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RESEARCH PAPER

Contributions of Leguminosae to young and old stands of neotropical forests under different environmental conditions

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Abstract

• ***Key message*** **Potentially nodulating Leguminosae species had high density and biomass in young stands of forests in Northeast Brazil, except in a dry forest on a low-fertility soil.**

• ***Context*** Leguminosae species, especially potentially nodulating ones, appear to be important components of tropical secondary forests, although information is still scarce concerning their contributions to richness and biomass under different environmental conditions.

• ***Aims*** To evaluate the contribution of Leguminosae to the aboveground biomass and density of young and old forest stands in six sites, with different climate and soil conditions, in northeastern Brazil.

• ***Methods*** The biomass of plants was estimated using allometric equations in ten plots in one young and one old forest stand in each site. Leguminosae were separated into nodulating and non-nodulating species based on literature.

• ***Results*** Leguminosae, mainly nodulating species, displayed the largest number of species among all families and the largest biomass and density in young stands. There was more similarity in Leguminosae species composition between young and old stands in dry than in humid forests.

• ***Conclusion*** Nodulating species make considerable contributions to the biomass of the initial successional stages of forests in Northeast Brazil — confirming the importance of the family for natural forest regeneration, especially in dry environments.

Keywords Aboveground biomass · N-fixing species · Nodulation · Plant density · Species richness

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Contribution of the co-authors Tânia Lúcia da Costa (doctorate student) did the field sampling, analyzed and interpreted the data, and wrote the article. Everardo Valadares de Sá Barreto Sampaio and Ana Dolores Santiago de Freitas (advisers) designed the project, choose the sampling sites, and helped with data analysis and writing of the article. Aleksandro Ferreira da Silva (doctorate student) helped with field sampling and data analysis. Elcida de Lima Araújo (member of the advisory committee) participated in discussing and writing the article.

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1 Introduction

Secondary forests are becoming predominant in the tropics as a result of the substitution of old-growth forests by crops and pastures and the eventual abandonment of these activities, leading to the natural regeneration of the native vegetation (Aide and Grau 2004; Arroyo-Rodríguez et al. 2017; FAO 2018). Leguminosae species are particularly abundant in secondary neotropical forests (Gei et al. 2018), in both dry (Lebrija-Trejos et al. 2008; Souza et al. 2012; Lopes et al. 2012) and humid regions (Aidar et al. 2001; Pereira et al. 2003; Oliveira-Filho et al. 2004; Romero-Duque et al. 2007; Guedes et al. 2012; Souza et al. 2012). The Leguminosae appear to have competitive advantages over the species of other families due to their symbiotic relationships with nitrogen-fixing bacteria, particularly in soils with low N availability (Freitas et al. 2010; Gei et al. 2018). As succession advances, the density of Leguminosae decreases in some areas (Oliveira et al. 2006; Álvarez-Yépiz et al. 2008), while remaining high in others (Souza et al. 2012; Cabral et al. 2013). No clear explanation has been provided for this difference, but it could be related to the ecological advantage of fixation, since in the areas where the density of Leguminosae remains high, the pioneer N-fixing species tended to be replaced by non-N-fixing species (Souza et al. 2012; Cabral et al. 2013).

The role of Leguminosae, especially potentially nodulating species, can vary not only along successional stages but also under different environmental conditions (Gehring et al. 2008; Gei et al. 2018). In general, total species richness tends to be higher, but the proportion of Leguminosae lower, in humid as compared to dry forests (Ferraz et al. 1998; Alcoforado-Filho et al. 2003; Valdez-Hernández et al. 2014). A higher proportion of Leguminosae plant density and stem basal areas has also been reported in dry than in humid forests (Lebrija-Trejos 2008; Valdez-Hernández et al. 2014; Gei et al. 2018). Dry tropical forests usually have higher soil N losses than humid forests, due to lower recycling in the plant-soil system, as evidenced by their higher soil and plant ^{15}N signals (Amundson et al. 2003; Aranibar et al. 2004; Freitas et al. 2015), making N fixation especially advantageous under dry conditions (Gei et al. 2018). The importance of Leguminosae may also differ between forests growing in high- and low-fertility soils. Under low fertility, nutrients other than N may be more limiting, and N-fixing Leguminosae would have fewer ecological advantages (Vitousek et al. 2013; Freitas et al. 2015). However, there is little specific information available in terms of the proportions of Leguminosae and nodulating Leguminosae biomass in relation to the total taxa, particularly considering successional stage, type of climate, or soil fertility (Gehring et al. 2008; Souza et al. 2012; Gei et al. 2018).

Therefore, we addressed the following questions: (1) Are the species richness, plant density, and total aboveground biomass of Leguminosae greater in younger than in older forests? Our hypothesis is that Leguminosae, especially N-fixing species, dominate in initial successional stages. (2) Does the relative importance of Leguminosae in terms of species richness, plant density, and biomass differ under different climates? And does the stand age (successional stage) interact with climate? Our hypothesis is that Leguminosae presence is higher in forests in drier climates. (3) Are the richness, plant density, and biomass of Leguminosae species greater in forests growing on high-fertility soils than on low-fertility soils? Our hypothesis is that nutrient limitations (other than N) may restrict the advantages of N-fixing Leguminosae species growing in low-fertility soils, reducing their participation in the forest. And (4) is Leguminosae species composition different under diverse environmental conditions? Our hypothesis is that the adaptations of Leguminosae will lead to a larger dissimilarity of species composition between younger and older stands growing under humid as opposed to dry conditions.

2 Material and methods

2.1 Study area

The study was carried out in tropical forests in northeastern Brazil which are exposed to a wide range of environments and contain considerable diversity of species of the Leguminosae family. Rainfall decreases in an east to west direction, from the humid coastal zone to a sub-humid transition zone and to the semi-arid interior lands, where isolated montane areas have slightly higher rainfall than the surrounding areas (Table 1). The transition and semi-arid zones have a large diversity of soil types, with contrasting fertility of those derived from highly weathered sedimentary material and those less weathered soils derived from crystalline parent material. Regolithic Neosols and the Latosols of the sub-humid and semi-arid zones are typically low-fertility soils while Argisols and Luvisols have higher fertility levels (Sampaio 2010). The coastal zone was originally covered with humid forests, mostly substituted by sugarcane fields. The montane areas were also covered by humid forests, but only small forest patches remain. The sub-humid and semi-arid zones were mostly covered by thorny deciduous dry forests (known as *caatinga*), and about half of the area is still covered by native vegetation, mostly regenerating forests that are the fallow part of the prevalent slash and burn agricultural system (Sampaio 2010). In the Araripe plateau, with highly weathered and low-fertility soils, the vegetation is a non-thorny deciduous dry forest (known as *carrasco*), with some characteristics similar to those of savannas (*cerrado*). That heterogeneity also includes higher soil N losses in dry areas (Freitas et al. 2015), which could result in greater advantages for nitrogen-fixing

Table 1 Site characteristics of the different native tropical forest fragments of different ages studied in northeastern Brazil

Vegetation type (municipality)	Altitude (m.a.s.l.)	Rainfall (mm)	Temperature (°C)	Soil type, fertility	Age	Coordinates	Previous use history
Humid coastal, evergreen (Igarassu)	20–115	1687	24.9	Argisol, deep, medium	20	7° 47′ 53.6″ S 35° 02′ 25.6″ W	Sugarcane followed by pasture.
					>40	7° 42′ 51.7″ S 34° 59′ 35.4″ W	Unknown; already forested 40 years ago
Sub-humid, high fertility, deciduous (Caruaru)	561	764	21.7	Argisol, shallow, high	21	08° 13′ 54″ S 35° 55′ 13″ W	Caatinga clear-cut; *Opuntia ficus indica* Mill planted and abandoned
					>50	08° 13′ 47″ S 35° 55′ 09″ W	Unknown; no use for at least 50 years
Sub-humid, low fertility, deciduous (São João)	716	885	21.1	Regolithic Neosol, deep, low	10	08° 48′ 40.34″ S 36° 24′ 3.75″ W	Corn and beans crops in itinerant agriculture
					>50	08° 52′ 32″ S 36° 22′ 00″ W	Unknown; no use for at least 50 years
Humid montane, evergreen (Triunfo)	1028	1250	18–22.5	Cambisol, shallow, high	20	7° 50′ 32″ S 38° 07′ 15″ W	Corn and bean crops in itinerant agriculture
					>80	7° 51′ 51.7″ S 38° 07′ 49.4″ W	Unknown; forest for at least 80 years, with selective cutting of trees 30 years ago
Semi-arid, high fertility, deciduous (Serra Talhada)	500	686	26	Luvisol, shallow, high	15	7° 54′ 24″ S 38° 18′ 02″ W	Caatinga opened to be used as native pasture
					>50	7° 53′ 49.9″ S 38° 18′ 14.7″ W	Selective cutting of plants 30 years ago
Semi-arid, low fertility, deciduous (Araripe)	867	700	24–26	Latosol, deep, low	18	7° 20′ 05.6″ S 40° 03′ 33.2″ W	Cassava crops in itinerant agriculture
					>40	7° 19′ 25.5″ S 40° 05′ 00.1″ W	Cassava crops in itinerant agriculture

Leguminosae species (despite the generally low soil N concentrations in all areas).

Young and old stands of six native forest types were selected along an east-west transect approximately 560 km long in northeastern Brazil (7° 42′ 51.7″ S and 34° 59′ 35.4 W to 7° 19′ 25.5″ S and 40° 05′ 00.1″ W) (Table 1). The forest fragments selected (from east to west) correspond to (1) humid coastal forest, part of the Atlantic Forest; (2) sub-humid high-fertility forests typical of *agreste caatinga*; (3) sub-humid low-fertility sandy *caatinga* forest; (4) humid montane (*Brejo*) forest; (5) semi-arid high-fertility (*sertão caatinga*) forest; and (6) semi-arid low-fertility (*Carrasco*) forest (Fig. 1). Characteristics of the soils of the areas are listed in Appendix Table 4. Two different stands (between 0.3 and 17 km apart) were sampled in each area, one old and one young. Information concerning their ages and previous land uses were based on studies conducted in the areas and/or conversations with residents (Table 1).

Ten 20 × 20 m plots were established along a single transect through each forest stand, with 10 m between plots. In the sub-humid and semi-arid forests, all living plants with stem diameters ≥ 3 cm at 1.3 m above ground level (DBH) in every plot (except for lianas and epiphytes) were identified and had their stem diameters measured. In cases of plants branching below 1.3 m, the diameters of all of their branches were measured, their areas were determined and summed, and the equivalent diameter of that sum was calculated. In the humid forests, the inclusion criterion for measuring the living plants was DBH ≥ 5 cm and the other procedures were the same adopted for the sub-humid and semi-arid forests.

2.2 Biomass calculation

The aboveground biomass of each plant was estimated by allometric equations, using DBH as the independent variable. The general biomass equation used for the sub-humid and semi-arid forests was that established by Sampaio and Silva (2005): biomass (kg) = $0.173\text{DBH}^{2.295}{}_{(\text{cm})}$. The general equation of Chave et al. (2001) was used for humid forests: biomass (kg) = $\exp(-2.19 + 2.54\text{LN}(\text{DAP}_{(\text{cm})}))$.

2.3 Species identification

Botanical material from each species was collected for identification by specialists and/or by comparisons with specimens deposited in the Federal Rural University of Pernambuco herbarium (PEUFR). The scientific names of the species were confirmed by consulting the W3 Tropics database (www.tropicos.org). The current classification of the Leguminosae sub-families followed The Legume Phylogeny Working Group (LPWG 2017).

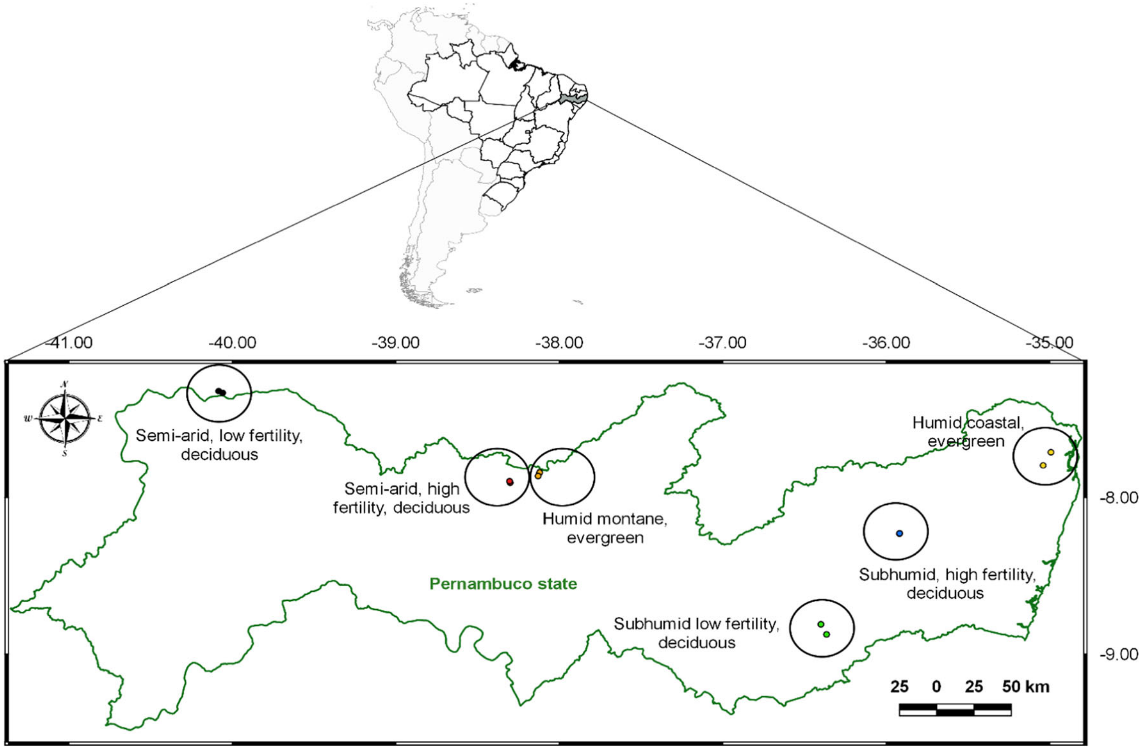

Fig. 1 Map of the study area with the distribution of young and old stands, along an east-west transect in Pernambuco state, Brazil

The Leguminosae species were separated into potentially N-fixing (henceforth designated as nodulating or N-fixing species) and non-N-fixing species (non-nodulating species) based on information published for the species or, in case of the absence of species information, for their genera (Faria and Lima 1998; Gehring et al. 2005; Sprent 2009; Freitas et al. 2010, 2015).

2.4 Statistical analysis

We analyzed differences in the biomass and in the plant density of pooled, Leguminosae, and nodulating species between young and old stands across the study sites using an analysis of variance. The analyses were conducted considering a split-plot (nested) design, in which the main plots corresponded to the six sites and the split plots to the young and old stands in each site. The 10 plots of each stand were considered replicates, but in fact they were pseudo-replicates. Therefore, the differences between forests may be due not only to their different climate and soil characteristics but also to local unknown characteristics. The data were log-transformed to attend normality criteria. The means were compared by the LSD (least significant difference) Student test at a significance level of 0.05. Analyses were carried out using the split-plot function of the agricolae package of the R program (R Core Team 2020).

3 Results

3.1 Biomass and density

The total aboveground biomass in the young stands of all forests varied from 20 to 24 Mg ha^{-1}, except in the humid coastal forest where it reached 124 Mg ha^{-1} (Fig. 2). The total aboveground biomass in the old stands varied from 28 to 68 Mg ha^{-1} in the sub-humid and semi-arid forests and from 227 to 273 Mg ha^{-1} in the humid coastal and montane forests, respectively. The total biomass was significantly higher in the old stands of most forests, but not in the two low-fertility (sub-humid and semi-arid) forests.

Leguminosae biomass was similar in both young and old stands, and among the different forest types, except for a higher biomass in the old stand of the montane forest (Fig. 2), partly contradicting our first three hypotheses. However, relative to total forest aboveground biomass (Fig. 2) and plant density (Fig. 3), the proportions of the Leguminosae in the young sub-humid and semi-arid stands were higher than in the young humid costal and montane stands, confirming our second hypothesis (Table 2). The proportions of Leguminosae biomass in old stands tended to be lower than in the young stands in four of the forests (13 to 68%) but were similar in the sub-humid high-fertility and montane forests, partially confirming our first hypothesis.

Most of the Leguminosae in the young stands belonged to nodulating species (Fig. 2), representing between 74 and 99%

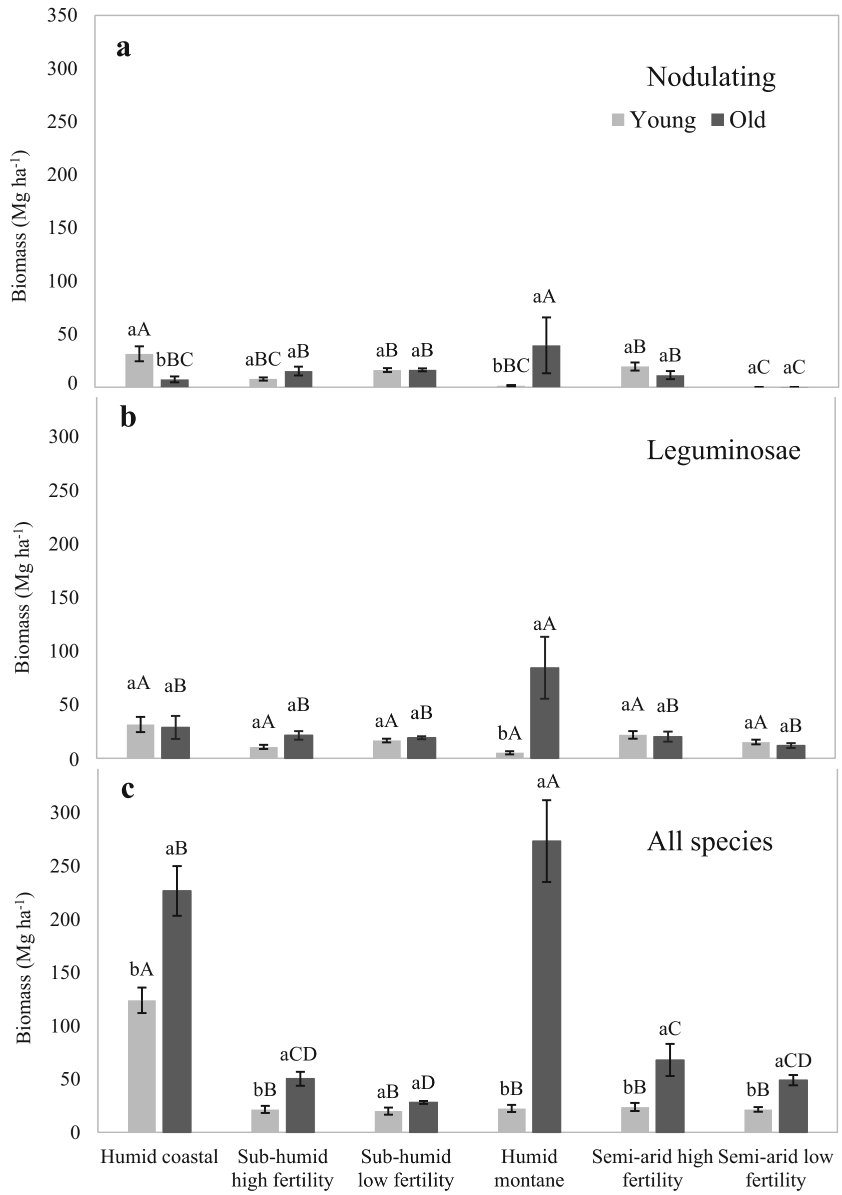

Fig. 2 Nodulating Leguminosae (A), all Leguminosae (B), and all tree and large shrub species (C) biomass in young and old stands of tropical forests under different environmental conditions in Northeast Brazil. Bars topped by the same small letter, comparing young and old stands in the same forest, and by the same capital letter, comparing young or old stands of the different forests, are not significantly different by the LSD test at a 0.05 probability level

of the Leguminosae biomass (except in the montane [29%] and in the semi-arid low-fertility forest [1%]) (Table 2). The biomass of those nodulating species did not significantly differ between young and old stands of sub-humid and semi-arid forests (0.2 to 19.5 Mg ha^{-1}) but were higher in the young stands of the coastal forest (31 versus 7 Mg ha^{-1}) and higher in the old stands of the montane forest (39 versus 2 Mg ha^{-1}) (Fig. 2).

3.2 Species composition

Leguminosae comprised the highest number of species among all plant families present in each forest type (Table 3; Appendix Table 6), the humid forests containing more Leguminosae species than the sub-humid or semi-arid forests, following the overall pattern of higher total numbers of taxa. The old stands had more Leguminosae species more than the young stands, except in the sub-humid low-fertility forest, where both stands had only three Leguminosae species.

In the sub-humid and semi-arid forests, species of the mimosoid clade (former Mimosoideae) of the Caesalpinioideae sub-family corresponded to more than half of the species in all localities (Appendix Tables 5 and 6) and had the largest proportions of Leguminosae biomass. Most of the mimosoids belonged to the tribe Mimoseae. A single species of Papilionoideae, belonging to the tribe Swartzieae (*Amburana cearensis* (Allemão) A.C.Sm.), was present in the young stand of the semi-arid high-fertility forest. Of all Leguminosae species, only those of the mimosoid clade of the tribes Mimoseae and Ingeae have been referred to as capable

Table 2 Proportions (%) of nodulating species aboveground biomass and plant density in relation to those of all Leguminosae and all tree and large shrub species and proportion of Leguminosae in relation to all tree species in young and old stands of tropical forests under different environmental conditions in Northeast Brazil

Forest	Nodulating/Leguminosae		Nodulating/all		Leguminosae/all	
	Young	Old	Young	Old	Young	Old
Biomass						
Humid coastal	99.6	25.7	25.3	3.3	25.4	12.7
Sub-humid high fertility	73.6	71.5	36.1	30.4	49.1	42.5
Sub-humid low fertility	97.6	85.4	81.0	58.2	83.0	68.1
Humid montane	28.8	46.7	6.7	14.4	23.1	30.9
Semi-arid high fertility	89.0	56.4	81.6	16.8	91.6	29.7
Semi-arid low fertility	1.3	1.7	0.9	0.4	70.4	24.2
Density						
Humid coastal	99.6	40.0	26.7	4.0	26.8	10.0
Sub-humid high fertility	59.6	46.1	23.7	19.2	39.8	41.8
Sub-humid low fertility	90.0	70.1	87.2	53.9	96.9	76.9
Humid montane	29.0	23.6	7.3	3.3	25.1	14.0
Semi-arid high fertility	85.6	39.8	70.6	12.3	82.4	30.8
Semi-arid low fertility	4.1	2.5	1.8	0.8	44.5	30.4

of forming nodules with N-fixing bacteria (Appendix Table 5). In the semi-arid low-fertility forest, only the species of the tribes Ingeae (mimosoid clade), Sophoreae, and Swartzieae (Papilionoideae sub-family) were considered nodulating species.

In the young stand of the humid montane forest, however, the largest proportion of Leguminosae biomass belonged to Caesalpinioideae species outside the mimosoid clade (Appendix Tables 5 and 6). This difference in predominant clades in relation to the drier forests confirmed our fourth hypothesis. In the young stand of the humid coastal forest, the mimosoid clade comprised the largest number of species and the greatest biomass, followed by the Papilionoideae sub-family, with the mimosoid species belonging to the tribe Ingeae and the Papilionoideae species belonging to the tribes Dalbergieae, Sophoreae, and Swartzieae. All species or genera of mimosoid and Papilionoideae have been reported as nodulating. The tribes in the montane forest were almost identical to those in the coastal forest, although the genera differed in most cases. All mimosoid species, and two of the three species of Papilionoideae in the montane forest, have been considered nodulating.

In all young stands (except in the sub-humid high-fertility forest), the species with the highest plant density belonged to Leguminosae: *Mimosa tenuiflora* (Willd.) Poir in the sub-humid low-fertility and semi-arid high fertility forests, *Senegalia langsdorffii* (Benth.) Seigler & Ebinger in the semi-arid low-fertility forest, *Inga ingoides* (Rich.) Willd in the coastal forest, and *Copaifera langsdorffii* Desf. in the montane forest (Appendix Table 5). The dominant species (32%) in the young stand of the sub-humid high-fertility forest (Appendix Table 6) was *Croton blanchetianus* Baill. (Euphorbiaceae), followed by two Leguminosae: *Piptadenia stipulacea* (Benth.) Ducke and *Poincianella pyramidalis* (Tul.) LP Queiroz. Contrasting with those young stands, the highest density in all old stands belonged to non-Leguminosae species, except in the species-poor sub-humid low-fertility forest, where *M. tenuiflora* comprised 55% of all plants.

4 Discussion

4.1 Biomass and density

The biomass of the young stands of sub-humid and semi-arid forests were in the same range as those of other tropical dry forests throughout the world with up to 25 years of regeneration (17 to 31 Mg ha^{-1}) (Becknell et al. 2012; Raharimalala et al. 2012; Rozendaal et al. 2017). The biomass of the old stands, however, was lower than those of most other dry forests, which usually had more than 72 Mg ha^{-1} (Read and Lawrence 2003; Raherison and Grouzis 2005; Vargas et al. 2008; Raharimalala et al. 2012; Becknell and Powers 2014). Low water availability is the probable cause of the low biomass in Brazilian dry forests, the closest to the equator with the highest potential evapotranspiration (Silva Filho et al. 2020). The biomass of the humid forests was within the ranges reported elsewhere (Fonseca et al. 2011; Poorter et al. 2016; Stas et al. 2017) for both young (76 to 100 Mg ha^{-1}) and old stands (100 to 334 Mg ha^{-1}), except for the low biomass of the young stand of the montane forest. The ranges were higher in humid forests than in dry forests, probably because of their greater water availability.

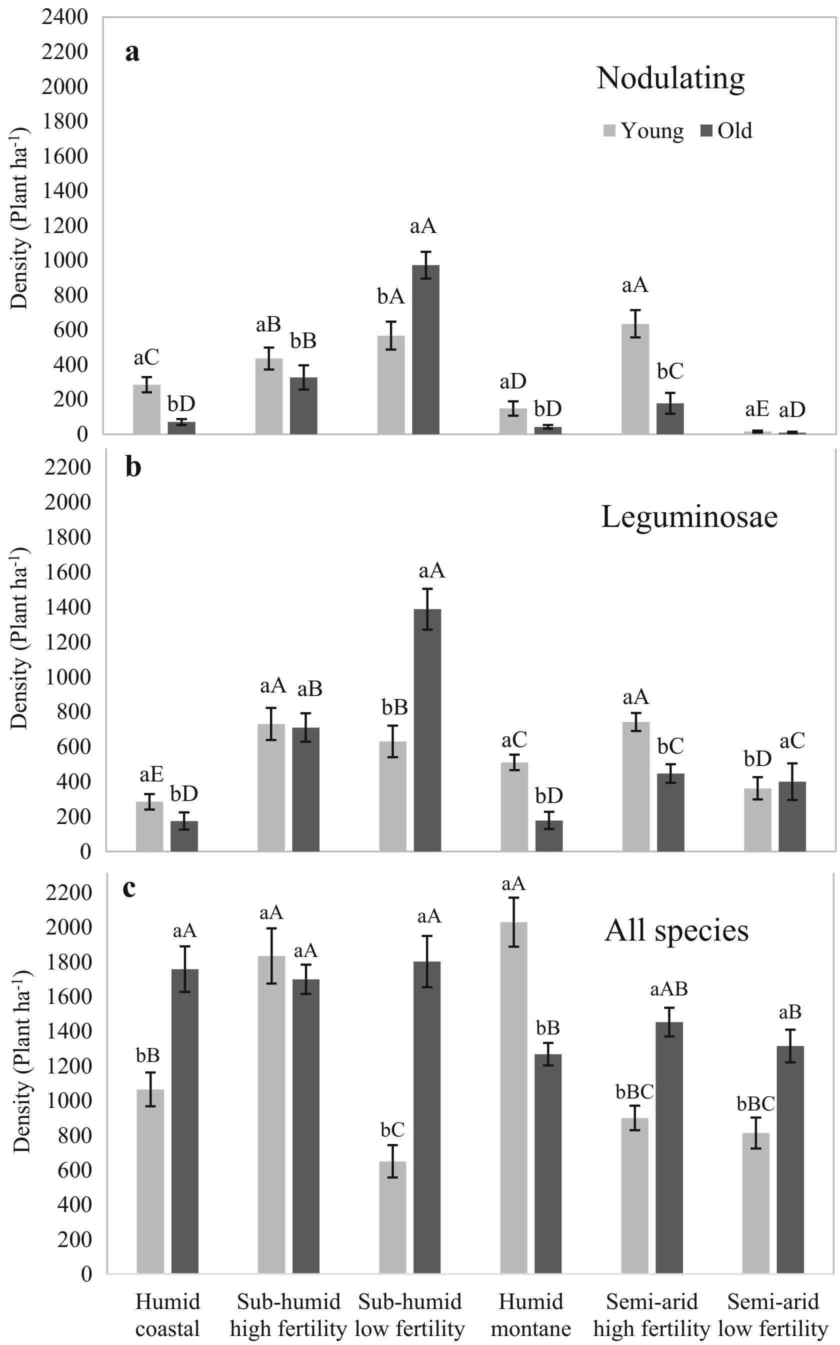

Fig. 3 Nodulating Leguminosae (A), all Leguminosae (B), and all tree and large shrub species (C) plant density in young and old stands of tropical forests under different environmental conditions in Northeast Brazil. Bars topped by the same small letter, comparing young and old stands in the same forest, and by the same capital letter, comparing young or old stands of the different forests, are not significantly different by the LSD test at a 0.05 probability level

Table 3 Numbers of all families and species, all Leguminosae and nodulating Leguminosae species of trees and large shrubs in young and old stands of tropical forest under different environmental conditions in Northeast Brazil. Total of 10 plots (0.4 ha)

Forest	Families		Species		Leguminosae		Nodulating	
	Young	Old	Young	Old	Young	Old	Young	Old
Humid coastal	19	29	35	58	9	10	7	7
Sub-humid high fertility	11	16	21	37	6	8	3	4
Sub-humid low fertility	7	11	9	17	3	3	1	1
Humid montane	25	22	45	50	9	11	5	5
Semi-arid high fertility	6	18	12	40	6	11	3	6
Semi-arid low fertility	8	11	15	27	5	6	3	3

Our results with a high proportion of Leguminosae biomass and species richness in the sub-humid and semi-arid forests confirm the importance of the family in neotropical forests reported in previous studies (Aidar et al. 2001; Pereira et al. 2003; Oliveira-Filho et al. 2004; Romero-Duque et al. 2007; Lebrija-Trejos et al. 2008; Araújo et al. 2011; Crescencio et al. 2011; Souza et al. 2012; Guedes et al. 2012; Nascimento et al. 2014). High density and basal area proportions of Leguminosae plants have also been reported in other forests and tend to be higher in dry than in humid forests (Lebrija-Trejos et al. 2008; Valdez-Hernández et al. 2014; Gei et al. 2018). These results of basal area are similar to ours of biomass, which we estimated based on allometric equations using diameter as the independent variable.

The lower proportion of Leguminosae biomass in humid forests indicates that the family has a lower contribution to the forest stand where water is not limiting, partially confirming our second hypothesis. However, the absolute values of Leguminosae biomass were not lower in humid forests than in sub-humid and semi-arid forests, suggesting that greater water availability is not detrimental to Leguminosae. Higher water availability allows the establishment of more species, which together accumulate a higher total biomass. Higher species richness and aboveground biomass in humid than dry forests have been repeatedly reported, including those of Leguminosae (Lebrija-Trejos et al. 2008; Valdez-Hernández et al. 2014; Gei et al. 2018).

The low proportion of nodulating Leguminosae species in the semi-arid low-fertility forest indicates that N fixation is not a critical process in that environment, probably because of nutrient availability limitations, mainly phosphorus (Sampaio 2010). These low proportions confirm our third hypothesis. Most of the Leguminosae plants in this site were *Senegalia langsdorffii*, a non-nodulating species. Conversely, the high proportion of nodulating Leguminosae species found in most of the other forests suggests that N fixation is an important ecological process, especially in drier forests (Gei et al. 2018). However, data to support this hypothesis are scarce, highlighting the need of measurements of actual N fixation in tropical forest.

The similarities of the Leguminosae biomass between young and old forest stands (except the montane forests, where their biomass was higher in the old stand) lead to the conclusion that the family maintains its occupation of forest spaces even with advancing successional stages. That occupation may correspond to fewer plants with higher average biomass or greater numbers of plants with lower average biomass. The higher proportions of legume biomass in relation to the total biomass in young rather than old stands, however, do indicate that Leguminosae participation decreases along successional stages, confirming our first hypothesis. As the relative biomass and plant density of species other than N-fixing Leguminosae increase with age, it could be argued that N fixation during the initial successional stages increases N availability and allows other species to become established and prosper (Gehring et al. 2005; Sullivan et al. 2014; Gei et al. 2018).

In the humid forest, later successional species included other Leguminosae that eventually substituted pioneer species, while most of the Leguminosae species in the sub-humid and semi-arid forests were the same in both young and old stands. These later successional Leguminosae species could have N-fixation patterns different from those of the pioneer species of young stands, probably related to other environmental variables, such as shading. Detailed information concerning changes in N fixation along successional stages in tropical forests, however, remains scarce.

The probable initial ecological advantage of N fixation is corroborated by the lower biomass proportions of nodulating species in the old stands of some forests, although with two notable exceptions. The first refers to the semi-arid low-fertility forest, where N-fixing Leguminosae were almost absent in both young and old stands, probably due to phosphorous deficiencies (Sampaio 2010), confirming our third hypothesis. The second exception was the montane forest, where the old stand accumulated high total Leguminosae and N-fixing Leguminosae biomass, following initial slow growth. The cause of this slow growth, of similar magnitude as seen in young stands of drier forests, is not clear but could be related to the shallow, rocky montane soils. Larger proportions of nodulating species in young than in old stands have been reported in other Brazilian semi-arid forests (Pereira et al. 2003; Cabral et al. 2013), as well as in the Amazon Forest (Gehring et al. 2008). These articles confirm our results, but studies on other forests in Northeast Brazil with similar characteristics to those we analyzed are necessary to avoid the confounding effects of our pseudo-replications.

4.2 Species composition

Nodulating Leguminosae belonging only to the mimosoid clade of the Caesalpinioideae sub-family were observed in all forests. Although predominant, and comprising larger proportions of the total Leguminosae than in other tropical dry forests (Romero-Duque et al. 2007; Álvarez-Yépiz et al. 2008; Crescencio et al. 2011), mimosoid clade genera were different in the humid and the sub-humid and semi-arid forests, confirming our fourth hypothesis. The predominance of the mimosoid clade agrees with global observations that the highest proportions of nodulating species occur in this group, considering that the mimosoid clade is equivalent to the former Mimosoideae sub-family (LPWG 2017), with 90% of its species being potentially nodulant (Sprent 1995).

The Caesalpinieae and Cassieae (both Caesalpinioideae) species in all forests belonged to non-nodulating genera, although those tribes do have species with proven nodulation

(Roggy et al. 1999; Sprent 2009). With only a few exceptions, the nodulating genera of those tribes occur in South America and are mostly represented by lianas, herbaceous, or small shrub species (Alcoforado-Filho et al. 2003; Sprent 2009; Freitas et al. 2012). Therefore, nodulating species of Caesalpinioideae outside of the mimosoid clade might have been found if other strata had been sampled in this study.

5 Conclusions

The high plant density and aboveground biomass of Leguminosae species confirm their high contribution to the forest growth in the initial stage of succession during the natural regeneration of neotropical forests. The lower relative density and biomass of the Leguminosae species in the humid than in the dry forests (27% or less versus 40 to 90%) indicate that the importance of Leguminosae is lower when water is not a limiting factor and plant richness is higher. Most of the Leguminosae in both young and old stands were potentially N-fixing species, except in the semi-arid low-fertility forest, indicating a possible ecological advantage of N fixation.

Appendix

Table 4 Characteristics of the superficial soil layer in the sites where the study was conducted (0–20 cm)

	Humid coastal	Sub-humid low fertility	Sub-humid high fertility	Humid montane	Semi-arid high fertility	Semi-arid low fertility
Sand (g kg^{-1})	620	864	631	478	693	790
Clay (g kg^{-1})	280	62	140	89	178	180
pH	5.0	5.3	5.2	5.2	6.8	4.8
P (mg kg^{-1})	4.4	4.5	2.8	11.0	4.4	0.7
Ca (mmol kg^{-1})	10.0	8.7	25.0	45.0	16.0	1.3
Mg (mmol kg^{-1})	9.0	5.8	11.0	20.0	10.0	2.3
Al (mmol kg^{-1})	0.4	2.1	3.0	0.3	1.5	4.0

References from left to right column: Nascimento (2010), Silva et al. (2017), Alcoforado-Filho et al. (2003), Ferraz et al. (2003), Freitas et al. (2010), Faria et al. (2016), Freitas et al. (Dados não publicados)

Table 5 Density (plants ha^{-1}) of Leguminosae species and indication of the nodulation potential of specie, in tropical forest fragments with different ages (*Y* young, *O* old) in the northeast of Brazil

Sub-family-tribe-species	Nodulation[1]	Y	O
Humid coastal			
Detarioideae			
Detarieae/*Hymenaea courbaril* L.	–	0	5
Dialioideae			
Cassieae/*Apuleia leiocarpa* (Vogel) J.F. Macbr.	–	2	95
Caesalpinioideae			
Mimosoida**			
Ingeae/*Albizia pedicellaris* (DC.) L. Rico	+	0	5
Albizia polycephala (Benth.) Killip ex Record	+	85	0
Albizia saman (Jacq.) F. Muell.	+	25	0
Abarema cochliacarpos (Gomes) Barneby & J.W. Grimes	(+)	0	15
Inga cayennensis Sagot ex Benth.	+	0	2
Inga cf. *ingoides* (Rich.) Willd.	+	128	0

Table 5 (continued)

Sub-family-tribe-species	Nodulation[1]	Y	O
Inga thibaudiana DC.	+	0	5
Inga sp.	(+)	0	8
Papilionoideae			
Dalbergieae/*Andira nitida* Mart. ex Benth.	+	2	12
Machaerium hirtum (Vell.) Stellfeld	+	30	0
Sophoreae/*Bowdichia virgilioides* Kunth	+	2	28
Swartzieae/*Swartzia pickelii* Killip ex Ducke	(+)	8	0
Leguminosae indeterminada 1	s.i.	0	2
Leguminosae indeterminada 2	s.i.	2	0
Sub-humid, high fertility, deciduous			
Cercidoideae			
Cercideae/*Bauhinia cheilantha* (Bong.) Steud.	−	15	72
Caesalpinioideae			
Cassieae/*Senna* cf. *spectabilis* (DC.) H.S. Irwin & Barneby	−	15	0
Caesalpinieae/*Poincianella pyramidalis* (Tul.) L.P. Queiroz	−	262	278
Mimosoida**			
Mimoseae/*Anadenanthera colubrina* (Vell.) Brenan	+	50	225
Mimosa arenosa (Willd.) Poir.	+	118	7
Piptadenia stipulacea (Benth.) Ducke	+	268	28
Acacieae/*Senegalia* cf. *polyphylla* (DC.) Britton & Rose	(−)	0	8
Senegalia tenuifolia (L.) Britton & Rose	(−)	0	8
Ingeae/*Chloroleucon* cf. *foliolosum* (Benth.) G.P. Lewis	+	0	80
Sub-humid low fertility, deciduous			
Caesalpinioideae			
Caesalpinieae/*Poincianella pyramidalis* (Tul.) L.P. Queiroz	−	30	0
Mimosoida**			
Mimoseae/*Mimosa tenuiflora* (Willd.) Poir.	+	575	990
Acacieae/*Senegalia* sp.1	(−)	0	182
Senegalia sp.2	(−)	25	215
Humid montane			
Cercidoideae			
Cercideae/*Bauhinia* cf. *forficata* Link	(−)	0	10
Detarioideae			
Detarieae/*Copaifera langsdorffii* Desf.	−	268	15
Hymenaea courbaril L.	−	82	40
Caesalpinioideae			
Cassieae/*Senna macranthera* (DC. ex Collad.) H.S. Irwin & Barneby	−	10	0
Senna sp.	(−)	0	5
Mimosoida**			
Mimoseae/*Anadenanthera colubrina* (Vell.) Brenan	+	0	15
Piptadenia stipulacea (Benth.) Ducke	+	5	0
Parapiptadenia zehntneri (Harms) M.P. Lima & H.C. Lima	+	0	12
Ingeae/*Albizia* cf. *polycephala* (Benth.) Killip ex Record	+	45	2
Enterolobium contortisiliquum (Vell.) Morong	+	2	0
Inga thibaudiana DC.	+	15	0
Papilionoideae			
Swartzieae/*Amburana cearensis* (Allemão) A.C.Sm.	−	0	10
Dalbergieae/*Machaerium* sp.	(+)	0	2

Table 5 (continued)

Sub-family-tribe-species	Nodulation[1]	Y	O
Platymiscium floribundum Vogel	+	80	10
Leguminosae indeterminada 3	s.i	2	0
Leguminosae indeterminada 4	s.i	0	50
Semi-arid, high fertility, deciduous			
Cercidoideae			
Cercideae/*Bauhinia cheilantha* (Bong.) Steud.	−	85	115
Caesalpinioideae			
Cassieae/*Senna macranthera* (DC. ex Collad.) H.S. Irwin & Barneby	−	0	2
Caesalpinieae/*Libidibia ferrea* (Mart. ex Tul.) L.P. Queiroz	−	3	2
Poincianella pyramidalis (Tul.) L.P. Queiroz	−	25	142
Mimosoida**			
Mimoseae/*Anadenanthera colubrina* (Vell.) Brenan	+	13	70
Mimosa ophtalmocentra Mart. ex Benth	+	0	8
Mimosa tenuiflora (Willd.) Poir.	+	612	28
Parapiptadenia zehntneri (Harms) M.P. Lima & H.C. Lima	+	0	32
Piptadenia stipulacea (Benth.) Ducke	+	5	30
Ingeae/*Chloroleucon dumosum* (Benth.) G.P. Lewis	+	0	8
Papilionoideae			
Swartzieae/*Amburana cearensis* (Allemão) A.C.Sm.	−	0	10
Semi-arid, low fertility, deciduous			
Cercidoideae			
Cercideae/*Bauhinia acuruana* Moric.	−	0	72
Caesalpinioideae			
Cassieae/*Senna* sp.	(−)	78	18
Mimosoida**			
Acacieae/*Senegalia langsdorffii* (Benth.) Seigler & Ebinger	(−)	258	290
Ingeae/*Chloroleucon dumosum* (Benth.) G.P. Lewis	+	8	2
Papilionoideae			
Sophoreae/*Bowdichia* cf. *virgilioides* Kunth	+	8	2
Swartzieae/*Swartzia psilonema* Harms	(+)	8	5

+ nodulating, − non-nodulating, (+)/(−) probably nodulating or not based on nodulation information for the genera, *s.i.* no information

[1] Information about the occurrence of nodulation: Faria and Lima (1998), Freitas et al. (2010, 2015), Gehring et al. (2005), Sprent (2009)

**Former Mimosoideae sub-family (LPWG 2017)

Table 6 Number of individuals (n), total plant density (PD, plants ha^{-1}), total aboveground biomass (B, Mg ha^{-1}), and total basal area (BA, m^2 ha^{-1}) of species in tropical forest fragments with different ages in Northeast Brazil

Family	Species	*n*	PD	B	BA
Humid coastal, evergreen (Igarassu), 20 years					
Anacardiaceae	*Tapirira guianensis* Aubl.	6	15	6.3	0.7
Annonaceae	*Xylopia frutescens* Aubl.	6	15	0.4	0.1
Apocynaceae	*Rauvolfia* sp.	1	2.5	0.0	0.0
Araliaceae	*Schefflera morototoni* (Aubl.) Maguire et al.	13	32.5	0.7	0.1
Bixaceae	*Cochlospermum vitifolium* (Willd.) Spreng.	4	10	0.2	0.1
Boraginaceae	*Cordia sellowiana* Cham.	3	7.5	0.1	0.0
Lamiaceae	*Aegiphila pernambucensis* Moldenke	2	5	0.0	0.0
Lecythidaceae	*Eschweilera ovata* (Cambess.) Mart. ex Miers	29	72.5	2.4	0.5
	Gustavia augusta L.	20	50	1.0	0.2
Leguminosae	Leguminosae unidentified 2	1	2.5	0.0	0.0
Leguminosae-Caesalpinioideae	*Apuleia leiocarpa* (Vogel) J.F.Macbr.	1	2.5	0.1	0.0
Mimosoida*	*Albizia polycephala* (Benth.) Killip ex Record	34	85	2.6	0.5
	Albizia saman (Jacq.) F. Muell.	10	25	7.7	0.9
	Inga cf. *ingoides* (Rich.) Willd.	51	127.5	17.4	2.4
Leguminosae-Papilionoideae	*Andira nitida* Mart. ex Benth.	1	2.5	0.0	0.0
	Bowdichia virgilioides Kunth	1	2.5	0.5	0.1
	Machaerium hirtum (Vell.) Stellfeld	12	30	3.0	0.4
	Swartzia pickelii Killip ex Ducke	3	7.5	0.1	0.0
Malpighiaceae	*Byrsonima sericea* DC.	3	7.5	0.4	0.1
Malvaceae	*Apeiba tibourbou* Aubl.	45	112.5	24.2	3.1
	Guazuma ulmifolia Lam.	9	22.5	2.4	0.4
Melastomataceae	*Miconia minutiflora* (Bonpl.) DC.	6	15	0.3	0.1
	Miconia prasina (Sw.) DC.	4	10	0.3	0.1
Moraceae	*Brosimum discolor* Schott	24	60	2.1	0.4
Myrtaceae	*Eugenia* sp. 8	3	7.5	0.5	0.1
	Psidium guineense Sw.	3	7.5	0.8	0.1
Polygonaceae	*Coccoloba mollis* Casar.	46	115	12.3	1.8
Rhamnaceae	*Ziziphus joazeiro* Mart.	1	2.5	0.1	0.0
Salicaceae	*Casearia javitensis* Kunth	2	5	0.1	0.0
	Casearia sylvestris Sw.	20	50	2.6	0.5
Sapindaceae	*Cupania impressinervia* Acev.-Rodr.	13	32.5	2.0	0.3
	Cupania oblongifolia Mart.	15	37.5	0.9	0.2
	Talisia esculenta (A. St.-Hil) Radlk.	1	2.5	0.1	0.0
Urticaceae	*Cecropia pachystachya* Trécul	26	65	30.2	3.4
Unidentified	Unidentified 1	7	17.5	2.1	0.3
Humid coastal, evergreen (Igarassu), >40 years					
Anacardiaceae	*Tapirira guianensis* Aubl.	46	115	66.9	6.9
	Thyrsodium spruceanum Benth.	49	122.5	5.9	1.1
Annonaceae	Annonaceae unidentified	2	5	0.1	0.0
	Guatteria schomburgkiana Mart.	12	30	10.0	1.2
	Xylopia frutescens Aubl.	4	10	0.7	0.1
Apocynaceae	*Himatanthus phagedaenicus* (Mart.) Woodson	17	42.5	2.0	0.4
Araliaceae	*Schefflera morototoni* (Aubl.) Maguire et al.	12	30	8.6	1.1
Bignoniaceae	*Tabebuia* sp.	1	2.5	0.1	0.0
Boraginaceae	*Cordia superba* Cham.	10	25	0.6	0.1
Burseraceae	*Protium giganteum* Engl.	1	2.5	0.1	0.0
	Protium heptaphyllum (Aubl.) Marchand	8	20	0.6	0.1

Table 6 (continued)

Family	Species	*n*	PD	B	BA
Celastraceae	*Maytenus distichophylla* Mart. ex Reissek	8	20	1.3	0.2
	Maytenus obtusifolia Mart.	2	5	0.3	0.1
Chrysobalanaceae	*Couepia rufa* Ducke	2	5	0.1	0.0
	Licania sp.	3	7.5	0.1	0.0
Clusiaceae	*Clusia nemorosa* G.Mey.	4	10	1.2	0.2
Combretaceae	*Buchenavia tetraphylla* (Aubl.) R.A.Howard	1	2.5	7.4	0.6
Erythroxylaceae	*Erythroxylum mucronatum* Benth.	9	22.5	0.3	0.1
Humiriaceae	*Sacoglottis mattogrossensis* Malme	14	35	9.0	1.1
Lauraceae	*Ocotea glomerata* (Nees) Mez	4	10	0.6	0.1
Lecythidaceae	*Eschweilera ovata* (Cambess.) Mart. ex Miers	122	305	16.1	2.7
	Lecythis pisonis Cambess.	7	17.5	0.3	0.1
Leguminosae	Leguminosae unidentified 1	1	2.5	2.5	0.3
Leguminosae-Caesalpinioideae	*Apuleia leiocarpa* (Vogel) J.F.Macbr.	38	95	18.9	2.3
	Hymenaea courbaril L.	2	5	0.0	0.0
Mimosoida*	*Abarema cochliacarpos* (Gomes) Barneby & J.W.Grimes	6	15	0.4	0.1
	Albizia pedicellaris (DC.) L.Rico	2	5	0.7	0.1
	Inga cayennensis Sagot ex Benth.	1	2.5	0.0	0.0
	Inga thibaudiana DC.	2	5	0.1	0.0
	Inga sp.	3	7.5	0.4	0.1
Leguminosae-Papilionoideae	*Andira nitida* Mart. ex Benth.	5	12.5	0.9	0.1
	Bowdichia virgilioides Kunth	11	27.5	4.9	0.7
Malpighiaceae	*Byrsonima sericea* DC.	12	30	4.9	0.6
Malvaceae	*Eriotheca macrophylla* (K.Schum.) A.Robyns	5	12.5	7.6	0.8
Melastomataceae	*Henriettea succosa* (Aubl.) DC.	2	5	0.1	0.0
	Miconia pyrifolia Naudin	1	2.5	0.1	0.0
Moraceae	*Brosimum discolor* Schott	7	17.5	0.3	0.1
	Brosimum guianense (Aubl.) Huber	5	12.5	0.3	0.1
	Sorocea hilarii Gaudich.	3	7.5	0.1	0.0
Myrtaceae	*Calyptranthes brasiliensis* Spreng.	10	25	1.1	0.2
	Eugenia sp. 7	5	12.5	0.2	0.0
	Myrcia bergiana O.Berg	2	5	0.3	0.1
	Myrcia guianensis (Aubl.) DC.	6	15	0.2	0.0
Nyctaginaceae	*Guapira nitida* (Mart. ex J.A.Schmidt) Lundell	15	37.5	1.4	0.3
	Guapira opposita (Vell.) Reitz	10	25	1.3	0.2
Peraceae	*Chaetocarpus myrsinites* Baill.	2	5	0.2	0.0
	Pera glabrata (Schott) Poepp. ex Baill.	31	77.5	25.9	3.1
	Pogonophora schomburgkiana Miers ex Benth.	106	265	9.5	1.8
Polygonaceae	*Coccoloba latifolia* Lam.	3	7.5	0.3	0.1
	Coccoloba mollis Casar.	16	40	5.5	0.7
Rubiaceae	*Alseis pickelii* Pilg. & Schmale	8	20	1.1	0.2
Salicaceae	*Casearia javitensis* Kunth	10	25	0.4	0.1
Sapindaceae	*Cupania racemosa* (Vell.) Radlk.	9	22.5	0.3	0.1
	Sapindaceae unidentified	10	25	1.0	0.2
	Talisia sp.	1	2.5	0.0	0.0
Sapotaceae	*Pouteria* sp.	1	2.5	0.1	0.0
Schoepfiaceae	*Schoepfia brasiliensis* A.DC.	3	7.5	0.2	0.0
Unidentified	Unidentified 2	11	27.5	3.3	0.5
Sub-humid, high fertility, deciduous, Caruaru, 21 years					
Anacardiaceae	*Myracrodruon urundeuva* Allemão	29	72.5	2.83	0.61

Table 6 (continued)

Family	Species	*n*	PD	B	BA
	Schinopsis brasiliensis Engl.	55	137.5	2.96	0.70
Boraginaceae	*Cordia* cf. *trichotoma* (Vell.) Arráb. ex Steud.	64	160	0.55	0.17
Burseraceae	*Commiphora leptophloeos* (Mart.) J.B.Gillett	6	15	0.22	0.05
Capparaceae	*Capparis jacobinae* Moric. ex Eichler	5	12.5	0.05	0.01
	Cynophalla flexuosa (L.) J.Presl	6	15	0.14	0.04
Euphorbiaceae	*Croton blanchetianus* Baill.	236	590	3.56	0.98
	Euphorbiaceae unidentified	2	5	0.06	0.01
	Jatropha mollissima (Pohl) Baill.	7	17.5	0.06	0.02
Leguminosae-Caesalpinioideae	*Bauhinia cheilantha* (Bong.) Steud.	6	15	0.08	0.02
	Poincianella pyramidalis (Tul.) L.P.Queiroz	105	262.5	2.01	0.53
	Senna cf. *spectabilis* (DC.) H.S.Irwin & Barneby	6	15	0.69	0.15
Mimosoida*	*Anadenanthera colubrina* (Vell.) Brenan	20	50	5.03	0.94
	Mimosa arenosa (Willd.) Poir.	47	117.5	0.63	0.18
	Piptadenia cf. *stipulacea* (Benth.) Ducke	107	267.5	2.15	0.58
Malpighiaceae	*Ptilochaeta bahiensis* Turcz.	6	15	0.09	0.03
Nyctaginaceae	*Guapira* cf. *laxa* (Netto) Furlan	13	32.5	0.24	0.07
Rhamnaceae	*Ziziphus joazeiro* Mart.	2	5	0.15	0.03
Rutaceae	*Rutaceae* sp.	1	2.5	0.01	0.00
Verbenaceae	*Lippia* sp.	3	7.5	0.07	0.02
Unidentified	Unidentified 7	8	20	0.06	0.02
Sub-humid, high fertility, deciduous, Caruaru >50 years					
Anacardiaceae	*Myracrodruon urundeuva* Allemão	27	67.5	7.70	1.37
	Schinopsis brasiliensis Engl.	14	35	7.36	1.27
Bignoniaceae	Bignoniaceae unidentified	1	2.5	0.09	0.02
	Jacaranda sp.	2	5	0.06	0.01
Boraginaceae	*Cordia* cf. *trichotoma* (Vell.) Arráb. ex Steud.	12	30	0.81	0.18
Burseraceae	*Commiphora leptophloeos* (Mart.) J.B.Gillett	14	35	1.02	0.23
Capparaceae	*Cynophalla flexuosa* (L.) J.Presl	8	20	0.21	0.06
	Neocalyptrocalyx longifolium (Mart.) Cornejo & Iltis	1	2.5	0.08	0.02
Euphorbiaceae	*Croton blanchetianus* Baill.	159	397.5	2.98	0.81
	Croton heliotropiifolius Kunth	35	87.5	0.66	0.18
	Jatropha mollissima (Pohl) Baill.	6	15	0.12	0.03
	Manihot cf. *dichotoma* Ule	3	7.5	0.20	0.05
	Sebastiania cf. *jacobinensis* (Müll.Arg.) Müll.Arg.	8	20	0.58	0.13
Leguminosae-Caesalpinioideae	*Bauhinia cheilantha* (Bong.) Steud.	29	72.5	0.64	0.17
	Poincianella pyramidalis (Tul.) L.P.Queiroz	111	277.5	5.29	1.27
Mimosoida*	*Anadenanthera colubrina* (Vell.) Brenan	90	225	13.21	2.50
	Chloroleucon cf. *foliolosum* (Benth.) G.P.Lewis	32	80	1.74	0.41
	Mimosa arenosa (Willd.) Poir.	3	7.5	0.10	0.03
	Piptadenia cf. *stipulacea* (Benth.) Ducke	11	27.5	0.29	0.08
	Senegalia polyphylla (DC.) Britton & Rose	3	7.5	0.05	0.01
	Senegalia tenuifolia (L.) Britton & Rose	3	7.5	0.03	0.01
Malpighiaceae	*Ptilochaeta bahiensis* Turcz.	21	52.5	0.31	0.09
Malvaceae	*Ceiba glaziovii* (Kuntze) K.Schum.	4	10	3.81	0.59
	Helicteres sp.	3	7.5	0.03	0.01
Myrtaceae	*Eugenia pyriformis* Cambess.	33	82.5	0.96	0.25
	Eugenia sp. 1	1	2.5	0.01	0.00
Nyctaginaceae	*Guapira* cf. *laxa* (Netto) Furlan	1	2.5	0.04	0.01
Polygonaceae	*Ruprechtia laxiflora* Meisn.	1	2.5	0.02	0.00

Table 6 (continued)

Family	Species	*n*	PD	B	BA
Rhamnaceae	*Ziziphus joazeiro* Mart.	5	12.5	0.35	0.08
Rutaceae	*Zanthoxylum* cf. *rhoifolium* Lam.	3	7.5	0.61	0.11
Salicaceae	*Casearia* cf. *luetzelburgii* Sleumer	2	5	0.25	0.05
	Casearia sp. 1	3	7.5	0.10	0.03
Sapindaceae	*Allophylus quercifolius* (Mart.) Radlk.	10	25	0.34	0.09
Unidentified	Unidentified 8	5	12.5	0.06	0.02
	Unidentified 9	4	10	0.07	0.02
	Unidentified 10	3	7.5	0.08	0.02
	Unidentified 11	9	22.5	0.14	0.04
Sub-humid low fertility, deciduous, São João 10 years					
Anacardiaceae	*Spondias tuberosa* Arruda	1	2.5	2.26	0.34
Burseraceae	*Commiphora leptophloeos* (Mart.) J.B.Gillett	1	2.5	0.07	0.02
Euphorbiaceae	*Sapium* cf. *glandulosum* (L.) Morong	1	2.5	0.44	0.08
Leguminosae-Caesalpinioideae	*Poincianella pyramidalis* (Tul.) L.P.Queiroz	12	30	0.42	0.10
Mimosoida*	*Mimosa tenuiflora* (Willd.) Poir.	230	575	15.70	3.52
	Senegalia sp. 2	10	25	0.56	0.13
Nyctaginaceae	*Guapira* cf. *laxa* (Netto) Furlan	1	2.5	0.01	0.00
Rhamnaceae	*Ziziphus joazeiro* Mart.	3	7.5	0.49	0.09
Salicaceae	*Casearia luetzelburgii* Sleumer	1	2.5	0.01	0.00
Sub-humid low fertility, deciduous, São João >50 years					
Anacardiaceae	*Schinopsis brasiliensis* Engl.	5	12.5	1.37	0.26
Burseraceae	*Commiphora leptophloeos* (Mart.) J.B.Gillett	39	97.5	3.10	0.68
Capparaceae	*Cynophalla flexuosa* (L.) J.Presl	6	15	0.25	0.06
Erythroxylaceae	*Erythroxylum* sp. 1	1	2.5	0.06	0.01
Euphorbiaceae	*Sapium* cf. *glandulosum* (L.) Morong	21	52.5	1.73	0.38
Leguminosae-Caesalpinioideae	*Mimosa tenuiflora* (Willd.) Poir.	396	990	16.40	3.96
	Senegalia sp. 1	73	182.5	1.33	0.36
	Senegalia sp. 2	86	215	1.48	0.41
Myrtaceae	*Psidium rhombeum* O.Berg	1	2.5	0.01	0.00
Nyctaginaceae	*Guapira* cf. *laxa* (Netto) Furlan	24	60	1.10	0.26
Rhamnaceae	*Ziziphus joazeiro* Mart.	4	10	0.22	0.05
Rubiaceae	*Guettarda angelica* Mart. ex Müll.Arg.	1	2.5	0.01	0.00
Verbenaceae	*Lippia gracilis* Schauer	50	125	0.84	0.23
Unidentified	Unidentified 3	5	12.5	0.13	0.03
	Unidentified 4	5	12.5	0.06	0.02
	Unidentified 5	3	7.5	0.05	0.01
	Unidentified 6	1	2.5	0.08	0.02
Humid montane, evergreen, Triunfo, 20 years					
Annonaceae	*Annona leptopetala* (R.E.Fr.) H.Rainer	18	45	0.30	0.08
Apocynaceae	*Aspidosperma* sp.	53	132.5	1.35	0.33
Bignoniaceae	*Handroanthus impetiginosus* (Mart. ex DC.) Mattos	11	27.5	0.22	0.06
Boraginaceae	*Cordia curassavica* (Jacq.) Roem. & Schult.	15	37.5	0.19	0.06
Capparaceae	*Cynophalla flexuosa* (L.) J.Presl	2	5	0.02	0.01
Celastraceae	*Maytenus obtusifolia* Mart.	83	207.5	1.46	0.41
Ebenaceae	*Diospyros inconstans* Jacq.	20	50	0.24	0.07
Erythroxylaceae	*Erythroxylum* sp. 3	59	147.5	1.16	0.31
Euphorbiaceae	*Croton heliotropiifolius* Kunth	6	15	0.19	0.04
	Sapium glandulosum (L.) Morong	36	90	2.59	0.47
Lamiaceae	*Vitex* sp.	8	20	0.53	0.11

Table 6 (continued)

Family	Species	*n*	PD	B	BA
Lauraceae	*Ocotea duckei* Vattimo-Gil	3	7.5	0.10	0.02
Leguminosae	Leguminosae unidentified 3	1	2.5	0.01	0.00
Leguminosae-Caesalpinioideae	*Copaifera langsdorffii* Desf.	107	267.5	2.60	0.67
	Hymenaea courbaril L.	33	82.5	0.87	0.22
	Senna macranthera (DC. ex Collad.) H.S.Irwin & Barneby	4	10	0.14	0.03
Mimosoida*	*Albizia* cf. *polycephala* (Benth.) Killip ex Record	18	45	0.33	0.09
	Enterolobium contortisiliquum (Vell.) Morong	1	2.5	0.01	0.00
	Inga thibaudiana DC.	6	15	0.20	0.05
	Piptadenia stipulacea (Benth.) Ducke	2	5	0.01	0.00
Leguminosae-Papilionoideae	*Platymiscium floribundum* Vogel	32	80	0.98	0.22
Malpighiaceae	*Tetrapterys* sp.	3	7.5	0.05	0.01
Malvaceae	*Guazuma ulmifolia* Lam.	7	17.5	0.90	0.15
Myrtaceae	*Campomanesia aromatica* (Aubl.) Griseb.	15	37.5	0.39	0.09
	Campomanesia eugenioides (Cambess.) D.Legrand ex Landrum	9	22.5	0.15	0.04
	Eugenia luschnathiana (O.Berg) Klotzsch ex B.D.Jacks	5	12.5	0.23	0.05
	Myrcia multiflora (Lam.) DC.	3	7.5	0.23	0.05
	Myrtaceae unidentified 4	5	12.5	0.04	0.01
Nyctaginaceae	*Guapira laxa* (Netto) Furlan	42	105	1.38	0.33
	Guapira noxia (Netto) Lundell	9	22.5	0.10	0.03
	Guapira opposita (Vell.) Reitz	16	40	0.68	0.14
Ochnaceae	*Ouratea* sp.	3	7.5	0.41	0.07
Rhamnaceae	Rhamnaceae unidentified	2	5	0.03	0.01
Rubiaceae	*Chomelia* sp.	3	7.5	0.10	0.02
	Coutarea hexandra (Jacq.) K.Schum	57	142.5	0.76	0.22
	Guettarda sericea Müll.Arg.	8	20	0.18	0.04
	Tocoyena formosa (Cham. & Schltdl.) K.Schum.	11	27.5	0.14	0.04
Rutaceae	*Zanthoxylum rhoifolium* Lam	36	90	1.39	0.30
Salicaceae	*Casearia* sp. 3	3	7.5	0.05	0.01
Sapindaceae	*Allophylus* sp.	6	15	0.24	0.05
	Cupania impressinervia Acev.-Rodr.	20	50	0.43	0.11
Schoepfiaceae	*Schoepfia brasiliensis* A.DC.	6	15	0.25	0.06
Styracaceae	*Styrax* cf. *pohlii* A.DC.	3	7.5	0.34	0.06
Verbenaceae	*Lantana camara* L.	6	15	0.06	0.02
Unidentified	Unidentified 12	16	40	0.49	0.11
Humid montane, evergreen, Triunfo, >80 years					
Annonaceae	*Annona leptopetala* (R.E.Fr.) H.Rainer	17	42.5	9.03	0.94
Apocynaceae	*Aspidosperma* sp.	21	52.5	34.57	3.32
Araliaceae	*Aralia warmingiana* (Marchal) J.Wen	1	2.5	1.07	0.13
Bignoniaceae	Bignoniaceae unidentified 2	6	15	1.84	0.26
	Handroanthus sp.	14	35	29.38	2.96
Capparaceae	*Cynophalla flexuosa* (L.) J.Presl	10	25	0.31	0.08
Celastraceae	*Maytenus distichophylla* Mart. ex Reissek	39	97.5	3.81	0.59
Erythroxylaceae	*Erythroxylum* sp. 3	2	5	0.30	0.06
	Erythroxylum sp. 4	1	2.5	0.01	0.00
	Erythroxylum subrotundum A.St.-Hil.	4	10	0.70	0.12
Euphorbiaceae	*Sapium glandulosum* (L.) Morong	3	7.5	0.26	0.05
Leguminosae	Leguminosae unidentified 4	20	50	0.30	0.09
Leguminosae-Caesalpinioideae	*Bauhinia* cf. *forficata* Link	4	10	2.60	0.33
	Copaifera langsdorffii Desf.	6	15	5.36	0.62

Table 6 (continued)

Family	Species	*n*	PD	B	BA
	Hymenaea courbaril L.	16	40	23.48	2.54
	Senna sp.	2	5	0.14	0.03
Mimosoida*	*Albizia* cf. *polycephala* (Benth.) Killip ex Record	1	2.5	0.42	0.06
	Anadenanthera colubrina (Vell.) Brenan	6	15	31.09	2.54
	Parapiptadenia zehntneri (Harms) M.P.Lima & H.C.Lima	5	12.5	1.24	0.17
Leguminosae-Papilionoideae	*Amburana cearensis* (Allemão) A.C.Sm.	4	10	1.24	0.18
	Machaerium sp.	1	2.5	2.51	0.25
	Platymiscium floribundum Vogel	4	10	4.60	0.47
Malvaceae	*Ceiba glaziovii* (Kuntze) K.Schum.	6	15	32.29	2.44
Meliaceae	*Trichilia emarginata* (Turcz.) C.DC.	38	95	5.48	0.87
Myrtaceae	*Campomanesia eugenioides* (Cambess.) D.Legrand ex Landrum	2	5	3.87	0.36
	Campomanesia sp. 1	9	22.5	8.07	0.89
	Eugenia sp. 4	15	37.5	4.47	0.48
	Eugenia sp. 5	20	50	2.29	0.42
	Eugenia sp. 6	33	82.5	5.60	0.89
	Myrcia multiflora (Lam.) DC.	1	2.5	0.01	0.00
	Myrcia sp.	3	7.5	0.18	0.04
	Myrcia splendens (Sw.) DC.	2	5	0.03	0.01
	Myrtaceae unidentified 5	6	15	0.42	0.08
	Plinia cauliflora (Mart.) Kausel	3	7.5	0.65	0.11
	Psidium sp.	2	5	0.43	0.07
Nyctaginaceae	*Guapira opposita* (Vell.) Reitz	20	50	0.99	0.36
Ochnaceae	*Ouratea* sp.	2	5	2.59	0.28
Polygonaceae	*Coccoloba* sp.	5	12.5	0.37	0.07
	Ruprechtia laxiflora Meisn.	24	60	21.91	2.34
Rhamnaceae	*Ziziphus joazeiro* Mart.	1	2.5	0.43	0.06
Rubiaceae	*Randia armata* (Sw.) DC.	24	60	1.00	0.21
Rutaceae	*Zanthoxylum rhoifolium* Lam	4	10	0.04	0.01
Salicaceae	*Casearia sylvestris* Sw.	7	17.5	0.55	0.10
	Prockia crucis P.Browne ex L.	2	5	3.32	0.32
Sapindaceae	*Allophyllus edulis* (A.St.-Hil. et al.) Hieron. Ex Niederl.	36	90	1.25	0.29
	Cupania impressinervia Acev.-Rodr.	12	30	2.82	0.34
	Sapindaceae unidentified 2	3	7.5	3.30	0.40
Schoepfiaceae	*Schoepfia brasiliensis* A.DC.	14	35	2.48	0.38
Simaroubaceae	*Picrasma crenata* (Vell.) Engl.	13	32.5	0.65	0.14
Unidentified	Unidentified 13	13	32.5	13.62	1.56
Semi-arid, high fertility, deciduous, Serra Talhada, 15 years					
Anacardiaceae	*Myracrodruon urundeuva* Allemão	5	12.5	0.18	0.05
	Spondias tuberosa Arruda	2	5	0.08	0.02
Apocynaceae	*Aspidosperma pyrifolium* Mart.	3	7.5	0.15	0.03
Capparaceae	*Cynophalla flexuosa* (L.) J.Presl	4	10	0.13	0.03
Euphorbiaceae	*Croton blanchetianus* Baill.	45	112.5	1.13	0.29
Leguminosae-Caesalpinioideae	*Bauhinia cheilantha* (Bong.) Steud.	34	85	1.60	0.39
	Libidibia ferrea (Mart. ex Tul.) L.P.Queiroz	1	2.5	0.01	0.00
	Poincianella pyramidalis (Tul.) L.P.Queiroz	10	25	0.82	0.18
Mimosoida*	*Anadenanthera colubrina* (Vell.) Brenan	5	12.5	0.13	0.04
	Mimosa tenuiflora (Willd.) Poir.	245	612.5	19.33	4.16
	Piptadenia stipulacea (Benth.) Ducke	2	5	0.03	0.01
Rhamnaceae	*Ziziphus joazeiro* Mart.	4	10	0.30	0.07

Table 6 (continued)

Family	Species	*n*	PD	B	BA
Semi-arid, high fertility, deciduous, Serra Talhada, >50 years					
Anacardiaceae	*Myracrodruon urundeuva* Allemão	6	15	2.23	0.41
	Schinopsis brasiliensis Engl.	4	10	6.31	0.96
	Spondias tuberosa Arruda	1	2.5	2.75	0.41
Annonaceae	*Annona leptopetala* (R.E.Fr.) H.Rainer	68	170	1.89	0.47
Apocynaceae	*Aspidosperma pyrifolium* Mart.	6	15	0.74	0.15
Bignoniaceae	*Handroanthus impetiginosus* (Mart. ex DC.) Mattos	3	7.5	0.64	0.12
Burseraceae	*Commiphora leptophloeos* (Mart.) J.B.Gillett	13	32.5	17.81	2.57
Capparaceae	*Colicodendron yco* Mart.	2	5	0.10	0.02
	Cynophalla flexuosa (L.) J.Presl	4	10	0.07	0.02
Celastraceae	*Maytenus* sp.	3	7.5	0.11	0.03
Chrysobalanaceae	*Licania rigida* Benth.	2	5	0.04	0.01
Combretaceae	*Combretum monetaria* Mart.	26	65	0.75	0.19
Erythroxylaceae	*Erythroxylum caatingae* Plowman	2	5	1.33	0.22
Euphorbiaceae	*Croton blanchetianus* Baill.	68	170	2.65	0.65
	Croton heliotropiifolius Kunth	53	132.5	1.12	0.29
	Jatropha mollissima (Pohl) Baill.	8	20	0.22	0.06
	Manihot carthaginensis subsp. *glaziovii* (Müll.Arg.) Allem	44	110	1.80	0.43
	Sapium glandulosum (L.) Morong	7	17.5	0.29	0.07
	Sebastiania macrocarpa Müll.Arg.	16	40	0.76	0.17
Leguminosae-Caesalpinioideae	*Bauhinia cheilantha* (Bong.) Steud.	46	115	0.83	0.23
	Libidibia ferrea (Mart. ex Tul.) L.P.Queiroz	1	2.5	0.17	0.04
	Poincianella pyramidalis (Tul.) L.P.Queiroz	57	142.5	5.66	1.15
	Senna macranthera (DC. ex Collad.) H.S.Irwin & Barneby	1	2.5	0.01	0.00
Mimosoida*	*Anadenanthera colubrina* (Vell.) Brenan	28	70	4.55	0.79
	Chloroleucon dumosum (Benth.) G.P.Lewis	3	7.5	0.20	0.05
	Mimosa ophtalmocentra Mart. ex Benth	3	7.5	0.61	0.12
	Mimosa tenuiflora (Willd.) Poir.	11	27.5	3.06	0.57
	Parapiptadenia zehntneri (Harms) M.P.Lima & H.C.Lima	13	32.5	1.76	0.35
	Piptadenia stipulacea (Benth.) Ducke	12	30	1.17	0.25
Leguminosae-Papilionoideae	*Amburana cearensis* (Allemão) A.C.Sm.	4	10	2.22	0.37
Malvaceae	*Pseudobombax marginatum* (A.St.-Hil.) A. Robyns	19	47.5	1.65	0.34
Rhamnaceae	*Ziziphus joazeiro* Mart.	3	7.5	3.04	0.45
Rubiaceae	*Guettarda angelica* Mart. ex Müll.Arg.	3	7.5	0.05	0.01
Salicaceae	*Prockia crucis* P.Browne ex L.	15	37.5	0.40	0.10
Sapindaceae	*Allophylus quercifolius* (Mart.) Radlk.	2	5	0.03	0.01
Sapotaceae	*Sideroxylon obtusifolium* (Roem. & Schult.) T.D.Penn.	2	5	0.14	0.03
Unidentified	Unidentified 16	6	15	0.58	0.12
	Unidentified 17	4	10	0.05	0.02
	Unidentified 18	5	12.5	0.19	0.05
	Unidentified 19	7	17.5	0.08	0.02
Semi-arid, low fertility, deciduous, Araripe, 20 years					
Annonaceae	*Annona leptopetala* (R.E.Fr.) H.Rainer	54	135	1.48	0.38
Euphorbiaceae	*Croton* cf. *hemiargyreus* Müll.Arg.	18	45	1.53	0.32
	Manihot glaziovii Muell. Arg.	5	12.5	0.32	0.08
Leguminosae-Caesalpinioideae	*Senna* sp.	31	77.5	0.41	0.12
Mimosoida*	*Chloroleucon dumosum* (Benth.) G.P.Lewis	3	7.5	0.14	0.03
	Senegalia langsdorffii (Benth.) Seigler & Ebinger	103	257.5	14.40	2.85
Leguminosae-Papilionoideae	*Bowdichia* cf. *virgilioides* Kunth	3	7.5	0.09	0.02

Table 6 (continued)

Family	Species	*n*	PD	B	BA
	Swartzia psilonema Harms	3	7.5	0.05	0.01
Myrtaceae	Myrtaceae unidentified	4	10	0.12	0.03
Nyctaginaceae	*Pisonia* sp.	27	67.5	1.11	0.25
Rhamnaceae	*Colubrina cordifolia* Reissek	45	112.5	0.96	0.25
Rutaceae	*Pilocarpus jaborandi* Holmes	21	52.5	0.81	0.18
	Zanthoxylum hamadryadicum Pirani	5	12.5	0.19	0.05
Sapotaceae	*Chrysophyllum* sp.	2	5	0.03	0.01
Unidentified	Unidentified 20	1	2.5	0.01	0.00
Semi-arid, low fertility, deciduous, Araripe, >40 years					
Annonaceae	*Annona leptopetala* (R.E.Fr.) H.Rainer	24	60	0.41	0.11
Apocynaceae	*Aspidosperma* sp.	4	10	0.42	0.09
Bignoniaceae	*Jacaranda jasminoides* (Thunb.) Sandwith	1	2.5	0.02	0.01
Erythroxylaceae	*Erythroxylum* sp. 2	7	17.5	0.39	0.09
Euphorbiaceae	*Croton* cf. *hemiargyreus* Müll.Arg.	10	25	0.26	0.07
Leguminosae-Caesalpinioideae	*Bauhinia acuruana* Moric.	29	72.5	0.33	0.10
	Senna sp.	7	17.5	0.07	0.02
Mimosoida*	*Chloroleucon dumosum* (Benth.) G.P.Lewis	1	2.5	0.06	0.02
	Senegalia langsdorffii (Benth.) Seigler & Ebinger	116	290	11.23	2.36
Leguminosae-Papilionoideae	*Bowdichia* cf. *virgilioides* Kunth	1	2.5	0.02	0.00
	Swartzia psilonema Harms	2	5	0.08	0.02
Myrtaceae	*Campomanesia* sp. 2	4	10	0.14	0.03
	Campomanesia sp. 3	1	2.5	0.13	0.03
	Eugenia sp. 2	1	2.5	0.07	0.02
	Eugenia sp. 3	8	20	0.15	0.04
	Myrtaceae unidentified 2	9	22.5	0.45	0.11
	Myrtaceae unidentified 3	7	17.5	0.50	0.11
Nyctaginaceae	*Pisonia* sp.	8	20	0.42	0.10
Rhamnaceae	*Colubrina cordifolia* Reissek	11	27.5	0.30	0.08
Rutaceae	*Metrodorea mollis* Taub.	47	117.5	8.17	1.62
	Pilocarpus jaborandi Holmes	183	457.5	23.38	4.89
	Zanthoxylum hamadryadicum Pirani	3	7.5	0.02	0.01
	Zanthroxyllum sp.	1	2.5	0.01	0.00
Salicaceae	*Casearia* sp. 2	3	7.5	0.02	0.01
Unidentified	Unidentified 21	3	7.5	0.04	0.01
	Unidentified 22	6	15	0.28	0.07
	Unidentified 23	29	72.5	1.69	0.39

*Former Mimosoideae sub-family

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Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors declare no competing interests.

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