

Journal of Systematics and Evolution 00 (00): 1–10 (2012)

Research Article

Richness and diversity of Leguminosae in an altitudinal gradient in the tropical semi-arid zone of Brazil

¹Jacira R. LIMA ²Vidal F. MANSANO^{*} ³Francisca S. ARAÚJO

¹(Escola Nacional de Botânica Tropical, Rio de Janeiro, RJ 22460-030, Brazil)
 ²(Instituto de Pesquisas Jardim Botânico do Rio de Janeiro, Rio de Janeiro, RJ 22460-030, Brazil)
 ³(Universidade Federal do Ceará, Campus do Pici, Fortaleza, CE 60455-760, Brazil)

Abstract Many studies are based on the premise that, on a local scale, diversity is the result of ecological processes, whereas on a regional scale factors such as the topography, geology, hydrology, and historical and evolutionary events would influence this control. The Baturité Mountain Range (Ceará state), located in the Brazilian semi-arid zone, is considered an area of extreme importance for conservation with its vegetation varying with the altitude and slope (windward vs. leeward). On the windward (wet) slope, rainforest dominates, whereas the leeward (dry) slope is dominated by seasonal forests and thorny woodland. The aim of this study was to contribute to the knowledge of the patterns of richness and diversity of the family Leguminosae on a local scale (Baturité Mountain Range) as well as a regional scale (northeastern Brazil). The two slopes present quite distinct floras. The dry slope presents higher richness and diversity indices for Leguminosae than the wet slope. The highest diversity of Leguminosae in the dry areas did not corroborate the ideas of other studies carried out in neotropical forests (total flora) that the higher species richness was predicted for wet areas. The present study indicates that the historical and evolutionary processes influence the diversity patterns on a local scale (Baturité Mountain Range), as well as on a regional scale (Brazilian semi-arid). Our results reinforce the uniqueness of each portion of this area and its importance for conservation.

Key words Fabaceae, rainforest, seasonal forests, species diversity, thorny woodland.

Studies on biodiversity are becoming increasingly important, and one of the principal challenges for the ecologist is to understand the patterns of spatial and temporal variation on the diversity and richness of species (MacArthur, 1972; Ricklefs & Schluter, 1993; Whittaker et al., 2007; Lomolino et al., 2010). An understanding of these patterns and of the processes responsible for their creation and maintenance are of crucial importance for efficient implementation of biodiversity conservation (Diniz-Filho et al., 2004, 2007; Whittaker et al., 2005).

Many studies are based on the premise that, on a local scale, diversity is the result of ecological processes such as competition, whereas on a regional or global scale, factors such as the topography, geology, hydrology, and historical and evolutionary events would influence this control (Ricklefs, 1987). Gentry (1982, 1988, 1995) found that the areas of neotropical forests with more favorable climatic conditions (higher precipitation and lower seasonality) present a woody flora (all species with diameter at breast height >10 cm, in 0.1 ha) that is more diverse than areas with higher seasonality and lower precipitation.

One of the greatest challenges that we face today is the maintenance of the biodiversity in tropical forests. The Atlantic Forest is one example of such a forest and is one of the world's "hotspots" of biodiversity (Myers et al., 2000; Mittermeier et al., 2005). In the Brazilian semi-arid region, these forests once occupied an area of 11 960 km² (Silva & Casteleti, 2005). Currently, only 19.4% of this area is covered by forests, and it is found in scattered enclaves within the thorny woodland (Silva & Casteleti, 2005). Among these areas are the Serra Negra Mountain Range (Pernambuco state), the Chapada do Araripe, the Ibiapaba plateau, and the Baturité Mountain Range (Ceará state).

The Baturité Mountain Range presents high biological diversity and is considered a location of extreme biological importance for conservation (MMA, 2000). The windward slope is an area that is under the influence of forced convection rains, and has dense rainforest as its dominant vegetation. The leeward slope is an area with low precipitation and high temperatures (Gomes,

Received: 2 July 2011 Accepted: 22 March 2012

^{*} Author for correspondence. E-mail: vidalmansano@gmail.com. Tel.: 55-21-3204-2121. Fax: 55-21-3204-2070.

1978), and comprises areas of thorny woodland (below 200 m), deciduous seasonal forest (between 200 and 600 m), and semideciduous seasonal forest (above 600 m). The few floristic studies that have been carried out in the area indicate the presence of a very diversified flora, with the family Leguminosae being one of the richest (Araújo et al., 2006; Lima et al., 2012; Lima & Mansano, 2011).

Leguminosae is among the most diverse families in neotropical forests (Gentry, 1982, 1988, 1995; Wojciechowski et al., 2004) and is usually considered one of the most important families of the semi-arid region of Brazil (Queiroz, 1999, 2006). Evidence, such as the presence of various physiological and morphological adaptations to hot and dry climates and the high fossil richness in the areas of dry forests, indicates that the family originated in an area of seasonal forest on the margins of the Tethys Sea approximately 60 million years ago (Lavin et al., 2005; Schrire et al., 2005).

Due to these factors, this study had as a null hypothesis that areas of higher moisture in the Baturité Mountain Range (windward slope) will have a greater richness and diversity of Leguminosae. However, due to the evolutionary history of the family, this study adopted an alternative hypothesis, that the driest areas of the Baturité Mountain Range (leeward slope) would present higher species richness and diversity. We also attempted to verify whether the pattern observed on a local scale (Baturité Mountain Range) was similar to that found on a regional scale (northeastern Brazil).

Based on these ideas, the present study aimed to contribute data regarding the patterns of richness and diversity of the family Leguminosae on a local scale (across the different slopes and altitudes of the Baturité Mountain Range), as well as on a regional scale (the northeast of Brazil). We intended to determine: (i) which vegetation formations on a local and regional scale show greater richness and diversity of Leguminosae; (ii) whether the patterns of richness and diversity found are the same on a local scale (Baturité Mountain Range) and on a regional scale (northeast Brazil); (iii) which processes (ecological or historical/evolutionary) have a greater influence on the diversity patterns of the family Leguminosae on a local and regional scale; and (iv) what the implications are of the results for the conservation of the diversity in this semi-arid zone of Brazil.

1 Material and methods

1.1 Study area

The Baturité Mountain Range has altitudes ranging from 200 m to 1115 m (Souza, 1988). It covers an area of 3822 km² with a north–northeast/south– southwest orientation, located between the coordinates $38^{\circ}57'47''W$, $4^{\circ}08'21''S$ and $39^{\circ}02'32''W$, $4^{\circ}27'10''S$, and is 90 km from the north coast of northeastern Brazil (Souza, 1988) (Fig. 1).

The position of the relief in relation to the wind currents provides a higher humidity on the northern and northeastern slopes (windward slopes) due to the rain-forced convection. This results in different moisture gradients among the slopes and, in general, higher precipitation than the surrounding semi-arid region, where the average precipitation rate is 700 mm per year (Funceme, 2005). On the western and southern slopes (leeward sides), where a rain shadow is formed, higher temperatures and lower precipitation are observed compared to the windward slope.

The annual rainfall (Funceme, 2005) and temperature averages, estimated by regression, in the municipalities of Mulungu (~800 m), Guaramiranga (~850 m) and Pacoti (~900 m), located on the windward slope of the mountain, are 1221 mm, 1711 mm, and 1558 mm and 20.8 °C, 21.4 °C, and 21 °C, respectively. In contrast, in the town of Capistrano, located at the base of the leeward slope, the annual precipitation and temperature averages are 846 mm and 26 °C, respectively (Ipece, 2007). Along the altitudinal gradient on the leeward slope are thorny woodland, known as *Caatinga* (below 200 m), deciduous seasonal forest (200–600 m), and semideciduous seasonal forest (above 600 m).

On the windward slope, along the entire gradient, only dense rainforest is found (Araújo et al., 2006). The vegetation classification system adopted is that of Veloso et al. (1991). The concept of the Atlantic Forest adopted in this work is that of Oliveira-Filho & Fontes (2000), which includes rain, semideciduous, and deciduous forests.

1.2 Vegetation sampling

Plots were installed in five areas occurring at different altitudes and on different slopes of the Baturité Mountain Range. On the windward slope, the plots were installed at three altitudes: (i) 1000 m (WIN_1000), in the municipality of Guaramiranga; (ii) 800 m (WIN_800), in the municipality of Pacoti; and (iii) 600 m (WIN_600), in the municipality of Pacoti. At all altitudes sampled on the windward slope, the dominant vegetation was rainforest. On the leeward slope, the plots were installed in two elevational strips: (i) 800 m (LEE_800), an area of semideciduous seasonal forest, in the municipality of Mulungu; and (ii) 600 m (LEE_600), an area of deciduous seasonal forest, in the municipality of Guaramiranga. In addition to these areas, an area of thorny woodland, studied by Medeiros

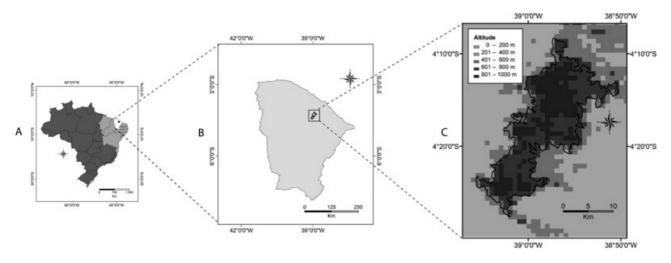


Fig. 1. Map of Brazil with the location of the state of Ceará (A), the position of Baturité Mountain Range in Ceará state (B), and detail of the studied area with altitudinal scale (C) where the delimited region comprises the protected area of the Baturité Mountain Range. Datum, SAD 69; Credit, NCCG / IPJBRJ; Date, March 2012.

(1995), was included in the analysis. This area is located at the base of the mountain at an altitude of approximately 200 m (LEE_200) in the municipality of Capistrano. Because the most severe climatic conditions are observed on the leeward side, the rocks are significantly eroded and the altitudes are lower than on the windward slope, justifying the fact that on the leeward slope plots were not installed at altitudes above 800 m.

A fragment representing the best-preserved site in each area was selected, and five plots of 20 m \times 50 m (Mueller-Dombois & Ellenberg, 1974), separated by an interval of 30 m with a total area of 0.5 ha, were selected. All of the living trees, shrubs, and woody vines of the Leguminosae family with a stem diameter at ground level equal to or greater than 3cm were sampled in these plots, the same inclusion criteria and sampling methods used in a study by Medeiros (1995) for the area LEE 200. The richness and diversity registered were compared among physiognomies on the same slope and between the two slopes. Species level identifications were made using published keys and/or taxonomic descriptions (e.g., Bentham, 1859–1862, 1870; Irwin & Barneby, 1982; Lewis, 1987; Barneby, 1991; Pennington, 1997) and by consulting digital images of type specimens online (http://collections.mnh.si.edu/search/botany/?ti=3, accessed 10 April 2012). Generic concepts were largely in accordance with Lewis et al. (2005), except the genera Bauhinia and Caesalpinia.

1.3 Richness and diversity of Leguminosae in the Baturité Mountain Range (local scale)

To determine which physiognomy presents higher richness and diversity, the total number of species at each of the altitudes studied on each slope was analyzed, and from these data and from the abundance of species, we calculated the Shannon–Wiener index (H'). We also calculated the Phylogenetic Diversity Index (PD) using the Tuatara package for Mesquite (Maddison & Maddison, 2008), the Taxonomic Diversity Index (Δ), and the Taxonomic Distinctness Index (Δ^*) using the PAST software (Hammer et al., 2001). The PD is a measure of diversity that incorporates the phylogenetic relationships of species (Magurran, 2004). This measure is obtained by summing the lengths of the branches of the phylogenetic species tree in a community (Faith, 1992). However, it is not always possible to use this index because it is necessary that all species of the analyzed community be sequenced. As some species of the Baturité Mountain Range have not been sequenced, a phylogenetic tree was assembled at the genus level using the PAUP* 4b10 application (Swofford, 2000) with the gene sequences of the plastid maturase K (matK), based on a study by Wojciechowski et al. (2004). This matrix was generated under the maximum parsimony criterion. The sequences of the genera Abarema, Anadenanthera, Mimosa, Piptadenia, and Ateleia were obtained from the NCBI website (http://www.ncbi.nlm.nih.gov/Genbank/, accessed May 23, 2011). As there were no matK sequences for Trischidium, we used the genus Ateleia for sequence comparisons because this genus is a sister to Trischidium (Torke & Schaal, 2008). We calculated the PD from this tree (see Doc. S1).

The Taxonomic Diversity (Δ) and Taxonomic Distinctness Indices (Δ^*) are simpler than the PD because they only count the number of nodes that separate the species in a phylogenetic tree (Webb, 2000). The Δ is estimated based upon the expected number of nodes

4 Journal of Systematics and Evolution Vol. 00 No. 0 2012

Table 1	Tree and shrub species of Leguminosae collected in plots along the altitudinal gradient in the Baturité Mountain Range, Ceará state, Brazil,
showing	the slopes and altitudes in which they were found (X).

	Leeward			Windward		
	800 m	600 m	200 m	1000 m	800 m	600 m
Subfamily Caesalpinioideae						
Bauhinia aromatica Ducke	Х	Х	Х			
Bauhinia outimouta Aubl.					Х	
Caesalpinia gardneriana Benth.		Х	Х			
Caesalpinia ferrea var. glabrescens Benth.			Х			
Caesalpinia ferrea var. parvifolia Benth.	Х					
Chamaecrista zygophyloides (Taub.) H. S. Irwin & Barneby var. zygophyloides	Х	Х				
Copaifera duckei Dwyer					Х	Х
Hymenaea courbaril L.						Х
Senna splendida (Vogel) H. S. Irwin & Barneby var. gloriosa H. S. Irwin & Barneby	Х					
Subfamily Mimosoideae						
Abarema jupunba (Willd.) Britton & Killip var. jupunba					Х	
Albizia polycephala (Benth.) Killip	Х					Х
Anadenanthera colubrina (Vell.) Brenan var. colubrina			Х			
Chloroleucon dumosum (Benth.) G. P. Lewis		Х				
Inga bollandii Sprague & Sandwith				Х		
Inga marginata Willd.				Х		
Mimosa arenosa (Willd.) Poir var. arenosa	Х	Х	Х			
Mimosa caesalpiniifolia Benth.	Х	Х	Х			
Mimosa tenuiflora (Willd.) Poir.			Х			
Parkia pendula (Willd.) Benth. ex Walp.					Х	
Piptadenia stipulacea (Benth.) Ducke	Х	Х				
Piptadenia viridiflora (Kunth) Benth.			Х			
Senegalia polyphylla (DC.) Britton & Rose		Х				
Senegalia tenuifolia (L.) Britton & Rose	Х	Х			Х	Х
Stryphnodendron guianense (Aubl.) Benth.					Х	
Subfamily Papilionoideae						
Amburana cearensis (Allemão) A. C. Sm.			Х			
Dalbergia cearensis Ducke			Х			
Dioclea megacarpa Rolfe		Х				
Lonchocarpus sericeus (Poir.) Kunth ex DC.						Х
Platymiscium floribundum var. nitens (Vogel) Klitg.	Х		Х			
Trischidium molle (Benth.) H. E. Ireland			X			

between any two randomly selected individuals in a community, whereas the Δ^* is estimated based upon the expected number of nodes between any two randomly selected individuals of different species in a community (Clarke & Warwick, 1998). To check which slope presents higher richness and diversity, data from all of the plots on the same slope were compiled, and the species richness and diversity indices (H', PD, Δ , and Δ^*) for each slope were estimated from the compiled data.

1.4 Species richness in vegetation formations in semi-arid zones (regional scale)

To ascertain whether the pattern found on a local scale (Baturité Mountain Range) also occurred on a regional scale (northeastern Brazil), we calculated the species richness of Leguminosae in different vegetation types in northeastern Brazil. To this end, we used the database TreeAtlan 1.0 (Oliveira-Filho, 2006). Because data on abundance were not available for all areas, only the species richness was calculated. The database used

Table 2 Number of individuals (No. ind.), species richness (Riq), Shannon–Wiener index (H'), Phylogenetic Diversity Index (PD), Taxonomic Diversity Index (Δ), and Taxonomic Distinctness Index (Δ ^{*}) for the family Leguminosae in an altitudinal gradient of the Baturité Mountain Range, Ceará state, Brazil. LEE, leeward slope; WIN, windward slope. The numbers after LEE and WIN correspond to the altitudinal strip of the areas.

	No. ind.	Riq	H′	PD	Δ	Δ^*		
Thorny woodland (LEE_200 m)	422	12	1.672	609.5	2.542	3.636		
Deciduous forest (LEE_600 m)	210	10	1.408	651.1	2.375	3.854		
Semideciduous forest (LEE_800 m)	218	10	1.853	587.5	3.113	3.859		
LEE Total	850	21	2.18	1006.5	3.178	3.816		
Rainforest (WIN_600 m)	35	5	1.416	583.5	2.763	3.779		
Rainforest (WIN_800 m)	54	6	1.2	424.5	2.391	3.979		
Rainforest (WIN_1000 m)	33	2	0.6816	133.5	0.5038	1		
WIN Total	122	10	1.988	756.5	2.839	3.393		

for this analysis included 125 areas in northeast Brazil, with 2934 individuals of 264 species of Leguminosae. We analyzed only the areas with physiognomies similar to those reported in the Baturité Mountain Range (dense rainforest, semideciduous seasonal forest, deciduous seasonal forest, and thorny woodland).

1.5 Variation in floristic composition between different altitudes and slopes of the Baturité Mountain Range

To determine how the floristic composition varies in different plots along each slope and between slopes, we carried out an ordination by multidimensional scaling with a similarity matrix calculated by the similarity index of Bray–Curtis, using the software Systat 10 (Wilkinson, 2000). The classification system used was that of Lewis et al. (2005) with adaptations of Lima & Mansano (2011).

2 Results

2.1 Richness and diversity of Leguminosae in the Baturité Mountain Range (local scale)

We recorded 972 individuals belonging to the three subfamilies of Leguminosae, representing 30 species and 22 genera (Table 1). Significant variations were not detected in the species richness or diversity indices analyzed among the forest formations on the same slope (Table 2). The thorny woodland (LEE_200) and dense rainforest (WIN_1000) presented the highest and lowest species richness, respectively (Table 2).

Although little difference was observed in the richness and diversity (Table 2) between the physiognomies of the same slope (except the WIN_100 area that showed a low richness and diversity), differences were observed between physiognomies of similar altitudes on different slopes (600 m and 800 m). These differed in both the richness and diversity indices, with the physiognomies of the leeward slope, in general, being richer and more diverse. When all of the data from a slope were compiled, the greatest richness (species, genera, and individuals) and diversity (H', PD, Δ , and Δ^*) were clearly found on the leeward slope (Table 2).

2.2 Species richness in vegetation formations in semi-arid zones (regional scale)

The species richness of Leguminosae on a regional scale (semi-arid areas) showed a similar pattern to that found on a local scale (Baturité Mountain Range); the thorny woodland had greater species richness of Leguminosae than the forest formations, especially those with more precipitation (Table 3). However, unlike the

 Table 3
 Species richness (Riq) of trees and shrubs of the family Leguminosae in different vegetation formations found in the semi-arid tropical zone-based database TreeAtlan (version 1.0)

Vegetation formations	Riq
Thorny woodland	200
Semideciduous seasonal forest	140
Rainforest	101
Deciduous seasonal forest	95

result found in the Baturité Mountain Range (local scale), on a regional scale there was greater species richness in the rainforest (101) than in the deciduous forests (95), although the difference was small. This difference may be due to the fact that many of the genera that have great diversity in drier areas, such as *Mimosa* and *Chamaecrista* (Polhill et al., 1981; Schrire et al., 2005; Queiroz, 2009), are mainly represented by herbaceous and shrub species, which were not included in the analysis. Moreover, the data collection among the areas examined was not systematic, which may also have generated this difference in observed richness.

2.3 Floristic composition

Multidimensional scaling (Fig. 2) showed that the two slopes have distinct floristic compositions. The presence of species and genera exclusive to each of the slopes studied was observed (Table 1). For example, species of the tribes Cassieae, Dalbergieae, Swartzieae, and Phaseoleae were found only on the leeward slope,

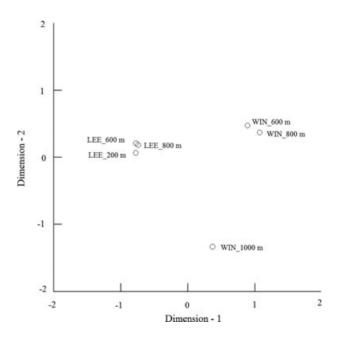


Fig. 2. Graph of ordination by multidimensional scaling summarizing the floristic variation among the inventory plots in the Baturité Mountain Range, Ceará state, Brazil. LEE, leeward slope; WIN, windward slope.

whereas species of the tribes Millettieae and Detarieae were restricted to the windward slope.

3 Discussion

3.1 Richness and diversity of species in the Baturité Mountain Range and the semi-arid region

The small difference in the richness and diversity of species among areas of the same slope can be due to small altitudinal differences and, consequently, a slight variation in the climatic conditions of the areas examined. Although the area of thorny woodland presented greater species richness of Leguminosae, it did not show greater diversity in relation to any of the indices examined (Table 2). The LEE 800 area showed the highest H' and Δ , and the LEE_600 area showed the highest PD. In addition to the number of species and individuals, the Shannon-Wiener index considers the ratio between them (i.e., equability). Although the area of thorny woodland presented a higher number of species and individuals, there were a large number of individuals from particular species, for example, Bauhinia aromatica Ducke, which represented more than 50% (216) of individuals found in the area.

The PD and Δ indices have the main premise that diversity is greater in a community where the species are more phylogenetically distinct. Despite the fact that the thorny woodland area presented higher species richness, many of those species belong to the same tribe or genera; for example, approximately 50% of the species in the thorny woodland belong to the tribe Mimoseae. Therefore, even though the LEE_600 area had a lower number of species in relation to the thorny woodland, they belonged to different genera, and there was little repetition at the tribal level, which explains the higher PD, because they were, indeed, more diverse from the phylogenetic point of view.

The greater richness and diversity of Leguminosae in seasonal forest formations (leeward slope) of the Baturité Mountain Range and in the tropical semi-arid zone of northeastern Brazil did not support the ideas of Gentry (1982, 1988), as, according to his theory, a greater diversity in wet areas would be expected, at least when the total flora is compared. However, in a study of the entire angiosperm flora of the Baturité Mountain Range, Araújo et al. (2006) found a positive correlation between precipitation and species richness and diversity, with the windward areas being the most diverse.

It should be noted that, although the Baturité Mountain Range is located in a region presenting a semi-arid tropical climate, where water is probably one of the main abiotic limiting factors for native species, the Leguminosae have a higher richness and diversity in exactly the driest and hottest part of the mountains. Punyasena et al. (2008), using data from Gentry (1988) for neotropical forests, found that while diversity patterns are analyzed individually for botanical families, each family responds differently to the different components of climate (rainfall and temperature). The authors found that the most important climatic variable for the family Leguminosae is temperature, but for other families, such as Bignoniaceae and Arecaceae, it is precipitation. According to Ricklefs (1987), taxonomic information provides evidence of the influence of historical factors on patterns of diversity.

Although Araújo et al. (2006) found a greater richness and diversity for total flora in the wetter areas of the Baturité Mountain Range, this result was not observed when the analysis was carried out only at the family level. Thus, using only the Leguminosae from the study by Araújo et al. (2006), we observed a similar result to that found in the present study, that is, the driest areas were the richest and most diverse. However, this pattern varied with the family studied; for example, with Myrtaceae, we observed an opposite pattern, with higher diversity in the wetter areas. Thus, the richness and diversity of species varies according to the taxonomic group analyzed, which may reflect the evolutionary history of each group. Similar results have also been reported in other studies, such as Murray-Smith et al. (2008), Schouten et al. (2009), and Punyasena et al. (2008).

Punyasena (2008) also found a positive correlation between the diversity of Leguminosae and high temperatures; however, this association was observed in areas where rainfall is high. Although the greatest species richness in the Baturité Mountain Range was found in the areas of thorny woodland, the highest diversity (H', Δ , and Δ^*) was observed in the area of semideciduous seasonal forest (800 m). This area has, in addition to a high annual average temperature, higher rainfall than the thorny woodland and deciduous seasonal forest, corroborating the results of Punyasena (2008).

To understand the diversity patterns in Leguminosae, it is necessary to understand the evolutionary history of the group because the pattern of diversity found in the Baturité Mountain Range for Leguminosae was the opposite of the expected results. Schrire et al. (2005) provided some evidence that the first species of Leguminosae emerged in areas of deciduous seasonal forest. Among these indications morphological and physiological adaptations to a hot and dry climate are observed, including the following: compound leaves, seeds with a hard testa and a long period of dormancy and viability, the ability to fix and store nitrogen, associations with insects that are promoted by the presence of extrafloral nectaries, and fruits and seeds with adaptations for wind dispersal. Thus, the Leguminosae are well adapted to arid climatic conditions, which explains the greater richness and diversity of species in the drier areas of the Baturité Mountain Range and in the semi-arid region of Brazil.

The preference for arid and semi-arid environments shown by the species of Leguminosae may also be related to their ability to fix nitrogen through a symbiotic association with bacteria in root nodules (Wojciechowski et al., 2004; Sprent, 2007). Based on data found in published reports (see Farias et al., 1994; Sprent, 2001), we verified that the driest areas (leeward slope) of the Baturité Mountain Range contain more species able to fix nitrogen compared to the wet areas (windward slope).

According to Tilman (1982), plants that fix nitrogen symbiotically are favored in soils with high phosphorus and low nitrogen contents. This is because nitrate reductase has phosphorus associated with the holoenzyme; therefore, nitrogen fixers need to have access to an adequate amount of this element (Vitousek & Howarth, 1991). Soils in areas with high precipitation have low phosphorus availability due to loss or immobilization, which also explains the greater richness and diversity of Leguminosae in drier areas.

3.2 Floristic composition

According to Schrire et al. (2005), the first legumes originated in a seasonal forest, with subsequent expansion to other plant communities. Among these were areas with wetter climates, such as rainforest, that were colonized more recently by the legume family than dry areas. Based on the super tree of Leguminosae presented by Schrire et al. (2005), there are some genera representing the basal lineages of Caesalpinioideae *sensu lato*, such as Cercideae, Cassieae, and Caesalpinieae, which are found almost exclusively on the leeward side, whereas clades of the tribes Ingeae and Millettieae, which represent more derived lineages with a more recent origin and diversification within Mimosoideae and Papilionoideae, respectively, are found only on the windward slope.

In addition, phylogenetic studies show that the Leguminosae have a phylogeny associated more with the biome than with geographical proximity, especially the dry-area clades (Schrire et al., 2005). Thus, some of the genera exclusive to the leeward slope of the Baturité Mountain Range (e.g., *Chloroleucon, Mimosa, Piptadenia*, and *Trischidium*) are among those that are characteristic of semi-arid environments (Schrire et al., 2005; Queiroz, 2009), found especially in areas of deciduous seasonal forest and thorny woodland (Lima et al., 2012). On the windward slope, many exclusive genera (e.g., *Abarema*, *Copaifera*, *Hymenaea*, and *Parkia*) were also cited by Schrire et al. (2005) as being characteristic of rainforests (rainforest biome) and are found mainly in areas of dense Amazon rainforest and dense Atlantic rainforest.

3.3 Implications for conservation

Although the Atlantic Forest is considered one of the world's hotspots of biodiversity (Myers et al., 2000; Mittermeier et al., 2005), this vegetation is continuously being devastated and is considered the most critically threatened tropical forest in the world (Metzger, 2009). With the goal of minimizing human impacts on an area of the Atlantic Forest located in the semi-arid region. the Baturité Mountain Range was designated an Environmental Protection Area (APA) in September 1990, through a decree of the state, No. 20 956. The APA is defined as the area from 600 m to the highest altitudes in this range, covering an area of 32 690 ha in the municipalities of Aratuba, Baturité, Capistrano, Guaramiranga, Mulungu, Pacoti, Palmácia, and Redenção (SEMACE, 1992). This APA is now considered by the Ministry of Environment of Brazil (MMA, 2000) as an area of extreme importance for the conservation of biodiversity.

Although one of the strategies for the conservation of biodiversity is the creation of Conservation Units, which contribute to the preservation of a significant portion of biological diversity among other things, an increase in the scientific knowledge of its biodiversity is also necessary (Pinto et al., 2006; Caro et al., 2009). This is especially important in areas with high environmental heterogeneity, such as the Baturité Mountain Range, which has very distinct floras on each slope and altitude, which contribute to the high diversity of the area.

In one of the few studies on the flora of the Baturité Mountain Range, Araújo et al. (2006) found 41 wood species of Leguminosae, while Lima et al. (2012), studying only the family Leguminosae, found 69 wood species. The study by Lima et al. (2012) showed an increase of 68% (28 tree and shrub species) for the area, in addition to species with other habits (32 shrub species, 16 climbers, 8 lianas, and 7 herbs). This result shows the importance of floristic studies for a better understanding of diversity, even in areas already recognized as being highly diverse. This result also confirms the great diversity of the Baturité Mountain Range and its value for the conservation of the remnants of Atlantic Forest in northeastern Brazil, considered one of the most critically threatened vegetation areas in Brazil (Silva & Tabarelli, 2001).

The APA of the Baturité Mountain Range only includes areas above 600 m. However, the areas of high diversity and richness of Leguminosae are those located at altitudes below 600 m. Thus, many genera and species found only in this area in the Baturité Mountain Range, such as *Trischidium molle* (Benth.) H. E. Ireland and *Amburana cearensis* (Allemão) A. C. Sm., the latter is included in the Red List of Threatened Species of the MMA (2008), are not in the protected areas of the Baturité Mountain Range and are thus at risk of local extinction.

For the Conservation Units to accomplish their mission of conserving biodiversity, greater oversight of these areas is necessary. Even after the creation of the APA, the Baturité Mountain Range remains ecologically fragile and susceptible to human interference. What has been observed is that the native vegetation cover remains low because of both agricultural activities, which are present on both slopes, and real estate speculation, especially on the windward slope. This low native vegetation cover indicates the need for better supervision by the agency responsible for the area.

3.4 Conclusion

The present study indicates that historical and evolutionary processes have a great impact on the patterns of diversity of the family Leguminosae on both local (Baturité Mountain Range) and regional scale (Brazilian semi-arid zone). We believe that because this family originated in dry habitats, the species of this group are strongly adapted to drier climatic conditions, justifying the results found in this study. Furthermore, many genera belonging to the basal clades of Leguminosae were found only in dry areas, whereas most other morederived genera were found only in wetter areas where the dominant vegetation is rainforest, supporting the ideas of Schrire et al. (2005).

Another point worth noting here is that if the species exclusive to those areas, such as *Amburana cearensis*, become extinct in the area, that genus or even the evolutionary lineage will no longer be found in the Baturité Mountain Range, leading not only to a decrease in species richness but also in the taxonomic and phylogenetic diversity of the area. Thus, an issue that should be taken into consideration in future zoning plans for the Baturité Mountain Range is that the vegetation at altitudes below 600 m includes important flora that are not currently covered in the protected area.

The fact that the Baturité Mountain Range presents such distinct vegetational formations and, as a consequence, such different floras, as was observed for the family Leguminosae, reinforces the uniqueness of each portion of this area and thus its overall importance for conservation. The singularity of the biogeographical elements present is also worth mentioning. Because the area is a Conservation Unit of sustainable use, this APA is susceptible to human intervention, as it can accommodate both private and public lands in its limits. Thus, we recommend an adjustment in the protection category of the Baturité Mountain Range, categorizing it as a Conservation Unit for full protection, thus guaranteeing the preservation of this important area of Atlantic Forest in northeastern Brazil.

Acknowledgements We acknowledge the Funcap (Fundação Cearense de Apoio ao Desenvolvimento Científico e Tecnológico) and CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico) for financial help through a PhD scholarship for the first author and a research grant to the second author (process 312766/2009–2). We are grateful to Andre Albernaz and Ernani Bellon for making the map shown in Figure 1. The manuscript was edited for correct English by Dewey Litwiller.

References

- 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. Fortaleza: UFC/COELCE. 137–162.
- Barneby RC. 1991. Sensitivae Censitae, a description of the genus *Mimosa* L. (Mimosaceae) in the New World. Memoirs of the New York Botanical Garden 65: 1–835.
- Bentham G. 1859–1862. Papilionaceae. In: Martius CFP, Eichler AW, Urban T eds. Flora Brasiliensis. Monachii: Typographia Regia. 1–396.
- Bentham G. 1870. Swartzieae et Caesapinieae. In: Martius CFP, Eichler AW, Urban T eds. Flora Brasiliensis. Monachii: Typographia Regia. 14–40.
- Caro T, Gardner TA, Stoner C, Fitzherbert E, Davenport TRB. 2009. Assessing the effectiveness of protected areas: Paradoxes call for pluralism in evaluating conservation performance. Diversity and Distributions 15: 178–182.
- Clarke KR, Warwick RM. 1998. A taxonomic distinctness index and its statistical properties. Journal of Applied Ecology 35: 523–531.
- Diniz-Filho JAF, Bini LM, Rangel TFLVB, Carvalho P, Pinto MP, Couto MSDS. 2007. Conservation biogeography of anurans in Brazilian Cerrado. Biodiversity and Conservation 16: 997–1008.
- Diniz-Filho JAF, Bini LM, Vieira CM, Souza MC, Bastos RP, Brandão D. 2004. Spatial patterns in species richness and priority areas for conservation of anurans in the Cerrado region, Central Brazil. Amphibia-Reptilia 25: 63–75.
- Faith DP. 1992. Conservation evaluation and phylogenetic diversity. Biological Conservation 61: 1–10.

- Farias SM, Lima HC, Carvalho AM, Gonçalves VF, Sprent JL. 1994. Occurrence of nodulation in legumes of the state of Bahia, Minas Gerais and Espirito Santo of Brazil. In: Sprent JI, Mcmey D eds. Advances in legume systematics. Richmond: Royal Botanic Gardens, Kew. 17–23.
- Fundação Cearense de Meteorologia e Recursos Hidrícos (Funceme). 2005. Relatório de pluviometria por faixa de anos – estado do Ceará. Departamento de Apoio Tecnológico (DETEC), Fortaleza (on-line). www.funceme.br/DEPAM/index.htm [Accessed 10 April 2010].
- Gentry AH. 1982. Patterns of neotropical plant species diversity. Evolutionary Biology 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: 1–34.
- Gentry AH. 1995. Diversity and floristic composition of neotropical forest. In: Bullock SH, Mooney H, Medina E eds. Seasonally dry tropical forest. Cambridge: Cambridge University Press. 146–194.
- Gomes MAF. 1978. O maciço de Baturité: Um enfoque ecológico. In: AGB, Universidade Federal do Ceará, Guia de Excursão. Fortaleza: III Encontro Nacional de Geógrafos. 43–59.
- Hammer Ø, Harper DAT, Ryan PD. 2001. Past: Paleontological statistics software package for education and data analysis. Palaeontologia Electronica 4: 1–9. (Available at http://palaeo-electronica.org/2001_1/past/issue1_01.htm).
- Instituto de Pesquisa e Estratégia Econômica do Ceará (Ipece). 2007. Perfil básico municipal: Capistrano. Fortaleza: Instituto de Pesquisa e Estratégia Econômica do Ceará (Ipece).
- Irwin HS, Barneby R. 1982. The American Cassiinae. Memoirs of the New York Botanical Garden 35: 1–918.
- Lavin M, Herendeen P, Wojciechowski MF. 2005. Evolutionary rates analysis of Leguminosae implicates a rapid diversification of lineages during the Tertiary. Systematic Biology 54: 530–549.
- Lewis GP. 1987. Legumes of Bahia. Richmond: Royal Botanic Gardens, Kew.
- Lewis GP, Schrire BD, Mackinder BA, Lock JM. 2005. Legumes of the world. Richmond: Royal Botanic Gardens, Kew.
- Lima JR, Mansano VF. 2011. The family Leguminosae in the Baturité mountain range, Ceará State, an area of Atlantic Forest in the semi-arid region of Brazil. Rodriguesia 62 (3): 563–613.
- Lima JR, Mansano VF, Araújo FS. 2012. 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.
- Lomolino MV, Riddle BR, Whittaker RJ, Brown JH. 2010. Biogeography. Sunderland: Sinauer Associates.
- MacArthur RH. 1972. Geographical ecology: Patterns in the distribution of species. New York: Harper & Row.
- Maddison WP, Maddison DR. 2008. Mesquite: A modular system for evolutionary analysis. Version 2.5, build j55 (on-line). http://mesquiteproject.org [Accessed 10 April 2010].
- Magurran AE. 2004. Measuring biological diversity. Oxford: Blackwell Publishing.

- Medeiros JBLP. 1995. Florística e fitossociologia de uma área de caatinga localizada na Fazenda Aracanga, Município de Capristano-CE. Graduation monograph. Fortaleza: Universidade Federal do Ceará.
- Metzger JP. 2009. Conservation issues in the Brazilian Atlantic Forest. Biological Conservation 142: 1138–1140.
- Mittermeier RA, Gil PR, Hoffmann M, Pilgrim J, Brooks T, Mittermeier CG, Lamourex J, Fonseca GAB. 2005. Hotspots revisited: Earth's biologically richest and most endangered terrestrial ecoregions. Washington: Conservation International.
- Ministério do Meio Ambiente (MMA). 2000. Avaliação e ações prioritárias para a conservação da Biodiversidade da Floresta Atlântica e Campos Sulinos. Brasília: MMA/SBF.
- Ministério do Meio Ambiente (MMA). 2008. Lista Oficial da Flora Ameaçada de Extinção (on-line). http://www.mma.gov.br/estruturas/179/_arquivos/179_051 22008033615.pdf [Accessed 30 June 2011].
- Mueller-Dombois D, Ellenberg H. 1974. Aims and methods of vegetation ecology. New York: John Wiley & Sons.
- Murray-Smith C, Brummitt NA, Oliveira-Filho AT, Bachman S, Nic Lughadha EM, Moat J, Lucas EJ. 2008. Plant diversity hotspots in the Atlantic Coastal Forests of Brazil. Conservation Biology 23: 151–163.
- Myers N, Mittermier RA, Mittermeier CG, Fonseca GAB, Kent J. 2000. Biodiversity hotspots for conservation priorities. Nature 403: 853–858.
- Oliveira-Filho AT. 2006. TreeAtlan 1.0. Tree flora of the South American Atlantic Forest: A database involving geography, diversity and conservation (on-line). http://www.icb.ufmg.br/treeatlan/ [Accessed 31 October 2011].
- Oliveira-Filho AT, Fontes MA. 2000. Patterns of floristic differentiation among Atlantic Forests in Southeastern Brazil and the influence of climate. Biotropica 32 (4b): 793–810.
- Pennington TD. 1997. The genus Inga: Botany. Richmond: Royal Botanic Gardens, Kew.
- Pinto LPS, Bede LC, Paese A, Fonseca M, Paglia AP, Lamas I. 2006. Mata Atlântica Brasileira: os desafios para a conservação da biodiversidade de um hotspot mundial. In: Rocha CFD, Bergallo HG, Van Sluys M, Alves MAS eds. Biologia da conservação: essências. São Carlos: RiMa. 91– 118.
- Polhill RM, Raven PH, Stirton CH. 1981. Evolution and systematics of the Leguminosae. In: Polhill RM, Raven PH eds. Advances in legume systematics. Richmond: Royal Botanic Gardens, Kew. 1–26.
- Punyasena SW. 2008. Estimating neotropical palaeotemperature and palaeoprecipitation using plant family climatic optima. Palaeogeology, Palaeoclimatology, Palaeoecology 265: 226–237.
- Punyasena SW, Eshel G, McElwain JC. 2008. The influence of climate on the spatial patterning of neotropical plant families. Journal of Biogeography 35: 117–130.
- Queiroz LP. 1999. Leguminosas de caatinga, espécies com potencial forrageiro. In: Araújo FD, Prendesgast HDV, Mayo SJ eds. Plantas do Nordeste: Anais do I Workshop Geral. Richmond: Royal Botanic Gardens, Kew. 53–62.
- Queiroz LP. 2006. The Brazilian caatinga: Phytogeographical patterns inferred from distribution data of the Leguminosae.

In: Pennington RT, Lewis GP, Ratter JA eds. Neotropical savannas and dry forests: Plant diversity, biogeography and conservation. Boca Raton: Taylor & Francis. 121– 157.

- Queiroz LP. 2009. Leguminosas da caatinga. Universidade Estadual de Feira de Santana. Bahia: Feira de Santana.
- Ricklefs RE. 1987. Community diversity: Relative roles of local and regional processes. Science 235: 167– 171.
- Ricklefs RE, Schluter D. 1993. Species diversity in ecological communities. Historical and geographical perspectives. Chicago: The University of Chicago Press.
- Schouten MA, Verweij PA, Barendregt A, Kleukers RMJC, Kalkman VJ, Ruiter PC. 2009. Determinants of species richness patterns in the Netherlands across multiple taxonomic groups. Biodiversity and Conservation 18: 203– 217.
- Schrire BD, Lavin M, Lewis GP. 2005. Biogeography of the Leguminosae. In: Lewis G, Schrire BD, Mackinder B, Lock M eds. Legumes of the world. Richmond: Royal Botanic Gardens, Kew. 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: Conservação Internacional. 43–59.
- Silva MG, Tabarelli M. 2001. Seed dispersal, plant recruitment and spatial distribution of Bactris acanthocarpa Martius (Arecaceae) in a remnant of Atlantic forest in northeast Brazil. Acta Oecologica 22: 259–268.
- Souza MJN. 1988. Contribuição ao estudo das unidades morfoestruturais do estado do Ceará. Revista de Geologia 1: 73– 91.
- Sprent JI. 2001. Nodulation in legumes. Richmond: Royal Botanic Gardens, Kew.
- Sprent JI. 2007. Evolving ideas of legume evolution and diversity: A taxonomic perspective on the occurrence of nodulation. New Phytologist 174: 11–25.
- Superintendência Estadual do Meio Ambiente (SEMACE). 1992. Zoneamento ambiental da APA da Serra de Baturité: diagnósticos e diretrizes. Fortaleza: SEMACE.
- Swofford DL. 2000. PAUP^{*}: Phylogenetic analysis using parsimony. Version 4. Sunderland: Sinauer Associates.
- Tilman D. 1982. Resource competition and community structure. New Jersey: Princeton University Press.

- Torke BM, Schaal BA. 2008. Molecular phylogenetics of the species-rich neotropical genus Swartzia (Leguminosae-Papilionoideae) and related genera of the swartzioid clade. American Journal of Botany 95: 215–228.
- Veloso PH, Rangel Filho ALR, Lima JCA. 1991. Classificação da vegetação brasileira, adaptada a um sistema universal. Rio de Janeiro. IBGE: Departamento de Recursos Naturais e Estudos Ambientais.
- Vitousek PM, Howarth RW. 1991. Nitrogen limitation on land and in the sea: how can it occur? Biogeochemistry 13: 87– 115.
- Webb CO. 2000. Exploring the phylogenetic structure of ecological communities: An example for rain forest trees. American Naturalist 156: 145–155.
- Wilkinson L. 2000. Systat Statistics version 10.0 for Windows. Chicago: SPSS.
- Whittaker RJ, Nogués-Bravo D, Araújo MB. 2007. Geographical gradients of species richness: A test of the waterenergy conjecture of Hawkins et al. (2003) using European data for five taxa. Global Ecology and Biogeography 16: 76–89.
- Whittaker RJ, Araújo MB, Jepson P, Ladle RJ, Watson JEM, Willis KJ. 2005. Conservation biogeography: Assessment and prospect. Diversity and Distributions 11: 3–23.
- 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.

Supplementary Material

The following supplementary material is available for this article at http://onlinelibrary.wiley.com/ doi/10.1111/j.1759-6831.2012.00190.x/suppinfo:

Doc. S1. Leguminosae phylogeny in parenthetical notation calculated for this analysis.

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.