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Original Paper

Floristic influence of Amazonian Lowland Dense Rain Forest on the pioneer vegetation with marine influence, Restinga of Pará state, Brazil

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Abstract

The coastal region of the municipalities of Curuçá and Maracanã, on the northeastern coast of Pará, shelters a valuable biological heritage, the last two remnants of Dense Rain Forest on the shores of the Atlantic Ocean. On the Ipomonga Island (Curuçá) and at the Marieta Beach (Maracanã), the Lowland Dense Rain Forest is notable for its abrupt contact with the pioneer formation with marine influence, called as Restinga. This geomorphological interface favors floristic connectivity between different ecosystems. The research objective was to evaluate, through vegetation inventories, whether these forests remnants, about Lowland Dense Rain Forest, are sources of dispersal of woody species in Restinga. A total of 189 species were recorded in 50 botanical families with the greatest richness corresponds to the dense forest (67 species). Of this flora, 46 species (24%) were common to both vegetation typologies, with 18 species considered new occurrences in Restinga of the Amazonian coastal plains. The floristic affinities founded support the effect of Lowland Dense Rain Forest acting as the source for propagule dispersion over the pioneer formation with marine influence (Restinga), mostly dispersed by animals (zoocory).

Key words: Amazonian coast, dispersal strategies, forests remnants, marine influence.

Resumo

A região costeira dos municípios de Curuçá e Maracanã, no litoral nordeste paraense, abriga um valioso patrimônio biológico vegetal. Trata-se, a princípio, de dois últimos remanescentes de Floresta Ombrófila Densa, banhados pelo oceano Atlântico. Na ilha de Ipomonga (Curuçá), bem como na praia de Marieta (Maracanã), a Floresta Ombrófila Densa das Terras Baixas se destaca pelo contato abrupto com a formação pioneira de influência marinha, conhecida por Restinga. Essa interface geomorfológica favorece uma conectividade florística entre estes ecossistemas distintos. O objetivo foi avaliar, através de inventários da vegetação, se estes remanescentes florestais, de Floresta Ombrófila Densa das Terras Baixas, são fontes de dispersão de espécies lenhosas em Restinga. Foram registradas 189 espécies, em 50 famílias botânicas. A maior riqueza corresponde à Floresta Ombrófila Densa das Terras Baixas (168 espécies), em detrimento à Restinga (67 espécies). Desta flora, 46 espécies (24%) foram comuns às duas tipologias de vegetação, sendo 18 espécies consideradas novas ocorrências para á Restinga do litoral amazônico. As afinidades florísticas encontradas embasam o efeito da Floresta Ombrófila Densa das Terras Baixas atuando como fonte de dispersão de propágulos na formação pioneira de influência marinha (Restinga), dipersos em sua maioria por animais (zoocoria).

Palavras-chave: litoral amazônico, estratégias de dispersão, remanescentes florestais, influência marinha.

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Introduction

The recent geological origin of the coastal plains afford the absence of endemic plant species in the pioneer formation with marine influence (Restinga) given the lack of sufficient time for speciation to have occurred in them (Scarano 2002). Therefore, the species that compose the Restinga vegetation are contributions from other surrounding ecosystems (Araújo 2000; Scarano *et al*. 2001) distinguished from one another according to their respective phytogeographic regions.

In the coastal plains of southern and southeastern Brazil, the stands of Restinga vegetation are associated to the Atlantic Forest domain and they are defined in various different ways (peripheral vegetation, marginal habitat, Atlantic forest sub-group and others) depending in the context in which the association is being addressed (Scarano 2001; Scherer *et al*. 2005; Fiaschi & Pirani 2009; Scarano 2009).

In the coastlands of northeastern Brazil, the Restinga receives floristic contributions from the neighboring Caatinga/Cerrado complex and from the low coastal sedimentary plateaus due to the geographic proximity of those various ecosystems (Freire 1990; Santos-Filho *et al*. 2015). However, the strongest influence on the flora composition of those restinga is attributed to the Atlantic Forest (Freire 1990; Zickel *et al*. 2007; Sacramento *et al*. 2007; Santos Filho *et al*. 2011, 2013, 2015). The flora of these lowland vegetation in the coastal plains is characterized by high endemism (about 41% of total species) and one of the most susceptible to vanish in with the global warming (Stehmann *et al.* 2009).

Unlike the coastal regions of southern, southeastern and northeastern Brazil, on the north (Amazonian) coast, the genesis of the woody flora of the restingas is mainly propitiated by Amazonian Lowland Dense Rain Forest (Amaral *et al*. 2015; Serra *et al*. 2016; Lima & Almeida Jr 2018). However, in contrast to the exuberance of their appearance inside the dense forest stands, many of the species have adapted to the limiting environmental conditions (sandy soils, leaching, salinity) of the sandy spits of Restinga formations exhibiting more rudimentary forms and trees of smaller stature (Amaral *et al*. 2015).

The Atlantic coast of the state of Pará has a history of exploitation of the natural flora and fauna resources that dates back to the settlement of the coastal lands in a region where one of the earliest of Amazonian colonizations occurred, the northeast of the state of Pará (Bragantina). The original vegetation cover, in which dense forests prevailed, was almost entirely converted (from the beginning of the 20th century on) to a matrix mainly occupied by secondary thicket-type vegetation known as *capoeira* (Vieira *et al*. 2007; Coelho *et al*. 2018).

The coastal region of the municipalities of Curuçá and Maracanã in the northeast of Pará is the site of a valuable biological vegetable heritage (Rocha & Miranda 2012). In principle it consists of the last surviving stands of Amazonian Lowland Dense Rain Forest on the shores of the Atlantic Ocean and in this study they will be referred to as forest relics.

Based on the premise that Restinga ecosystem does not have a flora of its own (in view of the relatively recent geological formation of the coastal plains), that its species are originally from adjacent ecosystems (Araújo 2000; Scarano 2002) and that the two stretches of Restinga that are the object of this study are exceptional insofar as they are interconnected with remnants of Amazonian Lowland Dense Rain Forest, this article seeks to answer the following research questions: 1) How the floristic composition of these stretches of Restinga differ from another Restinga on the Amazon coast, due to their proximity to the remaining stands of Lowland Dense Rain Forest formations (the dispersing matrix)? 2) Are there new records and new occurrences of species in relation to the known Restinga flora for the Amazonian coast? 3) What are the flora dispersal strategies of these restingas?

Against that background, this study, by means of a vegetation inventory, seeks to assess whether the remaining stands of Lowland Dense Rain Forest are sources for the dispersal of Restinga woody species in the northeast of Pará state.

Material and Methods

The study was conducted in two stretches of the state of Pará's Atlantic coast, namely the Ipomonga Island in the municipality of Curuçá and the Marieta Beach in the municipality of Maracanã, both in the northeastern part of the state (Fig. 1). The climate is equatorial, hot and humid, with a well-defined dry season from July to December with an average rainfall during the period of 300 mm and a wet season from January to June with an average rainfall of 2,350 mm (Moraes *et al*. 2005).

Four geomorphological units compose the northeastern coast of the state of Pará (Boulhosa & Souza-Filho 2009) namely: i) a lowland plateau

with average heights of less than 50 m above sea level; ii) an alluvial plain which is found in the fluvial domain of the estuary where fluvial rather than coastal processes are predominant; iii) a tidal plain strongly influenced by estuarine processes dominated by semi-diurnal macro-tides; and iv) a coastal plain that occurs along the length of the coast mainly influenced by aeolic and wave processes.

The two types of vegetation sampled in this study are classified, according to the technical manual of the brazilian vegetation (IBGE 2012), as

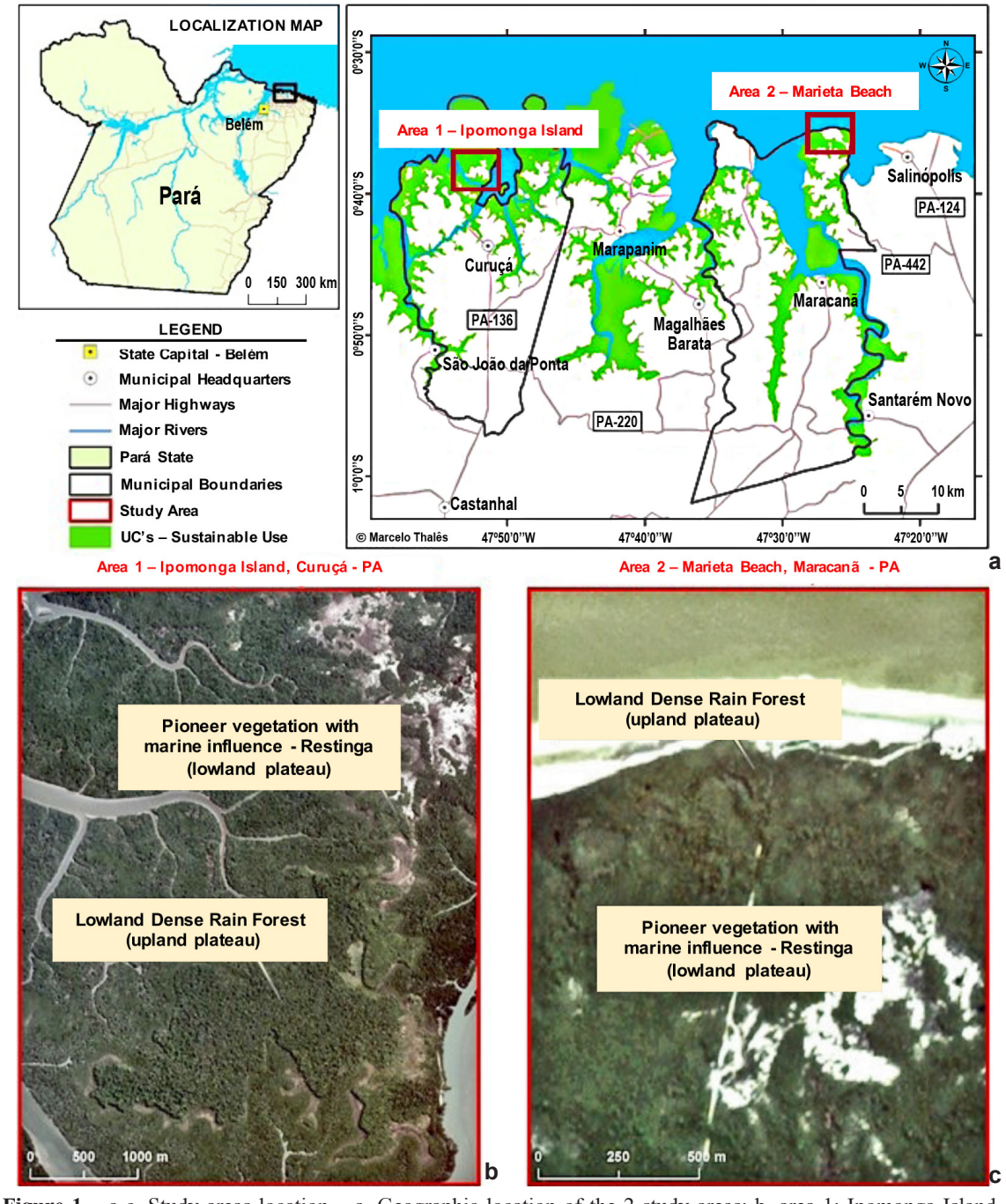

Figure 1 – a-c. Study areas location – a. Geographic location of the 2 study areas; b. area 1: Ipomonga Island, municipality of Curuçá; c. area 2: Marieta Beach, municipality of Maracanã, in the northeast of Pará state.

Restinga (pioneer formation with marine influence, representing a edaphic system of first occupation) and Lowland Dense Rain Forest (formation that in general occupies the coastal plains, covered by Pliopleistocene boards of the Barreiras Group).

The classification of the geomorphological units that support the vegetation investigated in this study, Lowland Dense Rain Forest and Restinga (pioneer formation with marine influence) is carried out specific studies in the areas of interest namely the Marieta Beach (Boulhosa & Souza-Filho 2009) and the Ipomonga Island (Rodrigues & Souza-Filho 2012).

The two study areas are located in Sector I of the Amazon Macro-tidal Mangrove Coast (*Costa de Manguezais de Macromaré da Amazônia*). The sector extends from the Marajó Bay to the Pirabas Bay and is characterized by the presence of a coastal plateau in direct contact with the shoreline where it forms cliffs supported on tertiary sediments of the Barreiras and Pirabas formations. The cliffs are subject to the action of the waves and currents of the tides (Fig. 2a). In turn, the Restinga is narrow (less than 2 km wide) and the estuarine channels extend for around 60 km (Souza-Filho 2005). At both Ipomonga Island and the Marieta Beach the Restinga is notable for its abrupt contact with the upland plateau, on the Lowland Dense Rain Forest (Boulhosa & Souza-Filho 2009; Rodrigues & Souza-Filho 2012) (Fig. 2).

The Restinga, formed by the deposition of marine and fluvial sediments are low, and relatively flat, bordering the sea (Muehe 1998). Within them are sub-environments consisting of sandy plains, mangrove swamps, cheniers, active and inactive sand dunes, tidal channels and estuarine channels all dominated by oceanographic processes (Souza-Filho 2005; Rodrigues & Souza-Filho 2012) (Fig. 2a).

The Restinga on the Ipomonga Island and at the Marieta Beach, which are the object of this study, are classified as floodable (subject to the temporary surfacing of the water table during the periods of heaviest rainfall) (Silva & Britez 2005) and they occupy the intercostal zones of the lowland plateau (Fig. 2b-c). Then intercostal zones are sandy ridges that occur in the coastal plains (remains of former beaches) formed by the action of the tide on the plain that results in progradation of the coastline in the direction of the continent as a result of sediment accumulation by wave action (Augustinus 1989; Souza-Filho & El-Robrini 1996; Mácola & El-Robrini 2004).

The two study areas are embedded in Federal Protected Areas of the Marine Extractive Reserve type (*Reserva Extrativista Marinha* - Resex). The Ipomonga Island is part of the Mãe Grande de Curuça Resex (Brasil 2002) and the Marieta Beach is attached to the Maracanã Resex (Brasil 2002) (Fig. 2c,e). The two locations have a common feature that is quite exceptional in the coastal region of Pará state, namely, the occurrence of surviving stands of Lowland Dense Rain Forest in contact with the Restinga in the lowland plateau (Fig. 2a). However, each area also has features of its own as described below.

Area 1 - Ipomonga Island

The island is situated between the mouth of the Pará river and the Curuçá bay. The forest remnants occupy 150 ha of terra firme almost entirely surrounded by mangrove and restinga vegetation on the lowland plateau (Fig. 2b-c).

The forest landscape presents a discontinuous canopy (strong luminosity) about 15 m above the ground with some emergent species like *Platonia insignis* Mart. and *Couratari guianensis* Aubl growing up to 25 meters tall, and an abundant understory of regenerating palms [*Attalea maripa* (Aubl.) Mart.] and low trees up to 5 meters tall among the big tree species typical of the exuberant Amazon forests such as *Bertholletia excelsa* Bonpl., *Couratari guianensis* Aubl., *Caryocar villosum* (Aubl.) Pers. and *Dipteryx odorata* (Aubl.) Willd (Fig. 2b).

The Restinga is segmented, forming various separated fragments of different sizes, but none greater than 1 ha, inserted in the midst of sandy strips between the sea and the mangrove forest (Fig. 2c). The fragments selected for the inventory are at a distance of about 1.2 km from the Lowland Dense Rain Forest formation.

Small statured trees predominate with an average circumference of 35 cm and height of 7 m. with absolute dominance of *Pradosia schomburgkiana* (A.DC.) Cronquist subsp. *schomburgkiana*, *Sacoglottis guianensis* Benth., *Pouteria ramiflora* (Mart.) Radlk. and *Humiria balsamifera* (Aubl.) A.St.-Hil (Fig. 2b-c).

In the open areas between fragments, herbaceous and bush species prevail such as *Chamaecrista ramosa* (Vogel) H.S.Irwin & Barneby, *Scleria cyperina* Willd. *ex* Kunth, *Axonopus purpusii* (Mez) Chase and *Xyris jupicai* Rich. The dominant species among the small-statured trees, isolated or in clumps, are *Byrsonima crassifolia*

Figure 2 – a. Remaining stands of Lowland Dense Rain Forest in contact with the coastline (seashore), Marieta Beach - Maracanã, Pará; b-c. inside Lowland Dense Rain Forest , Ipomonga Island - Curuçá, Pará; d. inside a pioneer formation with marine influence, Restinga, Ipomonga Island - Curuçá, Pará; e. external view of Restinga vegetation, Marieta Beach - Maracanã, Pará. Photo: Dário Amaral.

(L.) Kunth, *Chrysobalanus icaco* L., *Myrcia cuprea* (O.Berg) Kiaersk., *Protium heptaphyllum* (Aubl.) Marchand, *Pagamea guianensis* Aubl., *Ouratea racemiformis* Ule, *Eugenia biflora* (L.) DC., *Clusia grandiflora* Splitg. and *Anacardium occidentale* L.

Area 2 - Marieta Beach

The Marieta beach is 7 km long and lies in a NW-SE direction between the Maracanã and Urindeua bays. The lithostratigraphic units that support the Holocene sediments are: the Pirabas Formation of the Barreiras Group (Lower Tertiary), the Post-Barreiras Deposits and the more recent sediments. Because of the slight gradient and the amplitude of the macro-tides, the Marieta beach suffers the influence of the funneled estuaries associated to various sedimentary environments forming an extensive tidal plain with dune fields, estuarine channels, beach crests, cheniers, mangroves, saltwater marshes, elongated sandbanks perpendicular to the coastline and sandy spurs, all of which are typical features of the mouth of a macro-tidal estuary (El-Robrini *et al.* 2006; Guerreiro *et al*. 2013) (Fig. 2d-e).

The remaining stand of Lowland Dense Rain Forest occupies an area of approximately 30 hectares and is bordered to the south by mangrove, to the north by the sea, and to the east and west by dune fields where the Restinga occurs (Fig. 2e). Inside the forest there is a small stream which, before running into the sea, is responsible for the presence of lakes in the low-lying areas where species typical of floodable areas occur such as *Virola surinamensis* (Rol. *ex* Rottb.) Warb., *Symphonia globulifera* L.f., *Eriotheca globosa* (Aubl.) A.Robyns and *Licania heteromorpha* Benth (Fig. 2e).

The average height of trees registered was 12 meters and the circumference at breast height 50 cm. Among the most populous species composing the Lowland Dense Rain Forest canopy (15 m above the ground) were *Protium heptaphyllum* (Aubl.) Marchand, *Heisteria ovata* Benth., *Pouteria ramiflora* (Mart.) Radlk., *Maytenus guyanensis* Klotzsch *ex* Reissek and *Aniba citrifolia* (Nees) Mez (Fig. 2d). In the understory (up to 5 meters from the ground), the prevalent species are regenerating *Maytenus guyanensis* Klotzsch *ex* Reissek, *Calycolpus goetheanus* (Mart. *ex* DC.) O.Berg, *Cassipourea guianensis* Aubl., *Chaunochiton kappleri* (Sagot *ex* Engl.) Ducke, *Cupania scrobiculata* Rich., *Aniba citrifolia* (Nees) Mez and *Myrcia splendens* (Sw.) DC.

Contiguous with the remaining primary forest stand described above there is a Restinga marked by the presence of small species (30 cm circumference, height of 5 m.) covering strips of sandy ridges. The densest species are *Pradosia schomburgkiana* (A.DC.) Cronquist subsp. *schomburgkiana*, *Pagamea guianensis* Aubl., *Sacoglottis guianensis* Benth., *Clusia fockeana* Miq., *Humiria balsamifera* (Aubl.) A.St.-Hil., *Amaioua guianensis* Aubl. and *Protium heptaphyllum* (Aubl.) Marchand. Furthermore, given the presence of innumerable low-lying areas where rainwater accumulates inside the Restinga, it is common to find *Mauritiella armata* (Mart.) Burret (Fig. 2d-e) palms.

Among the fragments of Restinga (occupying little thickets) the commonest species are *Byrsonima crassifolia* (L.) Kunth, *Clusia grandiflora* Splitg., *Eugenia biflora* (L.) DC., *Ouratea cassinifolia* (A.DC.) Engl., *Pagamea guianensis* Aubl. e *Protium heptaphyllum* (Aubl.) Marchand. The herbaceous vegetation is dominated by *Sauvagesia erecta* L., *Scleria cyperina* Willd. *ex* Kunth, *Chamaecrista ramosa* (Vogel) H.S.Irwin & Barneby and *Axonopus purpusii* (Mez) Chase (Fig. 2d-e).

Vegetation sampling

The sampling plots method (Mueller-Dombois & Ellenberg 1974) was used in both the typologies studied, that is, the Lowland Dense Rain Forest and Restinga.

For the vegetation sampling, in the two stretches of the Atlantic coast of Pará investigated, referring to the Island of Ipomonga (municipality of Curuçá) and Praia da Marieta (municipality of Maracanã), in the northeast of Pará, we carried out the plots method (Mueller-Dombois & Ellenberg 1974) in both vegetation types studied; Lowland Dense Rain Forest and Restinga. All the plots were the same size: 25 × 10 m (*i.e.* 0.24 ha) and they were randomly allocated inside the forested areas.

In the stands of dense forest, 80 plots and (totaling 2 ha) and 40 plots (totaling 1 ha) were sampled at the Ipomonga Island and the Marieta beach respectively. In Restinga were sampled 44 plots (1.1 ha) and 40 plots (1 ha) sampled again at the Ipomonga Island and the Marieta Beach respectively. The total area sampled altogether was 5.1 ha (3 ha of dense forest and 2.1 ha of Restinga).

These inventories are part of a broader study (unpublished data) on the use of permanent plots to monitor the dynamics of woody vegetation in coastal forests on the Pará coast.

Preliminary identification was made in the field and subsequently the material was brought to the herbarium at the Emílio Goeldi Museum (Museu Paraense Emílio Goeldi - MG) where the identifications were revised. The fertile reference material was deposited in the abovementioned herbarium.

Data analysis

To support the floristic composition analysis the study made use of a flora checklist for the Restinga of the coast of Pará (Amaral *et al*. 2008), and a more recent study (Amaral *et al*. 2015) specifically addressing restinga forests with records of new occurrences (not listed in the checklist) for the woody flora of the said coast. The species dispersion syndrome was classified after field observations according to Amaral *et al*. (2008, 2009).

The synonymized nomenclatures in the studies referred to above were updated and doubtful classifications were unified when necessary. As an example, there were registrations for distinct occurrences of *Clusia fockeana* Miq. and *Clusia columnaris* Engl. among the restingas investigated. It was found, however, that there had been a mistake in the initial identification and in fact in all occurrences the species was the same one, namely, *Clusia fockeana* Miq.

The study adopted the APG IV (2016) classification system to classify the species and the spelling was based on the information in the List of Brazilian Flora Species (Lista de Espécies da Flora do Brasil) (<http://floradobrasil.jbrj.gov.br>).

To verify the possible existence of a gradient in the floristic composition related to the Restinga, data analysis made use of non-metric multidimensional scaling (NMDS) analysis and the Bray-Curtis index and Sorenson index were both used to assess similarity/dissimilarity (ecological distance). A dendrogram was constructed using the UPGMA algorithm to investigate linkage. The analyses were conducted using the PAST 2.08 program (Hammer *et al*. 2001).

In addition to all the data obtained in this study, secondary data from another Restinga in a nearby region, located on the Algodoal Island in the municipality of Maracanã (Amaral *et al*. 2016a), were introduced into the non-metric scaling analysis, maintaining the same inclusion criteria and sampling effort, standard in species per hectare.

The numbers of plots to compose the scaling analysis was standardized and they were made up into four large samples for each one of the three places under investigation (Ipomonga, Marieta and Algodoal). That adjustment optimized the graphic presentation of the data.

Results

The study registered 189 species in 50 botanical families (Tab. 1). The greater richness of species corresponds to the Lowland Dense Rain Forest (168 species of which 122 were exclusive to that formation), to the detriment of the Restinga (67 species of which 21 were exclusive to them). Of all the registered species, 46 (24%) were common to the two vegetation typologies. Among the latter were *Andira surinamensis*, *Copaifera martii*, *Eriotheca globosa*, *Himatanthus articulatus*, *Humiria balsamifera*, *Micropholis venulosa*, *Parinari campestris*, *Pouteria ramiflora*, *Protium heptaphyllum* and *Tapirira guianensis*.

Most of the species that were only found in the Lowland Dense Rain Forest were big tree species, like *Aspidosperma desmanthum*, *Bertholletia excelsa*, *Brosimum guianense*, *Caryocar villosum*, *Couratari guianensis*, *Diplotropis purpurea*, *Dipteryx odorata*, *Hymenaea courbaril*, *Peltogyne paniculata*, *Pouteria macrophylla*, *Simarouba amara*, *Tachigali glauca*, *Terminalia amazonia*, *Thyrsodium spruceanum*, *Trattinnickia rhoifolia* and *Virola sebifera*.

In the flora that was restricted to the Restinga, the majority of species were small trees and bushes such as *Anacardium occidentale*, *Bocageopsis multiflora*, *Byrsonima aerugo*, *Chrysobalanus icaco*, *Duguetia cadaverica*, *Erythroxylum leptoneurum*, *Eugenia biflora*, *Matayba elegans* and *Ouratea cassinifolia*.

Half of all the species registered for the two typologies of vegetation belong to just six families, as follows: Fabaceae (31), Chrysobalanaceae (15), Myrtaceae (15), Annonaceae (10), Sapotaceae (9), Lecythidaceae (8) and Clusiaceae (6). The other half of the species was distributed among the other 42 families.

At least 18 woody species were registered that are considered to be new occurrences for this type of vegetation on the Pará coast. Seven of them were found at the Marieta beach alone (*Duguetia cadaverica*, *Calophyllum brasiliense*, *Byrsonima aerugo*, *Ormosia flava*, *Pleurothyrium parviflorum*, *Virola surinamensis* and *Matayba elegans*) and four at Ipomonga Island alone (*Bocageopsis multiflora*, *Ocotea neesiana*, *Ficus malacocarpa* and *Ficus nymphaeifolia*). The other seven species were

Table 1 – List of species registered for the Restinga and to Lowland Dense Rain Forest at Ipomonga Island (Curuçá) and Marieta Beach (Maracanã), Pará. Dispersal: zooc = zoochory; anem = anemochory; auto = autochory; hydrochory = hydro.

Families / Species	Dispersion	Ipomonga Island		Marieta Beach	
		Restinga	Dense Forest	Restinga	Dense Forest
Achariaceae					
Lindackeria latifolia Benth.	zooc		x		x
Lindackeria paludosa (Benth.) Gilg	zooc		x		
Anacardiaceae					
Anacardium occidentale L.	zooc	x			
Tapirira guianensis Aubl.	zooc	x	x	x	x
Thyrsodium spruceanum Benth.	zooc		x		
Annonaceae					
Anaxagorea acuminata (Dunal) A.DC.	zooc				x
Annona exsucca DC.	zooc				x
Bocageopsis multiflora (Mart.) R.E.Fr.	zooc	x	x		
Duguetia cadaverica Huber	zooc			x	
Duguetia echinophora R.E.Fr.	zooc			x	x
Guatteria schomburgkiana Mart.	zooc		x		
Unonopsis guatterioides (A.DC.) R.E.Fr.	zooc		x		
Xylopia benthamii R.E.Fr.	zooc		x		
Xylopia cayennensis Maas	zooc		x		
Xylopia emarginata Mart.	zooc	x		x	x
Apocynaceae					
Aspidosperma desmanthum Benth. *ex* Müll.Arg.	anem		x		x
Himatanthus articulatus (Vahl) Woodson	anem	x	x	x	x
Araliaceae					
Didymopanax morototoni (Aubl.) Decne. & Planch.	zooc		x		
Arecaceae					
Astrocaryum vulgare Mart.	zooc		x	x	x
Attalea maripa (Aubl.) Mart.	zooc		x		x
Mauritiella armata (Mart.) Burret	zooc			x	x
Oenocarpus distichus Mart.	zooc		x		
Bignoniaceae					
Bignonia nocturna (Barb.Rodr.) L.G. Lohmann	anem				x
Jacaranda copaia (Aubl.) D.Don.	anem		x		
Memora magnifica (Mart. ex DC.) Bureau	anem		x		
Boraginaceae					
Cordia nodosa Lam.	zooc		x		
Burseraceae					
Brosimum guianense (Aubl.) Huber	zooc		x		
Protium heptaphyllum (Aubl.) Marchand	zooc	x	x	x	x
Protium krukovii Swart	zooc		x		
Protium tenuifolium (Engl.) Engl.	zooc		x		

Families / Species	Dispersion	Ipomonga Island		Marieta Beach	
		Restinga	Dense Forest	Restinga	Dense Forest
Trattinnickia rhoifolia Willd.	zooc		x		
Callophylaceae					
Calophyllum brasiliense Cambess.	zooc			x	x
Capparaceae					
Cynophalla flexuosa (L.) J. Presl	zooc	x			
Caryocaraceae					
Caryocar villosum (Aubl.) Pers.	zooc		x		
Celastraceae					
Cheiloclinium cognatum (Miers) A.C.Sm.	zooc		x		
Maytenus guyanensis Klotzsch *ex* Reissek	zooc	x		x	x
Monteverdia myrsinoides (Reissek) Biral	zooc		x		
Salacia impressifolia (Miers) A.C.Sm.	zooc				x
Chrysobalanaceae					
Chrysobalanus icaco L.	zooc	x			
Couepia bracteosa Benth.	zooc	x			x
Couepia guianensis Aubl.	zooc		x		
Hirtella glandulosa Spreng.	zooc		x		
Licania apetala (E. Mey.) Fritsch.	zooc		x		
Licania canescens Benoist	zooc		x		x
Licania egleri Prance	zooc	x			x
Licania heteromorpha Benth.	zooc		x	x	x
Licania membranacea Sagot *ex* Laness.	zooc		x		
Parinari campestris Aubl.	zooc	x		x	x
Clusiaceae					
Clusia fockeana Miq.	zooc	x		x	x
Clusia grandiflora Splitg.	zooc	x		x	x
Garcinia gardneriana (Planch. & Triana) Zappi	zooc				x
Garcinia madruno (Kunth) Hammel	zooc		x		
Platonia insignis Mart.	zooc	x	x		x
Symphonia globulifera L.f.	zooc				x
Combretaceae					
Buchenavia congesta Ducke	zooc				x
Buchenavia grandis Ducke	zooc				x
Terminalia amazonia (J.F. Gmel.) Exell	zooc		x		
Connaraceae					
Connarus angustifolius (Radlk.) G. Schllenb.	auto		x		
Connarus perrottetii var. *angustifolius* Radlk.	auto				x
Dichapetalaceae					
Tapura singularis Ducke	auto		x		
Dilleniaceae					
Doliocarpus dentatus (Aubl.) Standl.	zooc		x		x

Families / Species	Dispersion	Ipomonga Island		Marieta Beach	
		Restinga	Dense Forest	Restinga	Dense Forest
Tetracera willdenowiana Steud.	zooc				x
Elaeocarpaceae					
Sloanea terniflora (DC.) Standl.	auto		x		
Erythroxylaceae					
Erythroxylum leptoneurum O.E. Schulz	zooc	x			
Euphorbiaceae					
Croton matourensis Aubl.	auto		x		
Maprounea guianensis Aubl.	auto		x		
Fabaceae					
Abarema cochleata (Willd.) Barneby & J.W. Grimes	zooc		x		x
Abarema jupunba (Willd.) Britton & Killip	zooc	x	x		x
Andira surinamensis (Bondt) Splitg. *ex* Amshoff	zooc			x	x
Bauhinia guianensis Aubl.	auto		x		
Chloroleucon acacioides (Ducke) Barneby & J.W. Grimes	zooc				x
Copaifera martii Hayne	zooc	x	x	x	x
Diplotropis purpurea (Rich.) Amshoff	anem		x		
Dipteryx odorata (Aubl.) Willd.	zooc		x		
Hymenaea courbaril L.	zooc				x
Hymenolobium petraeum Ducke	anem	x		x	
Inga brachyrhachis Harms	zooc				x
Inga grandiflora Ducke	zooc				x
Inga heterophylla Willd.	zooc		x		
Inga lateriflora Miq.	zooc		x		
Inga laurina (Sw.) Willd.	zooc		x		
Inga paraensis Ducke	zooc				x
Inga thibaudiana DC.	zooc		x	x	x
Inga umbellifera (Vahl) Steud.	zooc		x		
Machaerium froesii Rudd.	hidro		x		
Machaerium latifolium Rusby	hidro		x		
Ormosia flava (Ducke) Rudd	zooc			x	x
Ormosia paraensis Ducke	zooc		x		
Parkia pendula (Willd.) Benth. *ex* Walp.	zooc			x	
Peltogyne paniculata Benth.	zooc				x
Pterocarpus rohrii Vahl	hydro		x		x
Stryphnodendron guianense (Aubl.) Benth.	zooc				x
Stryphnodendron pulcherrimum (Willd.) Hochr.	zooc		x		x
Swartzia laevicarpa Amshoff	zooc	x			
Swartzia laurifolia Benth.	zooc		x	x	x
Tachigali glauca Tul.	anem		x		x
Tachigali paniculata Aubl.	anem		x		

Families / Species	Dispersion	Ipomonga Island		Marieta Beach	
		Restinga	Dense Forest	Restinga	Dense Forest
Humiriaceae					
Humiria balsamifera (Aubl.) A.St.-Hil.	zooc	x	x	x	x
Sacoglottis guianensis Benth.	zooc	x	x	x	x
Vantanea guianensis Aubl.	zooc		x		
Vantanea parviflora Lam.	zooc		x		
Lamiaceae					
Vitex triflora Vahl	zooc		x		x
Lauraceae					
Aniba citrifolia (Nees) Mez	zooc	x		x	x
Ocotea canaliculata (Rich.) Mez	zooc		x		
Ocotea cernua (Nees) Mez	zooc				x
Ocotea glomerata (Nees) Mez	zooc		x		
Ocotea neesiana (Miq.) Kosterm.	zooc	x	x		
Pleurothyrium parviflorum Ducke	zooc			x	x
Lecythidaceae					
Bertholletia excelsa Bonpl.	zooc		x		
Couratari guianensis Aubl.	anem		x		
Eschweilera coriacea (DC.) S.A. Mori	auto		x		
Eschweilera ovata (Cambess.) Mart. *ex* Miers	auto				x
Eschweilera pedicellata (Rich.) S.A. Mori	auto		x		
Gustavia augusta L.	zooc		x		
Lecythis lurida (Miers) Mori	auto		x		
Lecythis pisonis Cambess.	auto		x		x
Linaceae					
Hebepetalum humiriifolium (G.Planch.) Benth.	zooc				x
Malpighiaceae					
Byrsonima aerugo Sagot	zooc			x	
Byrsonima crassifolia (L.) Kunth	zooc	x		x	x
Byrsonima densa (Poir.) DC.	zooc				x
Byrsonima densa (Poir.) DC.	zooc				x
Malvaceae					
Eriotheca globosa (Aubl.) A. Robyns	anem	x		x	x
Melastomataceae					
Miconia hypoleuca (Benth.) Triana	zooc		x		
Mouriri brachyanthera Ducke	zooc				x
Mouriri guianensis Aubl.	zooc	x			x
Menispermaceae					
Abuta grandifolia (Mart.) Sandwith	zooc		x		
Metteniusaceae					
Emmotum acuminatum (Benth.) Miers	zooc		x		

Families / Species	Dispersion	Ipomonga Island		Marieta Beach	
		Restinga	Dense Forest	Restinga	Dense Forest
Moraceae					
Ficus americana subsp. *guianensis* (Desv.) C.C. Berg	zooc			x	x
Ficus gomelleira Kunth	zooc		x		
Ficus malacocarpa Standl.	zooc	x	x		
Ficus nymphaeifolia Mill.	zooc	x	x		
Maquira guianensis Aubl.	zooc		x		
Myristicaceae					
Virola sebifera Aubl.	zooc				x
Virola surinamensis (Rol. *ex* Rottb.) Warb.	zooc			x	x
Myrtaceae					
Calycolpus goetheanus (Mart. *ex* DC.) O. Berg	zooc			x	x
Eugenia biflora (L.) DC.	zooc			x	
Eugenia egensis DC.	zooc		x		
Eugenia florida DC.	zooc			x	x
Eugenia patrisii Vahl	zooc		x	x	x
Eugenia punicifolia (Kunth) DC.	zooc		x		
Eugenia stictopetala Mart. *ex* DC.	zooc	x	x	x	x
Myrcia cuprea (O. Berg) Kiaersk.	zooc			x	x
Myrcia fallax (Rich.) DC.	zooc		x		
Myrcia multiflora (Lam.) DC.	zooc		x		
Myrcia rufipila McVaugh	zooc			x	x
Myrcia splendens (Sw.) DC.	zooc		x	x	x
Myrcia tomentosa (Aubl.) DC.	zooc		x		
Myrciaria floribunda (H.West *ex* Willd.) O. Berg	zooc	x	x	x	x
Myrciaria tenella (DC.) O. Berg	zooc				x
Nyctaginaceae					
Guapira opposita (Vell.) Reitz	zooc				x
Neea oppositifolia Ruiz & Pav.	zooc		x		
Ochnaceae					
Ouratea cassinifolia (A.DC.) Engl.	zooc			x	
Ouratea castaneifolia (DC.) Engl.	zooc	x	x		x
Ouratea racemiformis Ule	zooc				x
Olacaceae					
Chaunochiton kappleri (Sagot *ex* Engl.) Ducke	anem		x	x	x
Heisteria acuminata (Humb. & Bonpl.) Engl.	zooc		x		
Heisteria ovata Benth.	zooc	x		x	x
Opiliaceae					
Agonandra brasiliensis Benth. & Hook.	zooc		x		x
Pentaphylaceae					
Ternstroemia punctata (Aubl.) Sw.	zooc	x		x	x

Families / Species	Dispersion	Ipomonga Island		Marieta Beach	
		Restinga	Dense Forest	Restinga	Dense Forest
Peraceae					
Pogonophora schomburgkiana Miers *ex* Benth.	auto		x		
Putranjivaceae					
Drypetes variabilis Uittien	zooc		x		
Rhizophoraceae					
Cassipourea guianensis Aubl.	zooc		x	x	x
Rubiaceae					
Alibertia edulis (Rich.) A.Rich.	zooc				x
Amaioua guianensis Aubl.	zooc	x		x	x
Cordiera myrciifolia (K.Schum.) C.H.Perss. & Delprete	zooc				x
Pagamea guianensis Aubl.	zooc	x		x	x
Posoqueria latifolia (Rudge) Schult.	zooc		x		
Stachyarrhena spicata Hook.f.	zooc		x		
Tocoyena brasiliensis Mart.	zooc				x
Salicaceae					
Casearia javitensis Kunth	zooc		x		
Laetia procera (Poepp.) Eichler	zooc		x		
Sapindaceae					
Cupania diphylla Vahl	zooc				x
Cupania scrobiculata Rich.	zooc				x
Matayba elegans Radlk.	zooc			x	x
Talisia microphylla Uittien	zooc		x		
Talisia retusa Cowan	zooc		x		
Talisia veraluciana Guarim	zooc				x
Sapotaceae					
Chrysophyllum sparsiflorum Klotzsch *ex* Miq.	zooc		x		
Manilkara triflora (Allemão) Monach.	zooc			x	x
Micropholis venulosa (Mart. & Eichler) Pierre	zooc			x	x
Pouteria anomala (Pires) T.D.Penn.	zooc				x
Pouteria gongrijpii Eyma	zooc		x		
Pouteria guianensis Aubl.	zooc				x
Pouteria macrophylla (Lam.) Eyma	zooc		x		
Pouteria ramiflora (Mart.) Radlk.	zooc	x		x	x
Pradosia schomburgkiana (A.DC.) Cronquist subsp. *schomburgkiana*	zooc	x		x	x
Simaroubaceae					
Simaba polyphylla (Cavalcante) W.W. Thomas	zooc			x	
Simarouba amara Aubl.	zooc		x		x
Urticaceae					
Cecropia obtusa Trécul	zooc		x		
Total		**38**	**106**	**52**	**94**

found in both locations (*Xylopia emarginata*, *Couepia bracteosa*, *Licania egleri*, *Licania heteromorpha*, *Platonia insignis*, *Abarema jupunba* and *Inga thibaudiana*). All of these new occurrences were sampled in the restinga study areas as well as in the respective remaining stands of Lowland Dense Rain Forest associated to them.

Almost all (91%) of the Restinga species registered are dispersed by animals (zoochory) except for *Himatanthus articulatus*, *Hymenolobium petraeum*, *Eriotheca globosa* and *Chaunochiton kappleri* which are dispersed by the wind (anemochory) and *Clusia fockeana* and *Clusia grandiflora* which use autochory as the dispersion strategy for their propagules.

The graph obtained by the NMDS analysis reveals grouping of the Restinga forests of Ipomonga and Marieta and isolation of the Algodoal Restinga forest, based on the flora composition and vegetation abundance data for which the stress value obtained was 0.135 (Fig. 3).

Discussion

Up until the beginning of the 20th century, the main vegetation cover of the Amazon Atlantic sector (specifically the northeast of Para state where the research areas are located) was dense forest. The region, however, was the site of the earliest European colonization of the Amazon as far back as the 17th century (Huber 1909; Pires & Prance 1985; Vieira *et al*. 2007).

In more modern times, after almost 150 years of intensive exploitation of the land, this region (formerly covered by forests) now has a fragmented landscape from which many species of plants and animals have completely disappeared (Vieira *et al*. 2007). According to deforestation statistics, in those Pará state municipalities bordered by the sea only 34% of the original forest vegetation remains (IBGE 2012).

To make matters worse, the greater part of the territory of those municipalities is continental and only a narrow coastal strip is connected to the sea which reduces the areas covered by forest in the region even more (Rocha *et al*. 2003, 2007). Mainly due to the fact that the historically human occupation in Brazil (exploitation of natural resources) began in the coastlands (Martins *et al*. 2008).

The considerable changes in the landscape stem from historical, socioeconomic and geographic events that occurred in the region after the strong anthropic impact that began with the colonization of the Bragantina region following the opening up of the Belém-Brasília highway (BR-010) and the Pará-Maranhão Highway (BR-316) (Coelho *et al*. 2018).

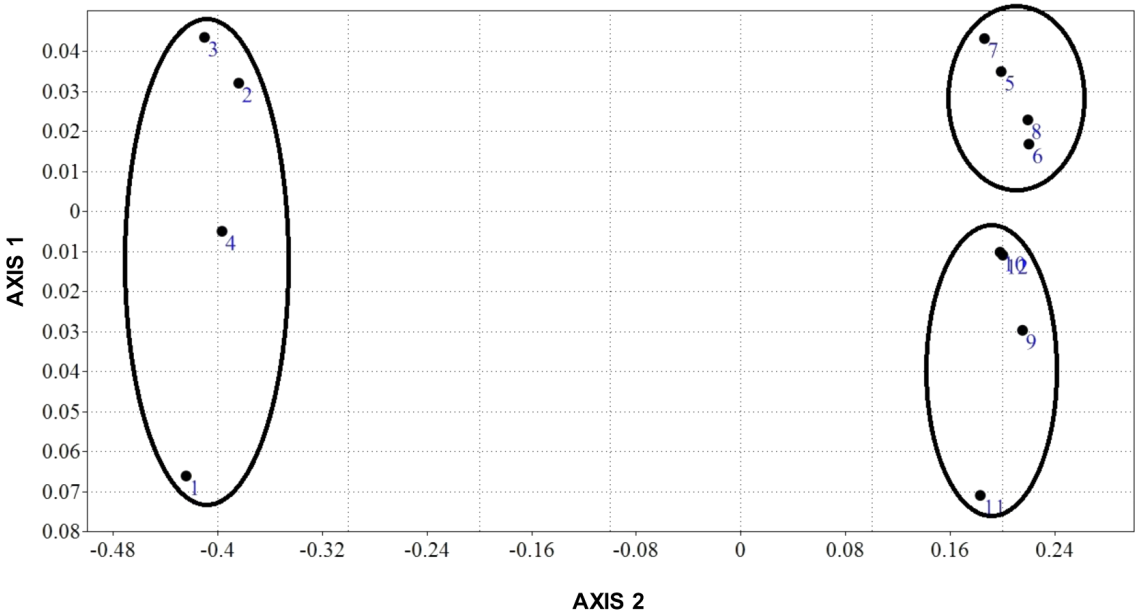

Figure 3 – Non-metric multidimensional scaling (NMDS) of three Restinga according to their floral composition. Ipomonga Island (Curuçá), Marieta Beach (Maracanã) and Algodoal (Maracanã), Pará, Brazil.

Thus, the two remaining forest stands investigated by this study are relics of the Alluvial Dense Rain Forest (IBGE 2012) that formerly occupied the coastal strip bordering the Atlantic Ocean along the Amazonian coast. They originally evolved from transgressive-regressive events associated to relative sea levels since the end of the Upper Pleistocene to the Holocene epochs (Souza-Filho 1995). The unique geological and geomorphological evolution of the sites on which those forest relics are found, together with the geographic aspect of their difficult access (insular regions) and the fact that they are enclosed within a Federal Conservation Unit of the RESEX type are conditions that explain the existence, at present, of these relics of coastal Amazonian forest.

Unlike the other four sectors of 650 km-long macro-tidal Mangrove Coast (*Costa de Manguezais* extending from the Marajó Bay in Pará to the Ponta de Tubarão in Maranhão), Sector 1, where the investigated forest formations are found, is the only one in which the coastal plateau reaches right to the shoreline, forming cliffs supported on tertiary sediments of the Barreiras and Pirabas formations. In the other sections, the lowland plateau is retracted further inland (to the south) leaving a space between it and the shoreline occupied by the expansion of the mangrove ecosystem (Souza-Filho 2005).

At both Ipomonga Island and Marieta Beach, the Restinga is notable for its abrupt encounter with Lowland Dense Rain Forest (Boulhosa & Souza-Filho 2009; Rodrigues & Souza-Filho 2012). That geomorphological interface between the areas favors floristic connectivity between the vegetable communities of restinga and dense terra firme forest. The spatial proximity and the similar physiognomy among vegetation types make the phytogeographical differentiation difficult leading to questions, especially for coastal lowland vegetation (Marques *et al.* 2011).

That fact explains the registration of the 18 woody species of the Restinga considered to be new occurrences for this type of vegetation on the Pará coast (Amaral *et al*. 2008, 2015) and it underscores the understanding that the Restinga are associated (in terms of history, flora and ecological functions) with other plant physiognomies to be found in the Brazilian coastlands (Scarano 2002; Scherer *et al*. 2007; Rodrigues *et al*. 2010; Marques *et al*. 2015). Given that scenario, it is necessary to consider the influence of distance between fragments on the success of the seed rain given that the greater the distance the lesser will be the flow of propagules (Cubiña & Aide 2001).

The new occurrences correspond to an increase of 15%, considering woody species only, in the checklist for the state of Pará (Amaral *et al*. 2008), and of 21% considering the woody flora of the coastal region alone (Amaral *et al*. 2015).

These relics of the Lowland Dense Rain Forest act as sources for the dispersion of propagules of some woody species that are dispersed through the action of animals (zoochory) in the contiguous areas occupied by Restinga (Scherer *et al*. 2007; Rodrigues *et al*. 2010; Giaretta *et al*. 2013). The aspects of local variation in the restingas such as topographic differences, natural clearings and the intensity of flooding control the establishment of those species which are adapted forms (Scarano *et al*. 2001; Kurtz *et al*. 2013) as in the case, for example, of *Virola surinamensis*, *Licania heteromorpha* and *Calophyllum brasiliense*, species that are generally tolerant in regard to flooding (Scarano 2002).

Virola surinamensis (Rol. *ex* Rottb.) Warb was registered at the Marieta Beach and it is a specie distributed in areas of the Amazon subject to flooding (varzea and igapó) (Ferreira *et al*. 2014), where it is intensely exploited for the value of its wood (Piña-Rodrigues & Mota 2000; Salomão *et al*. 2007) and it is inscribed on the current list of threatened species in Brazil (IUCN 2020). Based on molecular phylogeny, this species along with another 27 species registered for the dense forest formations investigated by this study, including *Chrysobalanus icaco*, *Symphonia globulifera* and *Terminalia amazonia*, was used to support the hypothesis that plants typical of neo-tropical coastal habitats also occur in the western Amazon thousands of kilometers away due to environmental events that occurred in the Neogene period (Bernal *et al*. 2019). They are species with wide distribution on the Amazon, which, when close to and associated with Restinga, can disperse their propagules in these Restinga environments.

Platonia insignis Mart. is another specie that had never been catalogued for the Brazilian coast Restinga (BFG 2018). It is known locally as *bacurizeiro* and has commercial value because of its fruits (Matos *et al*. 2009; Menezes *et al*. 2010). The specie is originally an eastern Amazonian species found in primary and secondary forests (thickets) and its area of greatest concentration is the estuary of the Amazon river, the island of Marajó and the micro-region of Salgado Paraense (Carvalho 2007; Homma *et al*. 2007).

The natural formations of the *bacurizeiro* that once occurred spontaneously along the Atlantic coast of Pará were constantly decimated by a process that eliminated all the vegetation cover in the region. Today what remain are managed groups of the species obtained by asexual reproduction (re-sprouting from the roots) in degraded areas of secondary vegetation. In the Ipomonga forest there is a considerable natural population of the species and there is interest in safeguarding it as a source of material for genetic improvement studies (Homma *et al*. 2007; Menezes *et al*. 2010, 2018). Although the sharing of a group of species between the Lowland Dense Rain Forest and the Restinga, prevailed in the dense forest remnants a restricted flora (64%), typical of this Amazonian plant typology. They are species of an advanced stage of ecological succession and as such they are specialized in regard to their environmental requirements (physical chemistry of the soil, shade and humidity) for their establishment and development. Examples of such species are *Aspidosperma desmanthum*, *Brosimum guianense*, *Caryocar villosum*, *Couratari guianensis*, *Diplotropis purpurea*, *Dipteryx odorata*, *Hymenaea courbaril*, *Peltogyne paniculata*, *Pouteria macrophylla*, *Thyrsodium spruceanum* and *Trattinnickia rhoifolia* (Salomão *et al*. 2007; Amaral *et al*. 2009).

There is ample proof in the literature of the prevalence of zoochoric dispersion in the Amazonian Restinga system (Amaral *et al*. 2015) and in various stretches of the Brazilian coastlands (Tarola & Morellato 2000; Marques & Oliveira 2005; Almeida Jr. *et al*. 2009; Rodrigues *et al*. 2010). Birds are the most important dispersal agents in Restinga and outweigh other groups of dispersers in the aspects of their mobility and great diversity of species (Scherer *et al*. 2007).

In turn the woody species are highly important to the avian fauna not only as a foraging substrate but also as a direct source of food (Gomes *et al*. 2008). The first registration of the occurrence of *Curatella americana* L. in Restinga of the Amazonian coast was in a Restinga on the island of Marajó. The distribution of its seeds was attributed to birds that obtained them in the contiguous areas of Cerrado (Amaral *et al*. 2016a).

The grouping diagram obtained with the NMDS analysis, bringing together the Restinga of Ipomonga and the Marieta Beach, show that the type of surrounding vegetation makes a decisive contribution to the composition of the Restinga floras, corroborating the finding of biogeographic studies of islands in general (Macarthur & Wilson 2001; Giaretta *et al*. 2013; Kurtz *et al*. 2013). Even though the Marieta beach is only 14 km from the Algodoal Island Restinga, there was greater similarity between the Marieta beach flora and that of the Ipomonga Island restinga which is more than 50 km away, thereby underscoring the evidence of the influence of the dense forest relics on the floristic occupation of those Restinga, different from the Restinga forest of Algodoal which is bordered by mangrove (Bastos & Lobato 1996; Amaral *et al*. 2016b).

Among the new occurrence registered are some species that are widely distributed throughout Brazil such as *Abarema jupunba*, *Inga thibaudiana* and *Xylopia emarginata*. However, the occurrence of the majority, like *Couepia bracteosa*, *Duguetia cadaverica*, *Matayba elegans*, *Ocotea neesiana*, *Ormosia flava* and *Platonia insignis* is restricted to the Amazon (BFG 2018), endorsing the understanding that the original base of the dispersion center for woody species in the occupation of the Restinga on the coast of Pará state is Amazonian Lowland Dense Rain Forest (Amaral *et al*. 2015).

In the context of the Amazonian Atlantic coast, the unique characteristics of where these remnants are located explain the existence, at present, of these relics of coastal Amazonian forest. The registration of 18 species what are considered new occurrences for the Restinga flora of the Amazon coast, with an increase of 15% in the resting checklist, obtained in this study, and the floristic affinities identified between the Restinga in the locations investigated, support the prior understanding of exceptionality of the presence of Amazonian Lowland Dense Rain Forest (on upland plateau), acting as the source for propagule dispersion over lowland plateau to woody Restinga vegetation, mostly dispersed (91%) by animals (zoocory dispersal strategy).

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References

Almeida Jr EB, Olivo MA, Araújo EL & Zickel CS (2009) Caracterização da vegetação de restinga da RPPN de Maracaípe, Pernambuco, com base na fisionomia, flora, nutrientes do solo e lençol freático. Acta Botanica Brasilica 23: 36-48.

Amaral DD, Costa DCT, Amaral CT & Costa-Neto SV (2016a) Seleção de espécies lenhosas destinadas à restauração florestal de áreas degradadas de restinga no litoral amazônico. Boletim do Museu Paraense Emilio Goeldi, Ciências Naturais 11: 167-179.

Amaral DD, Costa-Neto SV, Jardim MAG, Santos JUM & Bastos MNC (2016b) *Curatella americana* L. (Dilleniaceae): primeira ocorrência nas restingas do litoral da Amazônia. Revista Brasileira de Biociências 14: 257-262.

Amaral DD, Jardim MAG, Costa-Neto SV & Bastos MNC (2015) Síndromes de dispersão de propágulos e a influência da floresta amazônica na composição de espécies lenhosas de uma restinga no litoral norte brasileiro. Biota Amazônica 5: 28-37.

Amaral DD, Prost MT, Bastos MNC, Costa-Neto SV & Santos JUM (2008) Restingas do litoral amazônico, estados do Pará e Amapá, Brasil. Boletim do Museu Paraense Emílio Goeldi, Ciências Naturais 3: 35-67.

Amaral DD, Vieira ICG, Almeida SS, Salomão RP, Silva ASL & Jardim MAG (2009) Checklist da flora arbórea de remanescentes florestais da região metropolitana de Belém e valor histórico dos fragmentos, Pará, Brasil. Boletim do Museu Paraense Emílio Goeldi 4: 231-289.

APG IV - Angiosperm Phylogeny Group (2016) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. Botanical Journal of the Linnean Society 181: 1-20.

Araújo DSD (2000) Análise florística e fitogeográfica das restingas do estado do Rio de Janeiro. Tese de Doutorado. UFRJ - Universidade Federal do Rio de Janeiro, Rio de Janeiro. 141p.

Augustinus PGEF (1989) Cheniers and chenier plains: a general introduction. Marine Geology 90: 219-229.

Bastos MNC & Lobato LCB (1996) Estudos fitossociológicos em áreas de bosque de mangue na praia do Crispim e Ilha de Algodoal – Pará. Boletim do Museu Paraense Emílio Goeldi 8: 157-167.

Bernal R, Bacon CD, Balslev H, Hoorn C, Bourlat SJ, Tuomisto H, Salamanca S, Teunissen van Manen M, Romero I, Sepulchre P & Antonelli A (2019) Could coastal plants in western Amazonia be relicts of past marine incursions? Journal of Biogeography 46: 1749-1759.

BFG - The Brazil Flora Group (2018) Brazilian Flora 2020: innovation and collaboration to meet Target 1 of the Global Strategy for Plant Conservation (GSPC). Rodriguésia 69: 1513-1527.

Boulhosa MBM & Souza-Filho PWM (2009) Reconhecimento e mapeamento dos ambientes costeiros para geração de mapas de ISA ao derramamento de óleo, Amazônia Oriental. Revista Brasileira de Geofísica 27: 23-37.

Brasil (2002) Decreto de 13 de dezembro de 2002: cria a Reserva Extrativista Mãe Grande de Curuçá, no município de Maracanã, no estado do Pará, e dá outras providências. Diário Oficial da União, Brasília. Available at <http://www.planalto.gov.br/ccivil_03/dnn/2002/dnn9774.htm>. Access on 30 January 2019.

Carvalho JEU (2007) Aspectos botânicos, origem e distribuição geográfica do bacurizeiro. *In*: Lima MC (org.) Bacuri: agrobiodiversidade. Instituto Interamericano de Cooperação para a Agricultura, São Luís. Pp. 17-27.

Coelho AS, Toledo PM, Vieira ICG & Adami M (2018) Impactos das mudanças de uso da terra nas áreas prioritárias para conservação da biodiversidade no nordeste do estado do Pará, Brasil. Boletim do Museu Paraense Emilio Goeldi, Ciências Naturais 13: 107-120.

Cubiña A & Aide TM (2001) The effect of distance from forest edge on seed rain and soil seed bank in a tropical pasture. Biotropica 33: 260-267.

El-Robrini M, Silva MAMA, Souza-Filho PWM, El-Robrini MH, Silva-Júnior OG & França CF (2006) Atlas de erosão e progradação da zona costeira do estado do Pará - Região Amazônica: áreas oceânica e estuarina. *In*: Muehe D (coord.) Erosão e progradação do litoral brasileiro. Ministério do Meio Ambiente, Brasília. Pp. 41-86.

Ferreira LV, Cunha DA & Parolin P (2014) Effects of logging on *Virola surinamensis* in an Amazonian floodplain forest. Environment Conservation Journal 15: 1-8.

Fiaschi P & Pirani JR (2009) Review of plant biogeographic studies in Brazil. Journal of Systematics and Evolution 47: 477-496.

Freire MSB (1990) Levantamento florístico do Parque Estadual das Dunas de Natal. Acta Botanica Brasilica 4: 41-59.

Giaretta A, Menezes LFT & Pereira OJ (2013) Structure and floristic pattern of a coastal dune in southeastern Brazil. Acta Botanica Brasilica 27: 87-107.

Gomes VSM, Loiselle BA & Alves MAS (2008) Birds foraging for fruits and insects in shrubby restinga vegetation, southeastern Brazil. Biota Neotropica, Campinas 8: 21-31.

Guerreiro JS, Vila-Concejo A, El-Robrini M & Ranieri LA (2013) Seasonal changes and morphodynamic behavior of a high-energy macrotidal beach: case study of Marieta Beach (Pará - Amazon Coast/ Brazil). Journal of Coastal Research 1: 1780-1784.

Hammer O, Harper DAT & Ryan PD (2001) PAST: Paleontological Statistics Software Package for Education and Data Analysis. Palaeontologia Electronica 4: 9p.

Homma AKO, Carvalho JEU, Matos GB & Menezes AJEA (2007) Manejando a planta e o homem: os bacurizeiros do nordeste paraense e da Ilha de Marajó. Amazônia: Ciência e desenvolvimento 2: 119-135.

Huber H (1909) Mattas e madeiras amazônicas. Boletim do Museu Paraense Emilio Goeldi, História Natural e Ethnografia 6: 91-225.

IBGE - Instituto Brasileiro de Geografia e Estatística (2012) Manual técnico da vegetação brasileira. Série manuais técnicos em Geociências 1, 2ª edição revista e ampliada. IBGE, Rio de Janeiro. Available at <https://edisciplinas.usp.br/pluginfile.php/4228241/mod_resource/content/2/Manual%20Tecnico%20da%20Vegetacao%20Brasileira%20-%202012.pdf>. Access on 10 October 2019.

IUCN (2020) The IUCN red list of threatened species. Version 2020-1. Available at <https://www.iucnredlist.org>. Access on 19 March 2019.

Kurtz BC, Gomes JC & Scarano FR (2013) Structure and phytogeographic relationships of swamp forests of Southeast Brazil. Acta Botanica Brasilica 27: 647-660.

Lima GP & Almeida Jr EB (2018) Diversidade e similaridade florística de uma restinga ecotonal no Maranhão, Nordeste do Brasil. Iterciência 43: 275-282.

Macarthur RH & Wilson EO (2001) The theory of island biogeography. Princeton University Press, New Jersey. 224p.

Marques MCM & Oliveira PE (2005) Características reprodutivas das espécies vegetais da planície costeira. *In*: Marques MCM & Brites RM (orgs.) História natural e conservação da Ilha do Mel. Editora da Universidade Federal do Paraná, Curitiba. Pp. 169-188 .

Marques MCM, Swaine MD & Liebsch D (2011) Diversity distribution and floristic differentiation of the coastal lowland vegetation: implications for the conservation of the Brazilian Atlantic Forest. Biodiversity and Conservation 20: 153-168. <https://doi.org/10.1007/s10531-010-9952-4>

Marques MCM, Silva SM & Liebsch D (2015) Coastal plain forests in southern and southerastern Brazil: ecological drivers, floristic patterns and conservation status. Brazilian Journal of Botany 38: 1-18.

Martins SE, Rossi L, Sampaio PSP & Magenta MAG (2008) Caracterização florística de comunidades vegetais de restinga, em Bertioga, SP, Brasil. Acta Botanica Brasilica 22: 249-270.

Menezes AJEA, Schoffel ER & Homma AKO (2010) Caracterização de sistemas de manejo de bacurizeiro (*Platonia insignis* Mart.) nas mesorregiões do nordeste paraense e do Marajó, estado do Pará. Amazônia: Ciência e Desenvolvimento, Belém 6: 49-62.

Menezes AJEA, Watrin OS, Gusmão LHA & Menezes JFG (2018) Adoção da tecnologia de manejo de rebrotamento de bacurizeiros (*Platonia insignis* Mart.) por pequenos produtores nas regiões do nordeste paraense e do marajó, Pará. Brazilian Journal of Development 4: 3801-3820.

Moraes BC, Costa JMN, Costa ACL & Costa MH (2005) Variacão espacial e temporal da precipitacão no estado do Pará. Acta Amazônica 35: 207-214.

Muehe D (1998) Estado morfodinâmico praial no instante da observação: uma alternativa de identificação. Revista Brasileira de Oceanografia 46: 157-169.

Mueller-Dombois D & Ellenberg H (1974) Aims and methods of vegetation ecology. John Wiley & Sons, New York. Pp. 93-135.

Piña-Rodrigues FCM & Mota CG (2000) Análise da atividade extrativa de virola (*Virola surinamensis* (Rol.) Warb) no estuário Amazônico. Floresta e Ambiente 7: 40-5.

Pires JM & Prance GT (1985) The vegetation types of the Brazilian Amazon. *In*: Prance GT & Lovejoy TE (eds.) Key environments: Amazonia, Pergamon Press, Oxford. Pp. 109-145.

Rocha AES & Miranda IS (2012) Cobertura vegetal, biomassa aérea e teor de proteína do estrato herbáceo de ambiente savânico no município de Maracanã, Pará, Brasil. Revista Brasileira de Biociências 10: 513-520.

Rocha CFD, Bergallo HG, Alves MAS & Van Sluys M (2003) A biodiversidade nos grandes remanescentes florestais do estado do Rio de Janeiro e nas restingas da Mata Atlântica. Rima Editora, São Carlos. 163p.

Rocha CFD, Bergallo HG, Van Sluys M, Alves MAS & Jamel CE (2007) The remnants of Restinga habitats in the Brazilian Atlantic Forest of Rio de Janeiro state, Brazil: habitat loss and risk of disappearance. Brazilian Journal of Biology 67: 263-273.

Rodrigues MA, Barbosa JM, Santos NA & Paoli AAS (2010) Avaliação da chuva de sementes em áreas de restinga em diferentes estágios de regeneração. Revista Árvore 34: 815-824.

Rodrigues SWP & Souza-Filho P (2012) Mapping of environmental sensitivity index to oil spill from Landsat TM images: a study case on the Amazon coastal plain. Revista Brasileira de Geofísica 30: 533-543.

Sacramento AC, Zickel CS & Almeida-Júnior EB (2007) Aspectos florísticos da vegetação de restinga no litoral de Pernambuco. Revista Árvore 31: 1121-1130.

Salomão RP, Terezo EFM, Rosa NA, Ferreira LV, Matos AH, Adams M, Amaral DD & Morais KAC (2007) Manejo florestal na várzea: caracterização, restrições e oportunidades para sua adoção. *In*: Salomão RP, Terezo EFM & Jardim MAG (eds.) Manejo florestal nas várzeas: oportunidades e desafios. Museu Paraense Emílio Goeldi (Coleção Adolpho Ducke), Belém. Pp. 11-138.

Santos-Filho FS, Almeida Jr EB & Zickel CS (2013) Do edaphic aspects alter in the structures in the Brazilian restinga? Acta Botanica Brasilica 27: 613-623.

Santos-Filho FS, Almeida Jr EB, Bezerra LFM, Lima LF & Zickel CS (2011) Magnoliophyta, restinga vegetation, state of Ceará, Brazil. Check List 7: 478-485.

Santos-Filho FS, Almeida Jr EB, Soares CJRS & Zickel CS (2015) Flora and woody vegetation structure in an Insular area of restinga in Brazil. International Journal of Ecology and Environmental Sciences 41: 147-160.

Scarano FR (2002) Structure, function and floristic relationships of plant communities in stressful habitats marginal to the Brazilian Atlantic rainforest. Annals of Botany 90: 517-524.

Scarano FR (2009) Plant communities at the periphery of the Atlantic rain forest: rare-species bias and its risks for conservation. Biological Conservation 142: 1201-1208.

Scarano FR, Duarte HM, Ribeiro KT, Rodrigues PJFP, Barcellos EMB, Franco AC, Brulfert J, Deléens E & Lüttge U (2001) Four sites with contrasting environmental stress in southeastern Brazil: relations of species, life form diversity, and geographical distribution to ecophysiological parameters. Botanical Journal of the Linnean Society 136: 345-364.

Scherer A, Maraschin-Silva F & Baptista LRM (2005) Florística e estrutura do componente arbóreo de matas de Restinga arenosa no Parque Estadual de Itapuã, RS, Brasil. Acta Botanica Brasilica 19: 717-726.

Scherer A, Maraschin-Silva F & Baptista LRM (2007) Regeneração arbórea num capão de restinga no Rio Grande do Sul, Brasil. Iherengia, Série Botânica 62: 89-98.

Serra FCV, Lima PB & Almeida Jr EB (2016) Species richness in restinga vegetation on the eastern Maranhão state, Northeastern Brazil. Acta Amazônica 46: 271-280.

Silva SM & Britez RM (2005) A vegetação da planície costeira. *In*: Marques MCM & Britez RM (orgs.) História natural e conservação da Ilha do Mel. Ed. UFPR, Curitiba. Pp. 49-84.

Souza-Filho PW (2005) Costa de manguezais de macromaré da Amazônia: cenários morfológicos, mapeamento e quantificação de áreas usando dados de sensores remotos. Revista Brasileira de Geofísica 23: 427-435.

Souza-Filho PW & El-Robrini M (1996) Morfologia, processos de sedimentação e litofácies dos ambientes morfosedimentares da Planície Costeira Bragantina - Nordeste do Pará (Brasil). Geonomos 4: 1-16.

Stehmann JR, Forzza RC, Salino A, Sobral M, Costa DP & Kamino LHY (2009) Plantas da Floresta Atlântica. Instituto de Pesquisas Jardim Botânico do Rio de Janeiro, Rio de Janeiro. 516p.

Tarola DC & Morellato LPC (2000) Fenologia de espécies arbóreas em floresta de planície litorâneado sudeste do Brasil. Revista Brasileira de Botânica 23: 13-26.

Vieira ICG, Toledo PM & Almedia A (2007) Análise das modificações da paisagem da região bragantina, no Pará, integrando diferentes escalas de tempo. Ciência e Cultura 59: 27-30.

Zickel CS, Almeida Jr EB, Medeiros DPW, Lima PB, Souza TMS & Lima AB (2007) Magnoliophyta species of restinga, state of Pernambuco, Brazil. Check List 3: 224-241.

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