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A review of the palm genus *Acrocomia*: Neotropical green gold

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Abstract

The genus *Acrocomia*, popularly known as macaw palm or *macaúba*, occurs in savanna areas and open forests of tropical America, with distribution from Central to southern South America. They are important oleaginous palm trees, due to their role in ecosystems and local economies and their potential for biofuel production and vegetable oil. Although the taxonomy of the genus is not resolved because of observed phenotypic diversity in *A. aculeata* (Jacq.) Lodd. ex Mart., there are several conflicting treatments. Some authors recognize three caulescent spp. occurring in South America: *A. aculeata*, *A. intumescens* Drude, and *A. totai* Mart, although a new one was described recently—*Acrocomia corumbaensis*. Because some Latin American governments want to expand production of macaw palm in their territory as raw material for agro-energy, several groups have been encouraged to study this genus, focusing on the production of biodiesel, seed germination, phenotypic aspects, and genetic diversity. The goal of this review is to compile key information available in the literature and herbarium data, focusing on South American populations of the genus.

Keywords Arecaceae · Fossil record · Macaw palm · Raw material · Taxonomy

Introduction

The genus *Acrocomia* Martius (1823) belongs to the family Arecaceae (the palms), subfamily Arecoideae, tribe Cocoseae, and subtribe Bactridinae (Baker and Dransfield 2016; Dransfield et al. 2005, 2008). Its name derives from the Greek "*Akros*" (highest) and "*Kome*" (hair or tuff), which is related to the crown of leaves (Dransfield et al. 2008). Studies

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of species from this genus are permeated by incongruities concerning their taxonomy. Although it is a genus of economic importance, only recently has the number of studies of its genetics and systematics increased.

The species of *Acrocomia* are spiny, with solitary stems, ranging from 30 cm (acaulescent species) to 15 m height; they bear unisexual flowers of both sexes, arranged in the same inflorescence (monoecious), and annually produce abundant fruits eaten by several species of mammals and birds that are responsible for its dispersal (Lorenzi et al. 2010). Usually, the development of fruits begins during the rainy season and is completed at the beginning of the dry season (Mota et al. 2011).

There is no consensus about the taxonomy adopted by authors. For instance, Bailey (1941) recognized 25 species; Henderson et al. (1995), two species: *A. aculeata* (Jacq.) Lodd. ex Mart. (1834) (37 synonymized names) and *A. hassleri* ((Barb. Rodr.) W. J. Hahn (1991), four synonymized names). Lorenzi et al. (2010) described six species occurring in Brazil (*A. aculeata*, *A. emensis* (Toledo) Lorenzi (2010), *A. glaucescens* Lorenzi, (2010), *A. hassleri*, *A. intumescens* Drude (1881), and *A. totai* Mart. (1844).

Regarding taxonomy, the World Checklist of Monocotyledons supported by Royal Botanic Gardens (2016), Kew (http://www.kew.org/); Palmweb (n.d.) - Palms of the World Online, an encyclopedia of palm trees on-line

(http://www.palmweb.org/), which is also supported by Royal Botanic Gardens); and the eMonocot portal (http://e-monocot.org/) recognize eight distinct species in *Acrocomia*: *A. aculeata A. crispa* (Kunth) C. F. Baker ex Becc. (1912), *A. emensis*, *A. glaucescens*, *A. hassleri*, *A. intumescens*, *A. media* O. F. Cook, (1901), and *A. totai*. Although the taxonomy has not been resolved, due to the high phenotypic diversity of *A. aculeata*, several studies have attempted classification (Table 1).

Phylogenetic studies encompassing *Acrocomia*, in which analyses included at least two representative species from the genus, found statistical support among samples, for example, *A. crispa*, *A. aculeata* (Asmussen et al. 2006; Eiserhardt et al. 2011; Gunn 2004; Meerow et al. 2015; Roncal et al. 2013), *A. intumescens* (Meerow et al. 2015), and *A. media* (Gunn 2004). There are no phylogenetic studies including the acaulescent species: *A. hassleri* and *A. emensis.*

Phylogenetic studies with divergence dates that included *Acrocomia* species are not fully congruent. Eiserhardt et al. (2011) focused on studying relationships in subtribe Bactridinae and showed that *Acrocomia* and *Astrocaryum* do not have a phylogenetic relationship; however, the phylogenetic tree included *Astrocaryum* as a sister group of *Bactris*, and *Acrocomia* in a clade with *Desmoncus*. Roncal et al. (2013) found the same results, but this study focused on the genus *Astrocaryum* and some species of Cocoseae and Reinhardtieae tribes as outgroups. Meerow et al. (2015) included all genera of the tribe Cocoseae and found a branch average age of 33.4 million years for *Acrocomia*, as well as weak support for a relationship between *Acrocomia* and *Astrocaryum*. The choice of species and nuclear markers used by Eiserhardt et al. (2011) and Roncal et al. (2013) may explain the similarity between the observed results. However, as Meerow et al. (2015) included representatives of all genera of the Cocoseae in their ingroup, with *Roystonea* as outgroup, they found different results. A simple comparison between the three studies does not solve the issue due to differences in methodology.

Acrocomia species from South America are characterized by several phenotypes. Here, we aim to illustrate aspects from the literature discussing descriptive characters, and both convergence and divergence between *Acrocomia* species. Due to the few studies with certain species, i.e., *A. crispa* (Vianna et al. 2017c), *A. glaucescens* (Lorenzi et al. 2010; Vianna et al. 2017c), *A. hassleri* (Vianna et al. 2017c; Lorenzi et al. 2010), *A. emensis* (Amadeu et al. 2016; Vianna et al. 2017c; Lorenzi et al. 2010; Neiva et al. 2016)—previously *Acanthococos emensis* Toledo—, *A. media*, and the newly described *A. corumbaensis* (Vianna 2017a), in the following sections, we present specific data from the literature for *A. aculeata*, *A. intumescens*, and *A. totai*. We structured this review into paleontological, botanical, ecological, and genetic aspects. The survey is useful as an aggregate source organized into a single document for discussion and support for further taxonomic, ecological, biogeographic, and genetic studies.

Occurrence and characterization of *Acrocomia* spp. distribution

Acrocomia species occur in savannah areas and open forests of tropical America, distributed from Central to southern South America (Dransfield et al. 2008). This wide distribution indicates their adaptability to different soil and climatic conditions. However, according to (Motoike et al. 2013), the natural occurrence is associated with eutrophic soils (high fertility) with an average of pH 5.5 and with medium to clayey texture. Its distribution does not include Ecuador and Peru (Wandeck and Justo 1982), although it extends from the south of Mexico and the Caribbean (Belén-Camacho et al. 2005) to

Table 1 Studies available in the literature with several slices of evidence provided to explain *Acrocomia* diversity

Description	References
Proposition for classification of *A. aculeata* into three subspecies: *A. aculeata* ssp. *sclerocarpa*, *A. aculeata* ssp. *totai*, and *A. aculeata* ssp. *intumescens*; in some geographic regions (i.e., Maranhão, Brazil), it is possible to find all three subspecies	Pimentel et al. (2011)
Recognition of the existence of differences between the *Acrocomia* palm trees in Cerrado and Pantanal	Ciconini et al. (2013); Scariot et al. (1995)
Based on the distribution pattern and shared alleles, it showed the formation of different genetic clusters among populations located in the distribution area of *A. totai* and *A. aculeata*	Abreu et al. (2012); Lanes et al. (2015)
Recognition of at least three populations of macaw palm with distinct morphological traits	Motoike et al. (2013)
Suggested the idea of a process of specialization and speciation in progress	Lanes et al. (2015)
Recognition of ecotypes for the species representing the Pantanal (*A. totai*), the Cerrado (*A. aculeata* or *A. sclerocarpa*), and Caatinga (*A. intumescens*)	Machado et al. (2015); Pires et al. (2013)
Based on anatomy, differences (organization of their tissues, size, and structures of leaflets) were verified for *A. aculeata*, *A. crispa*, *A. emensis*, *A. glaucescens*, *A. hassleri*, *A. intumescens*, and *A. totai*	Vianna et al. (2017c)
In spite of the differences among *A. aculeata*, *A. intumescens*, and *A. totai*, micromorphological analysis of the mesocarp did not distinguish the three species	Vianna et al. (2017b)

northern Argentina and Paraguay, with the most abundant concentrations in Central America, Paraguay, and Brazil (Wandeck and Justo 1982).

In order to characterize the geographical occurrence of *Acrocomia* spp., we surveyed records in the literature and the following databases: "Lista de Espécies da Flora do Brasil" (http://floradobrasil.jbrj.gov.br/), "Flora Integrada da Região Centro-Oeste – Florescer" (http://www.florescer.unb.br/), "Global Biodiversity Information Facility – GBIF" (http://www.gbif.org/), speciesLink Network (http://splink.cria.org.br/), and "Herbário Virtual da Flora e dos Fungos – INCT" (http://inct.florabrasil.net/) (Fig. 1). Synonymized species were ignored to the extent possible, in order to avoid overlaps and duplicates.

These data showed 298 records of geographic occurrence with 213 points distributed in Brazil, almost 70% of the total. In this country, this is the palm genus with the largest distribution and a major number of records in the Cerrado biome. It has not been found in the southern region (Mota et al. 2011), nor in the central region of the Amazon biome. Mota et al. (2011) reported that the natural occurrence is restricted to altitudes ranging from 150 to 1000 m, temperatures from 15 to 35 °C, and rainfall from 1000 to 1900 mm. Areas with higher precipitation are less favorable.

According to the Köppen classification, available from the Brazilian Institute of Geography and Statistics (IBGE 2004),

by contrasting occurrence record (298) with climate characterization, most (186–62.4%) occur in Aw climate, characterized by tropical savanna or tropical wet and dry forest, with a summer rainy season (November to April) and a dry winter (May to October).

Acrocomia spp.: fossil record, humans, and biological anachronism

The Neotropical palm species with the greatest representation in archeological sites are *Acrocomia aculeata*, *Attalea butyracea*, *Bactris gasipaes*, *Elaeis oleifera*, and *Oenocarpus bataua* (Morcote-Ríos and Bernal 2001). Among them, *Acrocomia* has the most abundant record (Fig. 2). It is believed that utilization of *Acrocomia* fruits began approximately 10,000 years before the present (BP) (Behling et al. 1998).

The center of origin, diversity, and dispersion of *Acrocomia* is unclear. Weathering processes such as fire in forests and storms that uprooted large trees may have opened canopy forests and provided habitat for fast-growing species—such as *Acrocomia*—thus facilitating the possibility of establishment and seed production before being eliminated from the habitat by other dominant forest elements (Lentz 1990).
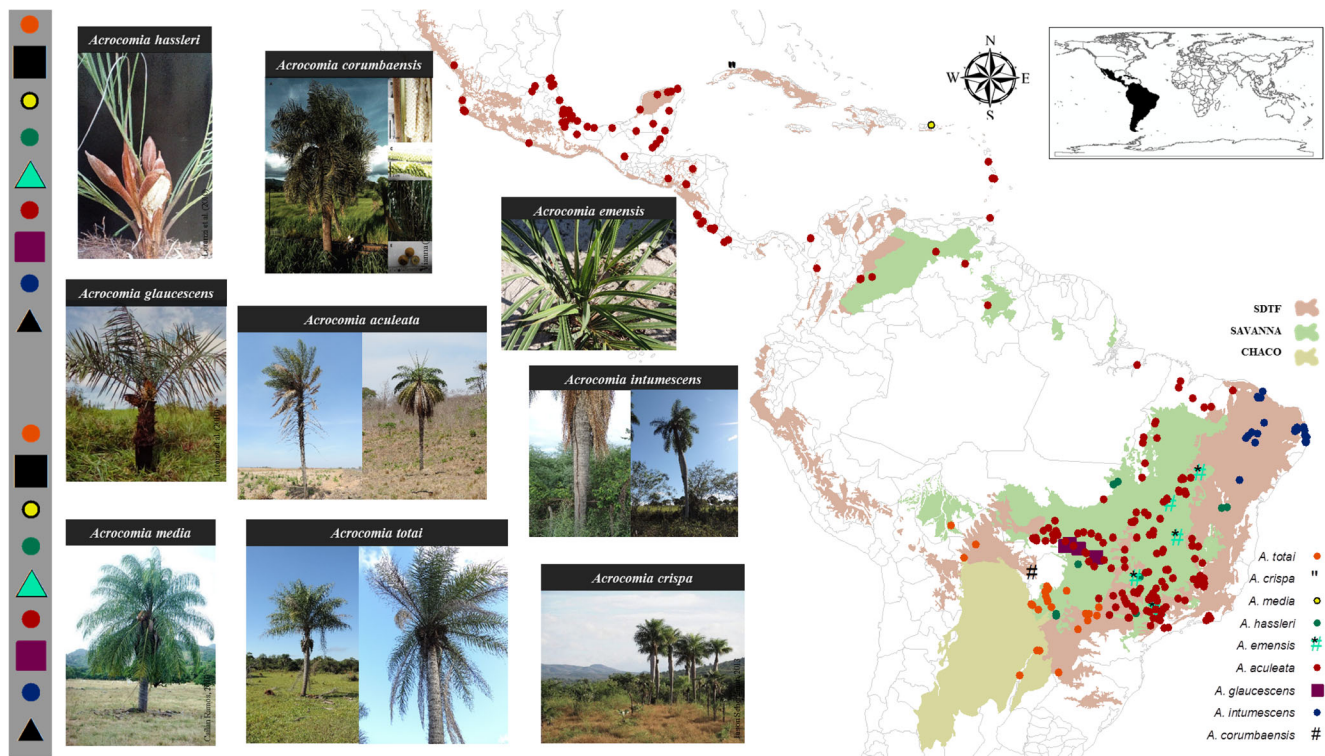
Fig. 1 Distribution of occurrence records of *Acrocomia* species from Central America to southern South America throughout the Neotropical region. STDF seasonally tropical dry forest. Image sources: *A. crispa* (Schoneman 2013), *A. corumbaensis* (Vianna 2017), *A. hassleri* and *A. glaucescens* (Lorenzi et al. 2010), and *A. media* (Ramos 2010)
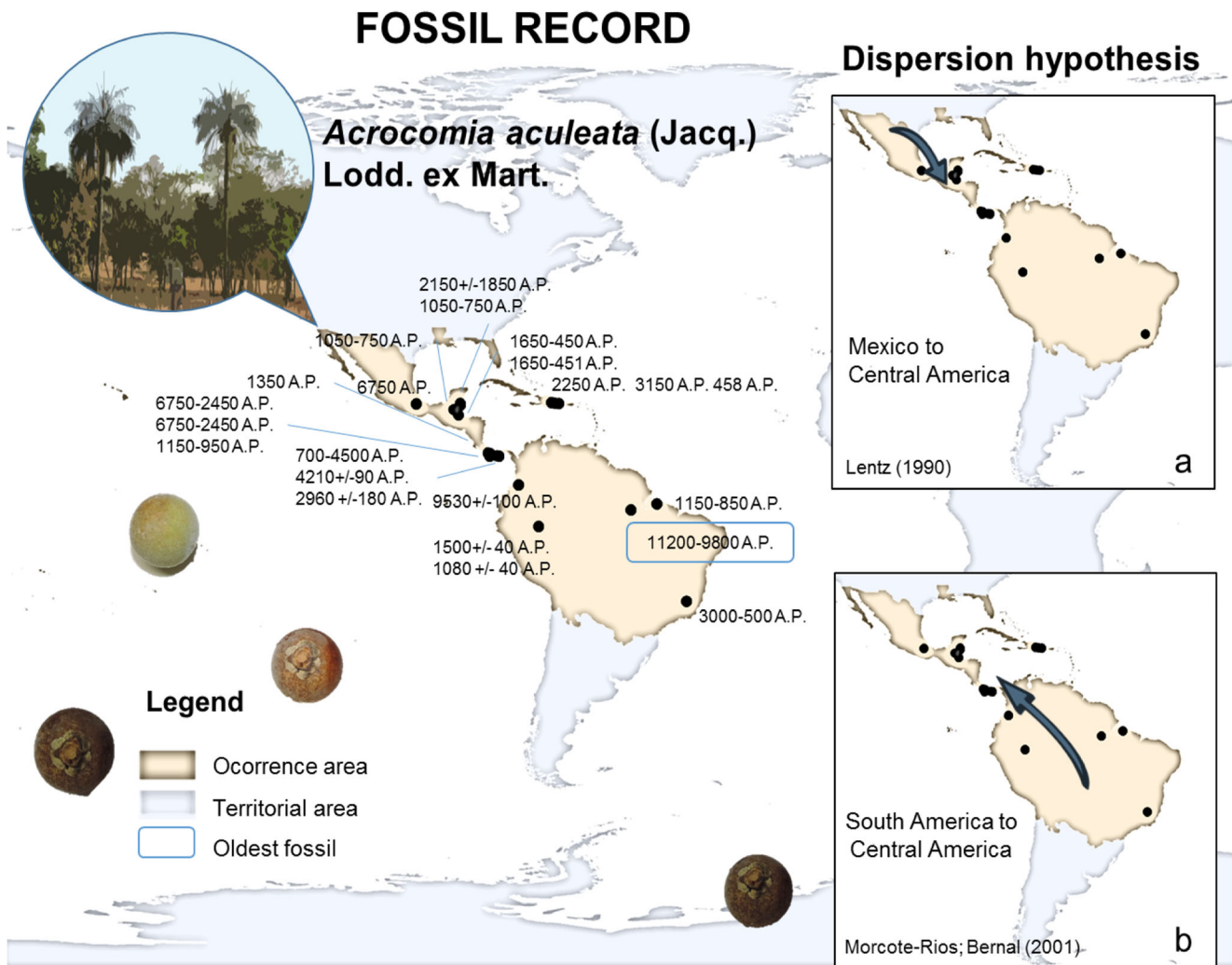
Fig. 2 Fossil record occurrence summarized from literature for *Acrocomia* with their ages BP. Hypothesis (a) dispersion of *Acrocomia* species by Mayans had started in Mexico toward Central America (Lentz 1990). (b) South America dispersion of fruits toward Central America (Morcote-Rios and Bernal 2001). The date highlighted in the rectangle refers to the oldest known record. References: 9530+/−100 (Gneeco and Mora 1997); 8040+/−390 (Cooke 1992); 7000–4500 (Cooke and Ranere 1992); 6750–2450 (Ranere 1980; Smith 1980); 6750 (Lentz 1990; Smith 1965); 4210+/−90; 2960+/−180 (Cooke and Ranere 1992); 3150 (Vega 1995); 2920+/−180 (Cooke and Ranere 1992); 2250 (Vega 1995); 2150 +/−1850 (Crane 1986; Lentz 1990); 1650–450 (Mckillop 1996); 1150–850 (Roosevelt 1991; 1999); 1500+/−40 (Morcote 1998); 1080+/−40 (Morcote 1998); 1350 (Ranere 1980; Smith 1980); 1150–950 (Ranere 1980; Smith 1980); 1050–750 (Lentz 1990; Turner and Miksicek 1984); 1050–750 (Caldwell 1980 apud Morcote-Rios and Bernal 2001); 458 (Vega 1995); 1550–885 (Roosevelt 1992; 1999 apud Morcote-Rios and Bernal 2001); 11,200–9800 (Roosevelt 1999); 3000–500 (Raczka 2009)

The genus easily develops in disturbed areas and is favored by fire; this may have contributed to their wide distribution by human dispersion. Lentz (1990) suggests that Mayans could have dispersed *A. aculeata* (reported as *A. mexicana*) from Mexico to Central America. However, due to the low frequency of *Acrocomia* in Panama forests, another point of view suggests that this palm crossed the land bridge as an introduced species already domesticated (Piperno and Pearsall 1998).

This land bridge in Central America, known as the Isthmus of Panama, is reported as a passage for movement of animals and humans between South and North America. By at least 11,000 BP, some pre-Columbian residents arrived in the Isthmus region and immediately altered the vegetation (Morcote-Rios and Bernal 2001). Crops for subsistence, between 9000 and 7000 BP could also be considered responsible for changes in the ecosystem (Cooke 2005).

After the first human migrations at the end of Pleistocene, contact was established between native people who lived in the Isthmus and others from continental areas where civilizations were more developed. According to known archeological sites, the time of this contact was around 1400 BP and is supported by the transfer of plantation crops, technology, and products (Richard Cooke 2005; Lentz 1990).

Based on dates of fossil records, Morcote-Rios and Bernal (2001) suggested that *A. aculeata* was dispersed by humans

from South to Central America, since the oldest fossil was described in Santarém, PA, in the north of Brazil (11,200 BP) followed by Panama (8040 BP) and Mexico (6750 BP). According to these authors, although there are more recent sites in the intervening areas, this decline in the age of the oldest dates suggests a northward migration accompanied by utilization of this species from South America. They suggested the dispersal process of *Acrocomia* was due to the abundant mesocarp that could be consumed directly, the good protection offered by the epicarp which could be removed easily, and the absence of quick fermentation, which could allow for consumption over a period of several weeks.

The dispersal hypothesis of *Acrocomia* from South America through Central America is also supported by the greater diversity of the genus in South America (Morcote-Rios and Bernal 2001), with Brazil being its possible center of origin as suggested by the high phenotypic diversity of the genus in that country (Pimentel et al. 2011).

In fact, the wide geographical distribution of *Acrocomia* may be in part a result of Amerindian utilization. Likewise, studies indicate that large mammals (> 1000 kg) during the Pleistocene, i.e., giant sloths, native horses, and *Gomphotheres* (elephants), ate and dispersed the fruits (Guimaraes et al. 2008; Janzen and Martin 1982). The megafauna used to live in open areas during the Pleistocene or at the end of Neogene when rainforests were reduced to small patches and dry forests occupied extensive areas. Climate change—resulting in forest area retraction—and human hunting are suspected as responsible for the mass extinction of the megafauna due to a reduction of its population sizes (Leiner et al. 2009).

The interaction between plants and frugivores can influence evolutionary processes on traits that affect demography, regeneration, and patterns of gene flow. Anachronism is a result of interaction between frugivores and plants, involving traits not related to the current fauna. Biological anachronisms differ from current dispersal systems that act on features already formed or molded (Guimaraes et al. 2008; Janzen and Martin 1982).

In terms of anachronisms on seed dispersal systems, the functional role of fruit traits in present interactions is probably substituted to some degree by abiotic factors such as water, gravity, wind, and secondary dispersers. Secondary dispersers of small and medium sizes, such as rodents, tapirs, and primates, were likely critical for persistence of *Acrocomia* when their original dispersers were extirpated (Guimaraes et al. 2008; Leiner et al. 2009).

The interaction with humans has been essential for the persistence of anachronistic species distributed over large geographic areas (Guimaraes et al. 2008). In all cases, profound changes in the pattern of seed dispersion are likely to have occurred. Although the contemporary system of seed dispersal generates a minimum recruitment of plants, there is a

reduction in the number of seeds dispersed and the distance of dispersion (Leiner et al. 2009).

If in the past, megafauna consumed and dispersed *Acrocomia* fruits, nowadays, cattle have a similar ecological role (Scariot 1998). Cattle consume the fruits and they are partly responsible for its wide current distribution (Lentz 1990). It is likely that when the herds are moving over the roads, in pasture areas between farms, they act as the greatest contemporary dispersers of seeds.

Among domestic animals, only adult cattle have an important role in dispersal, eating and dispersing seeds by regurgitation. The potential dispersion by horses, pigs, and young cattle can be disregarded because these animals remove the pulp of the fruit; however, they do not eat seeds, and under these conditions, fruits attract little or no attention from potential dispersers (Scariot 1998).

Acrocomia aculeata

The first classification of *Acrocomia aculeata* was made by Jacquin (Jacq.) in 1763 as *Cocos aculeatus* Jacq. It was included in the genus *Acrocomia* by Martius (Mart.) in 1824 and the scientific name transferred to *A. sclerocarpa*. In 1845, Loddiges (Lodd.) synonymized *C. aculeatus* and *A. sclerocarpa* under *A. aculeata*. In the scientific community, there is no consensus regarding its taxonomic determination and, therefore, many species are treated as synonymous (see Supplementary Material—Table S1).

The species is popularly known as macaw palm, due to its importance as a food source for the genus *Anodorhynchus* Spix (1824). In the Neotropics, it is known by several names such as the following: *amolado*, *amolada*, *bocaíuva*, *chonta*, *corozo*, *chiclete-de-baiano*, *coco-de-catarro*, *coco-de-espinho*, *coco-baboso*, *coco-xodó*, *imbocaia*, *jabara*, *korondía*, *macaúba*, *macaúva*, *macaíba*, *macacauba*, *macajuba*, *macaibeira*, *macajá*, *marcová*, *mucajá*, *mucaia*, *macaiá*, *palma de corozo*, *tamaco*, and *tamaca* (Smith 2015; Lorenzi et al. 2010; Galeano and Bernal 2010; Almeida et al. 1998). Indigenous names are *shakána*, *ñala*, *yawalaboto*, *maka-djiup*, *roi*, *roy rak*, and *pinawa* (Galeano and Bernal 2010; Smith 2015).

It has a wide distribution in the Neotropics, ranging from Caribbean islands and southern Mexico to Argentina (Dransfield et al. 2008). However, this and other descriptions of geographic distribution (Almeida et al. 1998; Henderson et al. 1995; Scariot et al. 1995) reflect the taxonomic disarray within the genus, since there is no consensus on the number of species, generating a bias in occurrence data. Vianna and Colombo (2013) conducted a survey on the geographical distribution of *A. aculeata*; however, for their database summary, they considered 29 species as synonyms, including *A. media*, which is recognized as a distinct species by the organizations cited in this work.

In Brazil, it occurs naturally in the following states: Bahia, Goiás, Mato Grosso, Mato Grosso do Sul, Maranhão, Minas Gerais, Piauí, Rio de Janeiro, São Paulo, and Tocantins. It is distributed in scattered areas of the Cerrado landscape such as *cerradões* and semi-deciduous forests (Almeida et al. 1998; Lorenzi et al. 2010).

Species studies are few, leaving doubts about its taxonomic classification. However, there are indications of high genetic diversity (Lanes et al. 2015; Oliveira et al. 2012) and natural populations with large phenotypic variability (Pires et al. 2013).

It is a diploid species (2n = 30), as described by (Röser et al. 1997), using microdensitometric of nuclei, and also by Abreu (Abreu et al. 2011), who detailed the karyotype with morphological characterization and determined the genome size as 2C = 5.81 pg, with base composition of AT = 58.3% and CG = 41.7%.

These palms are monoecious, with a mixed reproductive system, as verified in field experimentation (Scariot et al. 1995; Scariot et al. 1991) and by studies with microsatellite molecular markers (Abreu et al. 2012; Lanes et al. 2016). Flowering occurs between August and November and may extend until December. Usually, fruiting overlaps with this event and fruit drop occurs between June and March, with a peak in November (Scariot et al. 1995; Scariot et al. 1991).

Flowering follows the "multiple bang" model proposed by Gentry (1974), with isolated individual flowers blooming for a long period. At the population level, it follows the "cornucopia" model with a continuous offering of flowers throughout the flowering period (Scariot et al. 1991). The association of these two strategies with a long flowering period in *A. aculeata* is beneficial in reproductive terms since it increases the potential number of individuals contributing to gene flow and it reduces selfing and decreases the risk of reproductive failure or absence of pollinators by adverse climatic conditions (Scariot et al. 1991).

The pollination of *A. aculeata* is mainly by beetles, particularly *Andranthobius* sp., *Phyllotrox tatianae* Voeks (1985) (Curculionidae), *Mystrops* sp. Erichson (1843), *M. dalmasi* Grouvelle (1902), *M. debilis* Erichson (1843) (Nitidulidae), and *Cyclocephala forsteri* Endrodi (1963) (Scarabaeidae) (Brito 2013; Scariot et al. 1991). According to Brito (2013), these beetles remain on the same inflorescence, from the moment of its opening until night. Furthermore, *Apis mellifera* Linnaeus (1758) and *Trigona spinipes* Fabricius (1793) are considered occasional pollinators because they collect pollen but rarely visit female flowers.

The second major pollinator is the wind, probably due to the palm's occurrence in open environments and in groups, coupled with their capacity of releasing a large number of pollen grains at once (Scariot et al. 1991). Xenogamy is the main reproductive system, but as the species is self-compatible, geitonogamy accounts for a significant percentage of fruit production (Brito 2013; Scariot et al. 1995; Scariot et al. 1991). There are also records of apomixis (Brito 2013).

Macaw palm has a high fruit productivity, approximately 62 kg per plant (Scariot et al. 1991) and generating over 25 tons per hectare (Motoike and Kuki 2009). Usually, there is one seed per fruit; however, sometimes two or even three seeds can be found (Scariot 1998).

In a survey for dispersers and predators of *A. aculeata* seeds (A. O. Scariot 1998), the following species were captured: *Didelphis albiventris* Lund (1840) (white-eared opossum), *Nectomys squamipes* Brants (1827) (water rat), *Cebus apela* Linnaeus (1758) (capuchin monkey), and *Turdus* sp. Linnaeus (1758). As these wild animals are small and not all of them consume the fruits, they were considered as possible dispersers. In South America, the fruits are consumed and the seeds dispersed by *Tapirus terrestris* Linnaeus (1758) (tapir) (Rumiz 2001) and *Tapirus bairdii* Gill (1865) (Mesoamerican tapir) (Cortez and Pérez 2010; Olmos 1997), but not always in areas favored for germination.

It is reported, although without a proper confirmation, that fruits are an important food source for *Mazama americana* Erxleben (1777) (red brocket deer) and *M. gouazoubira* G. Fischer (von Waldheim) (1814) (brocket deer) (Rivero et al. 2005). *Anodorhynchus hyacinthinus* Latham (1790) (hyacinth macaw) consumes the nut of the fruit (Silva 2015). Even though it does not effectively contribute to dispersal because it damages the seed, the hyacinth macaw can drop undamaged fruit as it transports them during its flight (Scariot 1998).

Some animals consume the fleshy fruit without eating the seed, such as *Artibeus jamaicensis* (bat) (Ortega and Castro-Arellano 2001), *Ara ararauna* (canindé macaw) (Santos and Ragusa-Netto 2014), *Pecari tajacu*, and *Tayassu pecari* (jawbone pecari) (Beck 2006). Wild groups of *Cebus libidinosus* (capuchin monkey) break the seeds and consume the nuts (Waga et al. 2006).

Local communities modestly commercialize products derived from this species, although they are progressively gaining greater prominence by organizing into cooperatives, among them are the following: *Central do Cerrado Produtos Ecossociais*, *Cooperativa Grande Sertão*, and *Unidade de Beneficiamento do Coco Macaúba*. Cosmetic utilization has developed on an industrial scale, e.g., by manufacture of hair products by companies such as Macaúba Brasil, Lola Cosmetics, and Biodivér.

Fruit of *A. aculeata* is emerging as promising for biodiesel production and the secondary production of charcoal used in filters for the steel industry. The interest in this species for biodiesel production is justified by its high fruit production, concentration, and quality of oil derived from pulp and nut (Evaristo et al. 2016; Lanes et al. 2016; Lopes et al. 2013; Motoike et al. 2013; Pires et al. 2013).

The palm species is still exploited in an extractive way from the wild, and the collecting of fruits is inefficient.

There are also few industries operating, which leads to low productivity of products (Pires et al. 2013). In economic terms, a wide range of applications is described in Supplementary Material—Table S2.

Acrocomia intumescens

Acrocomia intumescens is known by several common names, such as *macaúba*, *macaíba*, *bocaiúva*, *coco-baboso*, *palmeira-barriguda*, *macaúba-barriguda*, and *coco de espinho* (Lorenzi et al. 2010). Some researchers assume that *A. aculeata* and *A. intumescens* are distinct species due to the morphological characters (Vianna et al. 2017b; Vianna et al. 2017c; Lorenzi et al. 2010) (e.g., epicuticular patterns of wax deposition, different colors of epicarp and mesocarp, tumescent stem and deciduous leafs at the sheath insertion point) and the information contained in Kew Royal Botanic Gardens and Palmweb. The phylogenetic study by Meerow et al. (2015) found a node with posterior probabilities = 1 resolving *A. aculeata* and *A. intumescens* as sister species, and the association of this data with morphological traits could elucidate if they are or not different species. However, some authors do not recognize this distinction and include *A. intumescens* as a synonym of *A. aculeata* (Govaerts and Dransfield 2005; Henderson 2002; Henderson et al. 1995). Thus, it is not possible to declare *A. intumescens* as a distinct species by reviewing the literature.

In the Web of Science platform, we found six articles that included the species in question. By refining the search and using the combination "*Acrocomia aculeata*" (in the case of adopting *A. intumescens* as a synonym) and "Northeast" (northeast) and/or "Caatinga," there was no result. This highlights the lack of ethnobotanical and ecological studies for this species. For example, there were no specific studies about consumption of *A. intumescens* fruits and seeds by fauna of the Brazilian northeast.

Acrocomia intumescens is distributed in Atlantic Forest along the Brazilian northeast coast and in the scattered areas of forest extensions into the Caatinga, with records occurring in Alagoas, Pernambuco, Paraíba, Bahia, and Ceará states, and in the endemic center of the São Francisco River (Lorenzi et al. 2010). We compiled 23 points of geographical distribution of this species based on records available in *Lista de Espécies da Flora do Brasil* (http://floradobrasil.jbrj.gov.br/), Global Biodiversity Information Facility - GBIF (http://www.gbif.org/), speciesLink (http://splink.cria.org.br/), *Herbário Virtual da Flora e dos Fungos* - INCT (http://inct.florabrasil.net/), and from personal observations in field.

A set of characteristics makes *A. intumescens* promising in the industry. Specific searches for the species show that besides being rich in carotenoids, it has a high oleic acid concentration in the pulp and lauric acid in the seed, which could serve as alternative sources of fat for the food industry and cookery. Its high oleic acid concentration makes it a promising species for the biodiesel industry (Bora and Rocha 2004; Silva 2015).

The presence of fatty acids in *A. intumescens* fruit differs positively in quality and quantity from the fruits of *A. aculeata* and *A. sclerocarpa* (synonymized as *A. aculeata*) (Bora and Rocha 2004). This species satisfactorily grows even in areas with low fertility, tolerates fire, and can be cultivated in areas characterized by prolonged drought, which makes it an excellent candidate for biomass and biofuel production in semi-arid areas (Silva 2015).

Local communities employ the fruits in their diet by producing cakes and jam and consuming them directly after boiling. They take advantage of the stem for building fences and houses and leaves for manufacturing handicraft products and home roofs. They also use the species as a source of income by selling the fruits and derived products (soap, oil, cosmetics) independently or in cooperatives (Cerratinga Macaúba: espécies de vários biomas n.d.) (De Lima, personal communication).

Acrocomia totai

Acrocomia totai is popularly known as *bocaiuva*, *totai*, *bocaiuveira*, *macabira*, *mocajuba*, and, in the Guarani language, as *mbokaja* (little coconut) (Lorenzi et al. 2010; Moraes 2015).

Publications recognizing *A. totai* as a distinct species are scarce (Vianna et al. 2017c; Lorenzi et al. 2010). This palm tree prefers moist wetlands and floodplains; however, sometimes it is associated with drier areas (Lorenzi et al. 2010). Its occurrence is reported in eastern Paraguay, north of Argentina, Bolivia, in Chaco region of Paraguay-Bolivia, and in Brazil in the south of Mato Grosso do Sul and the extreme west of Paraná (Lorenzi et al. 2010; Moraes 2015; Palmweb; WCSP 2016).

Scariot (1998) does not recognize *A. totai* as a distinct species but reported that fruits found in the Pantanal region are smaller than those in Cerrado. The seeds are dispersed by *Cerdocyon thous* Linnaeus (1766) (crab-eating fox) (Scariot 1998) and *Tapirus terrestris* (tapir) (Tófoli et al. 2006) and are key for the diet of *Anodorhynchus hyacinthinus* (hyacinth macaw) (Guedes 2009; Zorzi 2009). Despite seed predation, *Ara chloropterus* Gray (1859) (red macaw), by transporting the rachilla with fruits, could disperse fruits by dropping them on soil during flight (Yamashita and Valle 1993).

The pulp and nuts are rich in lipids, fiber, protein, and minerals. Recently, a study (Machado et al. 2015) that considered the species as ecotype *totai*, compared it to *A. aculeata* (considered there as *sclerocarpa* ecotype). They found a higher concentration of nitrogen, potassium, and calcium in nuts for *A. totai*; however, mineral composition and oil derived from nuts had higher mean values for *A. aculeata*, and pulp showed a higher concentration of manganese and zinc.

In the Pantanal, pulp flour is used for preparation of ice *lolly*, ice cream, cakes, and jam, with the same utilization as described for *A. aculeata*. The associations "Maria Coelho e Pescadores Artesanais de Iscas de Miranda" and "Cooperativa Mista dos Produtores Rurais de Poconé Ltda" commercialize some derivatives of the palm tree. In Paraguay, extraction and exportation of oil from nuts are related to industrial production (Poetsch et al. 2012). For more details about the potential use in biodiesel production, see Lapuerta et al. (2014).

A brief point of view and prospects

Considering morphological traits and habitat of *Acrocomia* spp., we observe some similarities and divergence points (see Supplementary Material—Tables S3 and S4, Figs. 1 and 3). Regarding the three species here detailed, *A. aculeata* has a persistent petiole base as a structural part of the stem—although not necessarily always—which does not occur in *A. intumescens* and *A. totai* (Fig. 3). The leaf bases of the latter two can be detached easily.

There is a clear difference in geographical distribution for *A. intumescens* and *A. totai*. Although a large area separates the species, in some rare cases, their representatives share similar morphological characteristics. The intumescent stem was seen on some *A. totai* individuals at the Brazilian frontier with Paraguay, and stems without intumescence were verified in adults from João Pessoa, Paraíba Brazilian state (De Lima, personal communication).

Regarding occurrence in Brazil, *A. aculeata* has a wider distribution (Fig. 1), located mainly in the Cerrado Savannah (71.7%) and followed by Atlantic Forest and a few points in the Amazon, covering most of the Paraná, the Tocantins, and the São Francisco River basins. *Acrocomia totai* records are located in the Paraná basin and abound in Cerrado Savannah (50%). It is also present in the Atlantic Forest (33.3%) and the Pantanal (16.7%). On the other hand, *A. intumescens* is restricted to the Brazilian northeast and has a fragmented distribution, mainly in Atlantic Forest near the coast (69.6%) and in some relict patches of rainforest (known as "Brejos de altitude") surrounded by Caatinga.

Comparing the information already provided, according to phylogenetic relationships, *A. intumescens* and *A. aculeata* appear to be well supported as distinct species (Meerow et al. 2015). However, there is no published phylogenetic study including all three ecotypes or potential species.

Nevertheless, differences between *Acrocomia* palms in the Cerrado and Pantanal have been described and recognized (Ciconini et al. 2013; Lorenzi et al. 2010; Scariot et al. 1995). These studies suggest the formation of distinct genetic groups among populations of both *A. aculeata* and *A. totai* (Abreu et al. 2012; Lanes et al. 2015), although these studies

Fig. 3 An overview of *Acrocomia* species. *A. aculeata*: stem aspects with persistent leaf base remnants; *A. intumescens*: enlarged stem without persistent leaf bases; *A. totai*: smooth stem without persistent leaf bases

included few populations of *A. totai*. Some authors consider that a possible speciation process is underway (Lanes et al. 2015), others hypothesize ecotypes (i.e., Machado et al. 2015; Pires et al. 2013), and still others include *A. totai* as a synonym of *A. aculeata* (Henderson et al. 1995). The few extant studies on genetics present a close relationship between *A. aculeata* and *A. totai*, supporting *A. totai* as a synonym or an ecotype of *A. aculeata*.

The studies discussed in this review by-and-large consider only a part of the available information, indicating that the available data is not able to clarify the current taxonomic issues. For example, if *Acrocomia* populations with taxonomic conflicts were regarded as ecotypes of *A. aculeata*, would it imply that they have the same potential for biodiesel production? Certainly, more studies specific to such considerations would be required to better manage what already seems to exist. However, we bring up this kind of questioning in order to reflect about conservation strategies for the species, since there is no detailed information regarding *A. intumescens* and *A. totai*. The uncertainty, by itself, would suggest caution. Many studies considered them all to be *A. aculeata*, potentially obscuring differences in support of a point of view.

Treating *A. intumescens* as an endemic species of the Northeast could favor a new point of view directed to this Brazilian region, which is full of social and structural problems. The improvement and targeting of conservation policies in the Caatinga could extend to other species, equally important but with unknown potential. It is noteworthy to look at this region, as well as the Cerrado Savanna, since they are not considered a national patrimony by the Brazilian Federal Constitution (art. 225, § 4°).

However, conservation strategies should not focus merely on the potential use of species, supporting only their economic value. In a short time, due to the presence of cattle and human intervention, it may not be possible to find and describe the evolutionary history of these palm species. The species from the Brazilian state of Rio Grande do Sul, for example, are derived from other regions of this country, as stated by the property owners where they were found (Soares et al. 2014).

While such considerations should not be a barrier to widespread dissemination or cultivation of the palm tree, however, it is important from a scientific perspective. Assuming that in the future species, it could be collected in a place different from where they originated due to anthropogenic actions, how can accurate research be conducted? *Acrocomia* have the potential for biodiesel, nourishment, alimentation, and handicraft. In other words, it is a natural patrimony. Additionally, if it is not possible to confirm the delimitation of species, the indiscriminate utilization of ecotypes without regard to proper identification will lessen the intrinsic value of these genetic resources for those dependent upon them.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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