

Soil attributes structure plant assemblages across an Atlantic forest mosaic

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Abstract

Aims

Community assembly persists as a key topic in ecology due to the complex variation in the relative importance of assembly forces and mechanisms across spatio-temporal scales and ecosystems. Here we address a forest–savanna vegetation mosaic in the Brazilian Atlantic forest to examine the role played by soil attributes as determinants of community assembly and organization at a landscape spatial scale.

Methods

We examined soil and plant assemblage attributes across 23 plots of forest and savanna in a 1600 km² landscape exposed to the same climatic conditions in the Atlantic forest region of northeast Brazil. Assemblage attributes included species richness, taxonomic and functional composition (community weighted mean, CWM) and functional diversity (quadratic diversity; Rao's quadratic entropy index) relative to plant leaf area, specific leaf area, leaf dry matter content, thickness and succulence.

Important Findings

Our results suggest that forest and savanna patches exposed to the same climatic conditions clearly differ in terms of soil attributes, plant assemblage structure, taxonomic and functional composition. By selecting particular plant strategies relative to resource economy, soil potentially affects community structure, with forest assemblages bearing more acquisitive resource-use strategies, while conservative plant strategies are more frequent in savannas. Accordingly, savanna–forest mosaics in the Atlantic forest region represent spatially organized plant assemblages in terms of taxonomic and functional features, with a signal of trait convergence in both vegetation types. Soil-mediated filtering thus emerges as a potential deterministic assembly force affecting the spatial organization of savanna–forest boundaries and mosaics.

Keywords: community assembly, habitat filtering, plant functional traits, savanna vegetation, tropical forest

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INTRODUCTION

Community assembly persists as a key topic in ecology due to the complex variation in the relative importance of assembly forces and mechanisms across spatio-temporal scales and ecosystems (Cavender-Bares *et al.* 2009; Kraft and Ackerly 2010). At the local scale, species interactions mediated by abundance, particularly species competition, result in limited similarity and have been highlighted as the predominant force in the assembly process (Laliberté *et al.* 2013; Stubbs and Wilson 2004). At landscape scale, environment filtering emerges as

the dominant driver of community assembly, while at regional and continental scales, evolutionary and biogeographic processes (i.e. speciation, species extinction and migration) play more important roles (Kraft and Ackerly 2010; Lambers *et al.* 2012; Paine *et al.* 2012). In contrast to such deterministic processes (i.e. limited similarity and environmental filtering), neutral theory (Hubbell 2001) recognizes individuals as being ecologically equivalent and communities as entities largely shaped by species demographic stochasticity.

Environmental filtering assumes that individuals immigrating into a community must have appropriate traits to pass

through both biotic and abiotic filters (Cornwell *et al.* 2009; Díaz *et al.* 1999; Weiher and Keddy 1995). From this perspective, communities tend to consist of a limited subset of species from the regional species pool, bearing similar functional traits or life-history strategies, particularly in harsh environments with low resource availability (Katabuchi *et al.* 2012; Lebrija-Trejos *et al.* 2010). Vegetation mosaics or gradients are often associated with environmental filtering imposed by variations in soil attributes (Dantas *et al.* 2013; Katabuchi *et al.* 2012; Oliveira Filho and Ratter 1995; Ruggiero *et al.* 2002; Réjou-Méchain *et al.* 2014). This occurs because plant species respond differently to variations in soil pH (Ejrnæs 2000), soil physical texture (Witkamp 1971), water content (Engelbrecht *et al.* 2007; Péliissier *et al.* 2003) and nutrient availability (Condit *et al.* 2013; Hodgson *et al.* 2011; John *et al.* 2007; Jager *et al.* 2015; Katabuchi *et al.* 2012). According to the environmental filtering hypothesis, spatial congruence between plant species distribution and soil attributes is mediated by plant traits, which constrains not only the taxonomic composition but also the functional structure of plant communities, and allows us to predict community-level responses to environmental changes (Westoby and Wright 2006; McGill *et al.* 2006).

Throughout the tropical region, forest and savanna coexist widely as a mosaic at landscape scale (Hoffmann *et al.* 2012). These two vegetation types differ not only in terms of tree density and vegetation structure, but also in species composition, with few species occurring in both ecosystems (Felfili and Silva Junior 1992). Generally, plant species distribution and vegetation boundaries are mediated by differences in species responses to a myriad of factors (Hoffmann *et al.* 2004, 2005, 2012), including fire and herbivory regimes (top-down forces, Bond 2008) and soil resource availability, with the distribution of savanna patches commonly associated with lower nutrient or water availability (Dantas *et al.* 2013; Furley 1992, 2007; Ruggiero *et al.* 2002; Silva *et al.* 2013). However, there is no consensus about the relative importance of these factors in mediating vegetation boundaries (Hoffmann *et al.* 2012). Fire is commonly assumed to be the main force allowing the persistence of savanna vegetation by reducing biomass and preventing canopy closure by forest species (Dantas *et al.* 2013; Hoffmann *et al.* 2012). Further, fire-driven nutrient losses may be a key feedback stabilizing savanna vegetation (Pellegrini 2016). On the other hand, at the landscape scale forest and savanna can coexist with well-defined boundaries without the presence of recent fires, suggesting a prominent role of nutrient stocks or soil conditions in preventing savanna stands from ever becoming a forest (Hoffmann *et al.* 2012).

Savanna and forest species are known to represent distinct functional types with different resource requirements (Dantas *et al.* 2013; Hoffmann *et al.* 2005; Nardoto *et al.* 2006; Silva *et al.* 2013). Specifically, forest species typically present more acquisitive resource-use strategies and thus have a higher nutrient requirement, which tend to limit its ingression in poor-soils dominated by savanna vegetation (Pellegrini

2016; Silva *et al.* 2013). This in turn limits the potential for soil enrichment and canopy closure by this group and the subsequent expansion of forests upon savannas (Hoffmann *et al.* 2012; Pellegrini *et al.* 2014). Despite some advances in the identification of functional differences between forest and savanna species, as well as soil differences between forest and savanna stands, the relationship between functional traits and environmental gradients remains as a key topic. In fact, it is a fundamental step to assess the importance of environmental filters on community assembly (McGill *et al.* 2006) and thus to elucidate the factors that determine the dynamic of forest–savanna boundaries and its response to disturbance regimes (Hoffmann *et al.* 2012).

The Brazilian Atlantic forest region, although markedly recognized by its forests, consists of several vegetation types, ranging from evergreen forests to savannas and grasslands (Barbosa and Thomas 2002; IBGE 2008). The regional distribution of different vegetation types is commonly explained by variations in climate (Good and Caylor 2011; IBGE 2008; Laughlin *et al.* 2011). However, at landscape scale, natural vegetation mosaics can also occur under the same climatic conditions, including mosaics with well delimited patches of forest and savanna (Barbosa and Thomas 2002). These natural landscape-level mosaics offer an interesting opportunity to investigate the role of soil as a driving force in structuring plant assemblages and to test the importance of soil in the coexistence of contrasting vegetation types (i.e. soil filtering structuring spatial distribution of plant functional groups as observed in some forest–savanna boundaries; see Laureto and Cianciaruso 2015; Neves *et al.* 2010).

Here we examine a vegetation mosaic in the Atlantic forest region of northeast Brazil, which is exposed to the same climatic conditions, to identify the role played by soil attributes in organizing plant assemblage structure, and taxonomic and functional composition at landscape spatial scale. Despite ambiguous results in the literature, we expected marked differences in terms of both soil conditions and plant assembly attributes between vegetation types, with forest patches supporting (1) more fertile soils, (2) more diverse and taxonomically/functionally distinct assemblages and (3) with forest species bearing more acquisitive resource-use strategies (as opposed to conservative resource-use in savanna). We also expected clear signals of trait convergence in both vegetation types and soil attributes correlated to the structure of plant assemblages. In synthesis, here we examine the hypothesis that soils play a role in the spatial organization of tropical plant assemblages.

MATERIAL AND METHODS

Study site

This study was carried out in a 1600 km² Atlantic forest landscape in northeast Brazil, which has been devoted to sugarcane cultivation, but still retains native vegetation patches (Fig. 1). This landscape consists of flat and undulating terrains

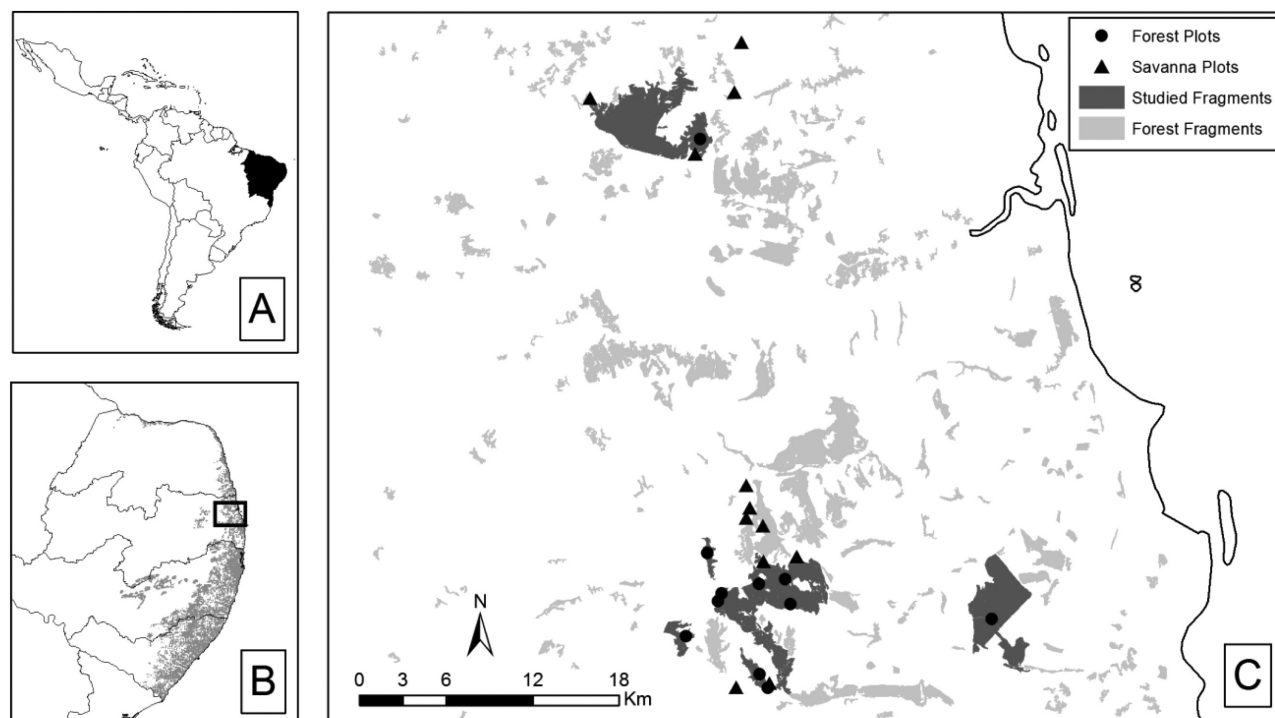


Figure 1: location of the study area in northeastern Brazil (A), with the Atlantic forest shown in gray (B) and details of the study area and location of the 23 plots represented by savanna (black triangle) and forest (black circle) patches (C).

not exceeding 230 m a.s.l. Argisol and latosol (i.e. ultisols and oxisols, according to USDA soil taxonomy) are the prevalent soil types and to a lesser extent neosol and espodosol also occur in the landscape. Mean annual temperature is 26°C and annual precipitation usually ranges between 1300 and 1700 mm, with a dry season (<60 mm per month) from October to December. The remaining native vegetation forms a mosaic consisting of semideciduous forest and savanna (locally named ‘Tabuleiro’, [Barbosa and Thomas 2002](#)), both types recognized as part of the Brazilian Atlantic forest ([IBGE 2008](#)). The transition between forest and savanna is sharp and clear, with differences in terms of vegetation structure and taxonomic composition ([Andrade-Lima 2007](#); [Barbosa et al. 2011](#); see supplementary material, including photos). Regionally, Leguminosae, Rubiaceae and Asteraceae are the most species-rich families ([Barbosa et al. 2011](#)).

Sample design and floristic inventory

In our focal landscape, we selected 23 vegetation patches (11 forests and 12 savannas) without visible signs of human disturbances such as fire and timber extraction. Patches were at least 1 km apart and in each we established a 300 m² plot comprised of three parallel transects of 2 × 50 m that were 10 m distant from each other, summing up to a total sampled area of 3300 m² of forest and 3600 m² of savanna. All trees and shrubs with diameter at breast height (DBH) > 7.5 cm were sampled and identified to the species level. We checked for families and synonyms in our species list according to

the Brazilian Flora (Brazilian Flora 2020). Plant vouchers are available at the UFP Herbarium, Federal University of Pernambuco, Brazil. In each plot, a single soil sample (0–20 cm deep) was obtained by mixing nine sub-samples, three from each transect (at the points 0, 25 and 50 m). Soil samples were analyzed for physicochemical properties, following the procedures recommended by the Brazilian Ministry of Agriculture for soil analyses ([Embrapa 1997](#)). These attributes are associated to different soils properties, such as soil texture, water availability and soil fertility ([Table 1](#)); important factors relative to plant species distribution and spatial organization of plant assemblages.

Plant functional traits

We examined five leaf functional traits: leaf area (LA), specific leaf area (SLA, leaf area per unit dry mass), leaf dry matter content (LDMC, leaf dry-matter content per unit of fresh mass), leaf thickness and leaf succulence (leaf water content per unit area), following [Pérez-Harguindeguy et al. \(2013\)](#). We adopted these traits because they have been widely recognized as valuable indicators of species’ responses to variation in soil conditions and resource availability ([Hodgson et al. 2011](#); [Jager et al. 2015](#); [Pérez-Harguindeguy et al. 2013](#); [Wilson 1999](#)). Mean values of leaf traits change from sapling to adult, but the rank of species tends to be consistent across ontogenetic stages ([Kitajima and Poorter 2010](#)). Thus, we measured leaf traits on saplings (1.5–3 m height) to calculate representative mean trait values for species (e.g. [Katabuchi et al. 2012](#)).

Table 1: soil physicochemical properties (mean \pm SD) exhibited by forest and savanna stands in a vegetation mosaic in the Atlantic forest of northeastern Brazil

Soil attributes	Forest	Savanna	<i>P</i> (<i>t</i> test)
Organic matter (g/kg)	29.06 \pm 20.81	11.08 \pm 5.37	0.01
Apparent density (g/cm ³)	1.46 \pm 0.008	1.56 \pm 0.04	< 0.01
True density (g/cm ³)	2.56 \pm 0.03	2.59 \pm 0.02	0.07
Fine sand (%)	15.09 \pm 5.90	24.16 \pm 6.30	< 0.01
Silt (%)	4.09 \pm 3.08	2.58 \pm 2.23	0.19
Clay (%)	9.63 \pm 2.94	7.41 \pm 2.06	0.04
Residual moisture (%)	1.88 \pm 0.58	1.39 \pm 0.31	0.02
Permanent wilting point (0.33 Atm)	11.3 \pm 4.18	7.23 \pm 1.76	0.01
Field capacity (15 Atm)	5.09 \pm 1.71	3.17 \pm 0.75	< 0.01
Water availability (mm/cm)	0.91 \pm 0.37	0.63 \pm 0.16	0.04
P (mg/dm ³)	2.18 \pm 0.60	1.91 \pm 0.28	0.20
pH (H ₂ O)	4.59 \pm 0.46	5.08 \pm 0.23	< 0.01
Ca (cmolc/dm ³)	0.74 \pm 0.59	0.57 \pm 0.32	0.41
Mg (cmolc/dm ³)	0.73 \pm 0.21	0.59 \pm 0.25	0.16
Na (cmolc/dm ³)	0.04 \pm 0.01	0.03 \pm 0.00	0.06
K (cmolc/dm ³)	0.05 \pm 0.01	0.05 \pm 0.01	0.85
Al (cmolc/dm ³)	0.57 \pm 0.69	0.27 \pm 0.21	0.16
H (cmolc/dm ³)	6.13 \pm 2.85	2.93 \pm 1.36	< 0.01
Sum exchangeable bases (cmolc/dm ³)	1.65 \pm 0.97	1.26 \pm 0.57	0.25
Cation exchange capacity (cmolc/dm ³)	8.46 \pm 3.41	4.51 \pm 1.89	< 0.01
V (%)	20.00 \pm 9.46	28.41 \pm 0.09	0.03
Al saturation (%)	33.09 \pm 16.41	22.16 \pm 9.52	0.07

Atm = standard atmosphere.

We analyzed leaf traits for only 70% of the species recorded in the floristic inventory, because of the difficulty in finding saplings with healthy leaves for some rare species. Species-level trait scores were obtained by measuring one leaf per individual across one to 23 individuals (mean = 6.4) per species, selected based on the absence of signs of severe herbivory or other physical damage, following previously established sampling protocols (Cornelissen *et al.* 2003; Pérez-Harguindeguy *et al.* 2013). For species with compound leaves, the smallest photosynthetic unit was taken, as adopted elsewhere (e.g. Lohbeck *et al.* 2012). After the collection of plant materials, leaves were rehydrated before trait measurement; otherwise, differences in trait values would reflect the environmental conditions at the moment of collection (Garnier *et al.* 2001). We did this by putting leaves and leaflets between moist paper towels for 24 h at 4°C (Ryser *et al.* 2008). Leaf area (mm²) was measured on scanned images using the software package ImageJ (Rasband 2008). Leaf mass was calculated before and after drying at 60°C to a constant weight. Leaf thickness (mm) was measured with a digital caliper, avoiding thick veins. Finally, we calculated the other traits: SLA (m² kg⁻¹) as saturated leaf area divided by dry mass; LDMC (mg g⁻¹) as leaf dry weight divided by water-saturated fresh weight; and leaf succulence (mg cm⁻²) by subtracting leaf dry mass from water-saturated fresh weight and dividing by leaf area.

Data analysis

We examined differences in soil and species richness between forest and savanna plots with Student's *t* tests. To test the hypothesis that forest and savanna plots were different in species composition we performed a non-metric multidimensional scaling (NMDS) ordination of all 23 plots using a Bray–Curtis dissimilarity matrix of species composition (Krebs 1989). To identify potential effects of the spatial configuration of vegetation patches on patterns of species similarity among plots, we verified the correlation of the species abundance matrix with the linear distance between plots via a Mantel test (Legendre and Fortin 1989), and found no effect of distance on species similarity. We tested the correlation of the matrix of species abundances per plot with the matrix of soil features controlling for the effect of the distance between plots using a Partial Mantel test, as available in the software PASSaGE (Rosenberg and Anderson 2011). We applied the Monte Carlo method, with 999 random permutations, to evaluate the test significance (Zar 2010). We used Euclidian distance in the three matrices.

To describe the functional trait composition of plant assemblages within each plot, each functional trait was scaled up from species to community level using the community weighted mean (CWM; Garnier *et al.* 2004; Lavorel *et al.* 2008), which can be considered as a community-level average value.

We also calculated the Rao's quadratic entropy (RaoQ) of each community (Rao 1982). While the CWM can be used to describe changes in the functional composition of plant communities due to environmental selection, the RaoQ is applied to examine patterns of trait convergence and/or divergence (Ricotta and Moretti 2011). To assess whether the observed RaoQ (RaoQ_{obs}) values of each plot were different than those that would be expected by chance (given the landscape species pool), we used a null model in which the occurrence of the species in each area was randomized, while maintaining the richness of each assemblage and the total abundance of each species. Thus, we obtained 1000 RaoQ randomized values (RaoQ_{null}) for each plot. To assess the direction and magnitude of non-random patterns of trait distribution in relation to that expected by chance, we calculated for each plot the standard effects size (SES): $SES\ RaoQ = (RaoQ_{obs} - RaoQ_{null}) / RaoQ_{SD}$; where RaoQ_{null} is the mean and RaoQ_{SD} is the standard deviation of 1000 randomized communities (Gotelli and Graves 1996). SES RaoQ values lower than zero indicate that the trait distribution patterns are less divergent than would be expected by chance, showing functional convergence of traits. On the other hand, positive values reflect plot trait distributions more divergent than would be expected by chance, a pattern commonly associated with limited similarity as a result of competitive interactions. Values of zero indicate that the dispersal of the attributes of the species in the area is no different than would be expected by chance (see Gómez et al. 2010; Hidasi-Neto et al. 2012). We adopted SES RaoQ instead of simply RaoQ values in regression analyses because, although this functional diversity metric is not directly correlated to species richness, this is a pairwise metric and thus the range of possible values is expected to decrease with species richness. Therefore, to allow comparative analyses, this potential bias must be removed by quantifying whether RaoQ values are higher or lower than expected given the observed species richness in each assemblage. These analyses were performed using package 'FD' in R (v 3.1 R; R Foundation for Statistical Computing, Viena, AT). Cross-habitat CWM and SES RaoQ scores were also compared between vegetation types with Student's t tests.

Finally, we investigate potential relationships between soil attributes and the functional trait composition of plant assemblages. First, we eliminated soil attributes that were potentially redundant and highly correlated. Second, the remaining attributes (Table 2) were integrated into a principal component analysis (PCA). The first two axes of the PCA ordination considering both habitats and combining variables related to bulk density, nutrient availability, and exchangeable Aluminum explained 74.8% of the variance in soil attributes (46.08% and 28.72%, respectively; Table 2), a proportion higher than the 46% expected by the broken stick model. Finally, we assessed the relation of the first axis of the PCA (high load for permanent wilting point, Mg, CEC, bulk density and Al) with CWM of leaf functional traits and SES RaoQ, to test for continuous change in community functional

Table 2: soil attributes used in principal component analysis (PCA) showing the correlation of the variables with the first axis

Soil attributes	PC1
Bulk density	-0.389
Permanent wilting point	0.420
pH	-0.226
Ca	0.301
Mg	0.409
Al saturation	0.166
S	0.348
CEC	0.444
K	0.132

properties in response to soil factors. As abrupt changes/differences between forest and savanna vegetation in response to soil factors are expected, differences were examined via four-parameter logistic regressions, i.e. a non-linear model with a sigmoidal shape and appropriate to fit to threshold curves (Pinheiro and Bates 2000; Morante-Filho et al. 2015). Analyses were performed in SigmaPlot 12.0.

RESULTS

Savanna and forest habitats differed greatly in terms of soil attributes (Table 1). On average, forest soils had two and half times the amount of organic matter, 45% higher water availability, 30% more clay, lower pH and 90% higher cation exchange capacity compared to savanna soils. The first axis of the PCA, used in further analyses, described a gradient from dense soils with low nutrient availability to soils with lower density and higher nutrient availability (Table 1).

A total of 2592 woody plants belonging to 188 species were recorded across the 23 plots; 1605 individuals and 128 species in forest and 987 individuals from 60 species in savanna plots (supplementary Table S1). Vegetation types differed in species richness and stem density (supplementary Table S2). Savannas exhibited on average half of the species richness recorded in forests: 14.08 ± 4.75 versus 29.54 ± 5.98 ($P < 0.001$). Also, stem density ($n\ ha^{-1}$) were significantly lower in savannas than in forests: 100.25 ± 41.87 versus 160.08 ± 49.23 ($P = 0.004$). Vegetation types also differed in taxonomic composition. Only 23 species (12.2%) were common to both habitats (supplementary Table S1). Plots from savannas and forests were well segregated into two groups in the non-metric multidimensional scaling (NMDS) ordination, which exhibited a low stress level (0.11; Fig. 2). Plot-level species similarity did not correlate with geographical distance among plots according to the Mantel test ($P = 0.54$), but did correlate with all soil attributes ($P \leq 0.001$; 999 permutations; Partial Mantel test).

In addition to differences in soil, species richness and taxonomic composition, savanna and forest habitats supported plant assemblages with large differences in functional trait

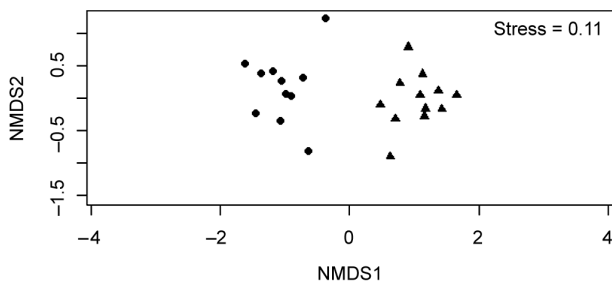


Figure 2: non-metric multidimensional scaling ordination (NMDS) based on Bray-Curtis taxonomic similarity of woody plants for 23 plots in forest (black circle) and savanna (black triangle) patches in the Atlantic forest, northeastern Brazil.

composition according to the CWM leaf traits (Fig. 3; supplementary Fig. S1). Specifically, savanna assemblages exhibited greater leaf thickness ($P \leq 0.0006$) and leaf succulence ($P \leq 0.0001$), while forest assemblages presented larger leaf area ($P \leq 0.0002$) and specific leaf area ($P \leq 0.0006$). On the other hand, the two habitats did not differ in terms of leaf dry matter content (Fig. 3). Collectively, these differences implied distinct functional trait composition. Soil attributes collapsed into the first PCA axis, and this axis was significantly related to most community-level functional measures, explaining up to 49% of the variation according to four-parameter sigmoidal regressions (Fig. 3). Further, forest and savanna vegetation were clearly composed by distinct plant functional trait composition separated by an abrupt threshold in response to soil attributes (Fig. 3). The decrease in soil density and increasing availability of nutrients (i.e. first PCA axis) correlated positively with leaf area and specific leaf area, and negatively with leaf succulence and thickness (Fig. 3). There was no significant relationship with leaf dry matter content. Plant assemblages differed in terms of RaoQ functional diversity ($P < 0.001$), with forest showing more of a convergent pattern (i.e. negative deviation from random expectation) than did savanna vegetation (Fig. 3). All forest plots exhibited effect sizes for RaoQ lower than zero, indicating that the attributes were less divergent than expected by chance; i.e. functional convergence of attributes. Conversely, half of savanna plots exhibited functional convergence while the other half exhibited scores indicating trait dispersion (Fig. 3). Finally, soil PC1 negatively correlated with RaoQ standardized effect size (Fig. 3).

DISCUSSION

Our results suggest that within a landscape exposed to the same climatic conditions, vegetation types can largely differ in terms of soil conditions, assemblage structure, taxonomic and functional composition. More precisely, forest soils are less dense, contain more organic matter and are more humid and acid, with forest and savanna plant assemblages exhibiting a small overlap in species composition, functional diversity

and trait distribution. Moreover, savanna supports plants with smaller, more succulents and thicker leaves with higher leaf mass per area, and exhibit some signals of trait convergence. On the other hand, forest plant assemblages are marked by a clear trait convergence towards more acquisitive strategies. Soil attributes associated with water and nutrient availability correlate with taxonomic and functional community properties, and thus appear to influence the spatial organization of plant assemblages in Atlantic forest mosaics.

These findings support key theories relative to patterns and mechanisms of plant assembly and the spatial organization of assemblages, particularly in the context of savanna–forest boundaries or mosaics. First, at landscape scale, plant assemblages do not consist of random sets from the regional flora (Davies *et al.* 1998; Katabuchi *et al.* 2012). Instead, they consist of reasonably predictable taxonomic and functional subsets, with a clear distinction between savanna and forest stands (see Dantas *et al.* 2013; Ruggiero *et al.* 2002). Such a deterministic assembly process results in differences beyond those in simple community-level attributes such as species richness and taxonomic composition. In fact, our findings support the notion that there is a profound functional distinction among assemblages at relatively small spatial scales, including leaf trait profile and related scores of functional diversity (see Dantas *et al.* 2013; Laureto and Cianciaruso 2015), with soil attributes playing an ecological role at larger spatial scales than local plots; i.e. landscape and regional scales (Dee and Ahn 2012; Katabuchi *et al.* 2012).

Although we did not explicitly examine the underlying mechanisms, it is reasonable to speculate that soil conditions are imposing some ecological filters on the establishment and performance of plant species, and thus operating as an assembly forces at the landscape scale as mentioned elsewhere (Furley 1992, 2007; Katabuchi *et al.* 2012; Laureto and Cianciaruso 2015; Moreno and Schiavini 2001; Martins *et al.* 2006; Pringle *et al.* 2016; Ruggiero *et al.* 2002). In other forest–savanna mosaics, the low supply of soil nitrogen, phosphorus and calcium seems to limit plants and thus the encroachment of forests upon savanna vegetation (Nardoto *et al.* 2006; Pellegrini 2016; Silva *et al.* 2013). Here we did not measure soil nitrogen, while soil phosphorus and calcium did not present significant differences between forest and savanna soils. However, our focal soils differed in terms of attributes related to fertility (e.g. CEC, pH, base sum) and to water availability (e.g. bulk density) as savanna is contrasted to forest.

As expected in response to the higher fertility and water availability, forest assemblages exhibited a signal of functional convergence towards more acquisitive resource-use strategies, while savannas were more associated with conservative plant strategies. Note that ‘conservative leaves’ (Wright *et al.* 2004; Westoby *et al.* 2002) have been widely interpreted as a responsive strategy to deal with resource scarcity (Jager *et al.* 2015; Reich 2014), and trait convergence has been interpreted as evidence of ecological filtering (Cornwell *et al.* 2006; Keddy 1992). Although leaf nutrient concentration was not

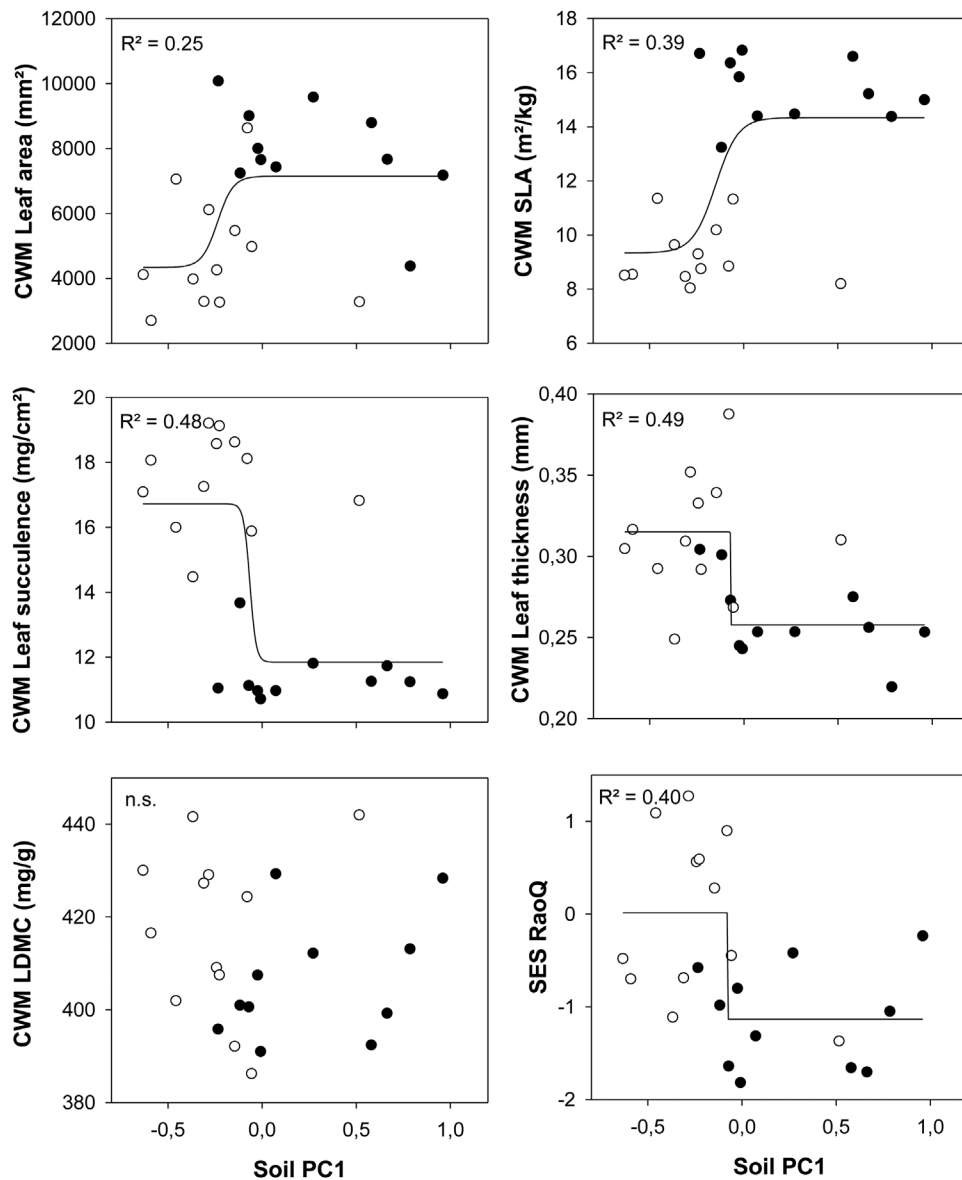


Figure 3: relationship between the first axis of Principal Component Analysis (PC 1) of soil attributes and functional properties of tree assemblages (community-weighted trait mean – CWM of leaf traits and the standard effect size of RaoQ functional diversity – SES RaoQ) in the Atlantic forest, northeastern Brazil. Empty circles represent savanna and filled circles forest plots. Only significant sigmoidal trends between PC 1 and functional properties are indicated ($P < 0.05$, in all cases). LDMC = leaf dry mass content; SLA = specific leaf area.

examined, i.e. a key feature that generally distinguish forest and savanna species and explain distinct effects from soil conditions (Pellegrini *et al.* 2014; Silva *et al.* 2013), leaf nutrient concentration is expected to be closely related to some morphological traits, such as specific leaf area (Díaz *et al.* 2016; Wright *et al.* 2004) as measured here. Plants with more acquisitive strategies tend to present higher SLA and also leaf nutrient concentration (e.g. N and P), reflecting its higher metabolic rates (Reich 2014; Wright *et al.* 2004).

Collectively, these findings support the hypothesis that soil-mediated filtering is one of the assembly forces in this Atlantic forest mosaic and reinforces the notion that the

distribution of forest and savanna is influenced by soil attributes via filtering (see Furley 1992; Ruggiero *et al.* 2002; Hoffman *et al.* 2004). It is worth considering that vegetation itself can alter soil conditions, with increased nutrient availability under forest trees due to higher litter amount and quality (Pellegrini *et al.* 2014) sometimes making unclear whether soil conditions determine the distribution of vegetation types or vice-versa. However, our focal soils differ in terms of genesis and texture with a higher percentage of fine sand in savanna due to coastal sediments deposited by winds (i.e. wind-blow sand, see Oliveira Filho and Carvalho 1995; Andrade-Lima 2007). Thus, it is reasonable to propose that

some soil conditions are permanently limiting the establishment of forest species and thus further modifications of soil properties that would allow forest expansion, such as higher nutrient availability (see Pellegrini *et al.* 2014; Silva *et al.* 2013). This perspective is in accordance with local researchers, which have considered the presence/persistence of these savanna-like patches associated with the occurrence of sandy soils and the stressful conditions they impose to plants (Andrade-Lima 2007; Barbosa *et al.* 2011).

We shall mention that half of our focal savanna assemblages did not exhibit signals of convergence, suggesting that in addition to soil-related filtering other mechanisms may be affecting plant assembly. In the lack of marked seasonality, blowdown (Australia) and intense herbivory by large-bodied vertebrates (African savannas), we shall speculate about the existence of other assembly forces. Recently, it has been proposed that the pressure of insect herbivore on seedlings (and soil type) may act as a biological filter, since tissue loss cannot be compensated in the nutrient-poor soils of savanna-like vegetation (Fine *et al.* 2004). Alternatively/ additionally, we shall speculate that past vegetation fires, although not acknowledged by local residents, might have been sufficiently frequent to reduce nutrient stocks or soil fertility below forest species requirements (see Barbosa *et al.* 2011; Silva *et al.* 2013). In this perspective, savanna stands might persist via a closed nutrient cycling (Pellegrini *et al.* 2014; Silva *et al.* 2013). In fact, fire has long been recognized as an assembly force operating in savanna–forest mosaics, maintaining two alternative stable states with distinct taxonomic and structural characteristics (Dantas *et al.* 2013) or exposing the soil to the erosive action of winds, what decreases water absorption and the persistence of heterogeneous landscapes (Ravi *et al.* 2009). On the other hand, savanna–forest mosaics can persist in the lack of fire regimes (Hoffman *et al.* 2012).

In synthesis, savanna–forest mosaics in the Atlantic forest region represent spatially organized plant assemblages distinguished by a comprehensive set of community-level attributes, from taxonomic to functional attributes, with evidence for a community-level threshold separating two vegetation states, with distinct functional characteristics associated with different edaphic conditions. Plant assembly emerges as influenced by deterministic processes, with soil-related environmental filtering probably playing a tangible role by affecting particular ecophysiological strategies, such as conservative plants with their small and dense leaves favored in savannas, and the opposite being true in forest stands, which harbor plants with more acquisitive strategies. This reinforces the role played by deterministic forces in the assembly of plant communities at landscape scales, particularly through soil-mediated filtering, including the delimitation of savanna–forest boundaries and mosaics. Future studies should investigate the contribution of complementary forces (e.g. fire) and the relative importance of soil resources, such as water and nutrients, in plant assembly.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Plant Ecology* online.

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