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BIOGEOGRAPHY AND CONSERVATION OF AMAZON PALMS

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Tese apresentada ao Programa de Pós-Graduação em Ecologia, Instituto de Ciências Biológicas da Universidade Federal de Juiz de Fora, como parte dos requisitos necessários para a obtenção do título de Doutor em Ecologia. Área de Biodiversidade, subárea Ecologia.

Orientador: Prof. Dr. Luiz Menini Neto

Co-orientador: Prof. Dr. Fabrício Alvim Carvalho

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Aprovado em ___/___/___

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ABSTRACT

Palms are abundant in tropical forests and are recognized as effective bio-indicators of hot climates. Moreover, play an important ecological and economic role for local populations. Though palms remain relatively well-conserved, they are under increasing pressure from deforestation. Therefore, endemicity is important for the delimitation of conservation areas. The purposes of the study is 1) to synthesize available information in the literature on species diversity, ecological aspects, use and conservation of Amazon palms (Chapter 1); to analyse palms species richness patterns relative to the latitudinal gradient, sample efforts, and deforestation in the Amazon region (Chapter 2); to compare richness and floristic similarities patterns among the Amazonian sub-regions (Chapter 2); to detect endemic areas for palms in the Amazon region (Chapter 3); and to determine whether the species that define these endemic areas are protected within conservation units (Chapter 3). Records of occurrences were extracted from the *Global Biodiversity Information Facility* (GBIF). The final dataset consisted of 17,310 records, for 177 species of Amazonian palms. The areas with the greatest richness were in the western, central and northeastern Amazon, principally at latitudes 0–5ºS. Most palms species grow in different habitats, but the highest species richness are found in *terra firme* forest. Palms are widely used with different category of use according to the regions and species, principally are used for human consumption, elaboration of utensils and tools, and construction of houses. Highest rates of deforestation ($\geq$2000 km^2) were found in the southern and eastern brazilian Amazon, which coincide with low species richness and gaps in records. Similarity analysis resulted in two groups of sub-regions: the first included the Amazon *s.s.*, Andes and Guiana, and the other group included the Plateau and Gurupi sub-region. The combination of PAE and NDM-VNDM analyses resulted in eight endemic palm areas in western Amazon shared with Andean sub-region. Of the species that define the endemic areas, five are threatened with extinction in one of three IUCN categories (EN, VU, NT), and they are not protected in any conservation units. In conclusion, the western Amazon, besides having high palm richness, also has palm endemic areas, especially, near the Andean sub-region and the Peruvian Amazon, and areas with low species richness, especially those areas with data deficiency, need to be further researched for a better knowledge of their diversity and richness patterns.

Keywords: Amazon region, ecology of palms, endemic areas, endemic species, richness patterns, species occurrence records, threatened species, western Amazon.

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GENERAL INTRODUCTION

Biological diversity is not evenly distributed on earth and this distribution is not random. Thus, there are areas that have greater species diversity than other areas (Carvalho 2004). For this reason, biogeography arises in order to understand the species distribution patterns, the relation of the biota to its distribution areas, and the relationship between the areas (Nelson & Platnick 1981; Morrone et al. 1996; Posadas et al. 2006). Two basic patterns of geographic distribution are recognized in biogeography (Brown & Lomolino 2006). First, the geographical distributions of organisms are limited by ecological or historical factors (Morrone et al. 1996). Second, the species that occur exclusively in certain locations are not randomly distributed, but tend to focus on some regions of the world, constituting a phenomenon called endemism (Silva et al. 2004). Therefore, to understand the biota distribution patterns, there are three components that must be evaluated together: space (geographical area of occurrence of organisms), time (historical events that influenced current patterns), and form (organisms groups) (Croizat 1964; Humphries 2000). In summary, biogeography is the science that studies the geographic distribution of living beings in space over time in order to understand the patterns of spatial organization of organisms and the processes that have resulted in such patterns (Gillung 2011). Therefore, biogeography applies theory to empirical data from the communion between diverse approaches of ecology, systematics, population genetics, evolution and geology (Brown & Lomolino 2006).

Since the 1980s it has been understood that the loss of biodiversity is caused by human action, and today most of the scientific community agrees that the main challenge is to prevent this loss of biodiversity (Fearnside 1992; Veríssimo et al. 1992; Johns et al. 1996; Holdsworth & Uhl 1997; Souza Jr et al. 2003; Brandon et al. 2005). Conservation of species is strongly based on the concept of endemism as well as on the number of existing species. Therefore, in the context of conservation, areas of endemism are biogeographic elements used to prioritize and to conserve places because they highlight their spatially unique biodiversity features (Löwenberg-Neto 2011). These decisions are best viewed through biogeographic methods that aim to critically understand the patterns of the spatial distribution of organisms and respond as these patterns were formed (Carvalho 2009). New techniques and software facilitated the advancement of research in biogeography. At present, several historical biogeographic methods are used to define strategies for conservation. These include PAE (Parsimony analysis of endemicity), panbiogeography, phylogeography and predictive models of species distribution (Crisci et al. 2003). In this study, PAE was used to find endemic areas of palms in the Amazon region (chapter 3). Thus, PAE unites areas based on their shared species and it is used to inform potential endemic areas (Nihei 2006).

The Amazon is a very rich and diverse region, comprising the Amazon basin and the lowlands of southern Colombia and Venezuela, northern and eastern Peru, eastern Bolivia, northern Brazil and the Guianas (Garzón-Orduña & Miranda-Esquivel 2007). According Eva and Huber (2005), the Amazon basin (7.5 million km^2; 4ºN–18ºS, 42–79ºW) can be divided into in the central Amazon (68%) (Amazon *sensu stricto*) and four peripheral sub-regions: Guiana (12%), Plateau (11%), Andes (7%), and Gurupi (2%). Amazon region presents favourable conditions for the development of the plants. Therefore, the Amazon has always been the crib of biological innovation and biodiversity (Hooghiemstra 2002).

Palms is composed of 183 genera and about 2,400 species distributed throughout the tropical regions, with some representative species in the subtropics (Uhl & Dransfield

1987; Baker et al. 2011). Their global influence on the structure and functioning of these ecosystems indicates that they represent key species (Balslev 2011) and are significant in terms of their high local densities, biomass, plant cover, effects on plant recruitment, influence on the nutrients, and their interactions with herbivores, dispersers and pollinators (Montúfar et al. 2011). Thus, the survival and development of palms in South America is due to several factors (Pintaud et al. 2008). The permanence of tropical rainforest, despite the fluctuations during the Tertiary and Quaternary (Haffer 1969; Wilf et al. 2003), ensured the habitat of a family basically in this physiognomy. The elevation of the Andes has introduced a very favourable environmental dynamics and diversity for the palm diversification. Some palms originating in the Andes have spread to the Pacific coast, Central America and Western Amazon (*e.g.*, species of *Aiphanes* and *Wettinia*).

In palaeobotanical literature, palms are generally recognized as effective bioindicators of hot climates (Mai 1995). Under current global climates, they reach their greatest proliferation in the tropics, being less richness in temperate regions (Good 1953; Jones 1995; Gibbons 2003). However, in recent years there is evidence that palms species more resistant to cold are occurring beyond the limit of their usual latitudinal range (Francko 2003). In addition, palms provide subsistence, providing food, such as fruit and oil, building materials, artisanal and fibers (Balslev 2011; Macía et al. 2011), which satisfy a relatively high proportion of the basic needs of local communities, indigenous populations and subsistence farmers living in the vicinity of tropical forests (Macía et al. 2011).

Thus, the purposes of this study is to analyse the geographic distribution and richness of palm species occurring in the Amazonian region; to determine areas of endemism based on the distribution of palm species; to analyse whether endemic palms are protected within any conservation unit.

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Chapter 1

AMAZON PALMS: DIVERSITY, ECOLOGY, USE AND CONSERVATION

Amazon palms: Diversity, ecology, use and conservation[1]

Abstract

Palms are widely distributed throughout the Amazon region with complex spatial patterns of species distributions and diversity. Moreover, plays an important ecological and economic role for the local population. We synthesize available information in the literature about species diversity and ecological aspects at level of habitat and factors that control the diversity, use and conservation of Amazonian palms. Highest palms richness are found in western Amazon. *Bactris*, *Astrocaryum*, *Attalea* and *Geonoma* are the most abundant genera and *Geonoma macrostachys*, *Euterpe precatoria* and *Iriartella setigera* are the species with most occurrence records. Most palms species grow in different habitats, but the highest species richness are found in *terra firme* forest. Small palms and large tall-stemmed palms dominate the communities both in terms of species richness and number of individuals. Thus, palm species richness and diversity seem related to climate particularly by water-related variables. Moreover, palms are widely used in different ways according to the regions and species, principally for human consumption, elaboration of utensils and tools, and construction of houses. Finally, the palms are threatened by the deforestation and non-sustainable destructive practices leading many species to reduce their population and, in worst cases, to extinction.

Keywords: Amazon region, category of use, endemic species, habitat, threatened species

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[1] Manuscript formatted following the instructions for authors given by *The botanical review* journal

Introduction

The palms are monocotyledon plants, have thick or thin stems, with smooth surface, ringed or with well pronounced spines; their leaves are simple or compound and their inflorescences branched with hermaphrodite or unisexual flowers (Valois-Cuesta et al., 2013). The fruits are berries or drupes with fleshy or fibrous pericarp (Galeano & Bernal, 2010). Palms have great diversity of habits and forms that range from delicate understory plants to climbing plants (*trepadeiras*) and robust of canopy. Palms may be monoecious or dioecious, solitary or clumpy (*touceira*), with thorns or unarmed, with entire, palmate or pinnate leaves. Although often associated with rainforests, palms are present in a wide variety of habitats (Leitman et al., 2013).

In the tropical rainforest, the palms represent one of the plant groups with high richness, diversity and endemism (Kahn & de Granville, 1992; Henderson, 1995; Henderson et al., 1995; Kahn, 2008; Pintaud et al., 2008; Balslev et al., 2015). In South America, 459 species and 50 genera coexist (Pintaud et al., 2008), which represent 19.5% of the species and 26.5% of the genera of palms known to date (Dransfield et al., 2008). Within the countries of Neotropical region, Colombia is the country with the highest palm richness: 220 species included in 43 genera (Galeano & Bernal, 2007). Palms play an important ecological role, being the main food source for several groups of vertebrates, especially in times of scarcity (Svenning, 2001; Galetti et al., 2006). Besides, palms constitute a resource of socio-cultural and economic importance for the local communities, since these plants have traditionally been used as raw material for various purposes (Moraes et al., 1995; Balslev et al., 2008; Nascimento, 2009; Macía et al., 2015). Therefore, palms are a group most economically exploited, behind only of grasses and legumes (Johnson et al., 1996). Oils, fibers, waxes, covers for houses, fruits, palm heart and drinks are extracted from palms. There are also uses in popular medicine and ornamentation (Uhl &

Dransfield, 1987; Johnson et al., 1996). The extraction is one of the great causes of reduction of the natural populations of palms, as is the case of the palm heart (*Euterpe edulis* Mart., *palmito*). However, loss of habitat (deforestation) and consequent loss of ecological interactions with pollinators and dispersers due to the fragmentation and destruction of natural environments are the major threats to this group of plants (Johnson et al., 1996; Galetti et al., 2006; Steffler et al., 2008).

Our study covers the entire Amazon watershed (8.121.313 km^2) divided into five sub-regions (Eva & Huber, 2005): Central sub-region (68%=Amazon *sensu stricto*) and four peripheral sub-regions: Andes (7%), Plateau (11%), Guiana (12%), and Gurupi (2%) (Fig. 1). A list of Amazonian palm species with information of their distribution was extracted from previous studies (Kahn & de Granville, 1992; Henderson, 1995; Henderson et al., 1995; Kahn, 2008; Pintaud et al., 2008; Balslev et al., 2015) (Table S1). In addition, to deepen information on diversity, ecology, use and conservation of Amazonian palms were complemented with available studies in the literature (Table 1).

Although there are many studies on palms, the purpose of the manuscript is to synthesize the information of the literature on species diversity and ecological aspect at level of habitat e factors that control to diversity, and use and conservation of Amazonian palms.

Palm species diversity in the Amazon region

It is difficult to give real number of palm species occurring in the Amazon region, but different researchers approximate numbers, as Henderson (1995) that mention 151 species, Pintaud et al. (2008) indicate 195 species (gradient 0-1000 m) and Balslev et al. (2015) mention 165 species approximately in Amazonian lowlands. In our review we found 177 palm species represented in 17,310 records (Table S1; Fig. 1) (see also Chapter 2). The sub-region with the largest palm species richness was the Amazonia *sensu stricto*

(167 species). The other sub-regions had substantially lower numbers of species: Guianas (91), and Andes (71), and with fewest palm species were the Gurupi (21 species) and the Plateau (17) (Fig. 2a) and > 50% palm species were found in western Amazon (Fig. 2b). Therefore in this region (western Amazon), Balslev et al. (2015) mention that in the Amazon region of Colombia are found 120 palm species, in Ecuador, the Amazon lodges 78 palm species (38 are exclusive to the Amazon region) and Peruvian Amazon are found 120 palm species. On a local scale, the diversity of palms can be very high in certain types of forests, with more than 30 different species in an area of half a hectare (Kahn & Mejía, 1991) but the total diversity of the Amazon region is surprisingly low considering its size and diversity at the ecosystem level (Pintaud et al., 2008). Thus, the palm diversity is low in comparison with the forests of the Pacific coast of Colombia and Ecuador that have 122 species in smaller areas (Balslev et al., 2015).

The diversity of palm species and genera reaches very high levels in Amazon unflooded (*terra firme*) forest, and less diversified in flooded and waterlogged forests (Kahn & de Granville, 1992; Balslev et al., 2015). The 10 species with the highest number of records were *Geonoma macrostachys* Mart. (1206), *Euterpe precatoria* Mart. (859), *Iriartella setigera* (Mart.) H. Wendl. (617), *Lepidocaryum tenue* Mart. (590), *Chamaedorea pauciflora* Mart. (577), *Desmoncus mitis* Mart. (549), *Astrocaryum aculeatum* G. Mey. (457), *Bactris hirta* Mart. (423), *Geonoma brongniartii* Mart. (400), and *Oenocarpus bacaba* Mart. (391) (Fig. 2c). More than 80 palms (>50%) are native species of Brazil, Colombia and Peru, and the rest are of Ecuador, Bolivia, Guiana and Venezuela (Fig. 2e). Four genera were represented by more than 20 palm species. *Bactris* with the highest species number (36), followed by *Astrocaryum* with 28 species, *Attalea* and *Geonoma* with 23 species, respectively (Fig. 2d). The genera *Geonoma*, *Bactris* and *Astrocaryum* (last two are thorny species) are rich in species particularly in the understory (*sub-bosque*) (Balslev et al., 2015).

Regarding endemic species, twenty-six species are endemic to different countries, 14 to Peru, five to Bolivia, three to Colombia, two to Ecuador and two species were endemic to Guyana (Fig. 2f), and 24 species were recorded in Amazon *sensu stricto*, 11 species in Andes, two in Guiana and one in Plateau sub-region (Table 2).

Ecological aspects

Habitat

Palms are present in a wide variety of habitats of tropical forests, such as *restingas*, savanna, mangroves, desert regions, floodplains, field formations and *terra firme* forest (Leitman et al., 2013). Most palm species can grow in different habitats, even though each one is usually more abundant in a particular habitat, either on *terra firme* forest, flooded forest or in marshes (Montúfar & Pintaud, 2006; Balslev et al., 2015). However, various studies showed that the highest species richness are found in *terra firme* forest, and less richness in flooded and waterlogged forests (Kahn & de Granville, 1992; Balslev et al., 2015). Balslev et al. (2015) mention that along the Guaviare, Caquetá and Amazonas rivers (Colombian Amazon) were found 74 palm species distributed in 21 genera, of which 68 species in 20 genera were in *terra firme* forest. The three most abundant palm species were *Oenocarpus bataua* Mart., *Iriartella setigera* (Mart.) H.Wendl. and *Oenocarpus bacaba* Mart. In flooded forest were recorded 60 species in 19 genera, and *Euterpe precatoria* Mart., *Attalea butyracea* (Mutis ex L.f.) Wess.Boer and *Socratea exorrhiza* (Mart.) H.Wendl. were the species most abundant (Balslev et al., 2015). In Ecuador, Yasuni National Park is covered by 80% of *terra firme* forest, and dominant palm species are *Iriartea deltoidea* Ruiz & Pav. and *Oenocarpus bataua* Mart. The flooded forests by white waters (that originate in the Andes) are dominated by *Phytelephas tenuicaulis* (Barfod) A.J. Hend., *Astrocaryum urostachys* Burret and *Attalea butyracea* (Mutis ex L.f.) Wess.Boer, while in black waters (that are born in lowlands) are dominated by *Astrocaryum jauari* Mart. and *Bactris riparia* Mart. (Balslev et al., 2015). Peruvian Amazon is very ecologically diverse and presents several types of habitats (Kahn and Mousa 1994). High palm species richness (70) were found in *terra firme* forest, followed with 16 species by periodically flooded white water forests, and with 22 species by seasonal swamp forests irregularly flooded. Other habitats in Peruvian Amazon present less palm species (Balslev et al., 2015). Similarly, Vormisto et al. (2004a) also found high palm species richness (54) in *terra firme* forest in the Pebas region (Peruvian Amazon), and most common species were *Lepidocaryum tenue* Mart., *Astrocaryum macrocalyx* Burret, *Socratea exorrhiza* (Mart.) H.Wendl. and *Geonoma macrostachys* Mart. Finally, in the Bolivian Amazon there are exclusive and very well represented species in the Amazon Basin (*e.g*., *Astrocaryum aculeatum* G. Mey, *Attalea maripa* (Aubl.) Mart., *Geonoma laxiflora* Mart.), others that grow both in the Amazon basin and in the Andes (*e.g*., *Aiphanes horrida* (Jacq.) Burret, *Chamaedorea angustisecta* Burret, *Geonoma deversa* (Poit.) Kunth, *Socratea exorrhiza* Mart.) H.Wendl.) and those found both in the Amazonian rainforests and in the *Cerrado* of eastern Bolivia (*Astrocaryum jauari* Mart., *Desmoncus horridus* Splitg. ex Mart., *Mauritiella armata* (Mart.) Burret and *Oenocarpus distichus* Mart.) (Moraes, 2007; Balslev et al., 2015).

Growth Forms of Amazonian Palms

Growth form is the morphological and physiological response of a plant species to ecological constraints (Kahn & de Granville, 1992; Henderson, 2002; Balslev et al., 2011). In a study of Balslev et al. (2011) with 789 native American palm species in 67 genera, they describe eight different growth forms (Table 3), and within each growth form, the species are classified as either solitary or cespitose (Table 4). The eight growth forms are differently represented in the palm communities, and the categories small palms and large tall-stemmed palms dominate the communities both in terms of species richness and number of individuals (Balslev et al., 2011). According to those different growth, the Amazonian palms have all growth forms mentioned by Balslev et al. (2011), except medium/small palms with stout stem, and the categories with highest species and genera were small palms (89 species, 17 genera) and large tall-stemmed palms (27 species, 8 genera). Moreover, in the categories large-leaved medium–short-stemmed palms were found 21 species in 4 genera and medium-sized palms with 10 species in 8 genera (Fig. 3).

The palms have characteristics that make them more vulnerable than other groups of plants: firstly, the stem of the palms only has one point of growth, the terminal meristem, thus if it is damaged or cutted, the stem dies. Therefore, palms that have only one stem implies the death of the individual, but in the cespitose palm (*e.g.*, *Euterpe oleracea* Mart.), the growth of the other stems guarantees their survival (Galeano & Bernal, 2005). Second, palms are mainly forest dwellers and require, at least in the initial stages, the lighting and humidity conditions provided by the forest; thus, although many adult palms survive in paddocks and deforested areas, their possibility of regeneration there is almost nil (Galeano & Bernal, 2005; 2010). Third, palms grow continuously since they germinate until they die, but the growth is not the same throughout life and follows a sigmoidal curve model (Henderson, 2002). At the beginning the palm go through a period of relatively slow growth (from the formation of the seedling to the end of the establishment phase), the stem increases in diameter until reaching its final size; then there is a period that presents the fastest growth of all life of the palm, with notorious elongation of the stem (Galeano & Bernal, 2010). Therefore, many of the palm species can take more than

25 years to reach reproductive age (Galeano & Bernal, 2005). Finally, some palms are dioecious, meaning that they have reproductive structures in separate individuals, which means that a greater number of adult plants is required to maintain a stable population Galeano & Bernal, 2005).

Factors that control the palm richness and diversity

Alternatively, species ranges may be controlled by soil or other environmental factors, or by non-environmental factors such as biotic interactions, dispersal barriers, intrinsic population dynamics, or time-limited expansion from place of origin or past refuge (Blach-Overgaard et al., 2010). Several studies showed that palm richness and diversity patterns are particularly related to the climate (Bjorholm et al., 2005; Blach-Overgaard et al., 2010) and the evolutionary history (lineage) (Bjorholm et al., 2006).

Bjorholm et al. (2005) showed that palm species richness of the Chocó area, western and eastern Amazon basin, and east Andean slopes have relationship to water-related variables such as annual rainfall and number of wet days, and are the main richness predictors (Table 5). In the Africa, Blach-Overgaard et al. (2010) also showed similar results. At the continental scale, climate constitutes the only strong environmental control of African palm species distributions and water-relates factors were most important for 25 of the 29 species.

Eiserhardt et al. (2011) determined the influence of the abiotic environment (climate, soil chemistry, hydrology and topography), the biotic environment (vegetation structure and species interactions) and dispersal in the ecology of palms, its distribution, community composition and species richness on different spatial scales. They showed that for species distributions, climate is important at landscape and larger scales, soil, topography and vegetation at landscape and local scales, hydrology at local scales, and dispersal at all scales. For community composition, soil is important at regional and finer scales, hydrology, topography and vegetation at landscape and local scales, and dispersal again at all scales. Finally, for species richness, climate and dispersal appear to be important at continental to global scale, soil at landscape and broader scales, and topography at landscape and finer scales (Fig. 4).

On the other hand, palm species richness also is related with the latitudinal gradient. Highest richness are near the equatorial line and declines strongly with latitude (Fig. 5) (Bjorholm et al., 2005; Svenning et al., 2008; Alvez-Valles et al., unpublished – Chapter 2). The topography also influence at local distribution of many palm taxa (Vormisto et al., 2004b). However, due to the site-specificity, the distribution patterns of a palm taxon in a given area cannot be predicted from topography alone. This is probably because topography does not exerts influence on plants directly, but rather through its correlation with other environmental variables, such as drainage, exposure of originally different sediment layers, and forest architecture (Vormisto et al., 2004b).

Useful palm species in the Amazon region

Beyond to their ecological importance, the palms play a very important role for the local populations in the Amazon region (Fig. 6a-j) (Nascimento, 2009). Thus, palms are used for various applications, and have great economic potential and industrial value (Kahn & de Granville, 1992). In a recent study, Macía et al. (2015) present the diversity of use of palms in the northwest of South America. They present 194 useful species in the Amazon, of which 82% are of different use and an average of 15 uses per species (Table 6). Colombia and Ecuador are the countries with highest number of useful palm species, but in Ecuador, there is a best known ethnobotany of palms, therefore highest values in ethnobotanical indicators were records in this country (2010 use records and 83.3% of indigenous groups with ethnobotanical information). However, in Colombia this type of study are available for only half of the indigenous groups (48.9%) and, in Peru the studies on the ethnobotanical knowledge are most incomplete compared with the previous two countries (38.3%). Albán et al. (2008) recorded 136 palm species in Peru, 104 (76.5%) have at least one use and 32 species have no known uses in the country. Moreover, they mention that the information on ethnobotanical knowledge of Peruvian palms is essentially descriptive. In Bolivia although it has less palm species, it is widely used, presenting an average of 11 uses per species (Table 6) (Macía et al., 2015). Moraes et al. (1995), mention that most common species used in Bolivia is *Iriartea deltoidea*, and 55% of palm species are used to constructions, fibers, medicinal and crafts, and fruits for food and/or drink.

Currently, the commercialization of palm products has increased both in national and international markets, and many organizations seek to improve local living conditions promoting the processing and marketing of these products (Balslev et al., 2008). All parts of the palms including thorns and flowers are used, but the ones that are most used are fruits and palm heart for subsistence as food source (*e.g.*, *Euterpe precatoria*, *Mauritia flexuosa*, *Oenocarpus bataua*), the stem for the construction and preparation of tools and utensils (*e.g.*, *Iriartea deltoidea, Socratea exorrhiza, Wettinia drudei*), and for obtaining fibers (*e.g.*, *Astrocaryum chambira* Burret, *Aphandra natalia*), the leaves fundamentally for roofing (*e.g.*, many species of *Attalea*, *Lepidocaryum tenue*) in the construction of houses, the seeds for elaboration of crafts (*e.g.*, *M. flexuosa, O. bataua*), and different parts of the palm for medicinal purposes (e.g., *E. precatoria, O. bataua*, *S. exorrhiza*) (Paniagua-Zambrana et al., 2007; Balslev et al., 2008; Macía et al., 2015) (Table 7). Three species (*E. precatoria, I. deltoidea,* and *O. bataua*) are the most commonly used by the local communities (>80%) but *E. precatoria* and *O. bataua* are the species with most different uses and related to construction (Paniagua-Zambrana et al., 2007). Moreover, fruit of some species are main food source for various large vertebrates (Bodmer et al., 1999) and fish populations that feed during annual floods in areas where palms are dominant (Goulding, 1980).

Therefore, the importance of palms in the Amazon region are for many reasons: 1. the majority of the populations lives in rural areas and depends mainly on natural resources for their subsistence, particularly of the palms; 2. It is a place populated by diverse indigenous communities that in turn are human groups most studied; 3. There is a high species diversity and resources in a huge area of territory; 4. There is a small rate of deforestation and agricultural transformation particularly in the western Amazon, the forest are better conserved and therefore also the natural populations of palms and; 5. There is less development in road and service infrastructures (Macía et al., 2015).

Conservation status of palms

Tropical deforestation or habitat loss without doubt, is the most serious threat to the Amazonian palms, which reduce its populations and range of distribution (Balslev, 2011). Most species are forest dwellers and do not survive in deforested areas, or if they manage to survive and produce seeds, their seedlings fail to thrive in open sites (Galeano & Bernal, 2010). However, deforestation also facilitates the expansion of disturbance-resistant palms in secondary vegetation and cleared land (Balslev, 2011). Other threat is the extraction (destructive practice) and commercialization (Valencia et al., 2015). Some species have already been overexploited, which indicate that there was no sustainable management, such as the destructive extraction from the different *Wettinia* species, the palm heart harvest of *Euterpe precatoria* in Bolivia and fruit of *Mauritia flexuosa* in Peru (Bernal et al., 2014; Valencia et al., 2015). Thus, most of the products from the palms are harvested in an unsustainable way (Weigend et al., 2015). Moreover, the most commercialized palm products come mostly from very common and abundant species (*e.g.*, *Euterpe precatoria*, *Iriartea deltoidea* and *Oenocarpus bataua*). Despite their abundance, destructive management practices, overharvesting and demand for their products in the markets are a constant threat to these species, especially around more populated sites (Valencia et al., 2015). This risk is even greater for species that have restricted ranges of distribution (*e.g.*, *Oenocarpus circumtextus* Mart. and several species of *Aiphanes*), endemic or native species of threatened palms in extinction (Galeano & Bernal, 2010; Valencia et al., 2015). Some species can be endemic, of restricted geographic distribution, nevertheless having abundant population favors their conservation (Valencia et al., 2015).

We found 22 palm species cited in the IUCN (2017) list, being 11 species not threatened (LC); two as near threatened (NT) (*Attalea tessmannii* and *Prestoea tenuiramosa*); two with data deficient (DD) (*Oenocarpus makeru* and *Oenocarpus simplex*); and the rest are threatened: four species as vulnerable (VU) (*Astrocaryum carnosum*, *Oenocarpus circumtextus*, *Syagrus stratincola* and *Wettinia longipetala*); a critically endangered species (CR) (*Astrocaryum minus*); and two endangered (EN) (*Bactris setiflora* and *Ceroxylon amazonicum*) (Fig. 7). Therefore, anthropogenic action (unsustainable extraction and deforestation) and lack of protection in particular for the endemic and/or threatened palm species, could lead to their extinction (Svenning, 1998; Souza & Martins, 2004; WWF 2014; Alvez-Valles et al., 2017).

Conclusions

We conclude that Amazon palms richness is high, particularly in western Amazon with highest species richness in *terra firme* forest, and less richness in flooded and waterlogged forests. According to growth forms, the palm communities are dominated by small palms and large tall-stemmed palms, both in terms of species richness and number of individuals. Palm species richness seems to be controlled mainly by water-related variables (annual precipitation and number of wet days) to continental-scale. Topography, soil and hydrology are mains factors to local scale. The palms are widely used for various purposes, and the category of use varies according to the regions and species. Therefore, the number of products for human subsistence is probably greater than that attributed to another family of plants. Thus, the use of palms is fundamentally for human consumption, elaboration of utensils and tools, and construction of houses. Some palms with restricted geographic distribution are in threat category by the deforestation and destructive practices such as non-sustainable palm extraction. Therefore, palms are usually better preserved in areas far from human settlements and markets.

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Table 1 References used in this study

Title	**topic in the study**	**references**
Palms in forest ecosystems of Amazonia	Distribution, diversity and ecology	Kahn & de Granville (1992)
Richness and uses in a diverse palm site in Bolivia	Diversity and use of palm	Moraes et al. (1995)
Diversity and dominance in palms (Arecaceae) communities in terra firme forest in the western Amazon basin	Diversity and distribution	Vormisto et al. (2004a)
Palm distribution patterns in Amazonian rainforests: what is the role of topographic variation?	factors that control to diversity	Vormistoet al. (2004b)
Historical legacies in the geographical diversity patterns of New World Palms. (Arecaceae) subfamilies	Diversity and distribution	Bjorholm et al. (2006)
Environmental and spatial controls of palm (Arecaceae) species richness across the Americas	factors that control to diversity	Bjorholm et al. (2005)
Diversidad y abundancia de palmas	Diversity and distribution	Balslev et al. (2015)
Determinants of palm species distributions across Africa: the relative roles of climate, non-climatic environmental factors, and spatial constraints	factors that control to diversity	Blach-Overgaad et al. (2010)
Palmas (familia Arecaceae o Palmae)	Diversity and conservation	Galeano & Bernal (2005)
Palmas de Colombia, guía de campo	Ecology	Galeano & Bernal (2010)
Palmas (Arecaceae) útiles en los alrededores de Iquitos, Amazonía Peruana	Use and conservation	Balslev et al. (2008)
Arecaceae	conservation	Leitman et al. (2013)
Phytogeographical patterns of Bolivian palms	Diversity and distribution	Moraes (2007)
Riqueza e etnobotânica de palmeiras no território indígena Krahô, Tocantins, Brasil	Use and conservation	Nascimento (2009)
Usos de las palmas por poblaciones rurales	Use and conservation	Macía et al. (2015)
Diversity of palm uses in the western Amazon	Use and conservation	Paniagua-Zambrana et al. (2007)
Las Palmeras De América Del Sur : Diversidad , Distribución e Historia Evolutiva	Diversity and distribution	Pintaud *el al*. (2008)

Table 2 Endemic palm species in the Amazon region according to the countries and sub-region of the Amazon. Ass: Amazon *sensu stricto*, An: Andes sub-region, Gui: Guiana sub-region, Gu: Gurupi sub-region, Pla: Plateau sub-region.

Countries	**Endemic species**	**Ass**	**An**	**Gui**	**Gur**	**Pla**
Bolivia	*Attalea blepharopus* Mart.	•				
	Bactris faucium Mart.	•	•			
	Desmoncus latisectus Burret	•	•			
	Syagrus cardenasii Glassman	•	•			•
	Syagrus yungasensis M. Moraes		•			
Colombia	*Desmoncus interjectus* A.J. Hend.	•				
	Oenocarpus circumtextus Mart.	•				
	Oenocarpus makeru R. Bernal, Galeano & A.J. Hend.	•				
Ecuador	*Bactris setiflora* Burret	•	•			
	Ceroxylon amazonicum Galeano	•	•			
Guiana	*Asterogyne guianensis* Granv. & A.J. Hend.			•		
	Attalea guianensis (Glassman) Zona	•		•		
Peru	*Astrocaryum carnosum* F. Kahn & B. Millán	•				
	Astrocaryum huicungo Dammer ex Burret	•	•			
	Astrocaryum perangustatum F. Kahn & B. Millán	•	•			
	Astrocaryum scopatum F. Kahn & B. Millán	•				
	Attalea bassleriana (Burret) Zona	•	•			
	Attalea cephalotus Poepp. ex Mart.	•				
	Attalea moorei (Glassman) Zona	•				
	Attalea peruviana Zona	•				
	Attalea salazarii (Glassman) Zona	•				
	Attalea weberbaueri (Burret) Zona	•				
	Chamaedorea fragrans (Ruiz & Pav.) Mart.	•	•			
	Desmoncus loretanus A.J. Hend.	•				
	Desmoncus madrensis A.J. Hend.	•				
	Geonoma schizocarpa A.J. Hend.	•	•			
	number of species	**24**	**11**	**2**	**0**	**1**

Table 3 Growth form of 789 native American palm species across the Americas. Based in Balslev et al. (2011).

Growth Forms of Palm	number of species	genera	Description	Some Species
Large tall-stemmed Palms	102	19	These are mainly defined by their height and stem diameter. Tall stems 20–35 m long, and 20–100 cm in diameter. Their leaf size varies greatly from one group to another. They occur in all tropical forest ecosystems, in Andean vegetation at high elevation, and in savannas and open areas.	*Attalea speciosa*, *A. maripa*, *Astrocaryum aculeatum*, *Euterpe oleracea*, *Mauritia flexuosa*
Large-leaved medium–short-stemmed Palms	31	7	These have stems 1–20 m tall, usually 15–25 cm in diameter; when short stemmed they may be subacaulescent with the stem no more than 1 m long and entirely covered with the sheaths of dead leaves. Their leaves are 4–10 m long in adult palms.	*Aphandra natalia*, *Astrocaryum carnosum*, *Astrocaryum sciophilum*, *A. farinosum*, *Phytelephas macrocarpa*
Medium-sized Palms	95	21	These palms have stems 8–15 m long and 12–15 cm in diameter and their leaves are 2–4 m long.	*Oenocarpus balickii*, *Syagrus inajai*, *Wettinia maynensis*
Medium/Small Palms with Stout Stem	42	12	These palms have stems with diameter of 30–60 cm or with the stem diameter significantly enlarged by persistent skirt of dead leaves	*Acrocomia intumescens*, *Butia lallemantii*, *Coccothrinax spissa*
Small Palms	423	36	These palms have stems 0.1–8 m long and 0.4–12 cm in diameter	Many species of genera *Bactris*, *Geonoma*, *Hyospathe*, *Chelyocarpus*, some small species of *Syagrus* (*S. smithii*) and *Wettinia* (*W. maynensis*, *W. drudei*)
Large acaulescent Palms	28	2	These palms have 4–8 m long leaves and a subterranean stem that never grows above ground. The palm's leaf sheaths and bases of petioles and inflorescence peduncles emerge from the ground	*Astrocaryum acaule*, *Astrocaryum paramaca*, *Astrocaryum sociale*, various species of *Attalea* (*A. attaleoide*, *A. spectabilis*)
Small acaulescent Palms	56	13	the stem is apparently absent and subterranean or too short to be conspicuous and the leaves are less than 2 m long.	Species of *Aiphanes*, *Bactris*, *Geonoma*, *Lytocaryum*, *Neonicholsonia*, *Barcella odora*
Climbing Palms	12	2	These palms have stems unable to grow vertically without support, except in the seedling and juvenile stages	Genus *Desmoncus* (11 of the 12 species) except in *Desmoncus stans*, *Chamaedorea elatior*

Table 4 Number of solitary and cespitose palm species in Tropical America and in Amazon region (review data in this study). Dichotomous Branching was observed in rare cases in the Three Species. Based in Balslev et al. (2011).

Branching	**Tropical America**		**Amazon region**	
	Species	**Species (%)**	**Species**	**Species (%)**
Solitary	521	66	74	42
Cespitose	268	34	100	56
Dichotomous	3	>1	3	>1
Total	789	789	177	177

Table 5 Multiple linear regression of palm species richness in the Americas against five environmental and nine spatial explanatory variables using stepwise selection P–enter = 0.05 and P–leave = 0.05 at 10 grain sizes, from 1° × 1° grid squares (1°) to 10° × 10° grid squares (10°). The final models are shown, with the variables in decreasing order of F values. TEMP = mean annual temperature (°C), PREC = annual precipitation (mm year−1), WETD = number of wet days per year, TOPOR = topographical range (m), NoVegT = number of vegetation types, X, X 2, X 3, Y, Y 2, Y 3, X 2Y and XY 2 refer to the cubic trend surface coordinates, red: PREC and blue color: WETD. Extracted from Bjorholm et al. (2005)

Grain size	**Explanatory variable F value (sign of regression coefficient)**												**R²**	**d.f.**
1°	WETD 385(+)	Y^2 375(-)	X^2 231(-)	PREC 85(+)	TOPOR 35(+)	X 33(-)	Y 32(-)	XY^2 27(-)	TEMP 18(+)	X^3 16(-)	Y^3 10(-)	X^2Y 5(-)	0.79	2025
2°	Y^2 122(-)	WETD 91(+)	X^2 68(-)	Y 35(-)	PREC 32(+)	X 22(-)	XY^2 17(-)	TOPOR 15(+)	NoVegT 16(+)	X^3 6(-)			0.77	576
3°	Y^2 60(-)	X 34(-)	WETD 33(+)	X^2 31(-)	Y 30(-)	PREC 24(+)	TOPOR 13(+)	NoVegT 12(+)	XY^2 9(-)				0.78	279
4°	Y^2 40(-)	PREC 20(+)	NoVegT 17(+)	X 13(-)	X^2 13(-)	WETD 11(+)	Y 11(-)	XY^2 5(-)	TEMP 4(+)				0.77	161
5°	PREC 106(+)	Y^2 28(-)	TOPOR 11(+)	TEMP 8(+)	NoVegT 2(+)								0.72	113

6°	PREC 65(+)	Y^2 37(-)	NoVegT 25(+)	X 7(-)	TEMP 5(+)	0.75	79
7°	PREC 32(+)	Y^2 19(-)	TOPOR 10(+)	NoVegT 7(+)		0.71	60
8°	PREC 46(+)	NoVegT 27(+)	Y^2 10(-)			0.74	54
9°	PREC 38(+)	NoVegT 26(+)	Y^2 22(-)	X^2 8(-)	X^3 5(-)	0.81	38
10°	PREC 61(+)	TOPOR 22(+)	Y^2 10(-)	TEMP 5(+)		0.82	35

Table 6 Use of palms in the northwest of South America. Extracted from Macía et al. (2015)

Country / Ecoregion	**Useful species**	**Use**	**Use records**	**Average ± SD of palm uses per species**	**Indigenous groups with ethnobotanical information**	**Percentage of indigenous groups with ethnobotanical information**
Total	**194**	**2395**	**6141**	**12.3 ± 18.7**	**54**	**49.1**
Amazon	134	1972	5144	14.7 ± 20.0	47	47.5
Andes	68	344	439	5.1 ± 6.0	2	28.6
Choco	52	347	569	6.7 ± 7.3	5	83.3
Colombia	**105**	**814**	**1429**	**7.8 ± 10.1**	**22**	**48.9**
Amazon	70	615	1049	8.8 ± 10.6	19	48.7
Andes	18	35	39	1.9 ± 1.2	-	-
Choco	38	225	341	5.9 ± 5.7	3	75
Ecuador	**103**	**936**	**2010**	**9.1 ± 11.9**	**10**	**83.3**
Amazon	62	676	1494	10.9 ± 12.3	7	87.5
Andes	52	240	295	4.6 ± 5.3	-	-
Choco	30	167	228	5.6 ± 5.2	3	75
Peru	**96**	**785**	**1390**	**8.2 ± 10.1**	**18**	**38.3**
Amazon	93	772	1369	8.3 ± 10.1	18	38.3
Andes	4	19	21	4.8 ± 3.4	-	-
Bolivia	**62**	**655**	**1348**	**10.6 ± 14.7**	**11**	**61.1**
Amazon	54	603	1267	11.2 ± 14.6	10	58.8
Andes	13	77	84	5.9 ± 6.7	2	100

Table 7 Description of six use-categories employed concerning knowledge and use of Amazon palms. Based in Paniagua-Zambrana et al. (2007)

use category	Species	Description
food source	*Aphandra natalia* (Balslev & A.Hend.) Barfod; *Astrocaryum chambira* Burret; *A. jauari* Mart.; *Attalea butyracea* (Mutis ex L.f.) Wess.Boer; *A. insignis* (Mart.) Drude; *A. maripa* (Aubl.) Mart.; *A. microcarpa* Mart.; *A. phalerata* Mart; *A. plowmanii* (Glassman) Zona; *A. racemosa* Spruce; *Bactris acanthocarpa* Mart.; *B. bidentula* Spruce; *B. bifida* Mart.; *B. brongniartii* Mart.; *B. concinna* Mart.; *B. corossilla* H.Karst.; *B. halmoorei* A.J.Hend.; *B. hirta* Mart.; *B. macroacantha* Mart.; *B. riparia* Mart.; *B. schultesii* (L.H.Bailey) Glassman; *B. simplicifrons* Mart.; *Chamaedorea pauciflora* Mart.; *Chelyocarpus repens* F.Kahn & K.Mejia; *C. ulei* Dammer; *Euterpe precatoria* Mart.; *Geonoma macrostachys* Mart.; *Hyospathe elegans* Mart.; *Iriartea deltoidea* Ruiz & Pav.; *Iriartella stenocarpa* Burret; *Itaya amicorum* H.E.Moore; *Lepidocaryum tenue* Mart.; *Mauritia carana* Wallace ex Archer; *M. flexuosa* L.f.; *Mauritiella armata* (Mart.) Burret; *Oenocarpus bataua* Mart.; *Phytelephas tenuicaulis* (Barfod) A.J.Hend.; *Prestoea schultzeana* (Burret) H.E.Moore; *Socratea exorrhiza* (Mart.) H. Wendl.	Dietary products, consumed directly (fruits) or after processing, including oil extraction and indirect uses such as palm stems used for breeding edible larvae. Part of palm used: *Fruits, palm heart, seeds, stem.*
construction	*Aphandra natalia* (Balslev & A.Hend.) Barfod; *Astrocaryum chambira* Burret; *A. jauari* Mart.; *Attalea butyracea* (Mutis ex L.f.) Wess.Boer; *A. insignis* (Mart.) Drude; *A. maripa* (Aubl.) Mart.; *A. microcarpa* Mart.; *A. phalerata* Mart.; *A. plowmanii* (Glassman) Zona; *A. racemosa* Spruce; *Bactris acanthocarpa* Mart.; *B. concinna* Mart.; *B. corossilla* H.Karst.; *B.halmoorei* A.J.Hend.; *B. schultesii* (L.H.Bailey) Glassman; *B. simplicifrons* Mart.; *Chamaedorea pauciflora* Mart.; *Chelyocarpus repens* F.Kahn & K.Mejia; *Euterpe precatoria* Mart.*; Geonoma brongniartii* Mart.; *G. camana* Trail; *G. deversa* (Poit.) Kunth; *G. leptospadix* Trail; *G. macrostachys* Mart.; *G. poeppigiana* Mart.; *G. stricta* (Poit.) Kunth; *Hyospathe elegans* Mart.; *Iriartea deltoidea* Ruiz & Pav.; *Itaya amicorum* H.E.Moore; *Lepidocaryum tenue* Mart.; *Mauritia carana* Wallace ex Archer; *M. flexuosa* L.f.; *Mauritiella armata* (Mart.) Burret; *Oenocarpus bataua* Mart.; *Phytelephas tenuicaulis* (Barfod) A.J.Hend.; *Prestoea schultzeana* (Burret) H.E.Moore; *Socratea exorrhiza* (Mart.) H. Wendl.; *Wettinia augusta* Poepp. & Endl.; *W. drudei* (O.F.Cook & Doyle) A.J.Hend.	Used in the construction of permanent or temporary houses (palm stem, leaves for roofing). Part of palm used: *Leaves, stem.*

Tools and utensils	*Aphandra natalia* (Balslev & A.Hend.) Barfod; *Astrocaryum chambira* Burret; *A. jauari* Mart.; *Attalea butyracea* (Mutis ex L.f.) Wess.Boer; *A. insignis* (Mart.) Drude; *A. maripa* (Aubl.) Mart.; *A. phalerata* Mart.; *A. racemosa* Spruce; *Bactris bidentula* Spruce; *B. brongniartii* Mart.; *B. concinna* Mart.; *B. halmoorei* A.J.Hend.; *B.riparia* Mart.; *Chamaedorea pauciflora* Mart.; *Chelyocarpus repens* F.Kahn & K.Mejia; *Chelyocarpus ulei* Dammer; *Desmoncus giganteus* A.J.Hend.; *Euterpe catinga* Wallace; *E. precatoria* Mart.; *Geonoma deversa* (Poit.) Kunth; *G. leptospadix* Trail; *G. stricta* (Poit.) Kunth; *Hyospathe elegans* Mart.; *Iriartea deltoidea* Ruiz & Pav.; *Iriartella stenocarpa* Burret; *Itaya amicorum* H.E.Moore; *Lepidocaryum tenue* Mart.; *Mauritia flexuosa* L.f.; *Oenocarpus bataua* Mart.; *Phytelephas tenuicaulis* (Barfod) A.J.Hend.; *Socratea exorrhiza* (Mart.) H. Wendl.	Raw materials (palm stem, fibers) for the manufacture basket-making (fans, baskets, rush mat) and utensils used in the home and/or the agricultural activities. Moreover, for the manufacture of tools used in hunting and fishing (blow guns, darts). Part of palm used: *Leaves, fibers, roots, seeds, stem.*
Medicinal and cosmetic	*Astrocaryum chambira* Burret; *A.jauari* Mart.; *Attalea butyracea* (Mutis ex L.f.) Wess.Boer; *A. insignis* (Mart.) Drude; *A. maripa* (Aubl.) Mart.; *A. phalerata* Mart.; *Bactris acanthocarpa* Mart.; *B. riparia* Mart.; *B. simplicifrons* Mart.; *Chamaedorea pauciflora* Mart.; *Desmoncus giganteus* A.J.Hend.; *Euterpe catinga* Wallace; *E. precatoria* Mart.; *Geonoma brongniartii* Mart.; *G. macrostachys* Mart.; *Hyospathe elegans* Mart.; *Iriartea deltoidea* Ruiz & Pav.; *Iriartella stenocarpa* Burret; *Lepidocaryum tenue* Mart.; *Mauritia flexuosa* L.f.; *Oenocarpus bataua* Mart.; *Phytelephas tenuicaulis* (Barfod) A.J.Hend.; *Socratea exorrhiza* (Mart.) H. Wendl.	Materials used alone or as ingredients (extracts, oils) in medicinal and cosmetic remedies (creams, soaps, etc.). Part of palm used: *Flowers, fruits, palm hearth, roots, seeds.*
Decorative, ritual and religious	*Attalea phalerata* Mart.; *Euterpe precatoria* Mart.; *Iriartea deltoidea* Ruiz & Pav.; *Oenocarpus bataua* Mart.	Materials used in ceremonial or religious activities (perfumes, decoration) and others related to cultural activities (magic rituals). Part of palm used: *Flowers, leaves.*
Commercialization	*Aphandra natalia* (Balslev & A.Hend.) Barfod; *Astrocaryum chambira* Burret; *Bactris gasipaes* Kunth; *Desmoncus giganteus* A.J.Hend.; *Euterpe precatoria* Mart.; *Geonoma camana* Trail; *Mauritia flexuosa* L.f.; *Oenocarpus bataua* Mart.; *Phytelephas tenuicaulis* (Barfod) A.J.Hend.	Raw material for the manufacture of products that are commercialized, and/or material which is commercialized without processing. Part of palm used: *Fiber, fruits, leaves, palm hearth, seeds, stem.*

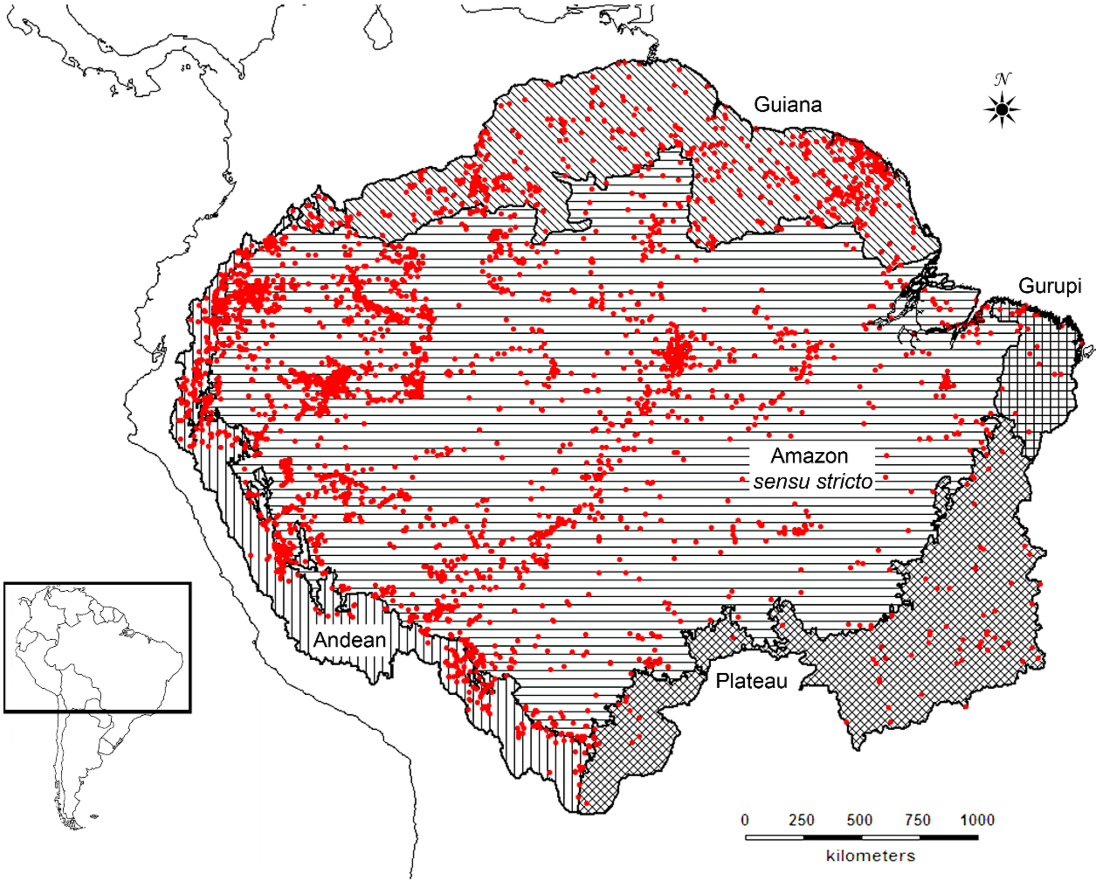

Fig. 1 Amazon region divided into sub-regions follows Eva and Huber (2005). Red dots are occurrence records 177 Amazon palms derived from the *Global Biodiversity Information Facility* (GBIF - http://www.gbif.org).

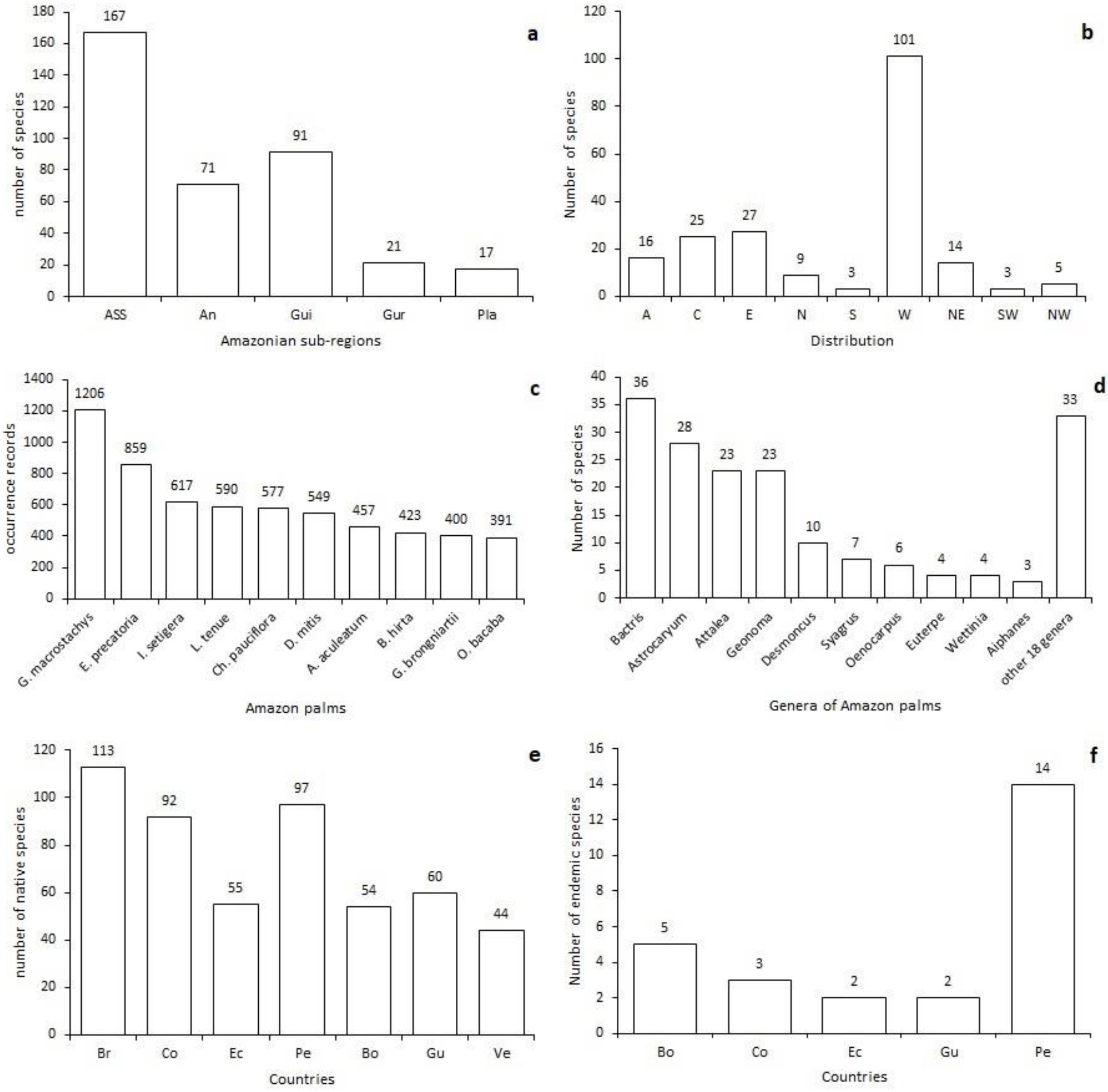

Fig. 2 Number of species by (a) Amazonian sub-regions and (b) Distribution in the Amazon region; (c) Amazon palms with high number of occurrence records; (d) Genera of Amazon palms with high number of species; (e) number of native species and (f) endemic species by contries. Ass: Amazônia sensu stricto, An: Andes sub-region, Gui: Guiana sub-region, Gu: Gurupi sub-region, Pla: Plateau sub-region, A: the entire Amazon region, C: central Amazon, E: eastern Amazon, N: north Amazon, S: south Amazon, W: western Amazon, NE: northeast of the Amazon, SW: southwest of the Amazon, NW: northwest of the Amazon, Br: Brazil, Co: Colombia, Ec: Ecuador: Pe: Peru, Bo: Bolivia, Gu: Guyana, Ve: Venezuela

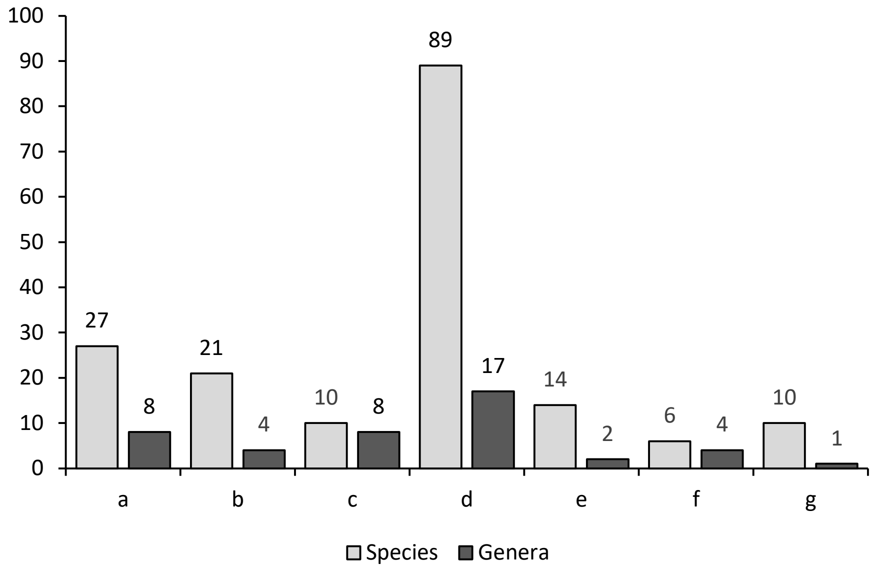

Fig. 3 number of Amazon palm species and genera in each growth forms. a. Large tall-stemmed Palms, b. Large-leaved medium–short-stemmed Palms, c. Medium-sized Palms, d. Small Palms, e. Large acaulescent Palms, f. Small acaulescent Palms, g. Climbing Palms.

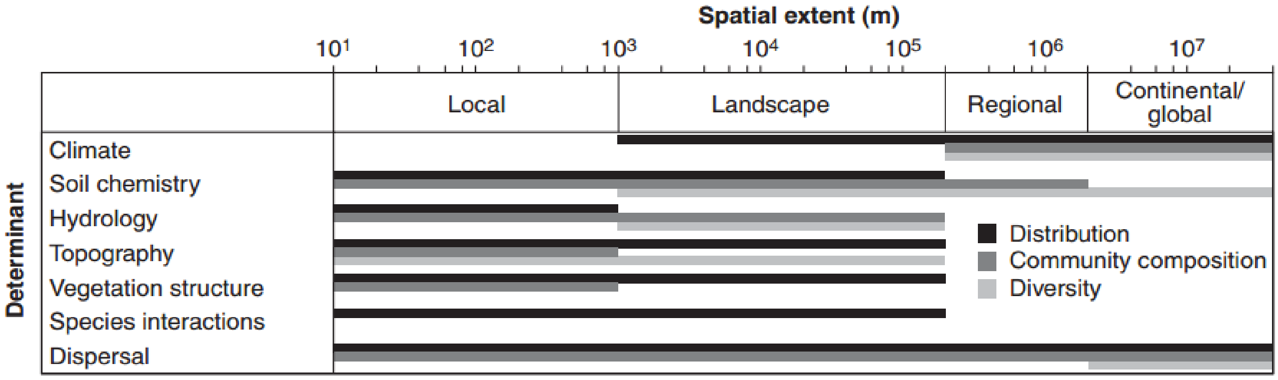

Fig. 4 Overview showing which processes (left column) have been shown to influence palm distributions, community composition and palm diversity, as indicated, on different scales (top row). Numbers show the upper and lower extents of the scale domains in metres. Extracted from Eiserhardt et al. (2011)

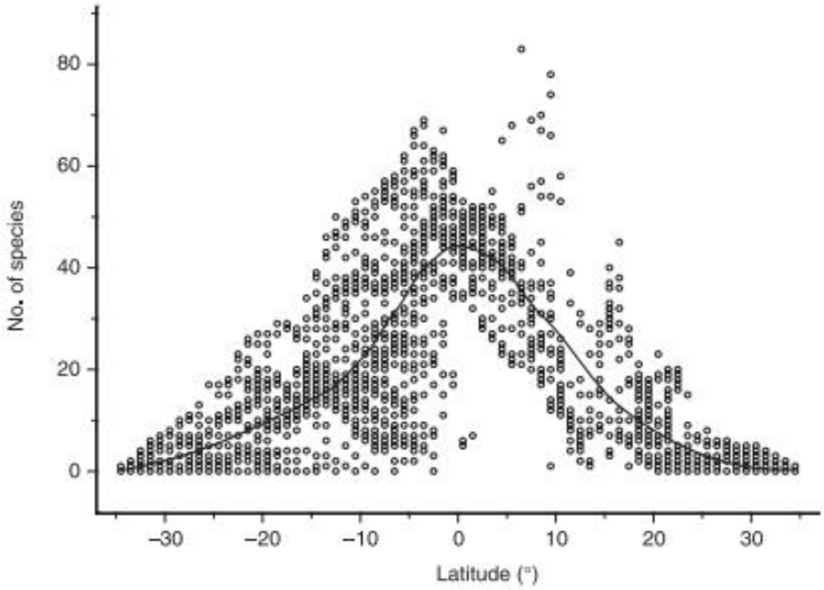

Fig. 5 Species number for each 1° grid square plotted against latitude. The curve is a linear Gaussian locally weighted regression curve with span = 0.5. This span closely approximates the span selected by the cross-validation procedure in S-PLUS. It is noteworthy that the latitude gradient is particularly steep within tropical latitudes. Extracted from Bjorholm et al. (2005)

Fig. 6 Different products made with Amazonian palms, a-b. Roof built with the leaves of *Euterpe precatoria* and walls with boards of the trunk of the same species, c. Trunks of *Dictyocaryum lamarckianum* cut into boards and drying for its use as housing walls, d. Leaves of *Lepidocaryum tenue* for the roof of dwellings, e. leaves of Attalea butyracea for later use in the roof of houses, f. Fruits of *Mauritia flexuosa* to prepare *chicha* (juice), g. Women's skirt made with the fibers of the tender leaves of *Mauritia flexuosa*, h. palm heart of *Euterpe precatoria* for commercialization, i. Bow and arrowheads manufactured with the trunk of *Bactris gasipaes*, j. Woven baskets with tender leaves of *Attalea phalerata*. Extracted from Macía et al. (2015)

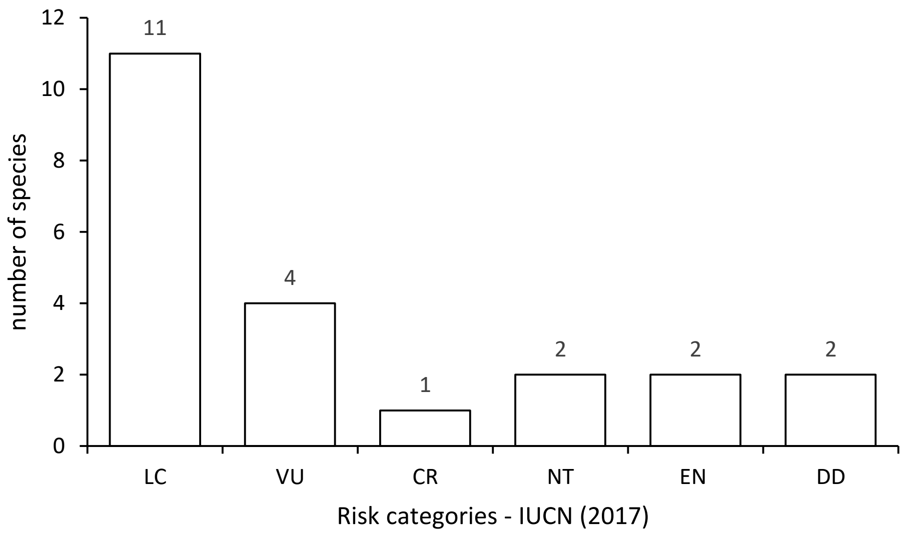

Fig. 7 Number of Amazon palm species in risk categories according IUCN (2017).

Chapter 2

PALM SPECIES RICHNESS, LATITUDINAL GRADIENTS, SAMPLING EFFORT, AND DEFORESTATION IN THE AMAZON REGION

Palm species richness, latitudinal gradients, sampling effort, and deforestation in the Amazon region[2]

Abstract

Palms are most diverse in warm and humid regions near the equator. Though palms remain relatively well conserved, they are under increasing pressure from deforestation. Here, we analyze patterns of palm species richness relative to latitudinal gradient, sampling effort, and deforestation in the Amazon, and compare patterns of richness and floristic similarity among Amazonian sub-regions. We built a database of 17,310 records for 177 species. The areas with the greatest richness were in the western, central and northeastern Amazon, principally at latitudes 0–5ºS. Species richness and the number of records were highly correlated ($R^2=0.76$, $P<0.005$). The highest rates of deforestation (≥ 2000 km^2) were found in the southern and eastern Amazon of Brazil, which coincide with low species richness and gaps in records. Similarity analyzes resulted in two groups of sub-regions: the first included the Amazon *s.s.*, the Andes and the Guiana sub-regions, while the second included the Plateau and Gurupi sub-regions. We conclude that the highest species richness is at low latitudes, and observed richness is affected by sampling effort and is vulnerable to deforestation. Therefore, areas with low species richness, especially areas with data deficiency, need to be further studied for a better understanding of their patterns of diversity and richness.

Keywords: Amazon palms, Amazon sub-regions, ecology of palms, richness patterns, species occurrence records

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Introduction

Understanding the spatial distribution of biodiversity is fundamental for its use, management and conservation (Mutke & Barthlott 2005). The Amazon presents high plant species richness not only at the regional scale (ter Steege *et al*. 2015), but also at very local scales (Gentry 1988; Balslev *et al*. 1998, 2011; Oliveira & Mori 1999; ter Steege *et al*. 2000). Moreover, the richness varies along latitudinal gradients (Barthlott *et al*. 2005; 2007), and floristic variability evolved also under the influence of climatic, soil and ecological drivers (Gentry 1988; Pitman *et al*. 2001; Vormisto 2002; ter Steege *et al*. 2003; Haugaasen & Peres 2006; Honorio *et al*. 2008). Although the Amazon is still relatively well-conserved, it is subject to deforestation with profound regional and global implications (WWF 2014), and uneven data records from the region makes it difficult to study.

Plant diversity is very unevenly distributed across the globe (Barthlott *et al*. 2005). In general, plant diversity increases toward the equator (Barthlott *et al*. 2005; 2007) but not all tropical regions are necessarily richer in plant species than subtropical or temperate ones (Barthlott *et al*. 2007). The biodiversity of a particular area depends not only on historical factors and its location, but also on the diversity of abiotic factors (*e.g*., soils, climate, altitudinal changes, and fire regimes) (Barthlott *et al*. 1996; 2005; Mutke & Barthlott 2005). Thus, several geographical studies on species distributions and diversity (*e.g*., ter Steege *et al*. 2000; 2003; 2006; Pitman *et al*. 2001; 2002; Bjorholm *et al*. 2005; 2006; Van Der Heijden & Phillips 2009; Blach-Overgaard *et al*. 2010; Eiserhardt *et al*. 2011b; Vedel-Sørensen *et al*. 2013) provide insights into the roles played by climate, topography, biotic interactions, and dispersal limitations in shaping the Amazon’s diversity (Pearson & Dawson 2003; Gaston 2009). In fact, most of the global centres of plant diversity (> 5,000 species per 10,000 km^2) are located in mountainous regions of humid tropics (Costa Rica to the Chocó, Tropical eastern Andes, Atlantic Brazil, northern Borneo, New Guinea), where suitable climatic conditions and high levels of geodiversity coincide (Barthlott *et al*. 2005; 2007). The patterns of plant richness related to climate (mean annual temperature, annual water deficit, and their interaction) are globally consistent and are independent of the diverse evolutionary histories and functional assemblages of plants in different part of the world (Francis & Currie 2003). In high energy regions, like the tropics and subtropics, the influence of water availability gains a stronger influence resulting in higher correlations coefficients with factors, like actual evapotranspiration, annual precipitation, or the number of dry months (Barthlott *et al*. 2005).

The Amazon region maintains a dynamic and suitable environmental heterogeneity for palms (Arecaceae) diversification. The Amazon has fewer threatened palm species than other Neotropical biogeographical regions such as the Caribbean, the Pacific coast, and the Andes (Balslev *et al*. 2015). There are some evident biogeographical patterns for palms in the Amazon region, whose diversity follows a gradient of rainfall with the humid areas being much richer, except for genera as *Attalea sensu stricto* and *Syagrus* which both show opposite tendencies (Pintaud *et al.* 2008). The western Amazon is distinguished by endemism at the generic level (*e.g*., *Aphandra*, *Itaya*, *Wendlandiella*) and especially by a high level of species endemism (Alvez-Valles *et al*. 2018). The central Amazon region also has its own endemisms, but at the species level (*e.g.*, *Astrocaryum ferrugineum* F. Kahn & B. Millán, *A. sociale* Barb. Rodr., *Bactris balanophora* Spruce, *B. tefensis* A.J. Hend., *Geonoma aspidiifolia* Spruce, *G. oligoclona* Trail, *Iriartella setigera* (Mart.) H. Wendl., *Oenocarpus minor* Mart.). This may relate to local geological features and a dry corridor barrier to the north, and possibly to the presence of refuges during the Pleistocene (Prance 1973). Other parts of the Amazon region are comparatively less diverse, but stand out for their floristic composition. The diversity is highest in non-flooded forests (*terra firme*), while flooded forests are less diverse (Kahn & de Granville 1992). Palms occur in different habitat types (Balslev *et al*. 2015), the topography determines their distribution (Kahn & de Castro 1985;

Vormisto *et al.* 2004), and have great influence on the forest structure (Kahn & Mejia 1990). In addition, their taxonomy is relatively well known (Gentry 1991; Henderson *et al*. 1995), making this group suitable for meta-analysis.

A commonly discussed pattern in palms and many other organisms is the variation in number of species per unit area, when latitude varies, which is referred to as the latitudinal gradient in which the number of species diminishes when moving away from the equator (Pianka 1966). Many explanations, both biotic and abiotic, have been proposed to explain the latitudinal gradient (Stiling 1996). Biotic explanations include the hypotheses of competition (Dobzhansky 1950), predation (Paine 1966) and, zoophilia (Stiling 1996). Abiotic explanations include the hypotheses of climate stability (Klopfer 1959), ecological time (Fischer 1960), productivity (Connell & Orias 1964) and area (Terborgh 1973). Some hypotheses include both biotic and abiotic factors such as spatial heterogeneity (Miller 1958, McArthur & MacArthur 1961) and ecological refuges (Haffer 1969, Vanzolini 1970, Brown & Ab'Saber 1979). Most of these hypotheses have not been tested and some are not testable (Stiling 1996). All of them, however, were proposed based on the number of species of one or a few taxa (genera, families, order, class, etc.), but still the findings were often generalized as if they were valid for all taxa in the community even if it is well known that some taxa have opposite trends in their species richness, a fact that must be considered for a deeper understanding of the latitudinal gradient. A meta-analysis showed that species richness of most taxa increases towards the equator (Hillebrand 2004) and this trend is substantially stronger at regional compared to local scales (Mittelbach *et al*. 2007).

Deforestation in the Amazon region increased explosively with clandestine road constructions that allowed human expansion and irregular occupation of lands, and predatory exploration of noble woods (Fearnside 1992). Consequently, illegal wood exploration that increases fire susceptibility, selective logging that cause extensive damage to nearby trees and soils, increase the risk of species extinction and carbon emissions. Open roads that encourage unplanned development, and explored forest converted into family agriculture and pasture are main causes of deforestation (Veríssimo *et al*. 1995; Johns *et al*. 1996; Holdsworth & Uhl 1997; Souza Jr *et al*. 2003). Moreover, the primary adverse effect of tropical deforestation is massive extinction of species (Whitmore & Sayer 1992, Turner 1996) and impacts on local and global climate (Laurance *et al.* 2004). Therefore, deforestation is a major threat to biodiversity (Skole & Tucker 1993; Turner 1996). In the last decades, the Amazon has experienced rapid land use change. An area that measured 763,000 km² had been deforested up to 2013 in the Brazilian Amazon (Nobre 2014), suggesting that 47% of the Brazilian Amazon would be deforested by 2050 (Soares *et al*. 2006). Additionally, deforestation rates within other Amazon countries are increasing (Soares *et al*. 2014). Hansen *et al*. (2013) mention that the tropics are the only domain to show statistically significant trend in annual forest loss, with an estimated increase in loss of 2101 km²/year. Tropical rainforest ecozones totaled 32% of global forest cover loss, nearly half of which occurred in South American rainforests (Hansen *et al*. 2013). In recent years, Brazil has substantially reduced deforestation rates (Hansen *et al.* 2013). However, large reductions in Amazon basin forest cover may still occur in the future (Spracklen & Garcia-Carreras 2015). Thus, all projections for the future of the Amazon over the current century, predict large-scale deforestation in the region (Laurance *et al.* 2004). Some palm species are adapted to high levels of disturbance and seem to benefit from deforestation and forest fragmentation, adjusting their reproductive strategies to better use these high-luminosity conditions (Barot *et al*. 2005). However, most palm species are vulnerable to such anthropogenic changes (Salm *et al*. 2001).

Species richness is widely used in ecological studies. Beyond the particular nature of the community, the calculated species richness is strongly affected by sampling effort (Lande *et al*. 2000). That is, the greater the collection effort, the greater the species richness (Melo &

Hepp 2008). Furthermore, species richness should be considered directly related to the number of individuals, area and variety of habitats sampled (Schluter & Ricklefs 1993). One of the most used forms of analysis is the construction of relationships between sample effort and number of species sampled. The analysis consists of figures relating the sample effort (number of individuals sampled or sample area) cumulative (X axis) to the cumulative number of species sampled (Y axis). This curve is logarithmic: as the sample area increases, at the beginning the number of species increases rapidly, then slowly and, finally very little (Pielou 1975; 1977).

Spatial scale has become increasingly important in ecology (Franklin 2009), using digital biodiversity databases, that permit assembly of species occurrence data from various sources, such as herbaria and museums, as well as data from the literature (Graham *et al.* 2004; Yesson *et al*. 2007). The current demand for reliable, easily accessible and free biodiversity data makes electronic infrastructures fundamental for facilitating access (Canhos *et al.* 2015). There are different international databases such as the *Global Biodiversity Information Facility* (GBIF), *Species link*, INCT - *Herbário Virtual da Flora e dos Fungos*, *NeoTropTree*, and others that strive to make the world’s biodiversity data globally accessible via the internet and data sharing protocols (Franklin 2009). These databases are used in plant ecology for analyses of species distribution (Bjorholm *et al.* 2006; Salm *et al.* 2007; Werneck *et al.* 2011), areas of endemism (Sigrist & Carvalho 2008; Werneck *et al.* 2011; Menini Neto *et al.* 2016; Alvez-Valles *et al*. 2018); effects of climate change on plants (Blach-Overgaard *et al*. 2010; Feeley & Silman 2011; Patiño *et al*. 2016) and others.

Previous palm studies (Bjorholm *et al*. 2005; 2006; Blach-Overgaard *et al*. 2010; Vedel-Sørensen *et al*. 2013) have analysed distribution in the new world as a whole and in the African continent. Here, we have assembled a large georeferenced database of locations for palm species in the Amazon region to answer the following questions: (1) How is palm species richness distributed spatially and latitudinally in the Amazon region? (2) Is the observed palm species richness related to sample effort? (3) Are low richness and record gaps related to deforestation? and (4) Are there floristic similarities in palms distribution patterns among the five Amazonian sub-regions?

Materials and Methods

Study area

Our study area covers the entire Amazon watershed from its highest altitude spring areas in the surrounding mountain systems, to the river mouth in the extreme east (8,121,313 km^2) (Eva & Huber 2005). This area can be divided into the central Amazon (68%) (Amazon *sensu stricto*) and four peripheral sub-regions: Guiana (12%), Plateau (11%), Andes (7%), and Gurupi (2%) (Fig. 1A). This delimitation, proposed by Eva and Huber (2005), was based on hydrographic, ecological, and biogeographical criteria as follows:

The Amazon sub-region (*sensu stricto*) (5,569,174 km^2) is defined by the boundary of the Amazon River Basin to the north, an outline of 700 m to the west and the Amazon forest (before exploration) to the south and southeast. Average annual temperature (AAT) is > 24°C, and mean annual rainfall (MAR) is > 1400 mm. Several tropical soil types with different chemical and physical properties are found in this sub-region. It harbours flooded or non-flooded terrain, including floodplains and so-called *igapó*, which is peculiar by being flooded by black waters. The region also includes coastal forest (mangroves) and marshes along the Atlantic Ocean.

The Andes sub-region (555,564 km^2) stretches from 700 m elevation to the sources of the Amazon River at the edge of the watershed along the top of the Andes. Therefore, the sub-region includes all submontane, mountainous, and high Andean (alpine) ecosystems, such as: humid montane forests, cloud forests, *yungas*, *páramos*, *punas*, *jalcas*, *chirivitales*, etc., with their corresponding faunistic associations that inhabit the eastern slopes of the Andean Cordillera, from Colombia in the north, through Ecuador and Peru to Bolivia in the south.

The Plateau sub-region (864,951 km^2) is the area between the confines of the Amazon rainforest in the plains and the limits of the Amazonas/Tocantins watershed spring areas in Bolivia and Brazil. This sub-region contains a considerable portion of savanna (*cerradão*) and shrubby savanna (*cerrado*), characteristic of the landscape of the Brazilian central plateau. The lowlands of eastern Bolivia, consists of an extensive mosaic of evergreen forest, with drier forest patches alternating with floodplain savannas and palm marshes, which in turn are bordered to the south by the dry forest of Chiquitania and the formation known as *chaco*.

The Guiana sub-region (970,161 km^2) is bordered to the north by the Atlantic coast and by the Orinoco and Vichada rivers, while the southern boundary is formed by the watershed of the Amazon basin. The mountains of the Guiana massif are surrounded by extensive promontory (*glacis*) that result from the continuous accumulation of erosion products on the heights and slopes of the *tepuis* and their subsequent transport to the downstream hydrological network. Only the rivers of the southern and southwestern sections of the Guiana massif pour into the Amazon River; the northwest and north sections pour into the Orinoco River; in turn, the rivers originating in the three Guianas flow directly into the northern coast of the Atlantic Ocean.

The Gurupi sub-region (161,463 km^2) is located to the east, outside the limits of the Amazonas/Tocantins watersheds, but it is included in the Amazon forest. This sub-region includes the basins of the following rivers that flow directly to the Marajó bay or the Atlantic Ocean, to the east of Tocantins: Mojú/Acará, Capim, Gurupi, Turiaçú and Pindaré; Pindaré River, towards the sources of the Mearim and, until reaching the division with the Tocantins in Serra do Gado Bravo in the state of Maranhão (Brazil).

Species occurrence data

A list of 217 palm species occurring in the Amazon was extracted from existing publications (Khan & de Granville 1992; Henderson 1995; Henderson *et al.* 1995; Kahn 2008; Pintaud *et al.* 2008; Balslev *et al.* 2015). After updating and making the nomenclature uniform using the TROPICOS website (http://www.tropicos.org/) we ended up with a final list of 177 palm species occurring in the Amazon region. For these 177 palm species we obtained 309,277 occurrence records from the *Global Biodiversity Information Facility* online website (GBIF - http://www.gbif.org). After doing the cleaning, and taking out duplicate and doubtful data, our final dataset included 17,310 occurrence records of which 11,462 records were georeferenced. For the remaining 5,848 records (34%) we were able to find coordinates using TROPICOS (http://www.tropicos.org/) and digital maps, such as Google Earth (http://earth.google.com/intl/pt/). (Fig. 1A) (Table S1).

Data analysis

Palm species distribution records in the Amazon region were plotted on a map divided into 494 grid squares of 1×1° representing our Operating Geographic Units (OGU). This was done to facilitate the manipulation of data, and partly to reduce the effects of sampling artifacts, such as mapping errors and grid squares positioning in sparsely populated areas (*roadmap effect*). All procedures used DIVA-GIS 7.5 (http://www.diva-gis.org/). For each grid square, the species richness was calculated as the total number of palm species present. This analysis was conducted for the entire Amazon basin and also separately for each sub-region. Additionally, at each latitudinal band (range of 1°) we also calculated the total number of palm species.

To evaluate if there was a correlation between the number of records and the observed richness (the sample effort), a Pearson correlation coefficient analysis was performed using

DIVA-GIS 7.5. This analysis was also conducted for the entire Amazon basin and for each sub-region.

Species richness were overlaid with deforestation shapefiles for the period 2001–2012 taken from WWF's deforestation report (2014), to infer whether the areas with lowest species richness and records gaps were due to suppression of forest vegetation or if they represent lack of research in these areas. The report (WWF 2014) use forest data generated by Global Forest Change 2013 (Hansen *et al*. 2013) supported by the University of Maryland, additional complementary data from PRODES of the *Instituto Nacional de Pesquisas Espaciais* (INPE) for Brazil, and literature reviews. Our data therefore, described the change in the dynamics of deforestation across the Amazon region, showed a significant decline in the rate of deforestation in the Brazilian Amazon but increasing rates of deforestation in the Andean Amazon countries (WWF 2014).

To determine the similarity between sub-regions, we analysed Jaccard distance (Gotelli & Ellison 2011) in the R sotfware version 3.3.1, that measures the similarity between two sets. This analyses were done with presence/absence data. The Jaccard distance is derived as 1 – *S* (the Jaccard's similarity coefficient between two samples). The formula for this analysis is: D_j=b+c/(a+b+c), where: D_j = The Jaccard distance between samples 1 and 2; a = number of species common to samples 1 and 2; b = number of species only found in sample 1, and c = number of species only found in sample 2. The result of this analysis was plotted in a dendrogram constructed using the UPGMA binding method (cluster analysis).

Results

The 177 palm species represented in 17,310 records, were distributed in all regions of the Amazon (Fig. 1). The sub-region with the largest palm species richness was the Amazonia *sensu stricto* (167 species). The other sub-regions had substantially lower numbers of species: Guianas (91), and Andes (71). The sub-regions with fewest palm species were the Gurupi (21 species) and the Plateau (17). Twenty-six species were endemic to different countries, 14 to Peru, five to Bolivia, three to Colombia, two to Ecuador and two species were endemic to Guiana. The 10 species with the highest number of records were *Geonoma macrostachys* Mart. (1206), *Euterpe precatoria* Mart. (859), *Iriartella setigera* (Mart.) H. Wendl. (617), *Lepidocaryum tenue* Mart. (590), *Chamaedorea pauciflora* Mart. (577), *Desmoncus mitis* Mart. (549), *Astrocaryum aculeatum* G. Mey. (457), *Bactris hirta* Mart. (423), *Geonoma brongniartii* Mart. (400), and *Oenocarpus bacaba* Mart. (391) (Table S1).

The greatest richness (29–71 species) were found in the western (Brasil, Colombia, Ecuador and Peru), central (Manaus) and northeastern (French Guiana) parts of the Amazon (Fig. 1B). Notably, the species richness was lower (1–14 species) on the outskirts of the Amazon region, especially in the eastern, southern and south-eastern Amazon (Fig. 1B). In relation to the latitudinal gradient, high species richness were found between 0–5°S (Fig. 1B), with most species (119) in the latitudes 2–3°S, followed by latitudes 4–5°S (116) and 3–4°S (109). All of them are under the equatorial line (Fig. 1B).

The Amazon *sensu stricto* sub-region (Fig. 2A) showed highest richness (44–71 species) in the Peruvian Amazon, around the city of Iquitos (Peru), followed by grid squares with 15–57 species in central Amazon (around Manaus, Brazil). Furthermore, 29–43 species were distributed in different parts of the western Amazon. The Andean sub-region (Fig. 2B) showed grid squares with highest richness (26 species) in two areas; in Pasco Departament, Peru (central Andes) and along border between Peru and Ecuador (northern Andes). In general, the greatest richness were found in northern (Colombia and Ecuador) and central (Peru) parts of the Andes sub-region, decreasing to the south (five species in Bolívia). The Guiana sub-region (Fig. 2C) showed greatest richness in the eastern parts of the sub-region. Specifically, the highest richness was found in French Guiana with 35 species. Other areas with high richness (15–28 species) were on the border of Colombia and Venezuela, and with 14 species near the Andes sub-region (western Guiana sub-region). The Gurupi sub-region (Fig. 2D) is a small area in eastern Brazil that showed high richness (10 species) along the border between the states of Pará and Maranhão and 5–8 species in the state of Maranhão. Finally, the Plateau sub-region (Fig. 2E) was the area where we found the lowest palm richness (up to 5 species) among all the sub-region.

The observed species richness and the number of database records per grid square were highly correlated (Pearson correlation, $R^2 = 0.76$, $P < 0.005$), showing that sampling effort strongly affects the observed species richness in each grid cell. In addition, in each sub-region we also performed this analysis resulting in high correlation, Amazon *sensu stricto* ($R^2 = 0.77$), Andes sub-region ($R^2 = 0.71$), Guiana ($R^2 = 0.81$), Gurupi ($R^2 = 0.66$) and Plateau ($R^2 = 0.79$).

Low species richness (1–14 species) and gaps in the records were found throughout the entire Amazon region, especially in Amazonia *sensu stricto* (Fig. 3). Highest rates of deforestation ($\geq$ 2000 km^2) were found in southern and eastern Brazilian Amazon. Therefore, in this areas the low richness and records gaps with the deforestation must be related. However, areas with higher richness (> 29 species) (western Amazon) also have deforested areas but they are $\leq$ 500 km^2 in extension.

Cluster analysis using Jaccard distance (Fig. 4) showed two group with similarity between them, with cophenetic correlation 0.843. The first group is composed for the three sub-regions

(Amazon *sensu stricto*, Andes and Guiana), and other group for Gurupi and Plateau sub-region.

Discussion

How is palm species richness distributed in the Amazon region?

Palm diversity is notoriously high and palms are widely distributed in Neotropical forests (Cintra *et al*. 2005; Montufar & Pintaud 2006) (Fig. 1A). This distribution pattern coincides with global patterns for angiosperm species (Barthlott *et al*. 1996; 2005; 2007; Francis & Currie 2003; ter Steege *et al*. 2006). Both individual palm species' distributions and patterns of palm species richness are related to current climate (Eiserhardt *et al*. 2011b). Global centres of vascular plants diversity coincide with highly structured, geodiversity areas in the tropics and subtropics such as the tropical eastern Andes, north-western Amazonia and eastern Brazil (Mutke & Barthlott 2005).

Of the 177 palm species (Table S1), the species with high number of records are small palms (*e.g.*, *Geonoma macrostachys* Mart., *Lepidocaryum tenue* Mart., *Chamaedorea pauciflora* Mart., *Desmoncus mitis* Mart.) and little collected species (e. x. *Euterpe precatoria* Mart., *Mauritia flexuosa* L. F., *Astrocaryum chambira* Burret), therefore they are easier to sample. This may be an explanation of the discrepancy in the number of records compared to species of larger size.

We found that palm species have the greatest richness in the western Amazon principally in the Colombian, Ecuadorian and Peruvian Amazon, in central Amazon (around Manaus) and north-eastern Amazon (French Guiana) (Fig. 1B). Several other studies of plants have demonstrated similar patterns, with high species richness and diversity, principally at local scales (*e.g.*, Kahn *et al*. 1988; 1985; 1990; Oliveira & Mori 1999; Cintra *et al*. 2005; Macía & Svenning 2005) and continental scales (*e.g.*, Barthlott *et al*. 1996; 2005; 2007; Bjorholm *et al*.

2005; Eiserhardt *et al*. 2011a,b) across the Americas. Salm *et al*. (2007) found the highest number of species in regions with high humidity (vapour pressure) and low seasonality in the Brazilian Amazon. Thus, not only water-related variables might be strong determinants of palm richness, but also temperature seasonality or extremes (Eiserhardt *et al*. 2011b) and species richness changes may be explained also by the availability of water and energy within megathermal climates, at least for strictly tropical taxa such as palms (Eiserhardt *et al*. 2011a).

In the Amazon *sensu stricto* (Fig. 2A), the western region is well known for its high diversity of plants (Gentry 1988; Duivenvoorden & Lips 1995; Pitman *et al*. 2002; Valencia *et al*. 2004) and that region presents one of the richest palm floras in the Neotropical region, with at least 121 species and 33 genera (Montufar & Pintaud 2006), as well as high endemism rates (Alvez-Valles *et al*. 2018). The north-western Amazon has a more recent relationship with Central America and the western Andes of Peru, Ecuador and Colombia (Souza-Amorin 2001). Several researchers have found high palm richness in different locations in the western Amazon, mainly in the Iquitos-Pebas region in Peru (Khan & Mejia 1991; Vormisto 2002; Vormisto *et al*. 2004a,b), the Yasuní National Park, Ecuador (Svenning 1999), and in the middle basin of Caquetá, Araracuara, Colombia (Galeano 1992; Balslev *et al.* 2017). The diversity in these areas is high due to species shared with the Andes and its altitudinal gradient (Pintaud *et al*. 2008). In addition, several studies have shown that the difference in local and regional diversity between the Iquitos-Pebas region (Peru) and the Yasuní region (Ecuador) can been attributed to soil fertility and soil types (Montufar & Pintaud 2006; Vormisto *et al*. 2004a; Eiserhardt *et al*. 2011b). Interestingly, the Iquitos-Pebas region supports more species (71 species in this study), although this region has poorer soils but presents a greater variety of soil types (Vormisto *et al*. 2004b). Another area with high richness (15–57 species) is the central Amazon near Manaus, where the floristic composition may be related to local and regional geological features, with a dry corridor barrier to the north, and possibly with Pleistocene refuges (Prance 1973). A particular phenomenon is the riverine flora of black waters and white sand. Therefore, these areas present two features: high biodiversity in extremely poor soils and large number of restricted species, principally the endemic genera *Barcella* and *Leopoldinia* (Oliveira *et al*. 2001; Pintaud *et al*. 2008).

The Andean sub-region present a broad range of landscapes and climatic conditions (Lozano *et al*. 2009) that result in a megadiverse flora in the equatorial sector (Romero-Saltos *et al*. 2001; Duque *et al*. 2001). In this sub-region (Fig. 2B), we found high species richness (11–26 species) in the north (Peru, Ecuador and Colombia), centre (Peru) and south (northern Bolivia). This pattern of high diversity, especially in the north, is related to greater topographic complexity and prevalence of humid environments (Pintaud *et al.* 2008). Therefore, palm richness decreases to the extremes of the sub-region (Borchsenius & Moraes 2006). In the northern parts of the Andes sub-region we found areas with high species richness especially along the border between Peru and Ecuador (26 species). In this area, the climate is very humid and regional isolation act as a natural barrier and is considered keys in the geographical distribution of plants (Lozano *et al*. 2009). Several palms studies made in the Ecuadorian Andean forest show that the southern regions of Ecuador may be the richest in species (Balslev *et al.* 2015). In central Peru in the Pasco department we also found high richness with 26 species. This area is important because it includes three protected natural areas (PNA): Yanachaga-Chemillén Natural Park, San Matias San Carlos Protection Forest, and Yanesha Community Reserve. Consequently, there is at present a good state of conservation of the forests. The diversity in this area is very heterogeneous (Vega *et al.* 2008), with high endemism (Kahn & Moussa 1994; León *et al*. 2006; Young 2007, 2009; Damián 2013) and palms were among the 15 most species rich families in the area (Vásquez *et al.* 2005).

The Guiana sub-region (Fig. 2C) is biogeographically unique with diverse and abundant vegetation, and many endemic species (Maguire 1970; Gibbs & Barron 1993; Kelloff & Funk 2004), principally in its eastern parts (Guiana, Suriname, and French Guiana – Guiana shield). We found high species richness (35) in French Guiana. In comparison with the western Amazon, the eastern Amazon — principally the Guiana shield — presents lower diversity in both mammals (Voss & Emmons 1996; Kay *et al.* 1997) and plants (ter Steege 1998), including palms (Kahn & de Granville 1992). The reduced diversity is not due to low rainfall or low nutritional status of the soil, but to the reduced extension of the area (ter Steege *et al.* 2000). Another area with high richness (15–28 species) is along the border between Colombia and Venezuela (the western part of this sub-region). Despite their high species richness and endemism, and presence of PNA such as Yapacana National Park and Sipapo forest reserve (Venezuela), these areas experience strong external pressure from mining and environmental degradation, and indirectly by mercury pollution and increased sediment load in rivers (Lasso *et al.* 2006; Castillo & Salas 2007).

Two remaining areas of the Amazon region (Gurupi and Plateau sub-regions) have low species richness (Fig. 2D-E), but stand out for their floristic composition (Pintaud *et al*. 2008). This low richness may be because this part of the Amazon has savannas with physiognomic similarity and affinities to the floristic composition of the *cerrado* (Brazilian savanna). Therefore, it is an area of transition between the Amazon rainforest and drier formations of southern and south-eastern Brazil (Pintaud *et al*. 2008). In the same way, the eastern Amazon (Gurupi sub-region) (Fig. 2D) has low palm richness and lacks endemism due to its environmental homogeneity, sedimentation, and floodplains around the mouth of the Amazon River (Pintaud *et al*. 2008; Alvez-Valles *et al*. 2018). Besides, the south-eastern Amazon (plateau sub-region) (Fig. 2E) has more recent relations with the Atlantic Forest than with the north-western Amazon (Souza-Amorin 2001).

The relationship between species richness and latitude in palms is driven mainly by a latitudinal gradient in net diversification rates that have been operative throughout the evolutionary history of New World palms (Svenning *et al*. 2008). Notably, this hypothesis proposes that more species-rich areas have experienced higher rates of net diversification due to higher speciation rates and/or lower extinction rates (Mittelbach *et al*. 2007; Svenning *et al*. 2008). The most species-rich grid square was found near the equator at latitudes 0–5°S (Fig. 1B) which coincides with the results of Bjorholm *et al*. (2005). Thus, the biogeographic patterns in the Amazon region involve a correlation of palm diversity with a gradient of rainfall from the central parts of the region to its periphery (Pintaud *et al.* 2008). Climatic influences vary strongly with latitude, principally in plants (Francis & Currie 2003). Thus, plant diversity generally present peaks where climatic conditions are warm, wet and more seasonally stable (Eiserhardt *et al*. 2011b). Therefore, the global distribution of the palms is concentrated in warm and humid climates (Eiserhardt *et al*. 2011b) with mean annual precipitation ≥2400 mm, ≥160 wet days per year, and mean annual temperatures ≥21°C. From such regions species richness declines strongly with latitude, as conditions become colder and drier, with more seasonally variable temperature (Francis & Currie 2003; Bjorholm *et al.* 2005). This decline is observed in our results, while latitude increases (north and south), the species richness declines (Fig. 1B).

Is the observed palm species richness related to sample effort?

According to results of Pearson correlation coefficient (R^2 = 0.76), the observed species richness is influenced by the sampling effort. Similar results were found in all five sub-regions. Therefore, areas with high species richness are those with highest number of records. However, there is strong evidence of sampling bias in this result, sometimes called “the museum effect” (Ponder *et al.* 2001), which implies that for historical reasons of efficiency, logistics and convenience, collectors tend to oversample near research institutions (Werneck *et al*. 2011) resulting in a greater number of species in those areas. For example, the greatest palms richness corresponded to areas of high overall plant diversity (Peruvian and Ecuadorian Amazon, and around Manaus) as recognized previously by several floristic inventories (Kahn & Castro 1985; Gentry 1988; Kahn *et al.* 1988; Kahn & Mejía 1990; 1991; Pitman *et al.* 2001; 2002; Haugaasen & Perez 2006; Honorio *et al.* 2008; Pintaud *et al.* 2008; Vedel-Sørensen *et al.* 2013). There are important research efforts in these areas, such as those of the Instituto Nacional de Pesquisas da Amazônia (INPA) around Manaus, Brazil, Instituto de Investigación de la Amazonía Peruana (IIAP) and Herbarium Amazonense HAMAZ) in Iquitos,Peru, Missouri Botanical Garden in Oxapampa, Peru, and Herbario QCA, Pontificia Universidad Católica del Ecuador, Quito, Ecuador.

Are low richness and record gaps related to deforestation?

The areas with highest rate of deforestation ($\geq$ 2000 km^2) are in the southern and south-eastern Amazon *sensu stricto*, areas which also have low richness and many record gaps (Fig 3A). The deforestation is a negative factor that puts a high proportion of plants at risk of extinction (ter Steege *et al*. 2015), which may also be the reason there are so few collections of the palms from there. The deforestation in those areas appears to be particularly severe due to high deforestation rates and ecological sensitivity to climate change (Coe *et al*. 2013). It is important to note that there are also deforestation (<2000 km^2) in areas with high species richness in the western Amazon and Andean sub-region. Therefore, greater emphasis should be given to conservation in these areas, because this activity may in the future lead to reduced richness and even extinction of some palms (ter Steege *et al*. 2015). On the other hand, there are areas with low richness and records gaps in non-deforested areas, which can be explained by other factors such a difficult access, lack of logistics and interest in researching these areas.

The Plateau and Gurupi sub-regions also presented low richness and record gaps. Those areas are located in the ecotone with the *cerrado* (Brazilian savanna), a phytogeographic domain where the palm diversity is lower in comparison with the Amazon (BFG 2015). Therefore, this result shows that the deforestation is not only responsible for the low richness and records gaps.

Are there floristic similarities in palms distribution patterns among the Amazonian sub-regions?

According to cluster analysis of Jaccard distance we found two groups of similarity. One group corresponded to Amazon *sensu stricto*, the Guiana and Andes sub-regions, and another group was composed by the Gurupi and Planalto sub-regions. Several palm species growing on the eastern slopes of the Andes are also found in the western Amazon (Pintaud *et al*. 2008) and there are species shared between eastern Amazon and Guiana shield (ter Steege *et al*. 2000). However, Gurupi and Plateau sub-region although they have low species richness, also present species shared between them, highlighting that several species extend until the *cerrado* domain and Atlantic Forest (Souza-Amorin 2001; Pintaud *et al.* 2008).

In conclusion, the greatest palm richness were found at latitudes near the equatorial belt (0–5°S), principally in the western Amazon (Andes sub-region and Amazon *sensu stricto*) and east of the Guiana sub-region. In contrast, low richness was found in the Plateau and Gurupi sub-regions. According to Pearson correlation coefficient in each sub-region, the species richness was highly related to the sampling effort. The low richness and records gaps may have been caused by deforestation principally in southern and south-eastern Brazilian Amazon, but in other areas with records gaps it may probably have been caused by difficult access, lack of logistics and research. Furthermore, the low richness must also be due to the existence of ecological transitional areas where palm species are known to have poor representation (Plateau and Gurupi sub-region). The pattern of species distribution played an important role for understanding the similarity between the sub-regions. Finally, we recommend giving greater focus of palm research in areas with few records of occurrence especially in areas with records gaps, for a better knowledge of their diversity and richness patterns. Therefore, the installation of research institutions and/or researches in areas of low sampling would increase the number of records, increasing the knowledge of the local flora.

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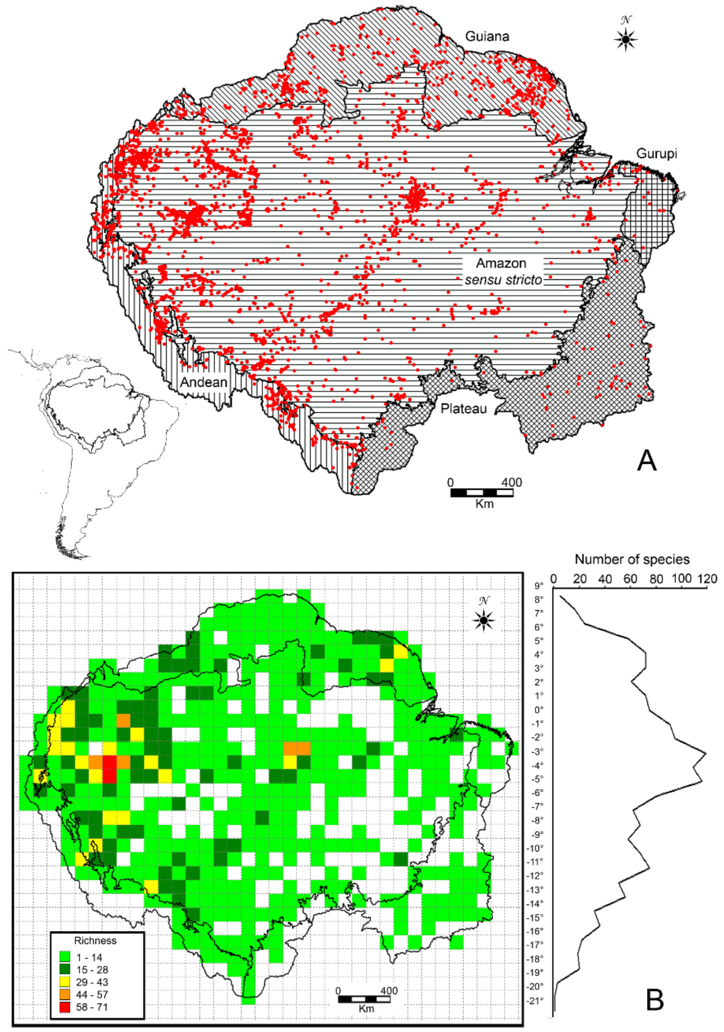
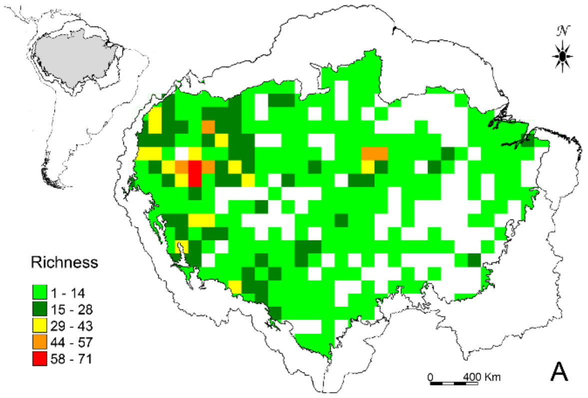
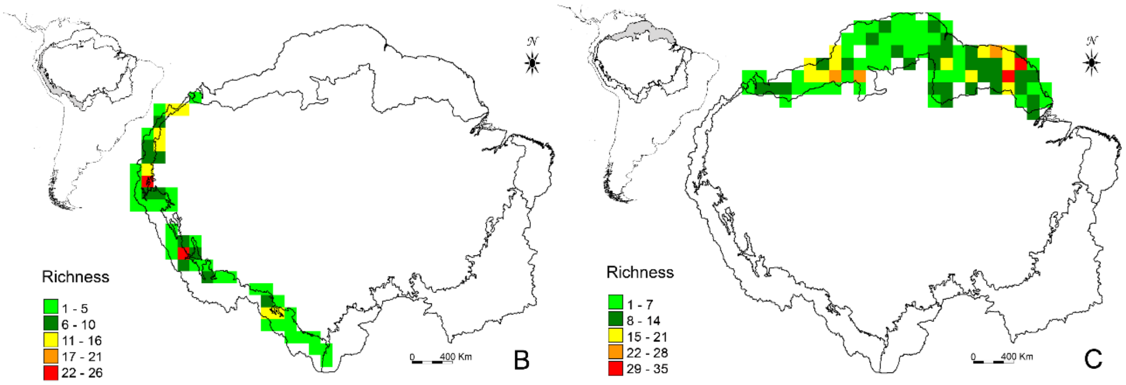


Figure 1. A - Distribution of 17.310 records of occurrence of 177 Amazonian palm species in the Amazon region (red dots). B - Left: Species richness of palms in the Amazon in grid squares of 1 º x 1 º. Right: Species richness distribution in latitude extents (in decimal degrees) for the distributional range of 177 Amazonian palms especies in the Amazon region. Area divided in a central sub-region - Amazon *sensu stricto*, and four peripheral sub-regions - Andes, Guiana, Gurupi and Plateau. Source: Eva and Huber (2005).

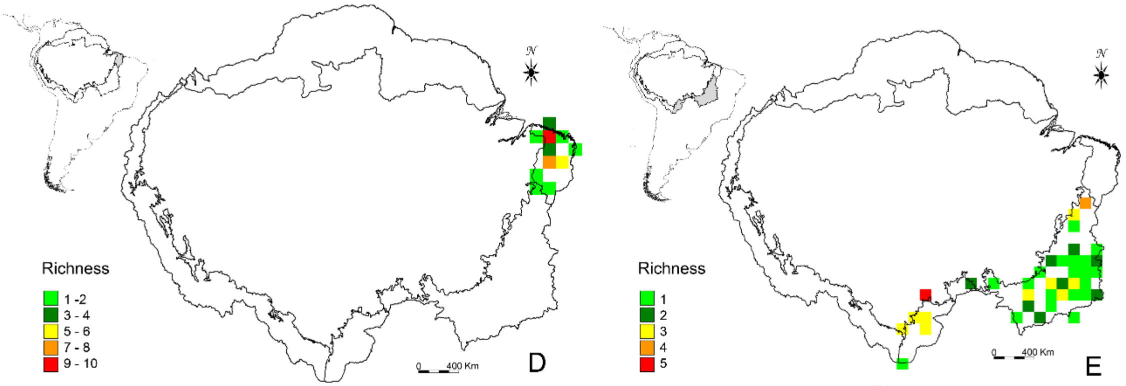


Amazon *sensu stricto*



Andean

Guiana



Gurupi

Plateau

Figure 2. Species richness of palms in the five sub-regions of Amazon region. A – Amazon *sensu stricto*; B – Andean; C – Guiana; D – Gurupi; E – Plateau. Grid squares: 1° x 1°.

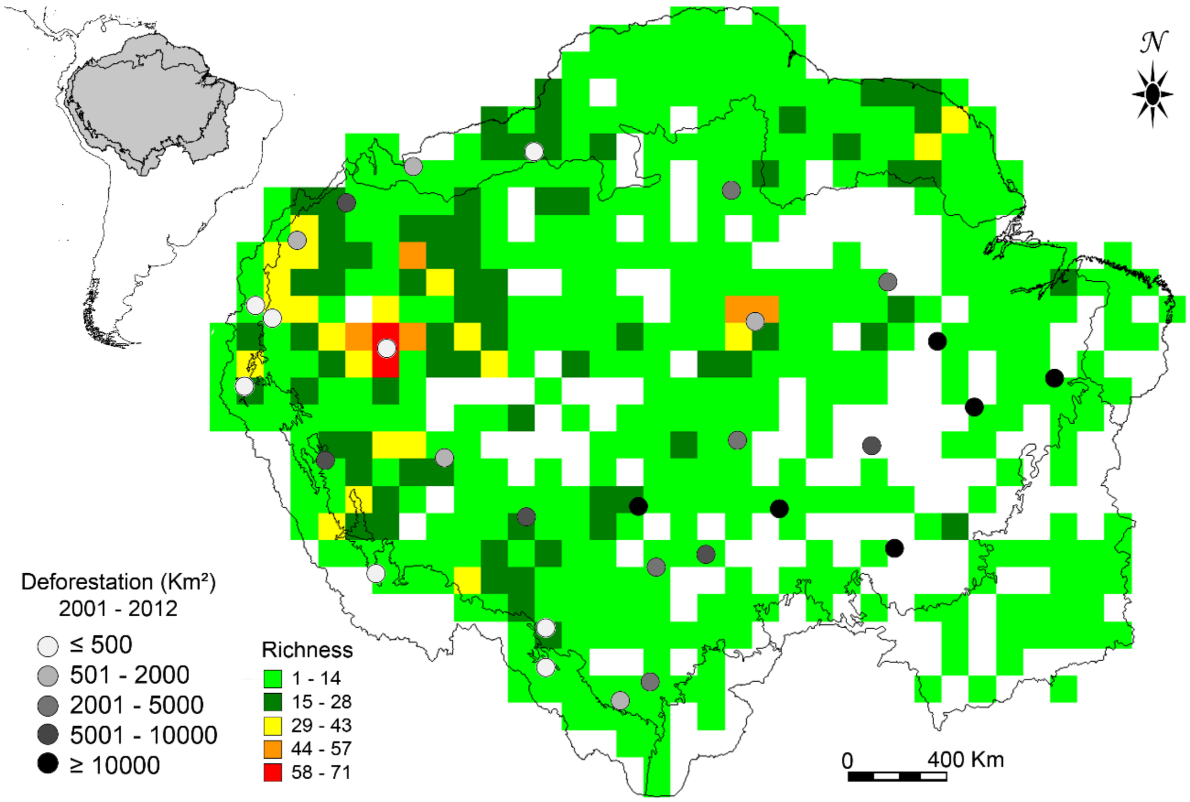


Figure 3. Comparison between the richness of Amazonian palms species and deforestation areas (circles) between the years 2001 and 2012.

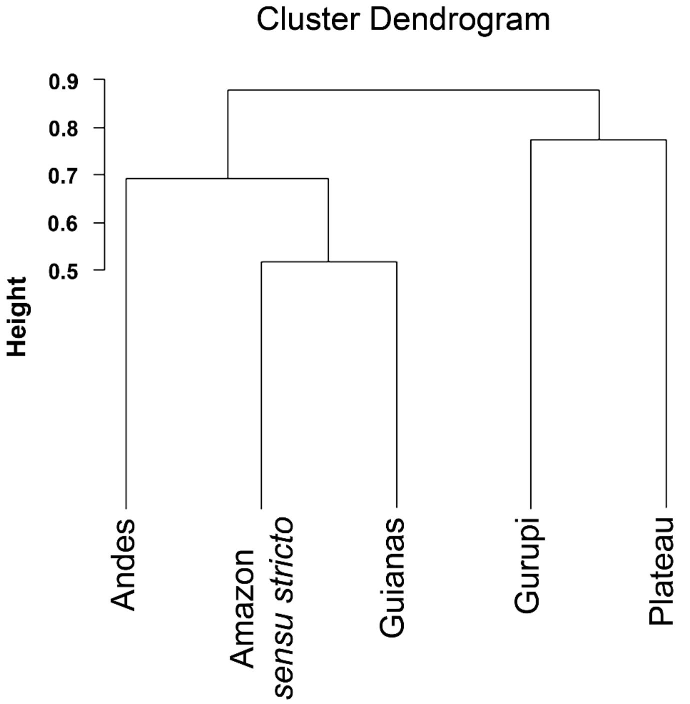


Figure 4. Dendrogram (Jaccard's similarity coefficient) obtained in the similarity analyzes with the five Amazon sub-regions based on a binary matrix of 177 Amazonian palm species. Ass – Amazon *sensu stricto*; An – Andes; Gui – Guiana; Gur – Gurupi; Pla – Plateau

Chapter 3

ENDEMISM AND CONSERVATION OF AMAZON PALMS

Endemism and conservation of Amazon palms

Abstract

Endemicity is important for the delimitation of conservation areas. Endemic areas are those that contain two or more taxa with their distribution restricted to the area. The aim of this study was to detect endemic areas for palms in the Amazon region and to determine whether the species that define these endemic areas are protected within conservation units. Records of occurrence were extracted from the *Global Biodiversity Information Facility* (GBIF). The final dataset consisted of 17,310 records, for 177 species of Amazonian palms. For analysis we used Parsimony Analysis of Endemicity (PAE) and NDM-VNDM program, and grid square size of 1º and 3º as Operational Geographic Units (OGUs). The distribution of endemic species was superimposed on occurrence of the Conservation Units (CUs). PAE did not show endemic areas in grid squares of 1º, but found 10 palm endemic areas in grid squares of 3º in the western Amazon and Andean sub-region. However, the NDM-VNDM program identified an endemic area in grid squares of 1º located at the eastern Guiana with endemicity score = 2.9, and in grid squares of 3º it identified seven consensus areas with endemicity score >6.0, all in the western Amazon. The combination of PAE and NDM-VNDM analyses resulted in eight endemic palm areas in the combined western Amazon and Andean sub-region. Of the species that define the endemic areas, five are threatened with extinction in one of three IUCN categories (EN, VU, NT), and they are not protected in any conservation units. The western Amazon, besides having high palm richness, also has palm endemic areas, especially, near the Andean sub-region and the Peruvian Amazon.

Keywords Biogeography, endemic areas, threatened species, western Amazon.

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Introduction

Palms are widespread in tropical and subtropical regions of the world (Dransfield et al. 2008) and they are very abundant in some habitats (Henderson et al. 1995; Balslev et al. 2015). This group of plants is generally recognized as having species that are good bioindicators of hot climates (Mai 1995). Under present global climates, palms reach their greatest proliferation in the tropics, being almost absent in temperate regions (Dransfield et al. 2008). Richness and diversity patterns of tropical American palms are strongly related to current, particularly climate related, ecological factors (Bjorholm et al. 2005) as well as historical factors (Bjorholm et al. 2006). Therefore, palms exhibit an amazing geographic variation in species richness, phylogenetic composition, and life form (Eiserhardt et al. 2011). Small-scale studies have emphasized how species and communities respond to environmental gradients and how species diversity is maintained locally (Eiserhardt et al. 2011). The Amazon region maintains a favourable environmental dynamic and diversity for palms and the region is the home to seven endemic palm genera and 121 endemic species (Pintaud et al. 2008). Large parts of the Amazon forests are dominated by palms growing under extremely limiting conditions (Kahn and Mejia 1990; Macía and Svenning 2005) and producing large quantities of fruits and other products (Kahn 1988; Peters and Hammond 1990).

Palms have important ecological roles, being the main food source for many groups of vertebrates, and economically they are the third most important plant family, following the grasses and the legumes (Johnson 1996). Palms are important for local communities (Nascimento 2009) and their products have great economic potential and industrial value (Kahn and de Granville 1992). In addition, palm products are renowned for their extraordinary utility that are exploited in broad economic scales worldwide (Borchsenius and Moraes 2006). The most frequent palm uses are for food, construction, fibres, animal fodder, and artisanal and medicinal purposes (Peters et al. 1989; Moraes et al. 1995; Borchsenius and Moraes 2006; Zambrana et al. 2007; Albán et al. 2008; Balslev et al. 2008; Macía et al. 2011, 2015). Furthermore, palms are useful for the regeneration of degraded areas (Anderson 1990; Salm et al. 2005). The commercialization of palm fruits (Weigend et al. 2015) is often mentioned as a promising alternative for reconciling the development and conservation of Amazonian forest (Peters et al. 1989). However, the export of wild palm products to regional and international markets (Weigend et al. 2015) have created incentives for destructive levels of palm extraction from natural forest stands (Vedel-Sørensen et al. 2013; Pintaud et al. 2015), driving several species to local extinction in some areas due to unsustainable harvest practices (Bernal et al. 2011). In addition, several factors cause the destruction of natural populations of the palms, especially extraction and habitat loss (Svenning 1998; Souza and Martins 2004; Pintaud et al. 2015), which interrupts the ecological interactions with pollinators and dispersers caused by fragmentation and destruction of natural environments (Johnson 1996; Svenning 1998; Souza and Martins 2004).

In recent years, endemicity has attained increasing importance in conservation biology and for the delimitation of conservation areas. In this context, an area of endemism is understood as a geographic region defined by the combination of areas of endemic species' distributions (Carvalho 2011). In other words, endemic areas are those that contain two or more taxa that have their distributions restricted to the area (Szumick et al. 2004). In the context of conservation, endemic areas are biogeographic elements that are used to prioritize and to conserve places because they highlight their spatially unique biodiversity features (Löwenberg-Neto 2011).

There are two main reasons to recognize endemic areas: (1) regarding the theoretical knowledge, they are the smallest units of analysis of historical biogeography and as such, they serve as a basis for constructing hypotheses about the processes responsible for the formation of the biota of a region; and (2) regarding the practice of conservation, endemic areas have a group of unique species that should be prioritized for conservation programs (Silva et al. 2005). Detecting endemic areas is an important step for any biogeographic study of a taxon, and can contribute to the conservation of the taxa (Morrone 2000).

Here we used two methods, Parsimony Analysis of Endemicity - PAE (Morrone 1994) and NDM/VNDM developed by Goloboff (2001) and Szumik et al. (2002, 2004), to identify endemic palm areas using a georeferenced dataset for Amazonian palms. Specifically we asked the following questions: (1) Which are the endemic palm areas in the Amazon region as identified by the PAE and NDM/VNDM programs? (2) Which palm species define the endemicity of each such area, and which of them are threatened? and (3) Are the encountered threatened endemic palms protected within any conservation unit?

Materials and methods

Study area

We follow the circumscription of the Amazon *sensu latissimo* by Eva and Huber (2005) which is divided into five sub-regions: Central sub-region (68%=Amazon *sensu stricto*) and four peripheral sub-regions: Andes (7%), Plateau (11%), Guyana (12%), and Gurupi (2%) (Fig. 1).

Data

A list of Amazonian palm species was extracted from previous studies (Khan and de Granville 1992; Henderson 1995; Henderson et al. 1995; Kahn 2008; Pintaud et al. 2008; Balslev et al. 2015). The locality records were obtained from the *Global Biodiversity*

Information Facility online website (GBIF - http://www.gbif.org) and consolidated in a geo-referenced database. When coordinates were not available for a GBIF-record, they were obtained from various sources: herbarium labels of a specific database (TROPICOS - http://www.tropicos.org/) and digital maps, such as Google Earth (http://earth.google.com/intl/pt/). Doubtful records of occurrence (e.g., incomplete or uncertain location) were excluded. In case of duplicated occurrence records only one of the records was used in the analyses. The resulting geo-referenced database that we used to identify endemic areas of palms, contained 17,310 records for 177 species distributed in the Amazon region (Fig. 1).

Data analyses

Parsimony Analysis of Endemism (PAE) unites areas based on their shared species and it is used to inform potential endemic areas (Nihei 2006). Here, the following steps were applied: (1) We drew grid square sizes of 1º and other of 3º (OGU - Operational Geographic Units) on a map of the Amazon region, considering grid squares only where at least one palm specimen was recorded. (2) We constructed a presence/absence data matrix for both grid square sizes, where columns represented the species and rows represented the grid squares. The matrix was uploaded in the program Nexus Data Editor 0.5.0 (Page 2001), with coding for presence (1) and absence (0) of the taxon in each OGU. A hypothetical area with the absent taxa was added as an out-group for rooting the cladogram. (3) Parsimony analysis was done with the program NONA (Goloboff 1993), with the interface WinClada 1.00.08 (Nixon 2002), using the tree-bisection-reconnection (TBR) method. (4) We collapsed the most parsimonious trees into strict consensus and the level of support was obtained through bootstrap analysis with 1000 replicates

(Felsenstein 1985). (5) Finally, we delimited the groups of grid squares defined by at least two endemic species (Morrone 1994).

In a second approach, the dataset was analysed using the heuristic algorithm of NDM/VNDM, version 3.0, developed by Goloboff (2001) and Szumik et al. (2002, 2004). This analysis determines endemic areas using an optimality criterion that takes into account the position of taxa in space as a component of the analysis (Szumik et al. 2002). The algorithm searches for endemic areas by evaluating the spatial concordance regarding the presence of two or more taxa for a given set of grid squares (endemic area) and calculates a endemicity score for a given taxon depending on how its distribution corresponds to a particular set of grid squares (Szumik et al. 2002). For this analysis, we also used two grid square sizes (1º and 3º) with standard parameters of the program: saving temporary sets within 0.99 of the current score; selecting areas with two or more restricted species (score ≥2.0), and we computed the consensus endemic areas using a cut-off at 50% similarity in species, and the strict consensus (Szumik et al. 2002).

Threatened endemic species vs conservation units

The conservation status of palm species that defined the endemic areas were checked on the existing red list of threatened species in IUCN (2017). The distribution of those threatened species was superimposed over the Conservation Units (CUs) in the Amazon region to verify if the species are protected within the CUs.

Results

Endemic areas and palms that support the endemicity (PAE – NDM/VNDM)

The Parsimony Analysis of Endemism (PAE) produced 1000 most parsimonious trees. The strict consensus tree in grid square size of 1º had 3341 steps with consistency index =5 and retention index =26. However, there was no endemic area at this scale, although it is important that a set of three grid squares (70, 71 and 86) were supported by one endemic species (*Desmoncus loretanus* – codified as 104). Additionally, the square 70 was supported by *Attalea peruviana* and *A. weberbaueri*, (species codified as 48 and 56) and square 71 by *Astrocaryum carnosum* (codified as 8). Those areas were located in the Peruvian Amazon (western Amazon) (Fig. 2a, Table 1). The strict consensus tree in grid square size of 3° had 1053 steps with consistency index =16 and retention index =48. The cladogram showed a large endemic area located in the western Amazon (composed by grid squares 1, 2, 3, 5, 6, 7, 8, 9, 12, 13) and defined by two species, *Aiphanes ulei* and *Wettinia maynensis* (see also Fig. 3a, where species are codified as 2 and 175). The grid squares with most endemic species were in the Peruvian Amazon, Loreto department (square 7; seven species) and the Andean region shared with the western Amazon (Peru, Ecuador) (square 3 with six species, square 2 with five species) (Fig. 3a). In this grid size, there were 13 palm species that supported different and nested endemic areas in the western Amazon (Table 1). Eight species were distributed in the Andean sub-region of Colombia, Ecuador, and Peru, and five species were restricted to areas of Peru and Brazil (squares 7 and 12).

The NDM-VNDM analysis using grid square size of 1º identified one endemic area in the eastern Guiana (Fig. 2b) with endemicity score of 2.9. This area is supported by four species of Amazonian palms: *Asterogyne guianensis*, *Attalea canopiensis*, *A. degranvillei* and *A. maripensis* (Table 2). However, the NDM-VNDM analysis using grid square size of 3º identified 47 endemic areas and 32 consensus areas (Fig. 4, Table 2), mainly associated with the western Amazon and shared with Andean sub-region (consensus areas 2, 3, 8, 10, 17, 26, 28, all with maximum score >6.0) (Fig. 4, Table 3). These consensus areas were supported for 38 species of Amazonian palms (Table 3). Thus, the overlapping patterns of the aforementioned endemic areas allowed the recognition of a large area composed by six grid squares located at the western Amazon (squares 6, 7, 8, 11, 12, 13; Fig. 3b). Furthermore, we identified six other important squares, three of them (2, 3, 5) shared with Andean sub-region and the other three distributed in north-western (10), western (19) and central Amazon (53) (Fig. 3b).

The combination of PAE and NDM-VNDM analyses, using the grid square of 3º showed a set of eight grid squares as a main area of endemism, located in Western Amazon (squares 6, 7, 8, 12, 13) and Andean sub-region (squares 2, 3, 5; Fig. 3b).

Threatened endemic species vs conservation units

According to IUCN (2017), three of the palm species that defined endemic areas in our PAE analyses (in both grid sizes) are threatened with extinction in two different categories: *Ceroxylon amazonicum* and *Bactris setiflora* are considered endangered (EN), and *Astrocaryum carnosum* (species found in both grid square size) as vulnerable (VU) (Table 1). Three species that defined the consensus areas in grid square size of 3º with maximum score >6.0 in our NDM/VNDM analysis were also found to be threatened in three different categories: *Attalea tessmannii* is considered near threatened (NT), *Wettinia longipetala* is vulnerable (VU), and *C. amazonicum*, also identified in the PAE analyses, is endangered (EN) (Table 3). The known distribution records of these threatened species were not located within any Conservation Units (CUs), although close to different protected natural areas of Brazil, Ecuador, and Peru (Fig. 5).

Discussion

Endemic areas and palms that define the endemicity (PAE – NDM/VNDM)

Pointing to the western Amazon as a main endemic area for palms by PAE and NDM/VDM analyses, agrees with other studies in South American forest, that consider this region important due to the presence of several endemic species. These include Cracraft (1985) and Morrone (2001, 2014), who reported various endemic areas for birds, Prado et al. (2014) who reported endemic areas for oryzomyine rodents, Costa et al. (2000) for marsupials, primates and rodents, and Noguera-Urbano and Escalante (2015) for mammals.

Many other studies have shown that the endemic areas identified in this study also have high palm species richness (Kahn et al. 1988; Khan and Mejia 1991; Duivenvoorden and Lips 1995; Henderson et al. 1995; Valencia et al. 2004; Vormisto et al. 2004a, b; Pintaud et al. 2008; Balslev et al. 2015). According to our PAE analysis at the scale of 3º, *Aiphanes ulei* and *Wettinia maynensis* supported all endemic areas found here (Fig. 3a), distributed in the western Amazon and shared with the Andean sub-region (Brazil, Colombia, Ecuador, Peru). The endemic palms of the western Amazon mostly belonged to the genera *Astrocaryum*, *Attalea*, and *Desmoncus* (Balslev et al. 2015). In our PAE analysis (grid square sizes of 1º and 3º) we found at least one species in each of these genera (*Attalea peruviana*, *A. salazarii*, *A. weberbaueri*, *Astrocaryum carnosum*, *Desmoncus loretanus*) that define endemic areas in the western Amazon. Of these, only *Astrocaryum carnosum* is in the vulnerable category according to IUCN (2017) (Table 1). It should be noted that this part of the Amazon region, mainly the Peruvian Amazon, was identified as endemic areas in PAE analysis of 1º and 3º supported by the species aforementioned.

The Andean sub-region (represented by squares 1, 2, 3, 5 in PAE analysis in grid square of 3º, although with only one shared endemic species, *Socratea rostrata*) was also identified as important for endemism in several studies on birds, marsupials, primates, rodents and mammals (Cracraft 1985; Costa et al. 2000; Morrone 2006; Noguera-Urbano and Escalante 2015). This region has high endemism due to altitudinal variation created by the geological formation of the Andes (Sigrist and Carvalho 2008) and also by the generally wet environments in this part of the Andes (Pintaud et al. 2008). An association between geological complexity and the number of endemic species may be common to all endemic areas (Sigrist and Carvalho 2008). In grid square of 3º, six restricted species were found in this part of the endemic areas, mainly in northern Andes (*Astrocaryum scopatum*, *Bactris setiflora*, *Ceroxylon amazonicum*, *Geonoma fosteri*, *Geonoma schizocarpa*, *Socratea rostrata*), of which two (*B. setiflora* and *C. amazonicum*) are threatened in the endangered category, according to IUCN (2017). The last species is endemic to the Ecuadorian Amazon (Balslev et al. 2015). Therefore, these areas in the northern Andes are important in most studies of conservation and protection, mainly because these endangered species were not found within any conservation units.

In our NDM/VNDM analysis using 3º grid squares, the central Amazon also had endemic areas but with lower endemism values (endemicity score 3.0–5.0, Table 2). The overlapping patterns of the endemic areas pointed to the recognition of the grid square 53 with 16–20 endemic species and the grid squares 36, 37, 46 and 47 with 11–15 species (Fig. 3b). The floristic composition of the central Amazon may be related to a confluence of distinct phytogeographic regions, grouping species from different provinces (Oliveira and Daly 1999). A particular aspect in these areas is the riverine flora of black waters and white-sand forest, *Campinarana*, which is the product of the erosion of Guianas shield in the Rio Negro basin. In the *Campinarana* areas, the geologic origin, characteristic of the soils, hydrology, and fire regimes, vary widely and have distinct impacts in different regions on vegetation structure and on flora, faunal, and fungal species composition (Adeney et al. 2016). Furthermore, these areas highlighted two features: high biodiversity on extremely poor soils and large number of restricted species, principally the endemic genera *Barcella* and *Leopoldinia* (Oliveira et al. 2001; Pintaud et al. 2008). Our NDM/VNDM analysis using 3º grid squares showed the presence of *Leopoldinia pulchra* as a species that defined three consensus areas in this part of the region with endemicity scores of 0.649 (consensus area 1), 0.655 (5) and 0.678 (6) (Table 2). Thus, this region should have special attention in the conservation efforts to ensure their persistence in the Amazon because it presents an extremely slow recovery after disturbance, and important contributions to basin-wide diversity patterns and ecosystem services (Adeney et al. 2016).

In Guiana sub-region, the same analysis (NDM/VNDM) also showed endemic areas in grid square of 1º with endemicity score of 2.9 (Fig. 2b), supported by four palm species (Table 2) among which *Asterogyne guianensis* is endemic to eastern French Guiana (Stauffer et al. 2003). In grid squares of 3º it showed four consensus areas (19, 23, 27, 32) in with endemicity scores of 2.0–4.0 (Fig. 4, Table 2) confirming the well known fact that the Guianas is a unique biogeographical region with diverse and abundant vegetation, and many endemic species (Maguire 1970; Gibbs and Barron 1993; Kelloff and Funk 2004). Thirteen palm species supported these areas (Table 2) among which *Prestoea tenuiramosa* (endemicity score 0.404, consensus area 23) stand out as an endemic species above 1000 m elevation in the mountains of the Guianas (Pintaud et al. 2008) and *Asterogyne guianensis* (endemicity score 0.700, consensus area 32) as a rare species in this area.

Threatened endemic species vs conservation units

The analysis of the geographical distribution of the threatened palm species that support the endemic areas, superimposed on the conservation units (CUs), portrays a negative picture regarding the effective conservation of these palms (Fig. 5). All threatened endemic species were found outside the CUs of Brazil, Ecuador, and Peru. *Attalea tessmannii* (NT) with a broader distribution does not have any populations that are protected by CUs, but there are three populations near important CUs, such as Serra do Divisor National Park in Brazil and Peru, Allpahuayo Mishana National Reserve, and Cordillera Azul National Park in Peru. Three species are near to CUs of Ecuador; *Bactris setiflora* (EN) is near to Sangay National Park and Llanganates National Park, *Wettinia longipetala* (VU) is near to Podocarpus National Park and Cerro Plateado Biological Reserve, and *Ceroxylon amazonicum* (EN) is distributed near all CUs aforementioned and also near to Colonso Chalupas Biological Reserve. *Astrocaryum carnosum* (VU) is found near the Pacaya Samiria National Reserve in Peru with a single record. The lack of protection, in particular for the endemic species, could lead to their extinction, attributable, for example, to anthropogenic action such as unsustainable extraction and deforestation (Svenning 1998; Souza and Martins 2004; WWF 2014).

In conclusion, our results showed that PAE analysis in small grid squares size (1º) there was no endemic area at this scale but recognized a small important area supported by one species (Peruvian Amazon) and NDM/VNDM analysis detected an endemic area in French Guyana. In contrast, larger grid square size (3º) (PAE and NDM/VNDM analyses) recognized large areas of endemism mainly in the western Amazon (Peruvian Amazon and near to Andes sub-region) with many species appearing as endemic in each area. The threatened endemic species found are not protected in conservation units. This underlines the continued need to define priority areas for conservation. It was comforting that the different methods available for identifying endemic areas (NDM-VNDM and PAE program) agreed in their general outcome, which suggests that they are adequate for this purpose; they only differed in the number of areas and endemic species found.

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Table 1 Palms species that support endemic grid squares of 1º and 3° in our Parsimony Analysis of Endemism (PAE), with indication of their presence in Operational Geographic Units (OGU), their distribution and country, and their threat category as defined by IUCN (2017)

Grid size	OGUs	Species	Distribution	Country	IUCN
1	(65) (67) (68)	*Desmoncus loretanus* A.J. Hend.	western Amazon	Peru	-
	67	*Attalea peruviana* Zona			-
		Attalea weberbaueri (Burret) Zona			-
	68	*Astrocaryum carnosum* F. Kahn & B. Millán			VU
3	(1) (2) (3) (5) (6) (7) (8) (9) (12) (13)	*Aiphanes ulei* (Dammer) Burret	Andes - western Amazon	Brazil, Colombia, Ecuador and Peru	LC
		Wettinia maynensis Spruce			-
	(7) (12)	*Attalea salazarii* (Glassman) Zona	western Amazon	Brazil, Peru	-
		Desmoncus loretanus A.J. Hend.			-
	7	*Astrocaryum carnosum* F. Kahn & B. Millán		Peru	VU
		Attalea peruviana Zona			-
		Attalea weberbaueri (Burret) Zona			-
	(1) (2) (3) (5)	*Socratea rostrata* Burret	Andes - western Amazon	Colombia, Ecuador and Peru	-
	(2) (3)	*Ceroxylon amazonicum* Galeano		Ecuador and Peru	EN
	2	*Bactris setiflora* Burret		Ecuador and Peru	EN
	3	*Astrocaryum scopatum* F. Kahn & B. Millán		Peru	-
		Geonoma schizocarpa A.J. Hend.			-
	1	*Geonoma fosteri* A.J. Hend.		Colombia and Ecuador	-

Table 2 Summary of information on the consensus areas of the palm species in the Amazon region in grid square of 1º and 3º, with information on number of the species for each area, species composition with their respective score, number of grid squares for each area and the maximum scores. *grid size of 1º

Consensus areas	number of species	Endemic species (score)	Number of grid squares	Maximum score
1*	4	*Asterogyne guianensis* (0.700), *Attalea canopiensis* (0.700), *Attalea degranvillei* (0.700), *Attalea maripensis* (0.800)	5	2.900
1	7	*Bactris bidentula* (0.807), *Bactris sphaerocarpa* (0.739), *Geonoma oligoclona* (0.596), *Bactris corossilla* (0.420), *Bactris macroacantha* (0.503), *Euterpe catinga* (0.336), *Leopoldinia pulchra* (0.649)	24	3.76796
2	12	*Aiphanes weberbaueri* (0.622), *Astrocaryum chambira* (0.558), *Attalea tessmannii* (0.833), *Bactris martiana* (0.700), *Chelyocarpus ulei* (0.730), *Geonoma orbignyana* (0.349), *Geonoma poeppigiana* (0.714), *Iriartella stenocarpa* (0.730), *Phytelephas tenuicaulis* (0.652), *Wendlandiella gracilis* (0.816), *Wettinia augusta* (0.816), *Wettinia drudei* (0.477)	20	6.26177
3	22	*Aiphanes deltoidea* (0.607), *Aiphanes ulei* (0.595), *Aiphanes weberbaueri* (0.818), *Aphandra natalia* (0.727), *Astrocayum chambira* (0.563), *Astrocaryum faranae* (0.636), *Attalea bassleriana* (0.607), *Attalea cephaloltus* (0.552), *Attalea tessmannii* (0.955), *Bactris martiana* (0.594), *Chelyocarpus ulei* (0.536), *Desmocus giganteus* (0.625), *Geonoma longepedunculata* (0.630), *Geonoma poeppigiana* (0.813), *Geonoma supracostata* (0.708), *Iriartella stenocarpa* (0.521), *Prestoea schultzeana* (0.714), *Socratea salazarii* (0.600), *Wendlandiella gracilis* (0.867), *Wettinia augusta* (0.393), *Wettinia drudei* (0.521), *Wettinia maynensis* (0.565)	15	9.475
4	7	*Astrocaryum ferrugineum* (0.647), *Attalea insignis* (0.467), *Bactris bidentula* (0.420), *Bactris bifida* (0.495), *Bactris fissifrons* (0.514), *Bactris killipii* (0.581), *Mauritia carana* (0.498)	17	3.87284

5	7	*Attalea insignis* (0.460), *Bactris bidentula* (0.810), *Bactris fissifrons* (0.573), *Bactris macroacantha* (0.474), *Bactris sphaerocarpa* (0.668), *Leopoldinia pulchra* (0.655), *Mauritia carana* (0.633)	22	3.69715
6	6	*Bactris bidentula* (0.810), *Bactris corossilla* (0.396), *Bactris macroacantha* (0.446), *Bactris sphaerocarpa* (0.668), *Leopoldinia pulchra* (0.678), *Mauritia cara* (0.633)	24	3.32331
7	5	*Attalea tessmannii* (0.752), *Bactris martiana* (0.615), *Geonoma atrovirens* (0.654), *Iriartella stenocarpa* (0.470), *Wendlandiella gracilis* (0.564)	13	3.30556
8	18	*Aiphanes deltoidea* (0.620), *Aiphanes ulei* (0.695), *Astrocaryum chambira* (0.563), *Attalea bassleriana* (0.714), *Attalea plowmanii* (0.667), *Attalea tessmannii* (0.833), *Chelyocarpus repens* (0.625), *Chelyocarpus ulei* (0.618), *Desmoncus giganteus* (0.755), *Geonoma longepedunculata* (0.714), *Geonoma poeppigiana* (0.787), *Geonoma supracostata* (0.679), *Iriartella stenocarpa* (0.521), *Prestoea schultzeana* (0.821), *Wendlandiella gracilis* (0.758), *Wettinia augusta* (0.383), *Wettinia drudei* (0.521), *Wettinia maynensis* (0.665)	16	8.475
9	5	*Astrocaryum chambira* (0.520), *Attalea plowmanii* (0.633), *Geonoma poeppigiana* (0.583), *Oenocarpus balickii* (0.073), *Wettinia drudei* (0.583)	15	2.64333
10	14	*Aiphanes weberbaueri* (0.792), *Astrocaryum perangustatum* (0.688), *Attalea cephalotus* (0.700), *Attalea moorei* (0.625), *Attalea tessmannii* (0.885), *Bactris chaveziae* (0.487), *Bactris martiana* (0.731), *Chelyocarpus ulei* (0.703), *Geonoma poeppigiana* (0.448), *Iriartella stenocarpa* (0.408), *Phytelephas tenuicaulis* (0.559), *Socratea salazarii* (0.950), *Wendlandiella gracilis* (0.831), *Wettinia augusta* (0.428)	14	7.06944
11	8	*Attalea insignis* (0.583), *Bactris bifida* (0.576), *Bactris cocinna* (0.536), *Bactris fissifrons* (0.591), *Bactris killipii* (0.741), *Bactris macroacantha* (0.669), *Bactris riparia* (0.597), *Geonoma laxiflora* (0.730)	28	4.48963
12	12	*Astrocaryum chonta* (0.495), *Astrocaryum gratum* (0.646), *Attalea cephalotus* (0.566), *Attalea moorei* (0.600), *Bactris chaveziae* (0.737), *Bactris martiana* (0.424), *Chamaedorea angustisecta* (0.570), *Chamaedorea fragrans* (0.303), *Desmoncus latisectus* (0.424), *Desmoncus madrensis* (0.600), *Socratea salazarii* (0.515), *wettinia augusta* (0.258)	12	5.4
13	7	*Astrocaryum ferrugineum* (0.656), *Attalea spectabilis* (0.502), *Bactris bidentula* (0.463), *Bactris killipii* (0.496), *Bactris sphaerocarpa* (0.673), *Itaya amicorum* (0.566), *Mauritia carana* (0.543)	21	3.375

14	7	*Astrocaryum ferrugineum* (0.656), *Bactris bidentula* (0.616), *Bactris sphaerocarpa* (0.673), *Euterpe catinga* (0.573), *Itaya amicorum* (0.566), *Mauritia carana* (0.800), *Syagrus smithii* (0.675)	22	3.875
15	8	*Aiphanes deltoidea* (0.450), *Aiphanes ulei* (0.050), *Astrocaryum ciliatum* (0.578), *Attalea plowmanii* (0.489), *Chelyocarpus repens* (0.578), *Oenocarpus makeru* (0.667), *Oenocarpus simplex* (0.667), *Manicaria martiana* (0.750)	6	4.47778
16	8	*Astrocaryum chambira* (0.630), *Chelyocarpus ulei* (0.698), *Dictyocaryum lamarckianum* (0.675), *Geonoma orbignyana* (0.667), *Iriartella stenocarpa* (0.810), *Oenocarpus balickii* (0.339), *Prestoea acuminata* (0.644), *Wettinia augusta* (0.677)	25	3.8836
17	21	*Aiphanes deltoidea* (0.607), *Aiphanes ulei* (0.595), *Aiphanes weberbaueri* (0.850), *Aphandra natalia* (0.778), *Astrocaryum faranae* (0.667), *Astrocaryum perangustatum* (0.517), *Attalea bassleriana* (0.607), *Attalea cephalotus* (0.564), *Attalea tessmannii* (0.955), *Bactris martiana* (0.500), *Chelyocarpus ulei* (0.524), *Geonoma longepedunculata* (0.635), *Geonoma poeppigiana* (0.685), *Geonoma supracostata* (0.778), *Iriartella stenocarpa* (0.288), *Prestoea schultzeana* (0.714), *Socratea salazarii* (0.615), *Wendlandiella gracilis* (0.867), *Wettinia augusta* (0.273), *Wettinia longipetala* (0.611), *Wettinia maynensis* (0.565)	13	10.22024
18	6	*Bactris bidentula* (0.714), *Bactris killipii* (0.606), *Bactris macroacantha* (0.565), *Geonoma camana* (0.625), *Geonoma laxiflora* (0.549), *Geonoma oligoclona* (0.658)	24	3.96726
19	3	*Bactris aubletiana* (0.636), *Geonoma oldemanii* (0.833), *Geonoma umbraculiformis* (0.657)	9	2.37626
20	4	*Attalea plowmanii* (0.654), *Attalea tessmannii* (0.747), *Geonoma atrovirens* (0.654), *Geonoma poeppigiana* (0.572)	13	2.8767
21	8	*Astrocaryum aculeatum* (0.250), *Astrocaryum murumuru* (0.630), *Desmoncus mitis* (0.782), *Geonoma macrostachys* (0.635), *Iriartella setigera* (0.833), *Attalea maripa* (0.367), *Bactris acanthocarpa* (0.606), *Geonoma leptospadix* (0.665)	60	5.01767
22	8	*Bactris killipii* (0.543), *Bactris macroacantha* (0.620), *Bactris riparia* (0.699), *Bactris schultesii* (0.674), *Geonoma brongniartii* (0.486), *Geonoma camana* (0.844), *Geonoma laxiflora* (0.844), *Phytelephas macrocarpa* (0.813)	33	4.53106
23	4	*Astrocaryum farinosum* (0.635), *Bactris ptariana* (0.833), *Dictyocaryum fuscum* (0.750), *Prestoea tenuiramosa* (0.404)	6	2.87179

24	3	*Bactris faucium* (0.700), *Attalea princeps* (0.750), *Syagrus cardenasii* (0.750)	10	2.45
25	6	*Astrocaryum aculeatum* (0.473), *Astrocaryum gynacanthum* (0.583), *Attalea maripa* (0.138), *Bactris elegans* (0.632), *Lepidocaryum tenue* (0.530), *Oenocarpus bacaba* (0.655)	56	3.2619
26	13	*Aiphanes ulei* (0.455), *Aiphanes weberbaueri* (0.357), *Aphandra natalia* (0.643), *Astrocaryum huicungo* (0.800), *Astrocaryum urostachys* (0.929), *Attalea bassleriana* (0.929), *Ceroxylon amazonicum* (0.700), *Geonoma longepedunculata* (0.500), *Geonoma multisecta* (0.700), *Geonoma supracostata* (0.643), *Prestoea schultzeana* (0.234), *Socratea rostrata* (0.900), *Wettinia maynensis* (0.422)	7	7.25325
27	4	*Astrocaryum rodriguesii* (0.700), *Attalea guianensis* (0.700), *Bactris aubletiana* (0.711), *Bactris constanciae* (0.667)	10	3.02778
28	20	*Aiphanes deltoidea* (0.688), *Aiphanes ulei* (0.675), *Aiphanes weberbaueri* (0.563), *Aphandra natalia* (0.813), *Astrocaryum faranae* (0.688), *Astrocaryum huicungo* (0.800), *Astrocaryum urostachys* (0.667), *Attalea bassleriana* (0.667), *Attalea plowmanii* (0.582), *Attalea salazarii* (0.625), *Attalea tessmannii* (0.508), *Ceroxylon amazonicum* (0.700), *Chelyocarpus repens* (0.688), *Desmoncus loretanus* (0.625), *Geonoma longepedunculata* (0.519), *Geonoma poeppigiana* (0.270), *Geonoma supracostata* (0.736), *Prestoea schultzeana* (0.649), *Socratea rostrata* (0.445), *Wettinia maynensis* (0.476)	9	9.6875
29	6	*Astrocaryum ferrugineum* (0.483), *Astrocaryum javarense* (0.636), *Attalea attaleoides* (0.599), *Attalea spectabilis* (0.558), *Bactris halmoorei* (0.558), *Bactris sphaerocarpa* (0.707)	11	3.79132
30	4	*Astrocaryum ciliatum* (0.875), *Attalea racemosa* (0.643), *Manicaria martiana* (0.643), *Syagrus orinocensis* (0.286)	4	2.69643
31	5	*Astrocaryum aculeatum* (0.918), *Astrocaryum gynacanthum* (0.737), *Attalea maripa* (0.639), *Bactris acanthocarpa* (0.555), *Geonoma macrostachys* (0.363)	67	3.46247
32	5	*Asterogyne guianensis* (0.700), *Attalea guianensis* (0.389), *Bactris constanciae* (0.500), *Bactris rhaphidacantha* (0.622), *Syagrus stratincola* (0.800)	5	3.26111

Table 3 Amazon palms that define the consensus areas with maximum score >6.0 according NDM/VNDM in grid square of 3º and comparison with IUCN (2017)

Amazonian species	Consensus endemic areas (maximum score >6.0)							IUCN (2017)
	2 (6.26177)	3 (9.475)	8 (8.475)	10 (7.06944)	17 (10.22024)	26 (7.25325)	28 (9.6875)	
Aiphanes deltoidea Burret		•	•		•		•	-
Aiphanes ulei (Dammer) Burret		•	•		•	•	•	LC
Aiphanes weberbaueri Burret	•	•		•	•	•	•	-
Aphandra natalia (Balslev & A.J. Hend.) Barfod		•			•	•	•	-
Astrocaryum chambira Burret	•		•					-
Astrocaryum faranae F. Kahn & E. Ferreira		•			•		•	-
Astrocaryum huicungo Dammer ex Burret						•	•	-
Astrocaryum perangustatum F. Kahn & B. Millán				•	•			-
Astrocaryum urostachys Burret						•	•	-
Astrocaryum chambira Burret		•						-
Attalea bassleriana (Burret) Zona		•	•		•	•	•	-
Attalea cephalotus Poepp. ex Mart.		•		•	•			-
Attalea moorei (Glassman) Zona				•				-
Attalea plowmanii (Glassman) Zona			•				•	-
Attalea salazarii (Glassman) Zona							•	-
Attalea tessmannii Burret	•	•	•	•	•		•	NT
Bactris chaveziae A.J. Hend.				•				-
Bactris martiana A.J. Hend.	•	•		•	•			-
Ceroxylon amazonicum Galeano						•	•	EN

Chelyocarpus repens F. Kahn & K. Mejía			•				•	-
Chelyocarpus ulei Dammer	•	•	•	•	•			-
Desmoncus giganteus A.J. Hend.		•	•					-
Desmoncus loretanus A.J. Hend.							•	-
Geonoma longipedunculata Burret		•	•		•	•	•	-
Geonoma multisecta (Burret) Burret						•		-
Geonoma orbignyana Mart.	•							-
Geonoma poeppigiana Mart.	•	•	•	•	•		•	-
Geonoma supracostata Svenning		•	•		•	•	•	-
Iriartella stenocarpa Burret	•	•	•	•	•			-
Phytelephas tenuicaulis (Barfod) A.J. Hend.	•			•				-
Prestoea schultzeana Mart.		•	•		•	•	•	-
Socratea rostrata Burret						•	•	-
Socratea salazarii H.E. Moore		•		•	•			-
Wendlandiella gracilis Dammer	•	•	•	•	•			-
Wettinia augusta Poepp. & Endl.	•	•	•	•	•			-
Wettinia drudei (O.F. Cook & Doyle) A.J. Hend.	•	•	•					-
Wettinia longipetala A.H. Gentry					•			VU
Wettinia maynensis Spruce		•	•		•	•	•	-

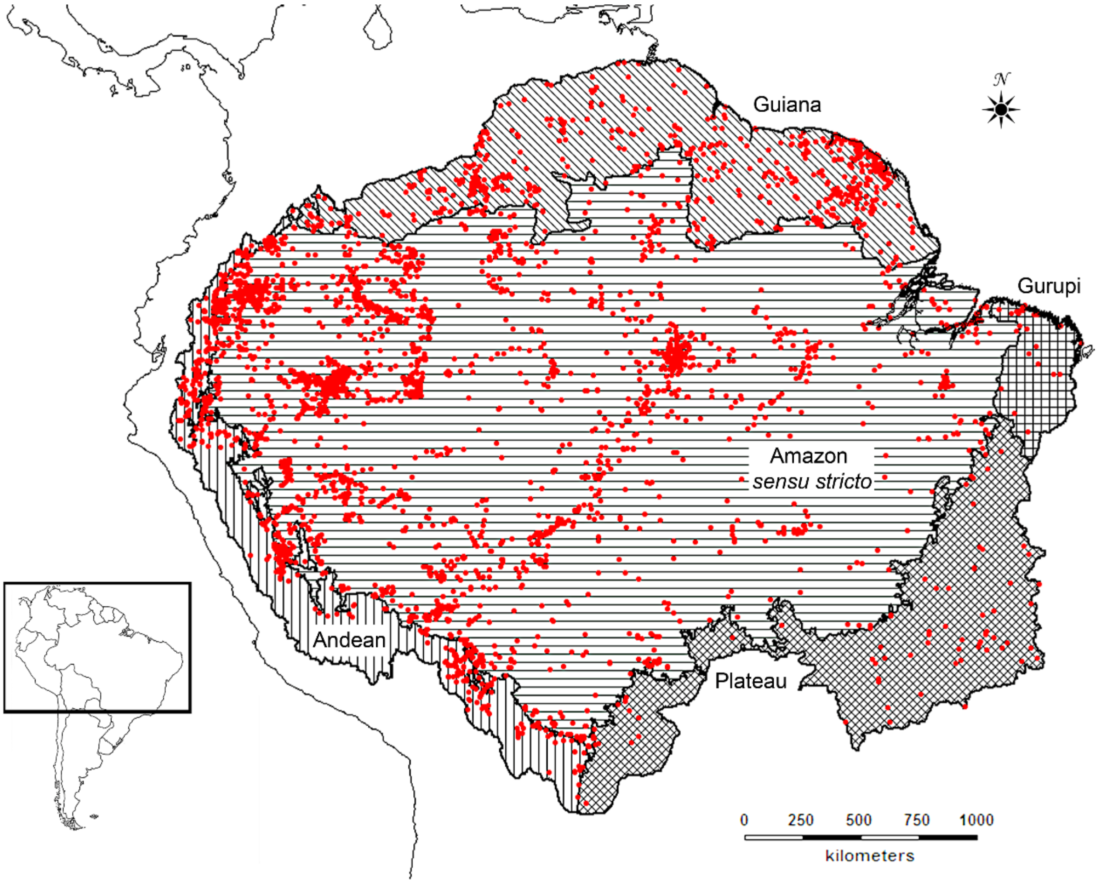

Fig. 1 Distribution of 17,310 records of occurrence of 177 Amazonian palm species in the Amazon region derived from the Global Biodiversity Information Facility (GBIF). The division into sub-regions follows Eva and Huber (2005)

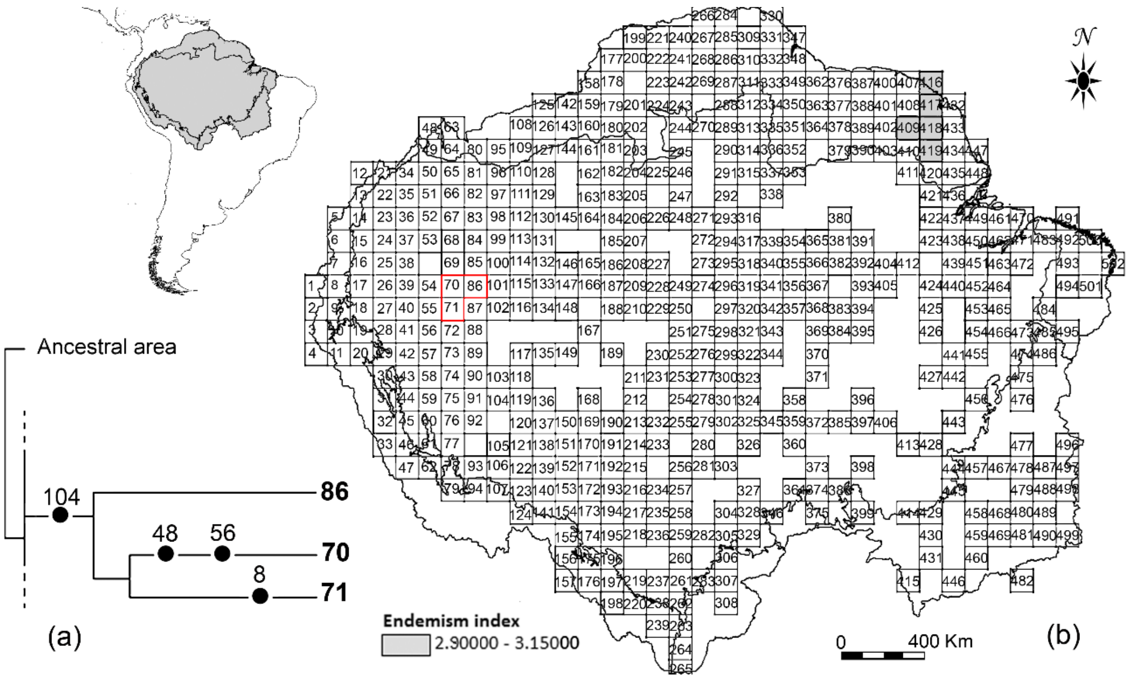

Fig. 2 a Informative part of cladogram obtained in our Parsimony Analysis of Endemism (PAE) in grid square of 1°. Internal numbers indicate the code (number) represented by the species defining the important secondary areas, and are presented in Table 1; **b** Overlapping of PAE and NDM/VNDM analyses in grid square of 1°. Darker tones are the main endemic areas by NDM/VNDM and the red line is the secondary area recognized by the PAE

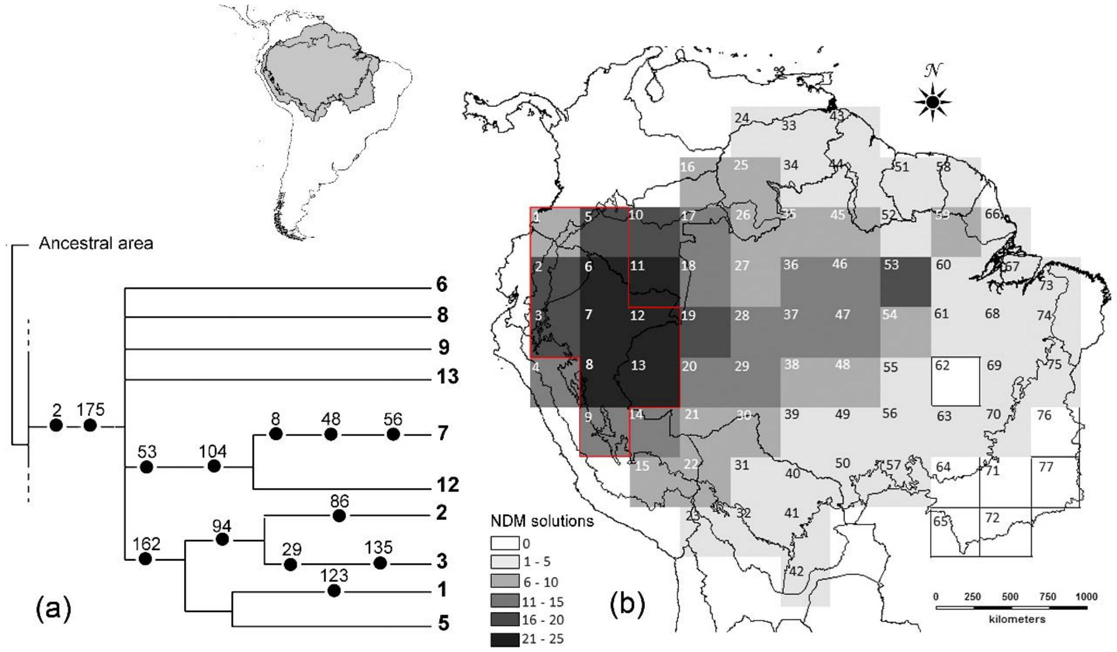

Fig. 3 a Informative part of cladogram obtained in our Parsimony Analysis of Endemism (PAE) in grid square of 3º. Internal numbers indicate the code (number) represented by the species defining the endemic areas, and are presented in Table 1; **b** Overlapping of PAE and NDM/VNDM analyses in grid square of 3º. Darker tones are the main endemic areas by NDM/VNDM and the red line is the endemic area recognized by the PAE

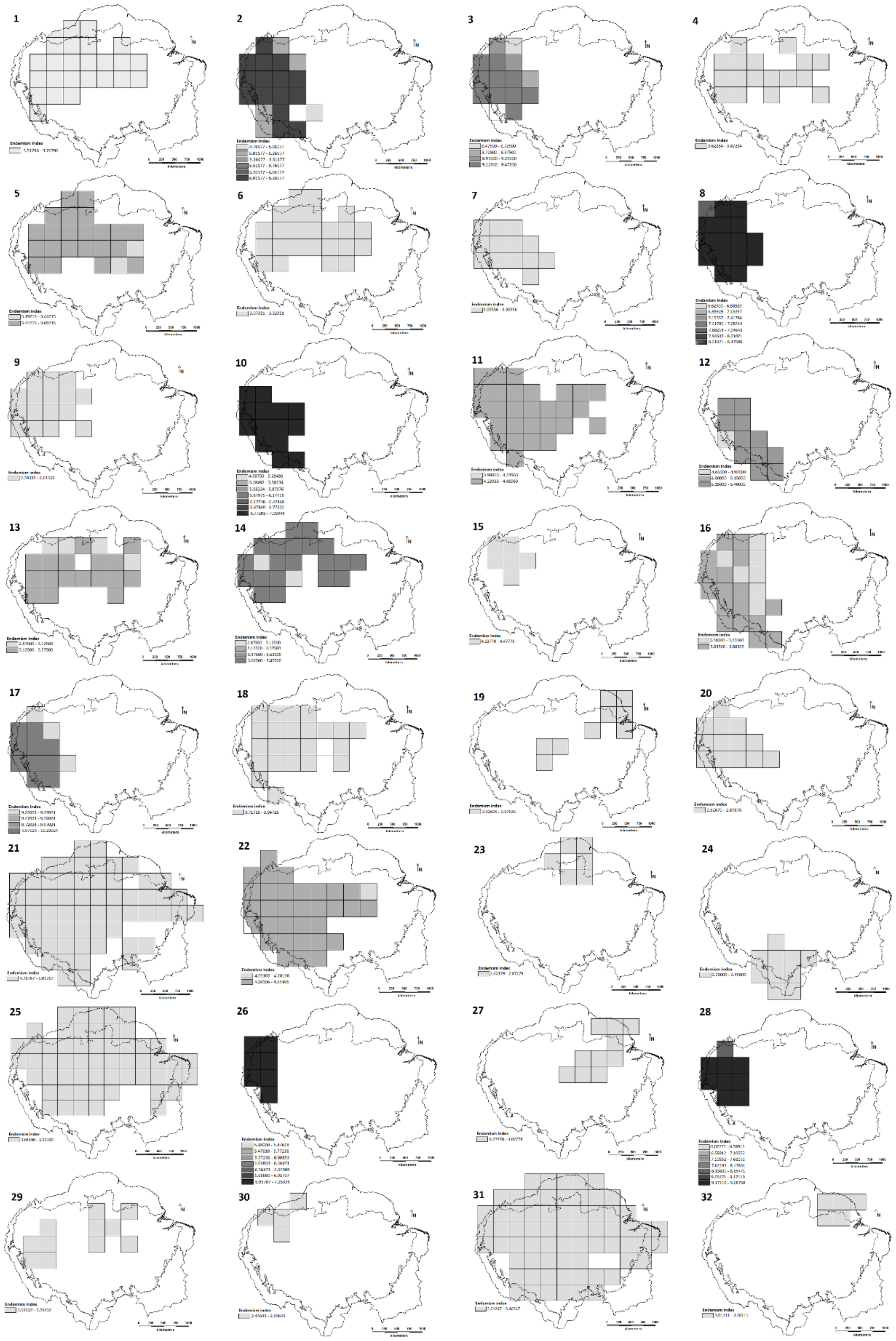

Fig. 4 Consensus endemic areas (32) detected for Amazonian palms by NDM/VNDM using three degree grids size in the Amazon region. Square with darker shades show greater endemicity

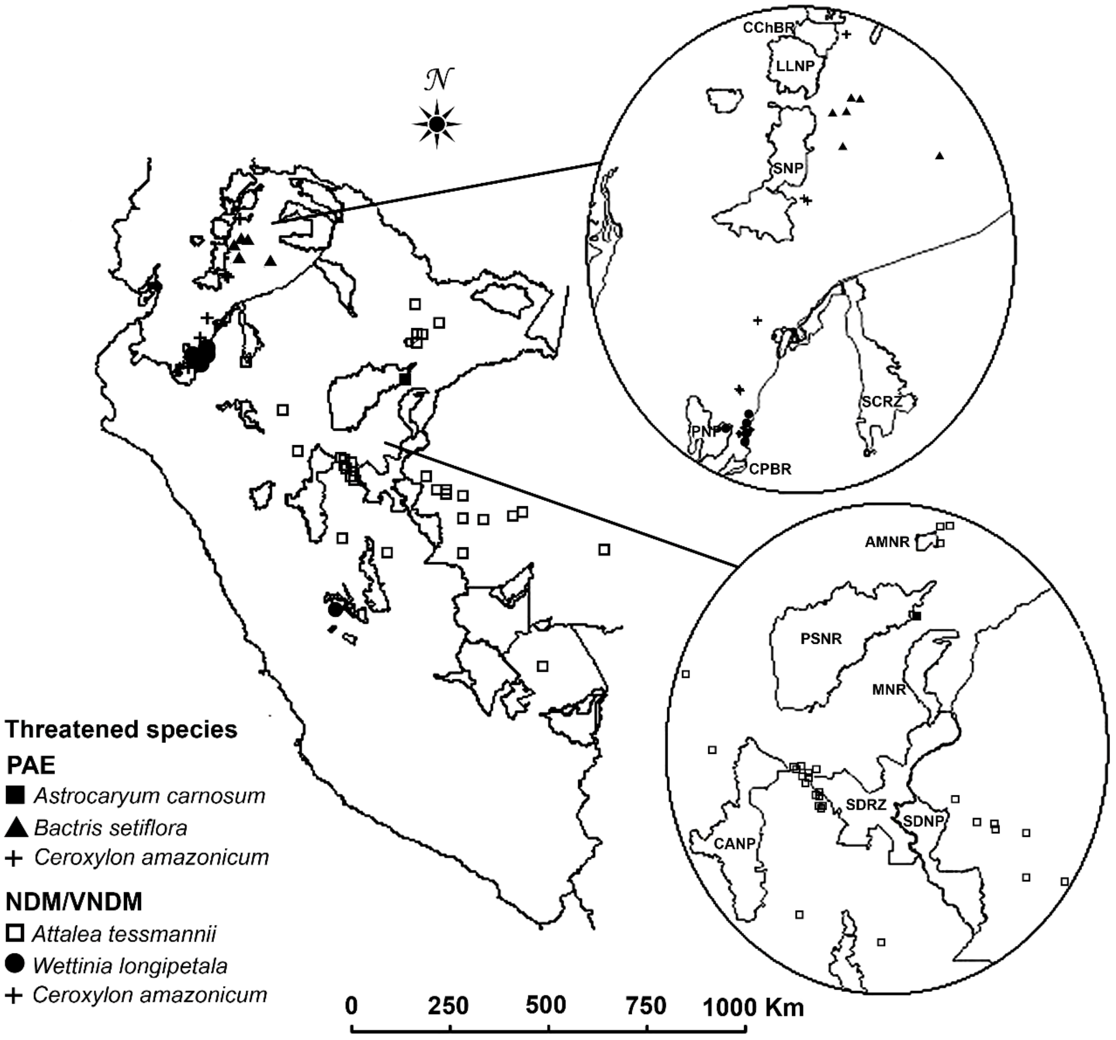

Fig. 5 Distribution of threatened species (according to IUCN, 2017) that support the endemic areas obtained in PAE and NDM/VNDM analysis. AMNR: Allpahuayo-Mishana National Reserve; CANP: Cordillera Azul National Park; CChBR: Colonso-Chalupas Biological Reserve; CPBR: Cerro Plateado Biological Reserve; LLNP: Llanganates National Park; MNR: Matsés National Reserve; PNP: Podocarpus National Park; PSNR: Pacaya–Samiria National Reserve; SCRZ: Santiago Comaina Reserved Zone; SDNP: Serra do Divisor National Park; SDRZ: Sierra del Divisor Reserve Zone; SNP: Sangay National Park

FINAL CONCLUSION

The thesis showed the diversity of palms existing in the Amazon region, especially with the greatest Amazon palms richness in western Amazon and near the equator. The areas with low richness and records gaps in the Amazon region may been caused by deforestation mainly in southern and south-eastern Brazilian Amazon, but it also may probably have been caused by difficult access, lack of logistics and research. According to habitat, highest palm species richness are found in *terra firme* forest, and less richness in flooded and waterlogged forests, and the growth form as small palms and large tall-stemmed palms dominate the communities both in terms of species richness and number of individuals. Climate seem be an important factor controlling the palm diversity and distribution, mainly water-related variables such as annual rainfall and number of wet days. Moreover, the western Amazon, besides having high palm richness, also has palm endemic areas, especially, near the Andean sub-region and the Peruvian Amazon, but the species that define the endemic areas, five are threatened with extinction, and they are not protected in any conservation units. Thus, the deforestation and non-sustainable palm extraction are threat for many palm species leading to reduce their population and in worst cases to extinction. Therefore, the need to delimit more priority conservation areas is important for the conservation of those threatened species. On the other hand, the palms play a very important role for the local populations, principally for human consumption, elaboration of utensils and tools, and construction of houses. Consequently, local communities depend mainly on natural resources for their subsistence, particularly of the palms.

Table S1. Palm species in the Amazon region used in this study. ASS: Amazon *sensu stricto*, An: Andes, Gui: Guiana, Gur: Gurupi, Pla: Plateau. En: Endemic. Br: Brazil, Bo: Bolivia, Co: Colombia, Ec: Ecuador, Gu: Guianas, Pe: Peru and Ve: Venezuela. A: All Amazonian region, C: Central region, E: Eastern region, N: North region, S: South region, W: Western region, NE: Northeast region, NW: Northwest region, SW: Southwest region, Ce: Cespitose, So: Solitary, p: Dichotomous, CR: Critically Endangered, DD: Data Deficient, EN: Endangered, LC: Least Concern, NT: Near Threatened, VU: Vulnerable, a: Large tall-stemmed Palms, b: Large-leaved medium–short-stemmed Palms, c: Medium-sized Palms, d: Small Palms, e: Large acaulescent Palms, f: Small acaulescent Palms, g: Climbing Palms. Reference: 1: Khan & de Granville (1992), 2: Henderson (1995), 3: Henderson et al. (1995), 4: Kahn (2008), 5: Pintaud *et al*. (2008), 6: Balslev *et al.* (2015).

Species	**Distribution in this study**					**Total**	**En**	**Native species**	**Distribution**	**Branch**	**UICN (2017)**	**Growth form**	**Reference**
	ASS	**An**	**Gui**	**Gur**	**Pla**								
Aiphanes deltoidea Burret	15					15		Br, Co, Pe	W	Ce		d	1, 2, 3, 5, 6
Aiphanes ulei (Dammer) Burret	178	35				213		Br, Co, Ec, Pe	W	So	LC	d	1, 2, 3, 5, 6
Aiphanes weberbaueri Burret	49	25				74		Ec, Pe	W	So		d	2, 3, 5, 6
Aphandra natalia (Balslev & A.J. Hend.) Barfod	94	9				103		Br, Ec, Pe	W	So		b	1, 2, 3, 5, 6
Asterogyne guianensis Granv. & A.J. Hend.			5			5	Gu	Gu	E	So		d	1, 2, 3, 5
Astrocaryum acaule Mart.	50		24			74		Br, Co, Gu, Ve	C, N, NE	So		e	2, 3, 4, 5, 6
Astrocaryum aculeatum G. Mey.	264		190	3		457		Br, Bo, Gu, Ve	C	So		a	2, 3, 4, 5, 6
Astrocaryum carnosum F. Kahn & B. Millán	1					1	Pe	Pe	W	Ce	VU	b	2, 3, 4, 5, 6
Astrocaryum chambira Burret	246	1	6			253		Br, Co, Ec, Pe, Ve	W	So		a	2, 3, 4, 5, 6
Astrocaryum chonta Mart.	57					57		Br, Pe, Bo	SW	So		b	2, 3, 4, 5, 6
Astrocaryum ciliatum F. Kahn & B. Millán	28		1			29		Co, Pe	NW	So		e	2, 3, 4, 5, 6
Astrocaryum faranae F. Kahn & E. Ferreira	72					72		Br, Pe	W	Ce		b	2, 3, 4, 5, 6
Astrocaryum farinosum Barb. Rodr.	4		2			6		Br, Gu	N, NE	So		b	2, 3, 4, 5

Astrocaryum ferrugineum F. Kahn & B. Millán	19					19		Br, Co	C	So		b	2, 3, 4, 5, 6
Astrocaryum giganteum Barb. Rodr.	1					1		Br	E	So		b	2, 3, 4, 5
Astrocaryum gratum F. Kahn & B. Millán	75	1				76		Pe, Bo	C, SW	So		b	2, 3,4, 5, 6
Astrocaryum gynacanthum Mart.	124		60	5	1	190		Br, Co, Pe, Bo, Gu, Ve	A	Ce		d	2, 3, 4, 5, 6
Astrocaryum huaimi Mart.	10				10	20		Br, Pe, Bo	C, W, S	Ce		d	2, 3, 4, 5, 6
Astrocaryum huicungo Dammer ex Burret	3	2				5	Pe	Pe	W	Ce		b	2, 3, 4, 5, 6
Astrocaryum jauari Mart.	101	1	9		1	112		Br, Co, Ec, Pe, Bo, Gu, Ve	A	Ce		a	2, 3, 4, 5, 6
Astrocaryum javarense (Trail) Drude	30					30		Br, Pe	W	So		b	2, 3, 4, 5, 6
Astrocaryum macrocalyx Burret	107		1			108		Co, Pe	NW	So		b	2, 3, 4, 5, 6
Astrocaryum minus Trail			2			2		Br, Gu	A	So	CR	d	2, 3, 4, 5
Astrocaryum murumuru Mart.	128	3	16			147		Br, Gu, Ve	C, NE	Ce		b	2, 3, 4, 5
Astrocaryum paramaca Mart.	2		46			48		Br, Gu	NW	So		e	2, 3, 4, 5
Astrocaryum perangustatum F. Kahn & B. Millán	7	2				9	Pe	Pe	W	So		b	2, 3, 4, 5, 6
Astrocaryum rodriguesii Trail	5		6			11		Br, Gu	C, NE	So		a	2, 3, 4, 5
Astrocaryum sciophilum (Miq.) Pulle	8		59			67		Br, Gu	NW	So		b	2, 3, 4, 5
Astrocaryum scopatum F. Kahn & B. Millán	2					2	Pe	Pe	W	Ce		b	2, 3, 4, 5, 6
Astrocaryum sociale Barb. Rodr.	15					15		Br	C, N	So		e	2, 3, 4, 5
Astrocaryum ulei Burret	11					11		Br, Pe, Bo	SW	Ce		b	2, 3, 4, 5, 6
Astrocaryum urostachys Burret	124					124		Co, Ec, Pe	NW	Ce	LC	b	2, 3, 4, 5, 6
Astrocaryum vulgare Mart.	21		24	8	1	54		Br, Gu	E, S	Ce		b	2, 3, 4, 5
Attalea attaleoides (Barb. Rodr.) Wess. Boer	12		5			17		Br, Gu	NE	So		e	2, 3, 5
Attalea bassleriana (Burret) Zona	17	2				19	Pe	Pe	W	So		a	2, 3, 5, 6
Attalea blepharopus Mart.	1					1	Bo	Bo	W	So		c	2, 3, 6
Attalea camopiensis (Glassman) Zona			2			2		Gu	NE	So		e	2, 3, 5
Attalea cephalotus Poepp. ex Mart.	11					11	Pe	Pe	W	So		a	2, 3, 5, 6
Attalea dahlgreniana Bondar) Wess. Boer	3		2	2		7		Br, Gu	NE	So		a	2, 3, 5
Attalea degranvillei (Glassman) Zona			3			3		Gu	NE	So		e	2, 3, 5
Attalea guianensis (Glassman) Zona	5		4			9	Gu	Gu	NE	So		e	2, 3, 5

Attalea insignis (Mart. ex H. Wendl.) Drude	93		6			99		Br, Co, Ec, Pe	W	So		e	2, 3, 5, 6
Attalea luetzelburgii (Burret) Wess. Boer	12		1			13		Br, Co	W	So		e	2, 3, 5, 6
Attalea maripa (Aubl.) Mart.	197		59	8		264		Br, Co, Ec, Pe, Bo, Gu, Ve	W	So		a	2, 3, 5, 6
Attalea maripensis (Glassman) Zona			4			4		Gu	NE	So		e	2, 3, 5
Attalea microcarpa Mart.	166		64			230		Br, Co, Pe, Gu, Ve	W, N	So		e	2, 3, 5
Attalea moorei (Glassman) Zona	2					2	Pe	Pe	W	So		a	2, 3, 5, 6
Attalea peruviana Zona	1					1	Pe	Pe	W	So		a	2, 3, 5, 6
Attalea phalerata Mart. ex Spreng.	237	8	1		11	257		Br, Co, Pe, Bo	W	So		a	2, 3, 5, 6
Attalea plowmanii (Glassman) Zona	42					42		Co, Pe	W	So		a	2, 3, 5, 6
Attalea princeps Mart.	7	1			5	13		Bo	W	So		a	2, 3, 5, 6
Attalea racemosa Spruce	1		2			3		Br, Co, Pe, Gu, Ve	W, N	So		e	2, 3, 5
Attalea salazarii (Glassman) Zona	3					3	Pe	Pe	W	So		a	2, 3, 5, 6
Attalea spectabilis Mart.	17		2			19		Br, Gu	NE	So		e	2, 3, 5
Attalea tessmannii Burret	110	1				111		Br, Pe	W	So	NT	a	2, 3, 5, 6
Attalea weberbaueri (Burret) Zona	1					1	Pe	Pe	W	So		a	2, 3, 5, 6
Bactris acanthocarpa Mart.	256	5	53	2		316		Br, Co, Ec, Pe, Bo, Gu, Ve	A	Ce		d	2, 3, 5, 6
Bactris acanthocarpoides Barb. Rodr.	31		53			84		Br, Gu	A	Ce		d	1, 2, 3, 5
Bactris aubletiana Trail	8		100			108		Gu	E	Ce		d	1, 2, 3, 5
Bactris balanophora Spruce	77		8			85		Br, Co, Ve	W	Ce		d	2, 3, 5, 6
Bactris bidentula Spruce	88		13			101		Br, Co, Pe, Ve	N	Ce		d	1, 2, 3, 5, 6
Bactris bifida Mart.	155					155		Br, Co, Pe	W	Ce		d	1, 2, 3, 5, 6
Bactris campestris Poepp. ex Mart.	26		23	1		50		Br, Co, Gu, Ve	W	Ce		d	2, 3, 5, 6
Bactris chaveziae A.J. Hend.	62	6				68		Br, Pe, Bo	W	Ce		d	2, 3, 5, 6
Bactris concinna Mart.	357	1	2			360		Br, Co, Ec, Pe, Bo	A	Ce		d	1, 2, 3, 5, 6
Bactris constanciae Barb. Rodr.	20		36			56		Br, Gu	A	Ce	LC	d	1, 2, 3, 5
Bactris corossilla H. Karst.	167	5	24			196		Br, Co, Ec, Pe, Bo, Ve	W	Ce		d	2, 3, 5, 6
Bactris cuspidata Mart.	17		11		1	29		Br, Gu	NE	Ce		d	2, 3, 5
Bactris elegans Barb. Rodr.	92		55	1		148		Br, Co, Bo, Gu	C, E	Ce		d	1, 2, 3, 5, 6

Bactris faucium Mart.	8	3				11	Bo	Bo	W	Ce		d	2, 3, 5, 6
Bactris fissifrons Mart.	123	1	8			132		Br, Co, Ec, Pe	W	Ce	LC	d	2, 3, 5, 6
Bactris gastoniana Barb. Rodr.	34		71			105		Br, Gu	C, E	Ce		f	1, 2, 3, 5
Bactris glaucescens Drude	9				4	13		Bo	W	Ce	LC	d	2, 3, 5, 6
Bactris halmoorei A.J. Hend.	56					56		Br, Co, Pe	W	Ce		d	2, 3, 5, 6
Bactris hirta Mart.	371		49	2	1	423		Br, Co, Ec, Pe, Bo, Gu, Ve	A	Ce		d	2, 3, 5, 6
Bactris killipii Burret	138	2				140		Br, Co, Pe	W	Ce		d	2, 3, 5, 6
Bactris macroacantha Mart.	158	5				163		Br, Co, Ec, Pe, Bo	W	Ce		d	2, 3, 5, 6
Bactris martiana A.J. Hend.	12					12		Br, Co, Ec, Pe	W	Ce		d	2, 3, 5, 6
Bactris oligocarpa Barb. Rodr.	29		60			89		Br, Gu	E	Ce		d	1, 2, 3, 5
Bactris oligoclada Burret	2		20			22		Gu, Ve	E	Ce		d	1, 2, 3, 5
Bactris pliniana Granv. & A.J. Hend.	3		32			35		Br, Gu	E	Ce		d	2, 3, 5
Bactris ptariana Steyerm.	2		11			13		Gu, Ve	E	Ce		d	2, 3, 5
Bactris rhaphidacantha Wess. Boer	2		34			36		Br, Gu	E	Ce		d	1, 2, 3, 5
Bactris riparia Mart.	54	1			1	56		Br, Co, Ec, Pe, Bo	W	Ce		d	2, 3, 5, 6
Bactris schultesii (L.H. Bailey) Glassman	156	2				158		Co, Ec, Pe	W	Ce		d	2, 3, 5, 6
Bactris setiflora Burret	3	3				6	Ec	Ec	W	Ce	EN	d	2, 3, 5, 6
Bactris simplicifrons Mart.					2	2		Br, Co, Ec, Pe, Bo, Gu, Ve	A	Ce		d	1, 2, 3, 5, 6
Bactris sphaerocarpa Trail	44		1			45		Br, Co, Pe	W	Ce		d	2, 3, 5, 6
Bactris syagroides Barb. Rodr. & Trail	13					13		Br	C	Ce		d	2, 3, 5
Bactris tefensis A.J. Hend.	3					3		Br	C	Ce		d	2, 3, 5
Bactris tomentosa Mart.	40		3	1		44		Br, Gu	E	Ce		d	2, 3, 5
Bactris turbinocarpa Barb. Rodr.	2					2		Br, Gu	E	Ce	LC	d	2, 3, 5
Barcella odora (Trail) Drude	42					42		Br	C	So		f	2, 3, 5
Ceroxylon amazonicum Galeano	2	16				18	Ec	Ec	W	So	EN	a	2, 3, 5, 6
Chamaedorea angustisecta Burret	129	34				163		Br, Pe, Bo	W	So		d	2, 3, 5, 6
Chamaedorea fragrans (Ruiz & Pav.) Mart.	21	9				30	Pe	Pe	W	Ce		d	2, 3, 5, 6
Chamaedorea pauciflora Mart.	523	53	1			577		Br, Co, Ec, Pe, Bo	W	So		d	1, 2, 3, 5, 6

Chelyocarpus chuco (Mart.) H.E. Moore	22					22		Br, Bo	W	Ce		d	1, 2, 3, 5, 6
Chelyocarpus repens F. Kahn & K. Mejía	24					24		Co, Pe	W	P		d	1, 2, 3, 5, 6
Chelyocarpus ulei Dammer	107					107		Br, Co, Ec, Pe	W	So		d	2, 3, 5, 6
Desmoncus giganteus A.J. Hend.	144		2			146		Br, Co, Ec, Pe, Bo	W	Ce		g	2, 3, 5, 6
Desmoncus interjectus A.J. Hend.	1					1	Co	Co	W	Ce		g	2, 3, 6
Desmoncus latisectus Burret	7	1				8	Bo	Bo	W	Ce		g	2, 3, 6
Desmoncus loretanus A.J. Hend.	8					8	Pe	Pe	W	Ce		g	2, 3, 6
Desmoncus madrensis A.J. Hend.	12					12	Pe	Pe	W	Ce		g	2, 3, 6
Desmoncus mitis Mart.	534	5	10			549		Br, Co, Ec, Pe, Bo, Ve	C, E	Ce		g	1, 2, 3, 5, 6
Desmoncus parvulus L.H. Bailey	5		7	2		14		Br, Co, Ec, Pe, Bo, Ve	W	Ce		g	2, 3, 5, 6
Desmoncus phoenicocarpus Barb. Rodr.	10		8			18		Br, Bo, Gu, Ve	C, E	Ce		g	2, 3, 5
Desmoncus pumilus Trail	4					4		Co	W	Ce		g	2, 3, 6
Desmoncus vacivus L.H. Bailey	47					47		Co, Pe	W	Ce		g	2, 3, 6
Dictyocaryum fuscum (H. Karst.) H. Wendl.			5			5		Ve	NE	So		a	2, 3, 5
Dictyocaryum lamarckianum (Mart.) H. Wendl.	4	74				78		Co, Ec, Pe, Bo	W	So		a	1, 2, 3, 5, 6
Dictyocaryum ptarianum (Steyerm.) H.E. Moore & Steyerm.	14		3			17		Co, Pe, Gu, Ve	C, E	Ce		a	2, 3, 5, 6
Euterpe catinga Wallace	129	8	55			192		Br, Co, Ec, Pe, Gu, Ve	C, W	Ce		c	1, 2, 3, 5, 6
Euterpe longibracteata Barb. Rodr.	9		1			10		Br, Gu, Ve	E	Ce		c	2, 3, 5
Euterpe oleracea	22		21	4	1	48		Br, Co, Ec, Bo, Gu, Ve	E, NE, N	Ce		a	2, 3, 5, 6
Euterpe precatoria	692	79	88			859		Br, Co, Ec, Pe, Bo, Gu, Ve	A	So		a	2, 3, 5, 6
Geonoma appuniana Spruce	13	1	11			25		Br, Gu, Ve	E	Ce		d	2, 3, 5
Geonoma aspidiifolia Spruce	29		8			37		Br	C	Ce		d	2, 3, 5
Geonoma atrovirens Borchs. & Balslev	37					37		Co, Ec, Pe	W	So		f	2, 3, 5, 6
Geonoma baculifera (Poit.) Kunth	73	3	126	4		206		Br, Co, Gu, Ve	C, E	Ce	LC	d	1, 2, 3, 5, 6
Geonoma brongniartii Mart.	377	20	3			400		Br, Co, Ec, Pe, Bo	W	Ce		d	1, 2, 3, 5, 6
Geonoma camana Trail	215	1				216		Br, Co, Ec, Pe	W	So		d	1, 2, 3, 5, 6
Geonoma euspatha Burret	19	11	16			46		Br, Co, Ec, Pe, Bo, Gu, Ve	A	Ce		d	2, 3, 5, 6
Geonoma fosteri A.J. Hend.	2	2				4		Co, Ec	W	Ce		d	2, 3, 6

Geonoma laxiflora Mart.	89	1	1			91		Br, Co, Ec, Pe, Bo	C, W	Ce		d	1, 2, 3, 5, 6
Geonoma leptospadix Trail	113	9	12	1		135		Br, Co, Ec, Pe, Bo, Gu, Ve	A	Ce		d	1, 2, 3, 5, 6
Geonoma longipedunculata Burret	34	6				40		Co, Ec, Pe	W	P		d	2, 3, 5, 6
Geonoma macrostachys Mart.	1097	42	66	1		1206		Br, Co, Ec, Pe, Bo, Gu, Ve	A	Ce		f	1, 2, 3, 5, 6
Geonoma multisecta (Burret) Burret	17	1				18		Co, Ec	W	So		d	2, 3, 5, 6
Geonoma occidentalis (A.J. Hend.) A.J. Hend.	17	2				19		Br, Pe, Bo	W	Ce		d	2, 3, 5, 6
Geonoma oldemanii Granv.	3		36			39		Br, Gu	E	Ce		d	1, 2, 3, 5
Geonoma oligoclona Trail	25					25		Br, Co, Ve	W	Ce		d	2, 3, 5, 6
Geonoma orbignyana Mart.	7	118	1			126		Co, Ec, Pe, Bo	W	Ce		d	2, 3, 5, 6
Geonoma poeppigiana Mart.	158	7				165		Br, Co, Ec, Pe	W	So		d	1, 2, 3, 5, 6
Geonoma poiteauana Kunth	6		9	1		16		Co	E	Ce		d	1, 2, 3, 6
Geonoma schizocarpa A.J. Hend.	7	1				8	Pe	Pe	W	Ce		d	2, 3, 6
Geonoma supracostata Svenning	35	1				36		Ec, Pe	W	So		d	2, 3, 5, 6
Geonoma triglochin Burret	38	13	11			62		Co, Ec, Pe, Bo	W	Ce		d	2, 3, 5, 6
Geonoma umbraculiformis Wess. Boer	2		16	1		19		Br, Gu	E	So		d	2, 3, 5
Iriartella setigera (Mart.) H. Wendl.	411	3	203			617		Br, Co, Gu, Ve	C, W	Ce		d	1, 2, 3, 5, 6
Iriartella stenocarpa Burret	205	4				209		Br, Co, Ec, Pe, Bo	W	Ce		d	1, 2, 3, 5, 6
Itaya amicorum H.E. Moore	44		1			45		Br, Co, Pe	W	So	LC	d	1, 2, 3, 5, 6
Leopoldinia piassaba Wallace	18		14			32		Br, Co, Ve	W	So		d	2, 3, 5, 6
Leopoldinia pulchra Mart.	100		60			160		Br, Co, Ve	W	Ce		d	2, 3, 5, 6
Lepidocaryum tenue Mart.	583	1	5	1		590		Br, Co, Pe, Gu, Ve	N	Ce		d	1, 2, 3, 5, 6
Manicaria martiana Burret	12					12		Co	N	Ce		b	1, 2, 3, 6
Mauritia carana Wallace	40		9			49		Br, Co, Pe, Ve	C, W	So	LC	a	1, 2, 3, 5, 6
Mauritia flexuosa L. F.	205	4	24	1	11	245		Br, Co, Ec, Pe, Bo, Gu, Ve	A	So		a	1, 2, 3, 5, 6
Mauritiella aculeata (Kunth) Burret	123		24		2	149		Br, Co, Pe, Ve	A	Ce		d	1, 2, 3, 5, 6
Mauritiella armata (Mart.) Burret	101	1	15	2	27	146		Br, Co, Ec, Pe, Bo, Gu, Ve	A	Ce		c	2, 3, 5, 6
Mauritiella pumila (Wallace) Burret	3		13			16		Co	W	Ce		d	2, 3, 6
Oenocarpus bacaba Mart.	128	2	261			391		Br, Co, Gu, Ve	C, E	So		a	1, 2, 3, 5, 6

Oenocarpus balickii F. Kahn	89		3			92		Br, Co, Pe, Bo	W	So		c	2, 3, 5, 6
Oenocarpus circumtextus Mart.	12					12	Co	Co	W	So	VU	d	2, 3, 5, 6
Oenocarpus distichus Mart.	28	1		5	6	40		Br, Bo	S	So		a	1, 2, 3, 5, 6
Oenocarpus makeru R. Bernal, Galeano & A.J. Hend.	6					6	Co	Co	W	So	DD	d	2, 3, 5, 6
Oenocarpus simplex R. Bernal, Galeano & A.J. Hend.	4	1				5		Br, Co	W	Ce	DD	d	2, 3, 5, 6
Phytelephas macrocarpa Ruiz & Pav.	230	6				236		Br, Co, Pe, Bo	W	P		b	2, 3, 5, 6
Phytelephas tenuicaulis (Barfod) A.J. Hend.	128					128		Co, Ec, Pe, Bo	W	Ce		b	2, 3, 5, 6
Prestoea acuminata (Willd.) H.E. Moore	11	114				125		Co, Ec, Pe, Bo	W	Ce		c	2, 3, 5, 6
Prestoea schultzeana (Burret) H.E. Moore	162	19				181		Br, Co, Ec, Pe	W	Ce		d	2, 3, 5, 6
Prestoea tenuiramosa (Dammer) H.E. Moore	8		19			27		Br, Gu, Ve	E	Ce	NT	c	2, 3, 5
Socratea rostrata Burret	7	10				17		Co, Ec, Pe	W	So		a	2, 3, 5, 6
Socratea salazarii H.E. Moore	80	5				85		Br, Pe, Bo	W	Ce		c	1, 2, 3, 5, 6
Syagrus cardenasii Glassman	7	11			2	20	Bo	Bo	W	Ce		f	2, 3, 5, 6
Syagrus inajai (Spruce) Becc.	91		56			147		Br, Gu	C, E	So		c	1, 2, 3, 5
Syagrus loefgrenii Glassman	3					3		Br	C	So		f	2, 3, 5
Syagrus orinocensis (Spruce) Burret	17		29			46		Co, Ve	W	Ce		d	2, 3, 5, 6
Syagrus smithii (H.E. Moore) Glassman	36	2	2			40		Br, Co, Ec, Pe	W	So	LC	d	2, 3, 5, 6
Syagrus stratincola Wess. Boer			23			23		Gu	E	Ce	VU	d	1, 2, 3, 5
Syagrus yungasensis M. Moraes		3				3	Bo	Bo	W	So		d	2, 3, 5, 6
Wendlandiella gracilis Dammer	86	4				90		Br, Ec, Pe, Bo	W	Ce		d	1, 2, 3, 5, 6
Wettinia augusta Poepp. & Endl.	227	10				237		Br, Co, Pe, Bo	W	Ce		d	1, 2, 3, 5, 6
Wettinia drudei (O.F. Cook & Doyle) A.J. Hend.	88	1	3			92		Br, Co, Ec, Pe	W	Ce	LC	d	2, 3, 5, 6
Wettinia longipetala A.H. Gentry		8				8		Ec, Pe	W	So	VU	d	2, 3, 5, 6
Wettinia maynensis Spruce	101	34				135		Co, Ec, Pe	W	So		c	1, 2, 3, 5, 6
Records	**13726**	**887**	**2554**	**56**	**87**	**17310**							
Species	**167**	**71**	**91**	**21**	**17**	**177**							