MARSCHNER REVIEW

Soil properties and geomorphic processes influence vegetation composition, structure, and function in the Cerrado Domain

Demetrius Lira-Martins · Diego Luciano Nascimento · Anna Abrahão · Patrícia de Britto Costa · André M. D'Angioli · Evérton Valézio · Lucy Rowland · Rafael S. Oliveira

Abstract

Background The Cerrado of central Brazil—the world's largest Neotropical savanna – is comprised of a mosaic of highly heterogeneous vegetation growing on an extremely diverse geologic and geomorphologic background. Geomorphic processes under stable tectonic and climatic conditions facilitated the development of diverse edaphic properties, which interact with disturbance events to form unique vegetation types.

Scope In this review, we detail how the geophysical environment affects soil formation and evaluate the mechanisms through which edaphic conditions control vegetation structure, floristic diversity and functional diversity.

Conclusion The influence of geomorphic processes on edaphic properties has a marked impact on the ecology and evolution of plant communities. Species exhibit morphological and physiological adaptations that optimise their successful establishment in particular soil conditions. Furthermore, fire disturbance alters these soil-vegetation associations further regulating the structural nature of these communities. Therefore, we propose an integrative view where edaphic, chemical and physical properties act as modulators of vegetation stands, and these conditions interact with the fire regime. The knowledge of plant edaphic niches, their functional traits related to resource acquisition and use, as well as the interaction of edaphic properties and disturbance regimes is paramount to research planning, conservation, and

Responsible Editor: Hans Lambers.

D. Lira-Martins (✉) · P. de Britto Costa ·
A. M. D'Angioli · R. S. Oliveira
Department of Plant Biology, Institute of Biology,
University of Campinas-UNICAMP, Campinas 13083970,
Brazil
e-mail: dema.liramartins@gmail.com

D. L. Nascimento
ICHNOS Research Group, Geology Graduate Program,
Unisinos University, Av. Unisinos, 950, São Leopoldo,
RS 93022-750, Brazil

A. Abrahão
Institute of Soil Science and Land Evaluation,
Soil Biology Department, Emil Wolff-Str. 27,
70593 Stuttgart-Hohenheim, Germany

P. de Britto Costa
School of Biological Sciences, The University of Western
Australia, Perth, WA, Australia

A. M. D'Angioli
Programa de Pós-Graduação Em Ecologia, Departamento
de Biologia, Vegetal, Instituto de Biologia, Universidade
Estadual de Campinas, Campinas, Brasil

E. Valézio
Institute of Geosciences, University of Campinas-
UNICAMP, Campinas 13083-970, Brazil

L. Rowland
College of Life and Environmental Sciences, University
of Exeter, Exeter EX4 4RJ, UK

successful restoration of the full diversity of Cerrado vegetation types.

Introduction

Tropical savannas represent the second-largest biome in the world. They have a wide geographic distribution, support significant biodiversity and provide essential ecosystem services (Wilsey 2018). Amongst neotropical savannas, the Cerrado is the largest and is characterised by its higher rainfall and lower soil nutrient status, relative to other savannas (Solbrig 1993). Most of this domain is located within the Brazilian territory and originally covered *ca.* 200 million hectares distributed over 22.5° of latitude of Central Brazil (Ab'Sáber 2003; Sano et al. 2010, 2019). A wet seasonal climate dominates, with mean precipitation of 1,486 mm ± 146.8 mm. However, the north is drier (ca. 760 – 1,000 mm) and the west is wetter (1,500 – 1,600 mm), with some regions in the northwest, which border the Amazon, reaching annual rainfall of 2,400 mm (Campos and Chaves 2020). The precipitation is concentrated in the rainy season and the dry season can vary in duration from 4 to 7 months. Herein, we use the term Cerrado to characterize the phytogeographic domain within the central region of Brazil that is formed, in its majority, by the following vegetation types: grasslands (regionally termed "*campos*"), shrublands (grasslands with the presence of shrubs, "*campos sujos*"), savannas (grasslands with the presence of trees) and woodland savannas (closed canopy savannas, "*cerradão*"). Hence, there is a rich variance in growth forms coexisting within the same ecosystems (Gardner 2006). In addition, other formation types occur in disjoint patches of vegetation across the landscape, such as evergreen and deciduous forests, as well as wetlands (Durigan et al. 2022). Many of these vegetation types can be found in close proximity, forming abrupt transitions of vegetation under the same climatic conditions (Furley and Ratter 1988; Cochrane 1989; Cruz Ruggiero et al. 2002). This complex mosaic of vegetation types enriches the structural arrangements of the landscape, and the co-occurrence of forbs, sedges, grasses, palms and trees superimposes layers of different plant growth forms (Sano et al. 2008). The causes of the complexity in this vegetation mosaic also underpins the large diversity of plants found in the Cerrado domain.

The Cerrado domain has the most diversified and complex geologies in Brazil and this results in a variety of soil types and conditions (Salgado et al. 2015). Most soils evolved in a warm and wet climate and under stable tectonic conditions. The landforms not only mark the environmental heterogeneity of the Cerrado, but also underpin the pedogenetic process of these soils (Alkmim 2015; Salgado et al. 2015). Cerrado soils are generally dystrophic (Lopes and Cox 1977; Furley and Ratter 1988) with low nutrient availability, high acidity and high iron (Fe) and aluminium (Al) oxide content (Haridasan 1982; Goedert 1983; Lopes and Guilherme 2016). For instance, soil effective cation exchange capacity (ECEC) varies from 0.35 cmol kg^{-1} to 8.10 cmol kg^{-1}, with soils exhibiting values lower than 2.0 cmol kg^{-1} being extremely frequent (Lopes and Guilherme 2016). Conversely, most of the soils have high Al saturation with values as high as 40% being common across the Cerrado (Lopes and Guilherme 2016). These soils are one of the poorest in Brazil in terms of total phosphorus (P) concentration (Pavinato et al. 2020) and the presence of the Al and Fe oxides increase P sorption (de Mesquita Filho and Torrent 1993; McDowell and Condron 2001). This results in higher rates of P immobilization in soil and hampers its availability to plants. For instance, available P can be as low as 0.1 mg kg^{-1} to 16.5 mg kg^{-1}, but with values as low as 0.4 mg kg^{-1} being frequently found (Lopes and Guilherme 2016). In terms of physical properties, most of the soils are well-drained and deep (Reatto et al. 1998; Lopes and Guilherme 2016; Sano et al. 2019) with no evident physical limitation for the development of deep root growth. This geological, geomorphological and edaphic diversity translates into diverse vegetation types and a plethora of plant forms and species (Klink and Machado 2005).

Many of the geomorphological landforms represent immovable patches of substrates that persisted over geological times (Corlett and Tomlinson 2020) thus allowing for the evolution of plants adapted to these diverse environments (Rajakaruna 2018). Adaptations to these soil conditions along lineages contribute to reproductive isolation and speciation, generating high endemism (Rajakaruna 2018; Vidal et al. 2019; Hayes et al. 2021). Specific local plant assemblages develop highly specialised traits, allowing them to survive in particular edaphic conditions (Oliveira et al. 2015; Abrahão et al. 2019). For example, many Cerrado plants have specific

traits that allow them to establish in acidic soils with P and cation limitation. Furthermore, adaptations to limiting nutrient availability can promote the diversification of specific groups in ecosystems limited in P and cations (Pekin et al. 2012; Hayes et al. 2021). Some species, like *Qualea grandiflora* and *Rudgea viburnoides* have physiological and structural traits involved in coping with the high concentrations of Al in soils (Haridasan 2008). Other species have root specializations that allow them to acquire strongly bound P from these soils (Abrahão et al. 2019; Teodoro et al. 2019). Alternatively, some species are capable to optimize nutrient use and storage, which results in efficient metabolic activity (Guilherme Pereira et al. 2018). Hence, soils generate significant environmental filtering effects on species in the Cerrado (Viani et al. 2014).

Alongside soils, other environmental conditions, such as fire, play important roles in determining species distribution and the occurrence of vegetation types. Nevertheless, some care should be taken when considering the importance of fire in determining Cerrado functions and structure. Although frequent fires do constrain a high build-up of tree cover, they interact with soil conditions as underlying mechanisms of this control. For instance, quartzite has a high resistance to erosion (Barreto et al. 2013) and their silica nature will result in nutrient-poor—especially in P—(Teodoro et al. 2019) shallow soils. Alongside a dry climate, these edaphic conditions favour the development of a shrubby-grassy vegetation types, with a high investment in carbon-rich structures (Negreiros et al. 2014; Tameirão et al. 2021) that generate a fire-prone environment (Silveira et al. 2016).

The Cerrado plays an important biodiversity role on a global scale by representing an important hotspot, with extraordinary richness of endemic species (Myers et al. 2000). Such impressive biodiversity also represents a comprehensive repository of genetic resources, with a great potential to improve the efficiency and resilience of agricultural systems, thus ensuring sustainable use of resources and food security (Lambers et al. 2020). Brazil is highly dependent on the provision of Cerrado ecosystem services. The domain spans three major watersheds in a country where the most important energy supply comes from hydroelectric power plants, thus making the Cerrado a central element for Brazilian water and energy security (Lima et al. 2011; Latrubesse et al. 2019). Despite this, the Cerrado is one of the most threatened domains in the world and

displays Brazil's highest native vegetation removal rates, which resulted in a loss of approximately 50% of its original area (Eloy et al. 2016; Strassburg et al. 2017). The latest frontiers of land conversion, in the northern Cerrado, also threaten the Cerrado's integrity, as this is the most conserved part of the domain (Strassburg et al. 2017; Lemes et al. 2020; Silva et al. 2021). Conservation of natural areas remains the most important action to counter the continuous loss of Cerrado ecosystems. Nevertheless, restoration is also urgent given the significant and continued loss of native vegetation. Understanding the mechanisms underpinning community assembly and functioning when planning conservation and restoration practice is essential (Laughlin 2014). To achieve this, significantly more attention is needed on how the geology and geomorphology interact on driving edaphic conditions that determine the observed community assembly as mediated by plant adaptations.

In this review, we evaluate the role played by geological and geomorphological conditions and by soil chemical and physical properties as important environmental factors influencing vegetation structure, species and functional composition in the Cerrado domain. We also assess how the geophysical mechanisms controlling the floristic composition of Cerrado vegetation types are mediated by species traits. Hence, we discuss i) the importance of geologic history and the geomorphology in the development of soil diversity in the Cerrado; ii) how edaphic conditions interact with fire disturbance to influence vegetation structure in Cerrado; iii) how floristic diversity of Cerrado is affected by geophysical and edaphic properties; iv) the role of soils as environmental filters affecting plant functional traits and functional diversity of Cerrado plant species, and we conclude with v) highlighting the importance of the interplay between soil properties and species functional traits to successfully guide restoration efforts of Cerrado vegetation types.

The Cerrado soils in the context of long-term geomorphology

Geologic and geomorphologic aspects of the Cerrado domain

The Cerrado represents the second most important domain in Brazil, given the magnitude of its territory.

It occupies at least 90% of the Central Brazilian Plateau (Fig. 1). The Cerrado encompasses a wide variety of vegetation types (Fig. 1a), geomorphic features represented by different landforms (Fig. 1b), and soils (Fig. 1c) developed before and during the Quaternary. The parent material, and its different chemical characteristics, is determined by the geological history of the area that comprises the Cerrado domain. The association between geomorphology, parent material and soil type contribute to generating a complex mosaic of vegetation under semi-humid climatic conditions previously described (Rizzini 1997; Ratter et al. 1997; Motta et al. 2002; Sano et al. 2019; Françoso et al. 2020). There is a consistent overlap between vegetation types and geomorphology (Fig. 1). The dominant savanna formations in the Cerrado occur over the dominant landforms, namely, plateaus and depressions. There is a prevalence of the deep and weathered Ferralsols that result from these ancient landforms (Fig. 1c).

From a regional perspective, Brazil can be divided into two tectonic compartments separated by the fault system called Transbrasiliano Lineament (Fig. 2a): (i) the "Amazonian Brazil" where the landscape is dominated by lowlands below 500 m in elevation; (ii) "Atlantic Brazil" or "Extra-Amazonian Brazil",

where the relief is more variable and with the presence of mountains and high plateaus that reach altitudes above 500 m (Saadi et al. 2005; Salgado et al. 2015) (Fig. 2a, b). This geological difference between "Amazonian Brazil" and "Atlantic Brazil" resulted from plate convergence events during Neoproterozoic (1000–545 million years ago) (Alkmim 2015) that define the main geological features within Brazil. The marked differences of geomorphological features between the Amazonian and Atlantic compartments underly structural and functional differences of the main vegetation types found across these compartments. From a digital elevation model of the Brazilian territory (Fig. 2b), a wide variation in topography across the Cerrado domain (Fig. 2b) distributed over the "Atlantic Brazil" is clear. This was created by the break-up of Gondwana, resulting in magmatic intrusions, uplift and reactivation of ancient faults. These factors affected their geomorphological configuration over time, and the development of hydrographic basins. In this region, the rugged topography comprises landforms such as mountains, plateaus, tablelands and flattened plains developed in sedimentary basins, cratons and Neoproterozoic orogens over a wide range of lithotypes such as granites, gneisses, quartzites, basalts, and sandstones. Conversely, the
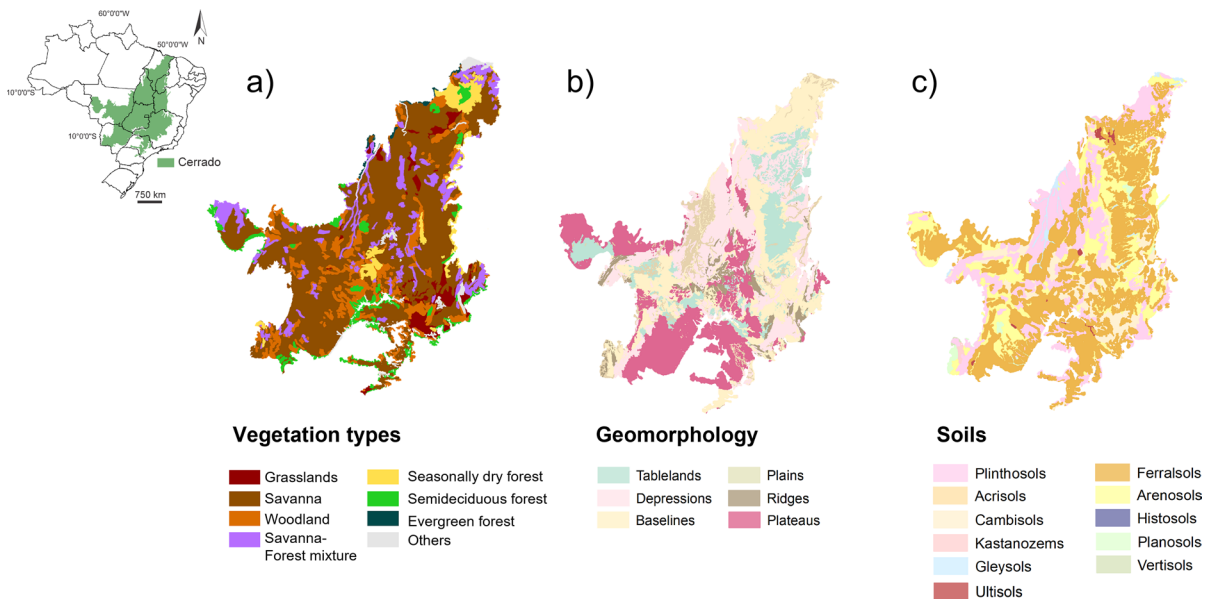

Fig. 1 a) Cerrado vegetation types (IBGE 2012) as indicated by the dominant vegetation in the area. **b)** There are six geomorphological units in Cerrado viz. depressions (29.1%), plateaus (22.9%), baselines (22.3%), tablelands (15.2%), plains (6.1%) and ridges (4.4%). Adapted from IBGE (2009). **c)** Soils of Cerrado domain. Adapted from dos Santos et al. (2011).
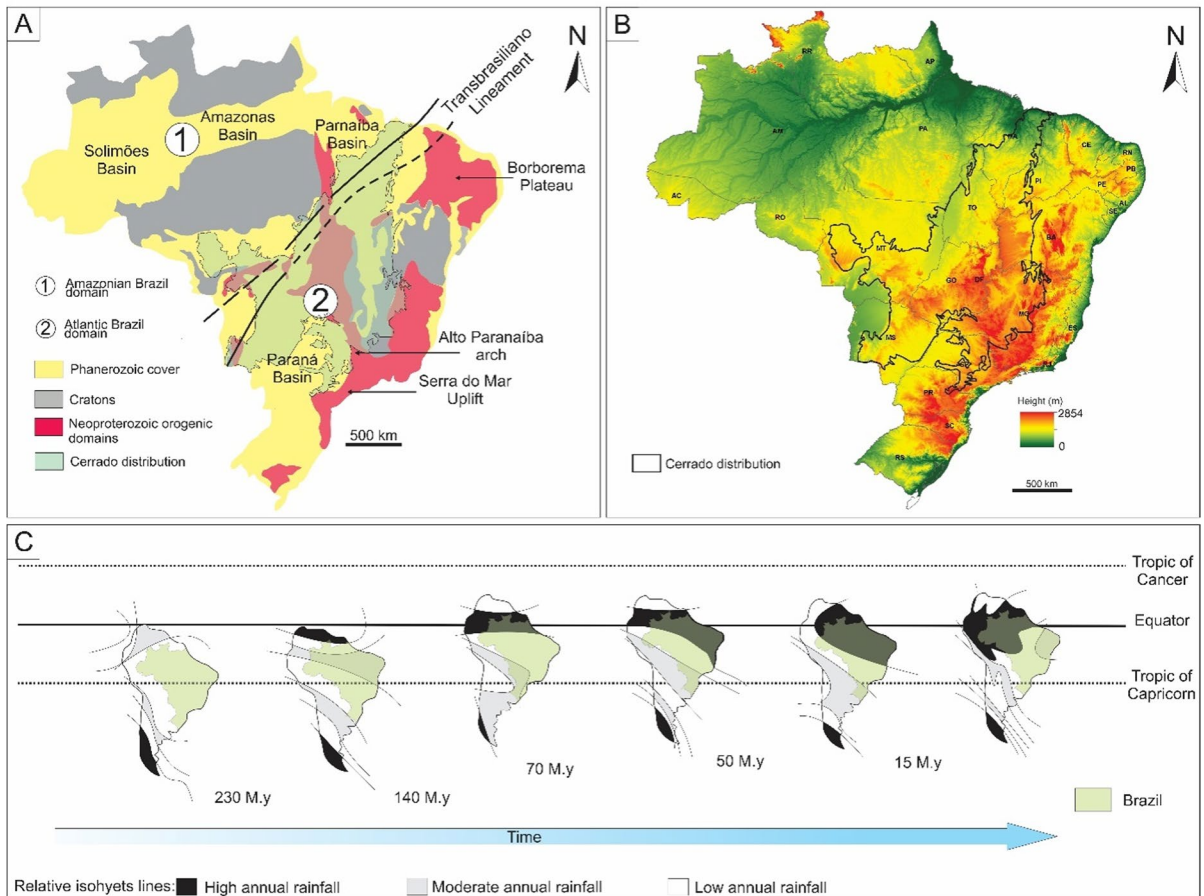
Fig. 2 a) Large-scale tectonic structures of Brazil and the Cerrado biome. Adapted from Saadi et al. (2005) and Alkmim and Reis (2021). **b)** Digital elevation model of Brazil. Note the difference in topographic features between Amazonian and Atlantic domains. **c)** Predicted rainfall distribution of South American plate position along Mesozoic and Cenozoic. Isohyetes represent line witj similar rainfall. Different colours indicate relative rainfall of different levels. Adapted from Tardy et al. (1991) and based in Parrish et al. (1982)

"Amazonian Brazil" compartment is composed by lowlands with more homogeneous landforms developed in cratonic region (i.e., Amazon craton).

Other important geomorphological aspect of the Cerrado domain is the relative tectonic and climatic stability from the Cretaceous (65 Ma) to present day (de Almeida and Carneiro 1998). The westward drift of the South American plate resulted in minimal latitudinal changes thus allowing the plate's maintenance in an intertropical position (between 30° S and 30° N) since the Gondwana break-up (Fig. 2c) (Parrish et al. 1982; Tardy et al. 1991). This intertropical stable position of the plate during millions of years provided constant warm and humid climatic conditions that resulted in the development of landforms and soils under intensive weathering. Under tectonic stability, surface erosion is minimal thus allowing the weathering products to remain in place and further resulting in kaolinitic deep weathered mantles and landforms capped by iron and silica-rich duricrusts (Tardy 1993; Ollier and Pain 1996), as observed in plateaus of central Brazil.

The geomorphological configuration of Cerrado comprises two general contexts at regional and local scale. At the regional scale, old landforms retain the geomorphic and pedological signature of tens of millions of years, such as pre-Cenozoic or Cenozoic geomorphic surfaces represented by tabular forms and large plateaus (i.e., *chapadas or chapadões*) and ridges. Peripheral depressions also mark these

old landforms and were developed during geomorphic cycles under relative tectonic stability prior to the Quaternary (Tardy 1993; Muggler et al. 2007) (Fig. 3a). At the local scale, landforms are marked by younger geomorphic elements, due to a dynamic evolution of the landscape, thus forming talus deposits, floodplains, and fluvial terraces (Ratter et al. 1997; Ab'Sáber 2003; Werneck 2011) created during the Quaternary. These dynamic local processes underly the topographic variation along the slopes (Fig. 3b).

Plateaus represent important landforms in the regional scale. They are elevated and extent landforms with tabular aspects limited by escarpments along the edges. Plateaus develop under different lithologies (sedimentary, metamorphic, or volcanic) and are formed by tectonic uplift and, or erosion (Fig. 4a, b) (Zinck 2013). Tablelands comprise flat-topped elevated areas also associated with escarpment retreat (Fig. 4c, d). Different from plateaus, tablelands occur in flat-lying sedimentary rocks such as sandstones. Erosion can destroy plateaus, resulting in ridges, canyons and dissected aspects of the surface by the deep incision of streams (e. g. dissected plateaus) (Fig. 4c). Lowlands are elaborated by erosive processes and form depressions, and residual relief, such as mesas and inselbergs
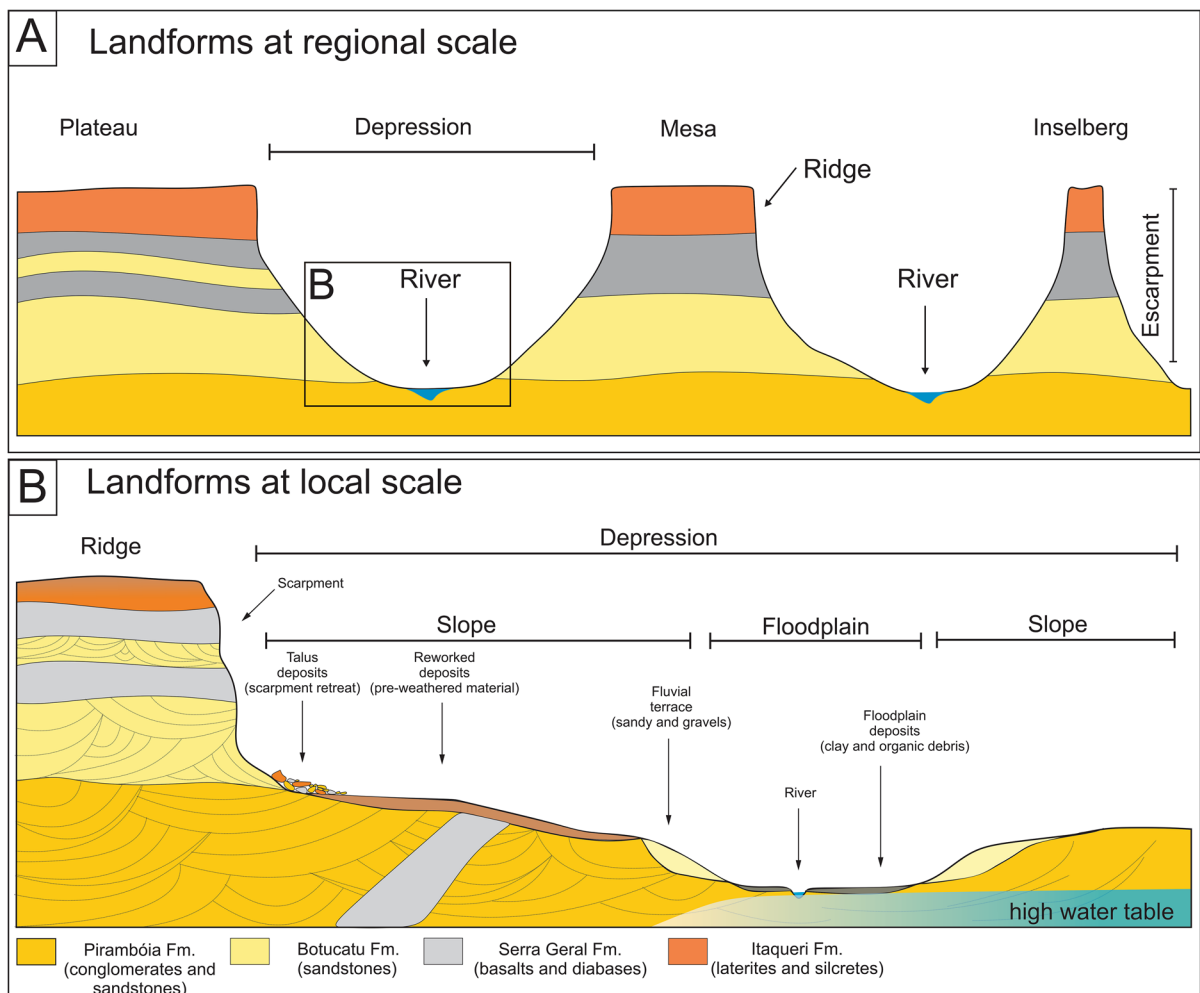

Fig. 3 General aspects of landforms in Cerrado domain. **a**) Plateaus, mesas, and inselbergs covered by soil or duricrusts are common at regional scales (modified from Duszyński et al. (2019)). **b**) At local scales, the deposit of material from plateau erosion to lower portions of the slopes represent important geomorphic processes of soil formation. The material deposited next to rivers form soils in fluvial terraces and floodplains

Fig. 4 a, **b**) Quarzitic plateaus in Espinhaço Range. Note the scarps and ridges in their border. **c**, **d**) Tablelands and dissected sedimentary plateau of Bahia. Yellow arrows indicate the fluvial channels that erode the plateaus thus resulting in the escarpment retreat of the plateau. **e**) Mesa and depression in Tocantins. The yellow arrow indicates the fluvial channel that enlarged the depression. **f**) Sedimentary plateau bordered by talus deposits and depression in Tocantins. **g**) Fluvial terrace in São Paulo covered by Cerrado. **h**) Fluvial terrace in São Paulo covered by Ferralsol
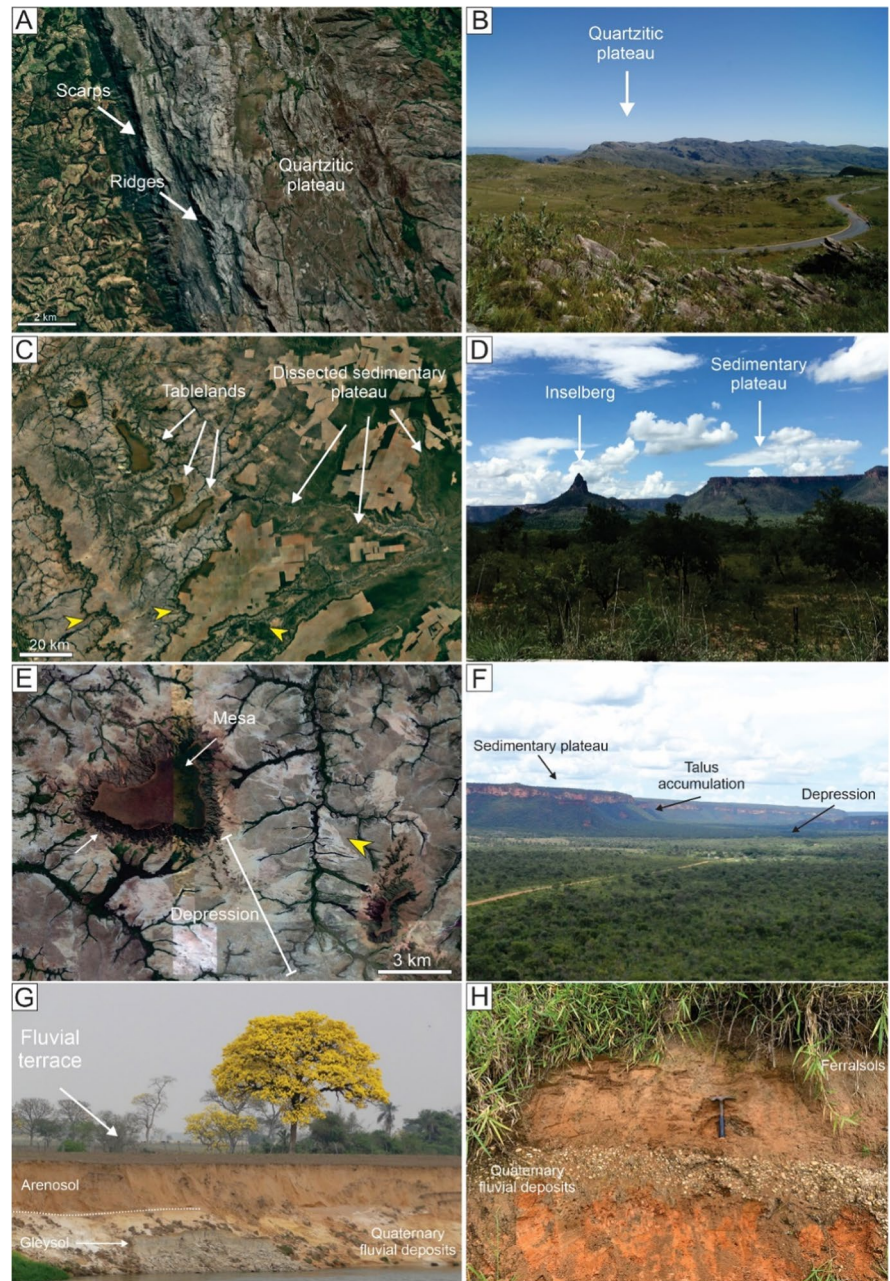
(Ollier and Pain 2000; Duszyński et al. 2019). The depressions are zones with lower elevations on plateau margins created by erosional process associated with fluvial activity and mass movement, which can generate escarpment retreat and landform fragmentation (Fig. 4e, f). The inselbergs and mesas represent the latter stages of geomorphic development. These landforms evidence plateaus erosion, process responsible for the development of lowland plains.

Examples of the latter are fluvial terraces and floodplains (Fig. 4g, h).

Geology and geomorphology as underlying factors of the vegetation and soil associations

Geology and geomorphology control the soil development (e.g., parent material distribution) (Box 1) and provide the underlying environmental heterogeneity

that drives abrupt vegetation transitions. Soils can develop from lithified parent material given by the underlying bedrock (quartzites, basalts or gneisses) or from unconsolidated materials, such as Quaternary deposits (Soil Survey Staff 2014). The majority of Cerrado soils consist predominantly of mineral matter, and thus are characterized as mineral soils (Brady and Weil 2016). The main physical and chemical properties of these soils are strongly determined by mineral composition (heterogeneous or homogeneous) of the parent material (Gray et al. 2016; Wilson 2019).

The geological perspective provides the conceptual basis to understand the chemical features of soils. The mineralogical properties of the parent material affect soil chemistry and represent the main source of mineral nutrients, such as P, thus characterizing overal soil nutrient availability. Mineralogy also controls the rates of pedogenesis, because the rock nature will affect the neoformation of secondary minerals (Ollier and Pain 1996; Porder 2019). For instance, soils developed from volcanic rocks, such as basalts, are composed by plagioclase, biotite and pyroxene, which are rich in Ca, Mg and Fe rich minerals and tend to be more clayey than soils developed from rocks rich in silica minerals (e.g., granite or quarztites) (Porder and Ramachandran 2013).

Alongside geology, geomorphology also plays an important role in soil formation. Soils developed from lithified parent material (i.e., sedimentation of finer materials) in stable areas are generally older and deeper than soils developed in steeper slopes, which tend to be shallow. In addition to topography, the fractures and bedding planes of bare rocks affect the location of soil development (patch soils) and plant distributions (Phillips 2019; Nascimento et al. 2021). Such patterns play a central role in some vegetation types, such as rocky grasslands and savannas. Geomorphic processes also control soil formation through the deposition of unconsolidated material, which varies according to chemical and physical properties of the source (erosional area). For instance, the erosion of sandstone plateaus caped by ironcrusts forms soils downslope composed sandstone and iron clasts mixed with sandy material, such as Arenosols, Leptsols and Cambisols. This process is responsible for the frequent occurrence of these soils in the lower parts of the relief. Two examples are described below, to illustrate the variability of landforms and their controls in Cerrado vegetation types: Veadeiros Tableland

(Chapada dos Veadeiros) in central Brazil and Espinhaço Range in eastern Brazil.

The landscape in Veadeiros Tableland (Chapada dos Veadeiros) can be used to illustrate these associations between vegetation types and geomorphology. It is located in Central Brazil and divides three important fluvial systems viz. Paraná, São Francisco, and Tocantins-Araguaia. The geomorphic aspects are highly variable and are composed of high plateaus, depressions, erosional scarps, and ridges with waterfalls (Fig. 5a, b, c). Shifts in vegetation types strikingly follow the geomorphology of the area where savannas cover the plateau upland and rocky grasslands—i.e., "*campos rupestres*"—grow on the rocky outcrops in the plateau edges. The eroded sediments from escarpments and plateau borders are deposited in the lowlands (talus and colluvial deposits) and depressions thus becoming the parent material of their soils. Vegetation with increased woodiness such as semideciduous forests can be found on these talus deposits (Fig. 5a). Furthermore, the area sits on impermeable quartzites that generate shallow, acidic and nutrient-limited soils (Cambisols. Leptosols and Arenosols). This impermeable quartzite in plateaus and floodplains favours the development of soils under water-saturated conditions (Fig. 5d) (de Carvalho Júnior et al. 2015), which exhibit hydromorphic features (e.g., Gleysols). These are covered by wet grasslands (*campos úmidos*), shrubby grasslands and, when *Mauritia flexuosa* palms are present, constitute the vegetation types called "Veredas" (de Carvalho Júnior et al. 2015) (Fig. 5e, f). In drier conditions, the constant process of wetting and drying of these soils results in hard forms of iron precipitates called plinthite (Motta et al. 2002) with more advanced stages of this process resulting in irreversible forms of precipitates called petroplinthite. These conglomerates can represent physical constraints to deep root development thus favouring the establishment of species with shorter roots such as grasses and herbs. These hydromorphic conditions result in common occurrences of Plinthosols with grasslands and grassy marshes at the intraplateau depressions (Correia et al. 2001). The transition between vegetation types is abrupt between uplands, well-drained fluvial terraces, and the floodplains covered by grasslands and palms.

The Espinhaço Range shows a complex relief morphology as a result of denudation process and fluvial incision. The differential weathering given

Fig. 5 General aspects of landforms in the Veadeiros Tablelands (*Chapada dos Veadeiros*) associated with a mosaic of vegetation types. **a**) Talus deposits from plateau edge erosion and formation of soils which allow forest establishment. **b**) Incision of streams formed by erosion. **c**) Satellite image from *Rio Preto* (black river) in Chapada dos Veadeiros National Park showing the formation of floodplains and fluvial terraces favoured by topography and impermeable soil quartzite. **d**) Abrupt transition of marsh and grasslands along with soils under different waterlogging conditions and these can provide different resources for the local fauna, indicated by the yellow arrows. **e**) Abrupt transition of wetlands "*Veredas*" and grasslands. **f**) "*Veredas*" with constant presence of *Mauritia flexuosa* palms
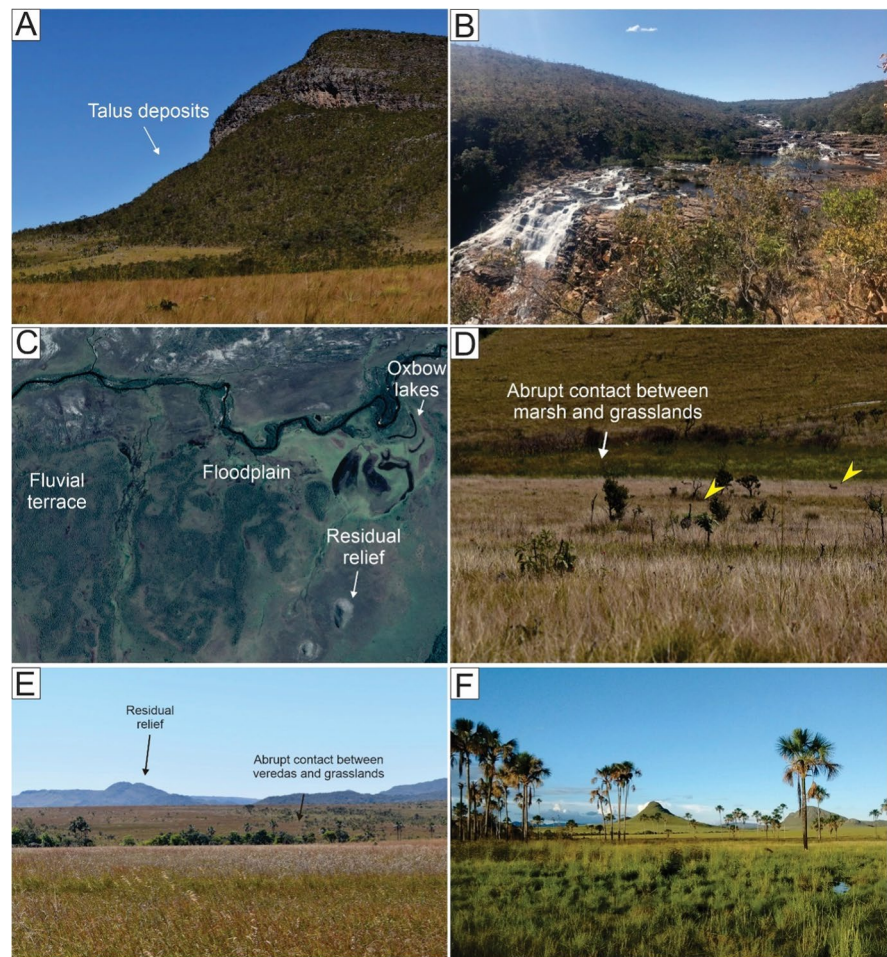

by variations in rock resistance results in impressive ridges of quartzite, scarps, deep valleys, depressions and ruiniform relief (Rezende and Salgado 2011; de Carvalho Júnior et al. 2015) (Fig. 6a, b, c, d). The landforms in the Espinhaço Range are predominantly erosional, with sediment accumulation restricted to specific segments of slopes and plains (Fig. 6e). Therefore, patches of impoverished, coarse-textured, and shallow soils, such as Cambisols and Leptosols are commonly found in the area (Silva 2005; Benites et al. 2007; Schaefer et al. 2016). They develop in situ and form from transported material produced by mechanical and biochemical erosion (Teodoro et al. 2019; Nascimento et al. 2021). Such edaphic conditions favour the occurrence of short-rooted plant species that are commonly observed in grasslands, shrubby grasslands and rocky grasslands. This geomorphic scenario underlies the complex disjunct pattern of plant distribution (Fig. 6f). The Ferralsols

in the area are associated with smooth relief and are covered by forests with varying phenologies. These Ferralsols exhibit iron-rich duricrusts developed in situ in addition to transported clasts of concretionary material (Camêlo et al. 2018). Furthermore, the local dry forests develop on carbonate-rich parent materials. The high soil heterogeneity at this local scale generated by shifting geological and geomorphological characteristics of the Espinhaço range creates abrupt vegetation transitions from grasslands, shrubby grasslands, and forests (Fig. 6g, h).

Characterization of the Cerrado soils and their associations with vegetation types

The determination of different soil orders in the Cerrado is based on their physical (colour, texture, and structure) and chemical (nutrient status, pH, organic matter) properties. The geologic material in which

Fig. 6 **a**, **b**, **c**) General aspects of landforms developed on a quartzite plateau of Espinhaço Range (MG). **d**) Runiform landscapes developed by weathering on a quartzite plateau. **e**) Hans Lambers examining the transported material that covers the slope and acts as parent material of Inceptsols and Arenosols. **f**, **g**, **h**) Abrupt contact between different physiognomies due to occurrence of rock outcrops
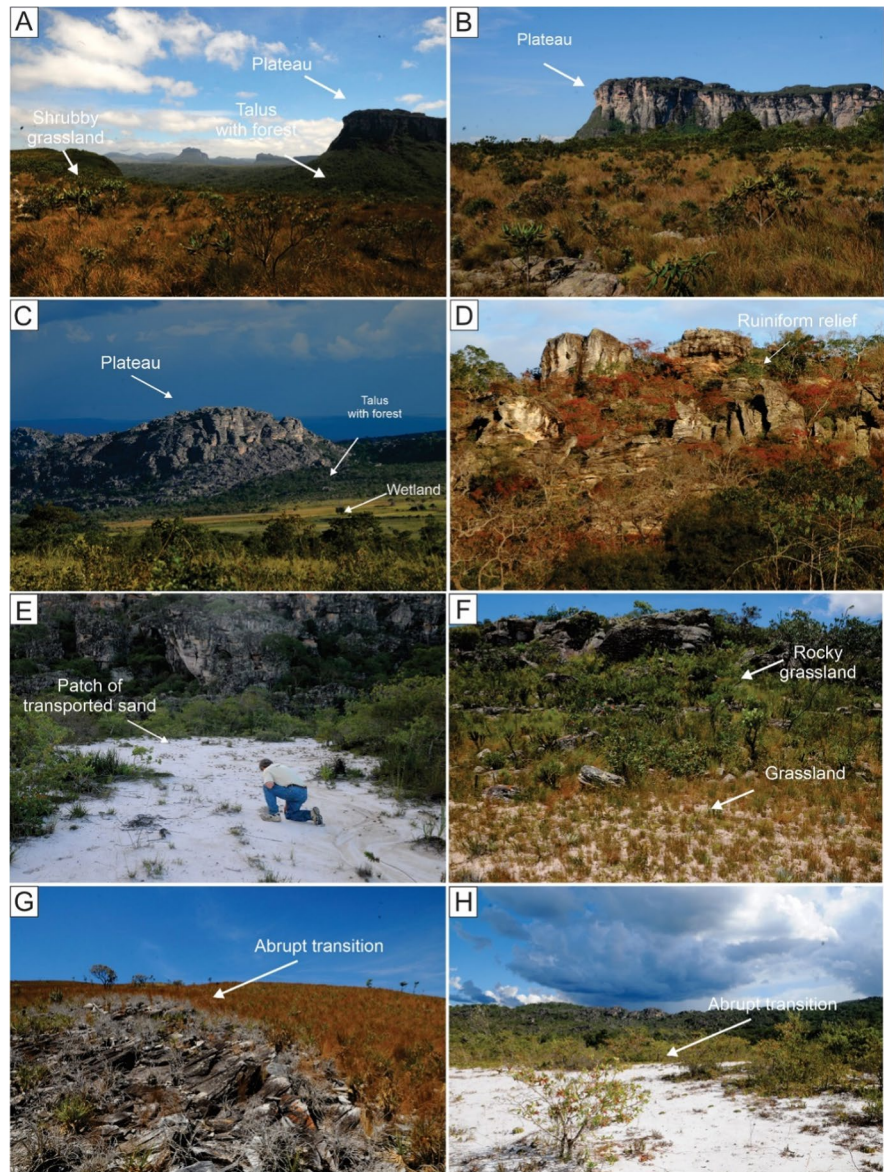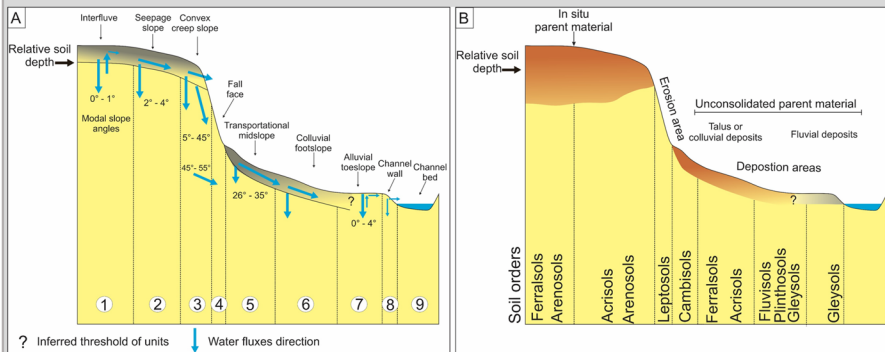

soil horizons are formed is designated as the parent material and determines the soil properties which distinguish each one of the soil orders (Box 1). The topography of the landscape also interacts with the parent material to determine the pedogenic development of these soils. These properties not only characterize the soils, but also affect the plant species they support. This soil-vegetation association is also mediated by species traits (Section 5). There are six soil types (Boxes 2, 3, 4, 5, 6, 7) covering approximately 98% of the Cerrado (Sano et al. 2019) and the other 2% are represented by soil orders restricted to specific conditions, such as Histosols, and Vertisols.

Mineral-rich rocks such as basalts, dolerites and gabbro are the parent material of soils with higher nutrient status which are covered by closed-canopy woody vegetation such as woodlands and forests. Conversely, mineral-poor rocks such as granites, gneisses, quartzites and sandstones provide the parent material of soils with low cation availability, low particle aggregation (i.e., friable) and high porosity. These soils can be covered by grasslands and savannas depending on the climate and water table level. Therefore, the soil chemical and physical properties determined by geophysical aspects have a close association with species composition and vegetation structure.

Box 1 Soil formation in Cerrado

Box 1 – Soil formation in Cerrado

The majority of Cerrado soils consist predominantly of mineral matter, therefore the mainly physical and chemical proprieties are strongly determined by mineral composition (heterogeneous or homogeneous) of the parent material (Gray et al., 2016; Wilson, 2019). Soils developed under volcanic rocks, such as basalts composed by plagioclase, biotite and pyroxene tend to be more clayey, fertile, and iron-rich than soils developed in silica-rich rocks (granite or quarztites) (Porder and Ramachandran, 2012). Soils occur as a "continuum" in the landscape, however, have a large variability in space due to changes in topography, such as hillslope inclination, parent material, erosional processes, hydrological regimes and biotic processes (Fig. a). These factors control the velocity, depth of water circulation, weathering processes and the spatial variability of soils. This results in multiple and developmental pathways and variation in soil characteristics at a short distance (tens to hundreds of meters) along the hillslope (Schaetzl and Randall, 2005) (Fig. b). Soils can develop in lithified parent material directly from the underlying bedrock or in unconsolidated allochthonous materials product of erosion processes. The erosional processes redistribute sediments along the hillslopes resulting in lateral differences in soil types due to changes in parent materials (Gerrard, 1992). Stable surfaces with low inclinations, such as interfluves, vertical water fluxes prevail, and chemical weathering process (cations and Si removal and secondary mineral neoformation) allows soil development and deepening without significative erosion. The unconsolidated parent material is a result of geomorphic processes which controls the soils development. It varies considerably in physical and chemical properties, thickness, distribution and can be multi layered given different erosion and deposition events, as observed in rocky grasslands. The proprieties of unconsolidated parent material are related to the characteristic of the source material (erosional area), such as rocks or pre-weathered material that is eroded and transported along the slopes (depositional area).

a) Two-dimensional soil and hillslope model and the general geomorphic process in relation to hydrologic behavior and declivity. Adapted from Wysock (2010) based in Dalrymple et al., (1968). b) Common soil orders developed in relation to geomorphic and hydrologic characteristics.

Box 2 Ferralsols

Box 2 - Ferralsols

a) Indication of a Ferralsol profile. Soil is richer in clay and with increased depth. **b)** Ferralsol covered by a high density of trees. Red soil coloration indicates high amounts of iron concentration in the soil.

Soil characteristics

From Latin *ferrum – iron.* These are the most abundant soil order in the Cerrado (40.8%). They are soils at the highest weathering stage and feature a red or yellow coloration (IUSS Working Group WRB, 2015). The development of Ferralsols is associated with intense and persistent weathering process, which results in strong cation, P and Si removal by leaching. Parent material can be derived from igneous, metamorphic and sedimentary rocks. The cations and Si removal results in the residual enrichment of Fe and Al (hydro)oxides, such as hematite (Fe_2O_3), goethite ($FeO(OH)$) and gibbsite ($Al(OH)_3$) (Buol and Eswaran, 1999; Schaefer, 2001; Muggler et al., 2007; Marcelino et al., 2010). These soils have high quantities of kaolinite and sesquioxides as constituents of the low activity clay, which are responsible for P sorption and occlusion (Schaefer et al., 2008; Fink et al., 2016). They have stable granular aggregates (100–1000 µm) that result in a friable consistency and low plant-available water-holding capacity (Buol and Eswaran, 1999; Schaefer, 2001). These are deep soils and can exhibit 30m depth on plateaus (Oliveira et. al. 2017), therefore do not impose any physical restrictions to root growth.

Vegetation types

Woody vegetation is commonly found on these soils, varying from savannas to forests. Nutrient availability is an important factor affecting the occurrence of these vegetation types. Savannas usually occur on low nutrient status Ferralsols, whilst higher cation availability favours development of woodlands such as dystrophic "*Cerradão*".

Box 3 Arenosols

Box 3 - Arenosols

a) Arenosol profile. This soil has a sandy texture and increased depth. **b)** Arenosol covered by an open savanna with sparse trees short in stature.

Soil characteristics

The Arenosols derive their names from Latin (*arena* – sand). Characteristically deep and of a sandy texture, these soils cover 23.3% of the Cerrado and have no evidence of pedogenic horizon development (i.e. diagnostic horizon) due to low weathering rates or resistance of the parent material (IUSS Working Group WRB, 2015). This order includes soils developed from usually quartz-rich bedrocks, such as sandstones, quartzites or unconsolidated sediments with a sandy texture. Arenosols developed in old geomorphic surfaces can show low quantities of clays (<15%), Fe and Al (hydro)oxides and can evolve from Ferralsols after weathering of low activity clay (kaolinite). The Arenosols normally feature low fertility and P availability, high acidity and exchangeable Al. Their sandy structure provides good drainage given their high porosity and, however, exhibit low water retention capacity.

Vegetation types

Grasslands and shrubby grasslands commonly cover these soils because of their high drainage and low water holding capacity. Some deep Arenosols developed *in situ* can be covered by woodlands.

Box 4 Acrisols

Box 4 - Acrisols
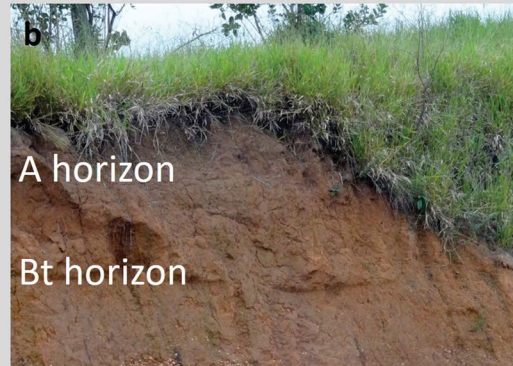
a) Acrisol profile developed over granite parent material. **b)** Acrisol developed over colluvial deposits in undulated relief.

Soil characteristics

From the Latin *acer* – acid, Acrisols cover 12.1% of the Cerrado. They have an argillic B horizon (argic horizons), i.e. with a greater amount of clay than A horizons (IUSS Working Group WRB, 2015). The clay accumulation in B horizon occurs due to vertical clay translocation in percolating soil water (illuviation processes) that fills the porous along the profile (Bockheim and Hartemink, 2013). Parent material of these soils are from sedimentary and metamorphic rocks, usually acid materials. Acrisols occur in a wide variety of parent materials in fluvial terraces, also in undulating topography at backslope, midslope and footslope positions (Reatto et al., 2008). They are mainly composed of low-activity clays and Fe and Al (hydro)oxides, therefore presenting high acidity and low fertility. The P sorption capacity in Acrisols is high and reduced P availability by sorption or occlusion can limit the plant productivity of the vegetation.

Vegetation types

The nutrient-poor Acrisols have no physical restriction to deep root growth and therefore are commonly covered by forest and savanna formations depending on the chemical status of the soils as determined by the parent material.

Box 5 Plinthosols

Box 5 - Plinthosols
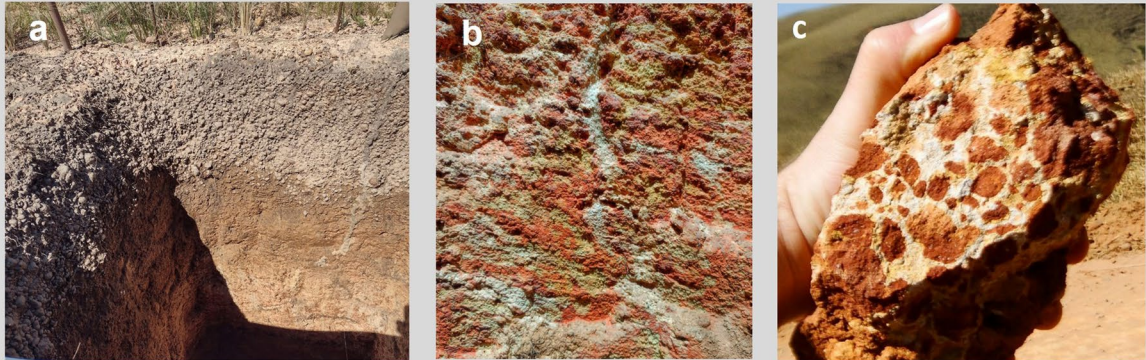
a) Plinthosol profile. **b)** Mottling as an indicative of iron mobilization. Orange colours indicate iron oxidation and grey colours indicate iron reduction. **c)** Sample of plinthite indicating past water table oscillations.
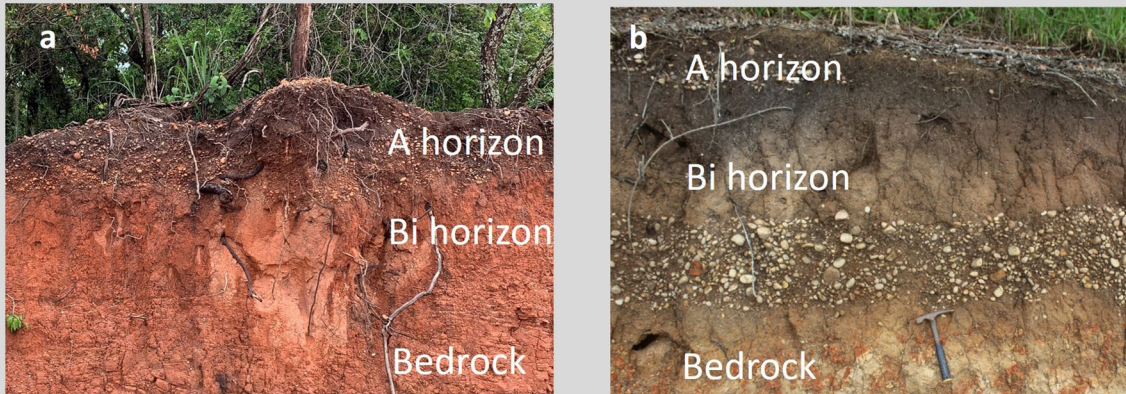
Soil characteristics

The name of these soils derives from Greek *plinthos* – brick. These soils cover 10.4 % of the Cerrado and are rich in Fe and Al (hydro)oxides made by a mixture of clay and quartz that form plinthite (IUSS Working Group WRB, 2015). The plinthic horizon of these soils shows a distinct red-mottled clay and is physically restrictive to deep root growth given its low permeability and high bulk density. The plinthite is an hydromorphic feature formed by the constant process of wetting and drying that results in hard forms of Fe precipitates (Schaetzl and Randall, 2005). Advanced stages of this process results in irreversible forms of precipitates called petroplinthite. Plinthosols are formed by unconsolidated parent material at foot slopes and floodplains with poor drainage conditions (Reatto et al., 2008). When formed on stable plateaus they are associated with Ferralsols and Acrisols and erosion can redistribute the petroplinthite along the landscape. They usually feature low fertility when developed on poor drainage conditions, but exhibit higher fertility when developed on foot slopes (Oliveira et al. 2017).

Vegetation types

Plinthosols with poor drainage are associated with grasslands and shrubby grasslands. They can also be associated with open savannas when under drier conditions after redistributed along the landscape by erosive processes.

Box 6 Cambisols

Box 6 - Cambisols

a,b) Cambisols with incipient B horizons developed under fluvial terraces.

Soil characteristics

These soils cover 9.4% of the Cerrado and are more abundant in the eastern part of the domain over the state of Minas Gerais (Reatto et. al., 2008). They are usually yellow or brownish and are characterized by a low weathering degree and absence of a distinct layer of accumulated clay, humus, soluble salts, or iron and aluminium oxides, therefore have a weak horizon differentiation (IUSS Working Group WRB, 2015). They usually have low activity clay and are poor in mineral nutrients. The formation of these soils is made from medium and fine-textured materials and they can be initially transformed from igneous, sedimentary or metamorphic rocks. Because of their more recent formation, they are usually of limited depth and their origin can be linked with fragmented pieces of their parent material close to the surface (Oliveira et al. 2017). Cambisols occur in many geomorphic configurations, however are more common on rugged topography (Oliveira et al. 2017). They also include the soils with diagnostic horizons that fail in the criteria for other soil orders. Cambisols are commonly of a limited depth

Vegetation types

These soils are usually covered by open savannas and rocky savannas. Gallery forest can be found on these soils when associated with floodplains (Reatto et al., 2008) in response to fluvial erosion processes that constrain the soil development. When Cambisols are developed in talus deposits, they are covered by woodlands, as observed in plateaus margins and in karstic regions (Maranhão et al., 2020).

Box 7 Gleysols

Box 7 - Gleysols

a) Gleysol from flooding terrace. Soil exhibits grey colouration of iron reduction due to development under redoximorphic conditions. **b)** Orange mottles indicating iron oxidation.

Soil characteristics

These hydromorphic soils cover 1.6% of the Cerrado. They exhibit a grey colour that indicates intense iron reduction given their development under continuous waterlogging conditions. They are developed under influence of water table on marshes, margins of lakes and floodplains along the streams (IUSS Working Group WRB, 2015). Gleysols are commonly associated with low parts of slopes intercepted by groundwater. Their texture is usually higher in clay and their chemical properties vary according to the parent material characteristics.

Vegetation types

Typical vegetation associated with wetlands, the poor drainage conditions of these soils favour the occurrence of grasslands, shrubby grasslands, gallery forests, and when along with *Mauritia flexuosa* palms, constitute the vegetation types called "Veredas" (de Carvalho Júnior et al., 2015).

Soil and fire interactions on vegetation structure

Climate is a central driver of tree cover at a global scale where higher precipitation favours the occurrence of increased tree coverage (Hirota et al. 2011; Staver et al. 2011). At intermediate levels of precipitation, forest and savanna formations can be observed and some studies suggest a top-down fire control over the stability of this bimodality, where fire determines savanna occurrence (Hirota et al. 2011; Staver et al. 2011; Murphy and Bowman 2012). According to predictions based on this assumption, grasslands and savannas are fire-prone ecosystems given their high fuel accumulation of grass biomass. These open ecosystems are kept in a dynamic equilibrium and forests retrocession to open ecosystems depend on severe perturbations (Lehmann et al. 2011; Hoffmann et al. 2012), such as varying frequency and intensity of fire events.

Alongside climate, soil is a key environmental determinant of vegetation structure and function in these tropical areas (Lloyd et al. 2015; Veenendaal et al. 2015). Increasing nutrient status allows for the growth of higher tree density with greater woody biomass accumulation (Fig. 7). Savanna trees have foliar tissues with increased concentrations of N, P, Ca, and Mg relative to grasses (Rossatto and Franco 2017) and therefore have higher nutritional demand. Furthermore, in Cerrado, increased soil nutrient status of forest stands represents an important factor associated with higher foliar tissue nutrient concentration than savanna trees (Viani et al. 2014). Intermediate soil conditions as induced by physical restriction and, or low nutrient availability will inhibit high woody biomass formation and, in these systems, fire events can impose an even harsher environment for the establishment of woody plant cover (Fig. 7). This can give rise to a feedback in which the post-fire vegetation will initially have lower woody biomass and higher grass biomass with greater predisposal for future fire events (Hoffmann et al. 2012; Murphy and Bowman 2012). Therefore, at restrictive soils (e.g., shallow and nutrient-limited) woody biomass accumulation is limited compared to soils with higher nutrient status as long as enough water is available, but fire frequency and intensity will inflict another restriction to
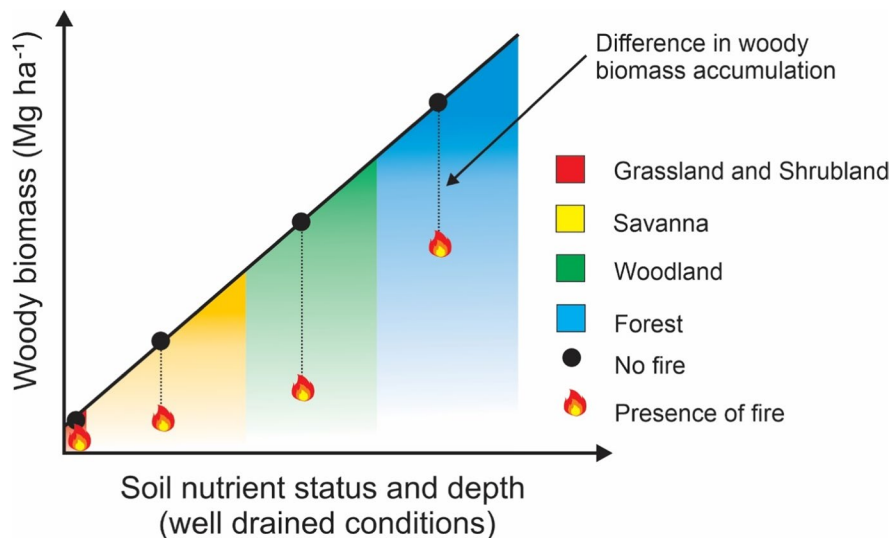
Fig. 7 Conceptual model of grassland, savanna and forest dominance in Cerrado mediated by soil and fire disturbance. Vegetation types are indicated by different colours. Lighter colours within vegetation types show lower values of woody biomass. The X-axis indicates an increment of soil nutrient content and depth; however, these two conditions are not associated with each other. Soils formed from richer parent material (e.g., basalt) can have a relatively higher nutrient content and exhibit greater depth when compared to soils derived from parent material with low P and cation availability (e.g., sandstone). Association between woody biomass accumulation and soil nutrient availability along with soil depth is expected to be linear. At no fire disturbance, vegetation biomass can reach its potential (black dots). Fire limits vegetation woody biomass accumulation at any given soil nutrient status and effective soil depth (fire dots) and this results in a large difference between accumulated biomass under different fire regimes

potential woody biomass accumulation. Although fire can favour the establishment of a grassy vegetation at higher soil nutrient status, the suppression of this disturbance should allow for a higher woody biomass accumulation (Fig. 7). Given increasing tree cover will naturally suppress fire (Hoffmann et al. 2012), fire disturbance in high nutrient soils generally has an anthropogenic source (Veenendaal et al. 2018).

Surveys in the southern Cerrado have indicated a shift from open savannas to closed-canopy woodlands during a 38-year period when anthropogenic fires were suppressed (Durigan and Ratter 2006). Nevertheless, this region is characterised by having relatively higher precipitation and an abundance of deep and well-drained Ferralsols with the influence of basaltic rocks, which increase soil fertility enough to accommodate agricultural activity (Sano et al. 2019). This set of environmental properties favours an increase in tree establishment and woody biomass accumulation. Some studies suggest that this shift from open savannas to closed-canopy woodlands (i.e. woody encroachment) is related to an increase in soil fertility through litter input from the established woody trees (Silva et al. 2008, 2013). However, there is limited evidence for this as indicated by formal tests of this hypothesis that do not support a causal effect of woody plant growth from increased litter production in savanna and woodland dystrophic soils (D'Angioli et al. 2021). Instead, evidence across different tropical vegetation types confirms a systematic edaphic effect on vegetation structure (Furley and Ratter 1988; Proctor 1989; Quesada et al. 2012; Cintra et al. 2013; Lloyd et al. 2015; Veenendaal et al. 2015; Lira-Martins et al. 2015). This suggests the shift from open savannas to closed-canopy woodlands are associated with soil characteristics and, in some edaphic and climatic conditions, potentially the suppression of fire, which allows the ecosystem to accumulate the woody biomass supported by soil physical and chemical properties (Fig. 7).

Notably, fire suppression alone will not inevitably result in the development of significant tree cover if edaphic conditions are unsuitable. For instance, even after 25 years of fire exclusion in *campos rupestres* of the Cipó Range (*Serra do Cipó*) at eastern Cerrado, grasslands growing on shallow and chemically depleted soils did not develop into savannas or woodlands (Le Stradic et al. 2018). However, these soil conditions favour the maintenance of a fire-prone vegetation. It should be emphasized that open grasslands or savannas cannot be assumed to be transient states, with forests representing the successional climax. Only if no climatic and soil restrictions exist and in the absence of fire can open ecosystems develop into woody vegetation type. Hence, soils, climate and fire should represent important environmental factors influencing structural vegetation shifts in Cerrado (Pinheiro and Monteiro 2010).

We conducted a simple analysis to give support to the conceptual model presented in this section. By using grass cover estimates for 906 plots across the Cerrado available from the NeoTropTree database (http://www.neotroptree.info/), we tested if soil chemical and physical properties, along with climate, could predict grass occurrence. Soil data for the plots were extracted from Soilgrids database at the spatial resolution of 250 m grid cell and 30 cm depth (Poggio et al. 2021). Precipitation data were obtained from WorldClim (Fick and Hijmans 2017). Figure 8 shows the model predictions for the soil and climate variables. Grass cover is higher in acidic soils (Fig. 8a). Soil pH is a primary driver of mineral nutrient solubility and controls their availability to plants, especially, phosphorus, iron, zinc, and manganese, essential elements for plant development (Tyler 2003; Lambers and Oliveira 2019). Soil bulk density can be interpreted as a proxy for physical restriction to deep root growth and the model indicates that grass occurrence rises in physically restrictive soils (Fig. 8b). Precipitation has a more subtle effect on grass coverage but suggests that drier areas tend to have increased grass occurrence (Fig. 8c). Altogether, this analysis suggests that soils along with climate have a significant effect on the establishment of grasses and trees, where grasses are more abundant in savanna vegetation types and very limited in forests (Fig. 8d).

Species distribution along soils gradients

A central issue in ecology is to understand to what extent the floristic composition of different sites is determined by environmental factors. Plant species respond to differences in soil fertility and many studies in the Neotropics have indicated soil properties exert strong controls on floristic composition (Oliveira-Filho et al. 1989; Tuomisto et al. 2003; ter Steege et al. 2006; Neri et al. 2012; Mews et al. 2016; Amaral et al. 2021). Geology and geomorphology
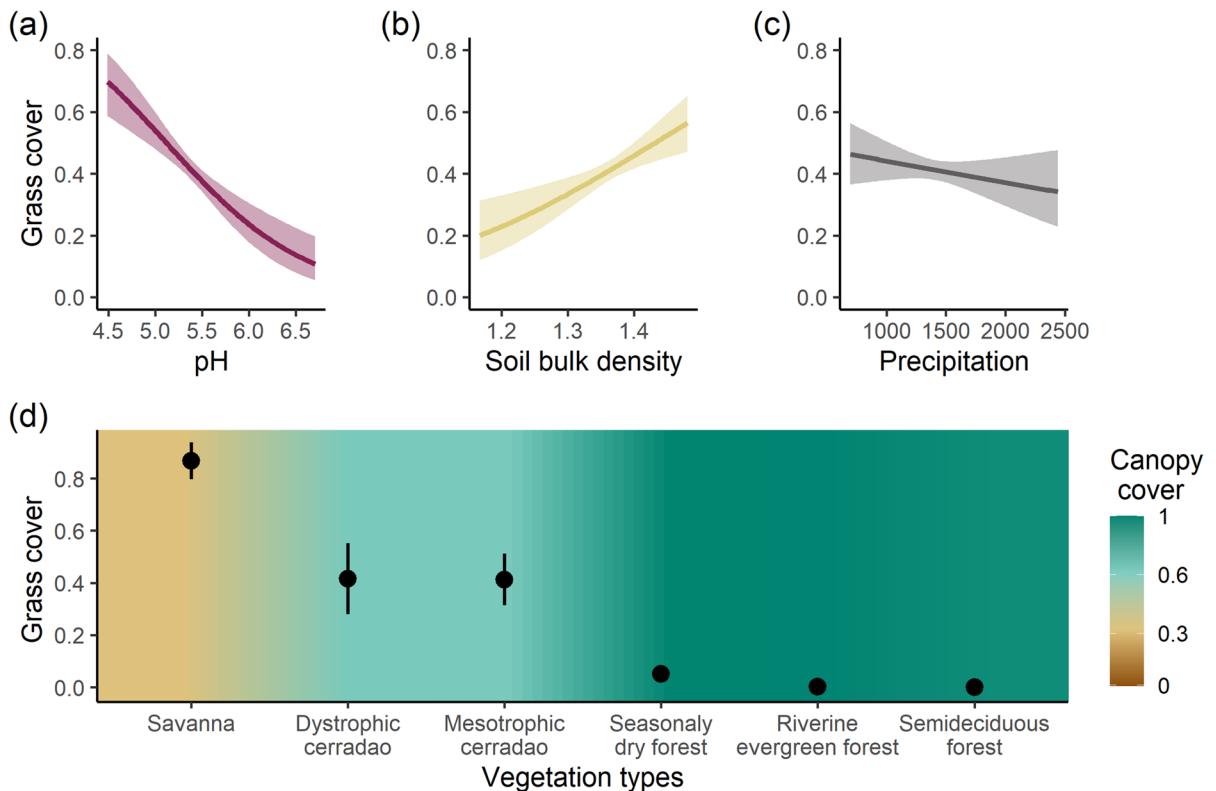
Fig. 8 a) Indicates the partial residuals plot of pH with grass cover (varying between 0 -1) for sites across the Cerrado domain. **b**) Shows partial residuals plot for soil bulk density (g cm^{-3}) from the same model as pH and **c**) mean annual precipitation (mm). Bands along the curves indicate 95% confidence intervals. **d**) Mean grass cover and standard deviation for the different vegetation types of forests and savannas

play significant roles in the deterministic effect of soil properties on floristic variation within a landscape. Chemical properties of the parent material along with soil depth and texture are key factors associated with species distribution (Messias et al. 2013; Schaefer et al. 2016) and structure the phylogenetic plant diversity of these communities (Zappi et al. 2017). These factors also contribute to the biogeographic history of habitats by selecting for edaphic specialists (Rajakaruna 2018; Corlett and Tomlinson 2020), thus acting as a mechanisms underpinning the diversity patterns in the Cerrado (Zappi et al. 2017; Vidal et al. 2019; Cássia-Silva et al. 2020; Silveira et al. 2020).

The Espinhaço Range on the eastern Cerrado (Minas Gerais state) can serve as an example of this geophysical control over edaphic conditions and floristic composition. The top of this stable landform is formed by chemically and physically resistant materials (e.g. quartzite) that limit soil nutrient availability and depth thus favouring a vegetation cover of shallow-rooted species with representatives from the families Velloziaceae, Poaceae, Cyperaceae and Xyridaceae (Conceição et al. 2007; Messias et al. 2013; Schaefer et al. 2016). The top of plateaus not only represent stable environments for the diversification of endemic species (Vidal et al. 2019), but the edaphic conditions also drive phylogenetic clustering of monocot clades such as Poaceae, Cyperaceae and Xyridaceae in open physiognomies (Zappi et al. 2017). The erosional process on scarps and cliffs transports rock debris and this colluvial deposition on less weathered materials from footslope forms deeper and relatively more fertile soils (Arruda et al. 2015) and with these geological, geomorphological and edaphic gradients exerting a strong control on species composition (Le Stradic et al. 2015; Mota et al. 2016; Mota et al. 2018). Hence, the conspicuous variation in vegetation structure are given by high species

turnover and are observed even in short distances along these gradients (Abreu et al. 2012; Mota et al. 2018; Chaves et al. 2019). These processes not only occur at the slope level but are also found at larger scales across the Cerrado domain.

Across many vegetation types in the Cerrado a negative association between soil Al and cation content represents a gradient that is important for species distribution and community assembly. This gradient is a result of the weathering processes responsible for cation depletion and formation of iron and aluminium oxides (Box 1) which inhibit P availability to plants by increasing the soils sorption capacity (Fontes and Weed 1996; Brenner et al. 2018). In the case of savannas and forests, floristic distinctiveness between these two vegetation types is clearly related to this Al-cation soil gradient. For instance, dry forests with high abundances of deciduous species and cation rich soils contrast with the Al-rich savannas soils dominated by grasses and shrubs (Oliveira-Filho and Ratter 1995; De Souza et al. 2007; Paula et al. 2021). Basalt or limestone rocks form these Ca-rich soils and the slope position where they occur will control their chemical properties thus characterizing their pedogenic development (Silva et al. 2017; Maranhão et al. 2020). Floristic differences determined by this soil chemical gradient are also observed between savannas and deciduous forests (Cruz Ruggiero et al. 2002) and with these edaphic differences being determined by geological and geomorphological aspects of the region (Ruggiero et al. 2006).

Although the woodlands (cerradão) exhibit a structural contrast with savannas because of the greater tree density of the former, floristic differences in some cases might not be as clear. When comparing soil and floristic composition of savanna and woodland Cruz Ruggiero et al. (2002) could not detect floristic or edaphic differences amongst them. Notably, the cerradão can be distinguished into two compositionally distinct categories viz. dystrophic cerradão and mesotrophic cerradão, associated with differences in soil nutrient status (Furley and Ratter 1988; Neri et al. 2012; Bueno et al. 2018). This distinction is related to increasing soil Ca availability towards the mesotrophic cerradão, derived from weathered limestone and in situ modification of calcareous parent material (Furley and Ratter 1988; Neri et al. 2012). Floristic dissimilarities between dystrophic woodlands and savanna are less evident based on soil nutrient status and other environmental properties such as fire dynamics or water availability represent important factors in this distinction (Bueno et al. 2018). It is interesting to note, however, that even within the same vegetation type, there is evidence for gradients in soil nutrient status influencing species composition. Mews et al. (2016) observed soil nutrients as significant factors associated with floristic composition among savannas and Bueno et al. (2013) found an increase in the abundance of Al-tolerant species such as *Qualea parviflora* and *Q. grandiflora* within areas of dystrophic cerradão with increments in soil Al.

Using the NeoTropTree database (http://www.neotroptree.info/) in the Cerrado domain, we analysed the species distribution response to soil pH with data from Soilgrids (Poggio et al. 2021). The species checklist in NeoTropTree database is defined by a single vegetation type and follows the proposed classification system of Oliveira-Filho (2015). Associating species occurrences to edaphic properties derived from Soilgrids can generate errors, given the limited capacity of this soil database to accurately capture in situ soil parameters (Moulatlet et al. 2017). However, our main objective is to capture a potential effect of soil chemical characteristics on habitat preferences of the most representative tree species of important Cerrado vegetation types at the domain-wide scale. From these analyses, we can observe that low pH soils, which usually have low nutrient availability and high Al concentrations (Furley and Ratter 1988; Cruz Ruggiero et al. 2002), seem to represent edaphic niches favoured by abundant savanna species (Fig. 9). Some of the dominant species in dystrophic *cerradão* are also abundant in savannas and there is a lack of distinguished patterns between the two vegetation types based on these data (Fig. 9). The higher soil nutrient status of mesotrophic *cerradão* (Neri et al. 2012) is captured by the pH data and some species response curves are shifted to higher values of pH (Fig. 9), thus indicating an intermediate vegetation type based on soil properties when compared to cation and P limited soils in savanna and dystrophic *cerradão* and cation-rich soils in dry forests (Fig. 9). The dominant species in seasonally dry forests are preferentially found on more alkaline soils (Fig. 9) with higher cation availability. These patterns suggest a deterministic effect of soil chemical properties on differentiating the floristic composition among Cerrado vegetation types.

Soil and functional trait associations

The concept of edaphic factors as associated with plant species distribution is not new (Grubb 1989;
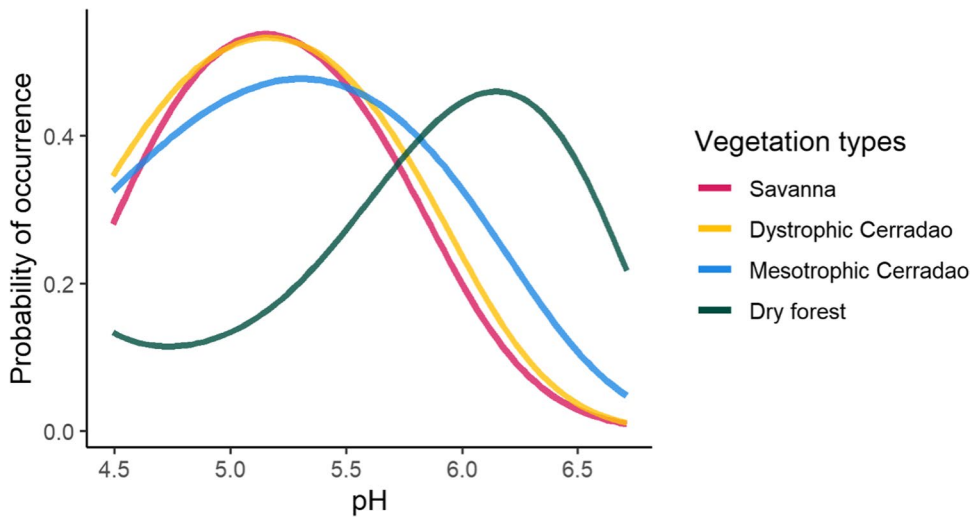
Fig. 9 Response curves for the probability of occurrence (0–1) of the 50 most common species in each vegetation type based on NeoTropTree database in savannas, dystrophic *cerradao*, mesotrophic *cerradao* and dry forests within the Cerrado relative to soil pH

Richter and Babbar 1991). However, ecological studies have long been interested in a mechanistic understanding underpinning species distribution patterns in terms of physiological processes. The development of trait-based ecological studies emerged with a focus on identifying specific suits of traits that allow for successful growth, reproduction, and survival across a range of environmental conditions (McGill et al. 2006). This approach is based on the determination of functional traits, which correspond to measurable morphological, physiological and phenological properties of the organisms which are heritable (Garnier et al. 2016). The use of specific trait characteristics in association with the functionality of organisms has been argued to provide powerful generalities in ecology (McGill et al. 2006, Ackerly and Cornwell 2007; Violle et al. 2007; Suding et al. 2008). Based on the idea that plant traits reflect species adaptations to environmental conditions, in the next sections we review functional differences of vegetation physiognomies and how they relate to differences in soil chemical and physical properties.

Variation in leaf economics with soil nutrient availability

The leaf economic spectrum describes a global-wide continuum of leaf strategies related to carbon

acquisition, leaf lifespan and nutrient use where conservative species sit in one end of the spectrum in opposition to acquisitive species in the other end. Nevertheless, environmental factors play important roles in the distribution of these foliar strategies. At the global scale, soils, along with climate, are important drivers of leaf nutrient concentration (Ordoñez et al. 2009; Vallicrosa et al. 2021) and these leaf-soil trait associations are also found in species across the tropics (Fyllas et al. 2009; Lloyd et al. 2015; Lira-Martins et al. 2019). For instance, the rocky grasslands (*campos rupestres*) are found on severely impoverished soils from mountaintops, with parent material with low cation and P availability such as quartzite, sandstone and ironstone causing very low leaf nutrient concentrations (Oliveira et al. 2015; Silveira et al. 2016). This is one trait of a set exhibited by these plant communities that converge into conservative use of resources as adaptations to tolerate environmental stress (Negreiros et al. 2014; Tameirão et al. 2021). Plant leaf nutrient concentrations in these areas closely follow edaphic variations (Abrahão et al. 2019) with an average foliar phosphorus concentration of 0.3 mg g^{-1} (Oliveira et al. 2015), comparable with severely P impoverished soils from south-western Australia (Lambers et al. 2011; Hayes et al. 2014). Comparisons of photosynthetic activity between savanna and *campos rupestres* plant communities

indicate that plants growing on nutrient poor Arenosols exhibit an average lower photosynthetic activity when compared with savanna communities on relatively richer Ferralsols (Abrahão et al. 2019).

In soils with low nutrient availability, many plant species exhibit physiological and morphological adaptations to use and acquire nutrients efficiently and one example is the lower nutritional investment in leaves (Lambers et al. 2011), which results in a high C:nutrient ratio (Lambers 1992). Conversely, plants on some cation rich soils are commonly deciduous and shed their leaves during the dry season, benefitting from short-lived, but nutritious leaves (Viani et al. 2014; Oliveira et al. 2021b). Early observations in savannas have directly associated high foliar investment of carbon relative to nutrients to the low soil nutrient availability, something termed oligotrophic sclerophylly (Arens 1958). One potential interpretation for this nutritional effect on leaf sclerophylly relies on the rationale of the nutrient dilution effect by high C structural investment in sclerophyll leaves as an adaptation to a conservative use of resources, such as limiting water and nutrient availability (Loveless 1961; Specht and Rundel 1990). Cross-domain comparisons in Brazil suggest that soil nutrient status should play a major role as an environmental factor influencing sclerophylly in these areas. Among important Brazilian vegetation types, the Cerrado plants tend to cluster at the conservative end of the leaf economic spectrum. They have a great foliar carbon investment as can be seen by their highest foliar C:N ratios (C:N = 34)—only comparable to vegetation types growing on nutrient-poor sandy soils (Martinelli et al. 2021). Conversely, trees growing under the semi-arid climate in the Caatinga vegetation exhibit much lower C:N ratios (C:N = 17) (Martinelli et al. 2021). Interestingly, these forests are located on eutrophic soils in northeastern Brazil (Arruda et al. 2017). The shifts in Cerrado vegetation types with increasing soil nutrient availability is associated with an incremental shift in foliar nutrient content (Viani et al. 2014; Miatto and Batalha 2016). Cation rich soils select for deciduous plants with nutritious leaves with a short lifespan (Bueno et al. 2018). These changes in leaf nutrition are associated with an increase in leaf mass per unit area (LMA) (Viani et al. 2014; Miatto et al. 2016; Abrahão et al. 2019; Tameirão et al. 2021). This pattern can also be found across growth forms. Grasses exhibit lower

foliar tissue nutrient content and a systematic higher LMA than trees (Rossatto and Franco 2017). The greater increment in LMA observed in plants growing on soils with low nutrient status is a structural consequence of anatomical and metabolic processes. These plants build leaves with a high investment in fibres, thick cell walls, sclerenchyma and important secondary plant compounds, which extends the lifespan and increase defence against herbivory and abiotic stress (Wright and Cannon 2001). Many of these structures being frequent in Cerrado species (Bieras et al. 2009; Rossatto et al. 2015).

Other leaf anatomical properties to increase nutrient-use efficiency also play an important role for plants adapted to low cation and P (Hayes et al. 2018). To increase photosynthetic P-use efficiency (PPUE) some plants preferentially allocate phosphorus to their leaf mesophyll, instead of metabolically inactive cells such as epidermal layers (Denton et al. 2007; Hayes et al. 2018; Guilherme Pereira et al. 2018). This discriminatory P allocation to mesophyll cells has been observed in Cerrado species, such as *Hymenaea stigonocarpa*, *Vochysia thyrsoidea*, *Qualea grandiflora* and *Q. parviflora* (Guilherme Pereira et al. 2018). Different biochemical mechanisms also generate efficient P-use. Ribosomal RNA represents the largest pool of organic P in leaves (Veneklaas et al. 2012) and a decrease of phosphorus allocation to rRNA represents a considerable economy in P, however, it necessitates lower cellular growth (Sulpice et al. 2014). Furthermore, the replacement of P-containing compounds (e.g. phospholipids) by galactolipids and sulfolipids (Lambers et al. 2012) also represents a trait to increase P-economy (Lambers et al. 2015). Given photosynthesis is highly dependent on foliar nutrient content (Franco et al. 2005; Domingues et al. 2010; Lambers and Oliveira 2019), such adaptations suggest traits associated with sclerophyllous leaf habit in Cerrado plants on dystrophic soils are likely to be associated with adaptations to increase photosynthetic output with limited nutrient availability.

Soils and leaf trait functional diversity associations

Functional diversity represents the various arrangements of functional traits from different species in terms of amplitude and abundance in a given community (Tilman 2001) and has a strong influence on ecosystem functioning (Díaz and Cabido 2001; Hooper

et al. 2005; Garnier et al. 2016). According to theory, environmental filters shape this metric according to the regional species pool (Grime 2006; Cornwell et al. 2006). Environmental filtering dominates in stressful habitats and can result in shifts in functional convergence because of the reduction in the range of suitable trait values (Fig. 10a) (Grime 2006; Cornwell et al. 2006). Conversely, in habitats where resources are more abundant, strategies associated with resource acquisition may be more frequent and functional diversity can be affected by other ecological processes, such as competition (Wilson 2007; Kunstler et al. 2016). For instance, in the case of foliar traits associated with nutrient use, species growing on soils limited in cations and, or P can have a lower variation in these traits, therefore driving convergent trait strategies (Guilherme

Fig. 10 **a**) Representation of environmental filter operating on species pools (different colours) by the selection of specific functional traits and the range of their variation (varying sizes). The effect of these filters will have an impact on the functional diversity of the communities. **b**) Variation of functional dissimilarity (FDis), a metric of functional diversity, of the distinct vegetation types along soil pH. Different letters on the right-side designate significant difference between FDis values
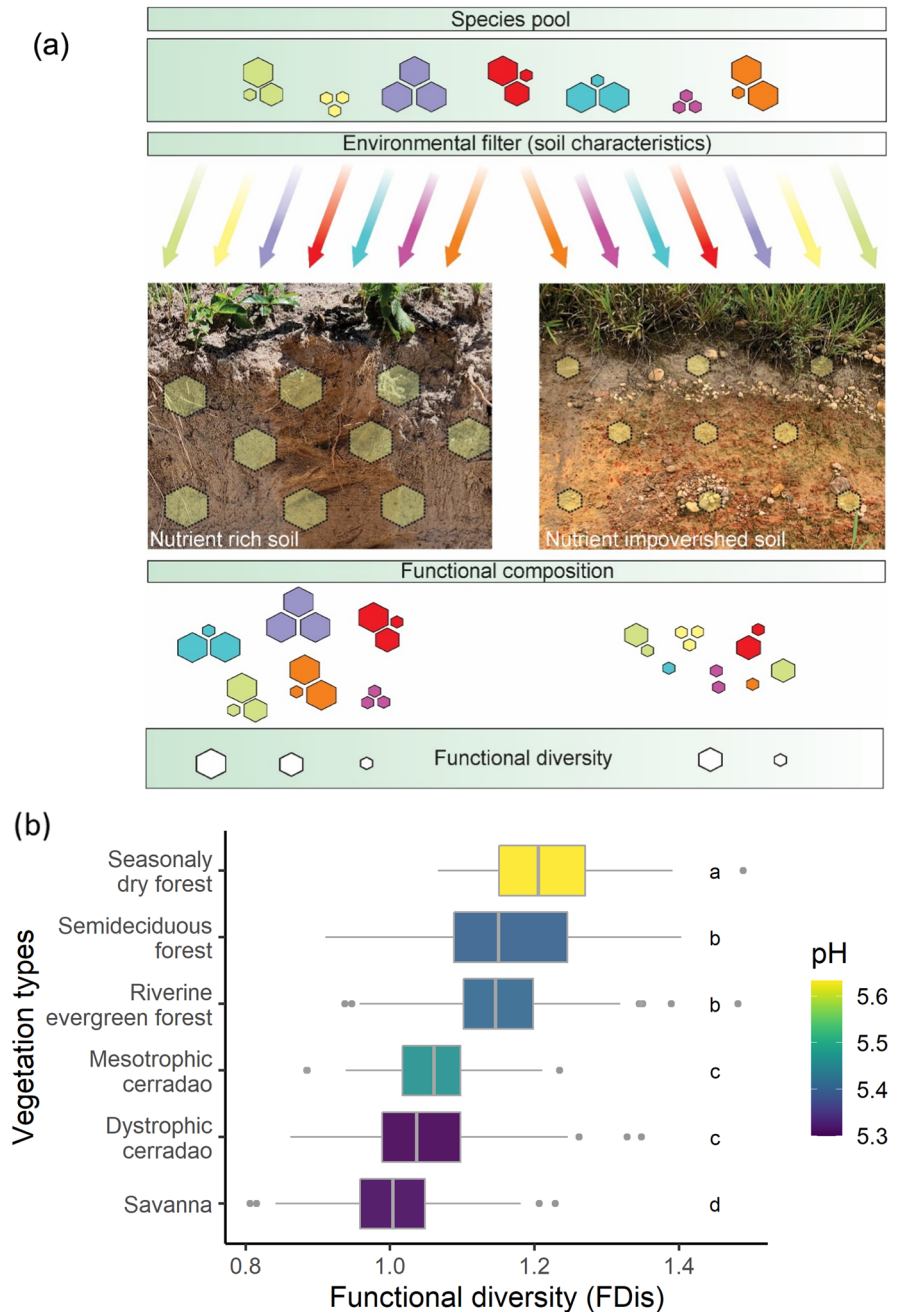
Pereira et al. 2019). Furthermore, species with contrasting leaf phenological habits co-occurring within savanna physiognomies do not seem to systematically differ in terms of leaf traits (Cianciaruso et al. 2013), which reiterates the importance of soil-induced shifts of leaf functional variation across vegetation types.

Soils play an important role in influencing leaf economy at the global scale (Joswig et al. 2021) and this should hold across the Cerrado domain, as suites of traits are filtered to be viable in specific environmental conditions (Kraft et al. 2015). Using the NeoTropTree and Soilgrids databases, we determined the leaf economic functional composition of communities on particular soils, deriving species leaf traits from the TRY database (Kattge et al. 2020) (specific leaf area—SLA, P and N foliar concentrations on a mass basis). We calculated the functional dispersion (FDis), a metric of functional diversity (Laliberté and Legendre 2010), based on the leaf traits for 906 plots which had identification for vegetation type based on Bueno et al. (2018). This analysis indicates that the typical savannas have the lowest FDis values, and this systematically increases towards forest formations with the seasonally dry forests showing the highest FDis values (Fig. 10b). Woodlands have a higher functional diversity than typicalsavannas. However, although there are differences in soil conditions between the woodlands, the dystrophic *cerradão* is not significantly different from the mesotrophic *cerradão* in terms of FDis (Fig. 10b). The evergreen and semi-deciduous forests overlap in terms of pH and FDis, but they can be distinguished from seasonally dry forests in relation to soil chemical properties and functional diversity of foliar traits. Based on these patterns we suggest that Cerrado soils with lower nutrient status act as environmental filters for leaf economic traits and communities of woody species in these edaphic conditions exhibit functional trait convergence. The increasing nutritional status of soils allows the establishment of denser vegetation with greater canopy cover. This is followed by a shift in species composition with increasing foliar trait diversity and therefore higher functional diversity.

Al tolerance

Soil acidity not only limits the availability of important cations (e.g. Ca, Mg and K), but also increases the solubility of Al. Below pH 5, toxic forms of Al, such as $Al(OH)^{2+}$ and Al^{3+} increase considerably (Kinraide 1991; Rahman and Upadhyaya 2021). The acidic nature of most Cerrado soils favours the occurrence of Al at many soil types (Lopes and Guilherme 2016). High concentrations of Al can harm plants via several mechanisms (Singh et al. 2017), such as: reduction of root growth (Marienfeld et al. 2000; Horst et al. 2010), impairment of gas exchange rates and photochemical performances (Chen et al. 2005; Jiang et al. 2008; Silva et al. 2018) and accumulation and alteration of DNA (Minocha et al. 1992; Silva et al. 2000). In addition, Al constrains the availability of important nutrients such as P by strong sorption of phosphate to Al (hydr)oxides (Fontes and Weed 1996; Brenner et al. 2018). Many plants on high Al soils in the Cerrado can however tolerate these conditions. Specialised adaptations enable Cerrado plants to acquire essential nutrients in these high Al environments (Malta et al. 2016). Approximately 30 Cerrado species have been identified as capable of tolerating high Al in soils across 17 families, including Melastomataceae and Vochysiaceae (Haridasan 1982). One Al tolerance strategy involves the accumulation of this element in the leaves, which does not necessarily translate into low tissue concentrations of other important elements such as Ca, Mg, K, Fe or Zn (Haridasan 1982). In Vochysiaceae all species show Al-accumulating capacity (Jansen et al. 2002b). Not surprisingly Vochysiaceae is one of the most dominant families in Cerrado (Ratter et al. 1997) and Al tolerance likely represents an important adaptation for this family's success in acidic Cerrado soils.

Given the physiological harms caused by Al, it is important to transform it into organic complexes with low toxicity, before internal accumulation occurs (Grevenstuk and Romano 2013). Some biochemical processes involve the formation of stable complexes with organic acids such as citrate, malate, and oxalate (Kochian et al. 2004; Grevenstuk and Romano 2013), whilst others involve the association with phenolic compounds (Tolrà et al. 2005; Malta et al. 2016), or the formation of aluminosilicate (Britez et al. 2002; Hodson and Evans 2020). Furthermore, the cellular structures involved in accumulation vary across species. For instance, in some species of *Qualea spp.* (Vochysiaceae) and *Miconia spp.* (Melastomataceae) Al is kept away from metabolically active cells and is accumulated in non-lignified cell walls via the use of aluminium silicates (Bressan et al. 2016). Similar

anatomic patterns were also observed by Guilherme Pereira et al. (2018) in other Cerrado plants. In *Rudgea viburnoides* (Rubiaceae) Al is predominantly accumulated in cell walls and in chloroplasts, involving the complexation of Al into silica and phenolic compounds (Malta et al. 2016). Other Vochysiaceae species, viz. *Qualea grandiflora* and *Callisthene* accumulate aluminium in their chloroplasts without negative effects on their leaf structures (de Andrade et al. 2011).

An important strategy for aluminium resistance also relies on mechanisms to exclude the impacts of Al in the rhizosphere (Horst et al. 2010). This mechanism involves root exudation of organic acids (e.g., citric, malic and oxalic) to stabilize Al in non-toxic forms (Brunner and Sperisen 2013). *Styrax campomum* (Styracaceae), which is a moderate Al-accumulating species (Bressan et al. 2020), relies on the exudation of citric and oxalic acids to chelate Al in the root environment (Bittencourt et al. 2020). Although being able to accumulate Al in their leaves and having organic acid exudations as means of coping with high Al in soils, this species is physiologically impaired at very high Al concentrations, which indicates that its tolerance is insufficient in extremely high Al soil concentrations (Banhos et al. 2016). In contrast, some common species on acidic soils are highly dependent on Al. For instance, *Vochysia tucanorum* shows compromised growth and low photosynthetic activity under low Al availability. This appears related to the root impairment of this species caused by the lack of available Al (Bressan et al. 2021). *Qualea grandiflora* is also highly dependent on Al for root metabolism involved in the structural synthesis of cell walls and lignin as well as in P uptake (Cury et al. 2020).

Metabolic dependence on this element should not be a rule amongst Al-tolerant species, and high levels of this element in soils may not determine the occurrence of these species (Haridasan and De Araújo 1988). Although Al-tolerance seems to be associated with a calcifuge strategy—species increased occurrence in acidic soils—some Al tolerant species fail to fall into this category. This is the case for *Callisthene fasciculata* (Vochysiaceae) which is restricted to Ca-rich soils (Haridasan and De Araújo 1988; Ratter et al. 2003a)—i.e. calcicole habit—most probably due to internal cation imbalance (de Souza et al. 2020). Calcicole species are a group of plants that have an edaphic niche associated with Ca-rich soils

and are not limited by soils poor in P (White and Broadley 2003). This group can be characterized as edaphic specialists (Corlett and Tomlinson 2020) and in the Cerrado are commonly distributed over alkaline soils covered by dry forest (Meira-Neto et al. 2017). Despite some exceptions, Al soil content should characterize the edaphic niche of Al tolerant species. We investigated the occurrence of these Al tolerant plants using published data (Haridasan 1982; de Oliveira et al. 2019) to investigate their occurrence along with soil pH. We observed that, although Al-tolerant species are more common on acidic soils, they can also be found on soils with higher pH (Fig. 11). Species featuring Al tolerance might also benefit from higher nutrient availability, thereby also growing in more fertile soils (Guilherme Pereira et al. 2018; Nogueira et al. 2019). However, they have an apparent ecological advantage over non-tolerant species that are physiologically impaired at higher Al concentrations (Mendonça et al. 2020). Hence, these Al-associated traits mediate the distribution of Al-tolerant species and these chemical soil conditions represent edaphic niches of these edaphic specialists. Along with their distribution, the previous traits seem to be phylogenetically constrained and indicate the life history of species that evolved under these edaphic conditions (Jansen et al. 2002a; Watanabe et al. 2007).

Plant nutrient acquisition

Together with the nutrient-use efficiency mechanisms described in the previous section, plants native to nutrient-impoverished soils have specific adaptations to acquire nutrients, such as specialized root architecture to explore superficial soil layers (Lambers et al. 2006) and carboxylate exudation through root structural specialization to mobilise poorly-available forms of P (Oliveira et al. 2015; Abrahão et al. 2020). Interestingly, root associations with arbuscular mycorrhizal fungi seem to be a nutrient acquisition strategy more commonly present among species dwelling on relatively less nutrient-impoverished soils (Zemunik et al. 2018), while root specializations based on mucilage and carboxylate exudation that conglomerate soil particles around the root surface (rhizosheaths) are common among species from relatively more nutrient-impoverished soils (Abrahão et al. 2019).

Soil-nutrient uptake by association with arbuscular mycorrhizal fungi has an elevated metabolic cost to

Fig. 11 Kernell density curves of 30 Cerrado Al accumulating species in relation to soil pH (Soilgrids). The dashed line indicates the median soil pH value for the Al-accumulators. Arrows with different colours represent median soil pH values (Soilgrids) of vegetation types with each plot location (NeoTropTree) representing a sample unit
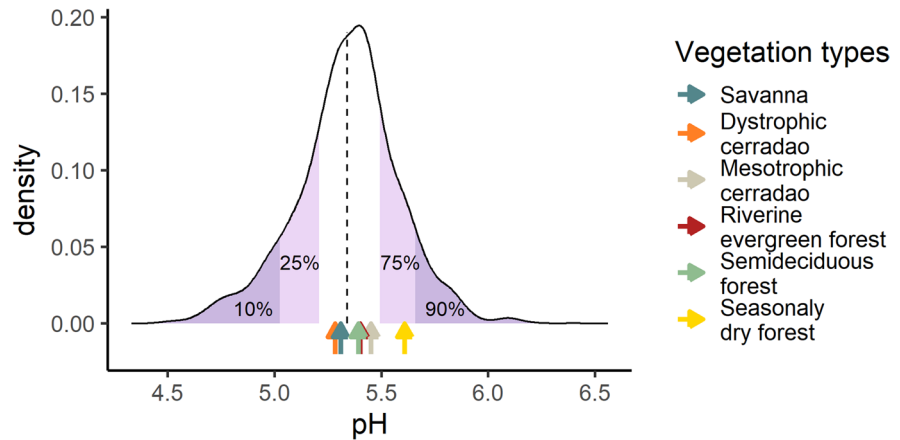
the plant at very low nutrient availability (Raven et al. 2018) and therefore, should be less common under such conditions. Conversely, specialized root structures such as rhizosheaths and cluster roots should be relatively more cost-effective because their metabolic cost considering the volume of soil explored for nutrient uptake should be lower relative to arbuscular mycorrhizal associations (Raven et al. 2018). In nutrient impoverished soils, where the majority of P is occluded in soil particles, the most effective acquisition mechanism is the exudation of carboxylates through the roots, because they complex metal cations that bind phosphates (e.g., Al, Fe and Ca) by ligand exchange (Shane and Lambers 2005; Johnson and Loeppert 2006).

Studies on plant mineral nutrition regarding below ground traits for nutrient uptake only considered the symbiotic association with arbuscular mycorrhizal fungus as an effective strategy in impoverished soils for a long time. From 1960, with the first description of specialized roots, cluster roots, studies on the mineral nutrition of OCBILs (old, climatically buffered, infertile landscapes) started to increase and now are well studied in OCBILs such as in the South-Western Australia floristic region (Hopper 2009; Lambers 2014). From these studies it was clear that despite the dominance of arbuscular mycorrhizal associations, other nutrient acquisition strategies were important, for example "mining" strategies, carnivorous species, parasitic plant species and others (Lambers et al. 2011). Although only the Brazilian *campos rupestres* vegetation type in the Cerrado domain is classified as an OCBIL, the Cerrado (*lato* sensu) occurs under nutrient impoverished soils compared to the

other vegetation domains in Brazil (e.g. Amazon and Atlantic forest) and even compared to other savannas worldwide (Solbrig 1993).

Despite the nutrient limitation, these places harbour incredibly high plant species diversity (Ratter et al. 2003b; Hopper 2009), relying on different mechanisms for efficient nutrient acquisition (Zemunik et al. 2018). Some studies have found a diverse community of arbuscular mycorrhizal fungi species in the Cerrado soils (Maia et al. 2020; Araujo et al. 2021). Thus, there is no doubt that mycorrhizal colonization can play an important role in the Cerrado soils. However, very few studies addressed the role of mycorrhizal colonization in native Cerrado species (Thomazini 1974) and even fewer relate the mycorrhizal colonization to species composition and distribution across the vegetation types. Mycorrhizal fungal species native to the Cerrado have been correlated with increasing water acquisition during the dry season (Junior et al. 2020). However, there is a wide range of other roles that mycorrhizas can play, including defence against soil pathogens (Lambers et al. 2018; Albornoz et al. 2021) and underground plant-plant signalling (Gilbert and Johnson 2017). Understanding these roles is crucial to set the scene for the importance of mycorrhizal colonization in Cerrado vegetation types.

Studies of other nutrient acquisition strategies in the native Cerrado species are beginning to increase. For example, studies of the soil microbiome and how it can promote nutrient turnover in impoverished substrates (Camargo et al. 2019, 2021). Studies on species that combine morphological and physiological adaptations to acquire and

use nutrients effectively such as dauciform roots (Oliveira et al. 2015) (Fig. 12a), Vellozioid roots (Teodoro et al. 2019) (Fig. 12b and c), and rhizosheaths (Abrahão et al. 2014, 2019) (Fig. 11d). Additionally, the recently described Vellozioid roots are carboxylate-releasing roots that function similarly to other specialised roots in nutrient-depleted soils, but on different substrates such as quartzite rocks, playing a pivotal role in nutrient acquisition and rock weathering (Teodoro et al. 2019) (Fig. 11b and c). More recently, studies of carnivorous species that can acquire nutrients by trapping and digesting nematodes with underground leaves (Pereira et al. 2012) have indicated further nutrient acquisitive strategies of these species. However, there is still much to be explored and studied regarding the diversity of nutrient acquisition strategies (i.e., parasitic plant species and species that rely on facilitations by other species), especially on other vegetation types in the Cerrado domain, since most of the studies are still concentrated in *campos rupestres*.

Most of the studies regarding root morpho-physiological adaptations to nutrient-depleted soils are focused on eudicot species. We find examples of dauciform roots mostly in the genus of *Lagenocarpus* in the Cyperaceae family. For Poaceae species there are very few studies of nutrient acquisition specialisations, most of which have focused on chelating substances, namely phytosiderophores. Phytosiderophores are root exudates found in grass species that mobilise cations on soils, more specifically solubilization of sparingly soluble inorganic Fe^{3+} compounds (Römheld and Marschner 1986). In the Cerrado, as most of the P in soil is occluded on soil particles, specially complexed with Fe and Al cations, these phytosiderophores compounds can contribute to P acquisition (de Tombeur et al. 2021). However, this topic must be further studied, since very few studies in this regard are found in Brazilian Cerrado ecosystems.

The knowledge of nutrient acquisition strategies in plant communities underpins the understanding of species distribution and co-occurrence in the Cerrado (Lambers et al. 2018). This knowledge of trait-based strategies in response to edaphic conditions is crucial for effective restoration of degraded ecosystems, the control of exotic species invasion (Leite et al. 2019), and for the conservation of ecosystem services (Lavorel and Grigulis 2012).

Fig. 12 **a**) Dauciform roots in *Lagenocarpus sp*. **b**) Vellozioid roots of *Barbacenia rubrovirens*. **c**) Vellozioid roots of *Barbacenia* sp. **d**) Rhizosheaths of *Discocactus placentiformis*

Future perspectives in restoration ecology

The understanding of the relationship between soil types, plant communities and their traits is essential to effective ecological restoration in the Cerrado. Ecological restoration is "the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed" (SER 2004). Functional trait-based restoration strategies enable species selection according to site-specific environmental conditions (Laughlin 2014; Valliere et al. 2021). In the Cerrado, this would mean selecting species according to their edaphic and hydrologic niches. As such, species would have resource-acquisition and -use traits suited to the soil types. This would allow functional recovery of ecosystems, including water, C and nutrient cycling, and their associated ecosystem services (Reid et al. 2005; Carlucci et al. 2020). However, sites that need to be restored have undergone substantial changes in land use, which affect soil chemical and physical structure. Soils used in agriculture have been homogenized via tillage and enriched via fertilisation (Silva et al. 2019; Sampaio et al. 2019), and lost soil organic C often acting as C sources (Braz et al. 2013). In addition, pastures are usually covered by exotic grasses and once abandoned, native grasses do not regenerate naturally, requiring interventions (Cava et al. 2018). Finally, more than 60% of the pastures in the Cerrado were degraded due to mismanagement or overgrazing (Galinari 2014; de Andrade and de Freitas 2018). Cerrado soils are often sensitive to erosion and loss of organic matter. Consequently, huge efforts are needed to recover degraded soils.

Unfortunately, most of the studies that used a trait-based framework to help design restoration projects were conducted in non-tropical forested areas, and only 26% of studies targeted open vegetation such as grasslands and savannas (Carlucci et al. 2020). In Brazil, only *ca.*16% of the studies on restoration were conducted in the Cerrado (Guerra et al. 2020), despite its representative coverage (22%) of the territory. Ecological restoration of the Cerrado is especially important in view of the International Agreements Brazil signed, such as the Bonn challenge launched in 2011 (Temperton et al. 2019) and joined by Brazil in 2017. Brazil developed a plan for the recovery of native vegetation, aiming to restore 12 million hectares of native vegetation by 2030 (Brasil 2017). The plan recommends restoration ecology to be based on

scientific knowledge to help solve social problems. To underpin large-scale restoration initiatives scientists and practitioners must understand plant and soil trait associations. The recent report from 2018 focuses on tree-planting in the Atlantic Forest, natural regeneration in the Amazon Forest and only mentions the Cerrado in the context of monitoring country-wide vegetation loss and recovery via remote sensing (Dave et al. 2018). Since both restoration methods and species-trait association in the Cerrado are mostly known for tree species and most of the Cerrado flora is composed of grasses and other herbaceous plants, the use of functional traits in the restoration of Cerrado depicts a significant knowledge gap. In order to restore the Cerrado, tree planting will not be enough and might even harm open ecosystems such as grasslands (Veldman et al. 2015; Temperton et al. 2019; Dudley et al. 2020; Buisson et al. 2021). It is, therefore, necessary to recover all plant functional types, and not only trees if we are to recover Cerrado ecosystem services and functions.

Ecological restoration of the Cerrado faces several challenges. The strategy to restore community assembly, ecosystem functions and services will depend on the previous land uses, which in the Cerrado are mainly pastures for livestock production or arable land (Guerra et al. 2020). Areas previously used as pastures are covered with fast-growing invasive African grass species, which increase the rate of C and nutrient cycling in the soil (Lannes et al. 2016). The challenge associated with removing these invasive grasses is a significant barrier to a successful restoration, and special techniques such as burning, and inversion tillage have been employed (Sampaio et al. 2019). However, conventional agricultural practices alter soil physical properties such as porosity, structure, soil bulk density as well as nutritional content (Hunke et al. 2015), hampering the establishment of native species. In addition, the nutritional input from fertilizers stimulates the growth of acquisitive grasses (Bustamante et al. 2012), which should also result in an increase in exotic grasses invasion. The techniques used for exotic-grass removal also decrease soil organic C. Soil organic C helps mitigate climate change through the reduction of CO_2 in the atmosphere (Lal et al. 2015). This is especially important in wetlands such as *Veredas* (Soares et al. 2021), where the waterlogged soils prevent C decomposition, generating exceptionally high soil C stores. In very dry

years, the soils can also dry, contributing to catastrophic fire events, as the soils themselves can burn (Flores et al. 2021). In order to protect the C stored in the wetlands, the biodiversity of open ecosystems, and the diversity of riparian forests, there is a need to integrate well-planned fire management practices in the Cerrado (Schmidt and Eloy 2020). Therefore, to prevent expensive restoration, the conservation of native areas is of the upmost importance to protect watersheds and their associated biodiversity.

Cerrado restoration techniques are diverse and vary from planting seedlings to direct seeding. In both cases however, the species selection based on their functional traits according to each soil condition is key. For this, small-scale soil surveys to evaluate the edaphic chemical and physical properties are paramount for the correct species selection. For example, only species growing on nutrient-poor soils can acquire nutrients where these have been depleted by poor management or long-term weathering (Abrahão et al. 2019). However, conditions of excess nutrients can also represent an obstacle to the establishment of species adapted to nutrient impoverished soils. Plants adapted to P-limited soils can exhibit toxicity for this element when exposed to slightly higher P availability than their edaphic niche (de Campos et al. 2013; Paganeli et al. 2020; Guilherme Pereira et al. 2021), especially when soils have been limed to increase pH (Hayes et al. 2019), a condition common in most post-agricultural soils (Hawkins et al. 2008). Knowledge of water table depth variation is also necessary for the correct assignment of reference ecosystems and the species selection based on their resistance to soil saturation or waterlogging conditions (*campos úmidos*) (Xavier et al. 2017).

In order to restore invaded tallgrass prairies in the United States, several studies recommend using species with functional traits similar to the invasive species, high-biomass producing plants with recalcitrant leaves (Young et al. 2008; Funk et al. 2008). In the Cerrado, several studies found an efficient coverage of the soil with native species using direct seeding techniques and mostly fast-growing grasses (Pellizzaro et al. 2017; Coutinho et al. 2019; Sampaio et al. 2019). This strategy is an excellent way to initially exclude exotic grasses (Mahaney et al. 2015). However, this may keep the restored site in a "fast" nutrient and carbon cycling state, which could prevent recovery of the functional traits of the native

reference system (Giles et al. 2021). Consequently, Cerrado grassland restoration using high density of species functionally similar to invasive species may not recover essential ecosystem functions, such as nutrient cycling and C cycling (D'Angioli et al. 2022), securing community drought resistance. However, restoration studies in the Cerrado are limited in terms of both their spatial resolution and geographical extent relative to other forest biomes in Brazil. Substantially more investment is needed into understanding how to rid these systems of exotic invasive plants and generate slow-growth native Cerrado plants after the initial establishment of the fast-growing native species (Mahaney et al. 2015).

Finally, the species choice also needs to consider the disturbance regimes of the Cerrado. As previously mentioned, the Cerrado is subject to anthropic and natural fires. Several species have underground buds and carbohydrate reserves that allow re-sprouting after fire (Pausas et al. 2018). Inclusion of species with underground buds in restoration projects, for example, via topsoil transfer may help the community resist occasional fires (Pilon et al. 2018). We conclude that an intervention is often needed to restore the Cerrado, since, after many years of agricultural management and soil tillage, there is a very low chance for natural regeneration. The combination of strategies such as direct seeding and topsoil transfer potentially increase the resilience of the sites under restoration (Standish et al. 2014).

Concluding remarks

The Cerrado shows a wide diversity in geology and geomorphology which govern the edaphic heterogeneity across the domain. Variation in the parent material and landforms controls soil formation (Fig. 13). For instance, rocks poor in cations and resistant to weathering will form shallow and nutrient-poor soils. Conversely, more stable landforms can form deeper soils that depending on the parent material will result in different soil nutrient conditions. We show that the floristic composition of the different vegetation types responds to the variation in edaphic conditions (Fig. 13). This fits with the views of early botanists who supported the concept of an edaphic effect on the distribution of vegetation types (Arens 1958; Goodland and Pollard 1973; Lopes and Cox 1977; Furley and Ratter 1988). Nevertheless, in the
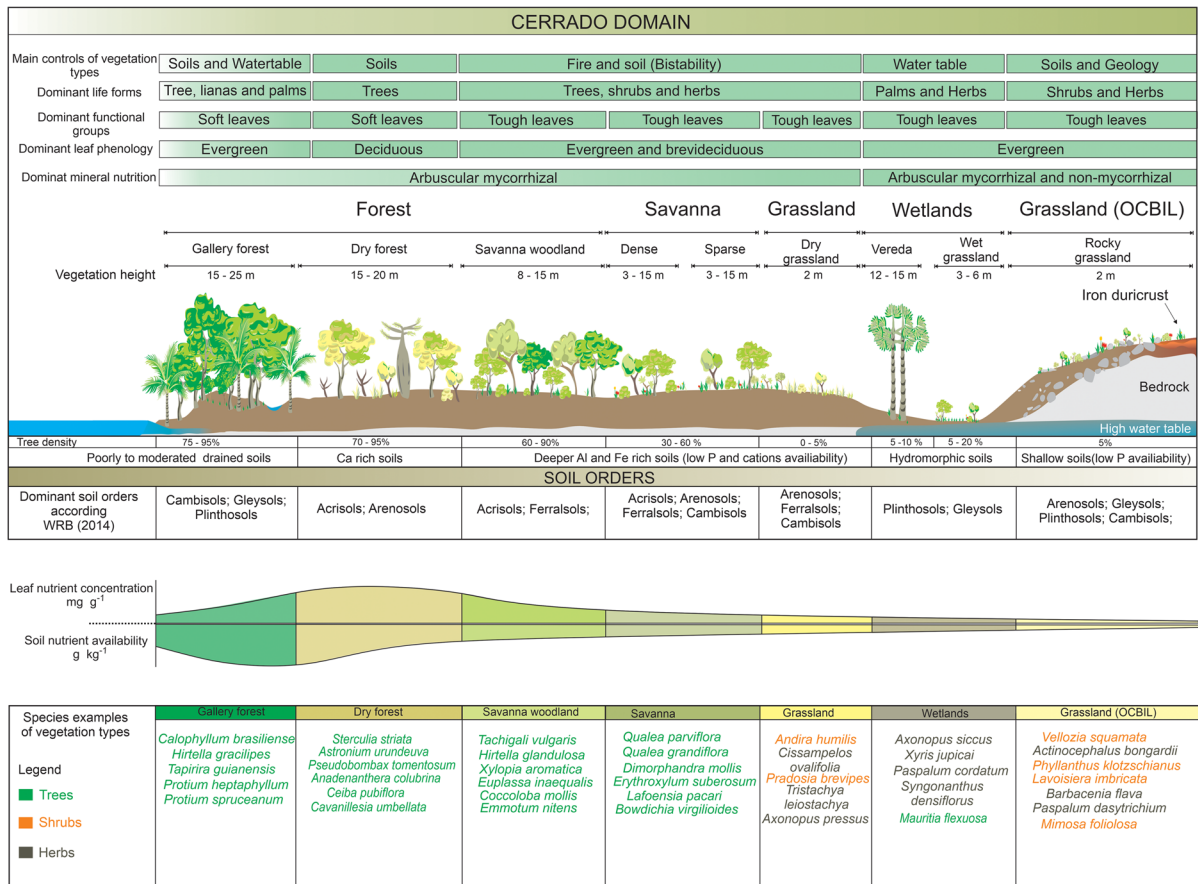
CERRADO DOMAIN

Main controls of vegetation types	Soils and Watertable	Soils	Fire and soil (Bistability)			Water table		Soils and Geology
Dominant life forms	Tree, lianas and palms	Trees	Trees, shrubs and herbs			Palms and Herbs		Shrubs and Herbs
Dominant functional groups	Soft leaves	Soft leaves	Tough leaves	Tough leaves	Tough leaves	Tough leaves		Tough leaves
Dominant leaf phenology	Evergreen	Deciduous	Evergreen and brevideciduous			Evergreen		
Dominat mineral nutrition	Arbuscular mycorrhizal					Arbuscular mycorrhizal and non-mycorrhizal		

	Forest		Savanna		Grassland	Wetlands		Grassland (OCBIL)
	Gallery forest	Dry forest	Savanna woodland	Dense / Sparse	Dry grassland	Vereda	Wet grassland	Rocky grassland
Vegetation height	15 - 25 m	15 - 20 m	8 - 15 m	3 - 15 m / 3 - 15 m	2 m	12 - 15 m	3 - 6 m	2 m

Iron duricrust

Bedrock

High water table

Tree density	75 - 95%	70 - 95%	60 - 90%	30 - 60 %	0 - 5 %	5 -10 %	5 - 20 %	5%
	Poorly to moderated drained soils	Ca rich soils	Deeper Al and Fe rich soils (low P and cations availiability)			Hydromorphic soils		Shallow soils(low P availiability)

SOIL ORDERS

Dominant soil orders according WRB (2014)	Cambisols; Gleysols; Plinthosols	Acrisols; Arenosols	Acrisols; Ferralsols;	Acrisols; Arenosols; Ferralsols; Cambisols	Arenosols; Ferralsols; Cambisols	Plinthosols; Gleysols		Arenosols; Gleysols; Plinthosols; Cambisols;

Leaf nutrient concentration mg g^{-1}

Soil nutrient availability g kg^{-1}

Species examples of vegetation types	Gallery forest	Dry forest	Savanna woodland	Savanna	Grassland	Wetlands	Grassland (OCBIL)
Legend: Trees / Shrubs / Herbs	*Calophyllum brasiliense* *Hirtella gracilipes* *Tapirira guianensis* *Protium heptaphyllum* *Protium spruceanum*	*Sterculia striata* *Astronium urundeuva* *Pseudobombax tomentosum* *Anadenanthera colubrina* *Ceiba pubiflora* *Cavanillesia umbellata*	*Tachigali vulgaris* *Hirtella glandulosa* *Xylopia aromatica* *Euplassa inaequalis* *Coccoloba mollis* *Emmotum nitens*	*Qualea parviflora* *Qualea grandiflora* *Dimorphandra mollis* *Erythroxylum suberosum* *Lafoensia pacari* *Bowdichia virgilioides*	*Andira humilis* *Cissampelos ovalifolia* *Pradosia brevipes* *Tristachya leiostachya* *Axonopus pressus*	*Axonopus siccus* *Xyris jupicai* *Paspalum cordatum* *Syngonanthus densiflorus* *Mauritia flexuosa*	*Vellozia squamata* *Actinocephalus bongardii* *Phyllanthus klotzschianus* *Lavoisiera imbricata* *Barbacenia flava* *Paspalum dasytrichium* *Mimosa foliolosa*

Fig. 13 Diagram of the main determinants of different Cerrado vegetation types. The dominant life forms, functional groups, leaf phenology, and mineral nutrition of each vegetation type presented in the text are indicated. Characteristic soil properties and soil order of each formation are depicted. Typical species are also indicated

past two decades, many savanna ecologists have been overlooking the effect of edaphic properties in favour of fire disturbance as the main environmental driver of shifts in vegetation (Murphy and Bowman 2012; Favier et al. 2012; Lehmann et al. 2014; Dantas et al. 2016). We propose an integrative view of both schools of thought, where edaphic chemical and physical properties act as modulators of vegetation stands and these conditions interact with the fire regime to affect woody plant growth (Fig. 13). Soils with low nutrient content and physical restriction represent edaphic conditions that predispose the occurrence of fire-prone open vegetation types (Figs. 8 and 13), where shallow-rooted plants (e.g., herbs and grasses) dominate. We propose that these edaphic conditions act as environmental filters for the convergence of economics traits (Fig. 13). Hence, plants evolving in these environments exhibit morphological and physiological adaptations based on the conservative use of resources. Under very low P availability, mycorrhizal associations are less cost-effective and strategies involving P mobilization prevail (Fig. 13). In contrast, deeper soils (i.e., no physical restriction) with higher nutrient concentrations favour the occurrence of deep-rooted plants with arboreal habit and more acquisitive strategies. This results in vegetation stands with greater woody plant growth (e.g., woodlands and forests) that prevent fire events. Therefore, edaphic conditions and fire regimes drive the ecology and evolution of these ecosystems.

We present an ecological framework based on a rationale towards a more mechanistic understanding of trait-based species and vegetation distribution (Fig. 13). It proposes a geomorphic and edaphic

control, along with climate conditions that interact with fire disturbance. Indeed, the use of combined soil and climate properties on dynamic vegetation models has recently gained more visibility (Arruda et al. 2017; Corlett and Tomlinson 2020; Oliveira et al. 2021a). Therefore, the rationale of this framework is imperative for accurate and reliable predictions of vegetation dynamics in response to climate change, especially in fire-prone areas with diverse geomorphic properties. In addition, this framework should provide important guidelines to enhance resource use and restoration efforts success given the impact of soil properties on plant performance.

Declarations

References

Abrahão A, de Costa P, B, Lambers H, et al (2019) Soil types select for plants with matching nutrient-acquisition and -use traits in hyperdiverse and severely nutrient-impoverished campos rupestres and cerrado in Central Brazil. J Ecol 107:1302–1316

Abrahão A, de Britto CP, Teodoro GS et al (2020) Vellozioid roots allow for habitat specialization among rock- and soil-dwelling Velloziaceae in campos rupestres. Funct Ecol 34:442–457

Abrahão A, Lambers H, Sawaya ACHF et al (2014) Convergence of a specialized root trait in plants from nutrient-impoverished soils: phosphorus-acquisition strategy in a nonmycorrhizal cactus. Oecologia 176:345–355

Abreu MF, Pinto JRR, Maracahipes L et al (2012) Influence of edaphic variables on the floristic composition and structure of the tree-shrub vegetation in typical and rocky outcrop cerrado areas in Serra Negra, Goiás State, Brazil. Brazilian J Botany 35:259–272

Ab'Sáber AN (2003) Os domínios de natureza no Brasil: potencialidades paisagísticas. Atelie Editorial

Ackerly DD, Cornwell WKK (2007) A trait-based approach to community assembly: Partitioning of species trait values into within- and among-community components. Ecol Lett 10:135–145. https://doi.org/10.1111/j.1461-0248.2006.01006.x

Albornoz FE, Dixon KW, Lambers H (2021) Revisiting mycorrhizal dogmas: Are mycorrhizas really functioning as they are widely believed to do? Soil Ecol Lett 3:73–82

Alkmim FF (2015) Geological background: a tectonic panorama of Brazil. In: Vieira BC, Salgado AAR, Santos LJC (eds) Landscapes and landforms of Brazil. Springer, Dordrecht, pp 9–17

Alkmim FF, Reis HLS (2021) Brazil and the Guianas. Encycl Geol 27:46

Amaral AG, Bijos NR, Moser P, Munhoz CBR (2021) Spatially structured soil properties and climate explain distribution patterns of herbaceous-shrub species in the Cerrado. Plant Ecol. https://doi.org/10.1007/s11258-021-01193-7

Araujo ASF, Melo VMM, de Pereira AP, A, et al (2021) Arbuscular mycorrhizal community in soil from different Brazilian Cerrado physiognomies. Rhizosphere 19

Arens K (1958) O Cerrado como Vegetação Oligotrófica. Boletim da Faculdade de Filosofia, Ciências e Letras, Universidade de São Paulo. Botânica 15:59

Arruda DM, Fernandes-Filho EI, Solar RRC, Schaefer CEGR (2017) Combining climatic and soil properties better predicts covers of Brazilian biomes. Naturwissenschaften 104:32

Arruda DM, Schaefer CEGR, Corrêa GR et al (2015) Landforms and soil attributes determine the vegetation structure in the Brazilian semiarid. Folia Geobot 50:175–184

Banhos OFAA, de Souza MC, Habermann G (2016) High aluminum availability may affect Styrax camporum, an Al non-accumulating species from the Brazilian savanna. Theor Exp Plant Physiol 28:321–332

Barreto HN, Varajão CAC, Braucher R et al (2013) Denudation rates of the Southern Espinhaço Range, Minas Gerais, Brazil, determined by in situ-produced cosmogenic beryllium-10. Geomorphology 191:1–13

Benites VM, Schaefer CEGR, Simas FNB, Santos HG (2007) Soils associated with rock outcrops in the Brazilian mountain ranges Mantiqueira and Espinhaço. In: Revista Brasileira de Botanica. 569–577

Bieras AC, Sajo M, das G, (2009) Leaf structure of the cerrado (Brazilian savanna) woody plants. Trees 23:451–471

Bittencourt BMOC, da Silva CMS, Filho SZ, Habermann G (2020) Aluminum (Al)-induced organic acid exudation in an Al-accumulating species from the Brazilian savanna. Trees 34:155–162

Bockheim JG, Hartemink AE (2013) Distribution and classification of soils with clay-enriched horizons in the USA. Geoderma 209–210:153–160

Brady NC, Weil RR (2016) The Nature and Properties of Soils, 15th edn. Pearson Education Limited, New Jersey and Columbus

Brasil MMA (2017) Planaveg: Plano Nacional de Recuperação da Vegetação Nativa. MMA, Brasília-DF

Braz SP, Urquiaga S, Alves BJR et al (2013) Soil carbon stocks under productive and degraded Brachiaria pastures in the Brazilian cerrado. Soil Sci Soc Am J 77:914–928

Brenner J, Porter W, Phillips JR et al (2018) Phosphorus sorption on tropical soils with relevance to Earth system model needs. Soil Res 57:17–27

Bressan ACG, Bittencourt BMOC, Silva GS, Habermann G (2021) Could the absence of aluminum (Al) impair the development of an Al-accumulating woody species from Brazilian savanna? Theor Exp Plant Physiol 33:281–292

Bressan ACG, Coan AI, Habermann G (2016) X-ray spectra in SEM and staining with chrome azurol S show Al deposits in leaf tissues of Al-accumulating and non-accumulating plants from the cerrado. Plant Soil 404:293–306

Bressan ACG, Schwab GS, Banhos OFAA, Tanaka FAO, Habermann G (2020) Physiological, anatomical and ultrastructural effects of aluminum on Styrax camporum, a native Cerrado woody species. J Plant Res 133:625–637

Britez RM, Watanabe T, Jansen S et al (2002) The relationship between aluminium and silicon accumulation in leaves of Faramea marginata (Rubiaceae). New Phytol 156:437–444

Brunner I, Sperisen C (2013) Aluminum exclusion and aluminum tolerance in woody plants. Front Plant Sci 4:172

Bueno ML, Dexter KG, Pennington RT et al (2018) The environmental triangle of the Cerrado Domain: Ecological factors driving shifts in tree species composition between forests and savannas. J Ecol 106:2109–2120

Bueno ML, Neves DRM, Souza AF et al (2013) Influence of edaphic factors on the floristic composition of an area of cerradão in the Brazilian central-west. Acta Bot Brasilica 27:445–455

Buisson E, Fidelis A, Overbeck GE et al (2021) A research agenda for the restoration of tropical and subtropical grasslands and savannas. Restor Ecol. https://doi.org/10.1111/rec.13292

Buol SW, Eswaran H (1999) Oxisols. In: Sparks DL (ed) Advances in Agronomy. Academic Press, pp 151–195

Bustamante MMC, Brito DQD, Kozovits AR et al (2012) Effects of nutrient additions on plant biomass and diversity of the herbaceous-subshrub layer of a Brazilian savanna (Cerrado). Plant Ecol 213:795–808

Camargo AP, de Souza RSC, de Britto CP et al (2019) Microbiomes of Velloziaceae from phosphorus-impoverished soils of the campos rupestres, a biodiversity hotspot. Sci Data 6:140

Camargo AP, de Souza RSC, Jose J, Gerhardt IR (2021) Plant-associated microbiomes promote nutrient turnover in impoverished substrates of a biodiversity hotspot. bioRxiv

Campos JD, Chaves HM (2020) Tendências e Variabilidades nas Séries Históricas de Precipitação Mensal e Anual no Bioma Cerrado no Período 1977–2010. Rev Bras Meteorol 35:157–169. https://doi.org/10.1590/0102-7786351019

Carlucci MB, Brancalion PHS, Rodrigues RR et al (2020) Functional traits and ecosystem services in ecological restoration. Restor Ecol 28:1372–1383

Cássia-Silva C, Cianciaruso MV, Dias PA et al (2020) Among cradles and museums: seasonally dry forest promotes lineage exchanges between rain forest and savanna. Plant Ecol Divers 13:1–13. https://doi.org/10.1080/17550874.2019.1709103

Cava MGB, Pilon NAL, Ribeiro MC, Durigan G (2018) Abandoned pastures cannot spontaneously recover the attributes of old-growth savannas. J Appl Ecol 55:1164–1172

Chaves DA, Ribeiro-Silva S, Proença CEB et al (2019) Geographic space, relief, and soils predict plant community patterns of Asteraceae in rupestrian grasslands, Brazil. Biotropica 51:155–164

Chen L-S, Qi Y-P, Smith BR, Liu X-H (2005) Aluminum-induced decrease in CO_2 assimilation in citrus seedlings is unaccompanied by decreased activities of key enzymes involved in CO_2 assimilation. Tree Physiol 25:317–324

Cianciaruso MV, Silva IA, Manica LT, Souza JP (2013) Leaf habit does not predict leaf functional traits in cerrado woody species. Basic Appl Ecol 14:404–412

Cintra BBL, Schietti J, Emillio T et al (2013) Soil physical restrictions and hydrology regulate stand age and wood biomass turnover rates of Purus-Madeira interfluvial wetlands in Amazonia. Biogeosciences 10:7759–7774. https://doi.org/10.5194/bg-10-7759-2013

Cochrane TT (1989) Chemical properties of native Savanna and forest soils in central Brazil. Soil Sci Soc Am J 53:139–141

Conceição AA, Pirani JR, Meirelles ST (2007) Floristics, structure and soil of insular vegetation in four quartzite-sandstone outcrops of "Chapada Diamantina", Northeast Brazil. Rev Bras Bot 30:641–656

Corlett RT, Tomlinson KW (2020) Climate Change and Edaphic Specialists: Irresistible Force Meets Immovable Object? Trends Ecol Evol 35:367–376

Cornwell WK, Schwilk LDW, Ackerly DD (2006) A trait-based test for habitat filtering: convex hull volume. Ecology 87:1465–1471

Correia JR, Lobo-Burle M, Calderano SB, et al (2001) Caracterização de ambientes na Chapada dos Veadeiros/Vale do

Rio Paraná: contribuição para a classificação brasileira de solos. Embrapa Cerrados-Documentos (INFOTECA-E)

Coutinho AG, Alves M, Sampaio AB et al (2019) Effects of initial functional-group composition on assembly trajectory in savanna restoration. Appl Veg Sci 22:61–70

Cruz Ruggiero PG, Batalha MA, Pivello VR, Meirelles ST (2002) Soil-vegetation relationships in cerrado (Brazilian savanna) and semideciduous forest, Southeastern Brazil. Plant Ecol 160:1–16

Cury NF, Silva RCC, Andre MSF et al (2020) Root proteome and metabolome reveal a high nutritional dependency of aluminium in Qualea grandiflora Mart. (Vochysiaceae). Plant Soil 446:125–143

Dalrymple JB, Blong RJ, Conacher AJ (1968) A hypothetical nine unit landsurface model. Z Geomorphol 12:60–76

Dave R, Saint-Laurent C, Murray L, et al (2018) Second Bonn challenge progress report. Application of the Barometer in 2019:

D'Angioli AM, Dantas VL, Lambais M et al (2021) No evidence of positive feedback between litter deposition and seedling growth rate in Neotropical savannas. Plant Soil 469:305–320

D'Angioli AM, Giles AL, Costa PB et al (2022) Abandoned pastures and restored savannahs have distinct patterns of plant-soil feedback and nutrient cycling compared with native Brazilian savannahs. J Appl Ecol. https://doi.org/10.1111/1365-2664.14193

Dantas V de L, Hirota M, Oliveira RS, Pausas JG (2016) Disturbance maintains alternative biome states. Ecol Lett 19:12–19. https://doi.org/10.1111/ele.12537

de Almeida FFM, Carneiro CDR (1998) Origem e evolução da Serra do Mar. Brazilian J Geol 28:135–150

de Andrade AG, de Freitas PL (2018) Prevenção do avanço da degradação e recuperação de terras degradadas. In: de Oliveira Y. M. M. Marques D. K. S. & Silva J. C. B. VGF de MBMP (ed) Vida terrestre: Conbtribuições da EMBRAPA. 63–72

de Andrade LRM, Barros LMG, Echevarria GF et al (2011) Al-hyperaccumulator Vochysiaceae from the Brazilian Cerrado store aluminium in their chloroplasts without apparent damage. Environ Exp Bot 70:37–42

Camêlo D de L, Gilkes RJ, Leopold M, et al (2018) The application of quartz grain morphology measurements to studying iron-rich duricrusts. CATENA 170:397–408. https://doi.org/10.1016/J.CATENA.2018.06.034

de Campos MCR, Pearse SJ, Oliveira RS (2013) Downregulation of net phosphorus-uptake capacity is inversely related to leaf phosphorus-resorption proficiency in four species from a phosphorus-impoverished …. Annals of

de Carvalho Júnior OA, Guimarães RF, de Martins É, S, Gomes RAT, (2015) Chapada dos Veadeiros: The Highest Landscapes in the Brazilian Central Plateau. In: Vieira BC, Salgado AAR, Santos LJC (eds) Landscapes and Landforms of Brazil. Springer, Netherlands, Dordrecht. 221–230

Denton MD, Veneklaas EJ, Freimoser FM, Lambers H (2007) Banksia species (Proteaceae) from severely phosphorus-impoverished soils exhibit extreme efficiency in the use and re-mobilization of phosphorus. Plant Cell Environ 30:1557–1565

de Mesquita Filho MV, Torrent J (1993) Phosphate sorption as related to mineralogy of a hydrosequence of soils from the Cerrado region (Brazil). Geoderma 58:107–123

de Oliveira AP, Dusi DM de A, Walter BMT, et al (2019) Avaliação de espécies do Cerrado quanto à tolerância ao alumínio. EMBRAPA, Brasília, DF

Oliveira-Filho AT, Shepherd GJ, Martins FR, Stubblebine WH (1989) Environmental factors affecting physiognomic and floristic variation in an area of cerrado in central Brazil. J Trop Ecol 5:413–431

De Souza JP, Araújo GM, Haridasan M (2007) Influence of soil fertility on the distribution of tree species in a deciduous forest in the Triângulo Mineiro region of Brazil. Plant Ecol 191:253–263

de Souza MC, Williams TCR, Poschenrieder C (2020) Calcicole behaviour of Callisthene fasciculata Mart., an Al-accumulating species from the Brazilian Cerrado. Plant

de Tombeur F, Cornelis J-T, Lambers H (2021) Silicon mobilisation by root-released carboxylates. Trends Plant Sci 26:1116–1125

de Xavier R, O, Leite MB, da Silva-Matos DM, (2017) Stress responses of native and exotic grasses in a Neotropical savanna predict impacts of global change on invasion spread. Austral Ecol 42:562–576

Díaz S, Cabido M, (2001) Vive la différence: plant functional diversity matters to ecosystem processes. Trends Ecol Evol 16:646–655

Domingues TF, Meir P, Feldpausch TR et al (2010) Co-limitation of photosynthetic capacity by nitrogen and phosphorus in West Africa woodlands. Plant Cell Environ 33:959–980

dos Santos HG, Carvalho Junior W de, Dart R de O, et al (2011) O novo mapa de solos do Brasil: legenda atualizada. Embrapa Solos-Documentos (INFOTECA-E)

Dudley N, Eufemia L, Fleckenstein M et al (2020) Grasslands and savannahs in the UN Decade on Ecosystem Restoration. Restor Ecol 28:1313–1317

Durigan G, Ratter JA (2006) Successional changes in Cerrado and Cerrado/forest ecotonal vegetation in Western São Paulo State, Brazil, 1962–2000. Edinb J Bot 63:119–130

Durigan G, Munhoz CB, Zakia MJB, Oliveira RS, Pilon NAL, do Valle RST, Walter BMT, Honda EA, Pott A (2022) Cerrado wetlands: multiple ecosystems deserving legal protection as a unique and irreplaceable treasure. Perspect Ecol Conserv. https://doi.org/10.1016/j.pecon.2022.06.002

Duszyński F, Migoń P, Strzelecki MC (2019) Escarpment retreat in sedimentary tablelands and cuesta landscapes–Landforms, mechanisms and patterns. Earth-Sci Rev

Eloy L, Aubertin C, Toni F et al (2016) On the margins of soy farms: traditional populations and selective environmental policies in the Brazilian Cerrado. J Peasant Stud 43:494–516

EMBRAPA (1983) Levantamento de reconhecimento de media intensidade dos solos e avaliacao da aptidao agricola das terras da margem direita do rio Parana- Estado de Goias. Empresa Brasileira de Pesquisa Agropecuária. Serviço Nacional de Levantamento e Conservação de Solos [SNLCS], Rio de Janeiro

Favier C, Aleman J, Bremond L et al (2012) Abrupt shifts in African savanna tree cover along a climatic gradient. Glob Ecol Biogeogr 21:787–797

Fick SE, Hijmans RJ (2017) WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. Int J Climatol 37:4302–4315. https://doi.org/10.1002/JOC.5086

Fink JR, Inda AV, Tiecher T, Barrón V (2016) Iron oxides and organic matter on soil phosphorus availability. Ciênc Agrotec 40:369–379

Flores BM, de Sá Dechoum M, Schmidt IB et al (2021) Tropical riparian forests in danger from large savanna wildfires. J Appl Ecol 58:419–430. https://doi.org/10.1111/1365-2664.13794

Fontes MPF, Weed SB (1996) Phosphate adsorption by clays from Brazilian Oxisols: relationships with specific surface area and mineralogy. Geoderma 72:37–51

Franco AC, Bustamante M, Caldas LS et al (2005) Leaf functional traits of Neotropical savanna trees in relation to seasonal water deficit. Trees 19:326–335

Françoso RD, Dexter KG, Machado RB et al (2020) Delimiting floristic biogeographic districts in the Cerrado and assessing their conservation status. Biodivers Conserv 29:1477–1500

Funk JL, Cleland EE, Suding KN, Zavaleta ES (2008) Restoration through reassembly: plant traits and invasion resistance. Trends Ecol Evol 23:695–703

Furley PA, Ratter JA (1988) Soil Resources and Plant Communities of the Central Brazilian Cerrado and Their Development. J Biogeogr 15:97–108

Fyllas NM, Patiño S, Baker TR et al (2009) Basin-wide variations in foliar properties of Amazonian forest: phylogeny, soils and climate. Biogeosciences 6:2677–2708

Galinari G (2014) Embrapa mapeia degradação das pastagens do Cerrado. In: EMBRAPA. https://www.embrapa.br/busca-de-noticias/-/noticia/2361250/embrapa-mapeia-degradacao-das-pastagens-do-cerrado. Accessed 15 Dec 2021

Gardner TA (2006) Tree-grass coexistence in the Brazilian cerrado: demographic consequences of environmental instability. J Biogeogr 33:448–463

Garnier E, Navas M-L, Grigulis K (2016) Plant Functional Diversity: Organism Traits, Community Structure, and Ecosystem Properties. Oxford University Press

Gilbert L, Johnson D (2017) Plant–plant communication through common mycorrhizal networks. Adv Bot Res 82:83–97

Giles AL, Costa P de B, Rowland L, et al (2021) How effective is direct seeding to restore the functional composition of neotropical savannas? Restor Ecol e13474

Goedert WJ (1983) Management of the Cerrado soils of Brazil: a review. J Soil Sci 34:405–428

Goodland R, Pollard R (1973) The Brazilian Cerrado Vegetation: A Fertility Gradient. J Ecol 61:219–224

Gray JM, Bishop TFA, Wilford JR (2016) Lithology and soil relationships for soil modelling and mapping. Catena 147:429–440

Grevenstuk T, Romano A (2013) Aluminium speciation and internal detoxification mechanisms in plants: where do we stand? Metallomics 5:1584

Grime JP (2006) Trait convergence and trait divergence in herbaceous plant communities: Mechanisms and consequences. J Veg Sci 17:255–260

Grubb PJ (1989) The role of mineral nutrients in the tropics: a plant ecologist's view. Mineral nutrients in tropical forest and savanna

Guerra A, Reis LK, Borges FLG et al (2020) Ecological restoration in Brazilian biomes: Identifying advances and gaps. For Ecol Manage 458

Guilherme Pereira C, Clode PL, Oliveira RS, Lambers H (2018) Eudicots from severely phosphorus-impoverished environments preferentially allocate phosphorus to their mesophyll. New Phytol 218:959–973

Guilherme Pereira C, Hayes PE, Clode PL, Lambers H (2021) Phosphorus toxicity, not deficiency, explains the calcifuge habit of phosphorus-efficient Proteaceae. Physiol Plant 172:1724–1738

Guilherme Pereira C, Hayes PE, O'Sullivan OS et al (2019) Trait convergence in photosynthetic nutrient-use efficiency along a 2-million year dune chronosequence in a global biodiversity hotspot. J Ecol 107:2006–2023

Haridasan M (1982) Aluminium accumulation by some cerrado native species of central Brazil. Plant Soil 65:265–273

Haridasan M (2008) Nutritional adaptations of native plants of the cerrado biome in acid soils. Braz J Plant Physiol 20:183–195

Haridasan M, De Araújo GM (1988) Aluminium-accumulating species in two forest communities in the cerrado region of central Brazil. For Ecol Manage 24:15–26

Hawkins H-J, Hettasch H, Mesjasz-Przybylowicz J et al (2008) Phosphorus toxicity in the Proteaceae: A problem in post-agricultural lands. Sci Hortic 117:357–365

Hayes PE, Clode PL, Oliveira RS, Lambers H (2018) Proteaceae from phosphorus-impoverished habitats preferentially allocate phosphorus to photosynthetic cells: An adaptation improving phosphorus-use efficiency. Plant Cell Environ 41:605–619

Hayes PE, Guilherme Pereira C, Clode PL, Lambers H (2019) Calcium-enhanced phosphorus toxicity in calcifuge and soil-indifferent Proteaceae along the Jurien Bay chronosequence. New Phytol 221:764–777

Hayes PE, Nge FJ, Cramer MD et al (2021) Traits related to efficient acquisition and use of phosphorus promote diversification in Proteaceae in phosphorus-impoverished landscapes. Plant Soil 462:67–88

Hayes P, Turner BL, Lambers H, Laliberté E (2014) Foliar nutrient concentrations and resorption efficiency in plants of contrasting nutrient-acquisition strategies along a 2-million-year dune chronosequence. J Ecol 102:396–410

Hirota M, Holmgren M, Van Nes EH, Scheffer M (2011) Global resilience of tropical forest and savanna to critical transitions. Science 334:232–235

Hodson MJ, Evans DE (2020) Aluminium–silicon interactions in higher plants: an update. J Exp Bot 71:6719–6729

Hoffmann WA, Geiger EL, Gotsch SG et al (2012) Ecological thresholds at the savanna-forest boundary: how plant traits, resources and fire govern the distribution of tropical biomes. Ecol Lett 15:759–768

Hooper DU, Chapin FS III, Ewel JJ et al (2005) Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. Ecol Monogr 75:3–35

Hopper SD (2009) OCBIL theory: towards an integrated understanding of the evolution, ecology and conservation

of biodiversity on old, climatically buffered, infertile landscapes. Plant Soil 322:49–86

Horst WJ, Wang Y, Eticha D (2010) The role of the root apoplast in aluminium-induced inhibition of root elongation and in aluminium resistance of plants: a review. Ann Bot 106:185–197

Hunke P, Mueller EN, Schröder B, Zeilhofer P (2015) The Brazilian Cerrado: assessment of water and soil degradation in catchments under intensive agricultural use. Ecohydrology 8:1154–1180

IBGE (2012) Manual técnico da vegetação brasileira. IBGE, Rio de Janeiro

IUSS Working Group WRB (2015) World Reference Base for Soil Resources 2014, update 2015. FAO, Rome, Italy

Jansen S, Broadley MR, Robbrecht E, Smets E (2002) Aluminum hyperaccumulation in angiosperms: A review of its phylogenetic significance. Bot Rev 68:235–269

Jansen S, Watanabe T, Smets E (2002) Aluminium accumulation in leaves of 127 species in Melastomataceae, with comments on the order Myrtales. Ann Bot 90:53–64

Jiang H-X, Chen L-S, Zheng J-G et al (2008) Aluminum-induced effects on Photosystem II photochemistry in citrus leaves assessed by the chlorophyll a fluorescence transient. Tree Physiol 28:1863–1871

Johnson SE, Loeppert RH (2006) Role of organic acids in phosphate mobilization from iron oxide. Soil Sci Soc Am J 70:222–234

Joswig JS, Wirth C, Schuman MC et al (2021) Climatic and soil factors explain the two-dimensional spectrum of global plant trait variation. Nat Ecol Evol. https://doi.org/10.1038/s41559-021-01616-8

Junior WGV, de Moura JB, de Souza RF et al (2020) Seasonal Variation in Mycorrhizal Community of Different Cerrado Phytophysiomies. Front Microbiol 11:2548. https://doi.org/10.3389/FMICB.2020.576764/BIBTEX

Kattge J, Bönisch G, Díaz S et al (2020) TRY plant trait database - enhanced coverage and open access. Glob Chang Biol 26:119–188

Kinraide TB (1991) Identity of the rhizotoxic aluminium species. In: Wright RJ, Baligar VC, Murrmann RP (eds) Plant-Soil Interactions at Low pH: Proceedings of the Second International Symposium on Plant-Soil Interactions at Low pH, 24–29 June 1990, Beckley West Virginia, USA. Springer Netherlands, Dordrecht, pp 717–728

Klink CA, Machado RB (2005) Conservation of the Brazilian cerrado. Conserv Biol 19:707–713

Kochian LV, Hoekenga OA, Pineros MA (2004) How do crop plants tolerate acid soils? Mechanisms of aluminum tolerance and phosphorous efficiency. Annu Rev Plant Biol 55:459–493

Kraft NJB, Adler PB, Godoy O et al (2015) Community assembly, coexistence and the environmental filtering metaphor. Funct Ecol 29:592–599

Kunstler G, Falster D, Coomes DA et al (2016) Plant functional traits have globally consistent effects on competition. Nature 529:204–207

Laliberté E, Legendre P (2010) A distance-based framework for measuring functional diversity from multiple traits. Ecology 91:299–305

Lal R, Negassa W, Lorenz K (2015) Carbon sequestration in soil. Curr Opin Environ Sustain 15:79–86

Lambers H (1992) Inherent Variation in Growth Rate Between Higher Plants: A Search for Physiological Causes and Ecological Consequences. Academic Press

Lambers H (2014) Plant life on the sandplains in southwest Australia: a global biodiversity hotspot. Apollo Books

Lambers H, Albornoz F, Kotula L et al (2018) How belowground interactions contribute to the coexistence of mycorrhizal and non-mycorrhizal species in severely phosphorus-impoverished hyperdiverse ecosystems. Plant Soil 424:11–33

Lambers H, Brundrett MC, Raven JA, Hopper SD (2011) Plant mineral nutrition in ancient landscapes: high plant species diversity on infertile soils is linked to functional diversity for nutritional strategies. Plant Soil 348:7

Lambers H, Cawthray GR, Giavalisco P et al (2012) Proteaceae from severely phosphorus-impoverished soils extensively replace phospholipids with galactolipids and sulfolipids during leaf development to achieve a high photosynthetic phosphorus-use-efficiency. New Phytol 196:1098–1108

Lambers H, de Britto CP, Oliveira RS, Silveira FAO (2020) Towards more sustainable cropping systems: lessons from native Cerrado species. Theor Exp Plant Physiol 32:175–194

Lambers H, Finnegan PM, Jost R et al (2015) Phosphorus nutrition in Proteaceae and beyond. Nat Plants 1:1–9. https://doi.org/10.1038/nplants.2015.109

Lambers H, Oliveira RS (2019) Plant Physiological Ecology. Springer International Publishing

Lambers H, Shane MW, Cramer MD et al (2006) Root structure and functioning for efficient acquisition of phosphorus: Matching morphological and physiological traits. Ann Bot 98:693–713

Lannes LS, Bustamante MMC, Edwards PJ, Olde Venterink H (2016) Native and alien herbaceous plants in the Brazilian Cerrado are (co-) limited by different nutrients. Plant Soil 400:231–243

Latrubesse EM, Arima E, Ferreira ME, et al (2019) Fostering water resource governance and conservation in the Brazilian Cerrado biome. Conservat Sci and Prac 1.: https://doi.org/10.1111/csp2.77

Laughlin DC (2014) Applying trait-based models to achieve functional targets for theory-driven ecological restoration. Ecol Lett 17:771–784

Lavorel S, Grigulis K (2012) How fundamental plant functional trait relationships scale-up to trade-offs and synergies in ecosystem services. J Ecol 100:128–140

Lehmann CER, Anderson TM, Sankaran M et al (2014) Savanna vegetation-fire-climate relationships differ among continents. Science 343:548–552

Lehmann CER, Archibald SA, Hoffmann WA, Bond WJ (2011) Deciphering the distribution of the savanna biome. New Phytol 191:197–209

Leite MR, Cassiolato AMR, Lannes LS (2019) Urochloa decumbens has higher mycorrhizal colonization in degraded than in pristine areas in the Brazilian cerrado. Floresta Ambient 26.: https://doi.org/10.1590/2179-8087.006019

Lemes L, de Andrade AFA, Loyola R (2020) Spatial priorities for agricultural development in the Brazilian Cerrado:

may economy and conservation coexist? Biodivers Conserv 29:1683–1700

Le Stradic S, Buisson E, Fernandes GW (2015) Vegetation composition and structure of some Neotropical mountain grasslands in Brazil. J Mt Sci 12:864–877

Le Stradic S, Hernandez P, Fernandes GW, Buisson E (2018) Regeneration after fire in campo rupestre: Short- and long-term vegetation dynamics. Flora 238:191–200

Lima J, Silva EM, Oliveira-Filho EC, et al (2011) The relevance of the Cerrado's water resources to the Brazilian development. In: Proceedings of the XIVth IWRA World Water Congress. IWRA, Montpellier

Lira-Martins D, Humphreys-Williams E, Strekopytov S, et al (2019) Tropical Tree Branch-Leaf Nutrient Scaling Relationships Vary With Sampling Location. Frontiers in Plant Science 10

Lira-Martins D, Schietti J, Feldpausch TR et al (2015) Soil-induced impacts on forest structure drive coarse woody debris stocks across central Amazonia. Plant Ecol Divers 8:229–241. https://doi.org/10.1080/17550874.2013.879942

Lloyd J, Domingues TF, Schrodt F et al (2015) Edaphic, structural and physiological contrasts across Amazon Basin forest–savanna ecotones suggest a role for potassium as a key modulator of tropical woody vegetation structure and function. Biogeosciences 12:6529–6571

Lopes AS, Cox FR (1977) A survey of the fertility status of surface soils under "cerrado" vegetation in Brazil. Soil Sci Soc Am J 41:742–747

Lopes AS, Guilherme LRG (2016) A career perspective on soil management in the Cerrado region of Brazil. Adv Agron 137:1–72

Loveless AR (1961) A Nutritional Interpretation of Sclerophylly Based on Differences in the Chemical Composition of Sclerophyllous and Mesophytic Leaves. Ann Bot 25:168–184

Mahaney WM, Gross KL, Blackwood CB, Smemo KA (2015) Impacts of prairie grass species restoration on plant community invasibility and soil processes in abandoned agricultural fields. Appl Veg Sci 18:99–109

Maia LC, Passos JH, Silva JA et al (2020) Species diversity of Glomeromycota in Brazilian biomes. Sydowia 72:181–205

Malta PG, Arcanjo-Silva S, Ribeiro C et al (2016) Rudgea viburnoides (Rubiaceae) overcomes the low soil fertility of the Brazilian Cerrado and hyperaccumulates aluminum in cell walls and chloroplasts. Plant Soil 408:369–384

Maranhão DDC, Pereira MG, Collier LS et al (2020) Pedogenesis in a karst environment in the Cerrado biome, northern Brazil. Geoderma 365

Marcelino V, Stoops G, Schaefer CEG (2010) Oxic and Related Materials. Interpretation of Micromorphological Features of Soils and Regoliths 305–327

Marienfeld S, Schmohl N, Klein M et al (2000) Localisation of Aluminium in Root Tips of Zea mays and Vicia faba. J Plant Physiol 156:666–671

Martinelli LA, Nardoto GB, Soltangheisi A et al (2021) Determining ecosystem functioning in Brazilian biomes through foliar carbon and nitrogen concentrations and stable isotope ratios. Biogeochemistry 154:405–423

McDowell R, Condron L (2001) Influence of soil constituents on soil phosphorus sorption and desorption. Commun Soil Sci Plant Anal 32:2531–2547

McGill BJ, Enquist BJ, Weiher E, Westoby M (2006) Rebuilding community ecology from functional traits. Trends Ecol Evol 21:178–185. https://doi.org/10.1016/j.tree.2006.02.002

Meira-Neto JAA, Tolentino GS, da Silva MCNA et al (2017) Functional antagonism between nitrogen-fixing leguminous trees and calcicole-drought-tolerant trees in the Cerrado. Acta Bot Brasilica 31:11–18

Mendonça AM, das C, Lira JMS, Vilela AL de O, et al (2020) High aluminum concentration and initial establishment of Handroanthus impetiginosus: clues about an Al non-resistant species in Brazilian Cerrado. Res J for 31:2075–2082

Messias MCTB, Leite MGP, Meira Neto JAA et al (2013) Soil-Vegetation Relationship in Quartzitic and Ferruginous Brazilian Rocky Outcrops. Folia Geobot 48:509–521

Mews HA, Pinto JRR, Eisenlohr PV, Lenza E (2016) No evidence of intrinsic spatial processes driving Neotropical savanna vegetation on different substrates. Biotropica 48:433–442

Miatto RC, Batalha MA (2016) Leaf chemistry of woody species in the Brazilian cerrado and seasonal forest: response to soil and taxonomy and effects on decomposition rates. Plant Ecol 217:1467–1479

Miatto RC, Wright IJ, Batalha MA (2016) Relationships between soil nutrient status and nutrient-related leaf traits in Brazilian cerrado and seasonal forest communities. Plant Soil 404:13–33

Minocha R, Minocha SC, Long SL, Shortle WC (1992) Effects of aluminum on DNA synthesis, cellular polyamines, polyamine biosynthetic enzymes and inorganic ions in cell suspension cultures of a woody plant, Catharanthus roseus. Physiol Plant 85:417–424

Motta PEF, Curi N, Franzmeier DP (2002) 2. Relation of Soils and Geomorphic Surfaces in the Brazilian Cerrado. In: The Cerrados of Brazil. Columbia University Press, pp 13–32

Mota NM, Rezende VL, da Silva MG et al (2016) Forces driving the regeneration component of a rupestrian grassland complex along an altitudinal gradient. Brazilian J Botany 39:845–860

Mota GS, Luz GR, Mota NM et al (2018) Changes in species composition, vegetation structure, and life forms along an altitudinal gradient of rupestrian grasslands in southeastern Brazil. Flora 238:32–42

Moulatlet GM, Zuquim G, Figueiredo FOG et al (2017) Using digital soil maps to infer edaphic affinities of plant species in Amazonia: Problems and prospects. Ecol Evol 7:8463–8477

Muggler CC, Buurman P, van Doesburg JDJ (2007) Weathering trends and parent material characteristics of polygenetic oxisols from Minas Gerais, Brazil: I. Mineralogy Geoderma 138:39–48

Murphy BP, Bowman DMJS (2012) What controls the distribution of tropical forest and savanna? Ecol Lett 15:748–758

Myers N, Mittermeier RA, Mittermeier CG et al (2000) Biodiversity hotspots for conservation priorities. Nature 403:853–858

Nascimento DL, Abrahão A, Lambers H et al (2021) Biogeo-morphological evolution of rocky hillslopes driven by roots in campos rupestres. Brazil Geomorphology 395. https://doi.org/10.1016/J.GEOMORPH.2021.107985

Negreiros D, Le Stradic S, Fernandes GW, Rennó HC (2014) CSR analysis of plant functional types in highly diverse tropical grasslands of harsh environments. Plant Ecol 215:379–388

Neri AV, Schaefer CEG, Silva AF et al (2012) The influence of soils on the floristic composition and community structure of an area of Brazilian Cerrado vegetation. Edinb J Bot 69:1–27

Nogueira MA, Bressan ACG, Pinheiro MHO, Habermann G (2019) Aluminum-accumulating Vochysiaceae species growing on a calcareous soil in Brazil. Plant Soil 437:313–326

Ollier C, Pain C (1996) Regolith, soils and landforms. John Wiley, Chichester, UK

Ollier C, Pain C (2000) The Origin of Mountains. Routledge, London, UK

Oliveira-Filho AT (2015) Um sistema de classificação fisionômico-ecológico da vegetação neotropical: segunda aproximação. Fitossociologia No Brasil: Métodos e Estudos De Casos 2:385–411

Oliveira-Filho AT, Ratter JA (1995) A study of the origin of central Brazilian forests by the analysis of plant species distribution patterns. Edinb J Bot 52:141–194

Oliveira RS, Galvão HC, de Campos MCR et al (2015) Mineral nutrition of campos rupestres plant species on contrasting nutrient-impoverished soil types. New Phytol 205:1183–1194

Oliveira VA, Jacomine PKT, Couto EG (2017) Solos do bioma Cerrado. Pedologia: Solos dos Biomas Brasileiros 177–226

Oliveira GC, C, Arruda DM, Fernandes Filho EI, et al (2021a) Soil predictors are crucial for modelling vegetation distribution and its responses to climate change. Sci Total Environ 780

Oliveira RS, Eller CB, de Barros F, V, et al (2021b) Linking plant hydraulics and the fast-slow continuum to understand resilience to drought in tropical ecosystems. New Phytol 230:904–923

Ordoñez JC, van Bodegom PM, Witte J-PM et al (2009) A global study of relationships between leaf traits, climate and soil measures of nutrient fertility. Glob Ecol Biogeogr 18:137–149

Paganeli B, Dexter KG, Batalha MA (2020) Early growth in a congeneric pair of savanna and seasonal forest trees under different nitrogen and phosphorus availability. Theor Exp Plant Physiol 32:19–30

Parrish JT, Ziegler AM, Scotese CR (1982) Rainfall patterns and the distribution of coals and evaporites in the Mesozoic and Cenozoic. Palaeogeogr Palaeoclimatol Palaeoecol 40:67–101

Paula GA, Fischer E, Silveira M et al (2021) Woody species distribution across a savanna-dry forest soil gradient in the Brazilian Cerrado. Braz J Biol 83

Pausas JG, Lamont BB, Paula S et al (2018) Unearthing belowground bud banks in fire-prone ecosystems. New Phytol 217:1435–1448

Pavinato PS, Rocha GC, Cherubin MR, Harris I (2020) Map of total phosphorus content in native soils of Brazil. Scientia

Pekin BK, Boer MM, Wittkuhn RS et al (2012) Plant diversity is linked to nutrient limitation of dominant species in a world biodiversity hotspot. J Veg Sci 23:745–754

Pellizzaro KF, Cordeiro AOO, Alves M et al (2017) "Cerrado" restoration by direct seeding: field establishment and initial growth of 75 trees, shrubs and grass species. Rev Bras Bot 40:681–693

Pereira CG, Almenara DP, Winter CE et al (2012) Underground leaves of Philcoxia trap and digest nematodes. Proc Natl Acad Sci U S A 109:1154–1158

Phillips JD (2019) Evolutionary Pathways in Soil-Geomorphic Systems. Soil Sci 184:1–12. https://doi.org/10.1097/SS.0000000000000246

Pilon NAL, Buisson E, Durigan G (2018) Restoring Brazilian savanna ground layer vegetation by topsoil and hay transfer. Restor Ecol 26:73–81

Pinheiro M, Monteiro R (2010) Contribution to the discussions on the origin of the cerrado biome: Brazilian savanna. Braz J Biol 70:95–102

Poggio L, de Sousa LM, Batjes NH et al (2021) SoilGrids 2.0: producing soil information for the globe with quantified spatial uncertainty. SOIL 7:217–240

Porder S (2019) How Plants Enhance Weathering and How Weathering is Important to Plants. Elements 15:241–246. https://doi.org/10.2138/GSELEMENTS.15.4.241

Porder S, Ramachandran S (2013) The phosphorus concentration of common rocks—a potential driver of ecosystem P status. Plant Soil 367:41–55

Proctor J (1989) Mineral nutrients in tropical forest and savanna ecosystems., 9th edn. Blackwell Scientific Publications, Oxford

Quesada CA, Phillips OL, Schwartz M et al (2012) Basin-wide variations in Amazon forest structure and function are mediated by both soils and climate. Biogeosciences 9:2203–2246. https://doi.org/10.5194/bg-9-2203-2012

Rahman R, Upadhyaya H (2021) Aluminium Toxicity and Its Tolerance in Plant: A Review. J Plant Biol 64:101–121

Rajakaruna N (2018) Lessons on Evolution from the Study of Edaphic Specialization. Bot Rev 84:39–78

Ratter JA, Bridgewater S, Ribeiro JF (2003) Analysis of the floristic composition of the brazilian cerrado vegetation iii: comparison of the woody vegetation of 376 areas. Edinb J Bot 60:57–109

Ratter JA, Ribeiro JF, Bridgewater S (1997) The Brazilian Cerrado Vegetation and Threats to its Biodiversity. Ann Bot 80:223–230

Raven JA, Lambers H, Smith SE, Westoby M (2018) Costs of acquiring phosphorus by vascular land plants: patterns and implications for plant coexistence. New Phytol 217:1420–1427. https://doi.org/10.1111/nph.14967

Reatto A, Correia JR, Spera ST (1998) Solos do bioma Cerrado: aspectos pedológicos. Cerrado: ambiente e flora

Reid WV, Mooney HA, Cropper A, Capistrano D (2005) Ecosystems and human well-being-Synthesis: A report of the Millennium Ecosystem Assessment

Rezende ÉA, Salgado AAR (2011) Mapeamento de unidades de relevo na média Serra do Espinhaço - MG. GEOUSP

Espaço e Tempo 15:45. https://doi.org/10.11606/issn.2179-0892.geousp.2011.74231

Richter DD, Babbar LI (1991) Soil Diversity in the Tropics. In: Begon M, Fitter AH, Macfadyen A (eds) Advances in Ecological Research. Academic Press, pp 315–389

Rizzini CT (1997) Tratado de fitogeografia do Brasil. Âmbito Cultural Edições 2a ed Rio de Janeiro, Brazil

Römheld V, Marschner H (1986) Evidence for a specific uptake system for iron phytosiderophores in roots of grasses. Plant Physiol 80:175–180

Rossatto DR, Franco AC (2017) Expanding our understanding of leaf functional syndromes in savanna systems: the role of plant growth form. Oecologia 183:953–962. https://doi.org/10.1007/s00442-017-3815-6

Rossatto DR, Kolb RM, Franco AC (2015) Leaf anatomy is associated with the type of growth form in Neotropical savanna plants. Botany 93:507–518

Ruggiero PGC, Pivello VR, Sparovek G et al (2006) Relação entre solo, vegetação e topografia em área de cerrado (Parque Estadual de Vassununga, SP): como se expressa em mapeamentos? Acta Bot Brasilica 20:383–394

Saadi A, Bezerra FHR, Costa RD, et al (2005) Neotectônica da Plataforma Brasileira Pp. 211--234. Quaternário do Brasil Ribeirão Preto, Holos, 378p

Salgado AAR, Bueno GT, Diniz AD, Marent BR (2015) Long-Term Geomorphological Evolution of the Brazilian Territory. In: Vieira BC, Salgado AAR, Santos LJC (eds) Landscapes and Landforms of Brazil. Springer, Netherlands, Dordrecht, pp 19–31

Sampaio AB, Vieira DLM, Holl KD et al (2019) Lessons on direct seeding to restore Neotropical savanna. Ecol Eng 138:148–154

Sano EE, Rodrigues AA, Martins ES et al (2019) Cerrado ecoregions: A spatial framework to assess and prioritize Brazilian savanna environmental diversity for conservation. J Environ Manage 232:818–828

Sano EE, Rosa R, Brito JLS, Ferreira LG (2010) Land cover mapping of the tropical savanna region in Brazil. Environ Monit Assess 166:113–124

Sano SM, de Almeida SP, Ribeiro JF (2008) Cerrado: ecologia e flora. Embrapa Informação Tecnológica

Schaefer CEG, Fabris JD, Ker JC (2008) Minerals in the clay fraction of Brazilian Latosols (Oxisols): a review. Clay Miner 43:137–154

Schaefer CEGR, Schaefer CEG, Corrêa GR, et al (2016) The Physical Environment of Rupestrian Grasslands (Campos Rupestres) in Brazil: Geological, Geomorphological and Pedological Characteristics, and Interplays. Ecology and Conservation of Mountaintop grasslands in Brazil 15–53

Schaefer CER (2001) Brazilian latosols and their B horizon microstructure as long-term biotic constructs. Soil Research

Schaetzl RJ, Anderson S (2005) Professor of Medicine Division of Nephrology and Hypertension Sharon Anderson. Genesis and Geomorphology. Cambridge University Press, Soils

Schmidt IB, Eloy L (2020) Fire regime in the Brazilian Savanna: Recent changes, policy and management. Flora 268

SER (2004) The SER International Primer on Ecological Restoration. Society for Ecological Restoration International Science and Policy Working Group, Tucson

Shane MW, Lambers H (2005) Cluster roots: A curiosity in context. Plant Soil 274:101–125

Silva AC (2005) Solos. In: Silva AC, Pedreira LCVSF, Abreu PAA (eds) Serra do Espinhaço Meridional: paisagens e ambientes. O Lutador, Belo Horizonte, p 271

Silva GS, Gavassi MA, Nogueira MA, Habermann G (2018) Aluminum prevents stomatal conductance from responding to vapor pressure deficit in Citrus limonia. Environ Exp Bot 155:662–671

Silva IR, Smyth TJ, Moxley DF et al (2000) Aluminum accumulation at nuclei of cells in the root tip. Fluorescence detection using lumogallion and confocal laser scanning microscopy. Plant Physiol 123:543–552

Silva LCR, Hoffmann WA, Rossatto DR et al (2013) Can savannas become forests? A coupled analysis of nutrient stocks and fire thresholds in central Brazil. Plant Soil 373:829–842. https://doi.org/10.1007/s11104-013-1822-x

Silva LCR, Sternberg L, Haridasan M et al (2008) Expansion of gallery forests into central Brazilian savannas. Glob Chang Biol 14:2108–2118

Silva MB, dos Anjos LHC, Pereira MG et al (2017) Soils in the karst landscape of Bodoquena plateau in cerrado region of Brazil. Catena 154:107–117

Silva MRSS, Pereira de Castro A, Krüger RH, Bustamante M (2019) Soil bacterial communities in the Brazilian Cerrado: response to vegetation type and management. Acta Oecol 100

Silva PS, Nogueira J, Rodrigues JA et al (2021) Putting fire on the map of Brazilian savanna ecoregions. J Environ Manage 296

Silveira FAO, Dayrell RLC, Fiorini CF et al (2020) Diversification in ancient and nutrient-poor neotropical ecosystems: How geological and climatic buffering shaped plant diversity in some of the world's neglected hotspots. Neotropical Diversification: Patterns and Processes. Springer International Publishing, Cham, pp 329–368

Silveira FAO, Negreiros D, Barbosa NPU et al (2016) Ecology and evolution of plant diversity in the endangered campo rupestre: a neglected conservation priority. Plant Soil 403:129–152

Singh S, Tripathi DK, Singh S et al (2017) Toxicity of aluminium on various levels of plant cells and organism: A review. Environ Exp Bot 137:177–193

Soares DM, Nascimento ART, Alves GS, de Oliveira CHE (2021) The importance of palm swamps for carbon storage in a multifunctional landscape in the Brazilian savanna. Regional Environ Change 21:116

Solbrig O (1993) Ecological constraints to savanna land use. The World's Savannas: Economic Driving Forces, Ecological Constraints and Policy Options for Sustainable Land Use Man and the Biosphere Series 12:

Specht RL, Rundel PW (1990) Sclerophylly and Foliar Nutrient Status of Mediterranean-Climate Plant Communities in Southern Australia. Aust J Bot 38:459–474

Standish RJ, Hobbs RJ, Mayfield MM et al (2014) Resilience in ecology: Abstraction, distraction, or where the action is? Biol Conserv 177:43–51

Staver AC, Archibald S, Levin SA (2011) The global extent and determinants of savanna and forest as alternative biome states. Science 334:230–232

Strassburg BBN, Brooks T, Feltran-Barbieri R et al (2017) Moment of truth for the Cerrado hotspot. Nat Ecol Evol 1:99

Suding KN, Lavorel S, Chapin FS et al (2008) Scaling environmental change through the community-level: a

trait-based response-and-effect framework for plants. Glob Chang Biol 14:1125–1140. https://doi.org/10.1111/j.1365-2486.2008.01557.x

Sulpice R, Ishihara H, Schlereth A et al (2014) Low levels of ribosomal RNA partly account for the very high photosynthetic phosphorus-use efficiency of Proteaceae species. Plant Cell Environ 37:1276–1298

Soil Survey Staff (2014) Keys to Soil Taxonomy, 12th edn. USDA-Natural Resources Conservation Service, Washington, DC, USA

Tameirão LBS, Caminha-Paiva D, Negreiros D et al (2021) Role of environmental filtering and functional traits for species coexistence in a harsh tropical montane ecosystem. Biol J Linn Soc Lond 133:546–560

Tardy Y (1993) Pétrologie des latérites et des sols tropicaux. Paris

Tardy Y, Kobilsek B, Paquet H (1991) Mineralogical composition and geographical distribution of African and Brazilian periatlantic laterites. The influence of continental drift and tropical paleoclimates during the past 150 million years and implications for India and Australia. J Afr Earth Sci 12:283–295

Temperton VM, Buchmann N, Buisson E et al (2019) Step back from the forest and step up to the Bonn Challenge: How a broad ecological perspective can promote successful landscape restoration. Restor Ecol. https://doi.org/10.1111/rec.12989

Teodoro GS, Lambers H, Nascimento DL et al (2019) Specialized roots of Velloziaceae weather quartzite rock while mobilizing phosphorus using carboxylates. Funct Ecol 33:762–773

ter Steege H, Pitman NCA, Phillips OL et al (2006) Continental-scale patterns of canopy tree composition and function across Amazonia. Nature 443:444–447

Thomazini LI (1974) Mycorrhiza in plants of the "cerrado." Plant Soil 41:707–711

Tilman D (2001) Functional Diversity Encyclopedia of Biodiversity 3:109–120

Tolrà RP, Poschenrieder C, Luppi B, Barceló J (2005) Aluminium-induced changes in the profiles of both organic acids and phenolic substances underlie Al tolerance in Rumex acetosa L. Environ Exp Bot 54:231–238

Tuomisto H, Ruokolainen K, Yli-Halla M (2003) Dispersal, environment, and floristic variation of western Amazonian forests. Science 299:241–244

Tyler G (2003) Some ecophysiological and historical approaches to species richness and calcicole/calcifuge behaviour — contribution to a debate. Folia Geobot 38:419–428

Vallicrosa H, Sardans J, Maspons J et al (2021) Global maps and factors driving forest foliar elemental composition: the importance of evolutionary history. New Phytol. https://doi.org/10.1111/nph.17771

Valliere JM, Ruscalleda Alvarez J, Cross AT et al (2021) Restoration ecophysiology: an ecophysiological approach to improve restoration strategies and outcomes in severely disturbed landscapes. Restor Ecol. https://doi.org/10.1111/rec.13571

Veenendaal EM, Torello-Raventos M, Feldpausch TR et al (2015) Structural, physiognomic and aboveground biomass variation in savanna-forest transition zones on three continents. How different are co-occurring savanna and forest formations? Biogeosciences 12:2927–2951

Veenendaal EM, Torello-Raventos M, Miranda HS et al (2018) On the relationship between fire regime and vegetation structure in the tropics. New Phytol 218:153–166

Veldman JW, Overbeck GE, Negreiros D et al (2015) Where tree planting and forest expansion are bad for biodiversity and ecosystem services. Bioscience 65:1011–1018

Veneklaas EJ, Lambers H, Bragg J et al (2012) Opportunities for improving phosphorus-use efficiency in crop plants. New Phytol 195:306–320

Viani RAG, Rodrigues RR, Dawson TE et al (2014) Soil pH accounts for differences in species distribution and leaf nutrient concentrations of Brazilian woodland savannah and seasonally dry forest species. Perspect Plant Ecol Evol Syst 16:64–74

Vidal JDD, de Souza AP, Koch I (2019) Impacts of landscape composition, marginality of distribution, soil fertility and climatic stability on the patterns of woody plant endemism in the Cerrado. Glob Ecol Biogeogr 28:904–916

Violle C, Navas ML, Vile D et al (2007) Let the concept of trait be functional! Oikos 116:882–892. https://doi.org/10.1111/j.0030-1299.2007.15559.x

Watanabe T, Broadley MR, Jansen S et al (2007) Evolutionary control of leaf element composition in plants. New Phytol 174:516–523

Werneck FP (2011) The diversification of eastern South American open vegetation biomes: Historical biogeography and perspectives. Quat Sci Rev 30:1630–1648. https://doi.org/10.1016/j.quascirev.2011.03.009

White PJ, Broadley MR (2003) Calcium in plants. Ann Bot 92:487–511

Wilsey B (2018) The Biology of Grasslands. Oxford University Press

Wilson JB (2007) Trait-divergence assembly rules have been demonstrated: Limiting similarity lives! A reply to Grime. J Veg Sci 18:451–452

Wilson MJ (2019) The importance of parent material in soil classification: A review in a historical context. Catena 182

Wright IJ, Cannon K (2001) Relationships between leaf lifespan and structural defences in a low-nutrient, sclerophyll flora. Funct Ecol 15:351–359

Young SL, Barney JN, Kyser GB et al (2008) Functionally similar species confer greater resistance to invasion: implications for grassland restoration. Restor Ecol 17:884–892

Zappi DC, Moro MF, Meagher TR, Nic Lughadha E (2017) Plant Biodiversity Drivers in Brazilian Campos Rupestres: Insights from Phylogenetic Structure. Front Plant Sci 8:2141

Zemunik G, Lambers H, Turner BL et al (2018) High abundance of non-mycorrhizal plant species in severely phosphorus-impoverished Brazilian campos rupestres. Plant Soil 424:255–271

Zinck JA (2013) Geopedology, Elements of geomorphology for soil and geohazard studies. ITC Special Lecture Notes Series ITC (Faculty of Geo-Information Science and Earth Observation), Enschede, The Netherlands