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

Marcelo Leandro Bueno*[1,2], Kyle G. Dexter[3,4], R. Toby Pennington[4,5], Vanessa Pontara[2], Danilo Mesquita Neves[6], James Alexander Ratter[4] & Ary Teixeira de Oliveira-Filho[1]

[1]Programa de Pós-Graduação em Biologia Vegetal, Universidade Federal de Minas Gerais – UFMG, Campus Pampulha, Belo Horizonte, MG 31270–090, Brazil.

[2]Laboratory of Ecology and Evolution of Plants, Universidade Federal de Viçosa, 36570-900, Viçosa, MG, Brazil

[3]School of Geosciences. The University of Edinburgh, Edinburgh EH9 3JN, UK

[4]Royal Botanic Garden Edinburgh, 20a Inverleith row, EH3 5LR, Edinburgh, UK.

[5]School of Geography. The University of Exeter, Exeter EX4 4RJ, UK

[6]Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721, USA.

*Correspondence author. E-mail: buenotanica@gmail.com

1. The Cerrado Domain of central Brazil houses the largest extent of savanna in the Neotropics, but despite its simple characterisation 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 cerradão 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.

Key words: cerrado, dystrophic cerradão, edaphic factors, fire, gallery forest, macroecology, mesotrophic cerradão, neotropical savanna, seasonally dry tropical forest, semideciduous forest

Running head: Savannas and forests in one climatic space of Cerrado Domain

Introduction

The main factors considered as determinants of worldwide savanna distribution, composition and structure are fire, herbivory, climate, soil fertility, and water availability, the latter being a product of climatic and edaphic factors (Eiten 1972; Cole 1986; Collinson 1988; Mistry 1998; Oliveira-Filho & Ratter 2002; Hirota *et al.* 2011; Staver, Archibald & Levin 2011; Dantas, Batalha & Pausas 2013; Lehmann *et al.* 2014; Bueno *et al.* 2017; Pellegrini 2016). 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; Staver, Archibald & Levin 2011; Pausas 2014; Lehmann *et al.* 2014; Pellegrini 2016).

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 (Neri *et al.* 2012; Dantas & Pausa 2013; Dantas, Batalha & Pausas 2013; Stevens *et al.* 2017). The flora of this region is dominated by fire-adapted species, including both fire-tolerant and fire-dependent plants (Eiten 1972, 1978; Coutinho 1990, 2006; Durigan & Ratter 2006; Hoffmann *et al.* 2009; Simon *et al.* 2009). Most savanna-inhabiting woody species show thick, corky bark and 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 (Ratter *et al.* 1973, 1977; Eiten 1978; Ratter & Dargie 1992; Oliveira-Filho & Ratter 1995, 2000; Ab'Saber 2003; Ribeiro & Walter 2008; Haidar *et al.* 2013; Oliveira-Filho *et al.* 2013a b, Dryflor 2016).

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 outcompete savanna species (Hoffmann, Orthen & Nascimento 2003; Dantas & Pausas 2003; Silva *et al.* 2013; Pausas 2014; Lehmann *et al.* 2014), 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 (Neri *et al.* 2012; Meira-Neto *et al.* 2017). 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 forest (SDTF) and evergreen and semideciduous forests (Oliveira-Filho & Ratter 2002; Ribeiro & Walter 2008; Oliveira-Filho *et al.* 2013a b). Under intermediate aluminium concentrations, another forest type, mesotrophic cerradão, is believed to act as an intermediate community, in terms of both soil properties and species composition (Ratter 1971; Ratter *et al.* 1973, 1978a; Ratter & Dargie 1992; Bueno *et al.* 2013). 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 (Furley & Ratter 1988; Oliveira-Filho & Ratter 2002; Amorim & Batalha 2007; Ribeiro & Walter 2008).

The variation of 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 *et al.* 1978b; Ratter 1992). Authors such as Oliveira-Filho and Ratter (2002) and Ribeiro & Walter (2008) have scaled these local studies up to the entire Cerrado Domain but using a qualitative approach. Whilst there are quantitative floristic comparisons across the Cerrado Domain (e.g., Ratter *et al.* 1997; Ratter, Bridgewater & Ribeiro 2003, 2006; Bridgewater, Ratter & Ribeiro 2004) 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 of 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 (Staver, Archibald & Levin 2011; Hirota et al. 2011; Silva *et al.* 2013; Lehmann *et al*. 2014).

Material and Methods

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 ca. 1/4 of the country's surface, plus smaller areas in north-western Paraguay and eastern Bolivia (Oliveira-Filho & Ratter 2002) (Fig. 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).

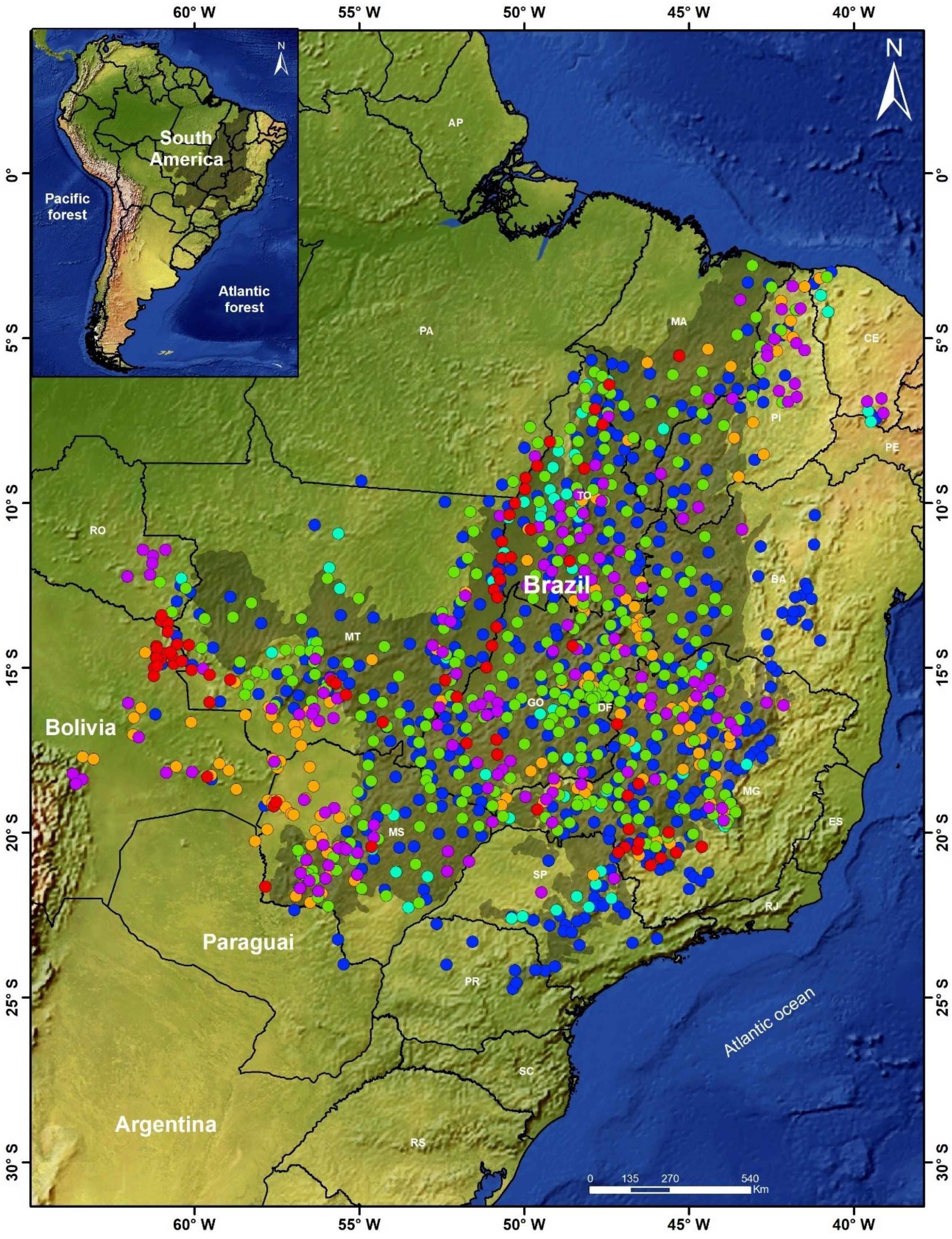

Figure 1. Geographic distribution of the Cerrado (IBGE 2012), with the location and vegetation types used in this study (cerrado woody savannas: blue circles, dystrophic cerradão: cyan circles, mesotrophic cerradão: purple circles, seasonally dry tropical forest: yellow circles, evergreen forest: green circles and semideciduous forest: red circles). Brazilian states are labelled as follows: Amapá (AP), Bahia (BA), Ceará (CE), Distro Federal (DF), Espírito Santo (ES), Goiás (GO), Maranhão (MA), Minas Gerias (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).

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. 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 and Walter 2008). We grouped the various vegetation formations that can be termed savanna, i.e. with a grassy understory and some frequency of fire, together 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 & 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 cerradão on richer soils (Ribeiro & Walter 2008). These two vegetation types can be structurally similar, but have distinct tree species composition (Araujo *et al*. 2011). Cerradão 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 cerradão, although grasses are often present (*Aristida*, *Axonopis*, *Paspalum* and *Trachypogon*, Ribeiro & Walter 2008). Mesotrophic and dystrophic cerradão 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 or Seasonally dry tropical forests (SDTF) occur on scattered patches of fertile soils (more fertile than in mesotrophic cerradão) 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; Ratter *et al.* 1973, 1977, 1978a b; Pennington, Prado & Pendry 2000; Bueno *et al.* 2013; Oliveira-Filho *et al.* 2013a b, Neves *et al.* 2015). 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 and Ratter 1995, 2000, 2002, Ribeiro & Walter 2008).

Dataset

We extracted the dataset from the NeoTropTree (NTT) database (Oliveira-Filho 2017, see http://prof.icb.ufmg.br/treeatlan), 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 standardised 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 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 projects *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 cerradão, 299 as evergreen forest, 76 as semideciduous forests, 140 as seasonally dry tropical forests (SDTF) and 153 as mesotrophic cerradão (Fig. 1). The final species matrix contained presence/absence data for 3,072 tree species, with a total of 148,718 presence records (see Fig. 1). The NTT database also included 27 environmental variables for all sites, derived from multiple sources (at a 30 arc-second resolution or ~1 km^2 near the equator; detailed below). Elevation at the NTT site centre was included as an integrative environmental variable. Eleven bioclimatic variables were obtained from WorldClim 1.4 (Hijmans *et al.* 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 et al. (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 data sets produced by Jones and Harris (2008).

Surface rockiness (% surface), soil texture class (% volume of sand), salinity class (ECe in dS·m-1) 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 diagram. This index is related with climate features and is related to both 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 was used as a proxy for fire return interval (i.e., fire frequency; Hoffmann *et al*. 2012; Archibald *et al*. 2013; Lehmann *et al*. 2014).

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 ($p < 0.05$) plotted as vectors. These analyses were conducted using the vegan package (Oksanen *et al.* 2016) in the R Statistical Software (R Core Development 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 toward a certain vegetation type. This analysis was performed using the statistical package indicspecies (De Caceres & Legendre 2009) in the R Statistical Environment (R Core Development Team 2017), with the method proposed by (Dufrêne & Legendre 1997).

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 (Fig. 2a; Fig. S1). Cerrado *sensu stricto*, comprising various savanna formations, grouped together in one corner of compositional space and was floristically distinct from seasonally dry tropical forest (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 three-dimensional NMDS was 0.11, indicating that three 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 $R^2 = 90\%$).

ANOSIM and MRPP analyses that distinguished the six vegetation types showed that, overall, these groups do differ significantly in tree species composition (ANOSIM, $R = 0.76$, $p < 0.001$; MRPP, $A = 0.18$, $p < 0.001$). When we categorised sites into three major floristic groups: savanna/cerradão (cerrado *sensu stricto*, dystrophic cerradão, mesotrophic cerradão), SDTF and semideciduous/evergreen (evergreen and semideciduos forests), the R value of ANOSIM increased ($R = 0.93$, $p < 0.001$), indicating that three groups provide a better categorisation of sites than six groups. The MRPP analysis suggested that three groups gave equivalent discrimination of sites compared to six groups ($A = 0.17$, $p < 0.001$).

Further, 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 (Fig. 2a-2d).

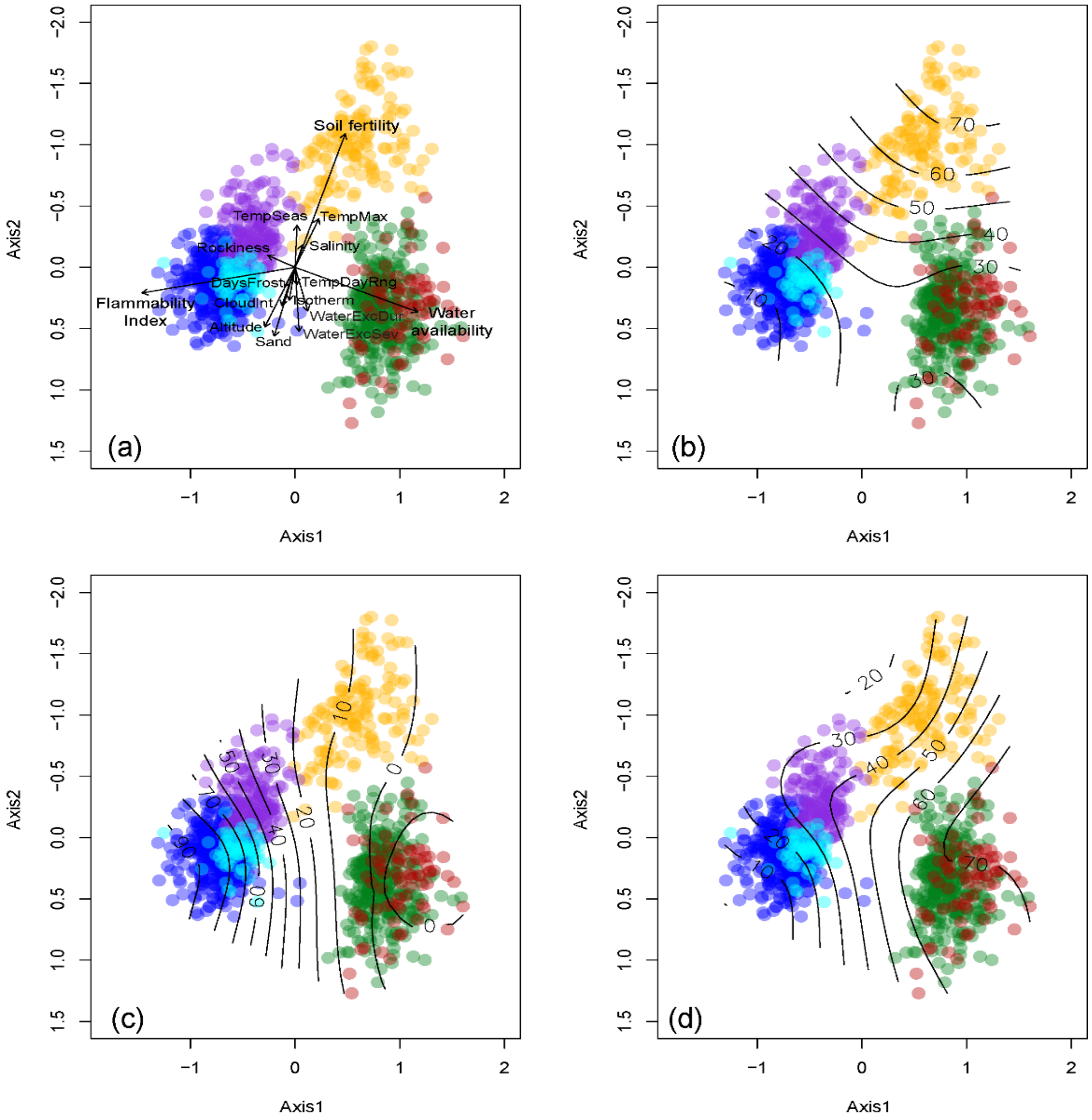

Figure 2. **(a)** Non-metric multidimensional scaling (NMDS) of 1,165 Cerrado Domain sites and their tree species composition into vegetation types (cerrado *sensu stricto*: blue circles, dystrophic cerradão: cyan circles, mesotrophic cerradão: purple circles, seasonally dry tropical forest: yellow circles, evergreen forest: green circles and semideciduous forest: red circles). 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 maximun; 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 fitted surface values for Soil fertility; **(c)** NMDS for vegetation types and black isolines fitted surface values for flammability index and **(d)** NMDS for vegetation types and black isolines fitted surface values for Water Availability.

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 the vegetation types in the Cerrado Domain.

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, seasonally dry tropical forest (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). The results clearly demonstrate the importance of edaphic factors in facilitating the coexistence of floristically divergent groups under similar climatic regimes (Fig. 2), which is evident from the complete spatial interdigitation of these floristic groups within the Cerrado Domain. 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 (Fig. 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; Fig. 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, realised between savanna and SDTF and unrealised between savanna and evergreen and semideciduous forests, lie between these vertices.

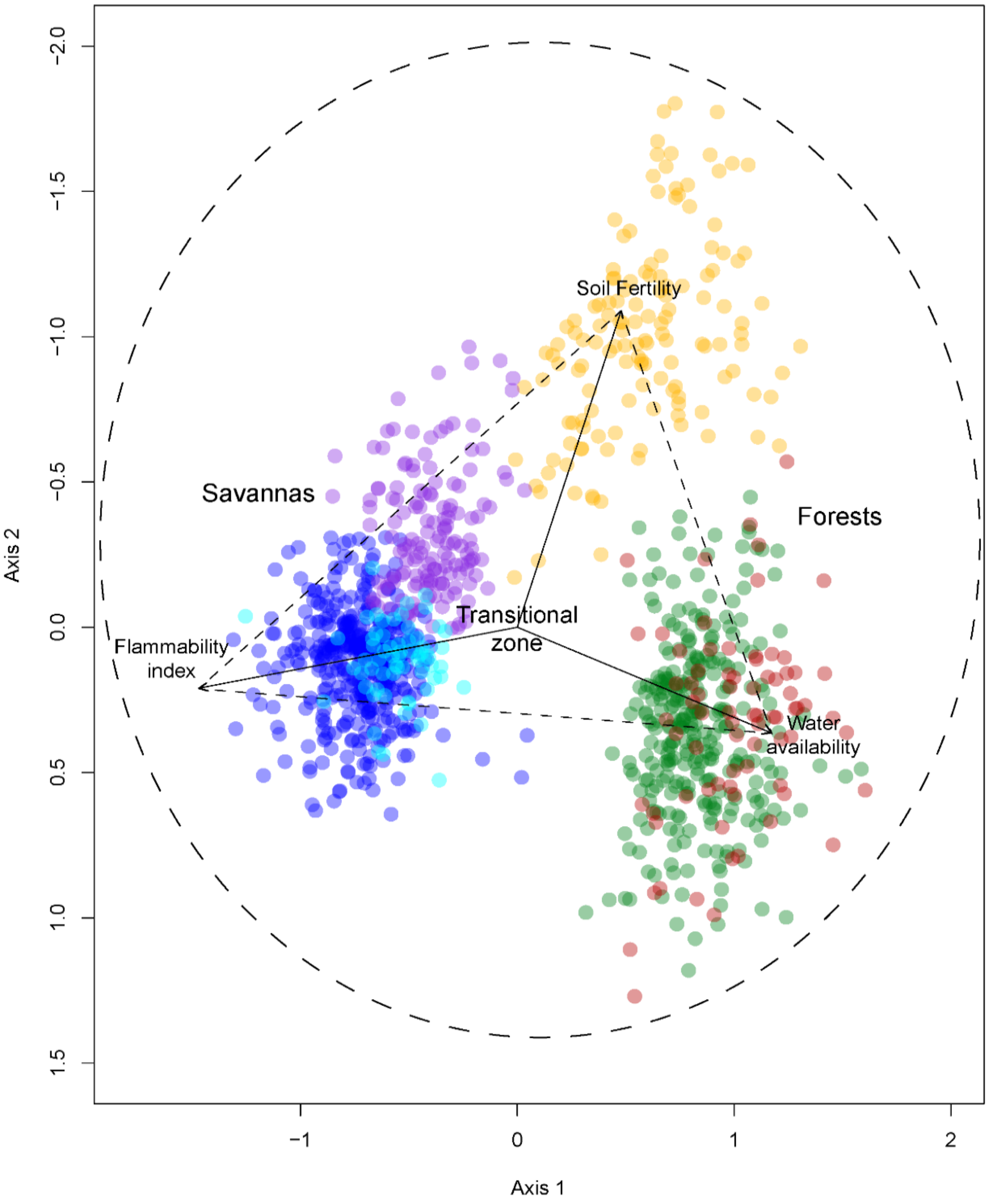

Figure 3. Proposed *Cerrado Vegetation Triangle* related to the NMDS results. The circle represents the climate, which influences the other factors in a general way; each vertex of the triangle represents a factor that leads to the occurrence of a major vegetation type, with the arrows on each side of triangle representing the increase of variables towards the vertices. The tree species composition are coloured according to vegetation types (cerrado *sensu stricto*: blue circles, dystrophic cerradão: cyan circles, mesotrophic cerradão: purple circles, seasonally dry tropical forest: yellow circles, evergreen forest: green circles and semideciduous forest: red circles)

Savannas have been strongly influenced and shaped by fire across the tropics (e.g. Gillon 1983; Coutinho 1990; Bond & van Wilgen 1996; Gottsberger & Silberbauer-Gottsberger 2006; Silva & Batalha 2010; Dantas, Batalha & Pausas 2013; Platt *et al.* 2016), as evidenced by key features of fire-tolerance or fire-dependency in the savanna flora (Simon *et al.* 2009; Silva & Batalha 2010; Simon & Pennington 2012; Lehmann *et al.* 2014; Pennington & Hughes 2014). 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 characterised 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 (San Jose & Farinas 1991; Moreira 2000; Woinarski, Risler & Kean 2004; Stevens *et al.* 2016). 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; Pinheiro & Durigan 2009, 2012; Pinheiro, Azevedo & Monteiro 2010; Durigan & Ratter 2016). 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 (Fig. 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 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.

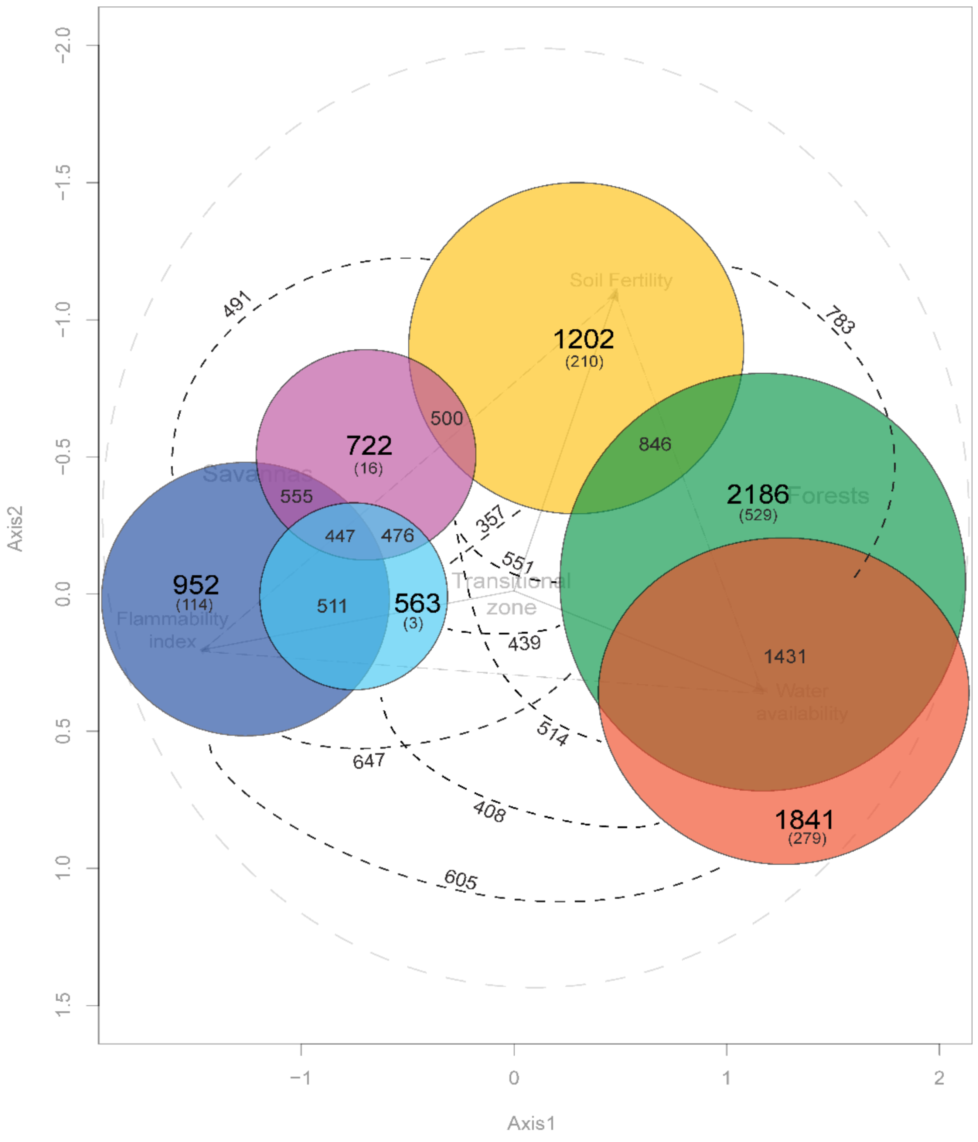

Figure 4. Species turnover among six vegetation types. The circles represent the vegetation types (cerrado *sensu stricto*: blue, dystrophic cerradão: cyan, mesotrophic cerradão: purple, seasonally dry tropical forest: yellow, evergreen forest: green and semideciduous forest: red). Numbers in bold represent the total species in the vegetation type and the number between brackets gives the number of exclusive species; numbers on the dashed lines and in the congruence of circles represent the shared species.

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 hypothesised 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; Silva *et al.* 2013; Pausas 2014; Lehmann *et al.* 2014). 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 *et al.* 2016a b). 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 (Lehmann *et al.* 2011; Hoffmann *et al.* 2012).

Mesotrophic cerradão is found on soils intermediate between the poor dystrophic soils of the savanna formations and dystrophic cerradão and the mineral-rich meso- 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 cerradão 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 cerradão, 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 cerradão and evergreen and semideciduous forests (Furley 1976; Adejuwon & Adesina 1992; Felfili & Silva Junior 1992). 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 (Fig. 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 (Furley 1992; Haridasan 2000; Ruggiero *et al.* 2002; Ribeiro & Walter 2008; Assis *et al.* 2011). 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 evegreen forests and *Garcinia gardneriana* (Planch. & Triana) Zappi*, Hieronyma alchorneoides* Allemão, *Unonopsis guatterioides* (A.DC.) R.E.Fr. for semideciduous forests) (Oliveira-Filho & Ratter 1995, 2000, 2002; Ribeiro

& Walter 2008). Despite present a similar tree species composition these vegetation types differ in soil drainage, being better drained soils 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 forests are also clearly floristically divergent from SDTF.

SDTFs and evergreen and semideciduous forests relate to the edge of the CVT with higher soil fertility and/or greater water availability (Scariot & Sevilha 2005; Ribeiro & Walter 2008). 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 interfluves, 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 indicator values, 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.

Conclusion

Our analyses suggest that, within one climatic zone in the Cerrado Domain of central Brazil, there is floristic heterogeneity and a complex mosaic of vegetations types, which form three major groups on the basis of tree species composition: fire-adapted vegetation (cerrado *sensu stricto* and cerradão), dry forests in high fertility soils with low water availability (STDF), 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 versus forest in the tropics (Hirota *et al.* 2011; Staver, Archibald & Levin 2011; Lehmann *et al.* 2014), 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.

Author's contributions

Bueno and Oliveira-Filho conceived the ideas; Oliveira-Filho, Ratter and Bueno compiled the data; Bueno, Pontara and Dexter designed methodology; Bueno and Pontara analysed the data; Pontara and Neves commented on earlier versions of the manuscript; Bueno, Dexter, Pennington and Oliveira-Filho led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Literature Cited

Abreu, R. C., Hoffmann, W. A., Vasconcelos, H. L., Pilon, N. A., Rossatto, D. R., & Durigan, G. (2017). The biodiversity cost of carbon sequestration in tropical savanna. Science advances, 3(8), e1701284.

Ab'Saber, A.N. (2003). *Os domínios de natureza no Brasil: Potencialidades paisagísticas*. Ateliê Editorial, São Paulo, Brazil.

Adejuwon, J.O. & Adesina. F.A. (1992). The nature and dynamics of the forest-savanna boundary in south-western Nigeria. In P.A. Furley, J. Proctor & J.A. Ratter (Eds.), *Nature and Dynamics of the Forest-Savanna Boundaries* (pp. 331-352). Chapman & Hall, London.

Amorim, P.K. & Batalha, M.A. (2007). Soil-vegetation relationships in hyperseasonal cerrado, seasonal cerrado, and wet grassland in Emas National Park (central Brazil). *Acta Ecologica* **32**, 319-327.

Araújo, G.M. & Haridasan, M. (1988). A comparison of the nutritional status of two forest communities on mesotrophic and dystrophic soils in central Brazil. *Communications in Soil Science and Plant Analysis* **19**, 1075-1089.

Araújo, G. M., Nascimento, A. R. T., Lopes, S. F., Rodrigues, R. F., & Ratter, J. A. (2011). Structure and floristics of the arboreal component of a dystrophic Cerradão and comparison with other Cerradões in Central Brazil. *Edinburgh Journal of Botany* **68(3)** 401-418.

Archibald, S., Lehmann, C.E.R., Gómez-Dansd, J.L. & Bradstocke, R.A. (2013). Defining pyromes and global syndromes of fire regimes. *PNAS* **110**, 6442–6447.

Assis, A.C.C., Coelho, R.M., Pinheiro, E. da S. & Durigan, G. (2011). Water availability determines physiognomic gradient in an area of low-fertility soils under Cerrado vegetation. *Plant Ecology* **212**, 1135-1147.

Bond, W.J. & van Wilgen, B.W. (1996). *Fire and Plants*. Chapman & Hall, London.

Bridgewater, S., Ratter, J.A. & Ribeiro, J.F. (2004). Biogeographic patterns, b-diversity and dominance in the cerrado biome of Brazil. *Biodiversity and Conservation* **13**, 2295-2318.

Bueno, M.L., Neves, D.R.M., Oliveira-Filho, A.T. Lehn, C.R. & Ratter, J.A. (2013). A Study in an Area of Transition Between Seasonally Dry Tropical Forest and Mesotrophic Cerradão, In Mato Grosso Do Sul, Southwestern Brazil. *Edinburgh Journal of Botany* **70**, 469–486.

Bueno, M.L.; Pennington, R.T; Dexter, K.G.; Kamino, L.H.Y.; Pontara, V., Neves, D.M. Ratter, J.A. & Oliveira-Filho, A.T. (2017). Effects of Quaternary climatic fluctuations on the distribution of Neotropical savanna tree species. *Ecography* **39**, 001–012.

Cole, M.M. (1986). *The savannas: biogeography and geobotany*. London: Academic Press, 438p.

Collinson, A.S. (1988). *Introduction to world vegetation*. London: Unwin Hyman Ltd. (2ed). 325p.

Coutinho, L. M. (1990). Fire in the ecology of the Brazilian cerrado. In: J.G. Goldammer, (Ed.), *Fire in the Tropical Biota* (pp. 82-105). Berlin: Springer-Verlag.

Coutinho, L. M. (2006). O conceito de bioma. *Acta Botanica Brasilica* **20**, 13-23.

Dantas, V.L., Batalha, M.A. & Pausas, J.G. (2013). Fire drives functional thresholds on the savanna-forest transition. *Ecology* **94**, 2454–2463.

Dantas, V.L. & Pausas, J.G. (2013). The lanky and the corky: fire-escape strategies in savanna woody species. *Journal of Ecology* **101**, 1265–1272.

De Caceres, M. & Legendre, P. (2009). Associations between species and groups of sites: indices and statistical inference. *Ecology* **90**, 3566-3574.

Dryflor (2016). Plant diversity patterns in neotropical dry forests and their conservation implications. *Science* 353: **6306**,1383-1387.

Dufrêne, M. & Legendre, P. (1997). Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* **67**, 345–366.

Durigan, G. & Ratter, J.A. (2006). Successional changes in cerradão and cerrado/forest ecotonal vegetation in western São Paulo State, Brazil, 1962-2000. *Edinburgh Journal of Botany* **6**, 119-130.

Durigan, G. & Ratter, J.A. (2016). The need for a consistent fire policy for Cerrado conservation. *Journal of Applied Ecology* **53**, 11–15.

Eiten, G. (1972). The cerrado vegetation of Brazil. *Botanical Review* **38**, 201-341.

Eiten, G. (1978). Delimitation of the cerrado concept. *Vegetation* **36**, 169-178.

Felfili J.M. & Silva Junior. M.C.D. (1992). Floristic composition. phytosociology and comparison of cerrado and gallery forests at Fazenda Agua Limpa, Federal District. Brazil. In P.A. Furley, J. Proctor & J.A. Ratter (Eds.), *Nature and Dynamics of the Forest-Savanna Boundaries* (pp. 393-429). Chapman & Hall. London.

Furley, P. & Ratter, J.A. (1988). Soil resources and plant communities of the central Brazilian cerrado and their development. Journal of Biogeography **15**, 97 – 108.

Furley, P.A. (1976). Soil-slope-plant relationships in the northern Maya mountains, Belize, Central America III – Variation in the properties of soil profiles. *Journal of Biogeography* **3**, 303-319.

Gillon, D. (1983). The fire problem in tropical savanna. In Bourliére. F. (Ed.), *Tropical Savannas (Ecossystem of the World 13)* (pp. 617-641). Elsevier, Amsterdam.

Gottsberger, G. and Silberbauer–Gottsberger I. (2006). Life in the Cerrado, a South American Tropical Seasonal Ecosystem. Vol. 1. Origin, Structure, Dynamics and Plant Use. Ulm, Germany: Reta Verlag.

Haidar, R.F., Fagg, J.M.F., Pinto, J.R.R., Dias, R.R., Damasco, G., Silva, L.C.R. and Fagg, C.W. (2013). Florestas estacionais e áreas de ecótono no estado do Tocantins, Brasil: parâmetros estruturais, classificação das fitofisionomias florestais e subsídios para conservação. *Acta Amzônica* **43**, 261-290.

Haridasan, M. (2000). Nutrição mineral das plantas nativas do Cerrado. *Revista Brasileira de Fisiologia Vegetal* **12**, 54-64.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. and Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* **25**, 1965-1978.

Hirota, M., Holmgren, M., Van Nes, E.H. & Scheffer, M. (2011). Global Resilience of Tropical Forest and Savanna to Critical Transitions. *Science* **334**, 232-235.

Hoffmann, W.A., Geiger, E.L., Gotsch, S.G., Rossatto, D.R., Silva, L.C.R., Lau, O.L., Haridasan, M. & Franco, A.C. (2012). Ecological thresholds at the savanna- forest boundary: how plant traits, resources and fire govern the distribution of tropical biomes. *Ecology Letters* **15**, 759–768.

Hoffmann, W.A. & Moreira, A.G. (2002). The role of fire in population dynamics of woody plants. In Oliveira, P.S. & Marquis, R.J. (Eds.), *The Cerrados of Brazil: Ecology and Natural History of a Neotropical Savanna* (pp. 159–177). Columbia University Press, New York.

Hoffmann, W.A., Adasme, R.A., Haridasan, M., Carvalho, M.T., Geiger, E.L., Pereira, M.A.B., Gotsch, S.G. & Franco, A.C. (2009). Tree topkill, not mortality, governs the dynamics of savanna–forest boundaries under frequent fire in central Brazil. *Ecology* **90**, 1326–1337.

Hoffmann, W.A., Orthen, B. & Nascimento, P.K.V. (2003). Comparative fire ecology of tropical savanna and forest trees. *Functional Ecology* **17**, 720– 726.

IBGE - Instituto Brasileiro de Geografia e Estatística (2012). *Manual Técnico da Vegetação Brasileira. Série Manuais Técnicos em Geociências 1*, (2nd ed.). IBGE, Rio de Janeiro.

Jones, P.D. & Harris, I.C. (2008). Climatic Research Unit (CRU) time-series datasets of variations in climate with variations in other phenomena. NCAS British Atmospheric Data Centre, date of citation. http://catalogue.ceda.ac.uk/uuid/3f8944800cc48e1cbc29a5ee12d8542d

Kellman, M. (1984). Synergistic relationships between fire and low soil fertility in Neotropical Savannas: A hypothesis. *Oecologia* **16**,158–160.

Lehmann, C.E.R., Archibald, S.A., Hoffmann, W.A. & Bond, W.J. (2011). Deciphering the distribution of the savanna biome. *New Phytology* **191**, 197–209.

Lehmann, C.E.R., Anderson, T.M., Sankaran, M., Higgins, S.I., Archibald, S., Hoffmann, W.A… Bond, W.J. (2014). Savanna vegetation-fire-cli- mate relationships differ among continents. *Science* **343**, 548–552.

Mccune, B. & Grace, J.B. (2002). Analysis of ecological communities. Mjm Software Design. Gleneden Beach.

Meira-Neto, J.A.A., Tolentino, G.S., Silva, M.C.N., Neri, A.V., Gatauer, M. Magnago, L.F.S…Valladares, F. (2017). *Acta Botanica Brasilica* **31**, 11-18.

Mistry, J. (1998). Fire in the Cerrado (savannas) of Brazil: an ecological review. *Progress in Physical Geography* **22**, 425 – 448.

Moreira, A.G. (2000). Effects of fire protection on savanna structure in Central Brazil. *Journal of Biogeography* **27**, 1021–1029.

Neri, A.V., Schaefer, C.E.G.R., Silva, A.F., Souza, A.L., Ferreira Junior, W.G. & Meira-Neto, J.A.A. (2012). The influence of soils on the floristic composition and community structure of an area of Brazilian Cerrado vegetation. *Edinburgh Journal of Botany* **69**, 1 – 27.

Neves, D.R.M., Dexter, K.G., Pennington, R.T., Bueno, M.L., Oliveira-Filho, A.T. (2015). Environmental and historical controls of floristic composition across the South American Dry Diagonal. *Journal of Biogeography* **42**, 1566–1576.

Neves, D.M., Dexter, K.G., Pennington, R.T., Valente, A.S.M., Bueno, M.L., Eisenlohr, PV., Fontes, M.A....(2017). Dissecting a biodiversity hotspot: The importance of environmentally marginal habitats in the Atlantic Forest Domain of South America. Diversity and Distribution **00**:1–12.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B…Wagner, H. (2016). Vegan: community ecology package. R package version 2.0–3. Available at: http://CRAN.R-project.org/package=vegan.

Oliveira-filho, A.T. (2015). Um Sistema de classificação fisionômico-ecológica da vegetação Neotropical. In: Eisenlohr, P.V.; Felfili, J.M.; Melo, M.M.R.F.; Andrade, L.A. & Meira-Neto, J.A.A. (Eds.). Fitossociologia no Brasil: Métodos e estudos de casos, vol.2, Editora UFV, Viçosa, cap. 19, pp. 452-473.

Oliveira-Filho, A.T. (2017). *NeoTropTree, Flora arbórea da Região Neotropical: Um banco de dados envolvendo biogeografia, diversidade e conservação*. Universidade Federal de Minas Gerais. (http://www.icb.ufmg.br/treeatlan/).

Oliveira-Filho, A.T. & Ratter, J.A. (1995). A study of the origin of Central Brazilian forests by the analysis of plant species distribution patterns. *Edinburgh Journal of Botany* **52**, 141-194.

Oliveira-Filho, A.T. & Ratter, J.A. (2000). Padrões florísticos das matas ciliares da região do cerrado e a evolução das paisagens do Brasil Central durante o Quaternário Tardio. In R.R. Rodrigues & H.F. Leitão Filho (Eds.). *Matas ciliares: conservação e recuperação* (pp.73-89). Edusp, São Paulo.

Oliveira-Filho, A.T. & Ratter, J.A. (2002). Vegetation physiognomies and woody flora of the cerrado biome. In Oliveira, P.S. & Marquis, R.J. (Eds.). *The cerrados of Brazil* (pp. 91-120). Columbia University Press, New York.

Oliveira-Filho, A.T., Cardoso D., Schrire, B.D., Lewis, G.P., Pennington, R.T., Brummer, T.J., Rotella, J., Lavin, M. (2013a). Stability structures tropical woody plant diversity more than seasonality:

Insights into the ecology of high legume-succulent-plant biodiversity. *South African Journal of Botany* **89**: 42-57.

Oliveira-Filho, A.T., Pennington, R.T., Rotella, J. & Lavin, M. (2013b). Exploring evolutionarily meaningful vegetation definitions in the tropics: a community phylogenetic approach. In D.A. Coomes, D.F.R.P. Burslem and William D. Simonsen (eds). *Forests and Global Change*. Pp. 239-260. Cambridge University Press (Ecological Reviews series).

Pausas, J.G. (2014). Alternative fire-driven vegetation states. *Journal of Vegetation Science* **26**, 4-6.

Pellegrini, A.F.A. (2016). Nutrient limitation in tropical savannas across multiple scales and mechanisms. *Ecology* **97**,313-324.

Pellegrini, A.F.A., Staver, A.C., Hedin, L.O., Charles-Dominique, T. & Tourgee, A. (2016a). Aridity, not fire, favors nitrogen- fixing plants across tropical savanna and forest biomes. *Ecology* **97**, 2177-2183.

Pellegrini, AFA, Franco, A.C. & Hoffmann, W.A. (2016b). Shifts in functional traits elevate risk of fire-driven tree dieback in tropical savanna and forest biomes. *Global Change Biology* **22**, 1235–1243.

Pennington, R.T., Prado, D.E. & Pendry, C.A. (2000). Neotropical seasonally dry forests and Quaternary vegetation changes. Journal of Biogeography **27**, 261 – 273.

Pennington, R. T. & C. E. Hughes. (2014). The remarkable congruence of New and old world savanna origins. *New Phytologist* **204**, 4-6.

Pinheiro, E.S. & Durigan, G. (2009). Dinâmica espaço-temporal (1962–2006) das fitofisionomias em unidade de conservação do Cerrado no sudeste do Brasil. *Revista Brasileira de Botânica* **32**, 441–454.

Pinheiro, E.S. & Durigan, G. (2012). Diferenças florísticas e estruturais entre fitofisionomias do Cerrado em Assis, SP, Brasil. *Revista Árvore, Viçosa* **36**, 181-193.

Pinheiro, M.H.O., Azevedo, T.S. & Monteiro, R. (2010). Spatial-temporal distribution of fire-protected savanna physiognomies in Southeastern Brazil. *Anais da Academia Brasileira de Ciências* **82**, 379–395.

Platt, W.J., Ellair, D.P., Huffman, J.M., Potts, S.E. & Beckage, B. (2016). Pyrogenic fuels produced by savanna trees can engineer humid savannas. *Ecological Monographs* **86**, 352–372

R Core Team (2017). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Ratter, J.A. (1971). Some notes on two types of cerradão occuring in northeastern Mato Grosso. In M.G. Ferri (Ed.), *III Simpósio Sobre o Cerrado* (pp. 110-112). São Paulo, EDUSP/Edgard Blücher.

Ratter, J.A. (1992). Transitions between cerrado and forest vegetation in Brazil. In P.A. Furley, J. Proctor & J.A. Ratter (Eds.), *Nature and dynamics of forest-savanna boundaries* (pp. 417 4300. Chapman & Hall, London.

Ratter, J.A., Richards, P.W., Argent, G. & Gifford, D.R. (1973). Observations on the vegetationof the northeastern Mato Grosso I. The woody vegetation types of the Xavantina-Cachimbo Expedition area. *Philosophical Transactions of the Royal Society B* **266**, 449-492.

Ratter, J.A., Askew, G.P., Montgomery, R.F. & Gifford, D.R. (1977). Observações adicionais sobre o cerradão de solos mesotróficos no Brasil central. In Ferri, M.G. (Ed.), *IV Simpósio sobre o Cerrado: Bases para a Utilização Agropecuária* (pp. 303-316). EDUSP, São Paulo.

Ratter, J.A., Askew, G.P., Montgomery, R.F. & Gifford, D.R. (1978a). Observations on forests of some mesotrophic soils in central Brazil. *Revista Brasileira de Botânica* **1**, 47-58.

Ratter, J. A., Askew, G. P., Montgomery, R. F. & Gifford, D. R. (1978b). Observations on the vegetation of northeastern Mato Grosso II. Forest and Soils of the Rio Suiá-Miçú area. *Proceedings of the Royal Society of London* **203**, 191-208.

Ratter, J.A. & Dargie, T.C.D. (1992). An analysis of the floristic composition of 26 cerrado areas in Brazil. *Edinburg Journal of Botany* **49**, 235-250.

Ratter, J. A., Ribeiro, J. F. & Bridgewater, S. (1997). The brazilian cerrado vegetation and threats to its biodiversity. *Annals of Botany* **80**, 223-230.

Ratter, J.A., Bridgewater, S. & Ribeiro, J.F. (2003). Analysis of the floristic composition of the Brazilian cerrado vegetation iii: comparison of the woody vegetation of 376 areas. *Edinburgh Journal of Botany* **60**, 57-109.

Ratter, J.A.; Bridgewater, S. & Ribeiro, F. 2006. Biodiversity patterns of the woody vegetation of the Brazilian Cerrado. In Pennington, R.T.; Lewis G.P. & Ratter, J.A. (Eds.). Neotropical savannas and seasonally dry forests: plant diversity, biogeography and conservation. (p.31-65). Taylor & Francis, London.

Ribeiro, J.F. & Walter, B.M.T. (2008). Fitofisionomias do bioma Cerrado. In Sano, S. M. & Almeida, S. P. (Eds.), *Cerrado: ecologia e flora* (pp.151-212). EMBRAPA-CPAC, Planaltina, DF.

Rodrigues, R.R. Uma discussão nomenclatural das formações ciliares (2009). In Rodrigues, R.R.; Leitão-Filho, H.F. (Eds.). Matas ciliares: conservação e recuperação. (p.101-107) São Paulo: EDUSP/FAPESP.

Rodrigues, R.R. & Shepherd, G.J. (2009). Fatores Condicionantes da Vegetação Ciliar. In Rodrigues, R.R.; Leitão-Filho, H.F. (Eds.). Matas ciliares: conservação e recuperação. (p.101-107) São Paulo: EDUSP/FAPESP.

Ruggiero, P.G.C., Batalha, M.A., Pivelo, V.R. & Meireles, S.T. (2002). Soil-vegetation relationships in cerrado (Brazilian savanna) and semideciduous forest, Southeastern Brazil. *Plant Ecology* **160**, 1-16.

Scariot, A. & Sevilha, A.C. (2005) Biodiversidade, estrutura e conservação de florestas estacionais deciduais no Cerrado. In: (eds.), A. Scariot, J.C. Sousa-Silva & J.M. Felfili. *Cerrado: Ecologia, Biodiversidade e Conservação*. pp. 123-139. Ministério do Meio Ambiente, Brasília, Distrito Federal.

San José, J.J. & Fariñas, M.R. (1991). Temporal changes in the structure of a *Trachypogon* savanna protected for 25 years. *Acta Oecologica* **12**, 237–247.

Santos, H. G., Jacomine, P. K. T., Anjos, L. H. C., Oliveira, V. A., Lumbreras, J. F., Coelho, M. R., … Oliveira, J. B. (2013). *Sistema brasileiro de classificação de solos*, 3rd ed. Brasília: Embrapa.

Silva, I.A. & Batalha, M.A. (2010). Woody plant species co-occurrence in Brazilian savannas under different fire frequencies. *Acta Oecologica* **36**, 85–91.

Silva, L.C.R., Corrêa, R.S., Doane, T., Pereira, E. & Horwath, W.R. (2013). Unprecedented carbon accumulation in mined soils: the synergistic effect of resource input and plant species invasion. *Ecological Applications* **23**, 1345-1356.

Silva, L.C.R., Hoffmann, W.A., Rossatto, D.R., Haridasan, M., Franco, A.C. & Horwath, W.R. (2013). Can savannas become forests? A coupled analysis of nutrient stocks and fire thresholds in central Brazil. *Plant Soil* **373**, 829–842.

Simom, M.F & Pennington, R.T. (2012). Evidence for Adaptation to fire regimes in the Tropical Savannas of the Brazilian Cerrado. *International Journal of Plant Sciences* **173**, 711-723.

Simon, M.F., Grether, R., Queiroz, L.P., Skema, C., Pennington, R.T. & Hughes, C.E. (2009). Recent assembly of the Cerrado, a Neotropical plant diversity hotspot, by in situ evolution of adaptations to fire. *PNAS* 106, 20359–20364.

Staver, A.C., Archibald, S. & Levin, S. A. (2011). The Global Extent and Determinants of Savanna and Forest as Alternative Biome States. *Science* **334**, 230-232.

Stevens, N., Lehmann, C. E. R., Murphy, B. P. and Durigan, G. (2017), Savanna woody encroachment is widespread across three continents. *Global Change Biology* **23**, 235–244.

Veloso, H.P., Filho, A.L.R.R. & Lima, J.C.A. (1991). *Classificação da vegetação brasileira, adaptada a um sistema universal*. IBGE. Rio de Janeiro, RJ. 124p.

Zomer, R.J., Trabucco, A., Bossio, D.A., van Straaten, O. & Verchot, L.V. (2008). Climate change mitigation: A spatial analysis of global land suitability for clean development mechanism afforestation and reforestation. *Agriculture Ecosystems and Environment* **126**, 67–80.

Walter, H. (1985). Vegetation of the earth and ecological systems of the geo-biosphere, (3nd ed.) Berlin: Springer-Verlag.

Woinarski, J.C.Z., Risler, J. & Kean, L. (2004). Response of vegetation and vertebrate fauna to 23 years of fire exclusion in a tropical Eucalyptus open forest, Northern Territory, Australia. *Austral Ecology* **29**, 156–176.