



Original Paper

Phytogeographic relationships of the species of Leguminosae presents in an area of the Atlantic forest domain in the semi-arid region of Brazil

Jacira Rabelo Lima^{1,3} & Vidal de Freitas Mansano²

Abstract

Worldwide, the Atlantic forest domain is considered one of the 34 biodiversity hotspots. In the Northeast region of Brazil, only 2% of its original territory is covered by forests, and part of these forested areas are found in the form of enclaves (“Northeastern brejos”) surrounded by the Thorny woodland. This study aimed to identify the phytogeographic patterns of the species of Leguminosae present in an area of Atlantic forest domain in Northeast Brazil and relate these patterns to abiotic and/or biotic factors to explain the current distribution. For this goal, a floristic inventory was carried out with assessments of dispersal syndromes for each species and construction of maps with distribution patterns. For Baturité Mountain, 60 genera and 128 species of Leguminosae were found. Twelve distribution patterns were identified, ranging from restricted to the Northeast region of Brazil to extracontinental. Long-distance dispersion events were the best explanation for the extracontinental distribution pattern, whereas vicariance can explain distribution restricted to the American continent.

Key words: dispersal syndromes, Fabaceae, hotspots, Northeastern atlantic forest, phytogeographic patterns.

Resumo

O domínio da Floresta atlântica é considerado um dos 34 hotspots de biodiversidade. Na região Nordeste do Brasil, apenas 2% da área original está coberta por florestas, e parte dessas áreas florestais são encontradas na forma de enclaves (“Brejos nordestinos”) em meio à Caatinga. O objetivo deste estudo foi identificar os padrões fitogeográficos das espécies de Leguminosae presentes em uma área de Floresta Atlântica no Nordeste do Brasil e relacionar os padrões fitogeográficos a fatores abióticos e/ou bióticos para explicar a distribuição atual das espécies. Para tanto, foi realizado um levantamento das espécies de Leguminosae da área, com suas síndromes de dispersão e confecção de mapas com padrões de distribuição. Na área de estudo foram encontrados 60 gêneros e 128 espécies de Leguminosae. Foram identificados 12 padrões de distribuição, variando de restrito ao Nordeste do Brasil à padrões extracontinentais. Eventos de dispersão a longa distância foram a melhor explicação para o padrão de distribuição extracontinental, enquanto vicariância pode explicar a distribuição restrita ao continente americano.

Palavras-chave: síndromes de dispersão, Fabaceae, hotspots, floresta atlântica nordestina, padrões fitogeográficos.

Introduction

The Atlantic forest domain (hereafter Atlantic forest) has an incredibly diverse biota (MMA 2000), likely having up to 8% of the world’s biodiversity (Silva & Casteleti 2005). About 90% of this domain

is deforested (Fundação SOS Mata Atlântica 2017; Fonseca *et al.* 2005) and can be considered the most devastated and seriously threatened area on the planet (Galindo-Leal *et al.* 2005). Despite all the devastation that was historically inflicted

See supplementary material at <<https://doi.org/10.6084/m9.figshare.16564215.v1>>

¹ Universidade Federal Rural do Rio de Janeiro, Inst. Ciências Biológicas e da Saúde, Depto. Botânica, Seropédica, RJ, Brasil. ORCID: <<https://orcid.org/0000-0002-5560-5619>>.

² Instituto de Pesquisas Jardim Botânico do Rio de Janeiro, Diretoria de Pesquisas, Jardim Botânico, Rio de Janeiro, RJ, Brasil. ORCID: <<https://orcid.org/0000-0002-7204-0744>>.

³ Author for correspondence: jacirabelo@gmail.com

on this domain, it still harbors high levels of biological richness and endemisms (MMA 2000). It is considered one of the 34 biodiversity hotspots worldwide (Mittermeier *et al.* 2005).

The Atlantic forest from the Northeast of Brazil occupies about 2% of its original territory (Tabarelli *et al.* 2006). Some of these areas are found in the form of enclaves (“Northeastern brejos”) inside the Thorny woodland (Caatinga) (Silva & Casteleti 2005). These areas are considered refuges for both flora and fauna because they present a more humid, colder climate than the dry vegetation surrounding them (Andrade-Lima 1982). Baturité Mountain, located in the state of Ceará, is considered one of the greatest “Northeastern brejos” (Silva & Casteleti 2005; Siqueira Filho & Leme 2006) with vegetation varying according to the slope (windward or leeward) and elevation on the slope, ranging from seasonal semideciduous forest, seasonal deciduous forest (leeward slope) to the rainforest (windward slope) (Oliveira & Araújo 2007). The few studies conducted in the area show a vibrant flora, and Leguminosae is one of the most diverse families in this area (Lima *et al.* 2012a, b; Figueiredo & Barbosa 1990; Cavalcante *et al.* 2000; Araújo *et al.* 2006).

Leguminosae Jussieu is composed of roughly 770 genera and 19,500 species (LPWG 2013). They are incredibly diverse, both in their ecology and morphology, from large trees to small annual herbs (Lewis 1987; Lewis *et al.* 2005). They have a worldwide distribution and are among the families with the highest species richness in neotropical forests (Gentry 1982, 1988, 1995), with greater diversity in the seasonal forest (Lima *et al.* 2015) and in temperate shrub vegetation with xeric climates (Wojciechowski *et al.* 2004).

The distribution of species may respond to both abiotic (climate and soil) and biotic factors and historical aspects (Motzkin *et al.* 1999). According to Schrire *et al.* (2005), the Leguminosae originated in an area of seasonal deciduous forest and later dispersed to other vegetation, including the rainforest. As a result, the family has a phylogeny more strongly associated with the type of vegetation than to the geographical proximity, particularly for those species from drier environments (Schrire *et al.* 2005). This suggests that abiotic factors, such as climate and soil, are essential variables for the distribution of Leguminosae. However, according to Krebs (1985), dispersion capacity is among the main factors influencing the distribution of a species. Dispersal syndromes are characterized as

plant’s strategy to succeed in the dispersion phase of their diaspores (Stebbins 1974). In general, in dry forests anemochoric species are predominant, while in the rainforests, zoochoric species dominate (Howe & Smallwood 1982). However, some studies have shown that autochoric and zoochoric species may also predominate in areas of dry forests (Barbosa *et al.* 2003; Silva & Rodal 2009; Griz & Machado 2001; Costa *et al.* 2004; Rocha *et al.* 2004; Toppa *et al.* 2004; Noguchi *et al.* 2009).

As the family has a phylogeny more strongly associated with the type of vegetation than the geographical proximity, it is expected that the phytogeography patterns of the species of Leguminosae of Baturité Mountain vary according to their presence on each slope; the species found on the leeward slope are those distributed mainly in dry vegetation, while the species present on the windward slope are mainly distributed in moist vegetation. However, if the dispersion syndromes also influence the distribution of Leguminosae, it is expected that anemochoric species, with their diaspores presenting structures that help their dispersion (*e.g.*, wings) exhibit broader phytogeographic patterns than those shown by species with other dispersion syndromes (autochoric, barochoric or zoochoric).

This study aimed to identify the phytogeographic patterns of the species of Leguminosae present in an area of Atlantic forest in Northeast Brazil. It also aimed to determine which domains and/or vegetation where the species occur, related to abiotic (slope) and/or biotic (dispersal syndromes) factors, to ascertain 1) what the phytogeographic patterns of the Leguminosae species present in the study area are, 2) in which domains and/or vegetation the species are found and 3) the relationships between the phytogeographic patterns, slope, domains and/or vegetation and dispersal syndromes.

Material and Methods

Description of the study area

Baturité Mountain (Fig. 1) is located in the semiarid region of Northeast Brazil in the state of Ceará and has an area of 3,822 km² with a NNE-SSW orientation, situated between the coordinates 04° to 04°30’S and 38°45’ to 39°15’W and is ca. 90 km from the coast. It is one of the largest areas of high elevation in the state of Ceará, with altitudes ranging from 500 to 1,115 m (Souza 1988). The disposition of relief compared to the displacement of winds provides the occurrence of convection

rains caused by the northern and northeast slopes, resulting in higher rainfall and relative humidity than in the surrounding regions (700 mm/year). As a result, a rain shadow is formed on the leeward slope (Funceme 2005). Thus, the average annual precipitation and the temperature estimated by regression at the headquarters of the cities of Mulungu, Guaramiranga and Pacoti, located on the windward slope of the mountain, were 1,221, 1,711 and 1,558 mm and 20.8, 21 and 21.4 °C, respectively (Sudene 1982; Funceme 2005). While the city of Capistrano, located on the leeward side, has a mean annual temperature and rainfall of 846 mm and 26 °C, respectively (Ipece 2007).

The vegetation found in the mountains varies with elevation and position of the slope. On the leeward slope there are the semideciduous seasonal forests above 600 m and deciduous seasonal forest below 600 m. On the windward slope, due to orographic rains caused by the shifting winds, the rainforest is observed (Araújo *et al.* 2006).

Floristic inventory of Leguminosae

All life forms were collected (tree, shrub, subshrub, herbaceous, climbing and lianas) in areas of different elevations and vegetation types of Baturité Mountain. More information about the floristic inventory can be found in Lima *et al.* (2012a, b). The classification of species into subfamilies followed LPWG (2017).

Phytogeographic patterns and occurrence of the species in different vegetations

The distribution patterns were characterized from the information of the geographical distribution of species obtained from the data from herbarium labels, taxonomic revisions and Lima *et al.* (2015) and the Flora do Brasil (2020). The patterns were characterized from the overlapping of the species occurrence of extensions adapted from those described in the literature (Morim 2006).

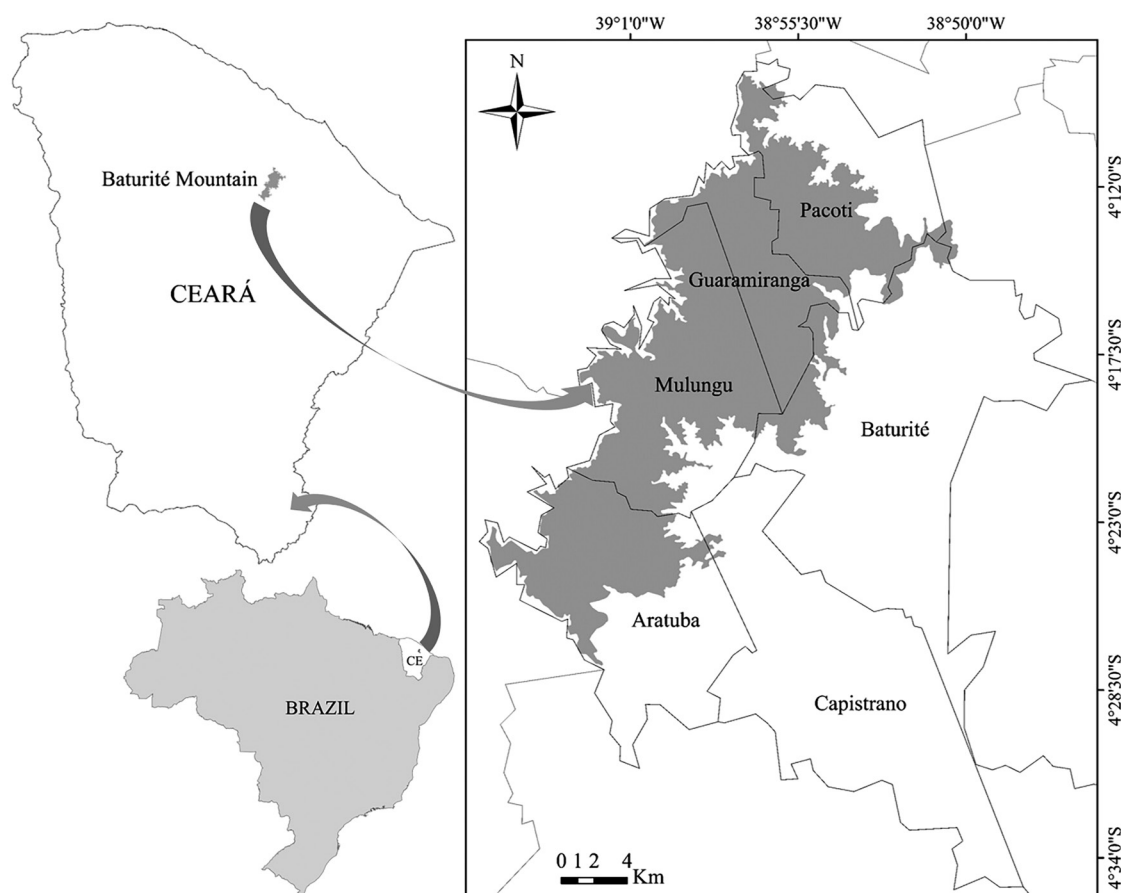


Figure 1 – Map of Brazil showing the location of the state of Ceará and the position of the Baturité Mountain range.

The following domains types are mentioned in the text (Fiaschi & Pirani 2009): Amazon, Thorny woodland (known as Caatinga), Savannah (known as Cerrado) and Atlantic forest. The concept of Atlantic forest (*sensu lato*) adopted in this work follows Oliveira-Filho & Fontes (2000), which includes rainforest and seasonal forests (semideciduous and deciduous).

Dispersal syndromes

The dispersal syndromes were established based on characteristics, such as type, consistency and color of fruit, according to Pijl (1982). Biotic syndromes were considered zoochoric, *i.e.*, species that produce fleshy fruits or arillated seeds, *e.g.*, diaspores with adaptations that allow dispersal by animals, while abiotic syndromes were considered anemochoric, *i.e.*, species whose diaspores present forms, structures or dimensions that allow wind dispersal; barochoric, *i.e.*, dispersion performed by free fall of diaspores via their own weight; or autochoric, *i.e.*, species with diaspores which do not have any of the characteristics listed above.

Results

Floristic inventory of Leguminosae

In the study area were registered 60 genera and 128 species of Leguminosae (Tab. 1, available on supplementary material <<https://doi.org/10.6084/m9.figshare.16564215.v1>>). Caesalpinioideae shows higher richness of both genera and species (24 and 63, respectively), followed by Papilionoideae (32 genera and 57 species), Cercidoideae (two genera and six species) and Detarioideae (two genera and two species). A higher species richness was observed on the leeward slope (91 species, 49 of them exclusive), whereas for the windward slope 79 species were found (37 of them exclusive).

The most diverse genera in the area were *Mimosa* L. (15), *Senna* Mill. (12), *Desmodium* Std. (seven), *Inga* Mill. and *Aeschynomene* L. (six each). Of the 60 genera, 45 were found on the leeward slope (14 exclusive) and 46 on the windward (15 exclusive). Many of the exclusive genera of the leeward slope, such as *Aeschynomene* and *Chloroleucon*, are among those characteristic of semiarid environments (Schrire *et al.* 2005; Queiroz 2009).

The analysis of the distribution of subfamilies by slope shows that Papilionoideae and Caesalpinioideae are the most diverse on

both the leeward (48% and 46.1% of the species present in the slope, respectively) and windward slopes (each with 45% of the species present in the slope) of Baturité Mountain. It is important to note that no species of the subfamily Detarioideae has been recorded on the leeward slope.

Phytogeographic patterns and occurrence of the species in different vegetations

A total of 12 geographical distribution patterns for the species of Leguminosae of Baturité mountain were found (Tab. S1, available on supplementary material <<https://doi.org/10.6084/m9.figshare.16564215.v1>>; Fig. 2). Of the 128 species analyzed, 97 (76%) had broader distribution patterns, also being found outside Brazil (seven patterns), while 31 species (24%) presented patterns restricted to Brazil (five patterns). The following patterns were found:

Pantropical – The species are distributed in tropical regions of the Americas, Africa and Asia. Nine species showed this pattern. Some of these species are considered native to the Americas and introduced on other continents [*Crotalaria incana* L. and *Senna occidentalis* (L.) Link], while some, like *Crotalaria retusa* L. and *Crotalaria pallida* Blanco, are native to Asia and Africa, respectively, and introduced in the rest of the world (Polhill 1982). However, some species are considered native to the Americas, Africa, tropical Asia [*Chamaecrista absus* (L.) H. S. Irwin & Barneby, *Mimosa pigra* L., *Indigofera microcarpa* Desv., *Rhynchosia minima* (Chiov.) Verdc. and *Vigna vexillata* (L.) A. Rich.]. All species of this pattern are widely distributed in different Brazilian domains (Amazon, Atlantic forest, Thorny woodland and Savannah). All species of this pattern are autochoric and were represented by herbaceous, shrub, subshrub and climbing plants.

African-American – *Lonchocarpus sericeus* (Poir.) Kunth ex DC, *Mucuna sloanei* Fawc. & Rendle, *Parkinsonia aculeata* L. and *Zornia latifolia* Sm. present disjunct distributions between America and tropical Africa, considered native to both continents. *Zornia latifolia* and *Parkinsonia aculeata* were found exclusively on the leeward slope and *Mucuna sloanei* only on the windward slope, while *Lonchocarpus*

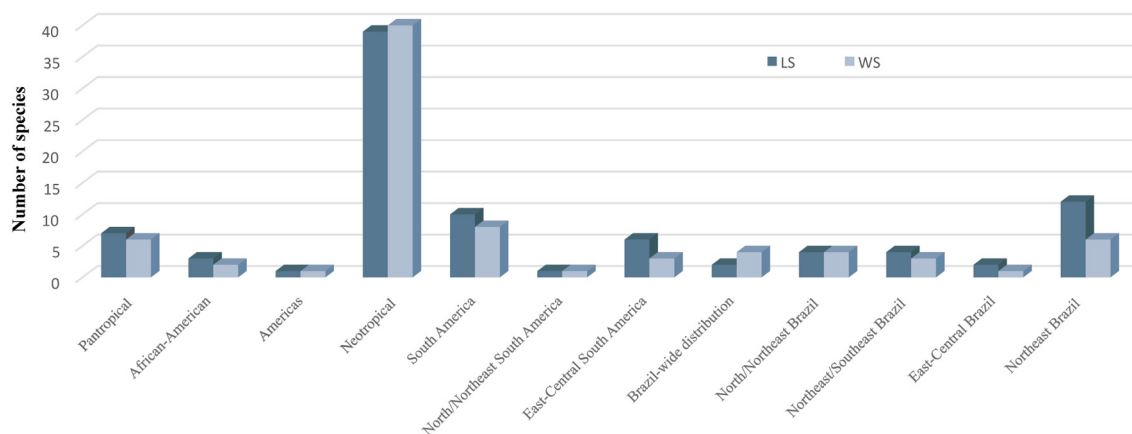


Figure 2 – Distribution patterns of species of Leguminosae on the leeward slope (LS) and windward slope (WS) of Baturité Mountain, Ceará, Brazil (see text for definitions).

sericeus was found on the two slopes, but in dry areas it occurs near the banks of rivers. All species of this pattern are widely distributed in different Brazilian domains (Amazon, Atlantic forest, Thorny woodland and Savannah). The species of this pattern have dispersal syndromes autochoric (two), anemochoric and zoochoric dispersal syndromes.

Americas – Only two species exhibit this pattern, *Aeschynomene evenia* C. Wright ex Sauvalle and *Senna hirsuta* (L.) H.S. Irwin & Barneby, which are found in tropical and subtropical regions of America. Both species are found in different Brazilian domains (Amazon, Atlantic forest, Thorny woodland and Savannah). These two species are subshrubs and have autochoric (*Senna hirsuta*) and zoochorous (*Aeschynomene evenia*) dispersal syndromes.

Neotropical (Fig. 3) – A total of 30 genera and 61 species (47.6%) of Leguminosae of Baturité Mountain are found from Mexico to southern Argentina. Of the 61 species, 40 were found on the windward slope (with 22 exclusive), 39 on the leeward slope (21 exclusive) and 18 were common to both sides. Various species of this pattern occur in different Brazilian domains, such as Amazon, Atlantic forest, Savannah, and Thorny woodland. Some exclusive species to the leeward slope, such as *Mimosa somnians* Humb. & Bonpl. ex Willd. subsp. *somnians*, *Mimosa tenuiflora* (Willd.) Poir., and *Mimosa ursina* Mart. are found only in areas of Savannah and Thorny woodland.

The most common dispersion syndrome found in the species with this pattern was the autochoric, represented by 34 species (55.7%), followed by zoochoric (41%) and anemochoric with only two species (3.3%). There was a predominance of subshrubs habit (17), followed by tree (15) and shrubs (12).

South America (Fig. 3) – Nine genera and 11 species of Baturité Mountain are distributed throughout South America, continuously or disjunct. On the windward slope eight species were found (one exclusive), while on the leeward slope ten were found (three exclusive). Various species of this pattern occur in different Brazilian domains, such as Amazon, Atlantic forest, Savannah and Thorny woodland. Of the 11 species, eight are autochoric, two are zoochoric, and one is anemochoric. Habits vary from climbing, subshrubs and shrubs (three species each), and lianas and scandent shrubs (one species each).

North and Northeast South America (Fig. 3) – The two species with this pattern [*Bauhinia acreana* Harms and *Chloroleucon acacioides* (Ducke) Barneby & J.W. Grimes] are distributed in North and Northeast Brazil, reaching the northern part of South America. On Baturité Mountain, *B. acreana* was exclusive to the windward slope, while *C. acacioides* was exclusive to the leeward slope. All the species are found in areas of Amazon and Atlantic forest, however *C. acacioides* also occurs in areas of Savannah and Thorny woodland. All are autochorous with tree and shrub habit.

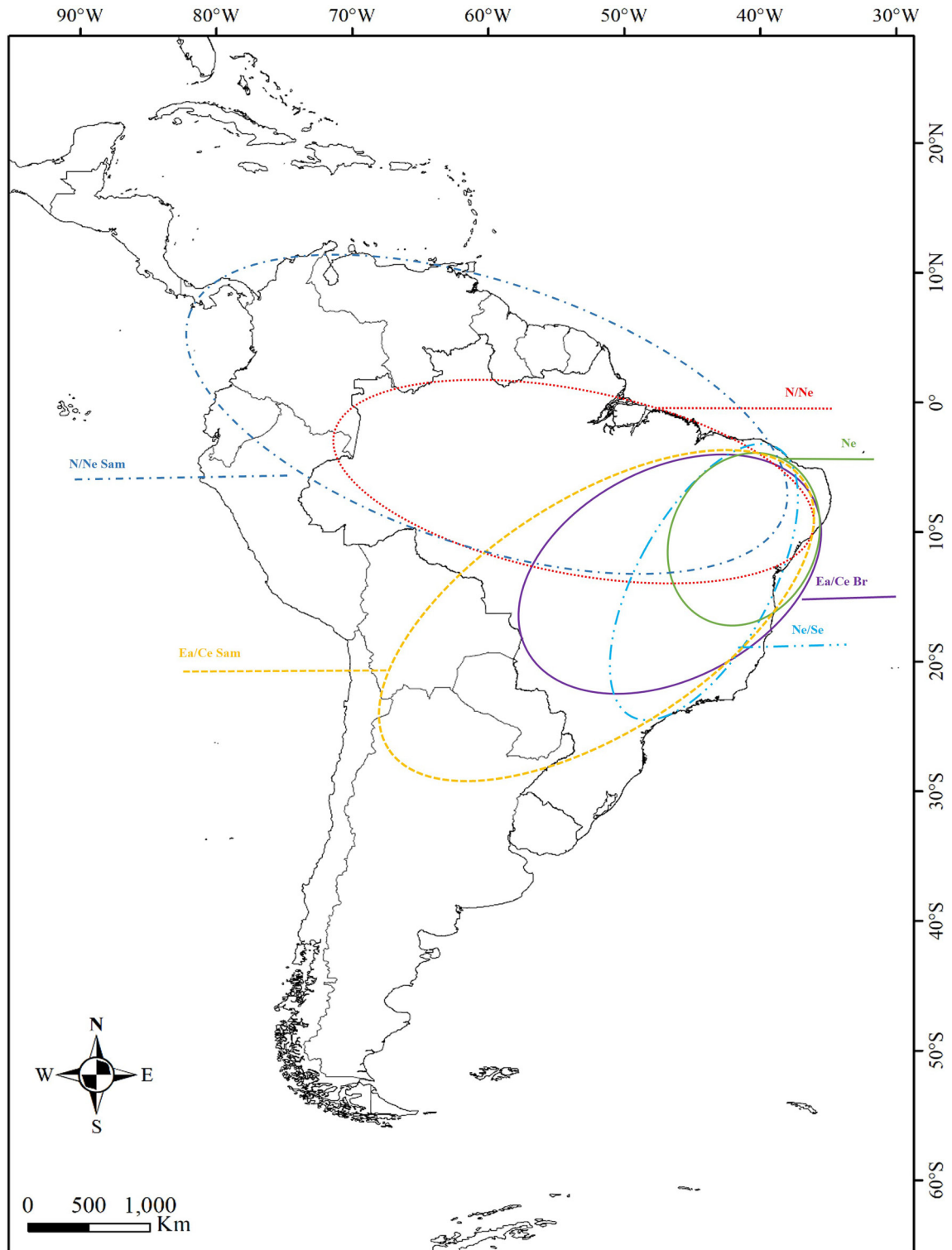


Figure 3 – Distribution patterns of the species of Leguminosae of Baturité Mountain, Ceará, Brazil. Ea/Ce Sam (yellow) = East-Central South America; N/Ne Sam (gray) = North and Northeast South America; Ea/Ce Br (purple) = Central-Eastern Brazil; N/Ne (red) = North/Northeast Brazil; Ne/Se (blue) = Northeast/Southeast Brazil; Ne (green) = Northeast Brazil. The broadest patterns (Pantropical, African-American, Americas, Neotropical, South America, and Brazil-wide distribution), are not included in this map because they are widely known.

East-Central South America (Fig. 3) – This pattern was observed in eight species that are distributed throughout the Northeast, Central-West and Southeast regions of Brazil to Bolivia, Paraguay and Argentina. Various species of this pattern occur in different Brazilian domains, such as Amazon, Atlantic forest, Savannah and Thorny woodland. On Baturité Mountain, three species were found on the windward slope, with two exclusive to this slope [*Ateleia guaraya* Herzog and *Mimosa bimucronata* (DC) Kuntze]. Six species were located in the leeward slope, five of which are exclusive. The species of this pattern showed four types of dispersion syndromes being autochory the predominant one (five species). Only two habits are found: tree and shrub (four species each).

Brazil-wide distribution (Fig. 3) – The four species with this pattern are restricted to Brazil and distributed in at least four of the five Brazilian regions. On Baturité Mountain, all species were found on the windward slope (two exclusive), and two are also found on the leeward slope. Three species of this pattern occur Atlantic forest, Savannah and Thorny woodland, and one occur in areas of the Amazon [*Periandra coccinea* (Schrad.) Benth.]. All species of this pattern have dispersal syndromes autochoric. Habits vary from tree (two), shrub, and climbing.

Central-Eastern Brazil (Fig. 3) – The two species [*Platymiscium floribundum* var. *nitens* (Vogel) Klitgaard and *Trischidium molle* (Benth.) H.Ireland] with this pattern are restricted to Brazil and distributed in the Northeast, Central-West, and Southeast regions of Brazil. Both species are found in areas of Atlantic forest and Thorny woodland, with *Platymiscium floribundum* var. *nitens* also occurring in areas of Savannah. These two species are trees and have anemochoric (*Platymiscium floribundum* var. *nitens*) and zoochorous (*Trischidium molle*) dispersal syndromes.

North/Northeast Brazil (Fig. 3) – The six species with this pattern are distributed in North and Northeast Brazil. On Baturité Mountain, four species were found on the windward slope (two exclusive) and four on the leeward slope (two exclusive). Various species of this pattern occur in different Brazilian domains, such as Amazon, Atlantic forest, Savannah, and Thorny woodland. We found species with autochoric and zoochoric dispersal syndromes (three each). There was a

predominance of tree species (four), followed by a subshrubs species and a liana.

Northeast/Southeast Brazil (Fig. 3) – Five species are distributed throughout the Northeast and Southeast regions of Brazil. On Baturité Mountain, three species are found on the windward slope (an exclusive) and four on the leeward slope (two exclusive). Species included in this pattern are distributed in areas of the Atlantic forest, Savannah and Thorny woodland. The species of this pattern present autochoric (four), and zoochoric (one) dispersal syndromes.

Northeast Brazil (Fig. 3) – The species of this pattern are distributed throughout Northeast Brazil. This pattern is represented by 14 species, of which 12 are found on the leeward slope (nine exclusive), while only five are found on the windward slope (two exclusive). All species occur in Thorny woodland (nine exclusive to this domain), except *Inga bollandii* Sprague & Sandwith, which is found only in rainforest (Pennington 1997). The autochorous species were predominant (11 species), followed by zoochoric (two species) and anemochoric (one species).

Dispersal syndrome

The predominant dispersal syndrome was autochoric (65%), followed by zoochoric (28%), anemochoric (6.2%) and barochoric (0.8%). Syndromes prevalent in two parts (windward and leeward) were autochoric (62% and 68.1%, respectively) and zoochoric (29% and 24.1%, respectively). The anemochory syndrome was represented by only 9% of the species of the windward slope and 6.6% of the leeward slope. The only species with barochoric syndrome (*Enterolobium timboíva* Mart.) was registered on the leeward slope. All anemochoric and barochoric species are tree, and the autochoric and zoochoric species are represented by all habits.

Discussion

Floristic inventory of Leguminosae

The high species richness on the study area and the greater diversity in the leeward slope may be related to the fact that Leguminosae species present compound leaves, seeds with hard testa, a long period of dormancy and viability (Schrire *et al.* 2005) and the ability to store nitrogen through symbiotic association with bacteria in root nodules

(Wojciechowski *et al.* 2004; Sprent 2007). These morphological and physiological characteristics give the family a great advantage, especially in dry vegetations. One of the reasons that can explain the competitive advantage over other families present in the arid and semiarid environments is that its species fix nitrogen have a higher photosynthetic rate because they present a higher concentration of leaf nitrogen (McKey 1994). Approximately 94% of the species of the areas studied belong to Caesalpinoideae and Papilionoideae, the subfamilies in which nitrogen fixation is most prevalent (Allen & Allen 1981; Sprent 2007).

The subfamily Papilionoideae showed a greater diversity of species on both slopes, which was expected because it is the subfamily of greater general diversity, with many species adapted to the most different types of vegetation, many with nitrogen fixation capacity (Wojciechowski *et al.* 2004; Sprent 2007). However, it is noteworthy that Caesalpinoideae has a high diversity of species on the leeward side (46.1% species). With the new classification of the family (LPWG 2017), the former subfamily Mimosoideae was recognized as a clade of Caesalpinoideae (mimosoid clade), increasing the general diversity of this subfamily by about 50%. The inclusion of the mimosoid clade in Caesalpinoideae means an increase of 28 species in the subfamily on the leeward side. It should be noted that many of these species belong to genera commonly associated with dry environments (Lewis *et al.* 2005; Queiroz 2009; Orchard & Maslin 2003) and that are exclusive to the leeward side, for example, *Chloroleucon*, *Lachesiodendron*, *Parkinsonia* and *Vachellia*.

Phytogeographic patterns, occurrence of the species in different domains and/or vegetations and dispersal syndromes

In general, it is expected that species with diaspores adapted to wind dispersal (samaras, for example) exhibit a larger geographical distribution range than those whose diaspores have no apparent adaptation to a particular type of transport (autochoric, for example). The so-called autochoric species have a more restricted pattern. However, for species of Leguminosae of Baturité Mountain, the broadest distribution patterns (Pantropical, African-American, Neotropical and South American) were mainly dominated by autochoric species, while all anemochoric species have distribution patterns more

restricted when compared to the autochoric ones. For example, *Dalbergia cearensis* is an anemochoric species restricted to Northeast Brazil. The only exception is *Lonchocarpus sericeus* which has an African-American distribution.

Higgins *et al.* (2003) conducted a study in which they attempted to associate the morphology of the diaspores (fruits or seeds) to the long-distance dispersion events. The authors concluded that there is no apparent relationship between the two factors analyzed. Thus, other factors may be responsible for long-distance dispersion of fruits and seeds. This result has been confirmed with phylogenetic studies showing that many species with transcontinental distribution have relatively recent age for their distribution to be explained by vicariance events, such as tectonic plates; these species are among examples within Leguminosae (Lavin *et al.* 2004; Richardson *et al.* 2004), Lauraceae (Chanderbali *et al.* 2001), Melastomataceae (Renner *et al.* 2001; Renner 2004a) and Annonaceae (Richardson *et al.* 2004).

For some authors, long-distance dispersion cannot be underestimated because the great diversity of Neotropical groups, such as Leguminosae, appear to be largely the result of recent transoceanic migration (Lavin *et al.* 2004; Richardson *et al.* 2004). Indeed, the Pantropical and African-American distribution patterns of the Leguminosae of Baturité Mountain cannot be explained based on vicariance due to plate tectonics since the estimated age of the family is 60 million years (Schrire *et al.* 2005), a period of time when the American and African continents were already disjunct. For Lavin *et al.* (2004), a possible explanation for such a distribution involves long-distance dispersions. Renner (2004b) analyzed the distribution of 110 African-American genera and found that the dispersion via oceanic currents is likely the main form of dispersion between those two continents, being more important than dispersal by birds or wind.

For Schrire *et al.* (2005), species with transcontinental distribution are frequently found in different domains and/or vegetation, while the species found only in the dry formations generally have distributions restricted to a continent. In fact, all species of Baturité Mountain presenting transcontinental distribution were found different domains and/or vegetation formations [Amazon, Atlantic forest (seasonal forests and rainforests), Savannah and Thorny woodland], while many species with more restricted distribution patterns are found only in a single vegetation type. Of the 14

species with Northeast Brazil distribution pattern, nine are exclusive to the Thorny woodland.

Among the exclusive species on each slope (Tab. S1, available on supplementary material <<https://doi.org/10.6084/m9.figshare.16564215.v1>>), excluding the Neotropical species that were prevalent on both slopes, a predominance of species on the leeward slope were observed with distribution patterns related to dry areas, such as those restricted to the Northeast (27.6%) and the East-central South American pattern (21%). In addition, 43% of the species exclusive to the leeward slope are found only in drier domains (Savannah and Thorny woodland). On the other hand, the exclusive species of the windward slope have the pattern associated with wetter areas, with the species of the pattern North/Northeast Brazil occurring in areas of the Amazon and rainforests of the Northeast, and species of the Northeast/Southeast Brazil pattern mainly occur in areas of rainforest. This result agrees with the ideas of Schrire *et al.* (2005), suggesting that abiotic factors, such as climate, are important variables for the distribution of Leguminosae.

The species of Baturité Mountain have distribution patterns ranging from transcontinental, such as Pantropical and African-American, to endemic, such as Northeast Brazil. The long-distance dispersal is the best hypothesis to explain transcontinental distribution patterns. For species with distribution patterns restricted to the American continent, the hypothesis is that the rainforests and seasonal forests were continuous during the Quaternary. However, the vegetation types are presently disjunct, which may explain patterns such as east-central South America, or endemic, such as those of Northeast Brazil.

The species showed a strong association with the environment, corroborating the data of Schrire *et al.* (2005). The exclusive species of the windward slope have distribution patterns that primarily involve areas of rainforests (North/Northeast and Northeast/Southeast Brazil patterns), while many of the leeward slope species show a pattern mainly involving areas of Thorny woodland and Savannah (Northeast Brazil and East-central South America).

References

- Allen ON & Allen EK (1981) The Leguminosae: a source book of characteristics, uses and nodulation. The University of Wisconsin Press, Madison. 812p.
- Andrade-Lima D (1982) Present day forest refuges in northeastern Brazil. *In*: Prance GT (ed.) Biological diversification in the Tropics. Columbia University Press, New York. Pp. 245-251.
- Araújo FS, Santos VG, Silveira AP, Figueiredo MA, Oliveira RF, Bruno MMA, Lima-Verde LW & Silva EF (2006) Efeito da variação topoclimática na fisionomia e estrutura da vegetação da Serra de Baturité, Ceará. *In*: Oliveira TS & Araújo FS (eds.) Diversidade e conservação da biota na Serra de Baturité, Ceará. Ufc/Coelce, Fortaleza. Pp. 137-162.
- Barbosa DCA, Barbosa MCA & Lima LCM (2003) Fenologia de espécies lenhosas de Caatinga. *In*: Leal IR, Tabarelli M & Silva JMC (eds.) Ecologia e conservação da Caatinga. Editora Universitária da UFPE, Recife. Pp. 657-694.
- Cavalcante AMB, Soares JJ & Figueiredo MA (2000) Comparative phytosociology of tree sinusiae between contiguous forests in different stages of succession. *Revista Brasileira de Biologia* 60: 551-562.
- Chanderbali AS, Van der Werff H & Renner SS (2001) Phylogeny and historical biogeography of Lauraceae: evidence from the chloroplast and nuclear genomes. *Annals of the Missouri Botanical Garden* 88: 104-134.
- Costa IR, Araújo FS & Lima-Verde LW (2004) Flora e aspectos auto-ecológicos de um enclave de Cerrado na Chapada do Araripe, nordeste do Brasil. *Acta Botanica Brasilica* 18: 759-770.
- Fiaschi P & Pirani JR (2009) Review of plant biogeographic studies in Brazil. *Journal of Systematics and Evolution* 47: 1-20.
- Figueiredo MA & Barbosa A (1990) A vegetação e flora da Serra do Baturité-Ceará. *Coleção Mossoroense (série B)* 747: 1-10.
- Flora do Brasil 2020. Jardim Botânico do Rio de Janeiro. Available at <<http://floradobrasil.jbrj.gov.br/>>. Access in March 2020.
- Fonseca GAB, Mittermeier RA & Seligmann P (2005) Mata Atlântica: biodiversidade, ameaças e perspectivas. *In*: Galindo-Leal C & Câmara IG (eds.) Mata Atlântica: biodiversidade, ameaças e perspectivas. Fundação SOS Mata Atlântica, Belo Horizonte. Pp. VIII-XV.
- Funceme (2005) Relatório de pluviometria por faixa de anos - estado do Ceará. Departamento de apoio tecnológico (Detec), Fortaleza. Available at <<http://www.funceme.br/DEPAM/index.htm>>. Access on 10 January 2019.
- Fundação SOS Mata Atlântica (2017) Atlas da evolução dos remanescentes florestais da Mata Atlântica, período 2015-2016: relatório final. Fundação S.O.S. Mata Atlântica/INPE, São Paulo. 60p.
- Galindo-Leal C, Jacobsen TR, Langhammer PF & Olivieri S (2005) Estados dos hotspot: a dinâmica da perda de biodiversidade. *In*: Galindo-Leal C & Câmara IG (eds.) Mata Atlântica: biodiversidade, ameaças e perspectivas. Fundação SOS Mata Atlântica, Belo Horizonte. Pp. 12-23.

- Gentry AH (1982) Patterns of Neotropical plant species diversity. *Evolution Biological* 15: 1-84.
- Gentry AH (1988) Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Annals of the Missouri Botanical Garden* 75: 01-34.
- Gentry AH (1995) Diversity and floristic composition of Neotropical Forest. *In: Bullock SH, Mooney H & Medina E (eds.) Seasonally Dry Tropical Forest*. Cambridge University Press, Cambridge. Pp. 146-194.
- Griz LMS & Machado ICS (2001) Fruiting phenology and seed dispersal syndromes in caatinga, a tropical dry forest in Northeast of Brazil. *Journal of Tropical Ecology* 17: 303-321.
- Higgins SI, Nathan R & Cain ML (2003) Are long-distance dispersal events in plants usually caused by nonstandard means of dispersal? *Ecology* 84: 1945-1956
- Howe HF & Smallwood J (1982) Ecology of seed dispersal. *Annual Review of Ecology and Systematics* 13: 201-228.
- Ipece (2007) Perfil básico municipal: Capistrano. Instituto de Pesquisa e Estratégia Econômica do Ceará. IPECE, Fortaleza. 17p.
- Krebs CJ (1985) *Ecology. The experimental analysis of distribution and abundance*. Harper & Row Publishers, New York. 816p.
- Lavin M, Schrire BD, Lewis GP, Pennington RT, Delgado-Salinas A, Thulin M, Hughes CE, Beyra-Matos A & Wojciechowski MF (2004) Metacommunity processes rather than continental tectonic history better explain geographically structured phylogenies in legumes. *Philosophical Transactions of the Royal Society, Biological Series* 359: 1509-1522.
- Lewis GP, Schrire BD, Mackinder BA & Lock JM (2005) *Legumes of the World*. Royal Botanic Gardens, Kew. 577p.
- Lewis GP (1987) *Legumes of Bahia*. Royal Botanic Gardens, Kew. 369p.
- Lima JR, Tozzi AMGA & Mansano VF (2015) A checklist of woody Leguminosae in the South American Corridor of Dry Vegetation. *Phytotaxa: a rapid international journal for accelerating the publication of botanical taxonomy* 207: 1-38.
- Lima JR, Mansano VF & Araújo FS (2012a) Richness and diversity of Leguminosae in an altitudinal gradient in the tropical semi-arid zone of Brazil. *Journal of Systematics and Evolution* 50: 433-442.
- Lima JR, Mansano VF & Araújo FS (2012b) Coexistence and geographical distribution of Leguminosae in an area of Atlantic forest in the semi-arid region of Brazil. *Journal of Systematics and Evolution* 50: 25-35.
- LPWG - The Legume Phylogeny Working Group (2013) Legume phylogeny and classification in the 21st century: progress, prospects and lessons for other species-rich clades. *Taxon* 62: 217-248.
- LPWG - The Legume Phylogeny Working Group (2017) A new subfamily classification of the Leguminosae based on a taxonomically comprehensive phylogeny. *Taxon* 66: 44-77.
- McKey D (1994) Legumes and nitrogen: the evolutionary ecology of a nitrogen-demanding lifestyle. *In: Sprent JI & McKey D (eds.) Advances in legume systematics 5: the nitrogen factor*. Royal Botanic Gardens, Kew. Pp. 211-228.
- Mittermeier RA, Gil PR, Hoffmann M, Pilgrim J, Brooks T, Mittermeier CG, Lamoureaux J & Fonseca GAB (2005) Hotspots revisited: earth's biologically richest and most endangered terrestrial ecoregions. *CEMEX and Conservation International*, Washington. 392p.
- MMA - Ministério do Meio Ambiente (2000) Avaliação e ações prioritárias para a conservação da Biodiversidade da Floresta Atlântica e Campos Sulinos. MMA/SBF, Brasília. 40p.
- Morim MP (2006) Leguminosae arbustivas e arbóreas da Floresta Atlântica do Parque Nacional do Itatiaia, sudeste do Brasil: padrões de distribuição. *Rodriguésia* 57: 27-45.
- Motzkin G, Wilson P, Foster DR & Allen A (1999) Vegetation patterns in heterogeneous landscapes: the importance of history and environment. *Journal of Vegetation Science* 10: 903-920.
- Noguchi DK, Nunes GP & Sartori ALB (2009) Florística e síndromes de dispersão de espécies arbóreas em remanescentes de Chaco de Porto Murinho, Mato Grosso do Sul, Brasil. *Rodriguésia* 60: 353-365.
- Oliveira TS & Araújo FS (2007) Diversidade e conservação da biota na Serra de Baturité, Ceará. *Edições UFC, Fortaleza*. 465p.
- Oliveira-Filho AT & Fontes MA (2000) Patterns of floristic differentiation among Atlantic Forests in Southeastern Brazil and the influence of climate. *Biotropica* 32: 793-810.
- Orchard AE & Maslin BR (2003) Proposal to conserve the name *Acacia* (Leguminosae: Mimosoideae) with a conserved type. *Taxon* 52: 362-363.
- Pennington TD (1997). *The genus Inga: Botany*. Royal Botanic Gardens, Kew. 844p.
- Pijl L (1982) *Principles of dispersal in higher plants*. Springer Verlag, Michigan. 214p.
- Polhill RM (1982) *Crotalaria in Africa and Madagascar*. Royal Botanic Gardens, Kew. 396p.
- Queiroz LP (2009) *Leguminosae da caatinga*. Universidade Estadual de Feira de Santana, Feira de Santana. 443p.
- Renner SS (2004a) Multiple Miocene Melastomataceae dispersal between Madagascar, Africa and India. *Philosophical transactions of the Royal Society of London* 359: 1485-1494.
- Renner SS (2004b) Plant dispersal across the tropical Atlantic by wind and sea currents. *The International*

- Journal of Plant Sciences 164: S23-S33.
- Renner SS, Clausing G & Meyer K (2001) Historical biogeography of Melastomataceae: the roles of Tertiary migration and long-distance dispersal. *The American Journal of Botany* 88: 1290-1300.
- Richardson JE, Chatrou LW, Mols JB, Erkens RHJ & Pirie MD (2004) Historical biogeography of two cosmopolitan families of flowering plants: Annonaceae and Rhamnaceae. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences* 359: 1495-1508.
- Rocha PLB, Queiroz LP & Pirani JR (2004) Plant species and habitat structure in a sand dune field in the Brazilian Caatinga: a homogeneous habitat harbouring an endemic biota. *Revista Brasileira de Botânica* 27: 739-755.
- Schrire BD, Lavin M & Lewis GP (2005) Biogeography of the Leguminosae. *In*: Lewis GP, Schrire BD, Mackinder B & Lock M (eds.) *Legumes of the world*. Royal Botanic Gardens, Kew. Pp. 21-54.
- Silva JM & Casteleti CHM (2005) Estado da biodiversidade da Mata Atlântica brasileira. *In*: Galindo-Leal C & Câmara IG (eds.) *Mata Atlântica: biodiversidade, ameaças e perspectivas*. Fundação SOS Mata Atlântica, Belo Horizonte. Pp. 43-59.
- Silva MCNA & Rodal MJN (2009) Padrões das síndromes de dispersão de plantas em áreas com diferentes graus de pluviosidade, PE, Brasil. *Acta Botanica Brasílica* 23: 1040-1047.
- Siqueira Filho JA & Leme EMC (2006) Atlantic Forest - an overview. *In*: Siqueira Filho JA & Leme EMC (eds.) *Fragmentos de Mata Atlântica do nordeste, biodiversidade, conservação e suas bromélias*. Andrea Jakobsson Estúdio, Rio de Janeiro. Pp. 46-79.
- Souza MJN (1988) Contribuição ao estudo das unidades morfo-estruturais do estado do Ceará. *Revista de Geologia* 1: 73-91.
- Sprent JI (2007) Evolving ideas of legume evolution and diversity: a taxonomic perspective on the occurrence of nodulation. *New Phytologist* 174: 11-25.
- Stebbins GL (1974) *Flowering plants: evolution above the species level*. Harvard University Press, Cambridge. 399p.
- Sudene - Superintendência do desenvolvimento do Nordeste (1982) *Climatologia e balanço hídrico. Ceará. Dados pluviométricos. Temperaturas do Ceará estimadas por regressão múltipla: altitude, latitude e distancia do mar. Projeto de delimitação e regionalização do Brasil semi-árido*. Sudene, Fortaleza. 30p.
- Tabarelli M, Melo MDVC & Lira OC (2006) A Mata Atlântica do nordeste. *In*: Campanili M & Prochnow M (eds.) *Mata Atlântica - uma rede pela floresta*. RMA, Brasília. Pp. 1-17.
- Toppa RH, Pires JSR & Durigan G (2004) Flora lenhosa e síndromes de dispersão nas diferentes fisionomias da vegetação da Estação Ecológica de Jataí, Luiz Antônio, São Paulo. *Hoehnea* 32: 67-76.
- Wojciechowski MF, Lavin M & Sanderson MJ (2004) A phylogeny of legumes (Leguminosae) based on analysis of the plastid matK gene resolves many well-supported subclades within the family. *American Journal of Botany* 91: 1846-1862.