

Landforms and soil attributes determine the vegetation structure in the Brazilian semiarid

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Abstract The semiarid region of Brazil consists of a great variety of landscapes, soils and vegetation forms, with complex interrelations. In order to better understand this interplay, we posed two questions: Are there greater pedological similarities among the different landforms of the same catena or among the same landforms from different catenas? Which soil attributes could be the most important to segregate communities of plants? We sampled soils and vegetation on different landforms in four different catenas and performed NMS (non-metric multidimensional scaling) and ANOVA (analysis of variance) to address the first question; also, we carried another NMS following GLM (general linear model regression) to answer the second question. The

first NMS indicated the existence of a fertility gradient, grouping communities in relation to similar landforms, confirmed by ANOVA. The second NMS indicated the same gradient whereas the GLM showed that is controlled by aluminum saturation, sodium saturation, phosphorous and sand content. One extreme of the gradient has uplands associated with cerrado vegetation forms whereas the other extreme slopes were associated with dry forests. The lowlands associated with dry forest represent the central position of the fertility gradient. In general, soils at similar landforms showed greater pedological similarity, and their physico-chemical attributes determined the formation and structure of vegetation. This similarity across the same landform refers to the

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comparable soil formation at each landform and soil age at landscape scale. The characteristics of the vegetation and soils in the Brazilian southern semiarid region indicated a previously wetter climate, during which deep weathered latosols (oxisols) were formed and remain as relics in the present semiarid.

Keywords cerrado · climate transition · gradient of vegetation · seasonally dry tropical forest · semiarid geomorphology · vegetation-soil relationship

Introduction

The southern region of the Brazilian semiarid comprises a transition zone with a tropical savanna climate (Aw sensu Köppen), resulting in the establishment of a mosaic of diverse vegetation forms in association with different lithologies. This region is the contact zone among three large and distinct floristic units – the ‘caatinga’ (semiarid savanna-steppe) to the north, ‘cerrado’ (Neotropical savanna) to the south and west, and Atlantic moist forests to the east (Ab’Sáber 2003). This phytogeographical contact results in the occurrence of several vegetation forms, in which the transitional character favours the occurrence of seasonally dry tropical forest (Murphy and Lugo 1986). The floristic patterns within this ecotone are determined by the specific soil characteristics related with forest establishment (Arruda et al. 2013).

Besides the dry forest (seasonally deciduous forest sensu IBGE 2012), other formations also occur in the region, such as semideciduous forests, cerradão (savanna woodlands), typical cerrado (savanna), campo rupestre (open vegetation on rock outcrops), cerrado rupestre (savanna on rock outcrops) and hyperxerophilous caatinga on limestone outcrops (Brandão 1994). At the local scale, the distribution of these formations seems to be strictly associated with landforms and soil characteristics.

Ecological studies in Brazil have demonstrated that plant communities often vary according to landforms and soil attributes, e.g. Botrel et al. (2002) and Ferreira-Jr et al. (2007) for semideciduous forests, Oliveira-Filho et al. (1998) for seasonally dry forests, and Budke et al. (2006) for gallery forests. These studies generally show topographic sectors with distinct soil characteristics,

with nutrient depleted soils at higher elevations and strong soil influence on plant communities.

Studies examining multiple catenas with diverse geologies and their influence on plant communities are scarce in Brazil, particularly in semiarid environments (see Figueiredo et al. 2014 for information about Amazon forest). This highly seasonal climate surely has a marked influence on landforms, soils and vegetation forms, and strongly contrasts with wet environments (Bigarella et al. 1994; Ab’Sáber 1998).

We examined the relationships among landforms, soils and plant communities in the semiarid region of Brazil, seeking to characterize the soils and the vegetation in different catenas of the southern portion of this climatic domain, aiming to answer the following questions: Are there greater soil similarities among the different landforms of the same catena or among the same landforms from different catenas? Which soil attributes could be the most important to segregate plant communities?

Material and methods

Study sites

The present study was undertaken at four different localities: three municipalities in Minas Gerais state (MG) and one in Bahia state (BA), Brazil (Fig. 1). These locations were chosen due to the presence of well-preserved vegetation fragments established on different geological formations, all representative of the regional landscape.

The localities chosen were: (1) Januária-MG, representing a catena between the sandstone plateaus to the west and the alluvial plains of the São Francisco River; (2) Porteirinha-MG, along the western border of the Espinhaço Range, representing a catena between the Santa Isabel Complex (granite-gneiss basement), which borders the Espinhaço Range Supergroup and the flattened depression of the Guanambi Complex (granite-gneiss basement); (3) Gameleiras-MG, catena in the western border of Palmas de Monte Alto Formation, a sandstone-quartzite plateau on the Sertaneja Depression; (4) Guanambi-BA, near the western border of the central part of the Espinhaço Range, representing a catena between the weathered quartzite highlands and the edge of the granite-gneiss basement.

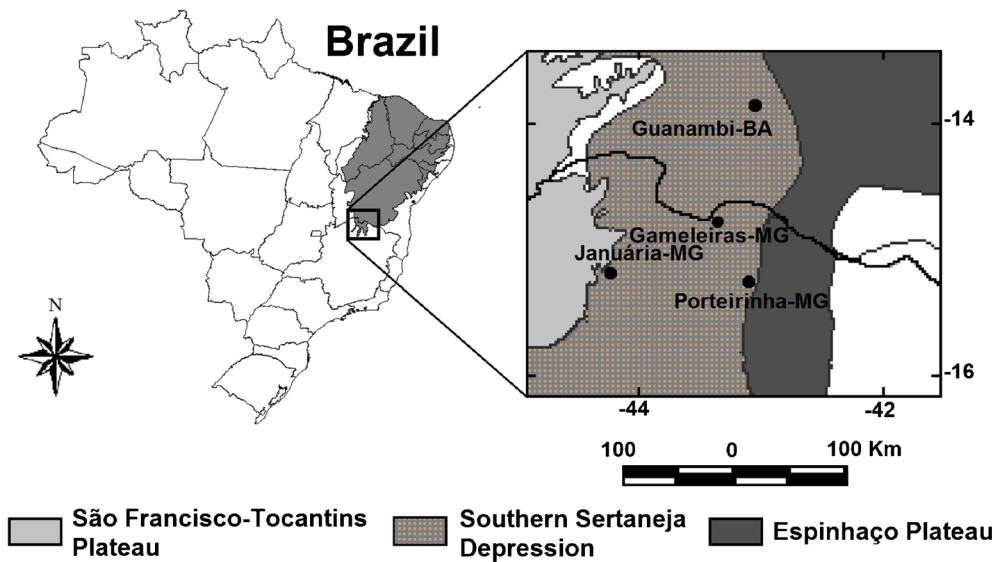


Fig. 1 Location of the semiarid region in Brazil (shaded on the left-side map) and the four study localities in Bahia (BA) and Minas Gerais (MG) states (dots on the enlarged right-side map), together with their three main geomorphological subdivisions: the sandstone plateaus of the Urucuia, to the west (São Francisco-

Tocantins Plateau); flattened depression associated with the mid São Francisco River basin in the central part (Southern Sertaneja Depression); and the quartzitic Espinhaço Range to the east (Espinhaço Plateau).

Sampling

The landform segment of each catena was distinguished as an upland, slope or lowland based on elevation, slope, rock exposure and soil type. Soil profiles were dug at each landform, described and sampled for further chemical and physical analyses, and subsequently classified following both the U.S. Soil Taxonomy (Soil Survey Staff 2010) and the Brazilian System of Soil Classification (EMBRAPA 2006). Soil material was air-dried and sieved (< 2 mm), and subjected to analysis according to the methods described by EMBRAPA (1997). The texture of fine-earth was analysed using the pipette method. The pH was determined in water and the exchangeable cations were extracted by KCl 1 mol L⁻¹ and quantified by atomic absorption spectrometry (Ca²⁺ and Mg²⁺) and by titration with NaOH (Al³⁺). Available P and exchangeable K were extracted by Mehlich⁻¹, P being measured by the ascorbic acid method as described by Kuo (1996) and K⁺ determined by flame photometry. Na⁺ was extracted with a solution of ammonium acetate 1.0 mol L⁻¹ at pH 7.0 and determined by flame photometry. The organic matter (OM) content was estimated after determining organic carbon by the Walkley Black method without heating (EMBRAPA 1997).

The vegetation forms were classified according to the IBGE (2012), a Brazilian classification system adapted to the universal system. For vegetation characterization, three 400 m² plots were established in the same soil pedon area representing each landform; all trees with diameter at breast height (DBH) ≥ 15 cm were sampled and identified. All plants and botanical material collected was deposited in the Federal University of Viçosa Herbarium (VIC).

Analyses

To answer the first question on soil similarity, non-metric multidimensional scaling (NMS-env) was performed using an environmental matrix at each community and Euclidean (Pythagorean) distance measure (Clarke 1993). The variables used were pH, phosphorus (P), bases sum (BS), aluminum saturation (m), sodium saturation index (ISNA), organic matter (OM) and sand content of the A horizon. The variables that were interdependent were not considered in model in order to minimize noise effects. In order to minimize the effects of the different scales of the environmental variables, they were standardized according to their respective standard errors (Webster and Oliver 1990). To test the significance of the groups formed in different axes of the

NMS-env diagram, two analyses of variance were performed. The significant axes were used as response variable in both ANOVAs and the explanatory variable ‘landform’ (upland, slope and lowland) and ‘catenas’ (Jan – Januária, Por – Porteirinha, Gam – Gameleiras and Gua – Guanambi) were assessed separately.

In order to answer the second question concerning the pedological influence on species distribution, a non-metric multidimensional scaling (NMS-sp) was performed, using an abundance matrix of the ten more abundant species (79 species, listed in Table A in the Electronic supplementary material) in each community and Sorensen’s (Bray-Curtis) index as a distance measure (Clarke 1993). We considered the NMS results (axes scores) as a measure of community structure (Barlow et al. 2010; Magnago et al. 2014), wherein the scores of the axes indicate the grouping of species/community in terms of the similarity. A general linear model regression (GLM) was performed using the significant axes of the NMS-sp as response variable and pH, phosphorus (P), bases sum (BS), aluminum saturation (m), sodium saturation (NaSat), organic matter (OM) and sand as explanatory variables. This regression indicates which soil attributes are most critical to segregate plant communities.

The NMS were performed using PC-ORD 6.0 software (McCune and Mefford 2006) and the ANOVAs and GLMs were carried out in R v. 3.1.2 (R Development Core Team 2014). In the GLM, the ‘dredge’ function from the ‘MuMIn’ package was used to test all possible combinations of the variables included in the full model. The lower value of the second-order Akaike Information Criterion (AICc) was used, which indicates the most parsimonious model (Burnham et al. 2011).

Results

Environment characterization

A general characterization of the landforms at the different catenas is illustrated below (Fig. 2). The information on lithology followed RADAMBRASIL (1982).

Januária: The transect between the Urucuia Formation and the São Francisco River terraces comprised four environments. The two highest sections of the transect, classified as uplands, were associated with the sandstone Tablelands of the Urucuia Formation; the first environment, at ca 600 m a.s.l., had a Typic Haplustox

(Red-Yellow Latosol; *Jan-up1*) covered by cerrado vegetation. The second environment, at ca 570 m a.s.l., consisted of the limit of the Cretaceous sandstones of the Urucuia formation, with Ustoxic Quartzipsamment (Quartzarenic Latossolic Neosol; *Jan-up2*) that were slightly sandier and with greater nutrients contents than the first environment, and covered by cerrado vegetation. The transition between the Urucuia Formation and the São Francisco Supergroup constituted the third environment, with the presence of Typic Haplustept (Eutric Leptic Cambisol; *Jan-slope*) at ca 540 m a.s.l., characteristic of the limestone slopes of the Bambuí group, covered mostly by seasonally dry forests. These lower slopes separate the sandstone plateau from the São Francisco River depression. This depression was characterized in the fourth environment, with Typic Haplustalf (Eutric, Latossolic, Red Argisol; *Jan-low*) associated with seasonally dry forests on the upper river terrace, at ca 480 m a.s.l.

Porteirinha: The transect between the granite-gneiss Santa Isabel Complex and the Guanambi Complex closely followed a base saturation gradient through three environments of two distinct landforms, all associated with seasonally dry forests. In this transect, we did not include the rocky uplands of the Espinhaço Massif, at altitudes above 900 m a.s.l. The higher slopes in the Santa Isabel Complex, at 660 m a.s.l., were dominated by typical Lithic Ustorthent (Eutric Litholic Neosol; *Por-slope1*). The lower slopes of the second environment were dominated by typical Typic Eutrochrept (Eutric Haplic Cambisol; *Por-slope2*), at 615 m a.s.l. The third environment was represented by the pediplain depression of the Guanambi Complex, at 580 m a.s.l., dominated by Inceptic Eustrtox (Eutric Latossolic Cambisol; *Por-low*).

Gameleiras: The transect between the Palmas de Monte Alto Sandstone Formation and the Bambuí Depression comprised three environments. The first environment corresponds to upland on the plateau, at ca 1,080 m a.s.l., had a Ustoxic Quartzipsamment (Quartzarenic Latossolic Neosol; *Gam-up*). This soil is formed by unconsolidated Plio-Pleistocene material covering the Precambrian metasedimentary rock (sandstone, quartzite and siltstone). The vegetation form on this environment is typical cerrado. The second environment is located in the slope on the lithology of glacial origin with mafic elements (conglomerate with greywacke matrix of the Macaúbas Formation), at 597 m a.s.l., covered by Typic Eutrochrept (Eutric Cambisol; *Gam-slope*) and dry forest. The third

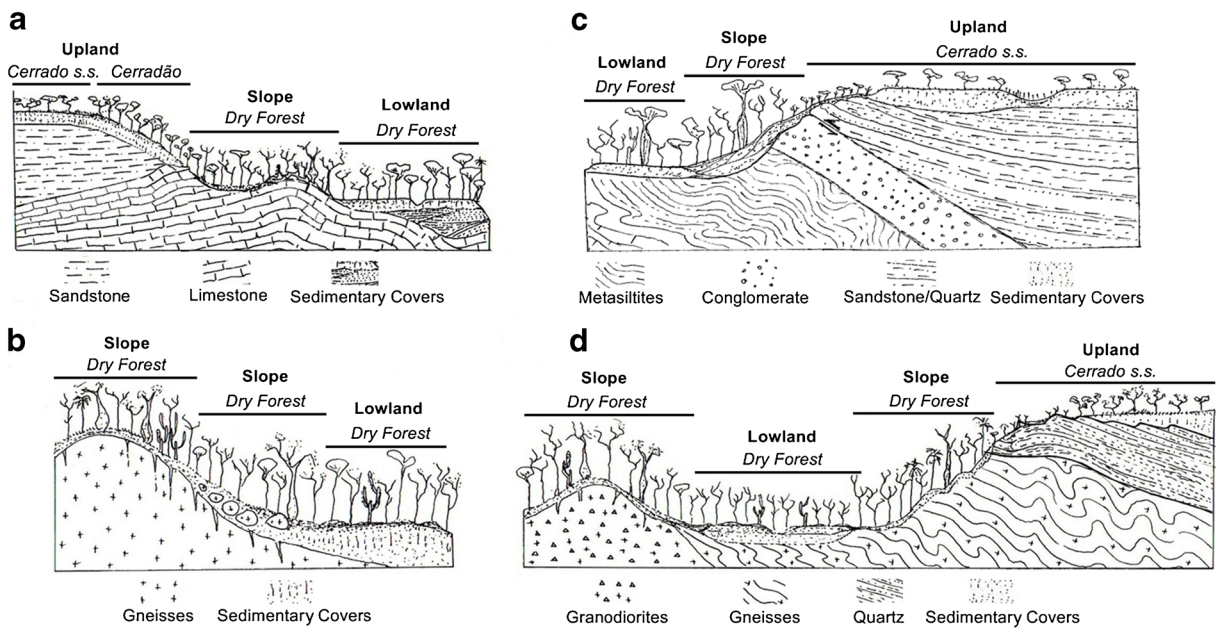


Fig. 2 Schematic diagram of the selected transects, showing the landforms and pedological-vegetational gradients at Januária (a), Porteirinha (b), Gameleiras (c) and Guanambi (d).

environment was a pediplain at 526 m a.s.l., with soils developed by the mix between colluvial matters and metapelitic rocks of the Bambuí Formation, dominated by Dystric Kandiusult (Dystric Yellow Argisol; *Gam-low*). This environment is vegetated by a dry woodland (dry forest of smaller height).

Guanambi: The transect between the Espinhaço Range and the depressions of the Guanambi Crystalline Basement could be divided into four pedo-environments with different lithologies. The first environment was associated with the Espinhaço Range – the upland segment of the transect, at 975 m a.s.l., mainly associated with Ustoxic Quartzipsamment (Quartzarenic Latossolic Neosol; *Gua-up*). This soil was derived from a Quaternary Sedimentary cover, on a slightly undulating topography interrupted by sparse quartzitic elevations above 1,000 m a.s.l. The vegetation form on this environment is typical cerrado. The second environment, towards the western slope of the Espinhaço Range, at 650 m a.s.l., on the Santa Isabel complex in a transitional zone with the Guanambi depression, is predominantly associated with Typic Eutrochrept (Eutric Cambisol; *Gua-slope1*) with medium texture, on a stony and sloping surface. The vegetation form occupying this landform is seasonally dry forest. The third environment is located in the Guanambi depression (Crystalline Basement), which is the lowest segment of the transect at 520 m a.s.l., covered by Dystric Paleustults

(Dystric Yellow Argisol; *Gua-low*). This forest environment possesses a large numbers of termite mounds approximately 1.2 m tall on a flat landscape, interrupted only by residual inselbergs. In general, the most elevated parts of the inselbergs are dominated by rock outcrops or shallow soils. The fourth environment, the inselberg slope surface, is composed of Lithic Eutrochrept (Eutric Leptic Cambisol; *Gua-slope2*), at 634 m a.s.l., on a steep slope with large stone blocks, under open seasonally dry forest.

Soil-landform relationship

Regarding the soil similarity, the NMS-env showed a significant gradient among the sampled soils, with solution of two axes ($P = 0.02$). We observed a grouping on axis 1 regarding landforms. The slopes were grouped in the positive portion on axis 1, the uplands in the negative portion, and the lowlands in the central portion (Fig. 3a). On axis 2, the grouping was in relation to catenas, where plant communities of Porteirinha (Por) and Gameleiras (Gam) were grouped in the positive portion of the axis 1 whereas Januária (Jan) and Guanambi grouped in the negative portion.

The landforms grouping of the axis 1 were confirmed by the ANOVA ($F = 16.73$; $P < 0.001$) with no effect regarding grouping among the landforms of the same catena ($F = 2.68$; $P = 0.103$; Fig. 3b). Axis 2 showed

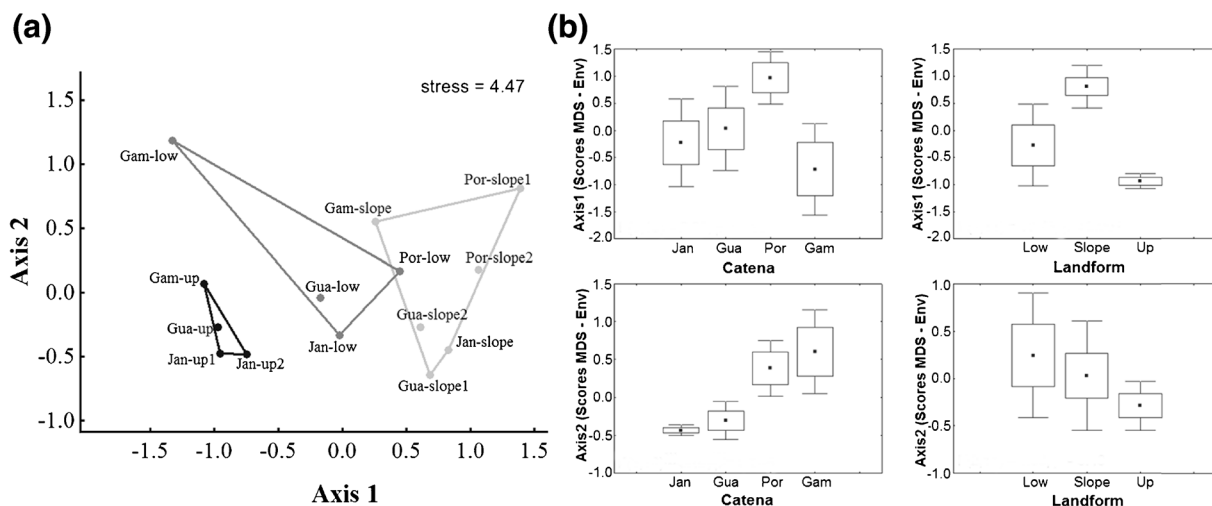


Fig. 3 Distribution of soil attributes in relation to landforms and catenas. **(a)** NMS diagram of the physico-chemical variables in 14 communities sampled. **(c)** Effects of physico-chemical variables in the landforms and catenas (axis 1 and 2 from NMS analysis).

significant grouping among the environments of the same catena ($F = 8.12$; $P = 0.005$), but no effect regarding landforms ($F = 0.99$; $P = 0.401$). Thereby, both grouping of catena and landforms were confirmed in relation to soil attributes, but greater significance was observed for the last group, according to the P -value.

Soil-plant community relationship

Regarding the influence of soil on plant communities, the NMS-sp revealed a significant gradient among the sampled communities, with solution of two axes ($P = 0.02$). Grouping on axis 1 regarding catenas was observed (Fig. 4a). In this axis, the uplands cerrado communities grouped in the positive portion whereas the dry forest species of the lowlands and slopes grouped in the negative portion. Therefore, like the previous analysis, there is greater similarity among similar landforms, even from different catenas. Although also significant, axis 2 was not observed a logical grouping in this axis.

The most parsimonious model to explain the distribution of species in the communities (axis 1) showed an effect of sodium saturation index ($T = -3.68$; $P = 0.005$), aluminum saturation ($T = 3.75$; $P = 0.004$), phosphorus content ($T = -2.89$; $P = 0.018$) and sand content ($T = 3.06$; $P = 0.013$), without interaction among the variables (Fig. 4b). The abundance of species and their scores of the axes are listed in Table A in the Electronic supplementary material.

Discussion

Physico-chemical attributes of soils in the same landform were similar, even from distant localities, and formed from different parent materials. Hence, this similarity refers to a comparable soil genesis and age at each landform. Landforms and soils, combined, determined the vegetation forms, in which cerrado covers old, stables, well-drained uplands whereas dry forests are associated with the slopes and lowlands. The effect of lithology and landforms in the control of soil and floristic similarity was also observed by Figueiredo et al. (2014) in central Amazonia.

In all catenas studied, the upper segments had soils with the lowest fertility, being related to chemically leached sediments on old and stable land surfaces. Their leached soils (low base contents, with a predominance of Al^{3+} in the exchange complex) and well drained (high sand content) reflect the high degree of evolution of these environments, when the desilicification process was facilitated. Therefore, these surfaces are regarded as relics of a time when the chemical weathering was more prevalent than currently.

These areas are commonly associated with escleromorph/xeromorph vegetation forms adapted to adverse environmental condition, such as the different formations of cerrado. Among these, cerrado and cerrado (closed savanna woodland) widespread in these uplands (Cole 1960; Askew et al. 1970), are differentiated in relation to chemical (Goodland and Pollard 1973; Furley and Ratter 1988; Neri et al. 2013) or physical

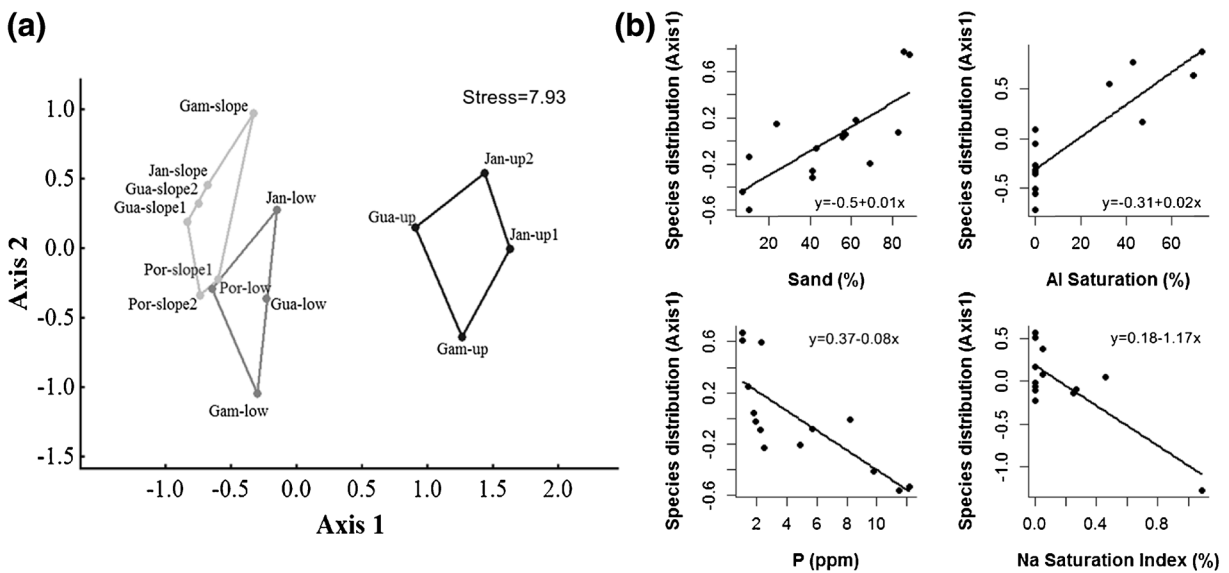


Fig. 4 Distribution of species in relation to physico-chemical soil attributes. **(a)** NMS diagram of the 79 most abundant species in 14 communities sampled. **(b)** Effects of physico-chemical variables

attributes (Haridasan 1992; Marimon-Júnior and Haridasan 2005; Schaefer 2013). On the other hand, cerrado forms of southeastern Brazil are not distinguished by physico-chemical attributes (Ruggiero et al. 2002), suggesting that the vegetation structure is more related to the degree of human disturbance and successional stage (Durigan and Ratter 2006; Pinheiro and Durigan 2009).

The other extreme of the fertility gradient was represented by the so-called slope (sloping surfaces). Soils there are recent colluvially transported materials related to the underlying rocks. As one moves downslope (from mid-slope to the bottom) chemically richer soils occur (little or without Al^{3+} in the exchange complex) on less weathered rocks. The Januária slopes contain limestone, dolomites, dolomitic limestone, carbonaceous claystones and schists. The rocks of the Santa Isabel Complex in Guanambi are basically Ca-rich gneisses and amphibolites, cut by granodiorite plutons (RADAMBRASIL 1982), affording high amounts of calcium, magnesium and potassium in these soils. Similarly, the slopes of Macaúbas Formation are chemically rich due to mafic rock influence. Also, leaves of dry forest species have a high content of nitrogen, phosphorus and calcium, which contributes to the nutrient concentration of soil surface (Jaramillo and Sanford, 1995).

Steep slope forests do not accumulate large biomasses (in terms of basal area and canopy height) as

(indicated by AICc as more significant in explain the distribution of species in the gradient) in the distribution of the communities.

do similar vegetation forms growing on flat surfaces (Scariot and Sevilha 2005; Arruda et al. 2011). Although mountain slopes are generally richer in nutrients, these environments are also unstable and prone to erosion, with shallow soils that constrain root development; landslide erosion is also common after torrential rains under this climate type.

Seasonally dry forest are common in nutrient richer (eutrophic to mesotrophic) soils, especially in shallow and well-drained substrates occurring in the Brazilian semiarid climate, which are normally associated with a deciduous phytophysognomy (Ratter et al. 1973; Ratter et al. 1978). However, dry forests on dystrophic soils, as that of Gameleira's pediplain, are rarely documented.

As observed by Cole (1960), neotropical seasonally dry forest are commonly found in semiarid-intermontane depressions in the central parts of northeastern Brazil. Soils under seasonally dry forest in the intermedial position of the fertility gradient – the lowland landscapes, allocated in the mid part of the axis 1 of the NMS-env – are considered mesotrophic (Askew et al. 1970), with nearly 50 % of base saturation. In this respect, Askew et al. (1970) and Ratter et al. (1978) associated the presence of seasonally dry forests within the Brazilian cerrado domain with the occurrence of these richer soils. These forests also occur associated with limestone in northeastern Goiás

State (Felfili et al. 2007) and on soils derived from basalt in southern Goiás and western Minas Gerais State (Oliveira-Filho et al. 1998). In all those localities, flat, stable landforms predominate, with tall seasonally dry forests growing on deep, richer soils.

In semi-arid environments, salts released by the rocks are transported and accumulated in the lower portions of the landscape (Bigarella et al., 1994; Gheyi, 2000), resulting in sodic to solodic soils (eg Oliveira et al 2009). Although the excess salts affect the growth and development of plants (Munns and Tester 2008), the sodium levels found in the samples of this study are considered low to establish a physiological effect on vegetation.

The vegetation is a reflection of the landform evolution. In general, late Quaternary climate oscillations from semiarid to humid, provided a bioclimatic scenario with enhanced pedogenesis and leaching. This context is favourable for the establishment of forest formations (Bigarella et al. 1994; Ab'Sáber 1998). In subsequent transition from humid climate to semiarid, the low plains were filled by sediments from the uplands following torrential rains, causing intense pediplanation and lateral degradation that removed most soils formed during the previous humid climate period, leaving shallow, rocky soils in the extensive lowland depressions (Bigarella et al. 1994; Ab'Sáber 1998). This is typical of the depressional core of the Brazilian semiarid (caatinga domain; Cole 1960; Andrade 1972). In contrast to that, the presence of well-developed soils associated with seasonally dry forest in the southern sector of the semiarid depression suggests that this landscape carries traits of different climatic phases. As such, the uncommon eutrophic latosols (oxisols) in the region reflect the influence of a previous wetter climate that was followed by the current semiarid regime. Although these soils are formed by the same processes in humid condition, nutrients are preserved under the present-day semiarid climate due to lower leaching intensity under dry conditions. Similar condition was reported in latosols of the 'Região dos Lagos' in the State of Rio de Janeiro (Ibraimo et al. 2004), where a similar recent onset of semiarid climate occurred.

The past distribution of seasonally dry forest in Brazil cannot be modelled or predicted by climate models without full consideration of the soils and landforms on which they developed and evolved. Hence, polygenetic soils with greater depths, and higher water

retention, can buffer, or limit, the expansion of a more xeric vegetation form, helping to maintain an ecotonal status.

Conclusions

(1) The landscapes at the southern semiarid domain in Brazil are associated with varying soil classes and the same landforms showed more similarity of the physico-chemical properties that different landforms in same catenas. (2) Soil and landform attributes are the main drivers of vegetation establishment. A soil fertility gradient is prominent, with decreasing nutrients followed upland < lowland < slope. The pedological differences between lowlands and slopes allowed the establishment of different plant communities. (3) Seasonally dry forest is the main vegetation at the lowlands and slopes, with different formations of cerrado on well-drained uplands. Chemically depleted sedimentary rocks account for the cerrado vegetation on the uplands, associated with deep weathered, well-drained soils. The eutrophic character on the slopes is due to the shallowness and direct influence of the chemically rich rocks, in agreement with present-day semiarid climate. The lowlands also have mesotrophic deep soils. Such lowland weathered soils were formed in a past wetter climate, being quite distinct from soils at the same lowland depressions at the core semiarid area further north. There, rocky, stony and shallow soils are typical of the caatinga domain.

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