



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 a 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), dispersos 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

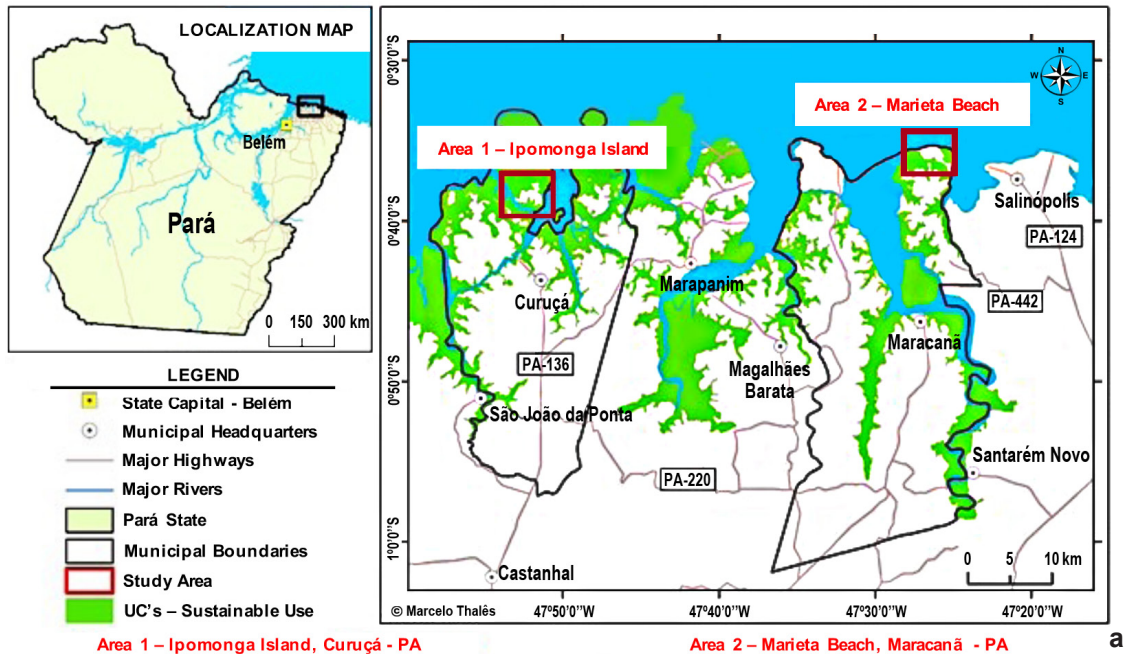
The study was conducted in two stretches of the state of Pará's Atlantic coast, namely the Ipomonga Island in the municipality of Curuçá and the Marieta Beach in the municipality of Maracanã, both in the northeastern part of the state (Fig. 1). The climate is equatorial, hot and humid, with a well-defined 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)

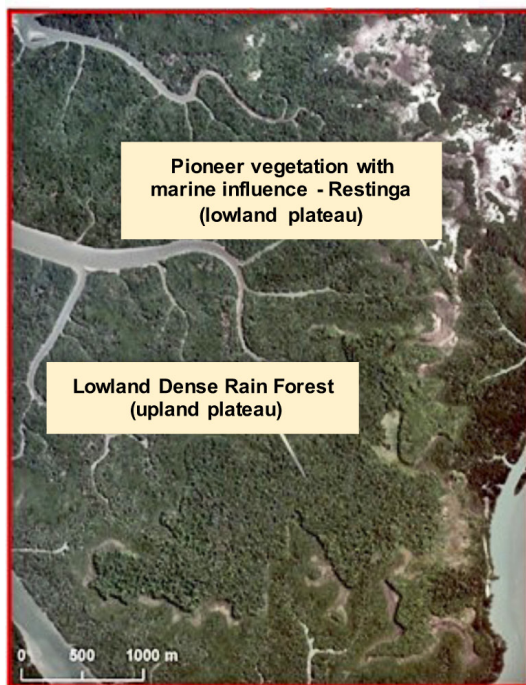
a coastal plain that occurs along the length of the coast mainly influenced by aeolic and wave processes.

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



Area 1 – Ipomonga Island, Curuçá - PA

Area 2 – Marieta Beach, Maracanã - PA



Pioneer vegetation with marine influence - Restinga (lowland plateau)

Lowland Dense Rain Forest (upland plateau)



Lowland Dense Rain Forest (upland plateau)

Pioneer vegetation with marine influence - Restinga (lowland plateau)

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 an 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 & Brites 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 Curuçá 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 macrotidal 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 Emilio Goeldi Museum (Museu Paraense Emilio 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 Algodual 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 Algodual). 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*, *Diploptropis 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					
<i>Lindackeria latifolia</i> Benth.	zooc		X		X
<i>Lindackeria paludosa</i> (Benth.) Gilg	zooc		X		
Anacardiaceae					
<i>Anacardium occidentale</i> L.	zooc	X			
<i>Tapirira guianensis</i> Aubl.	zooc	X	X	X	X
<i>Thyrsodium spruceanum</i> Benth.	zooc		X		
Annonaceae					
<i>Anaxagorea acuminata</i> (Dunal) A.DC.	zooc				X
<i>Annona exsucca</i> DC.	zooc				X
<i>Bocageopsis multiflora</i> (Mart.) R.E.Fr.	zooc	X	X		
<i>Duguetia cadaverica</i> Huber	zooc			X	
<i>Duguetia echinophora</i> R.E.Fr.	zooc			X	X
<i>Guatteria schomburgkiana</i> Mart.	zooc		X		
<i>Unonopsis guattertioides</i> (A.DC.) R.E.Fr.	zooc		X		
<i>Xylopia benthamii</i> R.E.Fr.	zooc		X		
<i>Xylopia cayennensis</i> Maas	zooc		X		
<i>Xylopia emarginata</i> Mart.	zooc	X		X	X
Apocynaceae					
<i>Aspidosperma desmanthum</i> Benth. ex Müll.Arg.	anem		X		X
<i>Himatanthus articulatus</i> (Vahl) Woodson	anem	X	X	X	X
Araliaceae					
<i>Didymopanax morototoni</i> (Aubl.) Decne. & Planch.	zooc		X		
Arecaceae					
<i>Astrocaryum vulgare</i> Mart.	zooc		X	X	X
<i>Attalea maripa</i> (Aubl.) Mart.	zooc		X		X
<i>Mauritiella armata</i> (Mart.) Burret	zooc			X	X
<i>Oenocarpus distichus</i> Mart.	zooc		X		
Bignoniaceae					
<i>Bignonia nocturna</i> (Barb.Rodr.) L.G. Lohmann	anem				X
<i>Jacaranda copaia</i> (Aubl.) D.Don.	anem		X		
<i>Memora magnifica</i> (Mart. ex DC.) Bureau	anem		X		
Boraginaceae					
<i>Cordia nodosa</i> Lam.	zooc		X		
Burseraceae					
<i>Brosimum guianense</i> (Aubl.) Huber	zooc		X		
<i>Protium heptaphyllum</i> (Aubl.) Marchand	zooc	X	X	X	X
<i>Protium krukovii</i> Swart	zooc		X		
<i>Protium tenuifolium</i> (Engl.) Engl.	zooc		X		

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

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

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

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

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

found in both locations (*Xylopia emarginata*, *Couepia bracteosa*, *Licania eglei*, *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 Algodual 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).

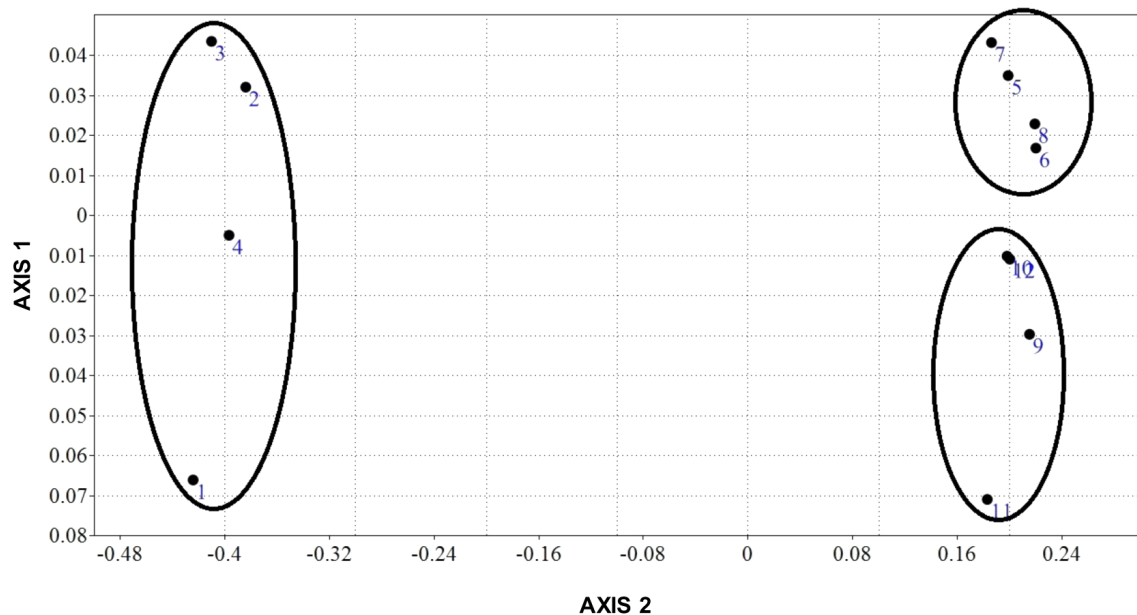


Figure 3 – Non-metric multidimensional scaling (NMDS) of three Restinga according to their floral composition. Ipomonga Island (Curuçá), Marieta Beach (Maracanã) and Algodual (Maracanã), Pará, Brazil.

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*, *Diploptropis 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; Giarretta *et al.* 2013; Kurtz *et al.* 2013). Even though the Marieta beach is only 14 km from the Algodual 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 Algodual 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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