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# Water availability drives gradients of tree diversity, structure and functional traits in the Atlantic–Cerrado–Caatinga transition, Brazil

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## Abstract

### Aims

Climate and soil are among the most important factors determining variation in tree communities, but their effects have not been thoroughly elucidated to date for many vegetation features. In this study, we evaluate how climate and soil gradients affect gradients of vegetation composition, species diversity and dominance, structure and functional traits (seed mass and wood density) using over 327 000 trees in 158 sites distributed along environmental gradients in the transitions among the Atlantic forest, Cerrado and Caatinga in Minas Gerais State (MG), Brazil (nearly 600 000 km<sup>2</sup>).

### Methods

Gradients in species, genus and family abundance in addition to basal area, stem density, species diversity (Fisher's alpha), dominance percentage, seed mass and wood density were correlated using multiple regressions with environmental variables, as summarized in four principal component analysis axes (two climatic—precipitation seasonality and temperature range—and two edaphic—soil

fertility and soil moisture). Additionally, ordinary kriging maps were used to better illustrate the gradients.

### Important Findings

Multiple regression models indicate that all variables but dominance percentage were affected by one or more of the environmental gradients, but the average  $R^2$  was low (26.25%). Kriging maps reinforced the patterns observed in the regression models. Precipitation seasonality and soil moisture gradients were the most important gradients affecting vegetation features. This finding suggests that water availability is an important determinant of vegetation features in these vegetation transitions.

**Keywords:** climate, environmental gradient, soil, southeastern Brazil, vegetation

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## INTRODUCTION

One of the most important challenges facing plant ecology is to understand and predict the variations of plant communities across environmental gradients. By examining how species abundance, structure and functional traits vary across spatial abiotic shifts, especially in broader scales, we can begin to unravel the processes driving such ecological transitions and provide more realistic scenarios in response to climate and land-cover change.

Vegetation transitions, or ecotones, are transitional border regions between communities, ecosystems or biomes, reflecting both local and regional changes in abiotic conditions (Kark and van Rensburg 2006; Oliveras and Malhi 2016). The transition between open vegetation physiognomies and different forest types has been described in several regions of the Neotropics (Hirota *et al.* 2011; Hoffmann *et al.* 2012a, b; Ratter 1992; Staver *et al.* 2011; Staal and Flores 2015). In central-eastern South America, a remarkable transition is found between vegetation belonging to the so-called ‘open dry diagonal,’ or simply ‘dry diagonal’ (Prado and Gibbs 1993; Werneck *et al.* 2012), and the Atlantic Forest (Oliveira-Filho and Ratter 1995; Oliveira-Filho and Fontes 2000). The dry diagonal represents a complex vegetation transition between its two main components: (i) the Seasonally Dry Tropical Forests (SDTFs), following the concept of Murphy and Lugo (1986), present in Caatinga in northeastern Brazil and in Chaco in southwestern South America and as patches of deciduous and semideciduous Atlantic forests along the Paraguay-Paraná Basin (Pennington *et al.* 2006; Werneck 2011); and (ii) the Neotropical Savanna (Cerrado) in central Brazil. The vegetation components of the “dry diagonal” share basic ecological conditions, being seasonally stressed by up to 10 months of drought (Dalmagro *et al.* 2014; Murphy and Lugo 1995; Pennington *et al.* 2006). Although these vegetation types are among the most fragmented and threatened ecosystems in the world (Miles *et al.* 2006), presenting a complex mosaic-types distributions with high species endemism, they have received far less attention than tropical rainforest in recent decades (da Silva and Bates 2002; Werneck 2011).

Several controversial attempts to understand the origin and evolution of this biogeographic picture were made (Mayle 2004; Neves *et al.* 2015). The combined influences of Paleogene–Neogene geological processes and the Quaternary climatic-vegetation fluctuations are hypothesized to have generated the current range of Seasonally Dry Tropical Forest found in South America (Pennington *et al.* 2006). Therefore, the current patches of SDTF in South America may represent a relic of a wider seasonally dry forest biome that reached its maximum expansion during the driest phases of the Pleistocene covering the dry diagonal, the dry inter-Andean valleys in Peru and Ecuador (Prado and Gibbs 1993; Prado 2000), and even possibly covering lands in the Amazon interior in areas of fertile soil (Pennington *et al.* 2000). These authors interpret the findings of repeated patterns of

fragmented populations as evidence that the current dry forest nuclei constitute remnants (i.e. refugia) of such former single formations, the Pleistocene Dry Forest Arc, split by vicariance after the subsequent climate and geological changes (for alternative hypotheses see Mayle 2004). As in South America, SDTFs grow under basically the same climatic conditions as the Cerrado, and recent adaptive shifts in the late Miocene (Cerling *et al.* 1997) driven by fire dynamics were identified as responsible by current Cerrado floristic and physiognomic distinctions from SDTFs (Dexter *et al.* 2015; Oliveira-Filho and Ratter 2002; Werneck *et al.* 2012).

In southeastern Brazil, Minas Gerais State harbors the transition among the Atlantic, Cerrado and Caatinga Brazilian domains. This transition represents a highly intricate mosaic of SDTFs, savanna and even rain forest in the extreme southern part of the state. At a large scale, this transition seems to be climate-driven, taking for instance the transition from the rain forest in the south towards the SDTFs in the center, north and west (Oliveira-Filho and Fontes 2000). However, at a smaller scale, the edaphic influence is conspicuous, as patches of different biomes exist in each of these domains under similar climate conditions, but different soil conditions (e.g. galleries and enclaves) (Oliveira-Filho and Ratter 1995; Ratter 1992). Therefore, local boundaries between the forests and the open-formations (Cerrado) in such transitions are related to soil conditions, with forest roughly occurring on more fertile soils and open-formation on dystrophic and well-drained soils (Coelho *et al.* 2016; Ratter 1992) and more frequent fires (Hoffmann *et al.* 2012b). These different drivers, acting simultaneously, result in a complex vegetation gradient that has been well-studied in terms of the occurrence of tree species but is poorly explored using abundance data. In this case, the use of species abundance data represents a step forward in the floristic understanding of these vegetation transitions by allowing a more accurate description of the vegetation patterns (population distributions and community diversity) over gradients. Moreover, observing the relative abundance at different taxonomic resolutions (species, genus and family) makes it possible to evaluate the consistency of the environmental drivers.

Among several structural parameters used to describe tree community patterns, stem density and basal area seem to be strongly climate-soil driven (Arellano *et al.* 2014; Magnago *et al.* 2015; Toledo *et al.* 2011). In tropical forests, they tend to be higher with a shorter dry season (Murphy and Lugo 1986; Toledo *et al.* 2011) and richer soils (Quesada *et al.* 2012; Wright *et al.* 2011). Therefore, in addition to providing a sense of the biomass and ecosystem productivity (Vieira *et al.* 2004), those parameters are also important to elucidate the outcomes of processes structuring a wide range of vegetation communities, and the main environmental drivers of such patterns (Toledo *et al.* 2011).

In addition to the composition and structural parameters, species functional traits allow us to understand the underlying determinants of species performance in a given environment

and to estimate the importance of environmental filtering in determining the assembly of tropical forests (Poorter *et al.* 2008). Traits such as seed mass and wood density seem to respond to environmental conditions and have been called ‘functional response traits’ (Lavorel and Garnier 2002; Prado-Junior *et al.* 2016). Sources differ on how seed size should be affected by stress gradients because seed mass is thought to reflect a tradeoff between viability and dispersal (Kitajima 2007). For instance, seeds are larger in the wetter areas or less dynamic forest in the Amazon (ter Steege *et al.* 2006), while larger seeds are also expected in stressful nutrient-limited environments (Lee and Fenner 1989; Mustart and Cowling 1992), such as the Cerrado. For wood density, there is a consensus on increasing density with environmental stress (King *et al.* 2006; Poorter *et al.* 2008; Reich 2014; Santiago *et al.* 2004).

In this study, we hypothesize that two main abiotic gradients drive current vegetation transition patterns in Minas Gerais, Brazil (approximately 600 000 km<sup>2</sup>): (i) one related to climate seasonality, which increases towards the north, and (ii) one relative to soil fertility, which decreases towards the northwestern part of the state. We address the implications of these gradients for the relative abundance of tree taxa (species, genera and families), diversity, species dominance, structure (basal area and stem density) and community-weighted mean (CWM) functional traits of seed mass and wood density. We expect patterns of composition, diversity, structure and functional traits in tree communities in Minas Gerais to be consistent with the shifts in soil and climate. More specifically, we expect tree species diversity, basal area and density to increase towards the south of the state mainly due to the decrease of stressful climatic conditions (shortened drought period), and seed mass and wood density to be higher in the north in response to increasing drought and fertility.

## MATERIALS AND METHODS

### Data collection

Our dataset included 158 vegetation sites in Minas Gerais State, Brazil (Fig. 1) from three main sources: the Minas Gerais Forest Inventory (Scolforo *et al.* 2008), the Federal University of Lavras (CONFLORA group) and the Federal University of Uberlândia. Our dataset covered three Brazilian vegetation domains (Atlantic Forest, Cerrado and Caatinga) and six vegetation types (Rain Forest – RF, Seasonally Dry Tropical Forest semideciduous—SDTF\_SD, Seasonally Dry Tropical Forest deciduous—SDTF\_D, Cerrado *sensu stricto*—CE, Cerradão—CD and Swamp—SW) (online supplementary Table S1). The sample area in those inventories varied from 0.12 to 17.2 ha (average 1.9 ha). The minimum diameter at breast height (DBH) of the trees recorded was 5 cm. Taxonomy was standardized to family, genus and species according to TNRS (Boyle *et al.* 2013; <http://tnrs.iplantcollaborative.org>). The total number of trees recorded was 354 956, but we worked with a final number of 327 606 by not including unidentified trees.

### Environmental gradients

From the coordinates at each site, we obtained 19 WorldClim bioclimatic variables and site altitudes (Hijmans *et al.* 2005; <http://www.worldclim.org/bioclim>). Two depths (0–5 cm and 5–15 cm) of soil data—cation exchange capacity (CEC), Sand content (Sand), Clay content (Clay), Silt content (Silt), pH, and Organic Carbon (ocarbon)—were extracted from ISRIC—World Soil Information (Hengl *et al.* 2017). To confirm the existence of the environmental gradients we ran principal component analysis (PCA) for both climate and altitude (PCA Climate) and soil (PCA Soil) variables. We used the *rda* function of *vegan* R package (Oksanen *et al.* 2016) for running principal component analyses and both PCAs were scaled to unit variance. We considered the first two axes of each PCA as summaries of the variation in these abiotic components.

### Composition, diversity and structure variables

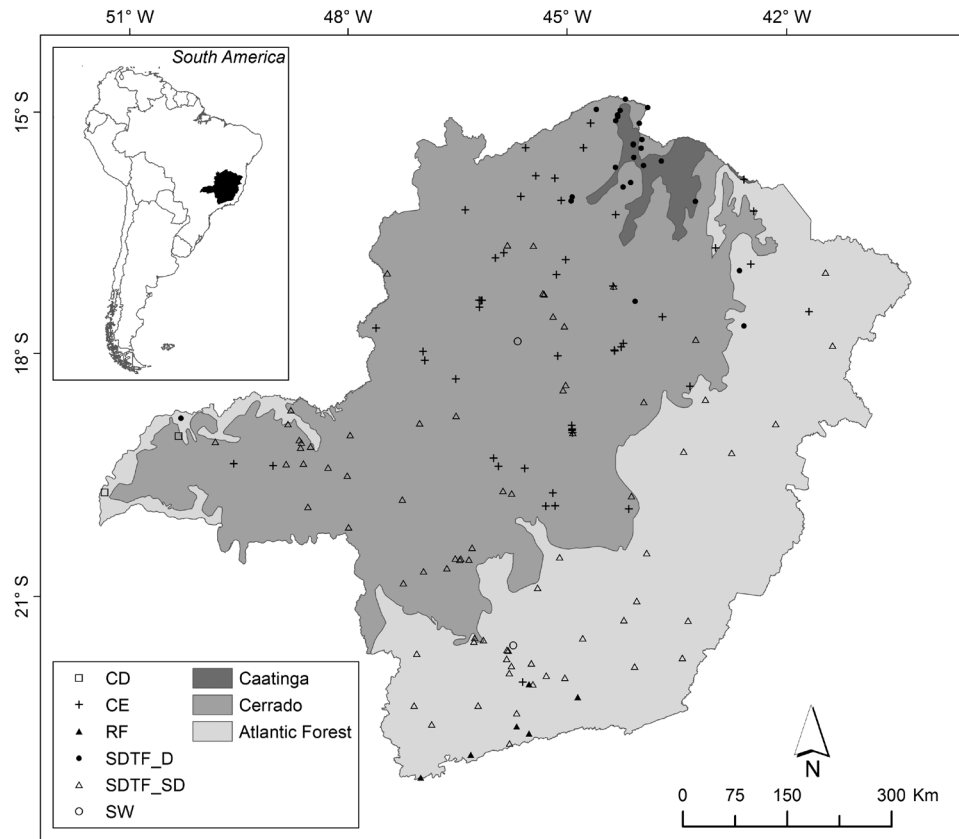
To access the turnover in species relative abundance we carried out detrended correspondence analysis (DCA) at different taxonomic resolutions (species, genera and families). We calculated Fisher’s alpha (Fisher *et al.* 1943) as a diversity index for each site and a dominance index (%Dom) as the number of individuals of the most abundant species in a site divided by the total number of individuals in this site. Structure was addressed in terms of basal area per hectare and the stem density (individuals per hectare). We used *vegan* R package (Oksanen *et al.* 2016) for diversity and ordination analyses.

### Community-weighted mean traits

We evaluated two functional traits that are important for responses as environmental conditions: community-weighted mean seed mass (CWM seed mass) and community-weighted mean wood density (CWM wood density). When calculating site scores for the functional tree traits, we followed ter Steege *et al.* (2006) and all individuals were counted. For seed mass, individuals were scored by genus and the trait values were obtained from SID-Kew (SID 2015). Eighteen genera (4.04% of the genera) were not found in this database. Wood density (oven-dried weight divided by green volume) was also scored by genus and the data were obtained from a global wood density database (Zanne *et al.* 2009; Global Wood Density Database, available online), which provided data for all genera recorded in the area.

### Multiple regression and ordinary kriging

To investigate the effects of the environmental gradients on vegetation composition gradients, species diversity and dominance, structural and functional variables, we used linear multiple regression. The four main environmental gradients (axes from the PCAs) were used as explanatory variables (tested by *t*-test) and each vegetation parameter as a response variable. To ensure that the models would be free of multicollinearity, the models were tested by the variance



**Figure 1:** location of the 158 sites in Minas Gerais State and their vegetation type classification. (Rain Forest—RF, Seasonally Dry Tropical Forest semideciduous—SDTF\_SD, Seasonally Dry Tropical Forest deciduous—SDTF\_D, Cerrado *sensu stricto*—CE, Cerradão—CD and Swamp—SW).

inflation factor (VIF). Explanatory variables with VIF lower than or equal to 10 are considered non-collinear (Dormann *et al.* 2013).

Finally, to better illustrate the variation in the vegetation variables, we mapped all variables using geostatistical interpolation (ordinary kriging). We checked for spatial dependency via an empirical semivariogram and fitted the Gaussian, Exponential and Spherical spatial models (Journel and Huijbregts 1978) using weighted least squares. Thus, the selection of the best spatial model was based on the cross-validation measurements (mean standardized error and root-mean-square standardized error) (Vieira 2000). The set of parameters of the best model for each variable were then used to proceed with the mapping (with a pixel size of 1 km<sup>2</sup>) by ordinary kriging.

We used geoR R package (Ribeiro and Diggle 2001) and ArcGis 10.1 (ESRI 2010) for geostatistical analysis.

## RESULTS

### Environmental gradients

The first axis of the PCA Climate explained 67.83% of the total variation and was regarded as a proxy for precipitation seasonality and total precipitation, separating the sites in rain

forest and deciduous forest (online supplementary Fig. S1a). The second axis explained far less variation (12.12%) and was determined mainly by the temperature (annual and diurnal) range, separating, for instance, semideciduous sites in the south from semideciduous sites in the Jequitinhonha (north-eastern) region. The first axis of PCA Soil explained 43.85% of the total variation in the soil data and is related to soil fertility and the second one explained 28.68% (online supplementary Fig. S1b). The second component was taken as a proxy of soil moisture, as it is related to soil texture and separated the deciduous sites from the rain forests in our dataset (see the PCA scores in online supplementary Tables S2 and S3). Therefore, the four main axes of the PCAs will hereafter be referred as Precipitation seasonality, Temperature Annual Range, Soil Fertility and Soil Moisture, respectively.

### Composition gradients

The first axis of the DCA species level analysis was long (eigenvalue = 0.7809) and represented the species turnover over a gradient between Cerrado and the deciduous forest in Caatinga. The second axis of the DCA (0.5175) reflected the variation within Deciduous and Semideciduous Forests in the Atlantic and Caatinga domains. The genus level DCA (eigenvalues: 0.6017 and 0.5503) displayed an approximation

between Cerrado and SDTF\_D, and at the family level (0.3391 and 0.3295), we observed that the three main groups (Cerrado, deciduous and semideciduous) were closer along the first axis. Atlantic forest was the most heterogeneous group in all scenarios and Cerrado the most homogeneous. The two main axes of the three DCAs will hereafter be referred to as species gradient (1 and 2), genus gradient (1 and 2), and family gradient (1 and 2), respectively (Fig. 2) (see the PCA scores in online supplementary Table S4).

### Regression and ordinary kriging

All the regressions between vegetation and environmental gradients were significant ( $F$ -test;  $P < 0.05$ ), except for the %Dom (Table 1). The average coefficient of determination ( $R^2$ ) was 26.25%, with the composition gradients (DCA axes) and Fisher's alpha having the highest values and the structural and functional trait variables the lowest ones. The models were free of multicollinearity as the VIF for the four explanatory variables (precipitation seasonality, temperature range, soil fertility and soil moisture) were lower than 10 (1.89, 1.04, 1.1 and 1.83, respectively). Precipitation seasonality and Soil moisture were more important for vegetation than Temperature Annual Range and Soil fertility according to the  $t$ -test.

All of the variables displayed spatial dependency fitted by different spatial models (see the semivariograms in online supplementary Fig. S2). The range of the fitted spatial models varied from 70 to 900 km. Longer ranges were found for the differentiation in species abundance (composition gradients) and diversity. On the other hand, basal area, stem density, seed mass and wood density displayed greater variances at shorter distances (shorter ranges) but maintained a pattern at longer distances. Especially for the functional traits, the maps displayed something of a 'bull's-eye' effect due to the shorter ranges of the spatial dependency. Overall, the kriging maps (Fig. 3) reinforced the results of the regressions, since the vegetation spatial patterns roughly coincide with the most important environmental variables (Precipitation seasonality and Soil moisture).

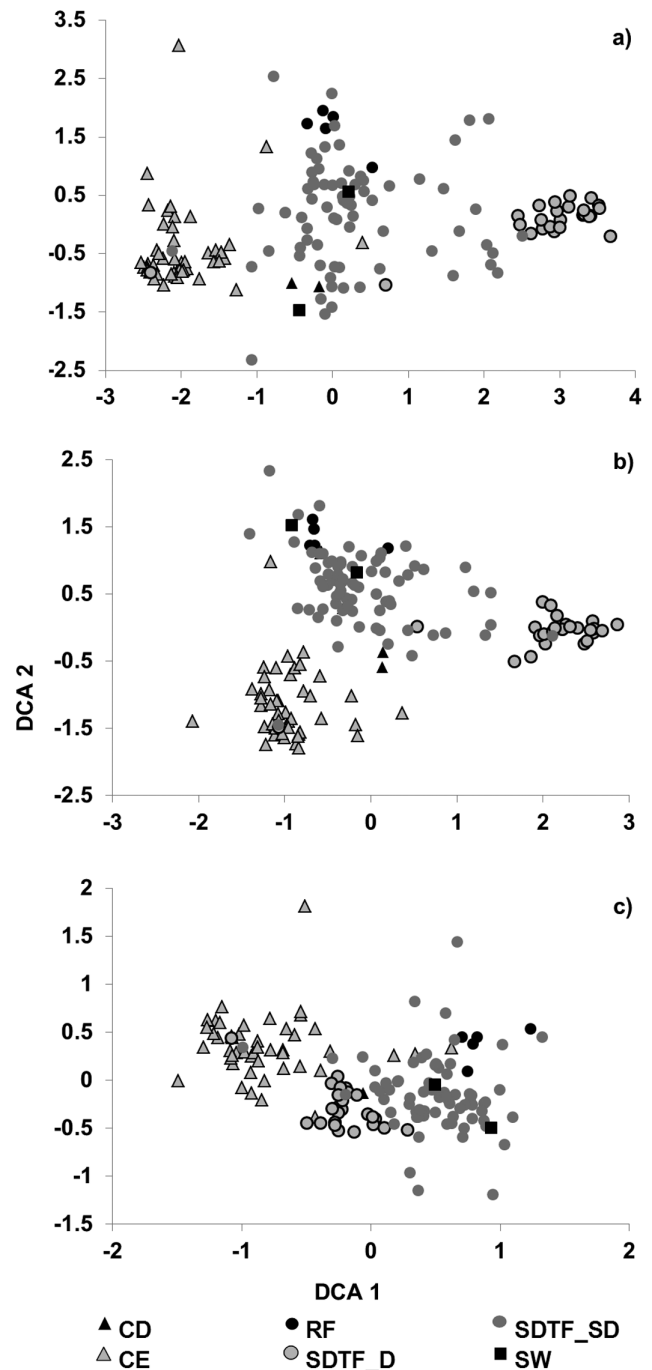
A combination between the regressions and maps led to the scheme presented in Fig. 4.

## DISCUSSION

This study aimed to evaluate to what extent patterns in vegetation attributes are driven by climate and soil in southeastern Brazil by correlating the attributes of diversity, structure and functional traits of tree communities in different vegetation types with abiotic environmental gradients (climate and soil). Our results showed the different roles played by the environmental drivers in each feature of the vegetation in Minas Gerais displaying highly complex patterns.

### Environmental gradients

Precipitation seasonality clearly displayed a gradient of sites of rain forests, semi-deciduous forests, Cerrado and deciduous



**Figure 2:** detrended correspondence analysis (DCA) ordination plots of the relative abundance of tree species (A), genera (B) and families (C) at 158 sites in southeastern Brazil. (Rain Forest—RF, Seasonally Dry Tropical Forest semideciduous—SDTF\_SD, Seasonally Dry Tropical Forest deciduous—SDTF\_D, Cerrado *sensu stricto*—CE, Cerradão—CD and Swamp—SW).

forests and its map illustrates this gradient, which has a north-south pattern (stronger seasonality in the north). Secondly, temperature annual and diurnal range seemed to be responsible for variations along longitude, as one can see in the

**Table 1:** linear multiple regression analysis (standardized coefficients) of vegetation composition gradients, species diversity and dominance, vegetation structure, and community-weighted mean functional traits variables against environmental variables (climatic and soil gradients) for 158 sites in southeastern Brazil. (Variables shaded in gray were significant—confidence level of 95%).

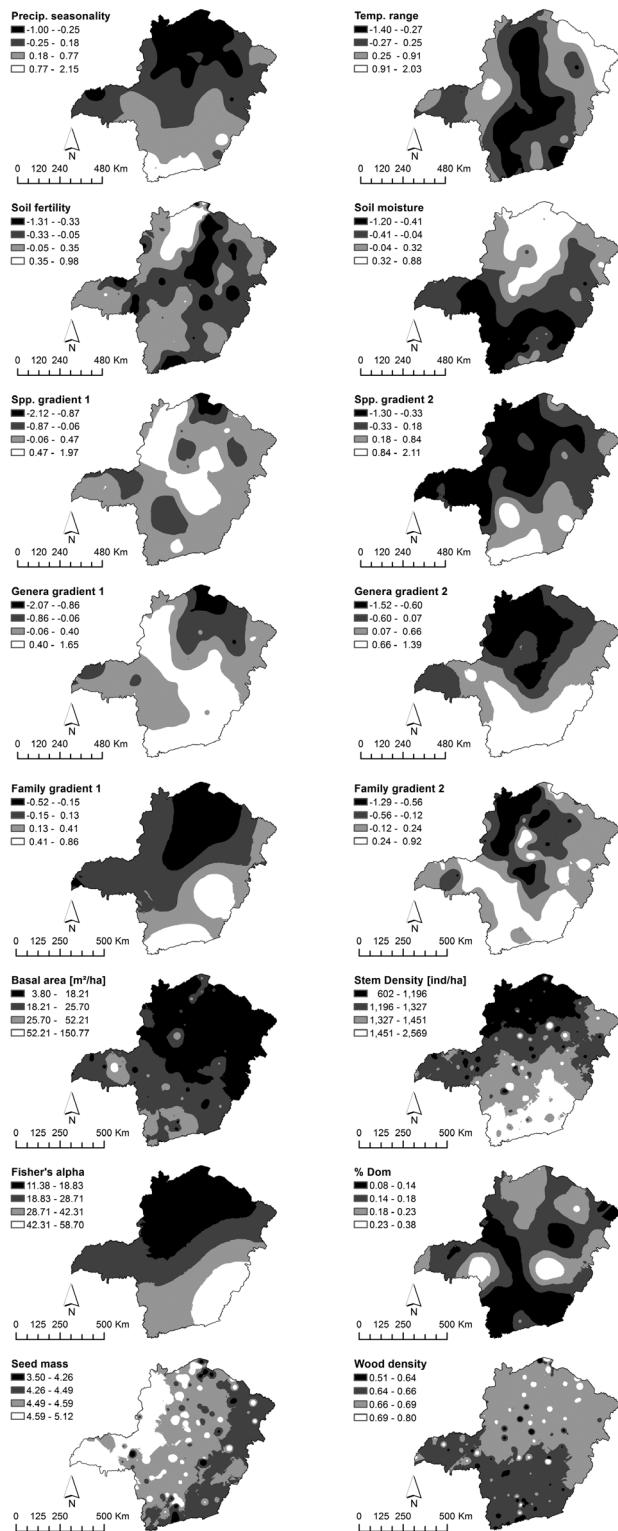
	Precip. seasonality	Temp. range	Soil fertility	Soil moisture	$R^2$	$P$ -value ( $F$ -test)
Spp. grad. 1	0.504	-0.004	0.203	0.243	15.45	3.393E-05
$P$ -value ( $t$ -test)	2.11E-06	0.953	0.010	0.017		
Spp. grad. 2	0.718	-0.152	-0.007	0.269	35.20	1.077E-13
$P$ -value ( $t$ -test)	2.51E-13	0.023	0.924	0.003		
Genus grad. 1	0.777	-0.038	0.184	0.193	42.71	< 2.2e-16
$P$ -value ( $t$ -test)	<2e-16	0.540	0.005	0.021		
Genus grad. 2	0.326	-0.016	-0.175	-0.315	39.27	8.386E-16
$P$ -value ( $t$ -test)	2.38E-04	0.803	0.009	3.09E-04		
Family grad. 1	0.855	-0.059	0.049	0.153	57.21	<2.2e-16
$P$ -value ( $t$ -test)	<2e-16	0.275	0.382	0.035		
Family grad. 2	0.010	-0.039	-0.289	-0.372	22.71	5.059E-08
$P$ -value ( $t$ -test)	0.920	0.591	1.53E-04	1.63E-04		
Basal area	0.139	-0.031	0.044	-0.275	14.72	6.290E-05
$P$ -value ( $t$ -test)	0.179	0.680	0.571	0.007		
Tree density	0.275	0.021	-0.123	-0.123	16.39	1.530E-05
$P$ -value ( $t$ -test)	0.008	0.777	0.115	0.222		
Fisher's alpha	0.241	-0.038	-0.038	-0.344	29.32	6.930E-11
$P$ -value ( $t$ -test)	0.011	0.589	0.594	2.57E-04		
%Dom	-0.072	-0.094	-0.078	0.122	4.03	0.176
$P$ -value ( $t$ -test)	0.512	0.247	0.346	0.256		
Seed mass	-0.247	-6.42E-04	0.198	-0.252	9.97	0.003
$P$ -value ( $t$ -test)	0.021	0.994	0.015	0.016		
Wood density	-0.279	0.183	0.183	0.047	17.23	7.370E-06
$P$ -value ( $t$ -test)	0.007	0.016	0.019	0.638		

(Precip. seasonality: precipitation seasonality; Temp. range: temperature range; Spp. grad. 1: species gradient—first axis of the DCA for species relative abundance; Spp. grad. 2: species gradient—second axis of the DCA for species relative abundance; Genus grad. 1: genus gradient—first axis of the DCA for genus relative abundance; Genus grad. 2: genus gradient—second axis of the DCA for genus relative abundance; Family grad. 1: Family gradient—first axis of the DCA for family relative abundance; Family grad. 2: Family gradient—second axis of the DCA for family relative abundance; %Dom: percentage of dominance—the number of individuals of the most abundant species in a site divided by the total number of individuals in this site; Seed mass: community-weighted mean seed mass; Wood density: community-weighted mean wood density).

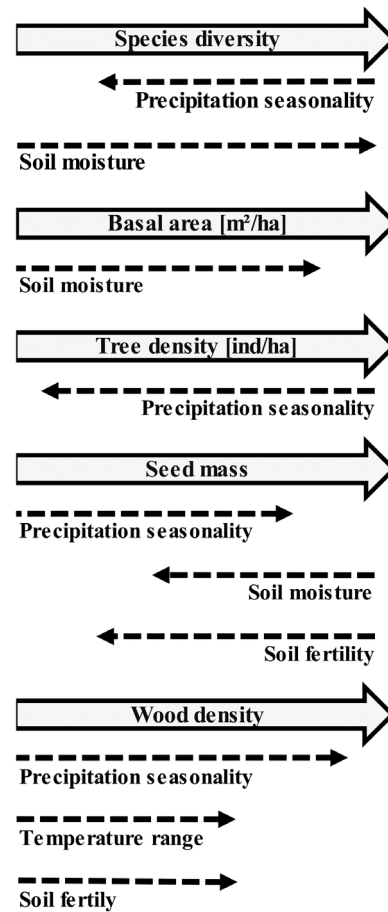
kriging map. The lower class in the temperature range map (the black one) coincided with the Espinhaço Range (altitude up to 1 700 m) (Fernandes *et al.* 2014), suggesting the effect of this mountain range on the regional climate, especially on the temperature ranges, which are higher in this region. In addition, the general pattern of the temperature range map roughly coincided with the Köppen climate classification for MG, with the two 'Tropical Zones' (Köppen's 'A') separated by a 'Humid Subtropical Zone' (Köppen's 'C') (Alvares *et al.* 2013). Soil fertility caused major a differentiation between deciduous forest—more fertile soils (de Albuquerque *et al.* 2012; Apgaua *et al.* 2014)—and Cerrado—more dystrophic soils (Coelho *et al.* 2016; da Silva and Batalha 2008). Soil moisture was responsible for differentiating the extremes of rain—higher soil moisture (Oliveira-Filho and Fontes 2000)—and deciduous forest—well-drained soils (Apgaua *et al.* 2014; de Albuquerque *et al.* 2012)—in the ordination.

### Composition and diversity gradients

Gradients in taxon composition (relative abundance) had different patterns for different taxonomic resolutions (species, genus and family). At the species level, we found a major differentiation between Cerrado and Deciduous forests, and the rain and semideciduous forests interleaved between them. The DCA first axis scores at the species level varied according to the precipitation seasonality and soil moisture. As the major differences were between Cerrado and dry forest, and they share some basic climatic conditions, subtle differences in the length of the dry season (slightly greater at deciduous forest) might contribute to differentiate them. Rain distribution acts as a selective force influencing the reproductive behavior of the plants and causing differential germination and mortality in the plant populations, especially in deciduous forest, with the predominant period of germination occurring during the rainy season (Araújo *et al.* 2007; dos Santos *et al.*



**Figure 3:** ordinary kriging interpolation maps of the variables considered in this study and the interval values for each class in the maps. (The class values of climate, soil and composition gradients represent site scores in the PCA and DCA analyses, respectively).



**Figure 4:** schematic diagram illustrating the relationships between the vegetation parameters and environmental gradients in southeastern Brazil. The length of the arrow represent the magnitude of the impact of the environmental gradient on each vegetation parameter.

2007; de Albuquerque *et al.* 2012). Regarding the soil, Cerrado is known as a soil climax vegetation (Pinheiro and Monteiro 2010), occurring mainly in well-drained soil with high Al levels (Ratter and Dargie 1992). Conversely, we have deciduous forest occurring in dry but highly fertile soils in northern MG (Apgaua *et al.* 2014). Those soil differences certainly filter species. For instance, many widespread dominant Cerrado genera, such as *Qualea* and *Eugenia* (Terra *et al.* 2017), are Al accumulators (Haridasan 2008; Jansen *et al.* 2002). In addition, the plant phylogenies presented by Simon *et al.* (2009) showed that Cerrado lineages are strongly associated with recent (4 Mya or less) adaptations to fire. Therefore, the synergistic interaction of all these factors (especially soil and fire) might be causing the differences observed here at the species level by selecting the species adapted to local conditions (da Silva and Batalha 2008).

The variation within deciduous and semideciduous forests and between semideciduous and rain forests at the species level (species gradient 2) are related to the temperature range and to

soil moisture. These forests present more idiosyncrasies related to altitude variation—especially semideciduous and rain forest (Eisenlohr and de Oliveira-Filho 2015; Oliveira-Filho and Fontes 2000)—and punctual soil and geological variation—mainly dry forest (Apgaua *et al.* 2014; Santos *et al.* 2012)—harboring a great species turnover. These ‘internal’ differences do not appear to reach Cerrado, which exhibits less species turnover, and they behave in a more stable way in regard to climate and soil moisture leading to a minor beta-diversity compared to forests in our dataset. Having less beta-diversity does not mean having little beta-diversity, as all three systems are reported to have great beta-diversity (Apgaua *et al.* 2014; Bridgewater *et al.* 2004; Franoso *et al.* 2016).

Despite all the differences shown at the species levels, the mutual influence between forest and savanna throughout the evolutionary history in our study region has been reported in the literature as occasional occurrences of species from a certain formation in another formation to which the species is less tolerant are not rare, especially in the edges and transitions (da Silva and Batalha 2008; de Albuquerque *et al.* 2012; Forni-Martins and Martins 2000; Simon *et al.* 2009). At the genus and family level, the three main vegetation types (Cerrado, semideciduous and deciduous) are closer, and we observed an approximation between Cerrado and Deciduous Forest in the DCA’s first axis. Simon *et al.* (2009) reported the existence of sister groups between the Cerrado and largely fire-free nearby wet forest, seasonally dry forest, subtropical grassland or wetland vegetation. For instance, the semideciduous forests are known for having strong links with the Cerrado at the genus and family levels, sharing important families such as the Rubiaceae and Melastomataceae (Oliveira-Filho and Fontes 2000). On the other hand, the relative importance of families such as the Myrtaceae and Fabaceae approximates the Cerrado and Deciduous forest at these taxonomic levels (Mendona *et al.* 1998; Pennington *et al.* 2006; Ratter *et al.* 2003). The Myrtaceae and Fabaceae are also important in semideciduous forests, especially at low altitudes (Fabaceae) (Oliveira-Filho and Fontes 2000).

A review of studies across environmental gradients found that the most common pattern is increasing species richness with gradients of water availability (Cornwell and Grubb 2003). We corroborate this pattern as the gradient in diversity (Fisher’s alpha) was highly correlated with the gradients of water availability in terms of both climate (the lower the precipitation seasonality, the higher the tree diversity) and soil (the higher the soil moisture, the higher the diversity). Therefore, in MG we observed a ‘counter-latitudinal’ pattern of tree species diversity. In the north of MG, drought can be interpreted as a strong environmental filter selecting species, as has been shown for other Neotropical regions (Esquivel-Muelbert *et al.* 2017). In the south, in less seasonal and more ‘favorable’ environments, more species can become established, leading to higher diversity. In addition, the internal variation in the south caused mainly by the topography may create more local niche opportunities (Leigh *et al.* 2004), increasing the diversity. Such patterns have an evolutionary

influence, since Atlantic forest, although contracted, remained forested throughout dry glacial times (Werneck *et al.* 2011), and this has potentially increased its relative diversity.

The percentage of dominance has not followed any environmental gradient, but the interpolations clearly show two regions of major dominance (white class in the interpolation map). The western one represents the effect of *Myracrodruon urundeuva* Allemo in patches of deciduous forest and the eastern one is *Eremanthus incanus* (Less.) Less. occurring in the region. Both of these species are among the most abundant tree species in these regions (Terra *et al.* 2017). In addition, it is possible to see a background trend of local dominance increasing towards the north, following the diversity pattern.

### Structure gradients

We observed vegetation structure patterns consistent with the literature. We found, in general, more basal area per hectare in the humid south and less in the dry north. The increase of basal area towards the west in the region better known as ‘Tringulo Mineiro’ is due to the existence in such regions of the Cerrado, a forest-like face of the Cerrado (Oliveira and Marquis 2002). The Cerrado is physionomically a forest but its species composition is related to Cerrado. Additionally, the Cerrado is one of the reasons we found a basal area significantly related to soil conditions, as this vegetation type has more basal area than Cerrado *sensu stricto* and typically occurs at dystrophic to mesotrophic soils (Neri *et al.* 2013; Oliveira and Marquis 2002). Another reason for the pattern presented is that deciduous forests up north, which have lower basal area per hectare, mainly as an effect of climate limitation (precipitation seasonality), occur in fertile soils (Apgaua *et al.* 2014).

With regard to density, we observed punctual differences within a general decreasing pattern towards the deciduous forest in the north. We found this pattern to be correlated to precipitation seasonality. Seasonally Dry forests usually have fewer individuals per area than humid ones (Murphy and Lugo 1986), mainly because the period of seedling recruitment is strongly restricted to the rainy period (de Albuquerque *et al.* 2012). The occurrence of a region of higher density in the northeast of MG is due to the effect of the transition from the Atlantic forest of coastal Bahia from evergreen to semideciduous, and then to deciduous forests up to a distance of 200–250 km inland (Saiter *et al.* 2015; Thomas *et al.* 2008). The occurrence of areas of lower density in the south is possibly due to anthropogenic interference. Human interference certainly produces long-lasting and complex effects on natural vegetation. Fragmentation (Santo-Silva *et al.* 2016) and human impacts (Pereira *et al.* 2015) might have masked some natural differences, especially in the Atlantic semideciduous and rain forests. For instance, Pereira *et al.* (2015) studying 20 areas in southeastern Brazil reported that forest structural parameters (basal area and tree density) are affected by cattle and outer roads. The presence of cattle in the forest fragments studied by Pereira *et al.* (2015) has a direct relationship with the trees that had larger diameters, suggesting that recruitment was affected

by trampling by livestock causing damage to smaller plants. In addition, outer roads lead to landscape changes and had a significant impact on the basal area and densities of less high trees.

### Functional traits gradients

We expected the CWM seed mass to increase towards the sites with lower precipitation seasonality, but instead, apparently, in semideciduous and rain forests where the environmental filter is weaker, we have a mix of seed sizes. Our results noted differences in the seed ecology between Cerrado and forest (semideciduous, deciduous and rain), with the CWM increasing towards Cerrado. Additionally, we found that CWM seed mass was related to both climate and soil conditions, with higher CWM seed mass in more seasonal sites and with lower soil fertility and soil moisture.

At a broader scale, our results seem to support experimental evidence (Lee and Fenner 1989; Mustart and Cowling 1992) that larger seeds enhance species fitness in nutrient-limited soil (Cerrado). Regarding the relationship of seed mass with soil fertility, Dainese and Sitzia (2013) also documented that seed mass decreases from low-fertility grasslands to high-fertility grasslands, which roughly explains the lower average in Atlantic forests and the higher values in the Cerrado region. Species with higher seed mass have larger seed reserves, which allows them to make large, robust seedlings that face fewer problems caused by defoliation and drought (Leishman et al. 2000; Paz et al. 2005; ter Steege 1994) and enhancing their fitness in stressful environments.

The interpolation map showed several areas occurring in the extremes (rain and deciduous forest) sharing the same class, the one with smaller seeds, and a major tendency to increase to towards the west. Both small and large seeds can be advantageous in stressful environments (Coyle et al. 2014; Leishman 2001; Moles and Westoby 2004). Again, the lower seed mass in the south can be a consequence of the fragmentation that led to proliferation of fast-growing pioneer species (Santo-Silva et al. 2016) which in general have lighter seeds. Hanley et al. (2007) recommended caution in attempting to link such traits as seed size to wider patterns of plant community ecology. The authors asserted that habitat-specific differences in regeneration conditions and/or evolutionary history may influence the role that seed size plays in dictating how seedlings of different species respond to nutrient shortage. Functional groups may be filtered by different traits, implying that processes of community assembly operate differently depending on the functional group (Hoffmann et al. 2004), which might explain the convergence between deciduous and rain forests regarding this trait.

We found that CWM wood density was also related both to climate gradients and soil fertility (higher CWM wood density in sites with higher precipitation seasonality, temperature range and soil fertility). The interpolation map showed a broader north-south variation but also a great variation in smaller scales. Low water and nutrient availability in a stressful environment favors high resource use efficiency

and resistance to embolism, leading to high wood density (Barajas-Morales 1987; Coyle et al. 2014; Hacke et al. 2001; Martinez-Cabrera et al. 2009; Markesteijn et al. 2011), as we could see in our dry forests in the north. On the other hand, competition favors fast growth and consequently low-wood-density species (Coyle et al. 2014; Hacke et al. 2001; Martinez-Cabrera et al. 2009), so we found lighter wood averages in the rain forest in the south. This might be enhanced by the increase in short-lived pioneer species in these forests (Santo-Silva et al. 2016). Chave et al. (2006) also found higher mean wood density for dry forest (Cerrado, deciduous and semideciduous) in South America compared with other Neotropical vegetation and attributed this pattern to the fact that higher wood density can better resist drought-induced embolism.

## CONCLUSIONS

Finally, in this report, we present evidence for a pattern that at a regional scale, variations in tree communities in tropical regions are related mainly to water and energy availability and energy–water balance (Oliveira-Filho and Fontes 2000; Pausas and Austin 2001; Qian 2013; Toledo et al. 2011). Precipitation seasonality and soil moisture were the most important drivers of vegetation parameters. Precipitation seasonality and soil moisture together determine tree water availability, which seems to be the key factor in vegetation ecology in MG. As climate change scenarios predict an increase in summer precipitation over southeastern South America and reduction of winter precipitation over most of the continent (Vera et al. 2006), we may expect potentially large changes in the structure, diversity and functioning of these and other tropical forests. Moreover, further studies are necessary in order to insert the effect of fragmentation and land use/cover on these vegetation parameters.

## SUPPLEMENTARY MATERIAL

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

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## REFERENCES

- de Albuquerque UP, de Lima Araújo E, El-Deir AC, et al. (2012) Caatinga revisited: ecology and conservation of an important seasonal dry forest. *Scientific World J* **2012**:205182.

- Alvares CA, Stape JL, Sentelhas PC, *et al.* (2013) Köppen's climate classification map for Brazil. *Meteorologische Zeitschrift* **22**:711–28.
- Apgaua DMG, dos Santos RM, Pereira DGS, *et al.* (2014) Beta-diversity in seasonally dry tropical forests (SDTF) in the Caatinga Biogeographic Domain, Brazil, and its implications for conservation. *Biodivers Conserv* **23**:217–32.
- Araújo EDL, de Castro CC, de Albuquerque UP (2007) Dynamics of Brazilian Caatinga – a review concerning the plants, environment and people. *Funct Ecosyst Commun* **1**:15–28.
- Arellano G, Cala V, Macía MJ (2014) Niche breadth of oligarchic species in Amazonian and Andean rain forests. *J Veg Sci* **25**:1355–66.
- Barajas-Morales J (1987) Wood specific gravity in species from two tropical forests in Mexico. *IAWA J* **8**:143–8.
- Boyle B, Hopkins N, Lu Z, *et al.* (2013) The taxonomic name resolution service: an online tool for automated standardization of plant names. *BMC Bioinformatics* **14**:16.
- Bridgewater S, Ratter JA, Ribeiro JF (2004) Biogeographic patterns,  $\beta$ -diversity and dominance in the Cerrado biome of Brazil. *Biodivers Conserv* **13**:2295–317.
- Cerling TE, Harris JM, MacFadden BJ, *et al.* (1997) Global vegetation change through the Miocene/Pliocene boundary. *Nature* **389**:153–8.
- Chave J, Muller-Landau HC, Baker TR, *et al.* (2006) Regional and phylogenetic variation of wood density across 2 456 Neotropical tree species. *Ecol Appl* **16**:2356–67.
- Coelho GAO, Terra MCNS, Almeida HS, *et al.* (2016) What can natural edges of gallery forests teach us about woody community performance in sharp ecotones? *J Plant Ecol* **10**:937–48.
- Cornwell WK, Grubb PJ (2003) Regional and local patterns in plant species richness with respect to resource availability. *OIKOS* **100**:417–28.
- Coyle JR, Halliday FW, Lopez BE, *et al.* (2014) Using trait and phylogenetic diversity to evaluate the generality of the stress-dominance hypothesis in eastern North American tree communities. *Ecography* **37**:814–26.
- Dainese M, Sitzia T (2013) Assessing the influence of environmental gradients on seed mass variation in mountain grasslands using a spatial phylogenetic filtering approach. *Perspect Plant Ecol Evol Syst* **15**:12–9.
- Dalmagro HJ, Lobo FA, Vourlitis GL, *et al.* (2014) The physiological light response of two tree species across a hydrologic gradient in Brazilian savanna (Cerrado). *Photosynthetica* **52**:22–35.
- Dexter K, Smart B, Baldauf C, *et al.* (2015) Floristics and biogeography of vegetation in seasonally dry tropical regions. *Int For Rev* **17**:10–32.
- Dormann CF, Elith J, Bacher S, *et al.* (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* **36**:27–46.
- Eisenlohr PV, de Oliveira-Filho AT (2015) Revisiting patterns of tree species composition and their driving forces in the Atlantic forests of southeastern Brazil. *Biotropica* **47**:689–701.
- Environmental Systems Research Institute [ESRI] (2010) *ArcGIS DeskTop: Release 10.1*. Redlands, CA: Environmental Systems Research Institute.
- Esquivel-Muelbert A, Baker TR, Dexter KG, *et al.* (2017) Seasonal drought limits tree species across the Neotropics. *Ecography* **40**:618–29.
- Fernandes GW, Barbosa NP, Negreiros D, *et al.* (2014) Challenges for the conservation of vanishing megadiverse rupestrian grasslands. *Nat Conserv* **12**:162–5.
- Fisher RA, Corbet AS, Williams CB (1943) The relation between the number of species and the number of individuals in a random sample of an animal population. *J Anim Ecol* **12**:42–58.
- Forni-Martins ER, Martins FR (2000) Chromosome studies on Brazilian Cerrado plants. *Genet Mol Biol* **23**:947–55.
- Françoso RD, Haidar RF, Machado RB (2016) Tree species of South America central Savanna: endemism, marginal areas and the relationship with other biomes. *Acta Bot Brasilica* **30**:78–86.
- Hacke UG, Sperry JS, Pockman WT, *et al.* (2001) Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia* **126**:457–61.
- Hanley ME, Cordier PK, May O, *et al.* (2007) Seed size and seedling growth: differential response of Australian and British Fabaceae to nutrient limitation. *New Phytol* **174**:381–8.
- Haridasan M (2008) Nutritional adaptations of native plants of the Cerrado biome in acid soils. *Braz J Plant Physiol* **20**:183–95.
- Hengl T, Mendes de Jesus J, Heuvelink GB, *et al.* (2017) SoilGrids250m: global gridded soil information based on machine learning. *PLOS ONE* **12**:e0169748.
- Hijmans RJ, Cameron SE, Parra JL, *et al.* (2005) Very high resolution interpolated climate surfaces for global land areas. *Int J Climatol* **25**:1965–78.
- Hirota M, Holmgren M, Van Nes EH, *et al.* (2011) Global resilience of tropical forest and savanna to critical transitions. *Science* **334**:232–5.
- Hoffmann WA, Geiger EL, Gotsch SG, *et al.* (2012) Ecological thresholds at the savanna-forest boundary: how plant traits, resources and fire govern the distribution of tropical biomes. *Ecol Lett* **15**:759–68.
- Hoffmann WA, Jaconis SY, McKinley KL, *et al.* (2012b) Fuels or microclimate? Understanding the drivers of fire feedbacks at savanna-forest boundaries. *Austral Ecol* **37**:634–43.
- Hoffmann WA, Orthen B, Franco AC (2004) Constraints to seedling success of savanna and forest trees across the savanna-forest boundary. *Oecologia* **140**:252–60.
- Jansen S, Watanabe T, Smets E (2002) Aluminium accumulation in leaves of 127 species in Melastomataceae, with comments on the order Myrtales. *Ann Bot* **90**:53–64.
- Journel AG, Huijbregts CJ (1978) *Mining Geostatistics*. New York, NY: Academic Press.
- Kark S, van Rensburg BJ (2006) Ecotones: marginal or central areas of transition? *Isr J Ecol Evol* **52**:29–53.
- King DA, Davies SJ, Tan S, *et al.* (2006) The role of wood density and stem support costs in the growth and mortality of tropical trees. *J Ecol* **94**:670–80.
- Kitajima K (2007) Seed and seedling ecology. In Pugnaire FI, Valladares F (eds) *Functional Plant Ecology*, 2nd ed. CRC Press, 549–79.
- Lavorel S, Garnier E (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Funct Ecol* **16**:545–56.
- Lee WG, Fenner M (1989) Mineral nutrient allocation in seeds and shoots of twelve *Chionochloa* species in relation to soil fertility. *J Ecol* **77**:704–16.

- Leigh EG, Davidar P, Dick CW, *et al.* (2004) Why do some tropical forests have so many species of trees? *Biotropica* **36**:447–73.
- Leishman MR (2001) Does the seed size/number trade-off model determine plant community structure? An assessment of the model mechanisms and their generality. *Oikos* **93**:294–302.
- Leishman MR, Wright IJ, Moles AT, *et al.* (2000) The evolutionary ecology of seed size. In Fenner M (ed) *Seeds. The Ecology of Regeneration in Plant Communities*. Wallingford: CABI International.
- Magnago LFS, Rocha MF, Meyer L, *et al.* (2015) Microclimatic conditions at forest edges have significant impacts on vegetation structure in large Atlantic forest fragments. *Biodivers Conserv* **24**:2305–18.
- Markesteyn L, Poorter L, Bongers F, *et al.* (2011) Hydraulics and life history of tropical dry forest tree species: coordination of species' drought and shade tolerance. *New Phytol* **191**:480–95.
- Martínez-Cabrera HI, Jones CS, Espino S, *et al.* (2009) Wood anatomy and wood density in shrubs: responses to varying aridity along transcontinental transects. *Am J Bot* **96**:1388–98.
- Mayle FE (2004) Assessment of the Neotropical dry forest refugia hypothesis in the light of palaeoecological data and vegetation model simulations. *J Quat Sci* **19**:713–20.
- Mendonça RC, Felfili JM, Walter BMT, *et al.* (1998) Flora vascular do bioma Cerrado. In Sano SM, Almeida SP (eds) *Cerrado: Ambiente e Flora*. Planaltina, Brasília: Empresa Brasileira de Pesquisa Agropecuária Embrapa-Cerrados, 288–556.
- Miles L, Newton AC, DeFries RS, *et al.* (2006) A global overview of the conservation status of tropical dry forests. *J Biogeogr* **33**:491–505.
- Moles AT, Westoby M (2004) Seedling survival and seed size: a synthesis of the literature. *J Ecol* **92**:372–83.
- Murphy PG, Lugo AE (1986) Ecology of tropical dry forest. *Annu Rev Ecol Syst* **17**:67–88.
- Murphy P, Lugo AE (1995) Dry forests of Central America and the Caribbean. In Bullock S, Mooney H, Medina E (eds) *Seasonally Dry Tropical Forests*. Cambridge: University Press, 9–29.
- Mustart PJ, Cowling RM (1992) Seed size: phylogeny and adaptation in two closely related Proteaceae species-pairs. *Oecologia* **91**:292–5.
- Neri AV, Schaefer CE, Souza AL, *et al.* (2013) Pedology and plant physiognomies in the Cerrado, Brazil. *An Acad Bras Cienc* **85**:87–102.
- Neves DM, Dexter KG, Pennington RT, *et al.* (2015) Environmental and historical controls of floristic composition across the South American dry diagonal. *J Biogeogr* **42**:1566–76.
- Oksanen J, Blanchet FG, Friendly M, *et al.* (2016) *Package 'vegan': Community Ecology Package. Version 2.4-1*.
- Oliveira-Filho AT, Fontes MAL (2000) Patterns of floristic differentiation among Atlantic forests in southeastern Brazil and the influence of climate. *Biotropica* **32**:793–810.
- Oliveira-Filho AT, Ratter J (1995) A study of the origin of central Brazilian forests by the analysis of plant species distribution patterns. *Edinb J Bot* **52**:141–94.
- Oliveira-Filho AT, Ratter JA (2002) Vegetation physiognomies and woody flora of the Cerrado biome. In Oliveira PS, Marquis RJ (eds) *The Cerrados of Brazil: Ecology and Natural History of A Neotropical Savanna*. New York, NY: Columbia University Press, 91–120.
- Oliveira PS, Marquis RJ (2002) *The Cerrados of Brazil: Ecology and Natural History of A Neotropical Savanna*. New York, NY: Columbia University Press.
- Oliveras I, Malhi Y (2016) Many shades of green: the dynamic tropical forest – savannah transition zones. *Philos Trans R Soc Lond B Biol Sci* **371**:20150308.
- Pausas JG, Austin MP (2001) Patterns of plant species richness in relation to different environments: an appraisal. *J Veg Sci* **12**:153–66.
- Paz H, Mazer SJ, Martínez-Ramos M (2005) Comparative ecology of seed mass in *Psychotria* (Rubiaceae): within- and between-species effects of seed mass on early performance. *Funct Ecol* **19**:707–18.
- Pennington RT, Lewis GP, Ratter JA (2006) An overview of the plant diversity, biogeography and conservation of Neotropical Savannas and seasonally dry forests. In Pennington RT, Lewis GP, Ratter JA (eds) *Neotropical Savannas and Seasonally Dry Forests: Plant Diversity, Biogeography, and Conservation*. Oxford: CRC Press, 1–29.
- Pennington RT, Prado DE, Pendry CA (2000) Neotropical seasonally dry forests and quaternary vegetation changes. *J Biogeogr* **27**:261–73.
- Pereira JA, de Oliveira-Filho AT, Eisenlohr PV, *et al.* (2015) Human impacts affect tree community features of 20 forest fragments of a vanishing neotropical hotspot. *Environ Manage* **55**:296–307.
- Pinheiro MH, Monteiro R (2010) Contribution to the discussions on the origin of the cerrado biome: brazilian savanna. *Braz J Biol* **70**:95–102.
- Poorter L, Wright SJ, Paz H, *et al.* (2008) Are functional traits good predictors of demographic rates? Evidence from five neotropical forests. *Ecology* **89**:1908–20.
- Prado D (2000) Seasonally dry forests of tropical South America: from forgotten ecosystems to a new phytogeographic unit. *Edinb J Bot* **57**:437–61.
- Prado DE, Gibbs PE (1993) Patterns of species distributions in the dry seasonal forests of South America. *Ann Mo Bot Gard* **80**:902–27.
- Prado-Junior JA, Schiavini I, Vale VS, *et al.* (2016) Functional traits shape size-dependent growth and mortality rates of dry forest tree species. *J Plant Ecol* **10**:895–906.
- Qian H (2013) Environmental determinants of woody plant diversity at a regional scale in China. *PLOS ONE* **8**:e75832.
- Quesada C, Phillips O, Schwarz M, *et al.* (2012) Basin-wide variations in Amazon forest structure and function are mediated by both soils and climate. *Biogeosciences* **9**:2203–46.
- Ratter JA (1992) Transition between Cerrado and forest vegetation in Brazil. In Furley P, Ratter J, Proctor J (eds) *Nature and Dynamics of Forest-Savanna Boundaries*. London: Chapman and Hall.
- Ratter JA, Bridgewater S, Ribeiro JF (2003) Analysis of the floristic composition of the Brazilian Cerrado vegetation III: comparison of the woody vegetation of 376 areas. *Edinb J Bot* **60**:57–109.
- Ratter JA, Dargie T (1992) An analysis of the floristic composition of 26 Cerrado areas in Brazil. *Edinb J Bot* **49**:235–50.
- Reich PB (2014) The world-wide 'fast-slow' plant economics spectrum: a traits manifesto. *J Ecol* **102**:275–301.
- Ribeiro PJ, Diggle PJ (2001) geoR: a package for geostatistical analysis. *R News* **1**:14–8.
- Royal Botanic Gardens Kew (2015) *Seed Information Database (SID)*. Version 7.1. <http://data.kew.org/sid/>
- Saiter FZ, Eisenlohr PV, Barbosa MR, *et al.* (2015) From evergreen to deciduous tropical forests: how energy–water balance, temperature, and space influence the tree species composition in a high diversity region. *Plant Ecol Divers* **9**:45–54.

- Santiago LS, Goldstein G, Meinzer FC, *et al.* (2004) Leaf photosynthetic traits scale with hydraulic conductivity and wood density in Panamanian forest canopy trees. *Oecologia* **140**:543–50.
- dos Santos JMFF, de Andrade JR, de Lima EN, *et al.* (2007) Dinâmica populacional de uma espécie herbácea em uma área de floresta tropical seca no Nordeste do Brasil. *Rev Bras Biocienc* **5**:855–7.
- Santos RM, Oliveira-Filho AT, Eisenlohr PV, *et al.* (2012) Identity and relationships of the Arboreal Caatinga among other floristic units of seasonally dry tropical forests (SDTFs) of north-eastern and Central Brazil. *Ecol Evol* **2**:409–28.
- Santo-Silva EE, Almeida WR, Tabarelli M, *et al.* (2016) Habitat fragmentation and the future structure of tree assemblages in a fragmented Atlantic forest landscape. *Plant Ecol* **217**:1129–40.
- Scoloro JRS, Oliveira AD, Carvalho LMT, *et al.* (2008) Inventário florestal de minas gerais. <http://www.inventarioflorestal.mg.gov.br/>
- da Silva DM, Batalha MA (2008) Soil-vegetation relationships in Cerrados under different fire frequencies. *Plant Soil* **311**:87.
- da Silva JMC, Bates JM (2002) Biogeographic patterns and conservation in the South American Cerrado: a tropical savanna hotspot. *BioScience* **52**:225–34.
- Simon MF, Grether R, de Queiroz LP, *et al.* (2009) Recent assembly of the Cerrado, a neotropical plant diversity hotspot, by in situ evolution of adaptations to fire. *Proc Natl Acad Sci USA* **106**:20359–64.
- Staal A, Flores BM (2015) Sharp ecotones spark sharp ideas: comment on “Structural, physiognomic and above-ground biomass variation 30 in savanna–forest transition zones on three continents – how different are co-occurring savanna and forest formations?” by Veenendaal *et al.* (2015). *Biogeosciences* **12**:5563–6.
- Staver AC, Archibald S, Levin SA (2011) The global extent and determinants of savanna and forest as alternative biome states. *Science* **334**:230–2.
- ter Steege H (1994) Seedling growth of *Mora gonggrijpii*, a large seeded climax species, under different soil and light conditions. *Vegetatio* **112**:161–70.
- ter Steege H, Pitman NC, Phillips OL, *et al.* (2006) Continental-scale patterns of canopy tree composition and function across Amazonia. *Nature* **443**:444–7.
- Terra MCNS, dos Santos RM, Fontes MAL, *et al.* (2017) Tree dominance and diversity in Minas Gerais, Brazil. *Biodivers Conserv* **26**:2133–53.
- Thomas WW, Carvalho AMV, Amorim AM, *et al.* (2008) Diversity of woody plants in the Atlantic coastal forest of southern Bahia, Brazil. In Thomas WW (ed) *The Atlantic Coastal Forests of Northeastern Brazil. Memoirs of the New York Botanical Garden*, Vol. **100**. New York, NY: The New York Botanical Garden Press, 21–66.
- Toledo M, Poorter L, Peña-Claros M, *et al.* (2011) Climate is a stronger driver of tree and forest growth rates than soil and disturbance. *J Ecol* **99**:254–64.
- Vera C, Silvestri G, Liebmann B, *et al.* (2006) Climate change scenarios for seasonal precipitation in South America from IPCC-AR4 models. *Geophys Res Lett* **33**:L13707.
- Vieira SR (2000) Geoestatística em estudos de variabilidade espacial do solo. In Novais RF, Alvarez VH, Schaefer GR (eds) *Tópicos em Ciência do Solo*. Viçosa: SBCS, 1–54.
- Vieira S, de Camargo PB, Selhorst D, *et al.* (2004) Forest structure and carbon dynamics in Amazonian tropical rain forests. *Oecologia* **140**:468–79.
- Werneck FP (2011) The diversification of eastern South American open vegetation biomes: historical biogeography and perspectives. *Quat Sci Rev* **30**:1630–48.
- Werneck FP, Costa GC, Colli GR, *et al.* (2011) Revisiting the historical distribution of seasonally dry tropical forests: new insights based on palaeodistribution modelling and palynological evidence. *Glob Ecol Biogeogr* **20**:272–88.
- Werneck FP, Gamble T, Colli GR, *et al.* (2012) Deep diversification and long-term persistence in the South American ‘dry diagonal’: integrating continent-wide phylogeography and distribution modeling of geckos. *Evolution* **66**:3014–34.
- Wright SJ, Yavitt JB, Wurzburger N, *et al.* (2011) Potassium, phosphorus, or nitrogen limit root allocation, tree growth, or litter production in a lowland tropical forest. *Ecology* **92**:1616–25.
- Zanne AE, Lopez-Gonzalez G, Coomes DA, *et al.* (2009) Data from: towards a worldwide wood economics spectrum. *Dryad Digital Repository*. <https://doi.org/10.5061/dryad.234>