Research Article
doi: 10.1590/01047760202329013189
vol(29), 2023

CERNE

Structures of tropical dry forests in the Andes: forest conservation, composition and the role of fabaceae and myrtaceae

Carlos Mario Galván-Cisneros[1iD], Luis Roberto Sánchez Montaño[2iD],
Andrey Enrique Ojeda-Rodríguez[3iD], João Augusto Alves Meira-Neto[1iD✤]

[1]Universidade Federal de Viçosa, Brazil
[2]Universidad de Pamplona, Colombia
[3]Fundación Trópico Alto, Colombia

FOREST ECOLOGY

ABSTRACT

Background: Tropical Dry Forests (TDFs) are repositories of biodiversity, ecosystem services and carbon that are threatened by fragmentation and climate change. Floristic and phytosociological studies are fundamental database for many studies of conservation and sustainability, but there is a knowledge gap concerning TDFs, especially in the Andes valleys. The aim of this study was to determine the phytosociological structure and composition of woody vegetation of seven TDFs in the Colombian Andes, and because the flora associated with this type of forest has a geographical distribution restricted to each locality where this biome exists, provide information on the main species, genera and families for conservation and restoration actions as well as for future meta-analyses. We sampled seven TDFs with 20 plots of 25 m × 4 m.

Results: In the 1.88 hectares of samples, 8422 individuals were surveyed, distributed in 170 species, 120 genera and 50 botanical families. Of these species, 78.82% were identified at the species level, 17.05% at the genus level, and 4.11% at the family level. The most important families were Fabaceae and Myrtaceae. Nitrogen-fixing Fabaceae species were prominent amongst the important species, especially in low altitude and more stressing sites.

Conclusion: The structure, composition and ecological importance of these forests must be considered for conservation and ecological restoration plans, in particular the habitat preference of species along the topographic gradient. Particularly noteworthy for conservation are the Myrtaceae species because promote connectivity and regeneration by providing resources for the fauna, a driver of dispersal, as well as nitrogen-fixing Fabaceae species, because promote the resilience and natural regeneration of TDFs in the Andes, a key feature of stability.

Keywords: Tropical Dry Forest; phytosociology; Fabaceae; nitrogen-fixing; conservation.

HIGHLIGHTS

The TDF is the most threatened biome in Colombia.
A prominent characteristic of the composition and structure of TDFs is the importance of species of the Fabaceae family.
Species with highest VIs: *Machaerium arboreum*, *Platymiscium pinnatum* and *Handroanthus ochraceus*.
Myrtaceae and Fabaceae species are promising for the conservation of TDFs in the Andes.

GALVÁN-CISNEROS, C.M.; SÁNCHEZ MONTAÑO, L.R.; OJEDA-RODRÍGUEZ, A.E.; MEIRA-NETO, J.A.A. Structures of tropical dry forests in the andes: forest conservation, composition and the role of fabaceae and myrtaceae. CERNE, v.29, e-1033189, doi: 10.1590/01047760202329013189

✤Corresponding author: j.meira@ufv.br
Received: November, 4/2022 Accepted: June, 26/2023

CERNE
ISSN 0104-7760
UNIVERSIDADE FEDERAL DE LAVRAS

INTRODUCTION

Floristic and phytosociological surveys in the Neotropics have generated, over more than 40 years, an extensive database that today allows us to understand how landscape, climate, altitude, soils and history affect phytogeography, diversity, evolution and ecology, from populations and communities to entire biomes (e.g., Bueno et al., 2016; Gastauer et al., 2015; Lima et al., 2020; Neves et al., 2020; A. T. Oliveira-Filho; Fontes, 2000). Tropical Dry Forests (TDFs) have less than 1000 mm of rainfall in tropical and equatorial latitudes (see Oliveira-Filho et al. 2015) and are less studied by floristic and phytosociological studies than other large biomes with woody vegetation (Andrade et al., 2011), but the absence of this type of study is especially worrying with the climate change predicted for the coming decades (IPCC, 2021) in mountains such as the Andes where isolated fragments of TDFs will have their climates altered in heavily anthropized landscapes (Galván-Cisneros et al., 2021).

The knowledge about neotropical biomes was greatly benefited by the extensive database of phytosociological studies set over the years (Oliveira-Filho, 2017; Oliveira-Filho & Fontes, 2000), but the TDFs in the Andes Mountains are still a gap in phytosociological data, which makes them necessary and important for many studies that need meta-analyses (Medina-García et al., 2020) such as conservation studies and sustainability diagnostic studies of human activities (Zerwes et al., 2018). In Colombia, more than 90% of the TDFs have been cleared, with only 5% of their original coverage remaining, with more than 70% of the transformed areas having soils with degradation and erosion, and more than 65% are in the process of desertification caused by continuous human activities (García et al., 2014).

The TDF biodiversity, its potential in carbon sequestration and its role in the provision of ecosystem services are important justifications for proposing changes in land use regulations and for promoting TDF conservation programs (Portillo-Quintero et al., 2015). In this context, compositional and phytosociological data are important to generate knowledge about the status of TDFs, their plant populations, their functioning and their responses to global changes (Siyum, 2020).

The most prominent characteristic of the TDFs' composition and structure is the importance of Fabaceae species, especially the nitrogen-fixers (Bhaskar et al., 2016; Vargas G. et al., 2015). The nitrogen-fixing Fabaceae species are abundant in neotropical forests in general and in TDFs in particular (Gei et al., 2018), especially at the very early regeneration (Avendaño-Yáñez et al., 2018) promoting resilience and shifts in succession in a forest type almost without pioneer species (Lebrija-Trejos et al., 2008). However, there is still knowledge gaps of composition and structure of TDFs concerning other important plant families and concerning some regions as Andes mountains, especially in Colombia.

In the Neotropics, the main areas with tropical dry forests are found in the northeast of Brazil (the 'Caatinga'), on the Caribbean coasts of Colombia and Venezuela. Other areas of tropical dry forests are found in the dry valleys of the Andes in Bolivia, Peru, Ecuador and Colombia, the coast of Ecuador and northern Peru (Tumbesina region). In Central America, dry forests are concentrated along the Pacific coast from Guanacaste in northern Costa Rica to the Mexican state of Sonora. Throughout the Antilles, there are areas with dry forests (Banda et al., 2016; Pennington et al., 2000). The original distribution of TDFs in Colombia covered regions of the Caribbean plain and the Andean slopes and valleys (IAvH, 1998) with some small enclaves (IAvH, 1998; González-M et al., 2018; Pizano & García, 2014). The Colombian North-Andean TDF region is formed by three nuclei: the Chicamocha river canyon, in the province of Santander (Albesiano; Fernández-Alonso, 2006), the Ocaña-Convencion nucleus (IAvH, 1998), and the nucleus of Cúcuta and its surroundings, in the province of Norte de Santander (Galván-Cisneros et al., 2021; Hernández et al., 1992). The Cúcuta nucleus forms a continuum with the dry enclave of Tachira in Venezuela (Hernández et al., 1992). It is estimated that less than 50% of the original coverage persists in this region (Hernández et al., 1992). In Colombia, most studies of TDFs on floristics and phytosociology have taken place in the Caribbean region and in the Magdalena River valley. Most floristic studies that have been carried out in the North-Andean region of Colombia have focused in the Chicachocha River canyon and its areas of influence (Albesiano et al., 2003; Albesiano; Fernández-Alonso, 2006; Albesiano; Rangel-Ch, 2006; Díaz-Pérez, 2012; Fajardo-Gutiérrez et al., 2018; Valencia-Duarte et al., 2012). In the nucleus of Cúcuta and surroundings there is an evident information gap in the literature with very few publications in which the work of Carrillo-Fajardo et al., (2007) stands out, who performed floristic and structural characterization of a TDF in Cerro Tasajero.

The information gap increases the problem that TDFs are one of the most threatened biomes in Colombia (Pizano et al., 2014) with urgent need for phytosociological data (Banda et al., 2016). Therefore, the aim of this study was to determine the phytosociological structure and composition of woody vegetation of seven TDFs along a topographic gradient in the TDFs of Cucuta and surrounding, in the eastern range of the Colombian Andes, and provide information on the main species, genera and families for conservation and restoration actions as well as for future meta-analyses.

MATERIAL AND METHODS

Study area

The study was carried out in the region of Cúcuta and its surroundings. All forests studied are on a south-north oriented slope that forms part of the eastern slope of the Cordillera Oriental de Colombia (Figure 1). The altitude range between the studied TDFs was from 282 m to 799 m ASL (Table 1). This slope still conserves TDFs remnants in a semi-arid corridor in the middle and lower part of the microbasins of the Zulia and Pamplonita rivers, within the Catatumbo river basin.

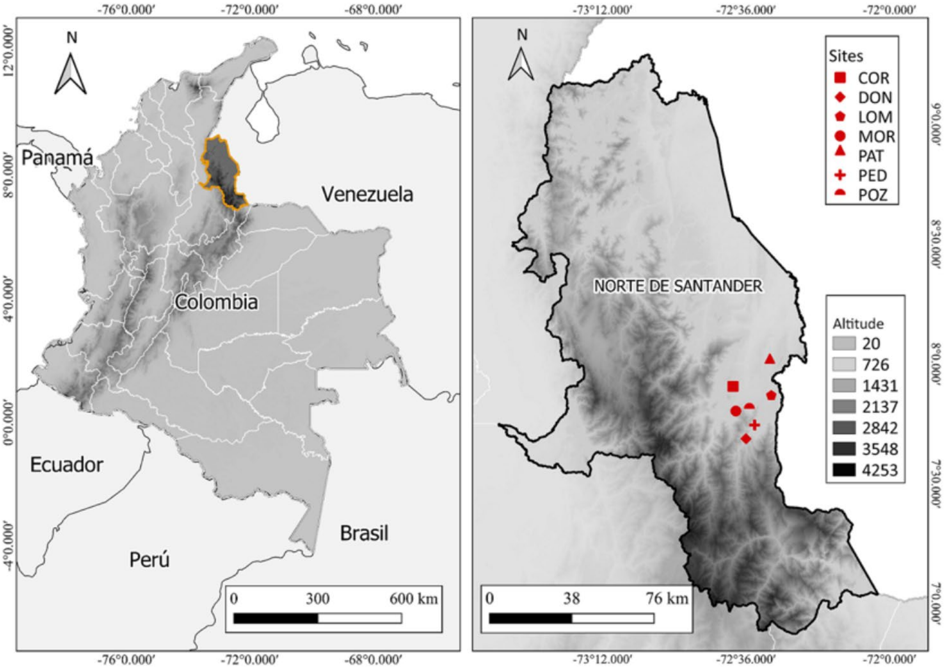

Figure 1: Sites of Tropical Dry Forest surveyed in Cúcuta and neighboring municipalities, province of Norte de Santander, Colombia.

Table 1: Geographical information of sampled sites of Tropical Dry Forests surveyed in Cúcuta and neighboring municipalities, province of Norte de Santander, Colombia.

Site code	Site	Municipality	Coordinates	Altitude (m.a.s.l.)
PAT	Patillales	Cúcuta	7° 59' 57,4'' N 72° 29' 58,1'' w	282
LOM	Las Lomas	Cúcuta	7° 52' 03,6'' N 72° 29' 36,6'' w	389
POZ	Pozo Azul	San Cayetano	7° 48' 50,2'' N 72° 35' 7,2'' w	505
DON	La Don Juana	Bochalema/Chinacota	7° 41' 14,4'' N 72° 35' 57,1'' w	799
PED	San Pedro	Cúcuta/Los Patios	7° 44' 39,9'' N 72° 33' 47,7'' w	656
COR	Cornejo	San Cayetano	7° 54' 20,5'' N 72° 39' 13'' w	393
MOR	Morretón Bajo	Durania	7° 48' 10,3'' N 72° 38' 30,6'' w	528

Sampling

We sampled seven sites. For each site, 20 plots of 25 m × 4 m were established, except for the locality of Patillales (PAT) where 68 plots were established, totaling 188 plots throughout the study area (Table 1). In each plot, all individuals with a diameter at breast height (DBH) of at least 1 cm were measured. The botanical material collected was identified from the specialized literature or by comparison in the HECASA Herbarium of the University of Pamplona, Colombia. Botanical identification followed APG IV (The Angiosperm Phylogeny Group, 2016).

Horizontal structure

To determine the horizontal structure of the communities, the phytosociological parameters of absolute density, absolute dominance, absolute frequency, relative density, relative dominance and relative frequency were used, as well as the importance value (VI) according to Curtis and McIntosh, (1950) and calculated with formulas described by Mueller-Dombois; Ellenberg, (1974). These calculations were carried out with basic functions in R statistical environment (R Development Core Team, 2021).

Species Density

To compare sites of different area sizes, it is advantageous to use species density [1] using the following equation (Vetaas; Grytnes, 2002). where S is the number of species in each location and A is the area (m^2) of each location.

$$SD = \frac{S}{\ln(A)} \qquad (1)$$

Floristic composition

We ordered the plots using non-metric multidimensional scale ordination (NMDS), with Bray-Curtis as the dissimilarity metric based on abundances, in order to assess the existence of a gradient in species composition along the topographic gradient. The NMDS was performed using the *'metaMDS'* function of the *"vegan"* package (Oksanen et al., 2018). We tested the significance of the groups generated with a permutational multivariate analysis of variance (PERMANOVA) with 999 permutations (Anderson, 2001), using the '*adonis*' function available within the "*vegan*" package (Oksanen et al., 2018). To generate the graphs for this study, we used the "ggplot2" package (Wickham, 2016). All analyzes were performed using packages of the R software (R Development Core Team, 2021).

RESULTS

Horizontal structure

In the 1.88 hectares of samples, 8,422 individuals were surveyed, distributed in 170 species, 120 genera and 50 botanical families (Table 2). Of these species, 78.82% were identified at the species level, 17.05% at the genus level, and 4.11% at the family level. The main limitation of identification was the absence of fertile botanical material during the survey period.

Table 2: Floristic list of 1.88 hectare of Tropical Dry Forest, Cúcuta and neighboring municipalities, province of Norte de Santander, Colombia.

Family	Species
Acanthaceae	*Aphelandra macrophylla* Leonard
Achatocarpaceae	*Achatocarpus nigricans* Triana
Anacardiaceae	*Astronium graveolens* Jacq.
	Spondias mombin L.
Annonaceae	*Duguetia lucida* Urb.
	Guatteria cargadero Triana & Planch.
	Guatteria sp
	Oxandra venezuelana R.E. Fr.
	Xylopia frutescens Aubl.
Apocynaceae	*Aspidosperma cuspa* (Kunth) S.F. Blake ex Pittier
	Aspidosperma darienense Woodson ex Dwyer
	Aspidosperma megalocarpon Müll. Arg
	Tabernaemontana grandiflora Jacq
Araliaceae	*Schefflera morototoni* (Aubl.) Maguire, Steyerm. & Frodin
Asteraceae	Asteraceae NI
	Chromolaena sp
	Piptocoma discolor (Kunth) Pruski

Continue.

Table 2: Continuation.

Family	Species
Bignoniaceae	*Crescentia cujete* L.
	Handroanthus ochraceus (Cham.) Mattos
	Jacaranda caucana Pittier
Boraginaceae	*Cordia alliodora* (Ruiz & Pav.) Oken
	Cordia bicolor A. DC
	Varronia curassavica Jacq.
Burseraceae	*Protium heptaphyllum* (Aubl.) Marchand
	Protium laxiflorum Engl.
Cactaceae	*Acanthocereus tetragonus* (L.) Hummelinck
	Cereus hexagonus (L.) Mill.
	Opuntia caracassana Salm-Dyck
	Pilosocereus lanuginosus (L.) Byles & G.D. Rowley
	Praecereus euchlorus (F.A.C. Weber ex K. Schum.) N.P. Taylor
Cannabaceae	*Celtis iguanaea* (Jacq.) Sarg.
Capparaceae	*Capparidastrum frondosum* (Jacq.) Cornejo & Iltis
	Crateva tapia L.
	Cynophalla polyantha (Triana & Planch.) Cornejo & Iltis
	Cynophalla verrucosa (Jacq.) J. Presl
	Monilicarpa tenuisiliqua (Jacq.) Cornejo & Iltis
	Morisonia americana L.
	Neocapparis pachaca (Kunth) Cornejo
	Quadrella indica (L.) Iltis & Cornejo
Celastraceae	*Monteverdia sieberiana* (Krug & Urb.) Biral
	Schaefferia frutescens Jacq.
Chrysobalanaceae	*Leptobalanus apetalus* (E. Mey.) Sothers & Prance
	Licania cf. *hypoleuca* Benth.
	Licania sp
	Parinari pachyphylla Rusby
Clusiaceae	*Garcinia madruno* (Kunth) Hammel
Combretaceae	*Terminalia amazonia* (J.F. Gmel.) Exell
Erythroxylaceae	*Erythroxylum macrophyllum* Cav.
	Erythroxylum novogranatense (D. Morris) Hieron.
	Erythroxylum sp.1
	Erythroxylum sp.2
Euphorbiaceae	*Adelia ricinella* L.
	Cnidoscolus urens (L.) Arthur
	Croton argyrophyllus Kunth
	Croton caracasanus Pittier
	Croton micans Sw.
	Croton sp
	Jatropha gossypiifolia L.
	Mabea nitida Spruce ex Benth.

Continue.

Table 2: Continuation.

Family	Species
Fabaceae	*Albizia guachapele* (Kunth) Dugand
	Albizia niopoides (Spruce ex Benth.) Burkart
	Apuleia leiocarpa (Vogel) J.F. Macbr.
	Bauhinia aculeata L.
	Bauhinia sp
	Brownea ariza Benth.
	Brownea sp
	Calliandra riparia Pittier
	Calliandra sp
	Clitoria arborescens R. Br.
	Crudia sp
	Cynometra cf. *fissicuspis* (Pittier) Pittier
	Fabaceae NI.1
	Fabaceae NI.2
	Fabaceae NI.3
	Fabaceae NI.4
	Hymenaea courbaril L.
	Inga marginata Willd.
	Lonchocarpus velutinus Benth. ex Seem.
	Machaerium arboreum (Jacq.) Benth.
	Machaerium biovulatum Micheli
	Ormosia sp
	Peltogyne paniculata Benth.
	Piptadenia flava (DC.) Benth.
	Pithecellobium dulce (Roxb.) Benth.
	Platymiscium pinnatum (Jacq.) Dugand
	Platypodium elegans Vogel
	Prosopis juliflora (Sw.) DC.
	Pterocarpus acapulcensis Rose
	Samanea saman (Jacq.) Merr.
	Senegalia riparia (Kunth) Britton
	Senna fruticosa (Mill.) H.S. Irwin & Barneby
	Senna robiniifolia (Benth.) H.S. Irwin & Barneby
	Swartzia pinnata (Vahl) Willd.
	Swartzia sp
Lauraceae	*Aiouea* sp
	Nectandra sp.1
	Nectandra sp.2
Lecythidaceae	*Gustavia poeppigiana* O. Berg
Malpighiaceae	*Malpighia glabra* L.
Malvaceae	*Guazuma ulmifolia* Lam.
	Helicteres baruensis Jacq.
	Luehea speciosa Willd.
Melastomataceae	*Miconia prasina* (Sw.) DC.
	Miconia stenostachya DC.
Meliaceae	*Trichilia hirta* L.
Menispermaceae	*Sciadotenia* sp

Continue.

Table 2: Continuation.

Family	Species
Moraceae	*Brosimum alicastrum* Sw.
	Brosimum sp
	Maclura tinctoria (L.) D. Don ex Steud.
	Sorocea affinis Hemsl.
	Sorocea sp
	Sorocea sprucei (Baill.) J.F. Macbr.
Myrtaceae	*Calyptranthes* sp
	Eugenia biflora (L.) DC.
	Eugenia punicifolia (Kunth) DC.
	Eugenia sp.1
	Eugenia sp.2
	Eugenia sp.3
	Myrcia sp
	Myrcia tomentosa
	Myrtaceae NI.1
	Myrtaceae NI.2
	Myrtaceae NI.3
	Psidium friedrichsthalianum (O. Berg) Nied.
Nyctaginaceae	*Guapira costaricana* (Standl.) Woodson
	Guapira sp
	Neea sp.1
	Neea sp.2
Ochnaceae	*Ouratea angulata* Tiegh.
Opiliaceae	*Agonandra brasiliensis* Miers ex Benth. & Hook. f.
Peraceae	*Pera arborea* Mutis
	Pera colombiana Cardiel
Petiveriaceae	*Seguieria americana* L.
Picramniaceae	*Picramnia latifolia* Tul.
Picrodendraceae	*Piranhea longipedunculata* Jabl.
Piperaceae	*Piper amalago* L.
Polygalaceae	*Bredemeyera floribunda* Willd.
	Bredemeyera lucida (Benth.) Klotzsch ex Hassk.
Polygonaceae	*Coccoloba padiformis* Meisn.
	Ruprechtia costata Meisn.
	Ruprechtia ramiflora (Jacq.) C.A. Mey.
	Triplaris americana L.
Primulaceae	*Clavija latifolia* (Willd. ex Roem. & Schult.) K. Koch
Proteaceae	*Roupala montana* Aubl.
Rubiaceae	*Amaioua corymbosa* Kunth
	Chomelia cf. *spinosa* Jacq.
	Randia armata (Sw.) DC.
	Rudgea marginata Standl.
	Warszewiczia coccinea (Vahl) Klotzsch

Continue.

Table 2: Continuation.

Family	Species
Rutaceae	*Amyris sylvatica* Jacq.
	Helietta plaeana Tul.
	Zanthoxylum fagara (L.) Sarg.
	Zanthoxylum cf. *lenticulare* Reynel
	Zanthoxylum sp
Salicaceae	*Banara ulmifolia* (Kunth) Benth.
	Casearia grandiflora Cambess.
	Casearia javitensis Kunth
	Casearia sp.1
	Casearia sp.2
	Casearia sylvestris Sw.
Sapindaceae	*Cupania latifolia* Kunth
	Melicoccus bijugatus Jacq.
Sapotaceae	*Chrysophyllum argenteum* Jacq.
	Pouteria caimito (Ruiz & Pav.) Radlk.
Solanaceae	*Solanum hazenii* Britton
Verbenaceae	*Lippia origanoides* Kunth
	Petrea cf. *rugosa* Kunth
	Petrea volubilis L.
Violaceae	*Pombalia phyllanthoides* (Planch. & Linden ex Triana & Planch.) Paula-Souza
Vochysiaceae	*Vochysia lehmannii* Hieron.

The families with the highest number of species in the total survey were Fabaceae with 35 species (20.59% of the total number of species), 19 of which are nitrogen fixing, Myrtaceae with 12 species (7.06%), Capparaceae and Euphorbiaceae with 8 (4.71%) each, Moraceae and Salicaceae with 6 (3.53%) each, Annonaceae, Cactaceae, Rubiaceae and Rutaceae with 5 each (2.94%). These ten families represent 55.88% of the total species found in the floristic survey. The richest genera were: *Casearia* and *Eugenia* with 5 species each, followed by *Croton* and *Erythroxylum* with 4 species each. The species with the highest number of individuals were *Machaerium arboreum* (1011), *Platymiscium pinnatum* (714), *Guapira costaricana* (577), *Handroanthus ochraceus* (573), *Croton micans* (489) and *Aspidosperma cuspa* (314).

Considering the seven TDFs studied, six species had the highest VIs: *Machaerium arboreum, Platymiscium pinnatum, Handroanthus ochraceus, Guapira costaricana, Croton micans* and *Machaerium biovulatum* with values of 9.71; 6.6; 5.63; 4.52; 3.82 and 3.03, respectively. Of these, three are nitrogen-fixing Fabaceae species and accounted for about 20% of the total VI. Another nine species had an importance value between 2.34 and 1.69. These fifteen species accounted for just over 50% VI of the seven TDFs (Figure 2).

Of the six species with VI above 3.0 in the TDFs studied, three are nitrogen-fixing Fabaceae species. Of the 170 surveyed species, one appears on the Red List of Endangered Species of Colombian Flora: *Parinari pachyphylla* Rusby, Endangered (EN). It also appears in the same category in Resolution No. 1912 of 2017, from the Colombian Ministry of Environment and Sustainable Development's list of threatened species in Colombia. However, the vast majority of species sampled have a low number of individuals and a small basal area, as shown in the phytosociological tables (See tables for supplementary material).

In Patillales, the species with the highest VI were *Machaerium arboreum* (13.6), *Platymiscium pinnatum* (9.9), *Guapira costaricana* (9.31) and *Croton micans* (7.2). These four species represented 40.19% of the total VI, with the two most important species being nitrogen-fixing Fabaceae species. An additional 21.95% of the VI is from another five species: *Neocapparis pachaca* (6.1), *Handroanthus ochraceus* (6.1), *Helietta plaeana* (5.8) and *Ruprechtia ramiflora* (3.8) (Table 3).

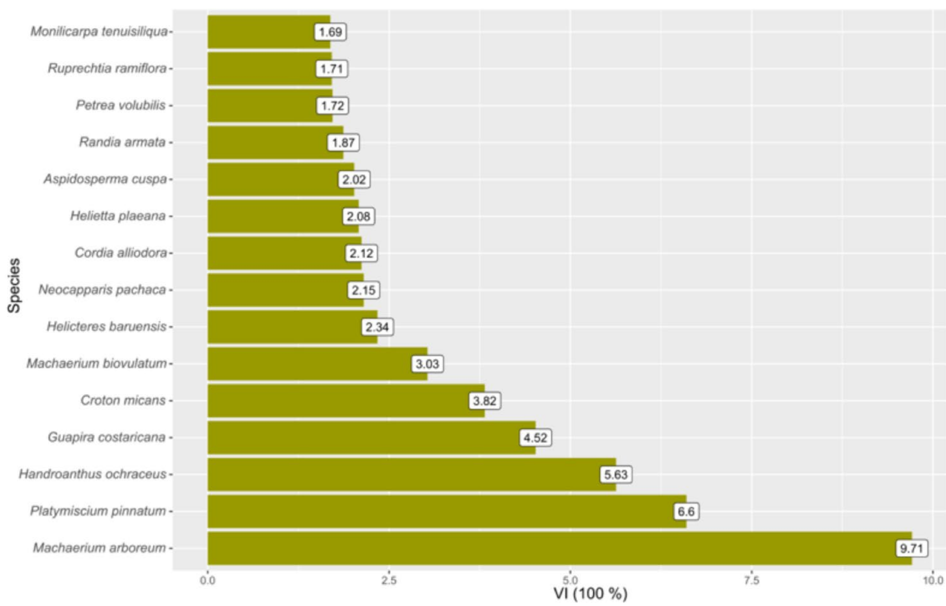

Figure 2: Percentages of species with the highest importance values (VI 100%) for the total of sampled forests.

Table 3: Phytossociological parameters of species sampled in 1.88 hectare of Tropical Dry Forest, Cúcuta and neighboring municipalities, province of Norte de Santander, Colombia. Ordered in decreasing value of importance, where DoA= absolute dominance (m^2 /ha), DoR = relative dominance (%), FA = absolute frequency, FR = relative frequency (%), DA = absolute density (number of individuals/ha), DR = relative density (%), VI 300 % = importance value (%) and VI 100 % = importance value (%).

Patillales (PAT), 282 m.a.s.l.								
Species	**DoA**	**DoR**	**FA**	**FR**	**DA**	**DR**	**VI 300**	**VI 100**
Machaerium arboreum	6.05	17.71	67.65	7.07	833.82	16.14	40.92	13.64
Platymiscium pinnatum	4.32	12.64	70.59	7.37	507.35	9.82	29.84	9.95
Guapira costaricana	2.43	7.12	66.18	6.91	719.12	13.92	27.96	9.32
Croton micans	0.92	2.69	82.35	8.60	545.59	10.56	21.85	7.28
Neocapparis pachaca	3.62	10.58	45.59	4.76	158.82	3.08	18.42	6.14
Handroanthus ochraceus	2.32	6.80	60.29	6.30	269.12	5.21	18.30	6.10
Helietta plaeana	3.02	8.83	41.18	4.30	232.35	4.50	17.63	5.88
Ruprechtia ramiflora	1.81	5.29	39.71	4.15	105.88	2.05	11.49	3.83
Helicteres baruensis	0.34	0.99	54.41	5.68	244.12	4.73	11.40	3.80
Monilicarpa tenuisiliqua	0.36	1.06	51.47	5.38	252.94	4.90	11.34	3.78
Praecereus euchlorus	0.71	2.07	50.00	5.22	179.41	3.47	10.77	3.59
Prosopis juliflora	1.73	5.05	22.06	2.30	125.00	2.42	9.77	3.26
Rest of species	6.55	19.17	305.88	31.95	991.18	19.19	70.31	23.44
Total	34.17	100	957.35	100	5164.71	100	300	100
Las Lomas (LOM), 389 m.a.s.l.								
Species	**DoA**	**DoR**	**FA**	**FR**	**DA**	**DR**	**VI 300**	**VI 100**
Platymiscium pinnatum	13.96	41.44	100.00	17.54	1740.00	45.19	104.17	34.72
Pilosocereus lanuginosus	7.34	21.78	60.00	10.53	445.00	11.56	43.87	14.62
Handroanthus ochraceus	2.74	8.12	70.00	12.28	635.00	16.49	36.90	12.30
Helicteres baruensis	0.45	1.35	50.00	8.77	240.00	6.23	16.36	5.45
Prosopis juliflora	2.98	8.83	30.00	5.26	80.00	2.08	16.17	5.39
Cynophalla polyantha	1.12	3.33	45.00	7.89	60.00	1.56	12.79	4.26
Randia armata	0.47	1.40	50.00	8.77	90.00	2.34	12.51	4.17
Acanthocereus tetragonus	0.21	0.63	25.00	4.39	80.00	2.08	7.10	2.37
Aspidosperma cuspa	0.34	1.00	15.00	2.63	125.00	3.25	6.87	2.29
Neea sp.1	1.49	4.42	5.00	0.88	55.00	1.43	6.72	2.24
Pithecellobium dulce	1.06	3.16	10.00	1.75	20.00	0.52	5.43	1.81
Lippia origanoides	0.03	0.09	10.00	1.75	80.00	2.08	3.93	1.31
Rest of species	1.50	4.45	100.00	17.54	200.00	5.19	27.18	9.06
Total	33.69	100	570.00	100	3850.00	100	300	100
Cornejo (COR), 393 m.a.s.l.								
Species	**DoA**	**DoR**	**FA**	**FR**	**DA**	**DR**	**VI 300**	**VI 100**
Handroanthus ochraceus	3.72	7.26	90.00	7.76	775.00	17.71	32.74	10.91
Cordia alliodora	5.08	9.90	75.00	6.47	385.00	8.80	25.17	8.39
Calliandra riparia	6.21	12.12	55.00	4.74	230.00	5.26	22.12	7.37
Machaerium arboreum	1.68	3.27	70.00	6.03	240.00	5.49	14.79	4.93
Aspidosperma cuspa	0.68	1.33	55.00	4.74	355.00	8.11	14.19	4.73

Continue.

Table 3: Continuation.

Cornejo (COR), 393 m.a.s.l.								
Species	**DoA**	**DoR**	**FA**	**FR**	**DA**	**DR**	**VI 300**	**VI 100**
Petrea volubilis	0.77	1.49	60.00	5.17	245.00	5.60	12.27	4.09
Croton micans	0.93	1.82	65.00	5.60	195.00	4.46	11.88	3.96
Samanea saman	5.53	10.79	5.00	0.43	5.00	0.11	11.34	3.78
Cynophalla verrucosa	0.47	0.92	65.00	5.60	195.00	4.46	10.98	3.66
Randia armata	1.13	2.21	40.00	3.45	185.00	4.23	9.89	3.30
Ormosia sp	3.92	7.64	10.00	0.86	55.00	1.26	9.76	3.25
Guapira costaricana	1.04	2.03	55.00	4.74	130.00	2.97	9.74	3.25
Rest of species	20.10	39.21	515.00	44.40	1380.00	31.54	115.15	38.38
Total	51.27	100	1160.00	100	4375.00	100	300	100
Pozo Azul (POZ), 505 m.a.s.l.								
Species	**DoA**	**DoR**	**FA**	**FR**	**DA**	**DR**	**VI 300**	**VI 100**
Machaerium arboreum	5.80	13.01	95.00	6.69	640.00	14.88	34.58	11.53
Pterocarpus acapulcensis	6.98	15.64	60.00	4.23	200.00	4.65	24.51	8.17
Machaerium biovulatum	4.11	9.21	65.00	4.58	180.00	4.19	17.97	5.99
Handroanthus ochraceus	2.15	4.81	80.00	5.63	300.00	6.98	17.43	5.81
Fabaceae NI.1	5.14	11.53	10.00	0.70	40.00	0.93	13.16	4.39
Calliandra riparia	1.57	3.52	40.00	2.82	225.00	5.23	11.57	3.86
Petrea volubilis	1.03	2.31	65.00	4.58	200.00	4.65	11.54	3.85
Luehea speciosa	3.14	7.04	25.00	1.76	55.00	1.28	10.08	3.36
Piptocoma discolor	1.32	2.95	30.00	2.11	205.00	4.77	9.83	3.28
Eugenia biflora	0.49	1.10	55.00	3.87	155.00	3.60	8.58	2.86
Astronium graveolens	0.66	1.48	50.00	3.52	85.00	1.98	6.97	2.32
Erythroxylum novogranatense	0.32	0.71	45.00	3.17	125.00	2.91	6.79	2.26
Rest of species	11.91	26.69	800.00	56.34	1890.00	43.95	126.99	42.33
Total	44.61	100	1420.00	100	4300.00	100	300	100
Morretón Bajo (MOR), 528 m.a.s.l.								
Species	**DoA**	**DoR**	**FA**	**FR**	**DA**	**DR**	**VI 300**	**VI 100**
Apuleia leiocarpa	8.54	13.21	60.00	3.61	115.00	2.98	19.80	6.60
Protium heptaphyllum	3.14	4.86	70.00	4.22	355.00	9.20	18.27	6.09
Brosimum alicastrum	4.36	6.75	20.00	1.20	130.00	3.37	11.32	3.77
Xylopia frutescens	1.17	1.80	50.00	3.01	220.00	5.70	10.52	3.51
Platypodium elegans	4.63	7.16	30.00	1.81	45.00	1.17	10.13	3.38
Hymenaea courbaril	4.06	6.28	30.00	1.81	55.00	1.42	9.51	3.17
Petrea volubilis	0.83	1.28	50.00	3.01	190.00	4.92	9.22	3.07
Myrcia sp	1.71	2.64	45.00	2.71	95.00	2.46	7.82	2.61
Oxandra venezuelana	1.43	2.21	40.00	2.41	95.00	2.46	7.08	2.36
Warszewiczia coccinea	0.33	0.50	40.00	2.41	150.00	3.89	6.80	2.27
Pterocarpus acapulcensis	3.03	4.69	20.00	1.20	35.00	0.91	6.80	2.27
Cupania latifolia	0.67	1.04	45.00	2.71	115.00	2.98	6.73	2.24
Rest of species	30.75	47.58	1160.00	69.88	2260.00	58.55	176.01	58.67
Total	64.62	100	1660.00	100	3860.00	100	300	100

Continue.

Table 3: Continuation.

San Pedro (PED), 656 m.a.s.l.								
Species	**DoA**	**DoR**	**FA**	**FR**	**DA**	**DR**	**VI 300**	**VI 100**
Machaerium arboreum	13.31	29.88	60.00	5.06	520.00	12.61	47.55	15.85
Randia armata	2.14	4.80	80.00	6.75	280.00	6.79	18.34	6.11
Machaerium biovulatum	3.81	8.55	55.00	4.64	165.00	4.00	17.19	5.73
Piptocoma discolor	1.81	4.07	40.00	3.38	330.00	8.00	15.44	5.15
Croton micans	1.01	2.26	60.00	5.06	330.00	8.00	15.33	5.11
Handroanthus ochraceus	2.25	5.05	45.00	3.80	170.00	4.12	12.97	4.32
Guapira costaricana	1.39	3.13	55.00	4.64	180.00	4.36	12.14	4.05
Cynophalla polyantha	1.14	2.56	60.00	5.06	185.00	4.48	12.10	4.03
Erythroxylum sp.2	1.43	3.21	30.00	2.53	205.00	4.97	10.72	3.57
Cordia alliodora	1.96	4.41	30.00	2.53	105.00	2.55	9.49	3.16
Helicteres baruensis	0.49	1.11	50.00	4.22	110.00	2.67	7.99	2.66
Chomelia spinosa	1.14	2.55	25.00	2.11	115.00	2.79	7.45	2.48
Erythroxylum sp.1	1.53	3.44	20.00	1.69	95.00	2.30	7.43	2.48
Rest of species	11.13	24.98	575.00	48.52	1335.00	32.36	105.87	35.29
Total	44.53	100	1185.00	100	4125.00	100	300	100
La Don Juana (DON), 799 m.a.s.l.								
Species	**DoA**	**DoR**	**FA**	**FR**	**DA**	**DR**	**VI 300**	**VI 100**
Machaerium arboreum	5.49	13.45	65.00	5.86	780.00	19.31	38.62	12.87
Machaerium biovulatum	6.15	15.07	95.00	8.56	255.00	6.31	29.94	9.98
Guazuma ulmifolia	5.35	13.11	45.00	4.05	110.00	2.72	19.88	6.63
Swartzia sp	4.06	9.93	30.00	2.70	270.00	6.68	19.32	6.44
Picramnia latifolia	2.22	5.44	45.00	4.05	325.00	8.04	17.54	5.85
Piper amalago	1.46	3.58	50.00	4.50	330.00	8.17	16.25	5.42
Casearia sp.1	0.66	1.63	70.00	6.31	240.00	5.94	13.87	4.62
Casearia sylvestris	2.72	6.66	30.00	2.70	135.00	3.34	12.70	4.23
Astronium graveolens	0.90	2.22	70.00	6.31	160.00	3.96	12.48	4.16
Cordia alliodora	1.90	4.65	25.00	2.25	160.00	3.96	10.86	3.62
Adelia ricinella	2.55	6.24	15.00	1.35	80.00	1.98	9.57	3.19
Zanthoxylum sp	0.88	2.15	40.00	3.60	100.00	2.48	8.23	2.74
Rest of species	6.48	15.88	530.00	47.75	1095.00	27.10	90.73	30.24
Total	40.83	100	1110.00	100	4040.00	100	300	100

The phytosociological structure of Las Lomas was mainly characterized by the dominance of the species *Platymiscium pinnatum* (VI = 34.7%), a nitrogen-fixing species belonging to the Fabaceae family, a family commonly prominent in tropical dry forests. Other important species were *Pilosocereus lanuginosus* (14.6) and *Handroanthus ochraceus* (12.3). These three species represented 61.64% of the total VI. This was the location that showed the lowest species richness.

In Cornejo, the species with the highest VI were *Handroanthus ochraceus* (10.9), *Cordia alliodora* (8.39), *Calliandra riparia* (7.3) and *Machaerium arboreum* (4.9). These four species represented 31.6% of the total VI. Another 17.27% corresponded to five other species: *Aspidosperma cuspa* (4.7), *Petrea volubilis* (4.09), *Croton micans* (3.9) and *Samanea saman* (3.7). Among these eight species, three are nitrogen-fixing Fabaceae species.

In Pozo Azul, three Fabaceae species stood out: *Machaerium arboreum* (11.5), *Pterocarpus acapulcensis* (8.1) and *Machaerium biovulatum* (5.9). These three species represented 25.69% of the total VI. Other important species were *Handroanthus ochraceus* (10.9), an unidentified

Fabaceae (4.3) and *Calliandra riparia* (7.3). Among the six identified species, four are nitrogen-fixing Fabaceae species.

Morretón Bajo stood out for its high number of species (89), and none of them surpassed 7% of the total VI. The species with the highest VI were *Apuleia leiocarpa*, *Protium heptaphyllum*, *Brosimum alicastrum*, *Xylopia frutescens*, *Platypodium elegans* and *Hymenaea courbaril*. Only *Platypodium elegans* is a nitrogen fixer.

In San Pedro, the species with the highest VI were *Machaerium arboreum* (15.8), *Randia armata* (6.1), *Machaerium biovulatum* (5.7) and *Piptocoma discolor* (5.1). These four species represented 33.44% of the total VI. Other highlighted species were *Handroanthus ochraceus*, *Guapira costaricana*, *Cynophalla polyantha* and *Erythroxylum* sp.2. The two mentioned species of the genus *Machaerium* are nitrogen fixing.

In La Don Juana, the species with the highest VI were *Machaerium arboreum* (12.8), *Machaerium biovulatum* (9.9), *Guazuma ulmifolia* (6.6) and *Swartzia* sp (6.4). These four species represented 35.92% of the total VI and only *Guazuma ulmifolia* is not a nitrogen-fixing Fabaceae species. An additional 24.28% correspond to five highlighted species: *Picramnia latifolia* (5.8), *Piper amalago* (5.4), *Casearia* sp.1 (4.6), *Casearia sylvestris* (4.2) and *Astronium graveolens* (4.1).

Richness, density and composition of species

The highest species richness was found in Morretón Bajo and Pozo Azul, while the lowest was recorded in Las Lomas. A similar pattern was found for species density, which tended to be higher in locations at higher altitudes (MOR, DON, POZ, PED), while locations at lower altitudes had the lowest values (LOM, PAT and COR). The locations with the highest values were Pozo Azul and Morretón Bajo, the location with the lowest value was Las Lomas (Table 4).

Table 4: Richness and Species density (SD) of seven the sites of Tropical Dry Forest, Cúcuta and neighboring municipalities, province of Norte de Santander, Colombia.

Sites code	Sites	Richness	SD	Altitude
LOM	Las Lomas	22	2.89	389
PAT	Patillales	58	6.57	282
COR	Cornejo	48	6.32	393
POZ	Pozo Azul	72	9.47	505
PED	San Pedro	51	6.71	656
DON	La Don Juana	57	7.5	799
MOR	Morretón Bajo	89	11.71	528

The NMDS of species composition showed significant differences. The groups formed in this analysis were considered consistent, according to the PERMANOVA results (F6.139 = 10.56; p <0.001). The variables generated by NMDS describe the variation in plant community composition along a topographic gradient (Figure 3), from sites at lower altitudes and less species richness to places at higher altitudes and greater species richness (Table 1). The wider dispersion of the plots in the Morretón Bajo (MOR) location in comparison with the other locations indicates that the forest in this location has a composition more variable than others.

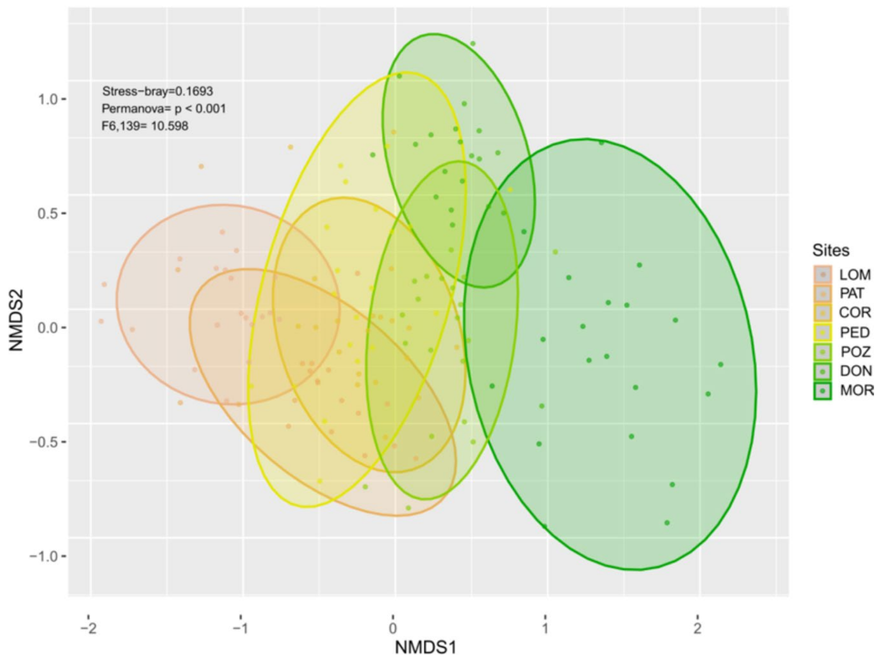

Figure 3: Non-metric multidimensional scaling (NMDS) plot based on a Bray-Curtis abundance matrix, showing patterns of community composition among all seven sites of Tropical Dry Forest, Cúcuta and neighboring municipalities, province of Norte de Santander, Colombia.

DISCUSSION

In our study, the Fabaceae family was dominant, followed by Myrtaceae, Capparaceae, Euphorbiaceae, Moraceae and Salicaceae. Fabaceae had the highest VI in six of the seven localities always with prominent nitrogen-fixing species importance. In general, the floristic composition of these tropical dry forests maintains a trend similar to those reported by Albesiano; Rangel-Ch, (2006) e Albesiano; Fernández-Alonso, (2006) for Chicamocha Canyon, in the department of Santander, that the families with the most important woody species were Fabaceae, Bignoniaceae, Euphorbiaceae, Cactaceae and Rubiaceae. These families are among the most representative in phytosociological surveys in the arboreal-shrubby layer of the dry tropical forests of the Neotropics (Gentry, 1995; Rodríguez et al., 2012).

Fabaceae was the family with the greatest representation in species richness of these TDFs, with 35 species, just over 20% of all species sampled. This high representation may be related to the ability to fix atmospheric nitrogen by symbiotic association with bacteria, which is capable of occurring in harsh environments (da Silva et al., 2017). Despite TDFs present low species richness of pioneers comparatively to wetter tropical forests (Chazdon et al., 2011; Lebrija-Trejos et al., 2008), TDFs recover structure and biodiversity readily through succession (Ruiz et al., 2005; Vieira; Scariot, 2006). Much of this resilience can be because nitrogen-fixing Fabaceae species are drivers of early ecological succession in TDFs by making nitrogen available in their plants and in the soil and, since nitrogen is available, these nitrogen-fixing plants can allocate it to seeds and leaves, improving germination performance and deterring herbivory (Dovrat et al., 2020). Regardless of whether Fabaceae species are nitrogen fixing or not, they have seed germination twice as fast as the germination of seeds from species of other families in TDFs, which gives an adaptive advantage in environments with long droughts by increasing seedling growth rates, increasing fecundity and avoiding seed predators (Vargas G. et al., 2015). Therefore, Fabaceae species in TDFs are drivers of resilience and stability. Among the 35 Fabaceae species, 19 species are of known nitrogen-fixing genera (Sprent, 2009). *Machaerium, Platymiscium, Calliandra, Pterocarpus* and *Prosopis*, were the genera that presented the highest IV in the Fabaceae family, and all of them are nitrogen-fixing (Sprent, 2009).

The high importance of Myrtaceae in these TDFs is not as common in other TDFs in Colombia, a result also obtained by Carrillo-Fajardo et al., (2007) in the area known as Cerro Tasajero, near the Patillales, a site of our study, which denotes a particularity of the studied region. According to Rocha; Silva, (2002), the Myrtaceae family is important because it has many vertebrate-dispersed species that are fundamental to natural regeneration and connectivity. Thus, is fundamental the importance of the prominent Myrtaceae species for the maintenance of these remaining TDFs, for regeneration processes and associated fauna that promote connectivity.

The species with the highest VI among all sites was *Machaerium arboreum*, a dominant nitrogen-fixing Fabaceae species in five out seven localities; this is the first work where this species appears as dominant in an TDF in Colombia. Other works in TDFs have shown the dominance of other species of the genus *Machaerium* in Colombia, such as in the Magdalena river valley and in the Caribbean region (Mendoza-C, 1999; Romero-Duque et al., 2019). *Platymiscium pinnatum*, was the second most important species in the VI general, and was very common in localities located at lower altitudes and more severe environments (Galván-Cisneros et al., 2021). This species is also prominent in the Neguanje TDF, within the Tayrona National Natural Park in the Colombian Caribbean, a zone with stressing bioclimatic characteristics similar to the areas where the species was recorded in our study (Carbonó-Delahoz; García-Q, 2010). *Handroanthus ochraceus, Guapira costaricana* and *Croton micans* are the third, fourth and fifth species with the highest overall VI, respectively; this result is quite similar to the finding in the Tayrona National Natural Park where species of the genus *Handroanthus, Platymiscium, Guapira* and *Croton*, were among the five highest VI (Carbonó-Delahoz; García-Q, 2010).

Morretón Bajo was the location that presented the most different and heterogeneous floristic composition of all, which can be observed in the floristic composition ordination (NMDS). Also, in this forest, the largest DAP was registered. The five species with the highest VI in this locality were *Apuleia leiocarpa, Protium heptaphyllum, Brosimum alicastrum, Xylopia frutescens* and *Platypodium elegans*. *A. leiocarpa* is a Fabaceae species but it is not nitrogen-fixing species (Sprent, 2009). *A. leiocarpa* was also found to be prominent in several Atlantic Forest forests in Brazil (Carvalho et al., 2007; Ruschel et al., 2009). *P. heptaphyllum, B. alicastrum, X. frutescens* and *P. elegans* are very common species, occurring widely in almost all lowland forests in the Neotropics (Dionisio et al., 2016; Gardner et al., 2021; Hufford; Hamrick, 2003). Due to the greater richness, trees with greater DAP and for having only one nitrogen-fixing Fabaceae species among the prominent species, this forest seems to be the most advanced in the successional process among the TDFs in our study.

Parinari pachyphylla, was the only species registered in an IUCN-Colombia threat category; in this study, the species was found only in a portion of the Morretón Bajo locality, the locality with the greatest floristic heterogeneity. The species was prioritized within the National Plant Conservation Strategy of Colombia (ENCP) (Pizano et al., 2014), and Program for the Integral Conservation of Ten Priority Plant Species of the TDF (Sofrony-Esmeral et al., 2020). The main cause of its threat is the drastic transformation of forest areas into areas of intensive agriculture (Calderón et al., 2002). In Colombia, this species is distributed in the Caribbean region, in the lower valley of the Magdalena River, in the Zulia region, in the Serranía de Perijá borders with Venezuela (Norte de Santander province), in the Urabá de Antioquia and Orinoquia (Calderón et al., 2002; Pizano & García, 2014); and it is estimated that the provinces of Norte de Santander and Vichada are home to the best preserved populations (Calderón et al., 2002). However, it is very likely that several other species will be threatened in the near future due to climate changes in fragmented landscapes that make connectivity difficult. (Galván-Cisneros et al., 2021; IPCC, 2021) because most species sampled has a low number of individuals and a small basal area. It is possible that a significant number of species will be at risk of extinction in the near future, which shows a clear need to protect these forests through public policies.

As a general trend, a greater number of species was found in locations at higher altitudes, decreasing in locations at lower altitudes and where climatic seasonality is more marked and filters out species from lineages that are less tolerant to stressful environments (Galván-Cisneros et al., 2021). The species richness of these TDFs in lower altitude is small, which contrasts with the species richness of humid tropical forests in low altitude (Janzen, 1988; Van Bloem et al., 2004).

In TDFs the number of species varies in response to altitudinal variation (Galván-Cisneros et al., 2021). Therefore, the variable species composition is a response to higher temperature and greater drought intensity at lower altitudes and contrasts with mild temperatures and less intense droughts at higher altitudes. Also, as altitude decreases and environmental stress increases, nitrogen-fixing Fabaceae species become more important. These environments reveal differences that must be observed in the elaboration of actions for the conservation and sustainability of human activities. A similar floristic gradient was found for eight TDF fragments at the confluence of Caatinga, Cerrado and Atlantic Forest in Brazil, where climatic seasonality was the main factor of floristic differentiation (Fagundes et al., 2020).

CONCLUSION

Fabaceae and Myrtaceae were consistent important families with high species richness in the studied TDFs in the Andes. The two species of greatest ecological importance in the region were *M. arboreum* and *P. pinnatum*, species belonging to the Fabaceae family, both nitrogen fixing species and easily found in most localities; *H. ochraceus* and *G. costaricana*, one Bignoniaceae and one Nyctaginaceae, respectively, also stood out. Las Lomas was characterized by its low number of species and the ecological dominance of *P. pinnatum*. In contrast, Morretón Bajo was characterized by its high number of species and its high variability. The locations (or fragments) of FTS's sampled in this study present a topographic gradient that influences species richness, floristic and structural composition driven by climatic factors (climate seasonality) and altitude. The structure, composition and ecological importance of these forests must be considered for conservation and ecological restoration plans, in particular the habitat preference of species along the topographic gradient. However, it is essential to consider the prominence of Myrtaceae species that promote connectivity and regeneration as they provide resources for fauna as well as the prominence of Fabaceae species, especially nitrogen-fixing ones, which promote resilience and natural regeneration of TDFs in the Andes.

AUTHORSHIP CONTRIBUTION

Project Idea: CMGC, JAAMN

Funding: CMGC, JAAMN, AEOR, LRS

Database: CMGC, AEOR

Processing: CMGC, LRS

Analysis: CMGC, JAAMN

Writing: CMGC, JAAMN, LRS

Review: JAAMN, CMGC

ACKNOWLEDGEMENT

Thanks to the Postgraduate Program in Botany at the Federal University of Viçosa. We thank to Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), CNPq (301913/2012-9, 307591/2016-6, 306335/2020-4), CAPES (PROAP), FAPEMIG (FORTIS, APQ-01309-16, PPM 00584-16), and DAAD (Project ID57393735). Thanks to the environmental consultancy RENATURAR S.A.S for the support. We thank biologists María Carmenza Rozo and Franklin Torres and forestry engineer Camilo Palacios, who were part of the floristic survey team.

REFERENCES

ALBESIANO, S.; FERNÁNDEZ-ALONSO, J. L. Catálogo comentado de la flora vascular de la franja tropical (500-1200m) del cañón del río Chicamocha (Boyacá-Santander, Colombia). Primera parte. Caldasia, v. 28, n. 1, p. 23–44, 2006.

ALBESIANO, S.; RANGEL-CH, J. O. Estructura de la vegetación del cañón del río Chicamocha, 500-1200m; Santander- Colombia: una herramienta para la conservación. Caldasia, v. 28, n. 2, p. 307–325, 2006.

ALBESIANO, S.; RANGEL-CH, J. O.; CADENA, A. La vegetación del cañón del río Chicamocha (Santander, Colombia). Caldasia, v. 25, n. 1, p. 73–99, 2003.

ANDERSON, M. J. A new method for non-parametric multivariate analysis of variance. Austral Ecology, v. 26, n. 1, p. 32–46, 2001.

ANDRADE, L. A.; FABRICANTE, J. R.; ARAÚJO, E. DE L. Estudos de fitossociologia em vegetação de Caatinga. In: FELFILI, J. M.; EISENLOHR, P. V.; MELO, M. M. R. F.; ANDRADE, L. A.; MEIRA-NETO, J. A. A. Fitossociologia no Brasil: métodos e estudos de caso. first ed. Viçosa, Brazil: Editora UFV, 2011. v. 1p. 339–371.

AVENDAÑO-YÁÑEZ, M. DE LA L.; LÓPEZ-ORTIZ, S.; PERRONI, Y.; PÉREZ-ELIZALDE, S. Leguminous trees from tropical dry forest generate fertility islands in pastures. Arid Land Research and Management, v. 32, n. 1, p. 57–70, 2018.

BANDA, K.; DELGADO, A.; DEXTER, K. et al. Plant diversity patterns in neotropical dry forests and their conservation implications. Science, v. 353, n. 6306, p. 1383–1387, 2016.

BHASKAR, R.; DAWSON, T. E.; BALVANERA, P. Ecological and evolutionary variation in community nitrogen use traits during tropical dry forest secondary succession. Ecology, v. 97, n. 5, p. 1194–1206, 2016.

BUENO, M. L.; PENNINGTON, R. T.; DEXTER, K. G.; KAMINO, L. H. Y.; PONTARA, V.; NEVES, D. M.; RATTER, J. A.; OLIVEIRA-FILHO, A. T. Effects of Quaternary climatic fluctuations on the distribution of Neotropical savanna tree species. Ecography, v. 40, n. 3, p. 403–414, 2016.

CALDERÓN, E.; GALEANO, G.; GARCÍA, N. J. Libro Rojo de Plantas Fanerógamas de Colombia. Volumen 1: Chrysobalanaceae, Dichapetalaceae y Lecythidaceae. Bogotá, Colombia: Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Instituto de Ciencias Naturales-Universidad Nacional de Colombia, Ministerio del Medio Ambiente, 2002. 218p.

CARBONÓ-DELAHOZ, E.; GARCÍA-Q, H. La vegetación terrestre en la ensenada de Neguanje, parque nacional natural Tayrona (Magdalena, Colombia). Caldasia, v. 32, n. 2, p. 235–256, 2010.

CARRILLO-FAJARDO, M.; RIVERA-DÍAZ, O.; SÁNCHEZ-MONTAÑO, R. Caracterización florística y estructural del bosque seco tropical del cerro Tasajero, San José de Cúcuta (Norte de Santander), Colombia. Actual Biol, v. 29, n. 86, p. 55–73, 2007.

CARVALHO, F. A.; NASCIMENTO, M. T.; BRAGA, J. M. A. Estrutura e composição florística do estrato arbóreo de um remanescente de Mata Atlântica submontana no município de Rio Bonito, RJ, Brasil (Mata Rio Vermelho). Revista Árvore, v. 31, n. 4, p. 717–730, 2007.

CHAZDON, R. L.; HARVEY, C. A.; MARTINEZ-RAMOS, M. et al. Seasonally Dry Tropical Forest Biodiversity and Conservation Value in Agricultural Landscapes of Mesoamerica. In: DIRZO, R.; YOUNG, H. S.; MOONEY, H. A.; CEBALLOS, G. Seasonally Dry Tropical Forests: Ecology and Conservation. Island Press, Washington, p. 195–219, 2011.

CURTIS, J. T.; MCINTOSH, R. P. The Interrelations of Certain Analytic and Synthetic Phytosociological Characters. Ecology, v. 31, n. 3, p. 434–455, jul. 1950.

DA SILVA, A. F.; DE FREITAS, A. D. S.; COSTA, T. L.; FERNANDES-JÚNIOR, P. I.; MARTINS, L. M. V.; SANTOS, C. E. de R. e S.; MENEZES, K. A. S.; SAMPAIO, E. V. de S. B. Biological nitrogen fixation in tropical dry forests with different legume diversity and abundance. Nutrient Cycling in Agroecosystems, v. 107, n. 3, p. 321–334, 2017.

DÍAZ-PÉREZ, C. N. Análisis florístico y fitogeográfico de la cuenca baja del cañón del río Suárez, (Santander, Colombia). Master's dissertation Universidad Nacional de Colombia, Bogotá, Colombia, 2012.

DIONISIO, L. F. S.; BONFIM FILHO, O. S.; CRIVELLI, B. R. S.; GOMES, J. P.; OLIVEIRA, M. H. S.; CARVALHO, J. O. Phytosociological importance of a fragment of dense rain forest in the state of Roraima, Brazil. Revista Agro@mbiente On-line, v. 10, n. 3, p. 243–252, 2016.

DOVRAT, G.; BAKHSHIAN, H.; MASCI, T.; SHEFFER, E. The nitrogen economic spectrum of legume stoichiometry and fixation strategy. New Phytologist, v. 227, n. 2, p. 365–375, 2020.

FAGUNDES, N. C. A.; PAIS, A. J. R.; DE SOUZA, C. R.; SANTOS, P. F.; ALMEIDA, H, S.; VIEIRA, F. A.; OLIVEIRA-FILHO, A. T.; VAN DER BERG, E.; CARVALHO, D.; DOS SANTOS, R. M. Floristic and structural relationships in seasonally dry tropical forests on limestone outcrops. Scientia Forestalis, v. 48, n. 127, 2020.

FAJARDO-GUTIÉRREZ, F.; MONTEALEGRE, C.; PARDO, M. E. Dinámica de la vegetación del Cañón del Chicamocha, análisis de la información nueva y preexistente sobre sus comunidades vegetales. In: PARDO, M. E.; MORENO-ARIAS, R. A. (Eds.). El enclave seco del cañón del Chicamocha: biodiversidad y territorio. Fundación Natura, 2018. p. 192.

GALVÁN-CISNEROS, C. M.; HERINGER, G.; DOMEN, Y. S. M.; SÁNCHEZ, L. R.; MEIRA-NETO, J. A. A. The environmental filtering and the conservation of tropical dry forests in mountains in a global change scenario. Biodiversity and Conservation, v. 30 n. 10, p. 2689-2705, 2021.

GARCÍA, H.; CORZO, G.; ISAACS-CUBIDES, P. J.; ETTER, A. Distribución y estado actual de los remanentes del bioma de Bosque Seco Tropical en Colombia: insumos para su gestión. In: PIZANO, C.; GARCÍA, H. (Eds.). El Bosque Seco Tropical en Colombia. Bogotá, Colombia: Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, 2014. p. 229–251.

GARDNER, E. M.; AUDI, L.; ZHANG, Q.; SAUQUET, H.; MONRO, A. K.; ZEREGA, N. J. C. Phylogenomics of *Brosimum* (Moraceae) and allied genera, including a revised subgeneric system. Taxon, v. 70, n. 4, p. 778–792, 2021.

GASTAUER, M.; SAPORETTI-JUNIOR, A. W.; MAGNAGO, L. F. S.; CAVENDER-BARES, J.; MEIRA-NETO, J. A. A. The hypothesis of sympatric speciation as the dominant generator of endemism in a global hotspot of biodiversity. Ecology and Evolution, v. 5, n. 22, p. 5272–5283, 2015.

GEI, M.; ROZENDAAL, D. M. A.; POORTER, L. et al. Legume abundance along successional and rainfall gradients in Neotropical forests. Nature Ecology & Evolution, v. 2, n. 7, p. 1104–1111, 2018.

GENTRY, A. H. Diversity and floristic composition of neotropical dry forests. In: BULLOCK, S. H.; MOONEY, H. A.; MEDINA, E. (Eds.). Seasonally Dry Tropical Forests. New York, USA: Cambridge University Press, 1995. p. 146–194.

GONZÁLEZ-M, R.; GARCÍA, H.; ISAACS, P.; ROJAS, A.; VERGARA, H.; PIZANO, C. Disentangling the environmental heterogeneity, floristic distinctiveness and current threats of tropical dry forests in Colombia. Environmental Research Letters, v. 13, n. 4, p. 045007, 2018.

HERNÁNDEZ, J.; WALSCHBURGER, T.; ORTIZ, R.; HURTADO, A. Origen y distribución de la biota suramericana y colombiana. In: HALFFTER, G. (Ed.). La diversidad biológica iberoamericana I. Xalapa, México: Acta Zoológica Mexicana, 1992. p. 55–98.

HUFFORD, K. M.; HAMRICK, J. L. Viability selection at three early life stages of the tropical tree, Platypodium elegans (Fabaceae, Papilionoideae). Evolution, v. 57, n. 3, p. 518–526, 2003.

IAVH. El bosque seco tropical (Bs-T) en Colombia. Programa de Inventario de la Biodiversidad Grupo de Exploraciones y Monitoreo Ambiental (GEMA)- Instituto de Investigación de Recursos Biológicos Alexander von Humboldt (IAvH). Bogotá, Colombia. 1998.

IPCC. Climate Change 2021 - The Physical Science Basis: Working Group I contribution to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. [Working Group I contribution to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change]. Intergovernmental Panel on Climate Change, 2021.

JANZEN, D. H. Tropical Dry Forests: The Most Endangered Major Tropical Ecosystem. In: WILSON, E. O.; PETER, F. M. (Eds.). Biodiversity. Washington, D.C.: National Academies Press (US), p. 130–137, 1988.

LEBRIJA-TREJOS, E.; BONGERS, F.; PÉREZ-GARCÍA, E. A.; MEAVE, J. A. Successional Change and Resilience of a Very Dry Tropical Deciduous Forest Following Shifting Agriculture. Biotropica, v. 40, n. 4, p. 422–431, 2008.

LIMA, N. E.; GUIMARÃES, R. A.; ALMEIDA-JÚNIOR, E. B.; VITORINO, L. C.; COLLEVATTI, R. G. Temporal trends, impact and partnership in floristic and phytosociology literature in the Brazilian Cerrado. Flora, v. 273, p. 151721, 2020.

MEDINA-GARCÍA, C.; VELÁZQUEZ, A.; GIMÉNEZ DE AZCÁRATE, J. et al. Phytosociology of a Seasonally Dry Tropical Forest in the State of Michoacán, Mexico. Botanical Sciences, v. 98, n. 4, p. 441–467, 2020.

MENDOZA-C, H. Estructura y riqueza florística del bosque seco tropical en la región Caribe y el Valle del río Magdalena, Colombia. Caldasia, v. 21, n. 1, p. 70–94, 1999.

MUELLER-DOMBOIS, D.; ELLENBERG, H. Aims and Methods of Vegetation Ecology. New York, USA: John Wiley and Sons, 1974.

NEVES, D. M.; DEXTER, K. G.; BAKER, T. R. et al. Evolutionary diversity in tropical tree communities peaks at intermediate precipitation. Scientific Reports, v. 10, n. 1, p. 1–7, 2020.

OKSANEN, J.; BLANCHET, F. G.; FRIENDLY, M. et al. Vegan: Community Ecology Package. R package version 2.0-7. 2018.

OLIVEIRA-FILHO, A. T. Um Sistema de classificação fisionômico-ecológica da vegetação Neotropical. In: EISENLOHR, P. V.; FELFILI, J. M.; MELO, M. M. R. F.; ANDRADE, L. A.; MEIRA NETO, J. A. A. (Orgs.), Fitossociologia no Brasil: Métodos e estudos de casos (V. 2,). Viçosa, Brasil: Editora UFV. 2015. p. 452–473

OLIVEIRA-FILHO, A. T. NeoTropTree, Flora arbórea da Região Neotropical: Um banco de dados envolvendo biogeografia, diversidade e conservação. Universidade Federal de Minas Gerais, 2017. Available in: http://www.neotroptree,info.

OLIVEIRA-FILHO, A. T.; FONTES, M. A. L. Patterns of Floristic Differentiation among Atlantic Forests in Southeastern Brazil and the Influence of Climate. Biotropica, v. 32, n. 4, p. 793–810, 2000.

PENNINGTON, R. T.; PRADO, D. E.; PENDRY, C. A. Neotropical seasonally dry forests and Quaternary vegetation changes. Journal of Biogeography, v. 27, n. 2, p. 261–273, 2000.

PIZANO, C.; GONZÁLEZ-M, R.; GONZÁLEZ, M. et al. Las plantas de los bosques secos de Colombia. In: PIZANO, C.; GARCÍA, H. (Eds.). El Bosque Seco Tropical en Colombia. Bogotá, Colombia: Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, p. 49–93. 2014.

PORTILLO-QUINTERO, C.; SANCHEZ-AZOFEIFA, A.; CALVO-ALVARADO, J.; QUESADA, M.; DO ESPIRITO SANTO, M. M. The role of tropical dry forests for biodiversity, carbon and water conservation in the neotropics: lessons learned and opportunities for its sustainable management. Regional Environmental Change, v. 15, n. 6, p. 1039–1049, 2015.

R Development Core Team. R: The R Project for Statistical Computing. https://www.r-project.org/. 2021.

ROCHA, A. E. S.; SILVA, M. F. F. Catalog of secondary forest species. Belem, Brazil: Museu Paraense Emilio Goeldi. 2002.

RODRÍGUEZ, G. M.; BANDA-R, K.; REYES, S. P.; ESTUPIÑAN, A. C. Annotated list of vascular plants of priority dry forests for conservation in the departments of Atlántico and Bolívar (Colombian Caribbean). Biota Colombiana, v. 13, n. 2, p. 7–39, 2012.

ROMERO-DUQUE, L.; ROSERO-TORO, J.; FERNÁNDEZ-LUCERO, M.; SIMBAQUEBA-GUTIERREZ, A.; PÉREZ, C. Trees and shrubs of the tropical dry forest of the Magdalena River upper watershed (Colombia). Biodiversity Data Journal, v. 7, n. e36191, 2019.

RUIZ, J.; FANDIÑO, M. C.; CHAZDON, R. L. Vegetation Structure, Composition, and Species Richness Across a 56-year Chronosequence of Dry Tropical Forest on Providencia Island, Colombia. Biotropica, v. 37, n. 4, p. 520–530, 2005.

RUSCHEL, A. R.; GUERRA, M. P.; NODARI, R. O. Tructure and floristic composition of two fragments of the Alto-Uruguay Seasonal Deciduous Forest, SC. Forest Science, v. 19, n. 2, p. 225–236, 2009.

SIYUM, Z. G. Tropical dry forest dynamics in the context of climate change: syntheses of drivers, gaps, and management perspectives. Ecological Processes, v. 9, n. 1, p. 25, 2020.

SOFRONY-ESMERAL, C.; CASTAÑO, A.; ROJAS, A.; SANTOS, A.; NIEVES, J.; OYUELA, G. Programa para la Conservación Integral de Diez Especies de Plantas Prioritarias del BST. v2.3. Red Nacional de Jardines Botánicos de Colombia. Dataset/Occurrence. 2020.

SPRENT, J. I. Legume Nodulation: A Global Perspective. Oxford, United Kingdom: Wiley-Blackwell, 2009.

THE ANGIOSPERM PHYLOGENY GROUP. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. Botanical Journal of the Linnean Society, v. 181, n. 1, p. 1–20, 2016.

VALENCIA-DUARTE, J.; TRUJILLO, L. N.; VARGAS, O. Dinámica de la vegetación en un enclave semiárido del río Chicamocha, Colombia. Biota Colombiana, v. 13, n. 2, p. 40–65, 2012.

VAN BLOEM, S. J.; MURPHY, P. G.; LUGO, A. E. TROPICAL FORESTS | Tropical Dry Forests. In: BURLEY, J. (Ed.). Encyclopedia of Forest Sciences. Oxford: Elsevier, 2004. p. 1767–1775.

VARGAS, G.; WERDEN, L. K.; POWERS, J. S. Explaining Legume Success in Tropical Dry Forests Based on Seed Germination Niches: A New Hypothesis. Biotropica, v. 47, n. 3, p. 277–280, 2015.

VETAAS, O. R.; GRYTNES, J.-A. Distribution of vascular plant species richness and endemic richness along the Himalayan elevation gradient in Nepal. Global Ecology & Biogeography, v. 11, n. 4, p. 291–301, 2002.

VIEIRA, D.; SCARIOT, A. Principles of Natural Regeneration of Tropical Dry Forests for Restoration. Restoration Ecology, v. 14, n. 1, p. 11–21, 2006.

WICKHAM, H. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York. 2016.

ZERWES, C. M.; REMPEL, C.; SCHNEIDER, J. K.; MARANHO, L. T. Importance of the review on floristic and phytosociological studies of the arboreal stratum of the seasonal deciduous forest of the Serra Geral slope, Rio Grande do Sul, Brazil, to support proposals for sustainable management. Ciência e Natura, v. 40, p. 41, 2018.