Mauritia flexuosa palm swamp communities: natural or human-made? A palynological study of the Gran Sabana region (northern South America) within a neotropical context

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Abstract

Mauritia flexuosa L.f. is one of the more widely distributed neotropical palms and is intensively used by humans. This palm can grow in tropical rainforests or can develop a particular type of virtually monospecific communities restricted to warm and wet lowlands of the Orinoco and Amazon basins. It has been proposed that, during the Last Glacial Maximum (LGM), the *Mauritia* swamp communities were restricted to the core of the Amazon basin from where they expanded favoured by the Holocene warmer and wetter climates. It has also been suggested that some of these palm communities might have been the result of human dispersal during the last millennia. Here, we evaluate both hypotheses using the case study of the Venezuelan Gran Sabana (GS) region, where the *M. flexuosa* swamp communities (locally called *morichales*) are common and well developed. The *morichales* did not reach the GS until the last 2000 years, as manifested by sudden increases of *Mauritia* pollen paralleled by similar trends in charcoal particles as proxies for fire. During the last two millennia, the situation was very similar to the present, characterised by extensive burning practices affecting savannas and savanna-forest ecotones but rarely morichales (selective burning). This strongly suggests that human activities could have been responsible for the penetration of the *morichales* to the GS. A meta-analysis of the available records of *Mauritia* pollen across northern South America shows that this palm has been present in the region since at least the last four glacial cycles. During the LGM, *Mauritia* was likely restricted to few but widespread sites of favourable microclimatic conditions (microrefugia) from where the palm expanded during the Holocene. During the last 2000 years, *Mauritia* underwent a remarkable expansion in northern South America, which includes the GS.

It is proposed that humans could have played a role in this regional expansion of *Mauritia* communities.

Keywords: *Mauritia*, palm swamps, Neotropics, human disturbance, paleoecology, last millennia

Introduction

There is an increasing interest on the potential role of historical human activities in the development of current neotropical landscape and biodiversity patterns. Some recent studies suggest that the pre-Columbian human footprint in the Amazon rainforests might be higher than previously thought. However, current palaeoecological evidence does not support the idea of the whole Amazonia as a primarily anthropogenic landscape, as some archaeologists contend. The intensity of human disturbance seems to be unevenly distributed across the Amazon basin, thus hampering generalisations (Bush et al., 2007; Arroyo-Kalin, 2012; McMichael et al., 2012; Levis et al., 2012, ter Steege et al., 2013, Whitney et al., 2014; and literature therein). Palms are among the plants more widely and intensely used by neotropical cultures through history, especially *Attalea butyracea*, *A. phalerata* and *Mauritia flexuosa*, which have been considered hyperdominant Amazon species (ter Steege et al., 2013). Several Amazonian palm forests have been considered as “cultural” forests or the result of past human clearance, management and manipulation; these include the forests dominated by *Astrocaryum vulgare*, *Elaeis oleifera*, and *Mauritia flexuosa*, among others (Balée, 1989; Goldhammer, 1992).

Mauritia flexuosa L.f. (Arecaceae) is among the more widespread palms across tropical South America where it dominates a distinct and peculiar type of wetland ecosystem within rainforest and savanna landscapes. The *M. flexuosa* swamp communities owe their structure and functional features to this dominant palm, which provides the structural complexity and the habitat diversity for the occurrence of a characteristic and unique terrestrial and aquatic flora and fauna that, otherwise, would not occur (e.g.

Marrero et al., 1976; González, 1987; Huber & Febres, 2000; Montaña et al., 2008; Tubelis, 2009). This contributes to enhance neotropical forest, savanna and wetland diversity not only from a taxonomic (α-diversity) but also from a landscape (β-diversity) perspective. The *M. flexuosa* palm swamps are widely distributed across the Orinoco and the Amazon basins and are -and have been historically- heavily exploited by a variety of cultures thus becoming a keystone human resource at a regional level (Kahn, 1991; Kahn et al., 1993; Meerow, 2008; Mesa & Galeano, 2013). *M. flexuosa* has been considered the more widely distributed and the more widely used South American palm (Kahn, 1988; Gragson, 1995). Therefore, it is pertinent to investigate to what extent the distribution and development of these palm communities has been influenced by human activities, an enquiry that may shed light on the potential influence of pre-Columbian cultures on neotropical landscapes and biodiversity. Of additional interest is the fact that the *M. flexuosa* palm wetlands have been considered preferred conservation targets as potential refugia for their unique biota (González & Rial, 2011; Machado-Allison & Lasso, 2011) and also as important ecosystems for the protection of watersheds (Tubelis, 2009).

In the Gran Sabana (SE Venezuela), *M. flexuosa* forms characteristic monospecific stands, locally called “morichales”, mostly within open savanna landscapes, along water courses and lake shores (Huber & Febres, 2000; Delgado et al., 2009). Similar communities are widespread across the savannas of the Orinoco Llanos of Venezuela and Colombia (González & Rial, 2011). Based on the present-day spatial arrangement of plant communities, some ecologists have considered the morichales as the initial stages of rainforest succession by providing an adequate microclimate for tree growing (González, 1987; Marrero, 2011). However, palaeoecological studies have shown that, rather, these palm communities have established after forest burning and soil degradation, followed by the onset of regional wetter climates (Rull, 1992). Burning is a common practice in the Gran Sabana and fires have been important drivers in the shaping of modern landscapes (Montoya & Rull, 2011). These fires usually affect large extensions of savannas and, occasionally, forest-savanna ecotones thus favouring savanna expansion and precluding forest recovery. The morichales are less affected by burning, except in the case of uncontrolled fires. The resources provided by *M. flexuosa* are and have been used historically by the indigenous inhabitants of the Gran Sabana, the “Pemón” people, mainly for food, fiber and housing materials. These resources are obtained by direct morichal exploitation (gathering), no cultivation practices have been observed or documented in the region in relation to *Mauritia* palms.

The whole picture suggests landscape management by fire favouring savanna expansion but the role of fire on the establishment and/or the persistence of morichales has not been fully addressed. Another question is for how long these fire practices have been operating. Owing to the lack of written history –the Pemón culture is exclusively based on oral transmission (Roroimökok Damük, 2010)- and the absence of archaeological studies (Gassón, 2002), palaeoecology seems to be the better suited approach to disentangle the socio-ecological history of the Gran Sabana. This paper analyses the palaeoecological studies carried out in the Gran Sabana encompassing the last millennia, in order to test whether human activities have been decisive for *M. flexuosa* establishment and expansion. The potential role of climate and of eventual synergies between climate and human disturbance are also considered. Vegetation dynamics are reconstructed by pollen analysis and fire incidence is deduced from charcoal records. Climatic trends are inferred from independent physicochemical evidence and/or from the available regional reconstructions. The paper begins with a biogeographical and ecological review of the palm species including human uses and potential exploitation. Then the Gran Sabana region is succinctly described and their palm swamps are characterised in more detail. The third part reviews the available palaeoecological records of the Gran Sabana, in order to unravel the origin of their *Mauritia* swamps and the potential role of humans in this process. Finally, these palaeocological studies are placed in the neotropical context by reviewing other studies from the Amazon and the Orinoco basins in which *Mauritia* occurs as an important element. The conclusions section summarises the information obtained from the former reviews, in relation to the potential role of either natural and human causes, or both, on the occurrence and distribution of extant *Mauritia* palm swamps.

***Mauritia flexuosa*: biogeography, ecology and uses**

Biogeographical and ecological overview

M. flexuosa is a straight-stemmed, tall (up to 30-40 m high) dioecious palm species with 8-25 large (up to 6 m long) costapalmate leaves and 8 inflorescences, on average (Fig. 1). The fruits are oval-shaped, small (5-7 cm long and about 7 g in weight) drupes covered by red scales (Delgado et al., 2007). The pollination of the species is still under discussion. Indeed, despite former proposals of several insects -notably beetles- as pollinators (Barfod et al., 2011), it has been suggested recently that *M. flexuosa* is a wind-pollinated species (Korshand Rosa & Koptur, 2013). This palm is widely distributed across tropical South America at both sides of the Equator, between approximately 12º N and 20º S, but it is restricted to the Orinoco and the Amazon

Figure 1. *Mauritia flexuosa* in the Gran Sabana. A) Crowns of two mature female individuals. B) Light palm stand around Lake Encantada. C) Closer view of the fruits, which size is similar to a chicken egg. D) Typical indigenous (Pemón) house which roof is made of *M. flexuosa* leaves (*Kako-parú* community, near Mapaurí). Photos V. Rull.

lowlands being absent from the Andes, the Pacific coasts and most of the Brazilian Atlantic coasts (Fig. 2). Between the Oligocene and the middle Miocene, the *Mauritia* ancestor -represented by the fossil morphospecies *Mauritiidites franciscoi*- was more widely distributed between the Atlantic and the Pacific coasts but the Middle-Late Miocene Andean uplift broke this pattern and restricted the range to the newly created Orinoco and Amazon basins (Rull, 1998). At present, the species of *Mauritia* (*M. carana* and *M. flexuosa*) and those from its sister genera *Mauritiella* (*M. aculeata* and *M. armata*) and *Lepidocaryum* (*L. tenue*) are restricted to these two basins; the only exception is *Mauritiella macroclada*, living on the northernmost Pacific coasts close to the Panama Isthmus (Henderson et al., 1995), which has been interpreted as the result of allopatric speciation after the emergence of the Andean barrier (Rull, 1998). Some authors combine the genera *Mauritia* and *Mauritiella*, but there are consistent differences in flower clusters and habits (Dransfield et al., 2008). Common names for

Figure 2. Map of tropical South America showing the main physiographic regions referred in the text (A) and the known distribution of *Mauritia flexuosa* (B). The red star shows the position of the planted *M. flexuosa* community called "Morichalito", referred in the text (Delascio, 1999).

M. flexuosa are diverse and vary according to the country; the more usual are “moriche” (Venezuela), “burití” (Brasil), “canangucho” (Colombia), “aguaje” (Perú), “palma real” (Bolivia), “ita” (Guyana) and “morete” (Ecuador). Accordingly, the characteristic communities dominated by the species are called “morichales”, “buritizais”, “canangunchales”, “aguajales”, etc.

M. flexuosa is confined to the lowlands (usually below 1000 m elevation) where it finds the required warm/wet climates needed for an optimal development (Rull, 1998). Although it can occur as one more component of the lowland rainforests (Cabrera & Wallace, 2007), this species is particularly abundant in permanently flooded soils –the presence of pneumatophores allows growing in anaerobic conditions (Delgado et al., 2007)- where it develops more or less dense and almost monospecific palm swamps. These characteristic communities can occur both in forest and savanna landscapes. In forested areas, the *M. flexuosa* palm swamps are typical of the interfluvial depressions that remain flooded during the dry season, when the surrounding terrains dry out (Kahn et al., 1993; Urrego, 1997). In the Orinoco delta and the Amazon estuary, *M. flexuosa* forms dense and extensive communities flooded by freshwaters reaching, but not crossing, the tidal boundary (Huber, 1995c; White et al., 2002; Vegas-Vilarrúbia et al., 2007). In more open landscapes, as for example the Orinoco savannas (including the Gran Sabana) and the Brazilian “cerrados”, these palm swamps occur chiefly along water courses and in lake shores, preferably on permanently or seasonally flooded soils (González, 1987; Montes & San José, 1995; Ratter et al., 1997; Sampaio, 2011). In spite of the biogeographical, ecological and economical importance of *M. flexuosa* palm swamps, detailed studies on their composition are rare (Endress et al., 2013). Some examples are provided at following.

In the Colombian Amazon region, the *M. flexuosa* palm swamps were grouped into the *Marliereo umbraticolae-Mauritietum flexuosae* association and described in detail by Urrego (1997). This is the more diverse community found within the rainforest floodplains with more than 300 species recorded, distributed into three strata. The canopy is dominated by *M. flexuosa*, *Virola surinamensis* (Myristicaceae) and *Marlierea spruceana* (Mytaceae), among others, whereas the more important species of the understory are *Macrolobium angustifolium* (Fabaceae) and *Qualea ingens* (Vochysiaceae), and the herbaceous stratum is dominated by the ferns *Adiantum tomentosum* and *Metaxya rostrata*, and the bromeliad *Pitcairnia sprucei*. This association grow on soils flooded for most of the year due to both river overflow and precipitation (Urrego, 1997).

A quantitative study developed in the Peruvian Amazonia reported 138 tree species belonging to 36 families, with *M. flexuosa* as the more common species (128 indiv/ha, representing over 40% of the basal area), followed by other palms (*Euterpe* and *Socratea*), as well as *Hevea* (Euporbiaceae) and *Virola* (Myristicaceae), all of them with ~50 indiv/ha or more. Taken by families, palms were the major component of the overstory (Endress et al., 2013). Despite the dominance of *M. flexuosa*, these communities are not monospecific showing considerable structural and compositional complexity, in contrast with similar palm swamps from other areas, especially those from more open landscapes, as for example savannas and cerrados. Destructive harvesting may account for very low densities of large woody species, such as *Virola pavonis*, which has been heavily exploited historically. Similar *Mauritia*-rich forests occur in the Ecuadorian Amazonia, where the soils are flooded up to about 2 m depth for ca. 200 days per year. In this case, *M. flexuosa* is accompanied by other palms such as *Bactris*, *Geonoma* and *Iriartea*, as well as by trees of the genera *Alchornea* (Euphorbiaceae), *Casearia* (Flaccourtiaceae), *Cecropia* (Cecropiaceae), *Mabea* (Euphorbiaceae), *Pourouma* (Moraceae) and *Pouteria* (Sapotaceae), among others (Bush et al., 2001).

The so-called "várzea" forests, in the Brazilian Amazonia, are periodically flooded by white-water rivers. One type of these forests is largely dominated by *M. flexuosa* and another palm, *Euterpe oleracea*, followed by *Virola* (Myristicaceae), *Tapirira* (Anacardiaceae), *Inga* (Fabaceae), *Pterocarpus* (Fabaceae) and *Ficus* (Moraceae) (Batista et al., 2011).

M. flexuosa also occurs as a minor component in the upland and lowland Amazon rainforests. For example, in the Peruvian Amazonia, this palm may occur in abundances around 10% in seasonal swamp forests dominated by other palms such as *Bactris*, *Jessenia*, *Geonoma* and *Euterpe* (Kahn & Mejía, 1990). In the Bolivian Amazonia under high-precipitation regimes (~3000 mm per year) with a short dry season between July and September, *Mauritia* occurs in lowland evergreen forests dominated by trees from families like Moraceae, Melastomataceae, Lauraceae, Fabaceae and Arecaceae. Among palms, the more abundant are *Geonoma*, *Oenocarpus*, *Bactris* and *Chamaedorea* (Cabrera & Wallace, 2007). *M. flexuosa* also occurs as a minor element in most of the floodable rainforests of the Colombian Amazonia (Urrego, 1997). In the Venezuelan Amazon region, *Mauritia* is typical of truly flooded forests growing on oxisols or ultisols from floodplains, where this palm coexists with other representatives of the same family (notably *Euterpe* and *Manicaria*), as well as of trees from others such as Apocynaceae (*Aspidosperma*), Fabaceae (*Pterocarpus*), Mimosaceae (*Parkia*), Lecythidaceae, Myrtaceae and Sapotaceae. *Mauritia* also grows on permanently inundated floodplains on oxisols, where it coexists with *Aspidosperma*, *Ormosia* (Fabaceae) and *Chaunochiton* (Olacaceae) (Huber, 1995c).

A typical palm swamp from the Orinoco basin is dominated by *M. flexuosa*, which form a closed canopy significantly reducing light penetration. Besides this typical structure, these communities may vary from savannas with isolated *M. flexuosa* individuals to swamp forests dominated by *Symphonia globulifera*, *Virola surinamensis* and *Protium heptaphyllum* (Burseraceae), with emerging *M. flexuosa* representatives - other components are *Cecropia* (Moraceae), *Euterpe* (Aracaceae), *Coccoloba* (Polygonaceae) and *Tapirira* (Marín et al., 2007; Dezzeo et al., 2008). There is a gradual transition in space between these two types of communities, with the closed palm swamp as an intermediate stage, which has been considered a chronosequence, that is, the spatial manifestation of a successional process (González, 1987; Marrero, 2011). In the Orinoco delta, these communities grow on deep and extensive peat accumulations until the tidal limit (middle delta, above 20 m elevation), where *M. flexuosa* is replaced by typical mangrove species such as *Rhizophora racemosa* and *Laguncularia racemosa*, with isolated individuals of the palm *Euterpe predatoria* and communties dominated by *Montricardia arborescens* (González & Rial, 2011). In these coastal environments, *M. flexuosa* can be found also as the dominant species of the typical palm swamps or in combination with *Symphonia*, *Virola*, *Carapa*, *Pterocarpus*, *Mora*, *Pachira* and other palms, on seasonally flooded terrains (Huber, 1995c). Another type of almost monospecific palm swamp occurs in permanently flooded areas of the Peruvian

Amazonia, where *M. flexuosa* dominates the canopy accompanied by *Geonoma*, *Oenocarpus* and *Euterpe* (Kahn & Mejía, 1990).

In contrast to other Amazon wetland forests, in which distribution is associated with geological and geomorphological features, the geographical distribution of *Mauritia* palm swamps seems to be almost independent of these physical factors and more linked to climatic conditions and flooding regime (De-Campos et al., 2013). The control of climate, especially precipitation seasonality, on *M. flexuosa* phenology was demonstrated by a study in the Roraima region of Brazil, where both male and female flowering occurred at the transition between wet and dry season (August-November) and fruit maturation took place during the wet season (May-August). This seems to be a general phenological feature over the distribution area of *M. flexuosa* (Urrego, 1987), but it should be taken into account that dry and wet seasons vary north and south of the Equator (Gragson, 1995). The influence of other physical factors was, as in the case of geographical distribution, negligible (Khorsand Rosa et al., 2013). In less seasonal climates, flowering and fructification can occur during the whole year, although the major abundance of fruits has been observed between August and October (Delgado et al., 2007).

The *Maurita* palm swamps are inhabited, permanently or temporarily, by many animal species. For example, in Perú, Gurgel-Gonçalves et al. (2006) found 135 species of insects and arachnids, the more important groups being Coleoptera (29%), Blattodea (22%), Collembola (11%) and Hemiptera (10%). Some crustaceans were also present. Among insects, it is especially worth mentioning the presence of *Rhodnius neglectus* (Hemiptera), suspected to transmit the protozoan *Trypanosoma cruzi*, the responsible for the Chagas disease (Gurgel-Gonçalves et al., 2003). Among birds, parrots (*Ara*, *Orthopsittaca* and *Amazona*) are the main fruit consumers, followed by tanagers (*Tangara* and *Schistochlamys*), hawks (*Caracara*), jays (*Cyanocorax*), and blackbirds (*Gnorimopsar*). *Orthopsittaca manilata* (the red-bellied macaw) is a key species for seed dispersal (Marín et al., 2007; Villalobos & Bagno, 2012). In the cerrados, it has been reported that none of the ~250 birds species that visit the *Mauritia* communities is restricted to them, although these palm swamps are important habitats for the biological cycle of ca. 30% of these bird species (Tubelis, 2009).

Fishes are also noteworthy components of the palm swamp ecosystems. Montaña et al. (2008) reported 107 fish species in a Venezuelan *M. flexuosa* swamp, corresponding to small-bodied cichlids, characins, lebiasinids, and silurids. Fish diversity was significantly higher in the palm swamp than in nearby river banks devoid of this vegetation type, likely due to the enhanced micro-habitat diversity created by the submerged aquatic and semi-aquatic vegetation (Montaña et al., 2008). On the same note, Antonio & Lasso (2001) reported the highest fish diversities of the Orinoco basin in the river Morichal Largo, whose gallery forest is a huge *M. flexuosa* swamp, with 109 species belonging to 9 orders. Similar results were obtained in the Orinoco delta (Campo, 2004). Among mammals, monkeys of the genus *Cacajao* (uakaris) and *Lagothrix* (woolly monkeys) actively eat *Mauritia flexuosa* fruits, especially during the dry season, when the availability of other fruits is low (Boubli 1999; Bowler & Bodmer, 2011). Other fruit consumers are Peccaris (*Tayassu*, *Peccari*), tapirs (*Tapirus*), deers (*Mazama*), rodents (*Agouti*, *Cuniculus*, *Dasyprocta*) and turtles (*Peltocephalus*, *Rhinoclemmis*) (Pérez-Emán & Paolillo, 1997; Cabrera & Wallace, 2007; Delgado et al., 2007; Rojas-Runjaic et al., 2011).

Human uses and exploitation

Mauritia flexuosa has been called by some cultures the "tree of life" because, owing to the varied resources it provides, these cultures are highly dependent on this palm in many basic aspects of their quotidian life such as nutrition, housing or clothing (Triana & Molina, 1998). Almost every part of this palm, from the roots to the leaves, can be harnessed. As in many other palms, the resource more used by humans is the fruit (Fig. 2), whose pulp may be eaten directly or may be used to prepare beverages (fermented or not), ice creams and cakes, and also to extract flour and oil. The oil is used for cooking and for treating dry hair, as well as to healing wounds and bites and to cure respiratory and heart problems (Kahn et al., 1993; Sampaio, 2011; Martins et al., 2012). The usual consumption of *M. flexuosa* fruits has been associated with a low risk of cardio-vascular diseases (Lares et al., 2011). This fruit is very rich in iron and vitamins, especially in vitamin A (ca. 20 times higher than carrots) (Sampaio, 2011), which might be useful to preventing deficiencies in local populations (Santos, 2005). In general, the *M. flexuosa* fruits are an important source of calories, proteins and vitamins for indigenous cultures (Meerow, 2008). The detailed chemical composition of the *M. flexuosa* fruit can be found in Silva et al. (2009). The stony seed is called "plant ivory" and is used in handycrafts (González & Rial, 2011; Trujillo et al., 2011), and also to help women during childbirth, once roasted and converted to powder (Martins et al., 2012). The nut is also used as an abortifacent (Gragson, 1995).

The leaves are used for thatching houses (Fig. 2) and also as a source for fibre to make baskets, fishing nets, curtains, hammocks and a variety of domestic ornaments and handicrafts (Kahn et al., 1993; Heinen et al., 1996; Gragson, 1995; Macía, 2004;

Rondón, 2005; Sampaio et al., 2008; Trujillo et al., 2011; Martins et al., 2012). They are also used in hunting rituals (Lewy, 2012). The stem may be utilised to build floating bridges on aquatic vegetation (Kahn et al., 1993). The stipe is rich in starch and is used to make flour for preparing bread and also to obtain a pap to treat dysentry and diarrhea (Heinen & Ruddle, 1974; Plotkin & Balick, 1984). The sap extracted from the stem can be drunk straightforward or be fermented to produce "palm wine", used for current consumption and also against diabetes (Martins et al., 2012). Another particular feature of the stipe is that, once pulled down and resting on the ground, is the substrate for the development of the so called "palm worms" (larvae of the coleopteran species *Rhynchophorus palmarum*), which are actively consumed by the indigenous people. These larvae have a high nutritional value for their content in fats, carbohydrates, proteins, vitamins A and E, as well as oils and minerals (Cerda et al., 2001). Pieces of *Mauritia* stems ("toras") are also used in ritual sports such as the "corrida da tora" (tora race) (Melatti, 1976; Nascimento et al., 2009). The roots are used to alleviate rheumatism symptoms (Martins et al., 2012). More detailed accounts of the traditional use of the diverse parts of *M. flexuosa* can be found in Heinen et al. (1996), Ponce et al. (2000), Martins et al. (2012), Santos & Coelho-Ferreira (2012) and Gilmore et al. (2013).

In addition to the direct resources obtained from *M. flexuosa* itself, other indirect benefits are derived from the use of other species associated with the palm swamps. For example, some indigenous groups use over 60 plant species (notably the palms *Astrocaryum*, *Attalea*, *Bactris*, *Desmoncus*, *Euterpe*, *Geonoma*, *Mauritiella*, *Oenocarpus* and *Socratea*) and hunt 20 animal species (mainly birds, mammals and turtles) living in these communities (Gilmore et al., 2013). Fishing is also an important practice (Gragson, 1995).

It has been suggested that some *Mauritia* swamps from the Amazon basin have been cultivated in the past by indigenous people (Triana & Molina, 1998) but no conclusive evidence has been provided so far. It has also been proposed that "the great extension of *Mauritia flexuosa* throughout and beyond the Amazon basin is likely to be the result of transport by humans" (Kahn & de Granville, 1992, p. 109) but factual support is equally lacking. Some archaeological studies based on seed records developed in the Colombian Amazonia suggest that *M. flexuosa* was exploited *in situ* by hunter-gatherer cultures since the early Holocene (Morcote-Ríos et al., 1998), which would provide indirect support to a potential role of humans in *Mauritia* expansion. Current cultivation experiences are scarce, although several proposals including specific recommendations are available (e.g. Triana & Molina, 1998; Vásquez et al., 2008; Sampaio, 2011). The better known cultivation experiences are in Perú, where several plantations are under exploitation and a research institute is conducting experiments on seed selection and germination (Delgado et al., 2007), and Venezuela, where some artificial plantations exist (Delascio, 1999). Some preliminary research on genetic features and germplasm viability has been conducted (Gonzales et al., 2006; Gomes et al., 2011; Menezes et al., 2012) but the potential application of these studies to cultivation practices is still in its infancy.

A handicap for successful cultivation is that *M. flexuosa* is a dioecious species and the sex of a given individual is not evident until maturity (7-8 years) and, therefore, the proportion of female plants in a crop able to produce fruits is hardly predictable (Kahn et al., 1993; Delgado et al., 2007). Commercial fructification occurs at the age of 12 to 20 years (Delgado et al., 2007). A potential pest for *M. flexuosa* is the moth *Eupalamides cyparissias*, which seems to have infested the palm species relatively recently (Delgado & Coutourier, 2003). A total of 13 phytophagous insects have been reported as potential pests for *M. flexuosa*, including butterflies, coleopters, aphids and shield bugs (Delgado et al., 2007). The more widespread opinion is that *Mauritia flexuosa* could provide significant economic gains for local human populations but *in situ* exploitation of the existing palm swamps, rather than intentional cultivation, is recommended (Kahn et al., 1993; Meerow, 2008; Virapongse et al., 2013). However, to ensure the proper continuity of this type of exploitation, it is indispensable to turn current extraction practices into more sustainable ones (Sampaio et al., 2008; Horn et al., 2012). For example, the widespread practice of palm felling for harvesting fruits should be replaced by the more classical and more sustainable climbing tradition (Holm et al., 2008; Manzi & Coomes, 2009; Endress et al., 2013). For example, low densities and the predominance of male over female individuals have been considered a sign of historical *Mauritia* over-exploitation using non-sustainable destructive practices (Kahn, 1988; Horn et al., 2012; Endress et al., 2013). There is also a current trend to promote industrial production and international distribution. Apparently, market demand for *Mauritia* fruits is increasing, at least in some places as for example in Perú, but several handicaps exist for suitable and sustainable production, namely adequate farming techniques, promotion and appropriate distribution channels (Ponce et al., 2000; Delgado et al., 2007; Horn et al., 2012).

Sometimes, *M. flexuosa* palm swamps are heavily exploited and require urgent conservation measures. For example, a study carried out in the Brazilian cerrados reported that most of the palm swamps surveyed were exploited by local farmers, and that almost half of these land owners were strongly dependant on *M. flexuosa* resources. The main activities were fruit harvesting, slash-and-burn agriculture, and cattle and pig farming. As a result, vegetation dynamics and structure, forest regeneration, water quality and soils were being severely affected (Sampaio et al., 2012). The *M. flexuosa* palm swamps are strongly affected by anthropic fires, whose main aims are to facilitate hunting and to promote pasture regrowth thus facilitating its consumption by cattle. Fires are especially active at the end of the dry season, when both aridity and dry biomass accumulation favour ignability. Some fires are superficial and burn only ground gasses, sedges and seedlings while others can reach the tree canopy and kill the palms by burning the growth buds. At present, fire is the more important environmental driver affecting palm swamp occurrence and distribution (González & Rial, 2011). However, fire is also an important element for *Mauritia* palm swamp management and the "best" practices in this sense have been explicitly described (e.g. Sampaio, 2011).

The Gran Sabana

Main landscape features

The GS is a region of approximately 18,000 km^2 located in southeastern Venezuela between the Orinoco and Amazon basins (Huber & Febres, 2000). It is part of a huge savanna patch, the Roraima savannas, with almost 70,000 km^2 shared by Venezuela, Brazil and Guyana, which lies within the dense and extensive Guayana and Amazon rainforests (Barbosa & Campos, 2011). The whole GS region is covered by a thick sedimentary layer of Precambrian sandstone and quartzite, spiked with intrusive rocks (mostly diabase) that penetrated this sedimentary cover during the Paleozoic and Mesozoic (Briceño et al., 1990). Geomorphologically, the GS is an undulated erosion surface developed on the Roraima sediments that forms an *altiplano* slightly inclined to the south, ranging from approximately 750 to 1450 m in elevation (Briceño & Schubert, 1990). Soils developed on the Roraima Group are mostly savanna oxisols, which are highly weathered and poor in nutrients, highly acidic and have very low cation exchange capacity. Soils originating from diabases are lower in silica and richer in nutrients, thus being more capable of supporting dense forests. Shallow inceptisols are common in floodplains and on mountain slopes.

Huber (1995a) classified the climates of the Venezuelan Guayana into six major types, of which two are present in the region under study. The submesothermic ombrophilous climate occurs between 500 and 1200 m elevation and is characterized by average temperatures between 18 and 24 ºC and 2000-3000 mm of total annual precipitation with a weak dry season from December to March. In the southern GS, the climate becomes submesothermic tropophilous, which is less humid (1600-2000 mm/year) and more seasonal, likely due to local rain shadows. The GS is mostly covered by treeless savannas dominated by grasses of the genera *Axonopus* and *Trachypogon*, accompanied by sedges such as *Bulbostylis* and *Rhynchospora*. Woody elements are rare in these savannas, and they are restricted to stunted plants that do not emerge above the herb layer (Huber, 1995c). Most GS forests are considered to fall within the category of lower montane forests because of their intermediate position between lowland and highland forests (Hernández, 1999). These forests are highly diverse and their composition varies with elevation (see Hernández et al., 2012, for more details). Gallery forests are also common along rivers and on lake shores. The GS shrublands usually occur between 800 and 1500 m elevation and are more frequent at the northern area than at the southern part (Huber, 1995c).

The morichales

In the GS, the *M. flexuosa* palm swamps, locally called morichales, develop on the wide alluvial plains of the Kukenán and Yuruaní valleys associated with seasonally flooded areas on lake shores and along water courses (Fig. 3). The total area of these morichales has been estimated in ca. 50,000 ha (Delgado et al., 2009). The upper elevational boundary of the morichales is approximately 1000 m (Huber & Febres, 2000); the uppermost morichal recorded in our extensive 2007 fieldtrip was found at 5º 8’ 28.4” – 61º 06’ 01.4” W and 1005 m elevation. Leal et al. (2013) report a *Mauritia* swamp at 1040 m elevation. However, the finding individual *M. flexuosa* representatives above this elevational boundary should not be dismissed, as we recorded three isolated palms of this species between 1240 and 1270 m elevation, within treeless savanna landscapes (Fig. 3). Climatically, the GS morichales occur in a broad precipitation range represented by a W-E gradient ranging from 3500 mm (Wonkén) to 1500 mm (Santa Elena) of total annual precipitation. Temperature seems to be more restrictive as the morichal communities commonly occur in areas with annual averages above 21ºC, which roughly coincides with the 1000 m contour. As a result, the morichales are restricted to the southernmost part of the GS, usually below 5º latitude N, between 750 and 1000 m elevation (Huber, 1995c). Soil moisture is guaranteed during most of the year, even during the driest month (February), when monthly precipitation is around 60 mm in the drier side (Santa Elena) and above 80 mm in the wetter sector (Wonkén) (Huber 1995a).

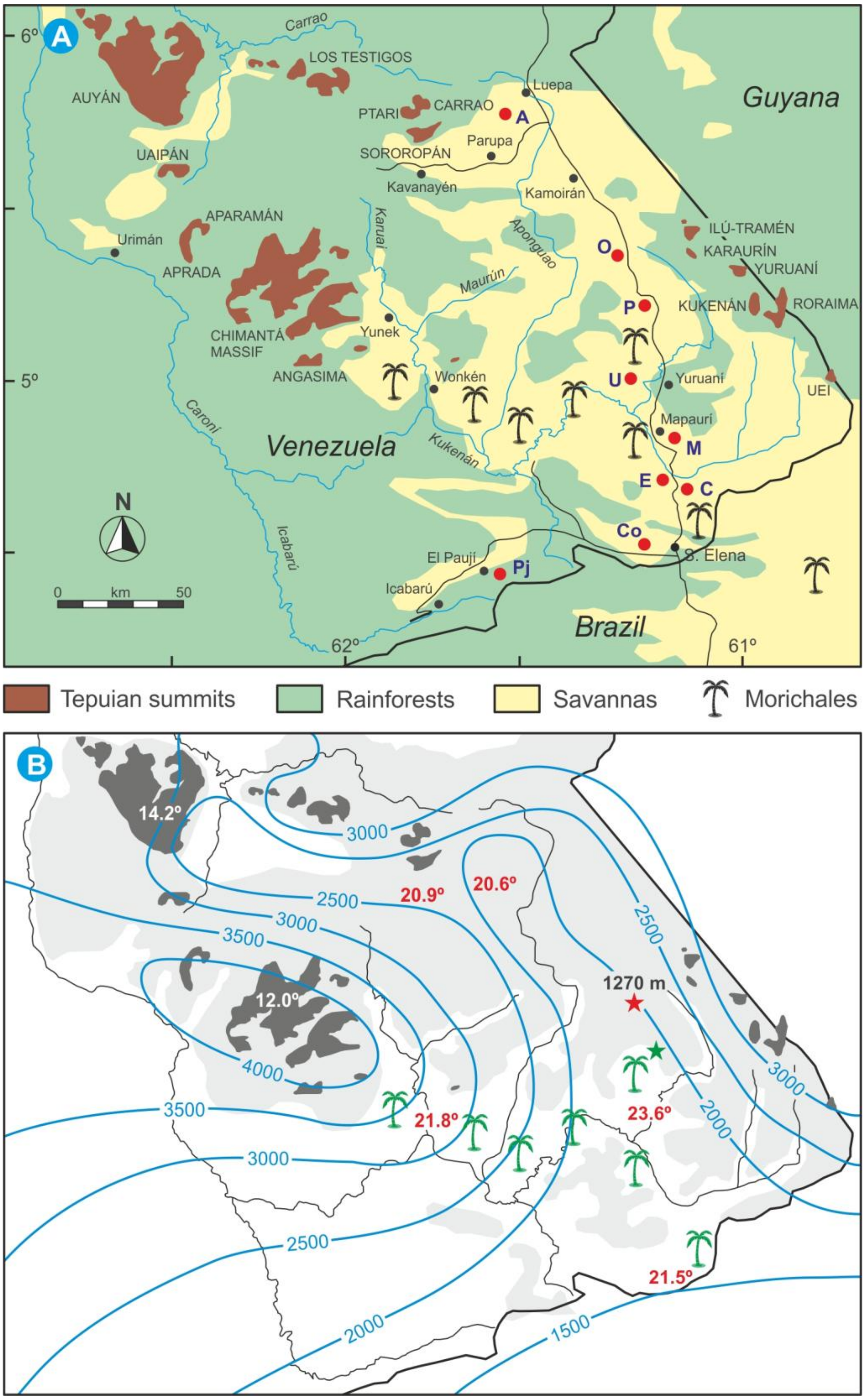

Figure 3. Map of the Gran Sabana. A) General map showing the main rainforest and savanna areas (shrubland patches occur within both of these vegetation types and are not represented). Sampling sites discussed in the text are represented as red dots. A – Ariwe, C – Chonita, Co – Colonia, E – Encantada, M – Mapaurí, O – El Oso, P –

Pacheco, Pj – Paují, U – Urué. B) Precipitation trends (blue lines) and annual average temperatures (red text) measured in the GS weather stations are displayed. The grey area indicates the terrains above 1000 m elevation and the white areas those areas below this elevation. The green star indicates the highest morichal community recorded in our 2007 fieldtrip and the red star shows the position of the isolated *M. flexuosa* records above 100 m elevation observed during the same campaign (see text for more details). Topographic, climatic and vegetation features based on Schubert & Huber (1989), Galán (1992), Huber (1995a), Huber & Febres (2000), Delgado et al. (2009).

An unpublished study carried out in the morichales of the Yuruaní river (Terán & Duno de Stefano, 1988; cited by Huber, 1995b, and Huber & Febres, 2000) distinguished three different strata in these communities. The lowermost herbaceous stratum was significantly more diverse than the surrounding savannas and was dominated by several grasses (*Andropogon*, *Schizachyrum*, *Panicum*, *Ischaemum*, *Thrasya*, *Echinolaena*), sedges (*Rhynchospora*, *Cyperus*, *Lagenocarpus*), Eriocaulaceae (*Eriocaulon*, *Phyllanthus*), Xyridaceae (*Xyris*) and Heliconiaceae. The intermediate stratum was characterised by several shrubs of the families Clusiaceae (*Mahurea*) Onagraceae, Melastomataceae (*Miconia*), Piperaceae (*Piper*), Sterculiaceae (*Byttneria*, *Waltheria*), Malvaceae and Asteraceae, whereas the uppermost stratum was composed of the dominant palm *M. flexuosa*. Close to the Gran Sabana, around the Auyan-tepui massif (Fig. 3), a detailed study of a morichal situated around 500 m elevation revealed the occurrence of 33 species of vascular plants distributed into a 12-m high *Mauritia* canopy, a shrubby stratum with *Rhynchanthera* (Melastomataceae) and *Turnera* (Turneraceae) and a herbaceous layer with *Chelonanthus* (Gentianaceae), *Urospatha* (Araceae), *Pterogastra* (Melastomataceae), *Buchnera* (Scrophulariaceae), *Rhynchospora* (Cyperaceae), *Rhytachne* (Poaceae) and *Eriocaulon* (Eriocaulaeae), among others. The morichal-savanna ecotone was characterised by *Echinolaena* (Poaceae), *Hyptis* (Lamiaceae), *Sipanea* (Rubiaceae), *Melananthus* (Solanaceae), *Polygala* (Polygalaceae) and *Macairea* (Melastomataceae) (Rodríguez & Colonello, 2009).

As stated above, the *M. flexuosa* palm swamps create suitable niches for peculiar faunal components that would not occur under other conditions. In the GS, some examples among the mammals are the otter (*Lontra longicaulis*), bats (*Noctilio*, *Micronycteris*, *Uroderma*), rats (*Proechimis*), mices (*Oecomys*), peccaries (*Tayassu*), the red brocket (*Mazama americana*) or the paca (*Agouti paca*). Characteristic birds of the GS morichal are the red-shouldered macaw (*Ara nobilis*), one of the main *Mauritia* fruit consumers, and the palm swift (*Tachornis squamata*), the oriole (*Ictherus chrysocephalus*) and the flycatcher (*Tyrannopsis sulphurea*), which build their nests in the *Mauritia* leaves. The GS morichales are also preferred breeding sites for diverse frogs and toads of the genera *Hyla*, *Scinax* and *Elachistocleis*. Reptiles such as caimans (*Paleosuchus trigonatus*), tupinambis (*Tupinambis teguixin*) or anacondas (*Eunectes murinus*) are also typical of these morichales (Huber & Febres, 2000).

Human occupancy and fire

The GS region is presently the homeland of the Pemón indigenous group, living in small villages, usually in open savannas. Although the GS population density is relatively low, the indigenous settlements have experienced an expansion since the arrival of modern-day European missions, and today more than 17,000 people live in GS (Medina et al., 2004). The date of arrival of the Pemón people at GS is still unknown. Based mainly on historical documents, it has been postulated that this culture settled in GS approximately 300 years ago, coming from Guyana to the east (Thomas, 1982; Colson, 1985), or approximately 500-600 years ago, migrating from Brazil, to the south (Huber, 1995a). In either case, these accounts do not necessarily represent their first arrival, so an early human occupation by the Pemón or other cultures cannot be dismissed. There is some archaeological evidence consisting of pre-Hispanic remains (spearheads and bifacial worked knives), similar in style to others about 9000 years old found in other Venezuelan localities (Gassón, 2002). Therefore, a definitive assessment is not yet possible.

Fire is a key component of the Pemón culture and they use it every day to burn savannas and the adjacent forests (Kingsbury, 2001). With time, the cumulative effects of these fires become evident in vast burnt areas that display different successional stages of re-colonization by savannas. In addition to the slow and continuous savanna expansion due to the edge effect of fires on the forest-savanna ecotone, accidental uncontrolled fires burning huge forest areas have also been observed on occasion (Fölster, 1986). The reasons for the extent and frequency of these fires include activities such as cooking, hunting, fire prevention, communication and magic, among others (Rodriguez, 2007). Surprisingly, land-use practices such as extensive agriculture or cattle raising, typical of other cultures strongly linked to fire, are not characteristic of the Pemón culture (Rodriguez, 2004a). The large number of fires today in the GS uplands (~10,000 each year; Huber, 1995d) are essentially human-made, which has resulted in a debate related to the sustainability of the present landscape and the possible factors that led to its development (Rodriguez, 2004b; Dezzeo et al., 2004; Rull, 2009a). It is estimated that most of the GS areas are burned every 1-3 years (Hernández and Fölster, 1994).

From a conservation perspective, fire is a key factor to consider. The GS region is under several protection figures including national parks, natural monuments, biosphere reserves and world heritage sites (Huber, 1995d) but, as it occurs in other neotropical areas (e.g. Nepstad et al., 2006), this has not inhibited fire practices. In addition, there is a special protection figure for the Venezuelan morichales that explicitly prohibits the use of fire (Anonymous, 1991). Since 1981, the government of the region has developed several actions focused mainly on direct fire suppression. The main executor has been the hydroelectric company called EDELCA, which developed extensive fire-fighting policies to protect the headwaters of the Caroní river, one of the main water suppliers of the downstream dams (EDELCA, 2004). However, the low effectiveness obtained (about 13% of fires are controlled and extinguished) has called the utility of these expensive measures into question (Sletto, 2008; Bilbao et al., 2010). This low success rate is mainly due to (i) the large extension of the area to monitor; (ii) the high number of daily fires; (iii) a bias in fire control measures focused only in specific locations; and (iv) the anthropogenic character of fires, which make any kind of prevention measures difficult (Rodriguez, 2007; Bilbao et al., 2010). An evident complication to deal with the problem of fire has been the permanent confrontation between indigenous people and non-indigenous actors with economic and conservation interests in the GS. Indeed, the Pemones perceive the attempts of EDELCA and a number of ecologists to combat fire as a threat to their culture. Suitable fire management policies will not be easy to attain in the GS due to this cultural conflict. Some initiatives for a synergistic management approach that considers all the potential actors involved are presently under way (Rodriguez et al., 2009; Sletto & Rodriguez, 2013).

In Venezuela, *Mauritia flexuosa* has been ranked as "vulnerable" and the main threats have been considered to be the human use of palm resources, farming activities (agriculture, cattle), wood extraction, commercialisation of exotic species, damming and draining works, fire, and oil exploration and extraction (Llamozas et al., 2003; Rodríguez et al., 2010).

In the context of this paper, it is worth mentioning that GS fires have a differential action on savannas, forests and morichales. Savanna is, by far, the more intensively and extensively burnt vegetation type, which is maintained in a quasi-permanent early stage of colonisation for this reason. When fires reach the forest-savanna ecotone they determine its retreat and prevent further forest regeneration thus resulting in net savanna expansion. The morichales, on the contrary, are less affected by fires or, if so, *M. flexuosa* palms are usually protected (selective burning), which results in light and pure *Mauritia* morichales with only two strata (i.e. the palms and the ground herbs), whereas trees and shrubs are lacking (Fig. 4). Occassionally, major damage by uncontrolled fires (crown fires) cannot be avoided. Unfortunately, no published studies are available on the consequences of fires on the GS morichales but, in other parts of the country, frequent burning reduces biodiversity, simplifies structure –and, as a consequence, niche heterogeneity- and determines shorter canopies (Colonnello et al., 2009). In addition, fire seems to be the main factor responsible for the current fragmentation of morichales in other savanna environments (Rodríguez et al., 2010). Most of the uses reported above for the diverse parts of *M. flexuosa* (roots, stem, leaves, fruits…) are common in the Pemón culture (Huber & Febres, 2000; Ponce et al., 2000).

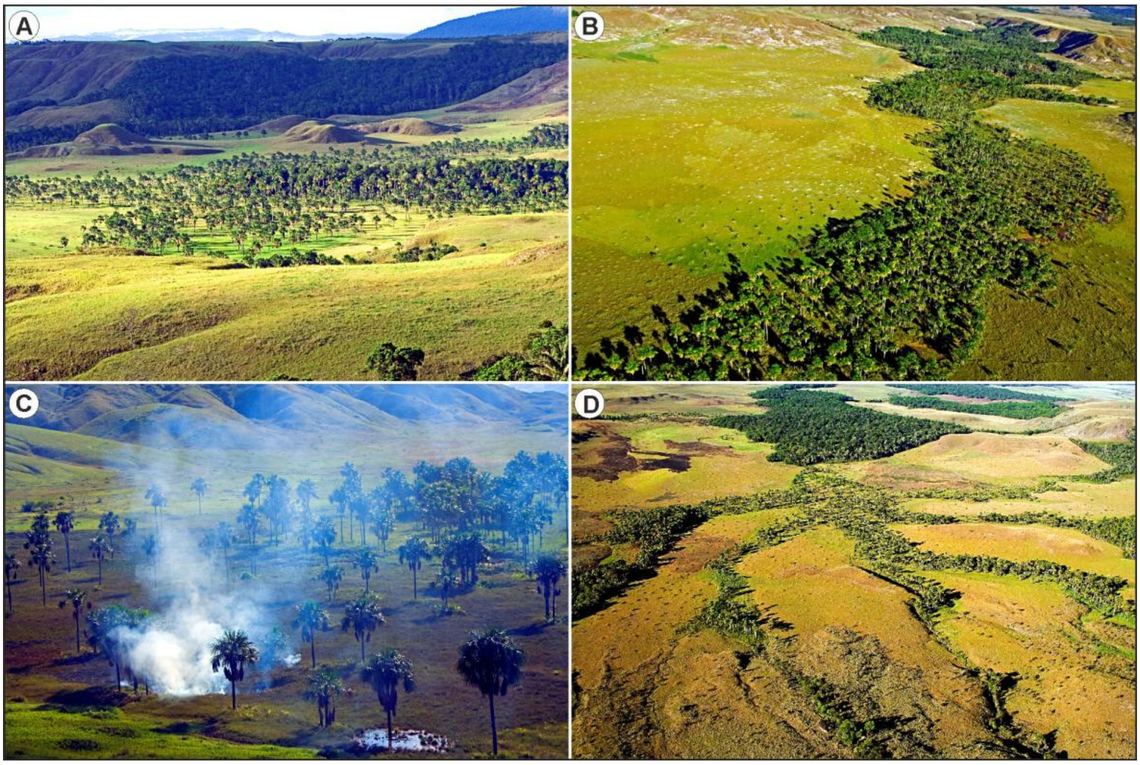

Figure 4. Morichales of the Gran Sabana. A) Extensive morichales in the Kukenán floodplain. B) Aerial view of a dense morichal along a small river around Wonkén. Note the mosaic of different green tones in the surrounding savannas, which are indicative of past fires corresponding to different years. C) Superficial fire inside a morichal burning only ground herbs and seedlings. D) Aerial view of a forest-savanna-morichal mosaic landscape where forest (at the background) is retreating while savanna and morichales are expanding due to selective burning. In this case, the savannas show evident signs of recent (dark-brown patches) and past (light-brown and green patches) fires. Photos V. Rull.

Palaeoecological records

The first GS palaeoecological studies based on pollen records revealed that morichales had been absent during most of the middle Holocene and did not colonise the studied sites until the last millennia. However, the lack of sufficient dating precision due to the use of conventional instead of AMS radiocarbon dating precluded the exact timing of *M. flexuosa* arrival and expansion being determined (Rull, 1992). It was concluded that present-day *Mauritia* palm communities represented the third stage of a process initiated with mid-Holocene forest retraction followed by treeless savanna expansion and morichal establishment coinciding with wetter climates. These studies did not provide information on the potential role of human activities in this colonisation process due to the lack of charcoal records as proxies for fires. Another handicap was the lack of reference collections to optimise pollen identification. The ensuing use of AMS dating on newly obtained sedimentary sequences, the incorporation of charcoal records in routine pollen analyses and the significant advances in pollen-morphological studies (Rull, 2003; Leal et al., 2012) provided the necessary details for more conclusive results.

Of the nine localities studied so far in the GS (Fig. 3), four were located within or near to a morichal and contained *Mauritia* pollen in the sedimentary record (Pacheco, Urué, Encantada and Chonita) (Rull, 1999; Montoya et al., 2009, 2011a; Leal et al., 2013). In the other sites, *Mauritia* and its pollen was absent for different reasons. The localities called Ariwe and El Oso were above the upper distribution boundary of this palm species but Mapaurí, Colonia and El Paují were below 1000 m elevation and the absence of *Mauritia* in these sites is still a matter of discussion (Rull, 2007; Montoya et al., 2011c; Leal et al., 2013). The summary pollen diagrams obtained in these localities show that *Mauritia* pollen had been absent during the Lateglacial and most of the Holocene, and did not colonised these sites until the last ~2000 years (Fig. 5). The first records of *Mauritia* pollen were from Chonita (~2500 cal y BP) and Encantada (~2000 cal y BP) (Montoya et al., 2009, 2011), at the south of the GS, whereas the youngest appearance occurred at Pacheco, situated in the central sector of the region, close to the upper *M. flexuosa* distribution limit (Leal et al., 2013). In later this case, dating resolution was insufficient to estimate the date of the first occurrence with the required precision, but using an age of ~600 cal y BP at 90 cm depth and assuming a modern age for the top of the sequence, it can be roughly estimated that *Mauritia* arrival ocurred during the last two centuries (20-30 cm depth) (Leal et al., 2013). In Urué, *Mauritia* pollen was already present at the beginning of the record, dated to ~1500 cal y BP (Rull, 1999); therefore, the arrival age is unknown. The presence of *Mauritia* pollen is indicative of the local occurrence of morichal communties. Indeed, modern sedimentation studies have revealed that this pollen has a very low dispersion ability and it is only found in soils below *Mauritia* palm swamps, even in the case of small pollen percentages (Rull, 1999; Leal et al., 2013).

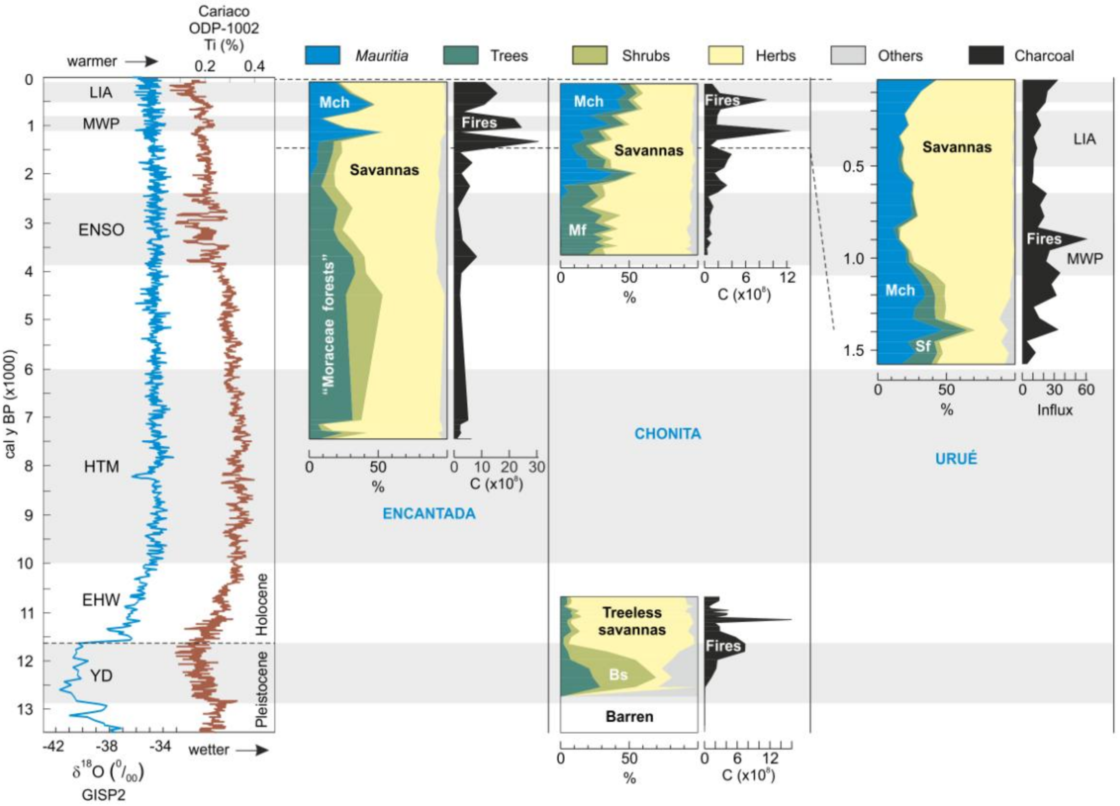

Figure 5. Lateglacial and Holocene summary pollen diagrams of the GS sequences with reliable dating resolution in which *Mauritia* pollen is present. Regional paleoclimatic trends are represented by temperature (oxygen isotop ratio) and moisture (Titanium content) proxies. The main climatic events recorded in northern South America are indicated (YD – Younger Dryas), EHW (Early-Holocene Warming), Holocene Thermal Maximum, ENSO – intensification of ENSO cyclicity, MWP – Medieval Warm Period, LIA – Little Ice Age). Fire incidence is represented by charcoal concentration (C) and influx. Bs – Bonnetia shrublands, Mch – Morichales, Mf – Moraceae forests, Sf –

Secondary forests. Modified from Rull et al. (2013). The complete pollen diagrams for each site can be seen in the supplementary material (Figs. S1 to S4)

According to the former results, the earliest recorded arrival and expansion of morichal communities in the GS occurred just after a phase of drier climates possibliy also due to an intensification of ENSO-related precipitation anoamlies that ended around 2500 cal y BP (Fig. 5). The ensuing wetter regional climates between ca. 2500 and 1000 cal y BP would have favoured the expansion of *M. flexuosa* swamps by facilitating the occurrence of permanent or seasonal flooding. There was also a slight increase in charcoal numbers, as indicative of a moderate intensification of fires, likely of anthropic origin (Montoya & Rull, 2011). During this phase of increased moisture availability and fire *Mauritia* pollen displays several oscillations, but since approximately 1000 cal y BP this pollen begins an increasing trend coinciding with a sudden increase in fire frequency and drier climates. It has been proposed that the combination of increased burning by humans and aridity –which increases vegetation flammability- would have exacerbated fire incidence (Vegas-Vilarrúbia et al., 2011; Rull et al., 2013). The expansion of morichales under unfavourable climates could be explained by selective burning, as is common nowadays (see above). In the case of Urué, the charcoal curve does not show an increase similar to those of Encantada and Chonita (Fig. 5) but the parallel trends of *Mauritia* pollen percentages and charcoal influx confirms that fire and morichal oscillations run almost parallel strongly suggesting a common forcing factor (Rull, 1999). In order to test the hypothesis of humans as major driving agents of fires and morichal expansion, interdisciplinary palaeoecological, anthropological and archaeological studies should be encouraged. So far, the only (circumstantial) evidence favouring this anthropogenic proposal is the similarity between palaeoecological results and the consequences of present-day human burning on GS extant ecosystems (charcoal increase, forest contraction, savanna and morichal expansion). The eventual finding of evidence for coupled human activities and vegetation changes in the past would be illuminating.

Contrastingly, charcoal values similar to those documented for the last millennia, but no trace of *Mauritia* pollen, were found in Lake Chonita Lateglacial sediments, peaking at ca. 12,000 cal y BP (Fig. 5). This is among the earliest burning evidence found in northern Sotuh America (Montoya et al., 2011c) although these fires could not be attributed to any known cause. As stated above, evidence for human occupation during that time is also lacking (Gassón, 2002). The absence of Lateglacial morichales could be explained by “dispersal debt”. It has been suggested that *Mauritia* experienced a general range contraction during the LGM followed by postglacial centrifugal expansions (Rull, 1998). This hypothesis has been recently supported by DNA phylogeographic studies showing that the current genetic diversity patterns of *M. flexuosa* populations across the Amazon Basin are consistent with glacial fragmentation into multiple scattered microrefugia (*sensu* Rull, 2009b), followed by interglacial range expansions from these microsites (De Lima et al., 2014). Within this framework, it is possible that the palm had not yet reached the GS where environmental conditions were suitable for its development. According to the results available so far, this hypothesis could be extrapolated to most of the Holocene (Fig. 5) but more studies in additional localities are needed for a conclusive assessment. A fact that indirectly supports the dispersal debt hypothesis is the occurrence of planted morichales beyond the current natural limits of distribution of *M. flexuosa*. For example, in Venezuela, two of these palm swamps exist beyond the northernmost *Mauritia* distribution area. In one of them, *M. flexuosa* was planted some 40 years ago –replacing a herbaceous community dominated by grasses-and now it dominates a morichal community of almost 6000 km^2 with more than 100 plant species that were formerly absent (Delascio, 1999). This demonstrates that the absence of morichales in a given place is not necessarily due to the lack of appropriate environmental conditions but to the fact that the dispersal potential of *Mauritia* has not yet been fully exploited (dispersal debt). In support to this, niche modelling shows that *M. flexuosa* is currently absent from areas whose environmental conditions are suitable for its growth, especially in the NW part of its actual range (De Lima et al., 2014). The case of planted morichales also provides partial support for the hypothesis of Kahn & de Granville (1992) about humans as successful dispersal agents for *M. flexuosa* palm swamps in the past. Additional dispersal agents are known to be rivers, which carry the fruit downstream, and a variety of animals, notably birds, which eat the fruit and carry the seeds elsewhere (see above).

The occurrence of isolated *M. flexuosa* palms above the altitudinal distribution limit of the species observed in our 2007 fieldtrip may be interpreted as dispersal forefronts whose successful establishment is still uncertain. In the case of *M. flexuosa*, a dioecious species, the potential success of one single individual as an effective coloniser is dependent on its sex (it should be a female palm) and its pollination possibilities. None of the pioneer palms observed were sexually mature and this point could not be confirmed. The fact that these individuals were migrating upwards might suggest some relationship with the ongoing global warming, which may be supported by the late arrival of the Quebrada Pacheco morichal, situated at 1040 m elevation, during the last few centuries (Leal et al., 2013). This would a relevant hypothesis for future *Mauritia* conservation to be confirmed or not with further studies.

Supra-regional context: tropical South America

In this section, we place the hypothesis of the late Holocene arrival of *M. flexuosa* to the GS in a regional context, including the whole distribution area of the species. First of all, it should be noted that *Mauritia* has likely been present in the Amazon Basin over the entire last glacial epoch. Indeed, the pollen of this palm shows a continuous presence since the Middle Pleistocene (>400,000 y BP) in the Amazon fan sediments reflecting the maintained occurrence of the palm in the watershed during the last glacial cycles (Hoorn, 1997, 2001). During the last glaciation, the occurrence of *Mauritia* pollen in the Amazon Basin is manifest as shown in both marine and continental cores embracing the last ~50,000 cal y BP (Ferraz-Vicenti & Salgado-Labouriau, 1996; Salgado-Labouriau et al., 1997; Haberle & Maslin, 1999; Colinvaux et al. 1996; Mayle et al., 2000; Burbridge et al., 2004; Bush et al., 2004). An eventual postglacial expansion of *M. flexuosa* would have left its palaeogeographical imprint in the form of coherent migration patterns in time and space, as has been well documented for many temperate tree species from Europe and North America (e.g. Davis, 1981; Huntley & Birks, 1983). In the Neotropics, the number of localities studied so far is still insufficient for a similar synthetic scenario but a mapping of the *Mauritia* pollen frequencies at each coring site at different time slices may be suggestive of some tendencies and may hopefully illuminate further research. Research on macrofossils, which are more reliable indicators of *in situ* occurrences of their parent plants (Birks & Birks, 2000), are still rare in the Neotropics. However, in the case of *Mauritia*, the pollen alone can be used as a reliable proxy for local ocurrence of this palm due to the low buoyancy and, hence, the low dispersal power of this pollen, as demonstrated by modern sedimentation studies (Rull, 1999; Leal et al., 2013).

Figure 6 is a first attempt to display graphically the available information on *Mauritia* pollen contained in neotropical sediments since before the LGM to the present (see also Table 1). It should be noted that some studies do not differentiate between *Mauritia* and *Mauritiella* pollen and their records might be mixed in some cases; however, the ecological requirements and the geographical distribution of the species of these two genera are similar (Henderson et al., 1995; Dransfield et al. 2008). It should also be noted that LGM and older records are scarce in the Amazon and Orinoco basins (Ledru & Mourguiart, 2001) and, as a consequence, the actual distribution of the parent palm during these times might be underestimated by their pollen record. This undervaluing effect becomes minimal or absent during the Holocene, of which sediments are present in most of the available neotropical records. In spite of these lower values, *Mauritia* pollen shows a widespread distribution during the LGM (22 to 20 ka BP) suggesting that the palm was well distributed across northern South America during glacial times. Abundances, however, were lower than in the Holocene, likely indicating that palm swamp populations were smaller. Exceptions are the southermost localities showing values over 40% during pre-LGM times (Fig. 6). During the Lateglacial (22 to 11.7 ka BP), the distribution of *Mauritia* pollen is similar to the LGM but abundances increase at two opposite Western and Eastern localities. In the Early Holocene (11.7-8.2 ka BP) the number of sites with *Mauritia* pollen increases to cover most localities sampled. The Orinoco basin began to be colonised by *Mauritia* during this time. This initial expansion was likely the result of the rising temperatures worldwide and a maintained increase in available moisture at a neotropical level culminating in the Holocene Thermal Maximum (HTM), as documented in the Cariaco record and others between about 9 and

7 ka BP (Haug et al., 2001) (Fig. 5). The W-E bi-polar pattern hint in the Lateglacial was reinforced in the early Holocene.

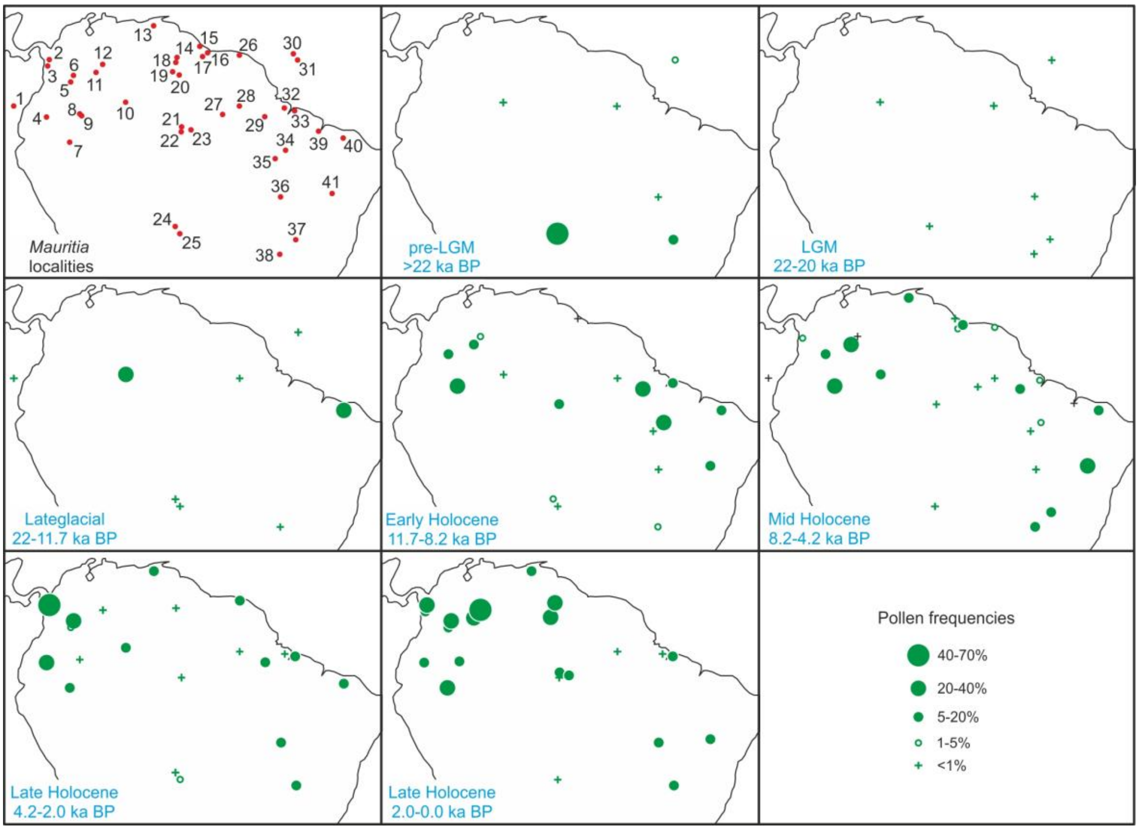

Figure 6. Map showing the neotropical localities containing *Mauritia* pollen in their Late Pleistocene and Holocene sedimentary records. Pollen abundances are represented as percentage classes and time is subdivided into several slices according to thee currently accepted chronostratigraphy (Walker et al., 2012). The Late Holocene has been subdivided into two parts, in order to emphasise the trends occurred during the last two millennia. See Table 1 for names and details of the localities surveyed.

Table 1
Localities with records of *Mauritia* pollen embracing the last glacial cycle, used to compose Fig. 6. ND: No data; SL: sea level. Numbers in the first column (N) indicate the position of each locality in the map (Fig. 6).

N	Locality	Country	Latitude	Longitude	Elev. (m)	References
1	TR 163-38	Pacific	1º 20' 24" N	81º 34' 48" W	SL	González et al. (2006)
2	Atrato	Colombia	6º 34' N	76º 34' W	18	Urrego et al. (2006)
3	Jotaordó	Colombia	5º 48' N	76º 42' W	50	Berrío et al. (2000a)
4	Anañgucocha	Ecuador	0º 40' S	76º 25' W	300	Frost (1988)

5	Agua Sucia	Colombia	3º 35' N	73º 31' W	300	Wymstra & van der Hammen (1966)
5	Las Margaritas	Colombia	3º 23' N	73º 26' W	290	Wille et al. (2003)
5	Loma Linda	Colombia	3º 18' N	73º 23' W	310	Behling & Hooghiemstra (2000)
6	Mozambique	Colombia	3º 58' N	73º 03' W	175	Berrío et al. (2002)
7	Quistococha	Peru	3º 50' 24" S	73º 19' 9.92" W	94	Roucoux et al. (2013)
8	Monica	Colombia	0º 42' S	72º 04' W	160	Behling et al. (1999)
8	Mariñame 1	Colombia	0º 45' 36.64" N	72º 03' 13.28" W	140	Urrego (1997)
8	Mariñame 2	Colombia	0º 45' 36.64" N	72º 03' 13.28" W	140	Urrego (1997)
9	Quinché 1	Colombia	0º 53' 54.35" S	71º 49' 00.66" W	120	Urrego (1997)
9	Quinché 2	Colombia	0º 53' 54.35" S	71º 49' 00.66" W	120	Urrego (1997)
9	Quinché 3	Colombia	0º 53' 54.35" S	71º 49' 00.66" W	120	Urrego (1997)
10	Dragão (Six Lakes)	Brazil	0º 16' N	66º 41' W	300	Bush et al. (2004)
10	Pata (Six Lakes)	Brazil	0º 16' N	66º 41' W	300	Bush et al. (2004) Colinvaux et al. (1996)
10	Verde (Six Lakes)	Brazil	0º 16' N	66º 41' W	300	Bush et al. (2004)
11	Angel	Colombia	4º 28' N	70º 34' W	200	Behling & Hooghiemstra (1998)
11	Carimagua-Bosque	Colombia	4º 04' N	70º 13' W	180	Berrío et al. (2000b)
11	Chenevo	Colombia	4º 05' N	70º 21' W	150	Berrío et al. (2002)
11	El Pinal	Colombia	4º 08' N	70º 23' W	180	Behling & Hooghiemstra (1999)
12	Sardinas	Colombia	4º 59' N	69º 28' W	80	Behling & Hooghiemstra (1998)
13	Mapire	Venezuela	9º 33' N	63º 40' W	80	Leal et al. (2011)
14	Urué	Venezuela	5º 10' N	60º 57' W	940	Rull (1999)
15	Ogle Bridge	British Guiana	6º 50' N	58º 10' W	SL	van der Hammen (1963)
16	Torani	British Guiana	5º 49' 05" N	57º 26' 57" W	13	van der Hammen (1963)
17	Kwakwani	British Guiana	5º 17' 20" N	58º 04' 19" W	8	van der Hammen (1963)
18	Chonita	Venezuela	4º 39′ N	61º 0′ W	884	Montoya et al. (2011a)
18	Encantada	Venezuela	4º 42' 39.6" N	61º 04' 55.6" W	867	Montoya et al. (2009)
19	Cigana-Indigena	Brazil	3º 34' N	61º 26' W	80-200	Meneses et al. (2013)
20	Galheiro	Brazil	3º 07' N	60º 41' W	90	Absy (1979)
21	Cajú	Brazil	2º 56' 51" S	60º 33' 04" W	50	Absy (1979)
22	Calado	Brazil	3º 16' S	60º 35' W	23	Behling et al. (2001)
23	Terra Nova	Brazil	3º 07' 20" S	59º 31' 50" W	25	Absy (1979)
24	Bella Vista	Bolivia	13º 37' S	61º 33' W	ND	Mayle et al. (2000) Burbridge et al. (2004)
25	Chaplin	Bolivia	14º 28' S	61º 04' W	ND	Mayle et al. (2000) Burbridge et al. (2004)
26	Mana	French Guiana	5º 44' N	53º 51' W	SL	Tissot et al. (1988)

						Tissot & Marius (1992)
27	Cumina	Brazil	1º 28' 12"	56º 07' 01"	25	Absy (1979)
28	Maicuru	Brazil	0º 30' S	54º 15' W	500	Colinvaux et al. (2001)
29	Curuá	Brazil	1º 44' 07" S	51º 27' 47" W	ND	Behling & da Costa (2000)
30	ODP-155	Brazil	6º 00' N	47º 30' W	SL	Hoorn (1997, 2001)
31	ODP-932	Brazil	5º 12' 42" N	47º 01' 48" W	SL	Haberle & Maslin (1999)
32	Arari	Brazil	0º 40' 40" S	49º 09' 09" W	SL	Absy (1985)
32	Pesqueiro	Brazil	0º 39' 34.0" S	48º 29' 0.3" W	SL	Behling et al. (2004)
32	Barra Velha	Brazil	0º 43' 10.5" S	48º 29' 32.4" W	SL	Behling et al. (2004)
33	São Caetano	Brazil	0º 43' S	48º 01' W	SL	Behling et al. (2004)
33	Curuça	Brazil	0º 46' S	47º 51' W	35	Behling (1996, 2001)
33	Crispim	Brazil	0º 46' S	47º 51' W	1-2	Behling & da Costa (2001)
34	Marabá	Brazil	5º 21' S	49º 09' W	70	Guimarães et al. (2013)
35	Maurítia	Brazil	6º 21' 6.2" S	50º 23' 36.6"	740	Hermanowski et al. (2012)
36	Confusão	Brazil	10º 38' S	49º 43' W	180	Behling (2002)
37	Águas Emendadas	Brazil	15º 34' S	47º 35' W	1040	Barberi et al. (2000)
38	Cromínia	Brazil	17º 17' S	49º 25' W	710	Ferraz-Vicentini & Salgado-Labouriau (1996) Salgado-Labouriau et al. (1997)
39	Aquiri	Brazil	3º 10' S	44º 59' W	10	Behling & Costa (1997)
40	Caço	Brazil	3º 50' S	41º 50' W	SL	Ledru et al. (2006)
41	Icatú	Brazil	10º 24' S	43º 13' W	ND	De Oliveira et al. (1999)

During the Middle Holocene (8.2-4.2 ka BP) *Mauritia* appears in the northernmost localities, close to or at the Caribbean and the Atlantic coasts with significant abundances. This time, the dipole slightly changes to adopt a NW-SE pattern, whereas the *Mauritia* pollen decreases at the centre of the Amazon basin. In the first half of the Late Holocene (4.2-2.0 ka BP), the eastern localities undergo a slight decline in *Mauritia* pollen, whereas this pollen remarkably increases at the NW. It is possible that the regional precipitation decrease recorded in the Cariaco basin between about 4 and 2.5 ka BP, linked to an ENSO intensification (Haug et al., 2001), was involved in this *Mauritia* decline. The fact that this decline occurred only in the E side is consistent with recent observations based on the isotopic composition of speleothems indicating a maintained asymetry in precipitation patterns between W and E Amazon regions, with the E part being constantly drier during the last 20 ka BP (Cheng et al., 2013). The W-E asymmetric pattern strengthens during the last 2000 years as a result of the increase of *Mauritia* at both N and NW localities. This time, climatic forcing is less evident as temperatures remained unchanged and moisture trends showed a general decreasing trend culminating in the Little Ice Age (Haug et al., 2001) but with heterogeneous local manifestations, especially in the GS region (Montoya & Rull, 2011). Therefore, additional and relatively independent forcing agents are required to explain the *Mauritia* expansion recorded during the last 2 ka BP in the NW part of Northern South America. In light of the available evidence, the more likely possibility is human disturbance by selective burning, as it has been observed in the GS region at present and suggested to have been occurring during the last 2000 years. This proposal is supported by several lines of evidence obtained in the GS, including: i) selective burning favours the expansion of *Mauritia* swamps at the expense of forests independently of moisture trends, ii) the sudden appearance and the abrupt expansion of *Mauritia* pollen at ~2000 y BP and iii) the exact coincidence of *Mauritia* trends with charcoal patterns as proxies for fire. Unfortunately, charcoal analyses are not available for most of the W localities surveyed.

Conclusions and final remarks

Mauritia flexuosa (Arecaceae) is widespread across tropical South America from the Atlantic to the Pacific coasts. This palm is restricted to warm and wet lowlands (up to ~1000 elevation) of the Orinoco and Amazon basins, where it can live as one more component of rainforests or can dominate characteristic palm swamps growing within both forest and savanna landscapes. *M. flexuosa* is, and has been historically, intimately linked to human life. Indeed, almost every part of Mauritia, from the roots to the fruits, is useful for human needs and activities such as fedding, clothing, housing, medicine, magic, etc. As a consequence, *M. flexuosa* has been considered an iconic palm for the neotropical region.

Mauritia palm swamp communities are particularly well developed in the Venezuelan Gran Sabana (GS) region, were they are known as morichales and greatly contribute to shape de characteristic regional savanna landscape. These GS morichales, however, are of relatively recent origin. The body of evidence analysed in this review suggests that *Mauritia* would have arrived to the GS in the late Holocene (the last two millennia) and that humans may have been involved in the dispersion and expansion of the palm and its communities in this region. This human influence, mainly in the form of selective burning, would have persisted during the last 2000 years, when the morichales have experienced rapid population increases at the expense of rainforests. Whether these hypothetical human cultures are or are not related with the modern Pemones cannot be resolved with the available evidence. A potential role for climate, and climate-human synergies, in *Mauritia* spreading cannot not be dismissed. However, the absence of *Mauritia* in the GS since the LGM to the Late Holocene despite the ocurrence of significant climate changes, the abruptness of the Late Holocene *Mauritia* expansion and the exact coincidence with the patterns of charcoal as the proxy for fire, point towards the incoming of an additional disturbing factor which manifestations coincide with well known present-day human activities. In the absence of archaeological evidence, this proposition should be considered as a working hypothesis to be tested with further studies but its is strongly supported by palaeoecological records.

The tempo and mode of colonisation of the GS region by *Mauritia* makes sense in a supra-regional context embracing the whole tropical South America. *Mauritia* has been present in the Amazon basin during the four last glacial cycles (~400,000 years BP) but only part the last glacial cycle displays a more or less continuous palynological record. During the LGM and the Lateglacial, *Mauritia* populations were likely small and widespread (microrefugia) and expanded since the beginnig of the Holocene owing to the increasing temperatures and available moisture. This expansion proceeded in a bipolar fashion with two main dispersal centres situated in the E and W, respectively, which remained during most of the Holocene. At about 4000 yr BP, however, the W dispersal centre remarkably increased in both palm swamps extent and popuation sizes, a situation that remained until the last millennia. The GS morichales, which had been absent from this region until the Late Holocene, were part of this latest western growing and expansion. If the anthropogenic character of *Mauritia* colonisation and expansion in the GS is finally confirmed, it would be asked whether the whole Late Holocene western expansion, at a neotropical level, would be the result of a supra-regional increase in human disturbance. Unfortunately, many palaeoecological records documenting the Late Holocene *Mauritia* increase did not record charcoal particles, a highly recommendable practice in light of the present supra-regional reconstrucction. Such a supra-regional manifestation of a hypothetical human disturbance would support the proposal of a significant and wide-ranging anthropization of present-day neotropical ecosystems. However, the fact that this phenomenon is especially noteworthy in the W sector would highlight the heterogeneous nature of this eventual humanization (Bush et al., 2007).

Among the recommendations for future studies, the following may be highlighted: i) the re-analysis of the available cores from NW localities showing *Mauritia* expansion with emphasis on charcoal particles, as proxies for fire, during the last millennia, ii) the development of synergistic palaeoecological-archaeological-historical programs in selected localities and regions, especially in order to check eventual W-E cultural asymmetries with emphasis on potential W expansions during the last millennia, iii) the careful reconstruction of local climatic trends using proxies independent from pollen (e.g. geochemistry and isotopic analyses) in selected coring sites, in order to disentangle natural and anthropic effects on *Mauritia* population trends, also during the interval of interest. A crucial tool in this type of studies is the availability of a comprehensive and updated pollen database for South America. The compilation used in this study (Fig. 6) has been based on a careful and time-consuming review of the existing literature. The recent initiative of updating and modernising the already existing Latin American Pollen Database (LAPD), which last updating dates from 2002, will hopefully facilitate this type of studies (Flantua et al., 2013).

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