Tropical forest refuge in peripheral soils of slags in Caatinga

José João Lelis Leal de Souza^{1¶*}, Bartolomeu Israel de Souza^{2¶}, Rubens Teixeira de Queiroz^{3¶}, Rony Lopes Lunguinho², Joseilson Ramos de Medeiros², Eini Celly Moraes Cardoso², Pedro André de Melo e Silva², Helder Cavalcante de Oliveira²

¹ Geography Department, Universidade Federal do Rio Grande do Norte, Caicó, Rio Grande do Norte, Brazil

² Geosciences Department, Universidade Federal da Paraíba, João Pessoa, Paraíba, Brazil

³ Ecology and Systematics Department, Universidade Federal da Paraíba, João Pessoa, Paraíba, Brazil

* Corresponding author

E-mail: jjlelis@gmail.com (JJLLS)

Abstract

The influence of environmental factors on the structure and composition of plant communities in the Caatinga is complex and poorly explored. Spatial variation of biodiversity in Caatinga is poorly know and strictly attributed to climatic conditions. We investigated the influence of slags on floristic composition and structure of a shrubby-arboreal community in one of the driest region in Brazil. Chemical and physical analyses of soils were performed in samples of seven plots from savannic formations and from forest formations. Vegetation was characterized floristically and structurally in all plots. Habitats were structurally distinct, and diversity differed

between peripheral and non-peripheral areas of slags. Nine of the ninety-seven species identified are reported to (sub)humid biomes. Soils are dominantly shallow, eutrophic and sandy loam. However, soils in the periphery of slags are more developed once paludization, melanization and bioturbation were verified. Our results suggest that soil fertility did not influence vegetable cover in Caatinga. The cover of plant species considered exclusive of (sub)humid biomes in Brazil extends beyond highlands in the semiarid, associated with high soil organic carbon content and water retention capacity of more developed soils than the typical of the Caatinga.

Introduction

Dryland biomes cover 41.5 % of the Earth's surface, with seasonally dry tropical forests occupying approximately 1,327 million hectares within this area [1]. The largest area of continuous dry tropical rainforests in Latin America occurs in Brazil, with approximately 800.00 km². Popularly called as Caatinga (Mata Branca), most trees and shrubs lose their leaves in the dry season, which can last up to nine months a year in certain regions [2].

Caatinga is a Brazilian exclusive biome composed by different plant formations [3] and its diversity is considered one of the most biodiverse among semiarid biomes [4,5]. Among the several ecosystems that exist in the Caatinga, granitic intrusions in the form of inselbergs, massive, slags (lajedos in portuguese) and bornhardts cover 15 % of the total area of the northern Brazilian Northeast [6].

Low developed, shallow and eutrophic soils are dominant in Caatinga due to tropical dry climate. However, high local diversity of soils has been attributed to variance of lithology and, or, relief by recent studies [7]. Understood soil diversity is a relevant task, especially considering that plant distribution is conditionate by soil

properties [8,9]. Soil influences plant physiognomies in Brazilian Savanna (Cerrado) [10], Restinga forest [11], Amazonia rainforest [12,13], Tundra [14] and other biomes around the world [15,16]. However, species diversity in Caatinga is poorly know [17] and strictly attributed to climatic conditions [18–20].

The purpose of this study was to investigate a vegetation gradient at preserved slabs in Caatinga, and to describe the main soil-vegetation relationships and the community structure. Thus, we hypothesized that variation in vegetation structure and composition is related to soil chemical and physical attributes.

Material and methods

Study area

The study area encompasses the occidental and oriental Cariri microregions, Paraíba state (Fig 1). They have a total area of approximately 11,225.736 km² and particular landscape diversity. Altitudes vary between 400 m, in the Paraíba valley, and 700 m, in highlands associated with resistant rocks and horst–graben systems. The mean precipitation of 350 mm year⁻¹, potential evapotranspiration four times higher than precipitation and mean temperature of 27 °C highlights Cariri as one of the driest regions of Brazil [21].

Fig 1. Paraíba State location (A), study area location (B) and sample distribution (C).

Cariri microregions are inserted in the Borborema province, characterized by the extensive erosive surfaces denominated the *sertanejas* depressions developed on Meso- and Neoproterozoic gneiss and schist [22]. Inselbergs, massives and slabs developed on

Neoproterozoic granites emerge due to differential weathering by mineralogical, petrographic or fracture pre-arrangement [6].

In Cariri microregions shallow and incipient weathered soils dominate, with Entisols (Neossolos according to Brazilian System of Soil Classification) and Alfisols (Luvisolos) representing 43 % of the study area [23]. Plant physiognomy is described as dry deciduous forest dominated by Bromeliaceae Juss., Cactaceae Juss. and Fabaceae Lindl. and members of Poaceae Barnhart and Cyperaceae Juss. families [24].

Data sampling and analysis

Sixty-five transects, 50 m x 2 m each one, were established in Environmental Protection Area of Cariri between January and November 2017, according to linear transect method for phanerophytes and camphids (LTMPC) [25]. The LTMPC was successfully adopted in previous studies in Caatinga [26]. Seven different vegetation plots (V.P.) were formed by grouping transects: a) V.P. on peripheral areas of slags: V.P. I, V.P. II, V.P. IV and V.P. VI; b) V.P. on a flat plain: V.P. III and V.P. V; c) V.P. on peripheral areas of slags and on flat plain: V.P. VII.

Height, the largest and the smallest diameters of individuals with diameter at breast height below 2 cm were measured. Individuals with diameter at breast height above 2 cm had their height and median crown radius measured. All live specimens were sampled and identified at field and consulting Brazilian Flora 2020 [27]. The APG IV classification system was adopted for the plant families [28].

The Jaccard similarity index was calculated to express the similarity between plots based on the number of common species. The resulting floristic similarity matrix was used for cluster analysis by simple binding method and generation of a dendrogram in the PAST software [29].

Soil sampling and analysis

Seven pedons were taken, described and classified according to Soil Taxonomy (Soil Survey Staff, 2014) and Brazilian Soil Classification System [30] to represent soil diversity of plots. Soil samples were collected from the surface down to the lithic contact at each pedon. For deeper soils a 200 cm control section was used. Because the absence of temperature soil data in Brazilian semiarid, we classified the moisture regime of soils according to previously studies [31].

Samples were air dried and sieved through a 2 mm sieve prior to physic and chemical analyzes according to methods established for tropical soils [32]. Coarse and fine sand, silt and clay were determined by the sieve-pipette method after dispersion with 0.1 M NaOH. Soil pH was measured with a glass electrode in a 1:2.5 suspension v/v soil and deionized water (H_2O pH) and 1 M KCl solution (KCl pH). Delta pH (ΔpH) was calculated by KCl pH minus H_2O pH. The potential acidity ($H + Al$) was extracted by 1 M ammonium acetate solution at pH 7. The content of exchangeable Ca^{2+} , Mg^{2+} and Al^{3+} were determined in a 1 M KCl extract. Exchangeable K^+ and Na^+ were determined after Mehlich-1 extraction. From these results, the sum of bases (SB), base saturation (V), aluminum saturation (m), equivalent cation exchange capacity (ECEC), total cation exchange capacity (CEC) and Na saturation (ISNA) were calculated.

The available phosphorus content (P_M) was determined by a Mehlich-1 extraction solution. Total organic carbon (C) was determined by wet combustion [33]. Total nitrogen (N) was determined by Kjeldahl method and titration [34]. Carbon to nitrogen ratio (C/N) was calculated on the mass basis. The P adsorption capacity of the soil was determined after stirring for 1 hour with 2.5 g of soil in 0.01 M $CaCl_2$

containing 60 mg of P L⁻¹. The suspension was filtered and the remaining P in solution (P_{REM}) was determined by photocolorimetry (Alvarez et al., 2000).

Bulk density, particle density and micropores (pores with diameter below 0.5 mm) were determined in undisturbed soil samples collected by volumetric rings [34]. Total porosity and macropores (pores with diameter above 0.5 mm) were calculated from these results. Total organic carbon and nitrogen stocks were calculated by using the total organic content, sampling depth and bulk density: Stock (Mg ha⁻¹) = bulk density (kg dm⁻³) x total organic carbon (or total nitrogen) content (%) x depth (cm).

Descriptive statistics were calculated for pedons according to its proximity of slags. Furthermore, Pearson correlation between soil properties was calculated. Principal Component Analysis (PCA) was performed to elucidate correlation between variables. Prior to PCA, analytical data of each horizon was logarithmic transformed and standardized to provide a normal distribution [35].

Results

A total of 2,563 specimens were identified in all transects (Table 1), exceeding the recommendation for phytosociological surveys aiming to characterize Caatinga [36]. Six hundred and thirty-seven specimens (24.9 % of total) composes the arboreal stratum. The richness of species is dominated by Fabaceae (14 species), followed by Euphorbiaceae Juss. (7 spp.), Myrtaceae Juss. (4 spp.), Anacardiaceae R. Br. (4 spp.) and Rubiaceae Juss. (3 spp.) families (S1 Table).

Table 1. Specimens distribution by strata.

Height (m)/ strata	Number of specimens	Relative frequency (%)
0 - 0.3/ herbaceous to sub shrubby	242	9.44

> 0.3 - 0.6/ sub shrubby	317	12.37
> 0.6 - 1.5/ shrubby	709	27.66
> 1.5 - 3/ shrubby to arboreal	658	25.67
> 3 – 5/ small tree	310	12.10
> 5 – 10/ medium tree	238	9.29
> 10 – 20/ large tree	73	2.85
> 20/ largest tree	16	0.62
All	2,563	100

Nine of the ninety-seven species identified are reported to other biomes (S1 Table): *Allophylus quercifolius* (Mart.) Radlk. is commonly associated to Amazon rainforest, Atlantic forest and Brazilian Savanna; *Calypttranthes lucida* Mart. ex DC and *Vitex orinocensis* Kunth are associated to Amazon rainforest and Atlantic forest; *Chloroleucon tortum* (Mart.) Pittier *Myroxylon peruiferum* L. F. are associated to Atlantic forest and Brazilian Savanna; *Erythroxylum suberosum* A. St.-Hil. is associated to Amazon rainforest and Brazilian Savanna; *Hymenaea rubriflora* Ducke, *Libidibia ferrea* var. *leiostachya* (Benth.) L. P. Queiroz and *Pisonia ambigua* Heimerl are associated to Atlantic forest.

The highest number of specimens were identified in vegetation plots (V.P.) peripheral to slags: V.P. 6 (755 specimens or 29.4 % of total), V.P. 4 (440 or 17.2 %), V.P. 2 (393 or 15.3 %) and V.P. 1 (370 or 14.4 %) (S1 Table). The highest number of specimens of the species associated to wetter biomes also are reported in V.P. peripheral of slags, corresponding to approximately 2.8 % of specimens in each V.P.

The values of coefficient of similarity vary from 27 % to 54 % (Fig 2). Higher Jaccard index values were observed for comparisons between V.P. II, V.P. IV and V.P. VI indicating that these plots share a high number of species in common.

Fig 2. Similarity index between vegetational plots.

Morphology and physic-chemical soil properties

Six of the nine collected soil profiles were classified as Entisols, which corresponds to the order of Neossolos in the Brazilian Soil Classification System [30]. Two Inceptisols were described: one Aridic Haplustepts with fragipan (Neossolo Regolítico) and the another one was identified as Oxic Haplustepts (Cambissolo Háplico). One Lithic Rhodustalfs (Luvisolo Crômico) were described to represent soil dominance of Brazilian semiarid (Table 2).

Table 2. Area description and classification of soils.

Soil profile	Soil Taxonomy	SiBCS	Related plot	Altitude (m)	Area description	Coordinates ¹
Slags peripheral soil profiles						
S1	'Vermic' Aridic Ustorthents	NEOSSOLO REGOLÍTICO Húmico léptico êutrico	II, IV, VI VII	498	Concave fracture in backslope of slag. Well drained soils, with no apparent erosion and derived from autochthonous granitoid colluvium. Soil is covered by litter and subperennial arboreal specimens. Gravelly sandy loam texture, mollic epipedon and gentle slope surface.	-7.36957 ° -36.27978 °
S2	Aridic Haplustepts	NEOSSOLO REGOLÍTICO Distrófico fragmentário organossólico fragipânico	II, IV, VI, VII	482	Footslope of slag. Well drained soils, with no apparent erosion and derived from autochthonous granitoid colluvium. Soil is covered by litter and subperennial arboreal specimens. Gravelly loamy sand texture, umbric epipedon and gentle slope surface.	-7.36990 ° -36.28043 °
S4	Vermic Ustorthents	NEOSSOLO REGOLÍTICO Distrófico saprolítico	I, VII	483	Footslope of slag. Well drained soils, with no apparent erosion and derived from autochthonous granitoid colluvium. Soil is covered by litter and subperennial arboreal specimens. Gravelly loamy sand texture, umbric epipedon and gentle slope surface.	-7.37221 ° -36.28064 °
S5	'Vermic' Aridic Lithic Ustorthents	NEOSSOLO LITÓLICO Eutrófico fragipânico	I, VII	510	Footslope of slag. Well drained soils, with no apparent erosion and derived from autochthonous granitoid colluvium. Soil is covered by litter and deciduous arboreal specimens. Gravelly loamy sand texture, mollic epipedon and gentle slope surface.	-7.37366 ° -36.28033 °
S6	Oxic Haplustepts	CAMBISSOLO HÁPLICO Tb Distrófico úmbrico	I, II, IV, VI	478	Concave shape in footslope of slag. Poorly drained soils, with no apparent erosion and derived from autochthonous granitoid colluvium. Soil is covered by litter and subperennial arboreal specimens. Sandy clay loam texture, umbric epipedon, gentle slope surface.	-7.36537 ° -36.27883 °
S7	Vermic	NEOSSOLO	II, IV,	479	Footslope of slag. Well drained soils, with no apparent erosion	-7.3653 °

	Ustorthents	REGOLÍTICO Eutrófico saprolítico arênico	VI		and derived from autochthonous granitoid colluvium. Soil is covered by litter and subperennial arboreal specimens. Gravelly loamy sand texture, umbric epipedon and gentle slope surface.	-36.28032 °
S8	'Vermic' Aridic Lithic Ustorthents	NEOSSOLO LITÓLICO Húmico fragipânico êutrico	II, IV, VI	476	Footslope of slag. Poorly drained soils, with no apparent erosion and derived from autochthonous granitoid colluvium. Soil is covered by litter and subperennial arboreal specimens. Gravelly loamy sand texture, mollic epipedon and gentle slope surface.	-7.36515 ° -36.28021 °
Non-peripheral soils of slags						
S3	'Fragipan' Lithic Ustorthents	NEOSSOLO LITÓLICO Eutrófico típico	III, VII	484	Gently inclined pediment. Well drained soils, with apparent laminar erosion and derived from autochthonous granitoid. Litter is absent due to sparse cover of herbaceous and deciduous arboreal specimens. Gravelly loamy sand texture, ochric and epipedon and gentle slope surface.	-7.37190 ° -36.28099 °
S9	Lithic Rhodustalfs	LUVISSOLO CRÔMICO Órtico vertissólico	V	464	Partially dissected pediment. Poorly drained soils, with apparent laminar erosion and derived from autochthonous gneiss. Litter is absent due to sparse cover of herbaceous and deciduous arboreal specimens. Desert pavement. Clay texture, ochric and epipedon and wavy surface.	-7.74847 ° -36.65791 °

175 ^{1/} Geographic coordinate system. World Geographic System 1984 Datum.

176   The depth of the soil varied between 20 cm and 100 cm with a mean of 72 cm
 177   (Table 3). Soils are shallow and transition between horizons was predominantly clear or
 178   abrupt, indicating that the parent material is low weathered. Structure is low to moderate
 179   developed, with sub angular blocky and single gran types dominantly. Worm hole sand
 180   filled animal burrows were observed in five Entisols, indicating widespread
 181   bioturbation. Soils without bioturbation were only observed in non-peripheral soils of
 182   slags.

Table 3. Morphological properties of soils.

Horizon	Depth (cm)	Boundary (distinctness, topography)	Moist color	Structure (grade, size, type)	Consistence (dry, moist, wetter, cementation)	Roots (quantity, size)	Pores (quantity, size, shape)
Slags peripheral soil profiles							
Profile S1 - 'Vermic' Aridic Ustorthents/ NEOSSOLO REGOLÍTICO Húmico léptico êutrico							
A1	0-5	G-S	10YR 2/1	0, -, sg	L, L, so, po, NC	1, f	3, m, DT
A2	5-25	G-S	10YR 2.3/1	0, -, sg	L, L, so, po, NC	1, f	3, m, DT
A3	25-50	G-S	10YR 2.7/1	1, f, sbk	L, L, so, po, NC	3, m	3, m, IR
A4	50-90	A-S	10YR 4/1	1, f, sbk	L, L, so, po, NC	2, co	2, m, IR
R							
Profile S2 - Aridic Haplustepts/ NEOSSOLO REGOLÍTICO Distrófico fragmentário organossólico fragipânico							
A1	0-5	G-S	5YR 2/2	2, m, gr	S, VFR, so, po, NC	3, f	2, f, VE
A2	5-35	C-S	2.5Y 2/2	1, f, sbk	S, FI, so, po, NC	2, m-co	3, m, VE
ACx	35-60	A-S	5Y 5/1	0, -, sg	L, L, so, po, M	1, m	1, f, IR
R							
Profile S4 - Vermic Ustorthents/ NEOSSOLO REGOLÍTICO Distrófico saprolítico							
A1	0-8	G-S	2.5Y 4/2	0, -, gs	L, L, so, po, NC	2, f	3, m, IR
A2	8-30	C-S	7.5YR 3/2	2, f-m, sbk	S, FI, so, po, NC	2, m	3, m, VE
C	30-50	C-S	2.5YR 4/2	2, f-m, sbk	S, FI, ss, ps, NC	1, f	1, f, IG
CR	50-100	A-S	2.5YR 4/4	1, m, sbk	L, FI, ss, ps, NC	absent	1, f, IG
R							

Profile S5 – 'Vermic' Aridic Lithic Ustorthents/ NEOSSOLO LITÓLICO Eutrófico fragipânico							
A	0-8	C-S	2.5Y 3/2	1, m, gr	L, FI, so, po, NC	1, f	3, m, DT
AC	8-35	C-S	2.5Y 3/2	2, m, sbk	SH, FI, ss, ps, NC	2, f-m	2, m, VE
Cx	35-50 (45-60)	A-B	10YR 3/3	0, -, m	L, FI, ss, ps, ST	absent	1, f, IG
R							
Profile S6 – Oxic Haplustepts/ CAMBISSOLO HÁPLICO Tb Distrófico úmbrico							
A1	0-5	G-S	5Y 2.2/1	1, m, gr	HA, FI, so, ps, NC	3, f-m	3, f, DT
AB	5-40	C-S	5Y 2.5/2	1, m, gr	HA, FI, ss, ps, NC	3, m-co-vc	3, m, DT
Bi1	40-65	G-S	5Y 2.8/2	2, m, sbk	SH, VFR, s, p, NC	2, f-m	1, m, VE
Bi2	65-82	C-S	5Y 3/2	2, m, sbk	SH, FI, s, ps, NC	3, f-m-co	3, m, VE
BC	82-92	C-S	2.5Y 4/4	1, f, sbk	S, FI, so, ps, NC	3, f-m	1, m, TU
C	92-105	C-S	2.5Y 4/4	1, f, sbk	S, FI, so, ps, NC	1, f	1, f, IR
Cr	105-200+		2.5Y 5/4	1, f, sbk	S, FI, so, po, NC	1, co-vc	1, f, IR
Profile S7 - Vermic Ustorthents/ NEOSSOLO REGOLÍTICO Eutrófico saprolítico arênico							
A1	0-15	G-S	10YR 2/1	1, f, gr	L, L, so, po, NC	3, f-m	3, m, DT
A2	15-40	C-S	2.5Y 3/2	1, f, gr	L, L, so, po, NC	3, co-vc	3, co, DT
Cr	40-90+		2.5Y 5/6	1, f, sbk	SH, FI, so, so	absent	1, m, IG
Profile S8 - 'Vermic' Aridic Lithic Ustorthents/ NEOSSOLO LITÓLICO Húmico fragipânico êutrico							
A1	0-8	G-S	2.5Y 2/1	2, m, gr	SH, L, so, po, NC	3, f	3, m, DT
A2	8-20	G-S	2.5Y 3/2	1, m, sbk	SH, FI, so, ps, NC	3, f-m	3, m, DT
A3	20-30	C-S	2.5Y 3/3	1, co, sbk	SH, FI, ss, ps, NC	2, m-co	2, f, TU
AC	30-40	A-S	10YR 3/4	0, -, m	SH, FI, so, po, M	absent	1, f, IG
R							
Non-peripheral soils of slags							
Profile S3 - 'Fragipan' Lithic Ustorthents/ NEOSSOLO LITÓLICO Eutrófico típico							
ACx	0-20	A-S	2.5Y 4/2	0, -, sg	L, FI, so, po, ST	absent	1, f, IR

R							
Profile S9 - Lithic RhodustalFs/ LUVISSOLO CRÔMICO Órtico vertissólico							
A	0-10	C-S	2.5YR 2.3/4	3, f, gr	S, FI, so, p, NC	absent	1, m, VE
Bt	10-40	C-S	2.5YR 2.8/4	3, co, abk	HA, FI, s, p, NC	1, m	1, f, VE
Btss	40-45	A-S	2.5YR 3/4	3, m, pr	EH, EF, vs, vp, NC	absent	1, f, VE
R							

184 Distinctness: A=abrupt, C=Clear, G=gradual. Topography: B=broken, S=smooth. Structure: Grade: 0=structureless, 1=weak, 2=moderate,
 185 3=strong. Size: co=coarse, f=fine, m=medium. Type: gr=granular, m=massive, sbk= subangular block, sg=single grain. /=principal structure
 186 parting to secondary one. Consistence: Dry: EH=extreme hard, EF=extreme firm, HA=hard, L= loose, S=soft, SH=slightly hard. Moist: FI=
 187 friable, L=loose, VRF=very friable, SH=slightly hard. Wetter: s=moderately sticky, so=nonsticky, ss= slightly sticky, p=moderately plastic,
 188 po=nonplastic, ps= slightly plastic. Cementation: M=moderately cemented, NC= non-cemented, ST=strong cemented. Roots and pores: 1= few,
 189 2= common, 3=many, co=coarse, f=fine, m= medium, vc=very coarse, vf=very fine, DT=dendritic tubular, IG=irregular, IR=interstitial,
 190 TU=tubular, VE=vesicular.

Fragipan and fragic soil properties were observed in four soil profiles. Roots are denser in shallow layers and its growing are limited by lithic contact or fragipan. Medium and coarse roots occur below 30 cm of depth.

The soil color ranged from dark olive gray in cambic horizon to dark gray in umbric epipedon. Mollic and umbric epipedons described in slags peripheral soil profiles indicates paludization and melanization. Organic horizons described according to Brazilian Soil Classification System were presented as mineral horizons due to the higher limit of organic carbon in the Soil Taxonomy's definition of organic soil material.

Texture is dominantly sandy loam and a slightly increase of clay content in deeper horizons is observed (Table 4). Feldspars were identified in the field as the main component of coarse fraction in all soils. Coarse sand is the main fraction of soil, once its mean content is 50 %. The deepest soil, Oxic Haplustepts, presented mean clay content until 2.4 times higher than the other soils.

Table 4. Physical soil properties.

Horizon	Depth	Coarse sand	Fine sand	Silt	Clay	Texture
	cm	----- % -----				
Slags peripheral soil profiles						
Profile S1 - 'Vermic' Aridic Ustorthents/ NEOSSOLO REGOLÍTICO Húmico léptico êutríco						
A1	0-5	82.9	7.3	1.1	8.7	gravelly sand
A2	5-25	59.5	19.9	7.3	13.2	gravelly sandy loam
A3	25-50	43.6	27.1	11.5	17.9	gravelly sandy loam
A4	50-90	55.7	15.5	13.0	15.9	gravelly sandy loam
R						
Profile S2 - Aridic Haplustepts/ NEOSSOLO REGOLÍTICO Distrófico fragmentário organossólico fragipânico						
A1	0-5	53.8	17.1	12.1	17.0	gravelly sandy loam
A2	5-35	71.0	13.1	7.3	8.6	gravelly loamy sand
ACx	35-60	72.4	10.2	9.2	8.2	gravelly loamy sand
R						
Profile S4 - Vermic Ustorthents/ NEOSSOLO REGOLÍTICO Distrófico saprolítico						
A1	0-8	55.3	21.2	10.6	12.9	gravelly sandy loam
A2	8-30	52.5	21.0	10.5	16.0	gravelly sandy loam
C	30-50	44.6	20.1	10.7	24.5	sandy clay loam
CR	50-100	46.9	13.3	14.8	25.0	sandy clay loam
R						
Profile S5 - 'Vermic' Aridic Lithic Ustorthents/ NEOSSOLO LITÓLICO Eutrófico fragipânico						
A	0-8	44.2	26.4	14.9	14.6	gravelly sandy loam
AC	8-35	42.4	23.5	16.3	17.8	gravelly sandy loam
CR	35-60	50.8	15.8	13.5	19.9	gravelly sandy loam
R						

Profile S6 - Oxic Haplusteps/ CAMBISSOLO HÁPLICO Tb Distrófico úmbrico						
A1	0-5	41.6	21.4	15.7	21.2	sandy clay loam
BA	5-40	38.8	22.4	15.3	23.4	sandy clay loam
Bi1	40-65	37.7	18.7	13.9	29.7	sandy clay loam
Bi2	65-82	39.3	14.8	19.1	26.8	sandy clay loam
Bi3	82-92	44.0	15.7	14.6	25.8	sandy clay loam
BC	92-105	48.8	16.6	13.2	21.5	sandy clay loam
CR	105-200+	55.5	13.7	13.2	17.6	sandy loam
Profile S7 - Vermic Ustorthents/ NEOSSOLO REGOLÍTICO Eutrófico saprolítico arênico						
A	0-15	54.7	20.6	9.4	15.3	gravelly sandy loam
AC	15-40	54.9	27.9	6.0	11.3	gravelly loamy sand
CR	40-90+	51.0	21.8	14.5	12.7	gravelly sandy loam
Profile S8 - 'Vermic' Aridic Lithic Ustorthents/ NEOSSOLO LITÓLICO Húmico fragipânico êutrico						
A	0-8	41.6	24.6	12.8	21.0	gravelly sandy clay loam
AC1	8-20	34.9	29.8	14.7	20.6	gravelly sandy clay loam
AC2	20-30	35.8	29.5	10.8	23.9	gravelly sandy clay loam
CR	30-40	38.8	28.2	16.8	16.3	gravelly sandy clay loam
Mean-CV		49.75-23	19.90-30	12.24-31	18.11-32	-
Non-peripheral soils of slags						
Profile S3 - 'Fragipan' Lithic Ustorthents/ NEOSSOLO LITÓLICO Eutrófico típico						
AC	0-20	53.1	20.3	16.8	9.8	gravelly sandy loam
R						
Profile S9 - Lithic Rhodustalfs/ LUVISSOLO CRÔMICO Órtico vertissólico						
A	0-10	26.4	27.6	21.5	24.6	gravelly sandy clay loam
AB	10-40	33.3	19.7	19.6	27.4	sandy clay loam
Btss	40-45+	23.8	12.9	20.0	43.3	Clay
R						

206

Mean-CV	-	34.15-39	20.12-30	19.47-10	26.28-52	-

207   The pedons are strongly acid to neutral and have base saturation (V) above 50 %
 208   in all horizons, except Oxic Haplustepts (Table 5). $\text{Ca}^{2+} > \text{Mg}^{2+} > \text{K}^+ > \text{Na}^+$ is the base
 209   dominance in the exchange complex. High variation of Mehlich-1 extractable P contents
 210   (P_M), sum of bases (SB), cation exchange capacity (ECEC and CEC), aluminum
 211   saturation (m), sodium saturation (ISNA), total organic carbon (C), total nitrogen (N)
 212   and carbon to nitrogen ratio (C/N) were detected. KCl pH is equal or below 5.0 and
 213   delta pH is negative in all horizons, indicating that, even the pedons with the lowest
 214   total organic carbon content, have dominance of negative charges.

Table 5. Chemical soil properties of massive influenced and non-influenced soils.

Hori zon	Dept h	H ₂ O pH	KCl pH	ΔpH	P _M	K ⁺	Na ⁺	Ca ²⁺ +	Mg 2+	Al ³⁺ +	H ⁺ Al	SB	EC EC	CE C	V	m	ISN a	C	N	C/N	P _{RE} M	
	cm				----- mg dm ⁻³ -- ----			----- cmolc dm ⁻³ ----- -----						----- % ----- -----					mg L ⁻¹			
					Slags peripheral soil profiles																	
Profile S1 - 'Vermic' Aridic Ustorthents/ NEOSSOLO REGOLÍTICO Húmico léptico êutrico																						
A1	0-5	5.94	5.16	- 0.78	24.1	129	8.3	3.3	0.7	0.0	1.4	4.4	4.42	5.82	76	0	0.62	1.07	0.06	17.8	50.0	
A2	5-25	5.42	4.41	- 1.01	12.4	147	12.4	3.9	0.7	0.0	4.2	5.1	5.08	9.28	55	0	0.58	3.06	0.16	19.1	43.4	
A3	25- 50	5.24	4.27	- 0.97	6.6	103	14.4	4.3	0.7	0.1	5.0	5.3	5.42	10.3 2	52	2	0.61	3.06	0.16	19.1	39.0	
A4	50- 90	5.02	4.02	- 1.00	7.5	71	14.4	2.8	0.4	0.6	5.0	3.5	4.05	8.48	41	14	0.74	1.72	0.13	13.2	34.7	
R																						
Profile S2 - Aridic Haplustepts/ NEOSSOLO REGOLÍTICO Distrófico fragmentário organossólico fragipânico																						
A1	0-5	5.65	4.77	- 0.88	31.2	103	26.5	7.0	1.6	0.0	6.4	8.9	8.9	15.3	58	0	0.75	8.41	0.33	25.5	44.2	
A2	5-35	4.94	3.91	- 1.03	21.9	61	16.4	2.1	0.6	0.9	4.6	2.9	3.79	7.53	39	23	0.95	1.22	0.07	17.4	37.0	
ACx	35- 60	5.02	3.95	- 1.07	25.0	55	10.4	1.7	0.5	0.8	4.2	2.3	3.1	6.54	36	25	0.69	0.96	0.04	24.0	33.1	
R																						
Profile S4 - Vermic Ustorthents/ NEOSSOLO REGOLÍTICO Distrófico saprolítico																						
A1	0-8	5.1	4.29	- 0.81	17.4	129	20.4	4.3	1.5	0.2	5.3	6.2	6.41	11.5 2	54	3	0.77	3.06	0.16	19.1	41.8	
A2	8-30	4.59	3.72	-	3.8	41	4.3	1.1	0.2	2.1	5.7	1.5	3.56	7.16	21	59	0.26	0.92	0.06	15.3	23.8	

				0.87																	
C	30-50	4.6	3.66	- 0.94	1.5	21	10.4	1.0	0.2	3.0	5.5	1.3	4.21	6.76	19	70	0.67	0.38	0.06	6.3	20.9
CR	50-100	5.06	3.56	- 1.50	0.6	11	28.5	1.8	0.2	2.6	3.8	2.2	4.75	5.98	37	54	2.07	0.23	0.03	7.7	23.9
R																					
Profile S5 - 'Vermic' Aridic Lithic Ustorthents/ NEOSSOLO LITÓLICO Eutrófico fragipânico																					
A	0-8	5.95	5.22	- 0.73	9.5	215	18.4	7.0	1.8	0	2	9.5	9.47	11.4 7	83	0	0.70	2.29	0.17	13.5	42.2
AC	8-35	5.17	3.84	- 1.33	2.4	55	34.5	3.2	1.7	0.7	3.1	5.2	5.83	8.26	63	12	1.82	0.77	0.07	11.0	40.1
Cx	35-60	5.28	3.73	- 1.55	1.6	23	46.6	2.7	3.4	0.7	2.5	6.4	7.05	8.88	72	10	2.28	0.31	0.03	10.3	39.6
R																					
Profile S6 - Oxic Haplustepts/ CAMBISSOLO HÁPLICO Tb Distrófico úmbrico																					
A	0-5	5.17	4.19	- 0.98	11.1	235	46.6	3.9	1.5	0.3	6.3	6.3	6.56	12.5 7	50	4	1.61	4.39	0.23	19.1	31.2
AB	5-40	4.63	3.77	- 0.86	2.6	69	10.4	1.2	0.3	3.1	6.8	1.7	4.87	8.53	20	65	0.53	1.91	0.14	13.6	20.9
Bi1	40-65	4.83	3.89	- 0.94	0.5	19	6.3	0.6	0.0	2.8	5.7	0.7	3.44	6.38	11	80	0.43	1.33	0.09	14.8	11.2
Bi2	65-82	4.64	4	- 0.64	0.5	17	10.4	0.7	0.0	2.0	5.0	0.8	2.77	5.77	13	72	0.78	0.92	0.09	10.2	7.5
BC	82-92	4.69	4.13	- 0.56	0.6	15	8.3	0.7	0.0	1.4	4.1	0.7	2.16	4.83	15	66	0.75	0.77	0.08	9.6	7.7
C	92-105	4.66	4.16	- 0.50	0.7	9	6.3	0.7	0.0	1.2	3.8	0.7	1.95	4.51	16	64	0.61	0.84	0.07	12.0	8.1
Cr	105-200+	5.07	4.25	- 0.82	2.8	7	14.4	0.7	0.0	1.1	3.0	0.8	1.81	3.76	20	58	1.67	0.46	0.05	9.2	9.6

Profile S7 - Vermic Ustorthents/ NEOSSOLO REGOLÍTICO Eutrófico saprolítico arênico																					
A1	0-15	5.63	4.85	- 0.78	17.8	355	58.7	4.6	2.3	0.0	3.9	8.1	8.07	11.9 7	67	0	2.13	3.44	0.21	16.4	46.8
A2	15- 40	5.17	3.9	- 1.27	3.9	225	26.5	1.1	0.9	0.6	4.1	2.7	3.23	6.76	39	18	1.70	1.15	0.07	16.4	47.3
Cr	40- 90+	5.06	3.74	- 1.32	0.8	245	44.6	0.7	1.0	0.9	3.0	2.5	3.31	5.45	45	26	3.56	0.69	0.03	23.0	43.8
Profile S8 - 'Vermic' Aridic Lithic Ustorthents/ NEOSSOLO LITÓLICO Húmico fragipânico eútrico																					
A1	0-8	6.02	5.33	- 0.69	17.2	355	70.8	9.4	3.3	0	3.3	13.9	13.9	17.2	81	0	1.79	6.11	0.30	20.4	44.8
A2	8-20	5.09	3.85	- 1.24	2.6	235	119. 1	2.7	2.3	0.4	4.7	6.1	6.47	10.7 9	56	6	4.80	1.83	0.11	16.6	43.9
A3	20- 30	5.02	3.61	- 1.41	1.7	189	191. 7	2.0	2.3	1.1	4.2	5.5	6.59	9.74	57	16	8.56	1.30	0.08	16.3	37.0
AC	30- 40	5.02	3.45	- 1.57	1.7	119	283. 5	1.5	1.9	1.1	4.1	4.9	5.99	8.95	54	19	13.7 7	0.99	0.07	14.1 a	39.2
R																					
Mean		5.13	4.12	- 1.00	8.2-	116	41.6	2.7-	1.1	1.0	4.3	4.3-	5.2-	8.58	45-	27-	2.01	1.91	0.11	15.4	33.6
-CV	-	-8	-12	-29	110	-89	-149	81	-94	-98	-31	75	50	-37	48	102	-142	-97	-70	-32	-42
Non-peripheral soils of slags																					
Profile S3 - 'Fragipan' Lithic Ustorthents/ NEOSSOLO LITÓLICO Eutrófico típico																					
ACx	0-20	6.23	5.19	- 1.04	19	355	28.5	4.2	1.3	0.0	0.9	6.5	6.49	7.39	88	0	1.68	0.53	0.06	8.8	50.7
R																					
Profile S9 - Lithic RhodustalFs/ LUVISSOLO CRÔMICO Órtico vertissólico																					
A	0-10	6.31	4.67	- 1.64	9.6	169	20.4	12.9	4.2	0.0	1.1	17.7	17.6 5	18.7 5	94	0	0.47	1.15	0.05	23.0	39.8
AB	8-40	6.53	4.85	-	2.0	67	64.7	19.5	5.7	0.0	0.8	25.7	25.6	26.4	97	0	1.06	0.61	0.04	15.3	37.4

				1.68									6	6							
Btss	40-45+	7.08	5	-2.08	4.3	25	253.2	25.1	13.5	0.0	0.5	39.8	39.82	40.32	99	0	2.73	0.23	0.02	11.5	41
R																					
Mean		6.54	4.93	-1.61	8.7-	154	91.7	15.4	6.2	0.0	0.8	22.4	22.4	23.2	95-		1.49	0.63	0.04	14.7	42.2
-CV	-	-6	-5	-27	87	-95	-119	-58	-84	-0	-30	-63	-63	-59	5	0-0	-65	-40	-40	-42	-14

Remaining P (P_{REM}) is dominantly above 30 mg L⁻¹ and low variable. The higher the value of P_{REM} , the lower is the affinity of soils for the P in the solution. High values of P_{REM} in all pedons, except by Oxic Haplustepts, indicates mineralogy dominantly silicate, and that iron oxides formation and brunification are limited.

Total organic carbon, N and C/N decrease with increase of depth. The C content in the upper horizon ranged between 3.6 ± 2.5 % (peripheral slags pedons) and 0.8 ± 0.4% (non-peripheral pedons of slags). In the 10–40 cm increment, the C content ranged from 1.8 ± 0.9% (peripheral slags pedons) to 0.4 ± 2.5% (non-peripheral pedons of slags). The mean C/N in the uppermost horizons ranges between 16.5 ± 3.7 (peripheral slags pedons) and 15.9 ± 10.0 (non-peripheral pedons of slags). In the 10–40 cm increment, the values ranged between 16.1 ± 0.04 (peripheral slags pedons) and 13.4 ± 13.8 (non-peripheral pedons of slags). Low correlation coefficient values indicated that P_{M} , SB, CEC and V are poorly correlated to C, N and C/N (Fig 3).

Fig 3. Correlation matrix between soil properties.

Both peripheral and non-peripheral soils of slags presented median values of particle density close to density of quartz (2.5-2.8 kg dm⁻³) (Table 6). Peripheral and non-peripheral soils of slags have median values of bulk density categorized as humic and sandy soils, respectively. Total porosity, macroposity, total organic carbon stock and total nitrogen stock in non-peripheral soils of slags are 16 %, 30 %, 69 % and 40 % lower compared to peripheral slags soils, respectively.

240 **Table 6. Physical soil properties determined by undisturbed samples and total organic carbon and total nitrogen stocks.**

Horizon	Depth	Particle density	Soil density	Total porosity	Micropores	Macropores	Stock (Mg ha ⁻¹)	
	(cm)	----- kg dm ³ -----		----- % -----			C	N
Peripheral soil of slags								
Profile 1 - 'Vermic' Aridic Ustorthents/ NEOSSOLO REGOLÍTICO Húmico léptico êutrico								
A1	0-5	2.62	1.15	0.56	0.12	0.44	6.14	0.35
A2	5-25	2.52	1.09	0.57	0.14	0.43	66.64	0.87
Profile 2 - Aridic Haplustepts/ NEOSSOLO REGOLÍTICO Distrófico fragmentário organossólico fragipânico								
A1	0-5	2.25	0.82	0.64	0.34	0.30	34.46	1.35
A2	5-35	2.62	1.36	0.48	0.11	0.37	49.94	2.86
Profile 4 - Vermic Ustorthents/ NEOSSOLO REGOLÍTICO Distrófico saprolítico								
A1	0-8	2.60	1.27	0.51	0.20	0.31	31.06	1.63
A2	8-30	2.56	1.08	0.58	0.21	0.37	21.78	1.43
Profile 5 - 'Vermic' Aridic Lithic Ustorthents/ NEOSSOLO LITÓLICO Eutrófico fragipânico								
A	0-8	2.62	1.35	0.48	0.20	0.28	24.75	1.83
AC	8-35	2.65	1.24	0.53	0.21	0.33	25.63	2.34
Profile 6 - Oxic Haplustepts/ CAMBISSOLO HÁPLICO Tb Distrófico úmbrico								
A	0-5	2.27	0.87	0.61	0.24	0.37	19.10	1.00
AB	5-40	2.50	0.90	0.64	0.19	0.45	60.11	4.41
Profile 7 - Vermic Ustorthents/ NEOSSOLO REGOLÍTICO Eutrófico saprolítico arênico								
A1	0-15	2.51	1.14	0.55	0.19	0.36	58.92	3.59
A2	15-40	2.47	1.01	0.59	0.11	0.48	28.99	1.77
Profile 8 - 'Vermic' Aridic Lithic Ustorthents/ NEOSSOLO LITÓLICO Húmico fragipânico êutrico								
A1	0-8	2.51	1.22	0.51	0.24	0.27	59.67	2.93
A2	8-20	2.62	1.08	0.59	0.20	0.39	23.75	1.42
Mean-CV		2.54-5	1.12-15	0.57-9	0.20-32	0.37-18	37.32-50	1.98-57

Non-peripheral soils of slags								
Profile 3 - 'Fragipan' Lithic Ustorthents/ NEOSSOLO LITÓLICO Eutrófico típico								
ACx	0 - 20	2.69	1.42	0.47	0.23	0.25	15.16	1.70
Profile 9 - Lithic Rhodustalfs/ LUVISSOLO CRÔMICO Órtico vertissólico								
A	0-10	2.64	1.34	0.49	0.22	0.27	15.39	0.67
Mean-CV		2.67-1	1.38-4	0.48-3	0.23-3	0.26-5	15.28-1	1.19-62

Two main components (PCs) presented eigenvalues above 1.0, and together they explained 72.3 % of the variance (Fig 4). Component 3 and higher had eigenvalues below 1.0 and hardly explained the variance better than the original variables (1/12 = 8.3 %), so they were excluded from subsequent analyzes [35,37].

Fig 4. Eigenvalues of correlation matrix and explained variance per PC (A). Projection of the variables on factor plane PC1 × PC2 (B).

The first component (PC1) explained 44.6 % of the total data variance. PC1 presented high negative charge of Al^{3+} and positive charges of P_M , C, N, C/N, and P_{REM} (Fig 4). The second component (PC2) accounted for 27.7 % of the total variance and presented large loads of CEC, coarse and fine sand, clay, silt contents. The antagonism between clay, silt, coarse and fine sand shown by PC2 could be associated to weathering process.

Discussion

Abundance of weatherable minerals in the coarse fraction, a sandy loam texture, shallow soils, high base saturation and fragipan indicates an incipient stage of pedogenesis compared to other biomes (Tables 4 and 5). Widespread occurrence of fragipan is attributed to the restricted removal of silica in semiarid climate, which favors fragipan formation in deeper horizons [38,39]. Low sodium saturation (ISNA) indicates that salinization and sodification did not occur in minimally disturbed areas, even in the driest region of Brazil.

Poorly known, soils in caatinga are described as monotonous and low variable [40]. However, differences between peripheral slags and non-peripheral slags soils in semiarid climate are notable. Soils in the periphery of slags are deeper, has a higher

number of horizons, has aggregates more developed, has lower chroma and values in topsoil, has higher total organic carbon and total nitrogen contents, and are more porous. Low value and chroma in peripheral slags soils is attributed to a higher supply of organic matter, probably related to the denser vegetation cover, higher C and N contents and C/N. These soils also presented granular structure, with larger and more frequently pores derived from intense fauna activity [41,42]. In tropical wet areas, bioturbation is related to well-structured soils through the increase of clay, carbon and nutrient contents and soil porosity [43–46].

Notification of Bi horizon is unexpected to Brazilian semiarid climate, once Inceptols are rare in soil maps [47,48]. A harder, firmer, more sticky and plastic consistence indicates more developed horizons. Development of Inceptsol seems to be drastically related to local geomorphology, once it covers a concave depression which accumulates water and sediments percolated on slags.

The absence of coatings in the argic horizon of Lithic Rhodustalfs can be attributed to neoformation of clays or elutriation, despite eluviation [49]. The eluviation can be defined as the translocation of soil particles from surface to deeper horizons. Once eluviation depends on vertical water movement, it occurs when precipitation exceeds evaporation. Occurrence of slickensides in the argic horizon indicate marked changes in moisture content [50].

Total porosity is composed by macro and microporosity. Micropores are formed by congruent dissolution of minerals and soil biota and are usually found within structural aggregates. The water within these pores is considered immobile, but available for plant extraction. So, these smaller pores are important to retain water required for plant during dry season. The lower values of microporosity in peripheral soils of slags suggest that the high vegetable cover explores water from other sources, as

litter [51] or atmosphere [52]. On the other hand, macroporosity is a highly dynamic soil property once it is influenced by environmental factors, as roots, soil biota and raindrop impact, wetting-drying cycles and human activities [53–55]. Low difference between macroporosity of surface horizon and its underlying guarantees water stocking by vertical water flux from surface to deeper horizons. The high density of roots close to lithic contact and fragipan suggests that water did not percolate below the active root zone by the force of gravity. Furthermore, sandy loam texture dominance reduces loss of water by capillarity-evaporation from soil surfaces [56].

Mean total organic carbon (C) is below other Brazilian biomes [57–60] and mean C/N is until 1.7 times lower than Amazonian rainforest [61]. The amount of C is determined by the net balance between the rate of input as leaf and root biomass and its mineralization. Soil structure is a key element in C dynamic. The increase of silt and clay contents during weathering, and its organization in aggregates, protects organic carbon from oxidation [62,63]. In dry tropical climates, carbon stock in the upper-most 30 cm of mineral soils estimate ranges from 31 Mg C ha⁻¹ in sandy soils to 38 Mg C ha⁻¹ in high activity clay soils [64]. However, the weak correlation between texture and C (Fig 3) suggest that stabilization of organic matter by the formation of stable complexes with clay minerals did not occurs or it is underestimated due to sand dominance.

Weak correlation between total organic carbon and CEC or base saturation indicates that soil fertility is not associated to total organic matter and, possibly related to parent material. This result indicates that paludization is incapable to influence geochemical processes in caatinga, in opposite to other biomes [65–68].

C/N also determines total organic matter decomposition. A decrease in C/N simultaneous to the proportion of stabilized organic carbon compounds has been shown in several studies [69–71]. Strong positive correlation between C/N and C indicates that

the organic carbon is stocked in less favorable conditions for microbial activity. Higher total organic carbon in peripheral slags soils highlights massive as crucial areas for the management of C sequestration in Caatinga.

The mean total organic carbon stock was 35 % higher than previously studies in Caatinga [72]. Soil organic carbon stock is commonly related to clay content and altitude [72], water availability and soil organic matter content in Caatinga [73]. Here, we observed that local geomorphology is more important to carbon sequestration in Caatinga, once massive influenced areas are larger than highlands. In opposite to previous studies [74], we did not observed a predominant decrease of total organic carbon and total nitrogen stocks with increasing of depth. This result can be attributed to several causes: a) total organic carbon and nitrogen are higher in denser vegetable cover V.P.; b) total organic carbon content is defined by an equilibrium between the low organic residue inputs [75] and high C/N values (Table 5); c) virtual absence of clay-organic complexes evidenced by low correlation between clay content and soil organic carbon (Fig 3); d) absence of eluviation evidences suggest that organic complexes are not transported by water vertical movement (Table 3).

Low similarity of plant communities between plots on peripheral areas of slags and plots on a flat plain (Fig 2) suggest that soil is the main limiting factor for phytogeographical patterns [76–79]. High tree species richness can be related to low levels of physiological stress, product of sites with high soil fertility [10,80]. Previous studies suggested that the same pattern in Caatinga [81], however the relative low coefficient of variation of base saturation suggest that shrub-arboreal diversity and abundance could be related to other soil properties.

The higher number of specimens in slags peripheral soils (S1 Table), especially of these species documented in (sub)humid biomes, is attributed to increase of water

retention due to high soil organic carbon, a valuable resource in xeric shrubland. Root depth in massive influenced pedons were higher than previously studies in Caatinga soils [82]. So, we believe that trees exploit a larger volume in peripheral slags soils, which guarantees them mechanisms of resistance to the climatic seasonality and consequently diversify the environments [83]. Although the proportion of humin, fluvic acids and humic acids influence the relation between water retention and soil organic matter content, a 1 % mass increase in soil organic matter content, on average, increases water content at saturation, field capacity, wilting point and available water capacity by: 2.95, 1.61, 0.17 and 1.16 mm H₂O 100 mm soil⁻¹, respectively [84]. The increase is larger in sandy soils, followed by loams and is least in clays [85].

These narrow areas around the slabs present floristic similarities with some tropical forests existing in highlands environments in the Brazilian semiarid [24,86]. This study reveals that cover of plant species considered exclusive of (sub)humid biomes in Brazil extends beyond highlands in the semiarid, associated with the high soil organic carbon content and water retention capacity of more developed soils than the typical of the Caatinga. These results corroborate the hypothesis that diversification of niches favors increase of plant species diversity in tropics [87].

However, if maintenance of this pedological and botanical conditions in a predominantly semiarid climate seems reasonably deciphered, questions arise about how high water-demand species reached semiarid regions. We believe that vegetable cover in areas influenced by slags and massives in the Caatinga are testimony to an old existing vegetable cover, inherited from a more humid past climate, and confined to refuges with the establishment of the current semiarid climate. Such vegetable cover would have existed between Late Miocene and Early Pleistocene, uniting the current Amazon, Atlantic and Caatinga biomes [6,88–92]. European colonization in the

sixteenth century and the advance of deforestation since then also could have contributed to the fragmentation of refugees [93].

Peripheral areas of slags are important today and can be decisive in future. Eighty percent of total transpiration in Caatinga is controlled by top layers of soil (0 – 20 cm) [94]. According to prevision of a rise in temperature between 0.5 and 4° C and a reduction of precipitation of 10–20 % for the Brazilian Northeast region by 2,100 [95] the Caatinga biome may become completely soil-water pulse dominated. Consequently, soil organic carbon stock also could be reduced by decrease of organic residue input. Future studies should investigate biotic responses from these refuges to climate changes [96].

Conclusions

Despite the semiarid surrounding context, pedogenetic processes typical of tropical wet conditions, such as paludization, melanization and bioturbation were verified in slags peripheral areas. Well-developed soils with high soil organic matter and water holding capacity support semi-deciduous forests of (sub)humid biomes. These areas constitute a refuge for several plant species that cannot develop on the typical soils of the semiarid. Furthermore, future vegetation surveys should focus different habitats to expand plant diversity knowledge of the Caatinga.

Carbon stock data is rare and soil diversity is poorly known in Caatinga. Further research could increase estimates of semiarid soil carbon stocks by 37 to 69 %, helping to reduce uncertainty about the global carbon budget. Our findings could also lead to the development of innovative conservation and land restoration actions in dryland biomes regions with low opportunity cost to mitigate climate change, combat desertification,

and support conservation of biodiversity and ecosystem services that underpin human livelihoods.

References

1. Bastin J, Berrahmouni N, Grainger A, Maniatis D, Mollicone D, Moore R, et al. The extent of forest in dryland biomes. *Science* (80-). 2017;638: 1–5. Available: <http://science.sciencemag.org/content/sci/356/6338/635.full.pdf>
2. Silva JMC da, Barbosa LCF, Leal IR, Tabarelli M. The Caatinga: Understanding the Challenges. *Caatinga*. Cham: Springer International Publishing; 2017. pp. 3–19. doi:10.1007/978-3-319-68339-3_1
3. MMA. Análise das variações da biodiversidade do bioma Caatinga: suporte a estratégias regionais de conservação. Araújo FS, Rodal MJN, Barbosa MR V, editors. Brasília: Ministério do Meio Ambiente; 2005.
4. Caetano S, Prado D, Pennington RT, Beck S, Oliveira-Filho A, Spichiger R, et al. The history of Seasonally Dry Tropical Forests in eastern South America: inferences from the genetic structure of the tree *Astronium urundeuva* (Anacardiaceae). *Mol Ecol*. 2008;17: 3147–3159. doi:10.1111/j.1365-294X.2008.03817.x
5. Pennington RT, Ratter J. An Overview of the Plant Diversity, Biogeography and Conservation of Neotropical Savannas and Seasonally Dry Forests. In: Pennington RT, Lewis GP, Ratter J, editors. *Neotropical Savannas and Dry Forests: plant diversity, biogeography and conservation*. CRC Press; 2006. pp. 1–29. doi:10.1201/9781420004496.ch1
6. Maia RP, Nascimento MAL. Relevos graníticos do Nordeste brasileiro. *Rev Bras Geomorfol*. 2018;19: 373–389. doi:10.20502/rbg.v19i2.1295

- 416 7. Araújo Filho JC, Ribeiro MR, Burgos N, Marques FA. Solos da Caatinga. In:
- 417 Curi N, Ker JC, Novais RF, Vidal-Torrado P, Schaefer CEGR, editors. Pedologia
- 418 - Solos dos Biomas Brasileiros. Viçosa-MG: Sociedade Brasileira de Ciência do
- 419 Solo; 2017. pp. 227–260.
- 420 8. Arruda DM, Fernandes-Filho EI, Solar RRC, Schaefer CEGR. Combining
- 421 climatic and soil properties better predicts covers of Brazilian biomes. Sci Nat.
- 422 The Science of Nature; 2017;104. doi:10.1007/s00114-017-1456-6
- 423 9. Rodrigues PMS, Schaefer CEGR, Silva J de O, Ferreira Júnior WG, dos Santos
- 424 RM, Neri AV. The influence of soil on vegetation structure and plant diversity in
- 425 different tropical savannic and forest habitats. J Plant Ecol. 2016;11: 226–236.
- 426 doi:10.1093/jpe/rtw135
- 427 10. Neri A V., Schaefer CEGR, Souza AL, Ferreira-Junior WG, Meira-Neto JAA.
- 428 Pedology and plant physiognomies in the cerrado, Brazil. An Acad Bras Cienc.
- 429 2013;85: 87–102. doi:10.1590/S0001-37652013000100007
- 430 11. Magnago LFS, Martins S V, Schaefer CEGR, Neri A V. Restinga forests of the
- 431 Brazilian coast: richness and abundance of tree species on different soils. An
- 432 Acad Bras Cienc. 2012;84: 807–22. doi:10.1590/S0001-37652012000300023
- 433 12. Hoorn C, Wesselingh FP, ter Steege H, Bermudez MA, Mora A, Sevink J, et al.
- 434 Amazonia Through Time: Andean Uplift, Climate Change, Landscape Evolution,
- 435 and Biodiversity. Science (80-). 2010;330: 927–931.
- 436 doi:10.1126/science.1194585
- 437 13. de Souza JJLL, Paulo M, Fontes F, Gilkes R, da Costa LM, de Oliveira TS.
- 438 Geochemical Signature of Amazon Tropical Rainforest Soils. Rev Bras Ciência
- 439 do Solo. 2018; 1–18. doi:https://doi.org/10.1590/18069657rbc20170192
- 440 14. Poelking EL, Schaefer CER, Fernandes Filho EI, De Andrade AM, Spielmann

- AA. Soil-landform-plant-community relationships of a periglacial landscape on Potter Peninsula, maritime Antarctica. *Solid Earth*. 2015;6: 583–594.
doi:10.5194/se-6-583-2015
15. Allié E, Pélissier R, Engel J, Petronelli P, Freycon V, Deblauwe V, et al. Pervasive local-scale tree-soil habitat association in a tropical forest community. *PLoS One*. 2015;10: 1–16. doi:10.1371/journal.pone.0141488
16. Jones MM, Ruokolainen K, Martinez NCL, Tuomisto H. Differences in topographic and soil habitat specialization between trees and two understorey plant groups in a Costa Rican lowland rain forest. *J Trop Ecol*. 2016;32: 482–497. doi:10.1017/S0266467416000419
17. Santos JC, Leal IR, Almeida-Cortez JS, Fernandes GW, Tabarelli M. Caatinga: The Scientific Negligence Experienced by a Dry Tropical Forest. *Trop Conserv Sci*. 2011;4: 276–286. doi:10.1177/194008291100400306
18. Lopes S de F, Ramos MB, Almeida GR de. The Role of Mountains as Refugia for Biodiversity in Brazilian Caatinga. *Trop Conserv Sci*. 2017;10: 194008291770265. doi:10.1177/1940082917702651
19. Barbosa WR, Romero RE, de Souza Júnior VS, Cooper M, Sartor LR, de Moya Partiti CS, et al. Effects of slope orientation on pedogenesis of altimontane soils from the Brazilian semi-arid region (Baturité massif, Ceará). *Environ Earth Sci*. 2015;73: 3731–3743. doi:10.1007/s12665-014-3660-4
20. da Silva FKG, de Faria Lopes S, Lopez LCS, de Melo JIM, de Brito Melo Trovão DM. Patterns of species richness and conservation in the Caatinga along elevational gradients in a semiarid ecosystem. *J Arid Environ*. 2014;110: 47–52. doi:10.1016/j.jaridenv.2014.05.011
21. Kayano MT, Andreoli R V. Clima da Região Nordeste do Brasil. In: Cavalcanti

- 466 IF, Ferreira NJ, Silva MGAJ, Dias MAFS, editors. Tempo e clima no Brasil. São
467 Paulo: Oficina de textos; 2009. pp. 213–234.
- 468 22. do Nascimento MAL, Galindo AC, de Medeiros VC. Ediacaran to Cambrian
469 magmatic suites in the Rio Grande do Norte domain, extreme Northeastern
470 Borborema Province (NE of Brazil): Current knowledge. J South Am Earth Sci.
471 Elsevier Ltd; 2015;58: 281–299. doi:10.1016/j.jsames.2014.09.008
- 472 23. EMBRAPA. Mapa de solos do Brasil [Internet]. 2011 p. 1. Available:
473 ftp://geofp.ibge.gov.br/informacoes_ambientais/pedologia/mapas/brasil/solos.pdf
474 f
- 475 24. de Queiroz LP, Cardoso D, Fernandes MF, Moro MF. Diversity and Evolution of
476 Flowering Plants of the Caatinga Domain. Caatinga. Cham: Springer
477 International Publishing; 2017. pp. 23–63. doi:10.1007/978-3-319-68339-3_2
- 478 25. Cámara R, Díaz del Olmo F. Directrices y Gestión para la Conservación y
479 Desarrollo Integral de un Humedal Centroamericano: Golfo de Montijo (Litoral
480 del Pacífico, Panamá). Panamá: Embajada de España en Panamá; 2004.
- 481 26. Souza BI, Artigas RC, Lima ERV de. the Caatinga and desertification. Mercator.
482 2015;14: 131–150. doi:10.4215/RM2015.1401.0009
- 483 27. da Silva LAE, De Fraga CN, De Almeida TMH, Gonzalez M, Lima RO, Da
484 Rocha MS, et al. Jabot - Sistema de gerenciamento de Coleções Botânicas: A
485 experiência de uma década de desenvolvimento e avanços. Rodriguesia. 2017;68:
486 391–410. doi:10.1590/2175-7860201768208
- 487 28. APG. An update of the Angiosperm Phylogeny Group classification for the
488 orders and families of flowering plants. Bot J Linn Soc. 2016;181: 1–20.
489 doi:10.1111/boj.12385
- 490 29. Hammer Ø, Harper DAT a. T, Ryan PD. PAST: Paleontological Statistics

- 491 Software Package for Education and Data Analysis. *Palaeontol Electron*.
492 2001;4(1): 1–9. doi:10.1016/j.bcp.2008.05.025
- 493 30. Santos HGS, Jacomine PK, Anjos LHC, Oliveira VA, Lumbrreras JF, Coelho
494 MR, et al. Sistema brasileiro de classificação de solos. Rio de Janeiro: Embrapa
495 Solos. Embrapa; 2013. doi:ISBN 978-85-7035-198-2
- 496 31. Ribeiro K, Sousa-Neto ER de, Carvalho JA de, Sousa Lima JR de, Menezes RSC,
497 Duarte-Neto PJ, et al. Land cover changes and greenhouse gas emissions in two
498 different soil covers in the Brazilian Caatinga. *Sci Total Environ*. Elsevier B.V.;
499 2016;571: 1048–1057. doi:10.1016/j.scitotenv.2016.07.095
- 500 32. Donagema GK, Campos DVB de, Calderano SB, Teixeira WG, Viana JHM.
501 Manual de métodos de análise de solos. 2nd ed. Rio de Janeiro: Embrapa Solos;
502 2011.
- 503 33. Yeomans JC, Bremner JM. A rapid and precise method for routine determination
504 of organic carbon in soil 1. *Commun Soil Sci Plant Anal*. 1988;19: 1467–1476.
505 doi:10.1080/00103628809368027
- 506 34. EMBRAPA. Manual de métodos de análises de solos. Embrapa; 1997.
- 507 35. Wackernagel H. *Multivariate Geostatistics: An Introduction with Applications*.
508 3rd ed. Springer -Verlag Berlin Heidelberg; 2003.
- 509 36. Moro MF, Martins FR. Métodos de levantamento do componente arbóreo-
510 arbustivo. In: Felfili JM, Eisenlohr P V, Melo MMRF, Andrade LA, Meira Neto
511 JAA, editors. *Fitossociologia no Brasil: métodos e estudos de casos*. Viçosa-MG:
512 Editora UFV; 2011. pp. 174–212.
- 513 37. McKillup S, Dyar MD. *Geostatistics Explained: An Introductory Guide for Earth*
514 *Scientists*. Cambridge University Press; 2010.
- 515 38. Smeck NE, Ciolkosz EJ, Smeck NE, Thompson ML, Norton LD, Shipitalo MJ.

Weathering Discontinuities: A Key to Fragipan Formation. 1989.

doi:10.2136/sssaspecpub24.c6

39. Monger HC, Martinez-Rios JJ, Khresat SA. TROPICAL SOILS | Arid and Semiarid. Encyclopedia of Soils in the Environment. Elsevier; 2005. pp. 182–187. doi:10.1016/B0-12-348530-4/00021-7
40. Cunha TJF, Petrete VG, Silva DJ, Mendes AMA, Melo RF de, Oliveira Neto MB de, et al. Principais solos do Semiárido tropical brasileiro: caracterização, potencialidades, limitações, fertilidade e manejo. [Internet]. Semiárido Brasileiro: pesquisa, desenvolvimento e inovação. 2010. p. 402. Available: <http://ainfo.cnptia.embrapa.br/digital/bitstream/item/80286/1/capitulo-2-principais-solos-do-semiArido.pdf>
41. Muggler CC, Van Loef JJ, Buurman P, Van Doesburg JDJ. Mineralogical and (sub) microscopic aspects of iron oxides in polygenetic Oxisols from Minas Gerais, Brazil. Geoderma. 2001;100: 147–171. doi:10.1016/s0016-7061(00)00084-7
42. Schaefer CER. Brazilian latosols and their B horizon microstructure as long-term biotic constructs. Aust J Soil Res. 2001;39: 909–926. doi:10.1071/SR00093
43. Nascimento AF, Furquim SAC, Graham RC, Beirigo RM, Oliveira Junior JC, Couto EG, et al. Pedogenesis in a Pleistocene fluvial system of the Northern Pantanal - Brazil. Geoderma. Elsevier B.V.; 2015;255–256: 58–72. doi:10.1016/j.geoderma.2015.04.025
44. Holt J, Lepage M. Termites and soil properties. In: Abe T, Bignell DE, Higashi M, editors. Termites: Evolution, Sociality, Symbioses, Ecology. Dordrecht: Springer Netherlands; 2000. pp. 389–407.
45. Sarcinelli TS, Schaefer CEGR, Fernandes Filho EI, Mafia RG, Neri AV. Soil

- 541   modification by termites in a sandy-soil vegetation in the Brazilian Atlantic rain
- 542   forest. *J Trop Ecol.* 2013;29: 439–448. doi:10.1017/S0266467413000497
- 543   46.   Rückamp D, Amelung W, Theisz N, Bandeira AG, Martius C. Phosphorus forms
- 544   in Brazilian termite nests and soils: Relevance of feeding guild and ecosystems.
- 545   *Geoderma.* Elsevier B.V.; 2010;155: 269–279.
- 546   doi:10.1016/j.geoderma.2009.12.010
- 547   47.   Brasil. Ministério da Agricultura. I - Levantamento Exploratório,
- 548   Reconhecimento de Solos do Estado da Paraíba. II - Interpretação para uso
- 549   agrícola dos solos do Estado da Paraíba. Boletim DPFS, EPE-MA. Rio de
- 550   Janeiro: M.A/CONTAP/USAID/BRASIL; 1972.
- 551   48.   SERVIÇO NACIONAL DE LEVANTAMENTO E CONSERVAÇÃO DE
- 552   SOLOS-EMBRAPA. Levantamento Exploratório – Reconhecimento de solos Rio
- 553   Grande do Norte. Boletim Té. Recife: SUDENE; 1971.
- 554   49.   Oliveira LB, Fontes MPF, Ribeiro MR, Ker JC. Micromorfologia e Gênese de
- 555   Luvisolos e Planossolos desenvolvidos de rochas metamórficas no semi-árido
- 556   brasileiro. *Rev Bras Ciência do Solo.* 2008;32: 2407–2423.
- 557   50.   Soil Survey Staff. Keys to Soil Taxonomy, 2010. 11th ed. SCS. USDA; 2010.
- 558   51.   Cesarano G, Incerti G, Bonanomi G. The Influence of Plant Litter on Soil Water
- 559   Repellency: Insight from ¹³C NMR Spectroscopy. *PLoS One.* 2016;11:
- 560   e0152565. doi:10.1371/journal.pone.0152565
- 561   52.   Vesala T, Sevanto S, Grönholm T, Salmon Y, Nikinmaa E, Hari P, et al. Effect of
- 562   Leaf Water Potential on Internal Humidity and CO₂ Dissolution: Reverse
- 563   Transpiration and Improved Water Use Efficiency under Negative Pressure.
- 564   *Front Plant Sci.* 2017;8: 1–10. doi:10.3389/fpls.2017.00054
- 565   53.   Sarcinelli TS, Schaefer CEGR, Lynch L de S, Arato HD, Viana JHM, Filho MR

- de A, et al. Chemical, physical and micromorphological properties of termite mounds and adjacent soils along a toposequence in Zona da Mata, Minas Gerais State, Brazil. *Catena*. Elsevier B.V.; 2009;76: 107–113. doi:10.1016/j.catena.2008.10.001
54. Zhao Y, Peth S, Horn R, Krümmelbein J, Ketzer B, Gao Y, et al. Modeling grazing effects on coupled water and heat fluxes in Inner Mongolia grassland. *Soil Tillage Res.* 2010;109: 75–86. doi:10.1016/j.still.2010.04.005
55. Hasenmueller EA, Gu X, Weitzman JN, Adams TS, Stinchcomb GE, Eissenstat DM, et al. Weathering of rock to regolith: The activity of deep roots in bedrock fractures. *Geoderma*. Elsevier B.V.; 2017;300: 11–31. doi:10.1016/j.geoderma.2017.03.020
56. Li X, Chang SX, Salifu KF. Soil texture and layering effects on water and salt dynamics in the presence of a water table: a review. *Environ Rev.* 2013;22: 41–50. doi:10.1139/er-2013-0035
57. Martins SC. Caracterização dos solos e serrapilheira ao longo do gradiente altitudinal da Mata Atlântica, estado de São Paulo. Universidade de São Paulo. 2010.
58. Martins BLF. Alterações nos fluxos de gases do solo e na ciclagem de carbono e nitrogênio após aquecimento do solo em áreas de Mata Atlântica. ESALQ. 2011.
59. dos Santos SN, Alleoni LRF. Reference values for heavy metals in soils of the Brazilian agricultural frontier in Southwestern Amazônia. *Environ Monit Assess.* 2013;185: 5737–48. doi:10.1007/s10661-012-2980-7
60. Duarte TG. Florística, fitossociologia e relações solo-vegetação em floresta estacional decídua em Barão de Melgaço, Pantanal de Mato Grosso. Universidade Federal de Viçosa- MG. 2007.

61. Woortmann BCPI. Equações alométricas, estoque de biomassa e teores de carbono e nitrogênio de campinaranas da Amazônia central. INPA. 2010.
62. Six J, Conant RT, Paul E a, Paustian K. Stabilization mechanisms of soil organic matter: Implications for C-saturatin of soils. Plant Soil. 2002;241: 155–176. doi:10.1023/A:1016125726789
63. Tan ZX, Lal R, Smeck NE, Calhoun FG. Relationships between surface soil organic carbon pool and site variables. Geoderma. 2004;121: 187–195. doi:10.1016/j.geoderma.2003.11.003
64. IPCC. Good practice guidance for land use, land use change and forestry [Internet]. Institute for Global Environmental Strategies. 2003. doi:citeulike-article-id:1260638
65. Marques JJ, Schulze DG, Curi N, Mertzman S a. Trace element geochemistry in Brazilian Cerrado soils. Geoderma. 2004;121: 31–43. doi:10.1016/j.geoderma.2003.10.003
66. de Souza JJLL, Abrahão WAP, de Mello JWV, da Silva J, da Costa LM, de Oliveira TS. Geochemistry and spatial variability of metal(loid) concentrations in soils of the state of Minas Gerais, Brazil. Sci Total Environ. Elsevier B.V.; 2015;505: 338–49. doi:10.1016/j.scitotenv.2014.09.098
67. Schucknecht A, Matschullat J, de Caritat P, da Silva J, Melo G, Pleßow A, et al. Pedogeochemistry in NE-Brazil - compared to Australia and Europe. Sci Total Environ. Elsevier B.V.; 2012;438: 342–56. doi:10.1016/j.scitotenv.2012.08.059
68. de Souza JJLL, Fontes MPF, Gilkes RJ, da Costa LM, de Oliveira TS. Geochemical Signature of Amazon Tropical Rainforest Soils. Rev Bras Ciência do Solo. 2018;42: 1–18. doi:https://doi.org/10.1590/18069657rbc20170192
69. Grüneberg E, Ziche D, Wellbrock N. Organic carbon stocks and sequestration

- rates of forest soils in Germany. *Glob Chang Biol.* 2014;20: 2644–2662.
doi:10.1111/gcb.12558
70. Pires C V, Schaefer CERG, Hashigushi AK, Thomazini A, Filho EIF, Mendonça
ES. Soil organic carbon and nitrogen pools drive soil C-CO₂ emissions from
selected soils in Maritime Antarctica. *Sci Total Environ.* Elsevier B.V.;
2017;596–597: 124–135. doi:10.1016/j.scitotenv.2017.03.144
71. Giongo V, Cunha TJF, Mendes AS, Gava CAT. Carbono no sistema solo-planta
no semiárido brasileiro. *Rev Bras Geogr Física.* 2011;6: 1233–1253.
doi:10.5935/1984-2295.20140015
72. Schulz K, Voigt K, Beusch C, Almeida-Cortez JS, Kowarik I, Walz A, et al.
Grazing deteriorates the soil carbon stocks of Caatinga forest ecosystems in
Brazil. *For Ecol Manage.* Elsevier B.V.; 2016;367: 62–70.
doi:10.1016/j.foreco.2016.02.011
73. Rieger I, Lang F, Kowarik I, Cierjacks A. The interplay of sedimentation and
carbon accretion in riparian forests. *Geomorphology.* Elsevier B.V.; 2014;214:
157–167. doi:10.1016/j.geomorph.2014.01.023
74. Torres-Sallan G, Schulte RPO, Lanigan GJ, Byrne KA, Reidy B, Simó I, et al.
Clay illuviation provides a long-term sink for C sequestration in subsoils. *Sci
Rep.* Nature Publishing Group; 2017;7: 1–7. doi:10.1038/srep45635
75. Menezes R, Sampaio E, Giongo V, Pérez-Marin A. Biogeochemical cycling in
terrestrial ecosystems of the Caatinga Biome. *Brazilian J Biol.* 2012;72: 643–653.
doi:10.1590/S1519-69842012000400004
76. Balvanera P, Quijas S, Perez-Jimenez a. Distribution Patterns of Tropical Dry
Forest Trees Along a Mesoscale Water Availability Gradient. *Biotropica.*
2011;43: 414–422. doi:DOI 10.1111/j.1744-7429.2010.00712.x

77. Arruda DM, Ferreira-Júnior WG, Duque-Brasil R, Schaefer CEGR. Phylogeographical patterns of dry forests sensu stricto in northern Minas Gerais State, Brazil. *An Acad Bras Cienc.* 2013;85: 623–634.
78. Neves DM, Dexter KG, Pennington RT, Bueno ML, Oliveira Filho AT. Environmental and historical controls of floristic composition across the South American Dry Diagonal. *J Biogeogr.* 2015;42: 1566–1576. doi:10.1111/jbi.12529
79. Moro MF, Nic Lughadha E, de Araújo FS, Martins FR. A Phylogeographical Metaanalysis of the Semiarid Caatinga Domain in Brazil. *Bot Rev. The Botanical Review*; 2016;82: 91–148. doi:10.1007/s12229-016-9164-z
80. ter Steege H. Contribution of current and historical processes to patterns of tree diversity and composition of the Amazon. In: Hoorn C, Wesselingh FP, editors. *Amazonia: Landscape and Species Evolution.* Wiley-Blackwell; 2010. pp. 349–359.
81. Sampaio EVS, Gamarra-Rojas CFL. A vegetação lenhosa das ecorregiões da Caatinga. In: Jardim EAG, Bastos MNC, Santos JUM, editors. *Desafios da Botânica brasileira no novo milênio: inventário, sistematização e conservação da diversidade vegetal.* Belém: Sociedade Brasileira de Botânica; 2003. pp. 85–90.
82. Pinheiro EAR, Costa CAG, De Araújo JC. Effective root depth of the Caatinga biome. *J Arid Environ.* Elsevier Ltd; 2013;89: 1–4. doi:10.1016/j.jaridenv.2012.10.003
83. Markesteijn L, Poorter L. Seedling root morphology and biomass allocation of 62 tropical tree species in relation to drought- and shade-tolerance. *J Ecol.* 2009;97: 311–325. doi:10.1111/j.1365-2745.2008.01466.x
84. Minasny B, McBratney AB. Limited effect of organic matter on soil available water capacity. *Eur J Soil Sci.* 2018;69: 39–47. doi:10.1111/ejss.12475

85. Hudson BD. Soil organic matter and available water capacity. *J Soil Water Conserv.* 1994;49: 189–194.
86. Rodal M, Barbosa M, Thomas W. Do the seasonal forests in northeastern Brazil represent a single floristic unit? *Brazilian J Biol.* 2008;68: 467–475. doi:10.1590/S1519-69842008000300003
87. Krebs CJ. *Ecologia. Análisis experimental de la distribución y abundancia.* 3rd ed. Madrid: Ediciones Pirámide; 1986.
88. Whitmore TC, Prance GT. *Biogeography and Quaternary History in Tropical America.* New York: Oxford University Press; 1987.
89. Werneck FP, Costa GC, Colli GR, Prado DE, Sites JW. Revisiting the historical distribution of Seasonally Dry Tropical Forests: New insights based on palaeodistribution modelling and palynological evidence. *Glob Ecol Biogeogr.* 2011;20: 272–288. doi:10.1111/j.1466-8238.2010.00596.x
90. Batalha-Filho H, Fjeldså J, Fabre PH, Miyaki CY. Verbindungen zwischen atlantischen und amazonischen Waldvogelfaunen spiegeln distinkte historische Ereignisse wider. *J Ornithol.* 2013;154: 41–50. doi:10.1007/s10336-012-0866-7
91. Sobral-Souza T, Lima-Ribeiro MS, Solferini VN. Biogeography of Neotropical Rainforests: past connections between Amazon and Atlantic Forest detected by ecological niche modeling. *Evol Ecol.* Springer International Publishing; 2015;29: 643–655. doi:10.1007/s10682-015-9780-9
92. Sobral-Souza T, Lima-Ribeiro MS. De volta ao passado: Revisitando a história biogeográfica das florestas neotropicais úmidas. *Oecologia Aust.* 2017;21: 93–107. doi:10.4257/oeco.2017.2102.01
93. Coimbra-Filho AF, Câmara IG. Os limites originais do bioma Mata Atlântica na região nordeste do Brasil. Rio de Janeiro: Fundação Brasileira para a

Conservação da Natureza; 1996.

94. Pinheiro EAR, de van Lier QJ, Bezerra AHF. Hydrology of a water-limited forest under climate change scenarios: The case of the Caatinga biome, Brazil. *Forests*.

2017;8. doi:10.3390/f8030062

95. IPCC. Part A: Global and Sectoral Aspects. (Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change).

Clim Chang 2014 Impacts, Adapt Vulnerability. 2014; 1132.

doi:10.1017/CBO9781107415324.004

96. Lenoir J, Hattab T, Pierre G. Climatic microrefugia under anthropogenic climate change: implications for species redistribution. *Ecography (Cop)*. 2017;40: 253–

266. doi:10.1111/ecog.02788

Supporting information

S1 Table. Number of specimens identified in vegetational plots by family, scientific name and its reported biomes according to literature.

Vegetational plot

Similarity

bioRxiv preprint doi: <https://doi.org/10.1101/317685>; this version posted May 8, 2018. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

Pearson correlation