







## Palm species richness, latitudinal gradients, sampling effort, and deforestation in the Amazon region

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### 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 0–5°S. Species richness and the number of records were highly correlated ( $R^2=0.76$ ,  $P<0.005$ ). The highest rates of deforestation ( $>2000$  km<sup>2</sup>) were found in the southern and eastern Amazon of Brazil, which coincide with low 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, while the second included the Plateau and Gurupi. 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

## 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 (Steege *et al.* 2015), but also at very local scales (Gentry 1988; Balslev *et al.* 1998; 2011; Oliveira & Mori 1999; 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; 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

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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., Steege *et al.* 2000; 2003; 2006; Pitman *et al.* 2001; 2002; Bjorholm *et al.* 2005; 2006; 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 centers of plant diversity (those with > 5,000 species per 10,000 km<sup>2</sup>) 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*, *A. sociale*, *Bactris balanophora*, *B. tefensis*, *Geonoma aspidiifolia*, *G. oligoclona*, *Iriartella setigera*, *Oenocarpus minor*). 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 & Granville 1992). Palms occur in different habitat types (Balslev *et al.* 2015), the topography determines their distribution (Kahn & Castro 1985; Vormisto *et al.* 2004b), 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-analyses.

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; MacArthur & 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 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 and selective logging that causes extensive damage to nearby trees and soils, increase the risk of species extinction and carbon emissions. Open roads that permits unplanned development, and exploration of forest that convert them into family agriculture and pasture are main causes of deforestation (Veríssimo *et al.* 1992; 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 of 763,000 km<sup>2</sup> had been deforested up to 2013 in the Brazilian Amazon alone (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 at 2101 km<sup>2</sup>/year. Tropical rainforest ecotones 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 analysis 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

analyzed distribution in the American and in the African continents. 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

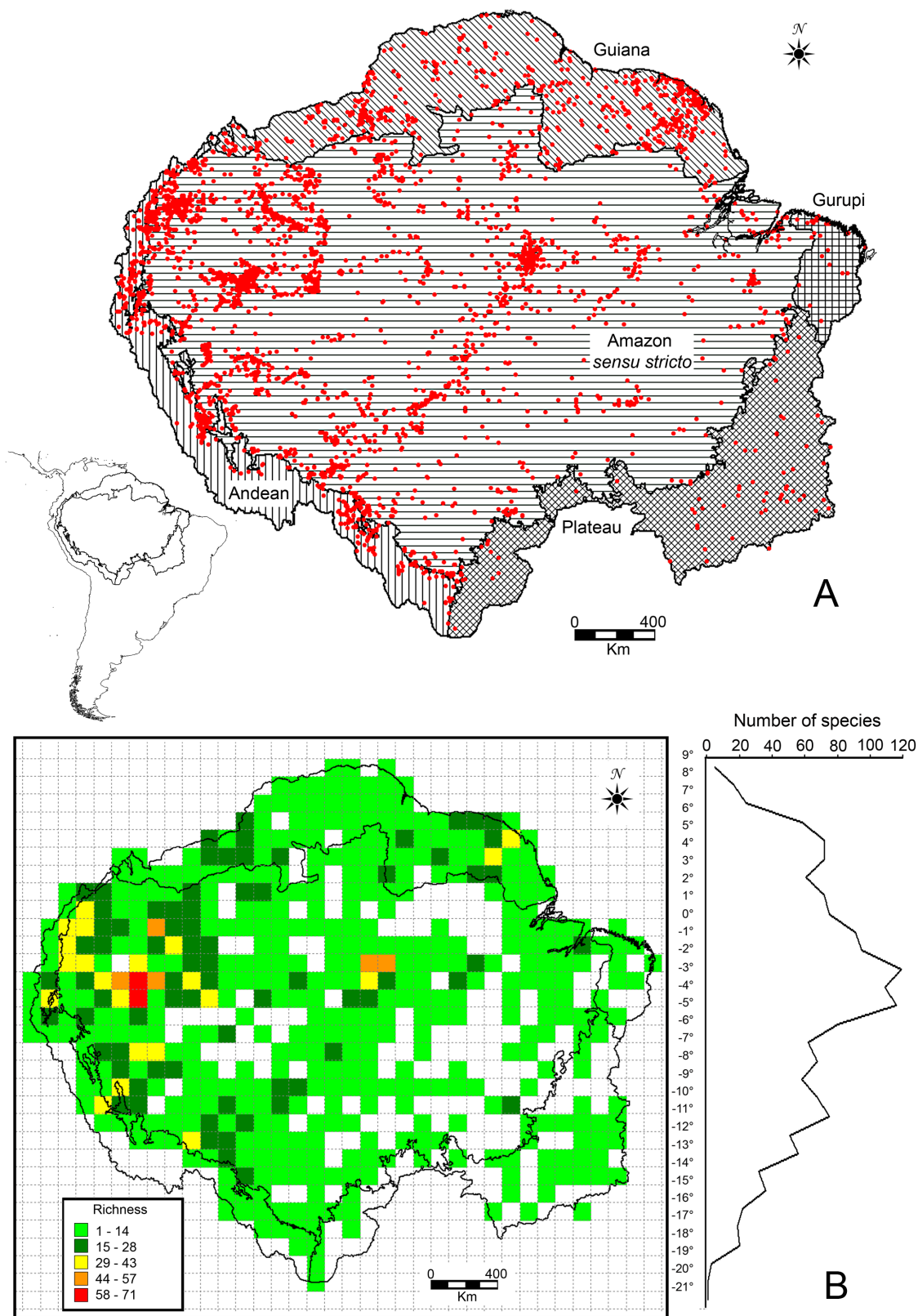
Our study area covers the entire Amazon watershed from its highest altitude spring areas in the surrounding mountain systems, to the river mouth in the extreme east (8,121,313 km<sup>2</sup>) (Eva & Huber 2005). This area can be divided into the central Amazon (Amazon *sensu stricto*) (68 %) and four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

The Amazon sub-region (*sensu stricto*) (5,569,174 km<sup>2</sup>) 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 harbors 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<sup>2</sup>) 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*, *chiriviales*, 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<sup>2</sup>) 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





**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  $1^{\circ} \times 1^{\circ}$ . Right: Species richness distribution in latitude extents (in decimal degrees) for the distributional range of 177 Amazonian palms species 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 & Huber (2005). Please see the PDF version for color reference.

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<sup>2</sup>) 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<sup>2</sup>) 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 (Kahn & 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) (Tab. S1 in supplementary material).

### Data analyzes

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 analyzes was performed using DIVA-GIS 7.5. This analyzes 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 analyzed Jaccard distance (Gotelli & Ellison 2011) in the R program version 3.3.1, that measures the similarity between two sets. This analyzes 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 analyzes 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) (Magurran 2011).

## Results

The 177 palm species represented in 17,310 records, were distributed in all regions of the Amazon (Fig. 1A). 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* (1206), *Euterpe precatoria* (859), *Iriartella setigera* (617),



*Lepidocaryum tenue* (590), *Chamaedorea pauciflora* (577), *Desmoncus mitis* (549), *Astrocaryum aculeatum* (457), *Bactris hirta* (423), *Geonoma brongniartii* (400), and *Oenocarpus bacaba* (391) (Tab. S1 in supplementary material).

The greatest richness (29–71 species) were found in the western (Brazil, 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 the 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 Department, 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 Bolivia). 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 five 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<sup>2</sup>) were found in southern and eastern Brazilian Amazon. Therefore, in this area the low richness and records gaps with the deforestation must be

related. However, areas with higher richness (> 29 species) (western Amazon) also had deforested areas but they were  $\leq 500$  km<sup>2</sup> in extension.

Cluster analyzes using Jaccard distance (Fig. 4) showed two groups with similarity between them, with cophenetic correlation 0.843. The first group was composed of the three sub-regions (Amazon *sensu stricto*, Andes and Guiana), and the other group of Gurupi and Plateau sub-region.

## Discussion

### *How is palm species richness distributed in the Amazon region?*

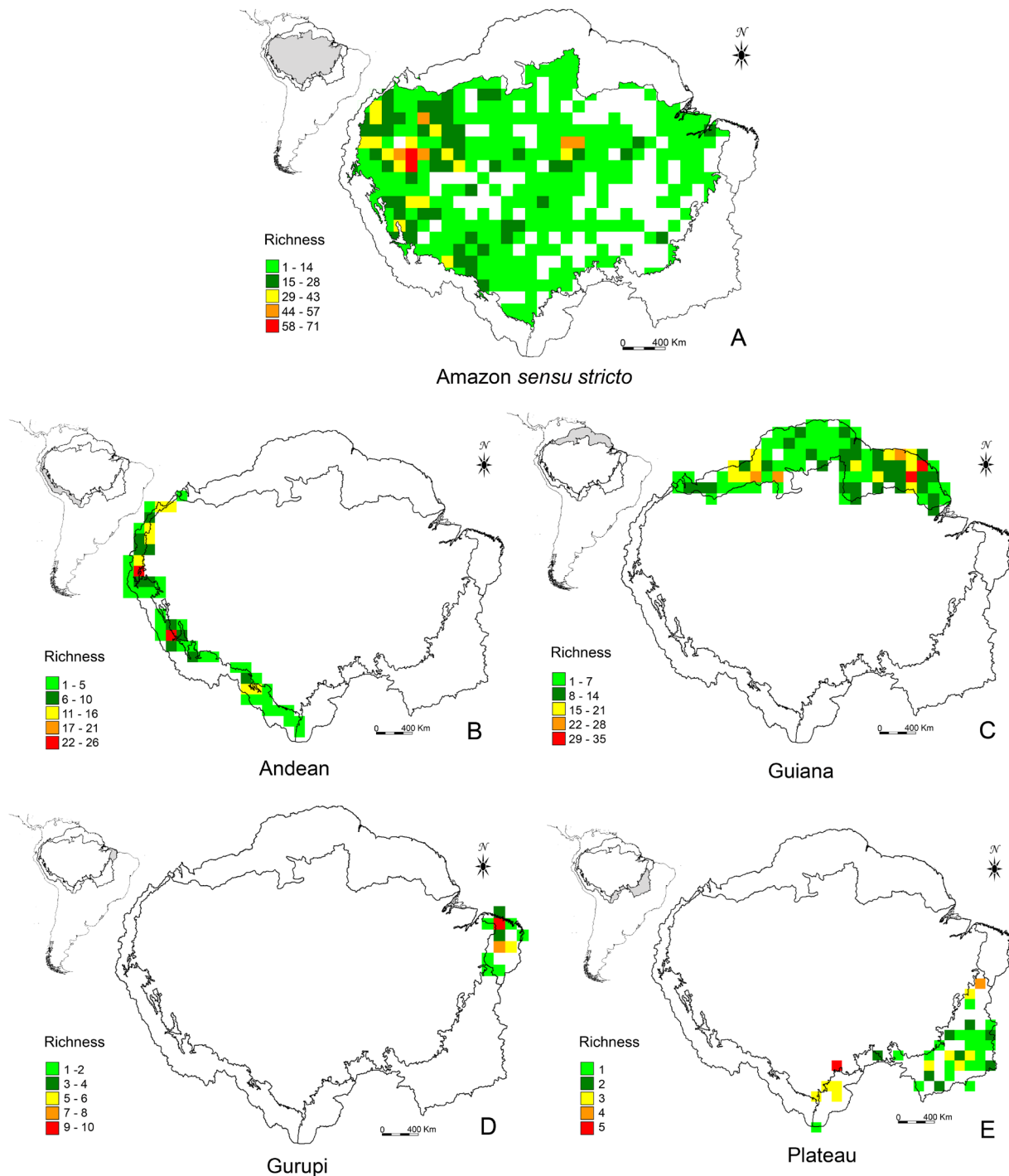
Palm diversity is notoriously high and palms are widely distributed in Neotropical forests (Cintra *et al.* 2005; Montufar & Pintaud 2006) (Fig. 1A). This distribution pattern coincides with global patterns for angiosperms (Barthlott *et al.* 1996; 2005; 2007; Francis & Currie 2003; Steege *et al.* 2006). 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, geodiverse 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 (Tab. S1 in supplementary material), those with high number of records are small palms (*e.g.*, *Geonoma macrostachys*, *Lepidocaryum tenue*, *Chamaedorea pauciflora*, *Desmoncus mitis*) 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 had 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; 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 (vapor 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*



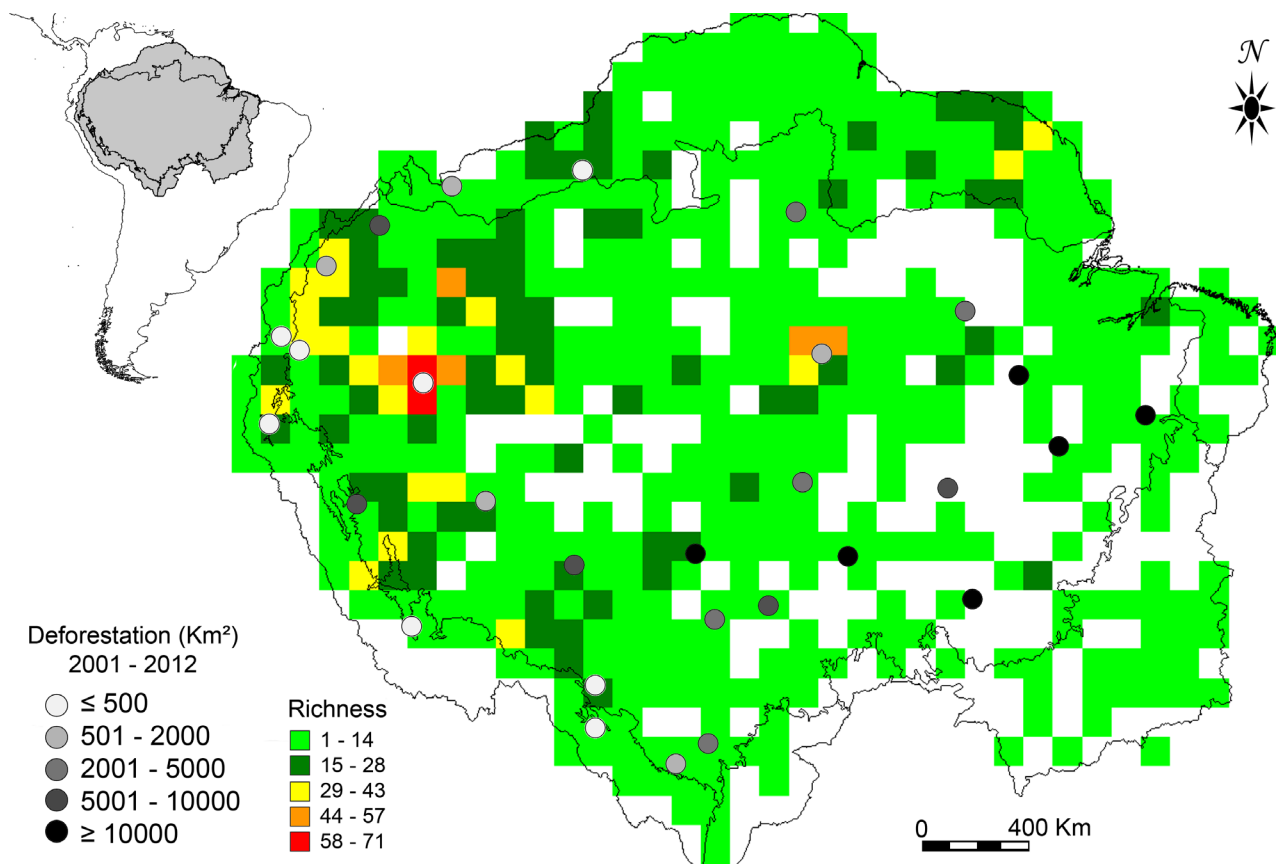


**Figure 2.** Species richness of palms in the five sub-regions of Amazon region. **A.** Amazon *sensu stricto*; **B.** Andean; **C.** Guiana; **D.** Gurupi; **E.** Plateau. Grid squares: 1° x 1°. Please see the PDF version for color reference.

*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 (Amorin 2001). Several researchers have found high palm richness in different locations in the western Amazon,

mainly in the Iquitos-Pebas region in Peru (Kahn & Mejia 1991; Vormisto 2002; Vormisto *et al.* 2004a; b), the Yasuni 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

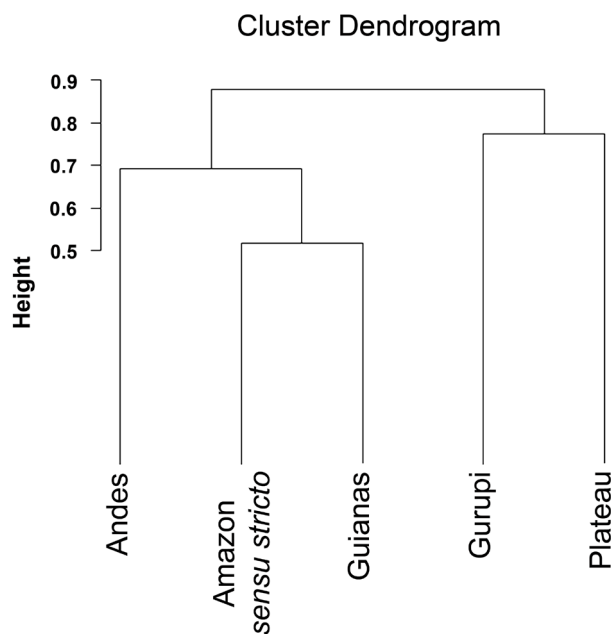




**Figure 3.** Comparison between the richness of Amazonian palms species and deforestation areas (circles) between the years 2001 and 2012. Please see the PDF version for color reference.

between the Iquitos-Pebas region (Peru) and the Yasuní region (Ecuador) can be 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 presents 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), center (Peru) and south (northern Bolivia). This pattern



**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.



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 Yanasha 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 (Steege 1998), including palms (Kahn & 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 (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 Yacapana 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 (Amorin 2001).

The relationship between species richness and latitude in palms is driven mainly by a 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  $\geq 2400$  mm,  $\geq 160$  wet days per year, and mean annual temperatures  $\geq 21$  °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 our results of the Pearson correlation coefficient analysis ( $R^2 = 0.76$ ), 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 & Peres 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<sup>2</sup>) 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 (Steege *et al.* 2015), which may also be the reason there are so few collections of 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 deforestation ( $<2000$  km<sup>2</sup>) also occur 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 (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, and lack of logistics and interest in exploring 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 analyzes 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 (Amorin 2001; Pintaud *et al.* 2008).

In conclusion, the greatest palm richness was 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 Amazonia, but in other areas with records gaps it may probably have been caused by difficult access and 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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