


The environmental triangle of the Cerrado Domain: Ecological factors driving shifts in tree species composition between forests and savannas

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Abstract

1. The Cerrado Domain of central Brazil houses the largest extent of savanna in the Neotropics, but despite its simple characterization as a giant savanna, it contains considerable vegetation heterogeneity that is poorly understood.
2. We aimed to determine how vegetation types in the Cerrado diverge in their tree species composition and what role ecological factors play in driving compositional patterns.
3. We used a dataset of 1,165 tree species inventories spread across the Cerrado Domain, which come from six vegetation types that have a substantial arboreal component: woody savannas, dystrophic cerradão, mesotrophic cerradão, seasonally dry tropical forests, semideciduous forests and evergreen forests. We found three extremes in terms of tree species composition, with clear underlying ecological drivers, which leads us to propose a ternary model, the *Cerrado Vegetation Triangle*, to characterize woody vegetation in the Cerrado. At one extreme, we found that semideciduous and evergreen forests are indistinguishable floristically and are found in areas with high water availability. At another extreme lie seasonally dry tropical forests which are found on more fertile soils. At the third extreme, we found that all types of savanna, and dystrophic cerradão, are highly similar in tree species composition and are commonly found in areas of poor soils and high flammability. Mesotrophic cerradão is transitional in tree species composition between savannas and seasonally dry tropical forest.
4. The lack of variation in tree species composition attributed to climatic variables indicates that within homogeneous macroclimatic zones, many types of forest and savanna co-exist due to complex mosaics of local substrate heterogeneity and fire history.

5. *Synthesis.* Our findings highlight the complexity of forest–savanna transitions in the Cerrado Domain, with relevance for understanding the future of Cerrado vegetation under environmental change. If nitrogen deposition is extensive, some savannas may be more likely to transition to mesotrophic cerrado or even seasonally dry tropical forest, whereas if water availability increases these same savannas may transition to semideciduous or evergreen forest. Our “Cerrado Vegetation Triangle” model offers a simple conceptual tool to frame discussions of conservation and management.

KEYWORDS

cerrado sensu stricto, dystrophic cerrado, fire, gallery forest, mesotrophic cerrado, neotropical savanna, seasonally dry tropical forest, semideciduous forest

1 | INTRODUCTION

The main factors considered as determinants of world-wide savanna distribution, composition and structure are fire, herbivory, climate, soil fertility and water availability, the latter being a product of climatic and edaphic factors (Bueno et al., 2017; Cole, 1986; Collinson, 1988; Dantas, Batalha, & Pausas, 2013; Eiten, 1972; Hirota, Holmgren, Van Nes, & Scheffer, 2011; Lehmann et al., 2014; Mistry, 1998; Oliveira-Filho & Ratter, 2002; Pellegrini, 2016; Staver, Archibald, & Levin, 2011). Although the relative weight of each driving factor varies from one region to another, most studies suggest that climatic and edaphic factors are most critical (Lehmann et al., 2014). While climate has a macro-scale effect (Hirota et al., 2011), soil and fire act at more local scales (Coutinho, 1990; Lehmann et al., 2014; Pausas, 2014; Pellegrini, 2016; Staver et al., 2011).

The main extent of Neotropical savanna is largely found within Brazil where it is often termed the cerrado (Ab'Saber, 2003; Gottsberger & Silberbauer-Gottsberger, 2006; Ribeiro & Walter, 2008). Brazil categorizes its large-scale phytogeographic regions into “Domains,” and the region of central Brazil that is dominated by savanna vegetation is termed the Cerrado Domain (Ab'Saber, 2003). In the Cerrado Domain, precipitation is seasonal, with well-defined wet and dry seasons, and fires are common in the dry season, hindering the establishment of forest species (Dantas & Pausas, 2013; Dantas et al., 2013; Neri et al., 2012; Stevens, Lehmann, Murphy, & Durigan, 2016). The flora of this region is dominated by fire-adapted species, including both fire-tolerant and fire-dependent plants (Coutinho, 1990, 2006; Durigan & Ratter, 2006; Eiten, 1972, 1978; Hoffmann et al., 2009; Simon et al., 2009). Most savanna-inhabiting woody species have thick, corky bark and/or subterranean meristems (xylopodia), which protect them from high temperatures and allow resprouting after fires (Gottsberger & Silberbauer-Gottsberger, 2006). However, this widely used “Cerrado Domain” label hides the complexity of vegetation found in this region, which is highly heterogeneous, including many different grassland and savanna formations as well as different types of forest (Ab'Saber, 2003; DRYFLOR, 2016; Eiten, 1978; Haidar et al., 2013; Oliveira-Filho, Cardoso, et al., 2013;

Oliveira-Filho, Pennington, Rotella, & Lavin, 2013; Oliveira-Filho & Ratter, 1995, 2000; Ratter, Askew, Montgomery, & Gifford, 1977; Ratter & Dargie, 1992; Ratter, Richards, Argent, & Gifford, 1973; Ribeiro & Walter, 2008).

Within the Cerrado Domain, the species composition of woody plants is expected to change along a fire gradient; in areas without fire, species associated with forest environments commonly out-compete savanna species (Dantas & Pausas, 2013; Hoffmann, Orthen, & Nascimento, 2003; Lehmann et al., 2014; Pausas, 2014; Silva, Corrêa, Doane, Pereira, & Horwath, 2013; Silva, Hoffmann, et al., 2013), and savanna can eventually convert to forest (Abreu et al., 2017). In the absence of fire, the levels of mineral nutrients and water availability are important factors in the distribution of vegetation types (Oliveira-Filho & Ratter, 2002). Most soils of the Cerrado Domain are dystrophic, with low pH and high levels of exchangeable aluminium (Furley & Ratter, 1988; Ratter, Ribeiro, & Bridgewater, 1997). Of the chemical elements in the Cerrado soil, one of the most important is aluminium, as emphasized by Haridasan (2000). This element, often toxic to plants, occurs at high concentrations in dystrophic soils and native plants of cerrado savanna formations show high levels of aluminium tolerance (Meira-Neto et al., 2017; Neri et al., 2012). In contrast, species occurring only in areas with higher levels of calcium and magnesium and lower levels of aluminium are characteristic of some kinds of forest in the Cerrado Domain, such as seasonally dry tropical forests (SDTF) and evergreen and semideciduous forests (Oliveira-Filho & Ratter, 2002; Oliveira-Filho, Cardoso, et al., 2013; Oliveira-Filho, Pennington, et al., 2013; Ribeiro & Walter, 2008). Under intermediate aluminium concentrations, another forest type, mesotrophic cerrado, is believed to act as an intermediate community, in terms of both soil properties and species composition (Bueno, Neves, Oliveira-Filho, Lehn, & Ratter, 2013; Ratter, 1971; Ratter, Askew, Montgomery, & Gifford, 1978a; Ratter & Dargie, 1992; Ratter et al., 1973). Meanwhile, permanently and temporarily waterlogged areas within the Cerrado are covered by evergreen and semideciduous forests or marshy “campos” (campos = grassland), while dry grasslands, savanna formations and SDTF occur in the higher and better drained areas (Amorim & Batalha,

2007; Furley & Ratter, 1988; Oliveira-Filho & Ratter, 2002; Ribeiro & Walter, 2008).

The variation in the ecological factors described above in the Cerrado Domain and their effect on the floristic composition of vegetation types has been studied primarily at small spatial scales, mostly at individual sites (e.g. Ratter, 1992; Ratter, Askew, Montgomery, & Gifford, 1978b). Authors such as Oliveira-Filho and Ratter (2002) and Ribeiro and Walter (2008) have scaled these local studies up to the entire Cerrado Domain but using a qualitative approach. While there are quantitative floristic comparisons across the Cerrado Domain (e.g. Bridgewater, Ratter, & Ribeiro, 2004; Ratter, Bridgewater, & Ribeiro, 2003, 2006; Ratter et al., 1997) these have been focused on savanna vegetation and have not included riparian habitats and most forest vegetation types. In addition, they did not include formal analyses of how environmental factors and fire correlate with broader floristic composition.

In this paper, we explore the tree species composition of different vegetation types proposed for the Cerrado Domain using quantitative analyses of the distribution of 3,072 tree species over 1,165 sites. We also analyse how compositional variation in tree species correlates with 27 climatic and edaphic variables. Based upon the results of these analyses, we develop a conceptual model that describes how the key ecological factors of soil fertility, water availability and fire influence the composition of tree species and vegetation types in the Cerrado Domain. Our results are key to understanding forest-savanna transitions under global environmental changes, such as nitrogen deposition and increasing temperatures, and have relevance for any seasonally dry region in the tropics where savannas and forests co-occur (Hirota et al., 2011; Lehmann et al., 2014; Silva, Corrêa, et al., 2013; Silva, Hoffmann, et al., 2013; Staver et al., 2011).

2 | MATERIALS AND METHODS

2.1 | Study area

The Cerrado Domain is the second largest phytogeographical domain in South America, surpassed in area only by the Amazon (Ab'Saber, 2003; Gottsberger & Silberbauer-Gottsberger, 2006), and spreads across central Brazil, comprising c. 1/4 of the country's surface, plus smaller areas in north-western Paraguay and eastern Bolivia (Oliveira-Filho & Ratter, 2002; Figure 1). The Cerrado Domain extends over 20 degrees of latitude and altitudes ranging from 100 m in the Pantanal wetlands (central-western Brazil) to 1,500 m in the tablelands of the Central Brazilian Highlands (Ribeiro & Walter, 2008). There is moderate variation in mean annual temperature across the Domain, ranging from 18 to 28°C. Variation in mean annual precipitation is relatively high, ranging from 800 to 2,000 mm, with a marked dry season during the austral winter (approximately April–September; Ab'Saber, 2003).

We classified the vegetation of individual sites following the criteria and nomenclature proposed by Oliveira-Filho (2015, 2017) for the vegetation of eastern tropical and subtropical South America.

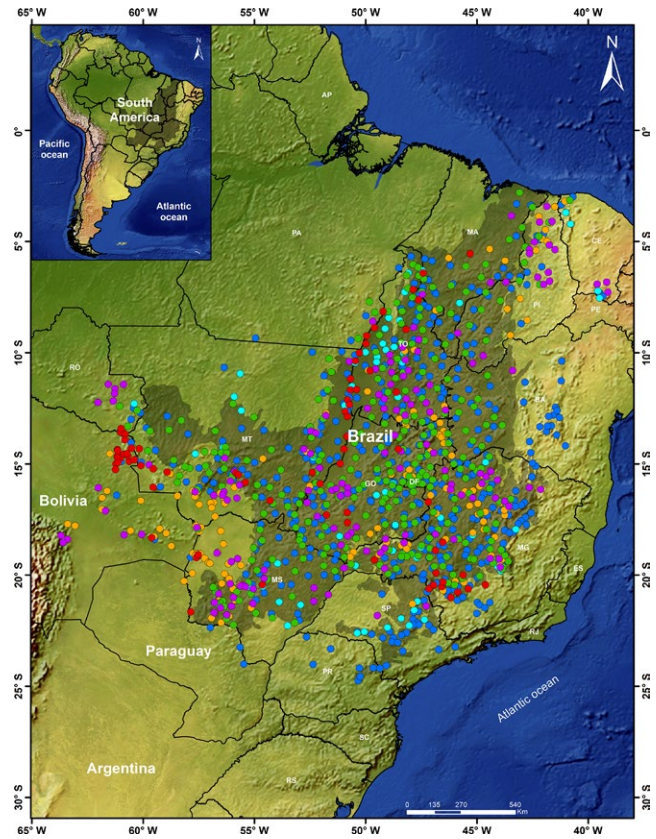


FIGURE 1 Geographic distribution of the Cerrado (IBGE, 2012), with the location of sites and their vegetation type (cerrado woody savannas: blue, dystrophic cerradão: cyan, mesotrophic cerradão: purple, seasonally dry tropical forest: orange, evergreen forest: green and semi-deciduous forest: red). Brazilian states are labelled as follows: Amapá (AP), Bahia (BA), Ceará (CE), Distrito Federal (DF), Espírito Santo (ES), Goiás (GO), Maranhão (MA), Minas Gerais (MG), Mato Grosso (MT), Mato Grosso do Sul (MS), Pará (PA), Paraná (PR), Pernambuco (PE), Rio de Janeiro (RJ), Rio Grande do Sul (RS), Rondônia (RO), São Paulo (SP), Santa Catarina (SC), Sergipe (SE), Tocantins (TO) [Colour figure can be viewed at wileyonlinelibrary.com]

This system is a further development of the widely accepted Instituto Brasileiro de Geografia e Estatística (IBGE) classification system for Brazilian vegetation (Veloso, Filho, & Lima, 1991; reissued by IBGE, 2012), although it describes physiognomic and environmental variations at much smaller scales than those covered by the IBGE.

Within the Cerrado Domain, we sampled six main vegetation types that consistently have a substantive arboreal component. We did not include vegetation types that largely lack trees (e.g. campo sujo or campo limpo, c.f. Ribeiro & Walter, 2008). We grouped the various vegetation formations that can be termed savanna, that is, with a grassy understorey and some frequency of fire, as one vegetation type: cerrado sensu stricto, occurring on poor and well-drained dystrophic soils, which is largely synonymous with the *cerrado sentido restrito* category of Ribeiro and Walter (2008). Cerradão is characterized by a more developed, almost closed canopy (with 50–90% tree cover), with trees reaching a height of 8–12 m, and we distinguished two vegetation types for cerradão: dystrophic cerradão

on poor soils and mesotrophic cerrado on richer soils (Ribeiro & Walter, 2008). These two vegetation types can be structurally similar, but have distinct tree species composition (Araújo, Nascimento, Lopes, Rodrigues, & Ratter, 2011). Cerrado can develop from cerrado *sensu stricto* in the prolonged absence of fire and thus the two vegetation formations often share many tree species (Abreu et al., 2017). In contrast to cerrado *sensu stricto*, there is generally not a continuous grassy layer in cerrado, although grasses are often present (*Aristida*, *Axonopis*, *Paspalum* and *Trachypogon*, Ribeiro & Walter, 2008). Mesotrophic and dystrophic cerrado are often considered as forests (Oliveira-Filho & Ratter, 2002; Ribeiro & Walter, 2008), although they are shorter in stature than the other forest types found in the Cerrado Domain. Deciduous forests or SDTF occur on scattered patches of fertile soils (more fertile than in mesotrophic cerrado) and are notable for experiencing little fire and housing a markedly different set of plant lineages from other vegetation types in the Cerrado (e.g. Cactaceae; Bueno et al., 2013; Neves, Dexter, Pennington, Bueno, & Oliveira-Filho, 2015; Oliveira-Filho, Cardoso, et al., 2013; Oliveira-Filho, Pennington, et al., 2013; Pennington, Prado, & Pendry, 2000; Ratter et al., 1977; Ratter et al., 1978a, 1978b; Ratter et al., 1973). Two other principal forests in the Cerrado Domain are evergreen and semideciduous forests, largely synonymous with mata de galeria and mata ciliar in the terminology of Ribeiro and Walter (2008), which are found in more humid areas, such as along river courses (i.e. gallery forest and semideciduous riparian forest), or in transition zones with the moist forests of either the Amazon or Atlantic Forests (Ribeiro & Walter, 2008). Evergreen and semideciduous forests tend to be richer in species than the other vegetation types in the Cerrado Domain (Oliveira-Filho & Ratter, 1995, 2000, 2002; Ribeiro & Walter, 2008).

2.2 | Dataset

We extracted the dataset from the NeoTropTree (NTT) database (Oliveira-Filho, 2017), which consists of tree species checklists (trees defined here as free-standing woody plants >3 m in height) compiled for geo-referenced sites, extending from southern Florida (U.S.A.) and Mexico to Patagonia. The NTT currently holds 6,000 sites/checklists, 14,878 tree species and 920,129 occurrence records. The data were originally compiled from an extensive survey of published and unpublished literature (e.g. PhD theses), particularly floristic surveys and forest inventories of individual sites. Sites were assigned vegetation formations based on the classification used by the original researcher, and then standardized to the system of Oliveira-Filho (2015, 2017). Sites are restricted to a circular area with a 10-km diameter. Where two or more vegetation formations co-occur in one 10-km area, there may be two geographically overlapping sites in the NTT database, each for a distinct vegetation type. In addition, new species occurrence records obtained from both major herbaria and taxonomic monographs were added to the checklists when they were collected within a 5-km radius of the original NTT site centre and within the same vegetation formation. All species and their occurrence records were checked regarding current taxonomic

and geographical circumscriptions, as defined (in the present case) by the team of specialists responsible for the online project *Flora do Brasil* (available at <http://floradobrasil.jbrj.gov.br/>). The compilation of NTT avoided, therefore, the inclusion of occurrence records with doubtful identification, location or vegetation formation, even when they were cited in published checklists. It also excludes species-poor checklists, which is an important filter because low sampling/collecting efforts often result in poor descriptive power.

The dataset extracted from NTT consisted of 1,165 checklists, of which 433 were classified a priori as savanna formations (cerrado *sensu stricto*), 64 as dystrophic cerrado, 299 as evergreen forest, 76 as semideciduous forests, 140 as SDTF and 153 as mesotrophic cerrado (Figure 1). The final species matrix contained presence/absence data for 3,072 tree species, with a total of 148,718 presence records (see Figure 1). The NTT database also includes 27 environmental variables for all sites, derived from multiple sources (at a 30-arc second resolution or c. 1 km² near the equator). Elevation at the NTT site centre was included as an integrative environmental variable. Eleven bioclimatic variables were obtained from WorldClim 1.4 (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005), including mean annual temperature, mean diurnal temperature range, isothermality, temperature seasonality, maximum temperature of the warmest month, minimum temperature of the coldest month, temperature annual range, mean annual precipitation, precipitation of the wettest month, precipitation of the driest month and precipitation seasonality. Potential evapotranspiration (mm) and an aridity index were derived from WorldClim layers by Zomer, Trabucco, Bossio, van Straaten, and Verchot (2008). WorldClim monthly temperatures and precipitation were also interpolated to obtain values for 5-day intervals by applying sinusoidal functions centred at day 15 by the mean value for each month. These functions yielded values for days 1, 5, 10, 20, 25 and 30, which, in addition to the mean value at day 15, were used to generate Walter's Climate Diagrams (Walter, 1985). These climate diagrams were used to generate four additional variables: duration (number of days) and severity (mm) of both the water deficit and water excess periods. Days of frost were obtained from gridded datasets produced by Jones and Harris (2008).

Surface rockiness (% surface), soil texture class (% volume of sand), salinity class (ECe in dS/m) and percent base saturation, a proxy for soil fertility, were obtained from the Harmonized World Soil Database v1.2 (available at <http://www.fao.org/soilsportal/soil-survey/soil-maps-and-databases/harmonized-world-soil-database-v12/en/>) and ranked afterwards by mid-class percentage. Due to imprecisions related to soil local heterogeneity all soil variables were eventually transformed to ranked mid-class values, in other words, the use of classes was adopted to add robustness to the data because of the high local soil heterogeneity that can make raw figures unrealistic. The soil drainage classes were obtained following EMBRAPA's protocol (Santos et al., 2013), which combines soil type, texture and depth with landforms, in order to characterize water availability. The seasonality index represents the sum of percent of rainfall across both deficit and excess periods from Walter climate diagrams. This index is related to climate

features, drought and the effects of flooding (albeit indirectly). Grass coverage (%) was obtained by direct observation of site surface on Google Earth® images in five 100 × 100 m areas, one at the central coordinates of the NTT site and four at 2.5 km away from it and towards the NE, SW, NW and SE (see Neves et al., 2017). The data were transformed to ranked mid-class values for each site and were used as a proxy for fire return interval (i.e. fire frequency; Hoffmann et al., 2012; Archibald, Lehmann, Gómez-Dansd, & Bradstocke, 2013; Lehmann et al., 2014).

2.3 | Data analyses

To analyse the floristic consistency of the vegetation types, we applied non-metric multidimensional scaling (NMDS) of species composition across sites (McCune & Grace, 2002) using Simpson distance as the floristic dissimilarity metric. In order to improve interpretability, ellipses showing 99% confidence levels were added around the vegetation type centroids. Multi-response permutation procedures (MRPP) and analysis of similarities (ANOSIM) were used to test the compositional differentiation of the vegetation types in the NMDS. The environmental variables were fit a posteriori to the NMDS

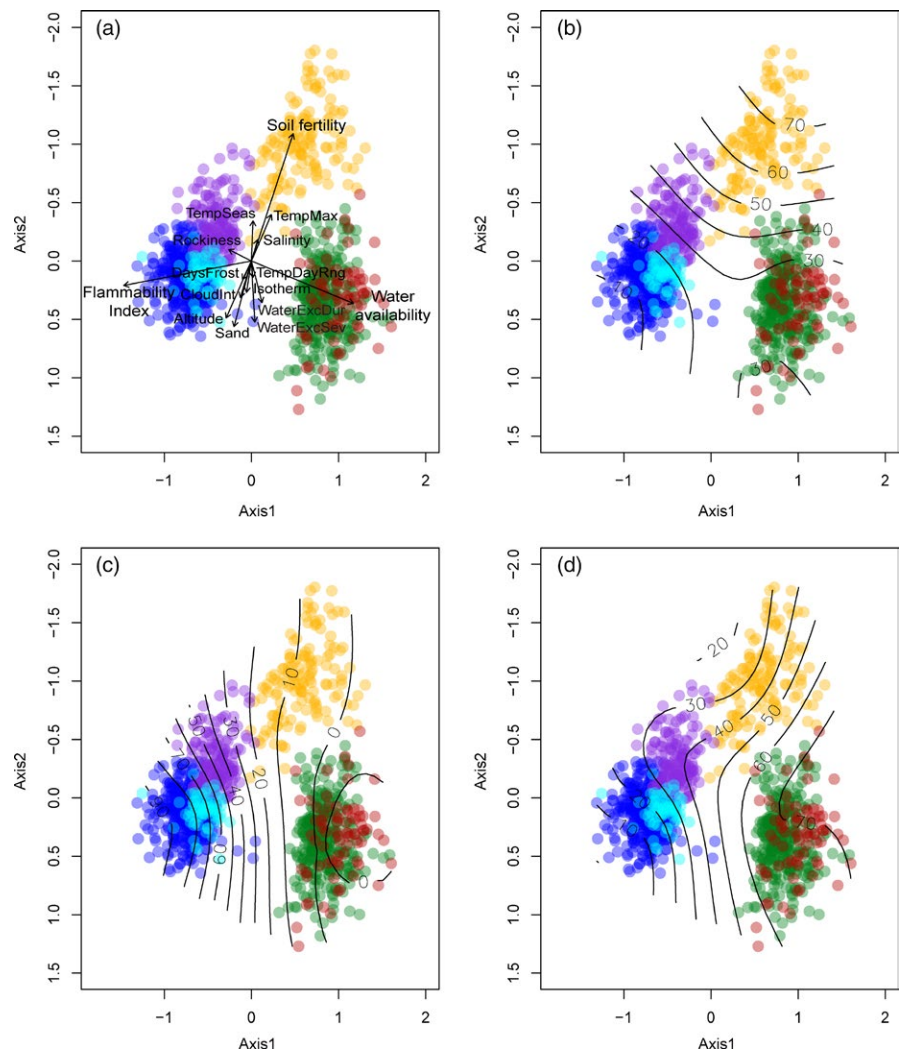
ordination, with the significant variables ($p < .05$) plotted as vectors. These analyses were conducted using the vegan package (Oksanen et al., 2016) in the R Statistical Software (R Core Team, 2017).

We also performed an indicator species analysis to test whether there are subsets of species with significant association with one or more vegetation types. In this analysis, an indicator value (IV) is derived, with higher IV values representing greater affinity of a given species towards a certain vegetation type. This analysis was performed using the statistical package indicpecies (De Cáceres & Legendre, 2009) in the R Statistical Environment (R Core Team, 2017), with the method proposed by (Dufrêne & Legendre, 1997).

3 | RESULTS

Several of the main vegetation types in the Cerrado Domain were consistently discriminated in the NMDS ordination, indicating differentiation in their tree species composition, while others were not, indicating their compositional similarity (Figure 2a; Figure S1). Cerrado sensu stricto, comprising various savanna formations, grouped together in one corner of compositional space and was floristically

FIGURE 2 (a) Non-metric multidimensional scaling (NMDS) of 1,165 Cerrado Domain sites based on their tree species composition (cerrado sensu stricto: blue, dystrophic cerradão: cyan, mesotrophic cerradão: purple, seasonally dry tropical forest: orange, evergreen forest: green and semideciduous forest: red). The arrows in diagram represent the correlations between the most explanatory environmental variables and ordination scores. CloudItcp, cloud intercept; DaysFrost, days of frost; flammability index, grass coverage (%); Isotherm, isothermality; Rockiness, surface rockiness (% exposed rock); salinity, soil salinity; Sand, soil coarseness (% sand); Soil Fertility, soil fertility (% base saturation); TempDayRng, temperature diurnal range; TempMax, temperature maximum; TempSeas, temperature seasonality; Water availability (representing the Soil drainage); WaterExcDur, water excess duration; WaterExcSev, water excess severity. (b) NMDS for vegetation types and black lines representing fitted surface values for soil fertility; (c) black isolines representing fitted surface values for flammability index and (d) black isolines representing fitted surface values for Water Availability [Colour figure can be viewed at wileyonlinelibrary.com]



distinct from SDTF and evergreen/semideciduous forests, which fell in opposite corners of the compositional space. Dystrophic cerradão grouped with cerrado sensu stricto, from which it was indistinguishable based on tree species composition, while semideciduous forests grouped with evergreen forests, from which they were compositionally indistinguishable. Mesotrophic cerradão was intermediate in composition between the cerrado sensu stricto/dystrophic cerradão group and SDTF.

The stress value in the two-dimensional NMDS was 0.11, indicating that two dimensions were adequate to represent the variation, and based on the stress plot, the overall configuration fits the data well (stress based $R^2 = 98\%$ and fit based $R^2 = 90\%$).

Analysis of similarities and MRPP analyses that distinguished the six vegetation types showed that, overall, these groups do differ significantly in tree species composition (ANOSIM, $R = .76$, $p < .001$; MRPP, $A = 0.18$, $p < .001$). When we categorized sites into three major floristic groups: savanna/cerradão (cerrado sensu stricto, dystrophic cerradão, mesotrophic cerradão), SDTF and semideciduous/evergreen (evergreen and semideciduous forests), the R -value of ANOSIM increased ($R = .93$, $p < .001$), indicating that three groups provide a better categorization of sites than six groups. The MRPP analysis suggested that three groups gave equivalent discrimination of sites compared to six groups ($A = 0.17$, $p < .001$).

Furthermore, we found that several ecological variables are key to explaining the tree species composition of these vegetation types, namely soil drainage class (related to water availability), grass coverage (related to flammability) and soil fertility (Figure 2a–d).

The main indicator species analysis yielded subsets of tree species that are significantly associated with each of the vegetation types (Table S1). Species that are significant indicators for evergreen forest are also frequent in semideciduous forests and vice versa, demonstrating their floristic similarity. The same holds for indicator species of cerrado sensu stricto being frequent in dystrophic cerradão and vice versa. Meanwhile, indicator species for mesotrophic cerradão have relatively high frequencies in SDTF, dystrophic cerradão and savanna sensu stricto, demonstrating the transitional nature of mesotrophic cerradão. The indicator species for evergreen and semideciduous forests are scarce to absent in other vegetation types, demonstrating the floristic distinctiveness of these two vegetation types in the Cerrado Domain.

4 | DISCUSSION

Our results confirm that the six tree-dominated vegetation types in the Cerrado Domain can be categorized into three principal floristic groups, based on tree species composition, namely savannas and cerradão, SDTF, and evergreen/semideciduous forest, the latter of which shows strong floristic affinities with tropical moist forests such as the Amazon and Atlantic Forests (Oliveira-Filho & Ratter, 2000, 2002; Miranda et al., in press). The results clearly demonstrate the importance of edaphic factors in facilitating the coexistence of floristically divergent groups under similar climatic regimes (Figure 2),

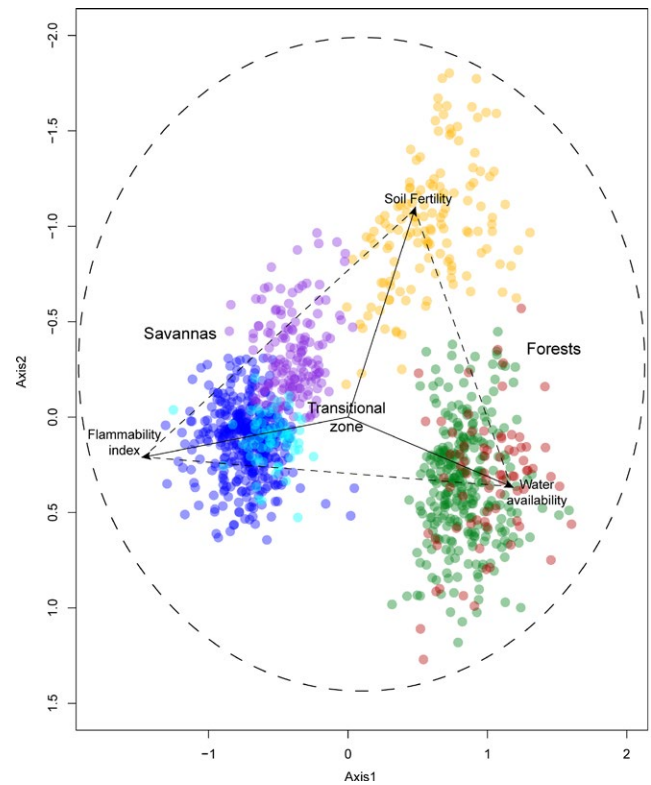


FIGURE 3 Proposed *Cerrado Vegetation Triangle* related to the NMDS results. The circle represents the climate, which influences the other factors in a general way; each vertex of the triangle represents a factor that leads to the occurrence of a certain vegetation types, with the arrows on each side of triangle representing the increase in variables towards the vertices. The tree species composition is coloured according to vegetation types (cerrado sensu stricto: blue, dystrophic cerradão: cyan, mesotrophic cerradão: purple, seasonally dry tropical forest: orange, evergreen forest: green and semideciduous forest: red) [Colour figure can be viewed at wileyonlinelibrary.com]

which is evident from the complete spatial interdigitation of these floristic groups within the Cerrado Domain (see also Miranda et al., in press). At any point in space within the Cerrado Domain, one is likely to be able to find all three of these floristic groups relatively nearby and experiencing the same climate (Figure 1).

In order to highlight the edaphic factors influencing the tree species composition of the Cerrado Domain, we propose a heuristic schematic that we refer to as the *Cerrado Vegetation Triangle* (CVT; Figure 3). The circle around the triangle represents the broad climatic envelope of the Cerrado Domain, which is strongly seasonal with respect to precipitation, while the triangle represents the three major factors that determine tree species composition. The arrowheads at the vertices of the triangle denote extreme values for a given ecological factor that give rise to each major floristic group of vegetation types: high fire frequency gives cerrado sensu stricto and cerradão, high soil fertility gives SDTF and high water availability gives evergreen and semideciduous forests. Meanwhile, potential transition zones, realized between savanna and SDTF and unrealized between savanna and evergreen and semideciduous forests, lie between these vertices.

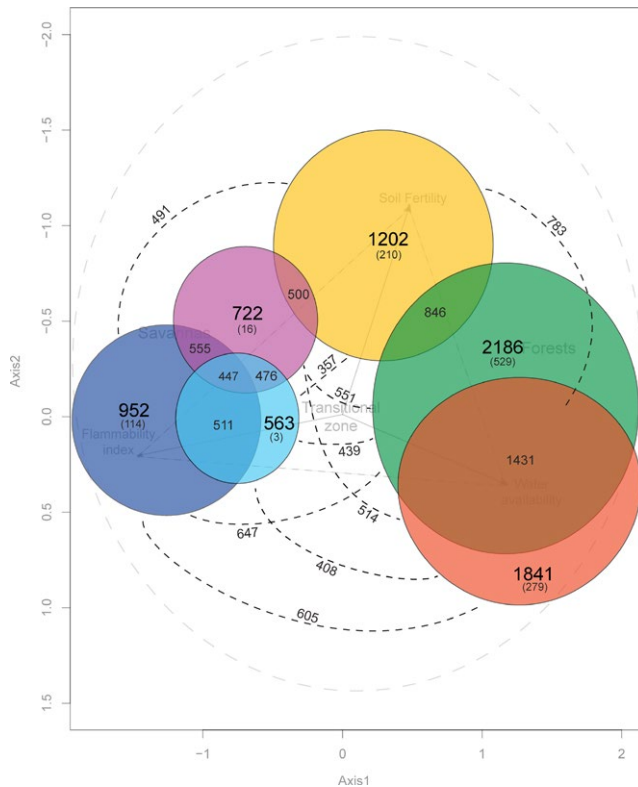


FIGURE 4 Species turnover among six vegetation types. The circles represent the vegetation types (cerrado sensu stricto: blue, dystrophic cerradão: cyan, mesotrophic cerradão: purple, seasonally dry tropical forest: yellow, evergreen forest: green and semideciduous forest: red). Numbers in bold represent the total species in the vegetation type and the number in brackets gives the number of exclusive species; numbers on the dashed lines and in the congruence of circles represent the shared species [Colour figure can be viewed at wileyonlinelibrary.com]

Savannas have been strongly influenced and shaped by fire across the tropics (e.g. Bond & van Wilgen, 1996; Coutinho, 1990; Dantas et al., 2013; Gillon, 1983; Gottsberger & Silberbauer-Gottsberger, 2006; Platt, Ellair, Huffman, Potts, & Beckage, 2016; Silva & Batalha, 2010), as evidenced by key features of fire tolerance or fire dependency in the savanna flora (Lehmann et al., 2014; Pennington & Hughes, 2014; Silva & Batalha, 2010; Simon & Pennington, 2012; Simon et al., 2009). Indicator species of savanna (cerrado sensu stricto), such as *Kielmeyera coriacea* Mart. & Zucc., *Palicourea rigida* Kunth, *Byrsonima coccolobifolia* Kunth, *Davilla elliptica* A.St.-Hil., *Dalbergia miscolobium* Benth and *Zeyheria montana* Mart. are characterized by thick corky bark and subterranean meristems that protect them from high temperatures and allow resprouting after fires (Gottsberger & Silberbauer-Gottsberger, 2006). In addition, the occurrence of these species is correlated with soils of low fertility and high aluminium levels and some of these species are obligate aluminium accumulators (Araújo & Haridasan, 1988; Haridasan, 2000; Meira-Neto et al., 2017).

In the absence of fire, existing trees in a savanna (cerrado sensu stricto) have increased growth and survival while additional tree individuals recruit. Thus, above-ground woody biomass and

tree density increase, in a process termed woody encroachment. Woody encroachment is occurring in tropical savannas across the globe (Moreira, 2000; San José & Fariñas, 1991; Stevens et al., 2016; Woinarski, Risler, & Kean, 2004). In the context of the Cerrado Domain, the increasing size and density of trees often leads to a forest formation termed cerradão (Durigan & Ratter, 2006, 2016; Pinheiro, Azevedo, & Monteiro, 2010; Pinheiro & Durigan, 2009, 2012). Given that many of the tree individuals in cerradão derive directly from a cerrado sensu stricto vegetation, the similarity in tree species composition between the two evident in our analyses is unsurprising (Figure 4). If cerradão does experience fire, it may revert to cerrado sensu stricto (Durigan & Ratter, 2006). The grasses that are present in cerradão (Ribeiro & Walter, 2008), albeit not as a continuous layer, may increase the chance of fire spreading through this forest vegetation formation. In contrast, the high water availability in evergreen/semideciduous forests and the rocky landscapes in which SDTF is found in the Cerrado Domain may inhibit fire spread in these forests. Overall, cerradão may be more likely to transition to savanna (cerrado sensu stricto) than the other forest types in the Cerrado Domain.

The floristic transition from cerrado sensu stricto/cerradão to the other forest formations is represented in the CVT by increasing soil fertility, lower flammability (a proxy for fire frequency) and higher water availability (i.e. low soil drainage). These factors can interact, and it has long been hypothesized that savanna formations on lower fertility soils are inherently more fire-prone than vegetation on fertile soils, because of the slow rates at which trees establish and grow, which then allows flammable grass to persist in the community (Kellman, 1984; Lehmann et al., 2014; Pausas, 2014; Silva, Corrêa, et al., 2013; Silva, Hoffmann, et al., 2013). Forest formations in the Cerrado Domain suppress flammable grasses because of their closed canopy and thus inhibit fire (Hoffmann & Moreira, 2002; Hoffmann et al., 2009). However, in this context, it is important to distinguish between dystrophic and mesotrophic cerradão. In dystrophic cerradão, low soil fertility may potentially limit the maximum amount of tree biomass such that it prohibits complete forest formation, irrespective of the fire regime, because nutrients may become increasingly limiting as a tree approaches the fire-resistance threshold (Hoffmann et al., 2012; Pellegrini, Franco, & Hoffmann, 2016; Pellegrini, Staver, Hedin, Charles-Dominique, & Tourgee, 2016). In addition to setting ultimate constraints on the ability of forests to form, nutrient availability also influences the distribution of tree species by regulating their growth rates and ability to overcome biomass loss in a fire (Hoffmann et al., 2012; Lehmann, Archibald, Hoffmann, & Bond, 2011).

Mesotrophic cerradão is found on soils intermediate between the poor dystrophic soils of the savanna formations and dystrophic cerradão and the mineral-rich mesotrophic or eutrophic soils of SDTF formations. Analysing the transition of tree species between SDTF and mesotrophic cerradão, Bueno et al. (2013) suggested that the floristic gradient was controlled mainly by soil fertility. It may be that under continued fire exclusion, mesotrophic cerradão, through litter deposition and nutrient cycling, may develop sufficient soil

fertility to transition to SDTF. These transitions between savanna, mesotrophic cerrado and SDTF must also be considered in the context of the potential for increased nitrogen deposition in the Cerrado Domain, which could encourage woody encroachment and conversion of savanna to forest vegetation.

In contrast with the smooth transition from savanna to SDTF, via mesotrophic cerrado, the distinction between the savanna and evergreen and semideciduous vegetation types is abrupt, not only in tree density in the field but also in species composition, with few species common to savanna or cerrado and evergreen and semideciduous forests (Adejuwon & Adesina, 1992; Felfili & Silva Junior, 1992; Furley, 1976). The evergreen and semideciduous forests are almost always present within a matrix of savanna vegetation, and the transition to non-forest vegetation is usually sharp. The transition is less perceptible physiognomically when it occurs with SDTF, but these transitions are rare as indicated by the sparsity of sites with a floristic composition intermediate between SDTF and evergreen and semideciduous forests (Figure 2).

With increasing tree size, the amount of nutrients required by forest trees becomes greater than that required by savanna trees, suggesting that evergreen and semideciduous forests species may be especially limited by nutrients (Pellegrini, 2016). For example, evergreen and semideciduous forests have higher water availability and are associated with higher soil nutrient levels, promoted by the higher presence of clayey soil (Assis, Coelho, da Pinheiro, & Durigan, 2011; Furley, 1992; Haridasan, 2000; Ribeiro & Walter, 2008; Ruggiero, Batalha, Pivelo, & Meireles, 2002). This combination of water availability and soil fertility may explain the distinctive indicator species from evergreen and semideciduous forests (e.g. *Cheiloclinium cognatum* (Miers) A.C.Sm., *Maprounea guianensis* Aubl., *Calophyllum brasiliense* Cambess. for evergreen forests and *Garcinia gardneriana* (Planch. & Triana) Zappi, *Hieronyma alchorneoides* Allemão, *Unonopsis gatteroides* (A.DC.) R.E.Fr. for semideciduous forests; Oliveira-Filho & Ratter, 1995, 2000, 2002; Ribeiro & Walter, 2008). Despite presenting a similar tree species composition, these vegetation types differ in soil drainage, being better drained in semideciduous forests and poorly drained in evergreen forests (Ribeiro & Walter, 2008; Rodrigues, 2009). These vegetation types also differ in the leaf-flush regime and in the structure of vegetation (Oliveira-Filho & Ratter, 1995; Ribeiro & Walter, 2008; Rodrigues & Shepherd, 2009). The CVT suggests a clear floristic distinction between evergreen and semideciduous forests and savanna formations, where the causal factor of vegetation change is water availability and the consequent absence of fire. The evergreen and semideciduous forests are also clearly floristically divergent from SDTF.

Seasonally dry tropical forest and evergreen and semideciduous forests relate to the edge of the CVT with higher soil fertility and/or greater water availability (Ribeiro & Walter, 2008; Scariot & Sevilha, 2005). Evergreen and semideciduous forests are more associated with watercourses and wetter soils, whereas SDTFs generally have no association with streams, but with fertile soil in the interflaves, for example, around calcareous outcrops. Indicator

species for SDTF such as *Ximenia americana* L., *Aspidosperma pyrifolium* Mart., *Trichilia hirta* L. and *Amburana cearensis* (Allemão) A.C.Sm. are characteristic of higher soil fertility (Ratter et al., 1973, 1978a,b). In contrast, the indicator species of evergreen and semideciduous formations show higher IVs, suggesting high specificity for environmental factors such as water availability and soil fertility. While we have noted that the transitions between evergreen and semideciduous forests and other vegetation types are generally abrupt in space, should precipitation patterns change dramatically in the Cerrado Domain under global climate change, such transitions may become possible.

5 | CONCLUSIONS

Our analyses suggest that, within one climatic zone in the Cerrado Domain of central Brazil, there is considerable floristic heterogeneity and a complex mosaic of vegetation types, which form three major groups on the basis of tree species composition: fire-adapted vegetation (cerrado sensu stricto and cerrado), dry forests in high fertility soils with low water availability (SDTF) and seasonal or evergreen forests where soil water availability is high (evergreen and semideciduous forest). We suggest a Cerrado Vegetation Triangle model that implicates ecological factors as fire, soil and water availability in controlling the variation in tree species composition of vegetation types in the Cerrado Domain. These factors act as important filters at local spatial scales to influence tree species composition across the entire Cerrado Domain, driving areas with high fire frequency and poor soils towards savanna formations and separating two distinct forest formations related to soil fertility (SDTF) and water availability (evergreen and semideciduous forests).

Much previous work has focused on the distribution of savanna vs. forest in the tropics (Hirota et al., 2011; Lehmann et al., 2014; Staver et al., 2011), but has treated forest as one vegetation type. There are in fact many kinds of forest in the Cerrado Domain. Transitions between savanna and each of these forest types are different, in terms of tree species turnover and environmental drivers. In order to understand future transitions between savanna and forest under global climate change or otherwise, distinguishing the environmental drivers and the kinds of forest involved will be essential.

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AUTHORS' CONTRIBUTIONS

M.L.B. and A.T.d.O.-F. conceived the ideas; A.T.d.O.-F., J.A.R. and M.L.B. compiled the data; M.L.B., V.P. and K.G.D. designed methodology; M.L.B., D.M.N. and V.P. analysed the data; V.P. and D.M.N. commented on earlier versions of the manuscript; M.L.B., K.G.D., R.T.P. and A.T.d.O.-F. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data used in this study is available at <http://www.neotropree.info> (Oliveira-Filho, 2017).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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