latter category; it was very abundant on the terraces, but absent from the Andean hills and the floodplain transects (Tab. 1). Another very abundant species, *Bactris brongniartii,* is likewise restricted but in this case almost entirely to the floodplains where it forms large colonies in wet depressions. *Genoma brongniartii* and *Oenocarpus bataua,* two other very abundant species, have a more even occurrence in several different habitat types and accordingly represent the other type of abundance, i.e., abundance attained by having a broad ecological niche.

Rare species, likewise, may be rare for different reasons. Among the ten rarest species encountered in our transects, *Chamaedorea pinnatifrons* is very widespread in the western Neotropical area from Mexico to Bolivia, but wherever it is found there are only few and scattered individuals. Others are rare because they have very restricted distribution ranges; *Geonoma triglochin* is an example of a range-restricted species that we found in only one of our 35 transects. Other species are rare because



10. Relative abundances of growth forms (large tree palms, medium sized palms, shrubs, acaulescents, lianas) among the species in the upper Ucayali river valleys, and indication of the relative proportions of solitary, cespitose and colonial species.

they are restricted to special habitats; both *Mauritia flexuosa* and *Mauritiella armata* grow in permanently water logged soils, a habitat that we did not sample well in our transects.

So the observation of a single super-abundant species, several abundant species and a long tail of species with low abundances in our palm community corresponds to a standard pattern in rain forests and in other ecosystems in general. But both abundance and rarity are driven by different mechanisms in different species, so for one to understand the species' relative position along the gradient from the most abundant to the rarest, each species must be looked at and interpreted individually.

Palm guilds – Rain forest organisms are sometimes grouped in guilds, depending on which part of the forest they exploit for resources. The most common growth form among the Ucayali palms was medium sized trees (Fig. 10), i.e., palms with stems up to five meters tall and five centimeters thick, reaching the lower mid-canopy layers in the forest. This category included 25 of the 66 taxa in the Ucayali river valley. Among the medium sized tree palms were very abundant ones such as *Lepidocaryum tenue, Bactris brongniartii, Iriartella stenocarpa* and *Geonoma maxima* var. *chelidonura*. The next most common growth form we found was large tree palms with tall stems to 40 centimeters in diameter and tall enough to reach the canopy; they were represented by 19 species of which the most abundant ones were *Astrocaryum chonta, Oenocarpus bataua* and *Wettinia augusta*. Shrub palms, that is small palms less than a couple of meters tall but with a clearly visible aboveground stem were represented with 15 species in our sample, and these included the very abundant *Geonoma brongniartii* and *Geonoma stricta* var. *trailii*. Acaulescent rosettes, i.e., palms with a subterranean stem and with only the leaves and inflorescences sticking above the ground, were not very rich in species and represented by only two varieties of *Geonoma macrostachys* and by *Aiphanes weberbaueri*, which elsewhere grows with aerial stems, but apparently not in this area. Finally we encountered four taxa of liana palms, all belonging to the genus *Desmoncus* (Fig. 10). This shows that in these upper Ucayali river valley rain forests the largest diversity of palms is found in the mid-canopy level, where 38% of the palm species, i.e., the medium sized tree palms, thrive, whereas the layer above (canopy), where the large tree palms (29%) occur, and below (lower canopy), where the shrub palms (22%) occur, have slightly lower species richness. The ground level (acaulescent rosette palms) and the liana palms make up much smaller fractions (5% and 6%, respectively) of the overall palm species richness. Such division of phylogenetically related species into guilds that occupy different strata of the rain forest have been given as one of the mechanisms that contribute to the packing of very high numbers of species in tropical rain forest ecosystems. Although previous examples have related to birds and other organisms (Terborgh 1992), our observations suggest that it may also be true for palms.

Palm architecture – A little less than half of the palms – 30 of the 66 taxa – in our study area had a cespitose growth, i.e., with stems originating through lateral budding at or below the ground level. Cespitose growth was found in several species in each of the different growth forms except acaulescent rosettes (Fig. 10). Solitary growth was found in 22 species representing all growth forms except the lianas. Solitary growth was particularly common among the large tree palms of which 14 of 19 species were solitary. Colonial growth, in which the stems are attached through below-ground rhizomes and forming dense stands over extended areas, was registered in seven species, four medium-sized trees and three shrubs, and it was absent among the large trees, acaulescent rosettes and lianas (Fig. 10, Tab. 1). Cespitose and colonial growth are two different ways of securing vegetative reproduction whereas the solitary palms depend entirely on sexual reproduction through seeds to survive. This division of the palm guilds into groups with different architecture (cespitose, colonial, solitary) can be interpreted as adaptations of reproductive strategies to divide the community into more complex niche structures in which the species competition is more finely differentiated, eventually making it possible for more species to co-exist and thereby increasing the local species richness.

Leaf architecture – All except four of the species have pinnate leaves. *Mauritia flexuosa* and *Mauritiella armata* have costapalmate leaves, and *Lepidocaryum tenue* and *Chelyocarpus ulei* have palmate leaves. The dominance of pinnate leaves among the species in the Ucayali palm community reflects the prevalence of lineages with pinnate leaves (subfamilies Ceroxyloideae and Arecoideae). The American rainforests are simply very poor in costapalmate and palmate-leaved palms.

After five weeks of field work in the Ucayali region we were tired and ready to go home, but we left the region with a feeling that much more could be done to understand fully the upper Ucayali palm flora. As expected we had encountered a very rich palm community with over 60 taxa and we also found very high local species richness, especially on the terraces above the floodplains. We were only able to scratch the surface of the enigmatic *terra firma* far away from the flood plains and hard to reach. Elsewhere the *terra firme* forest communities are known for their extremely high local species richness, and we would have liked to explore that further. The flood plains were relatively poor in species and also low in overall palm abundance. The palms occupied all strata of the forests from the ground level, where shrubby and acaulescent palms were common, to the canopy in which several large tree palms competed for the favorable light conditions. However, the richest stratum was the mid-canopy where about one-third of the species thrived. Another third of the species were found beyond their previously known distributional ranges, a testimony to the patchy nature of our knowledge of the Amazon palms and palm communities, and a reminder of the need for continued exploration of the magnificent Amazon rainforest and its palms.

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Literature Cited

Barbosa Rodrigues, J. 1875. Enumeratio Palmarum Novarum. Brown & Evaristo, Sebastianopolis.

Barbosa Rodrigues, J. 1903. Sertum Palmarum Brasiliensium, 2 vols. Veuve Monnom, Brussels.

Bjorholm, S., J.-C. Svenning, F. Skov and H. Balslev. 2005. Environmental and spatial controls of palm (Arecaceae) species richness across the Americas. Global Ecology and Biogeography 14: 423–429.

Borchsenius, F., H. B. Pedersen and H. Balslev. 1998. Manual to the Palms of Ecuador. Aarhus University Press, Aarhus.

Henderson, A. 1995. The Palms of the Amazon. Oxford University Press, Oxford and New York.

Henderson, A. 2000. Bactris. Flora Neotropica Monographs 79: 1–181.

Henderson, A., G. Galeano and R. Bernal. 1995. Field Guide to the Palms of the Americas. Princeton University Press, Princeton, New Jersey.

Humboldt, A. von. 1850. Aspects of Nature. Lea & Blanchard, Philadelphia.

Kahn, F. and F. Moussa. 1994a. Las Palmeras de Perú. Instituto Francés de Estudios Andinos, Lima.

Kahn, F. and F. Moussa. 1994b. Diversity and conservation status of Peruvian palms. Biodiversity and Conservation 3: 227–241.

Martius, C. 1823–1853. Historia Naturalis Palmarum, vols 1–3. Weigel, Leipzig.

Moraes Ramirez, M. 2004. Flora de Palmeras de Bolivia. Instituto de Ecologia, La Paz.

Mori, S., G. Cremers, C. Gracie, J.-J. de Granville, M. Hoff and J.D. Mitchell. 1997. Guide to the Vascular Plants of Central French Guiana. Part 1. Pteridophytes, Gymnosperms, and Monocotyledons. The New York Botanical garden, New York.

Spruce, R. 1871. Palmae Amazonicae. J. Proc. Linn. Soc. Bot. 11: 65–183.

Terborgh, J. 1992. Diversity and the Tropical Rain Forest. Scientific American Library, New York.

Valenzuela G., L., G. Calantayud H., J. Farfán V., I. Huamantupa Ch., A. Monteagudo M. and E. Suclli M. 1992. Flórula de la Reserva Ecologica Inkaterra. Missouri Botanical Garden and Inkaterra, Lima.

Wallace, A. R. 1853. Palm Trees of the Amazon and their Uses. Van Hoorst, London.