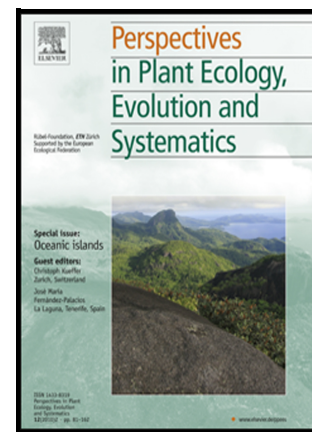


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Placing Brazil's grasslands and savannas on the map of science and conservation

Gerhard Ernst Overbeck¹, Eduardo Vélez-Martin², Luciana da Silva Menezes¹, Madhur Anand³, Santiago Baeza⁴, Marcos B. Carlucci⁵, Michele S. Dechoum⁶, Giselda Durigan⁷, Alessandra Fidelis⁸, Anaclara Guido⁹, Marcelo Freire Moro¹⁰, Cássia Beatriz Rodrigues Munhoz¹¹, Marcelo Reginato¹, Rodrigo Schütz Rodrigues¹, Milena Fermina Rosenfield¹², Alexandre B. Sampaio¹³, Fernando Henrique Barbosa da Silva¹⁴, Fernando A. O. Silveira¹⁵, Ênio Egon Sosinski Jr.¹⁶, Ingmar R. Staude¹⁷, Vicky M. Temperton¹⁸, Caroline Turchetto¹, Joseph W. Veldman¹⁹, Pedro L. Viana²⁰, Daniela C. Zappi²¹, Sandra C. Müller²²

1 Departamento de Botânica, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil

2 Programa de Pós-graduação em Ecologia, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil

3 School of Environmental Sciences, University of Guelph, Guelph, Canada

4 Departamento de Sistemas Ambientales, Facultad de Agronomía, Universidad de la República, Montevideo, Uruguay

5 Departamento de Botânica, Universidade Federal do Paraná, Curitiba, Brazil

6 Departamento de Ecologia e Zoologia, Programa de Pós-graduação em Ecologia, Universidade Federal de Santa Catarina, Florianópolis, Brazil

7 Floresta Estadual de Assis, Instituto de Pesquisas Ambientais, Assis, Brazil

8 Laboratory of Vegetation Ecology, Universidade Estadual Paulista, Rio Claro, Brazil

9 Instituto de Ecología y Ciencias Ambientales, Facultad de Ciencias, Universidad de la República, Montevideo, Uruguay

10 Instituto de Ciências do Mar, Universidade Federal do Ceará, Fortaleza, Brazil

11 Departamento de Botânica, Universidade de Brasília, Brasília, Brazil

12 The Nature Conservancy Brasil, São Paulo, Brazil

13 Centro Nacional de Avaliação da Biodiversidade e de Pesquisa e Conservação do Cerrado, Instituto Chico Mendes de Conservação da Biodiversidade, Brasília, Brazil

- 14 Instituto Nacional de Ciência e Tecnologia em Áreas Úmidas, Universidade Federal de Mato Grosso, Cuiabá, Brazil
- 15 Departamento de Genética, Ecologia e Evolução, Universidade Federal de Minas Gerais, Belo Horizonte, Brazil
- 16 Embrapa Clima Temperado, Pelotas, Brazil
- 17 German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany
- 18 Leuphana-University of Lüneburg, Institute of Ecology, Faculty of Sustainability, Lüneburg, Germany
- 19 Department of Ecology and Conservation Biology, Texas A&M University, College Station, Texas, USA
- 20 Museu Paraense Emílio Goeldi, Belém, Brazil
- 21 Programa de Pós-Graduação em Botânica, Instituto de Ciências Biológicas, Universidade de Brasília, Brazil
- 22 Departamento de Ecologia, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil

Abstract

In Brazil, the country with the highest plant species richness in the world, biodiverse savannas and grasslands – i.e., grassy ecosystems, which occupy 27% of the country – have historically been neglected in conservation and scientific treatments. Reasons for this neglect include misconceptions about the characteristics and dynamics of these ecosystems, as well as inconsistent or regionally restricted terminology that impeded a more adequate communication about Brazil's savannas and grasslands, both within the country and internationally. Toward improved communication and recognition of Brazil's diversity of ecosystems, we present the key drivers that control the main types of grassy ecosystems across Brazil (including in regions of the country where forests dominate). In doing so, we synthesize the main features of each grassy ecosystem in terms of physiognomy and ecological dynamics (e.g., relationships with herbivores and fire). We propose a terminology both for major grassland regions and for regionally relevant vegetation physiognomies. We also discuss terms associated with human land management and restoration of grassy ecosystems. Finally, we suggest key research needs to advance our understanding of the ecology and conservation

values of Brazil's grassy ecosystems. We expect that a common and shared terminology and understanding, as proposed here, will stimulate more integrative research that will be fundamental to developing improved conservation and restoration strategies.

Keywords

Campo; Cerrado; conservation; forest-bias; grassy ecosystem; neotropical

Introduction

Brazil is the country with the highest richness of plant species in the world (Ulloa Ulloa et al., 2017; BFG, 2022a). Both scientists and the public tend to credit this diversity to the humid tropical forests of the Amazon region and the Atlantic coast. Indeed, the Amazon Basin supports 10,000 tree species (ter Steege et al., 2019), and in the Atlantic Forest 140 tree species have been documented in 0.1 ha (Martini et al., 2007). But trees and forests are only one aspect of Brazil's immense biodiversity. Far less recognized is that one third of the country supports ecosystems that are not humid tropical forests, including the xeric forest-woodlands of the Caatinga (Moro et al., 2016) and extensive grasslands and savannas (Overbeck et al., 2015). In this paper, we focus on Brazil's underappreciated savannas and grasslands, which we collectively refer to as 'grassy ecosystems', because they are dominated by grasses and grass-like plants (Bond and Parr 2010).

Grassy ecosystems occur in all Brazilian biomes as defined by the Brazilian Institute of Geography and Statistics (IBGE 2019; see Box 1 for Brazil's grassy ecosystems in a global biome classification). Brazil's grassy ecosystems harbor a wealth of shade-intolerant plants, typically (but not always) with high dominance of perennial grasses and a relatively continuous layer of herbaceous plants, including many forbs and subshrubs (see also Veldman et al., 2015; Bond, 2019; Buisson et al., 2019). The characteristic species of grassy ecosystems evolved under, and are maintained by, frequent fires (e.g., Simon et al., 2009), megafaunal herbivores (e.g., Dantas and Pausas, 2020; Lopes et al., 2020), edaphic factors (e.g., Silveira et al., 2016) and climatic constraints (e.g., Behling et al., 2004), or a combination of these factors that limit tree growth. While we have a growing appreciation for the complex roles of all these factors that maintain grassy ecosystems, their relative importance in Brazil remains still poorly understood, with negative consequences for conservation and restoration.

Grassy ecosystems and their herbaceous plants are critically important to Brazil's biodiversity. In the Cerrado, the most biodiverse savanna of the world (Mendonça et al., 2008), grasses, sedges, forbs, and subshrubs, not trees and shrubs, account for the majority of plant diversity. Similarly, about 60% of the plant species of the Brazilian Pampa, which harbors 3,500 species (Andrade et al., 2018), occurs in grassy ecosystems (Boldrini et al., 2015). Like many

savannas and grasslands globally, local-scale plant diversity can be very high: da Silva Menezes and collaborators (2018) found 56 species in one square meter of Pampa, and densities of 30 to 35 plant species per square meter are common in grassy ecosystems across Southern Brazil. High species turnover (e.g., beta diversity) is another key element of grassy ecosystems: plant community composition can change dramatically along environmental gradients (e.g., Bueno et al., 2018; Andrino et al., 2020; Devecchi et al., 2020; de Souza et al. 2021; Amaral et al., 2022). Lineage turnover along geological time also seems to be high in some grassy ecosystems of Brazil, where some plant clades show some of the highest diversification rates in the world (Vasconcelos et al., 2020). Despite this growing evidence of the high biodiversity of Brazil's grassy ecosystems, to date there exists no comprehensive synthesis describing the savannas and grasslands of Brazil. We believe that such a knowledge gap is hindering national and international efforts to efficiently conserve and restore Brazil's grassy ecosystems.

Box 1: Brazil's grassy ecosystems

Definition of grassy ecosystems

Grassy ecosystems are composed of shade-intolerant plants, usually with high dominance of herbaceous (i.e., non-woody) plants, especially perennial grasses. These plants evolved with, and are maintained by, frequent fires, megafaunal herbivores, edaphic and climatic constraints, or a combination of these factors.

Distribution of grassy ecosystems in Brazil

Grassy ecosystems are found in all Brazilian biomes as defined by IBGE (2019). They are the dominant vegetation type in the Cerrado, Pampa and Pantanal, but also occur as enclaves in the Amazon, Atlantic Forest, and in the Caatinga. Overall, grassy ecosystems cover approximately 27% of Brazil's terrestrial surface (see Fig. 2).

Brazil's grassy ecosystems in global biome classifications

In the most widely used classification of Earth's biomes (Olson et al., 2001), many of Brazil's grassy ecosystems are part of the 'Tropical and Subtropical Grasslands, Savannas and Shrublands' biome, and, in the case of the Pantanal, of the 'Flooded Grasslands and Savannas' biome. Many other grassy ecosystems of Brazil do not appear on the global biome map at all: savannas and *campinas* in the Amazon are part of the 'Tropical Moist Broadleaf Forests' biome, and several savannas, *campos de altitude*, and *campo rupestre* in southeastern Brazil are part of the 'Tropical

Moist Broadleaf Forests' biome (in the Atlantic Forest) or the 'Deserts and Xeric Shrublands' biome (in the Caatinga).
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Despite their major importance in terms of biodiversity and ecosystem services (Bardgett et al., 2021), worldwide, savannas and grasslands have high conservation risks due to high levels of land conversion and low levels of protection (Hoekstra et al., 2005): In Brazil, where grassy ecosystems receive little public attention and are undervalued by conservation initiatives, anthropogenic impacts in grassy ecosystems, especially conversion to cropland and tree plantations, continues to be very high (Baeza and Paruelo, 2020; Sano et al., 2020; Souza et al., 2020). Until recently, the main legislation on nature conservation in Brazil was the Forest Code, introduced in 1934 and revised in 1965. In 2012, the Forest Code was replaced by the Law on the Protection of Native Vegetation; unfortunately, although the term 'native vegetation' is more inclusive, this law is widely referred to as 'The New Forest Code', reinforcing the notion that forests are more relevant than other vegetation types to the provisioning of ecosystem services in Brazil. Additionally, some parts of the new law continue to refer exclusively to forest. It is also notable, but not surprising, that Pampa, Cerrado and Caatinga are not considered national heritage in the Brazilian Constitution. Evidence is mounting that the forest bias in Brazilian laws and public perception results in poorly conceived conservation policies that harm biodiversity, compromise ecosystem services, and threaten human livelihoods (Silveira et al., 2020; Pimenta and Fonseca, 2021). The tension caused by valuing of forests, but not grasslands, poses a particular threat to conservation in regions with natural forest-grassland mosaics (Henderson et al., 2016).

Consideration of grassy ecosystems in Brazil's biodiversity strategy is further hindered by the lack of a synthetic understanding of the ecological characteristics of these systems, their uniqueness, and their similarities. With few exceptions, research is poorly integrated across ecosystems and has often focused on specific features and themes, rather than unifying features and ecological parallels among systems. For example, in the Cerrado, until recently, research focused on tree community dynamics; in the Pampa research focuses on use as grazing land; in Pantanal the focus is on flooding regime. Further, studies integrating research from Brazilian grassy ecosystems with those on other continents are scarce (but see Overbeck

et al. (2018) for *Campos Sulinos*, Silveira et al. (2016), Mucina (2018), Zappi et al. (2019) for *campo rupestre*, and Dantas and Pausas (2013), Stevens et al. (2017) for Cerrado woody species). Finally, local terminologies, many of which are inconsistent with internationally accepted ecological concepts, hamper the development of an integrated research agenda and a better general understanding of grassy ecosystems. A common language to study grassy ecosystems in Brazil is key to their scientific study and conservation within the country, and to their recognition by scientists globally.

Based on knowledge gleaned from a literature review and available geographic information, we here present a synthesis of the general characteristics of the grassy ecosystems in Brazil. We sought to summarize the similarities and particularities, and to also identify the main drivers that maintain biodiversity and determine vegetation structure. Further, we discuss the terminology currently used and propose general definitions to aid communication. Our synthesis is a critical first step to map grassy ecosystems on a broad spatial scale and to introduce a common terminology among scientists, conservation specialists and restoration practitioners. We hope that this paper will pave the way towards further efforts to fill knowledge gaps and develop a more accurate classification of grassy ecosystems in Brazil, ideally based on field data. This undertaking is especially important at the onset of the United Nations Decade on Ecosystem Restoration (2021-2030): The identification of reference ecosystems has been deemed a priority but grasslands still are not properly considered (Vetter 2020). Additionally, sound knowledge on grassy ecosystems, often prone to degradation due to inadequate management, is needed to better integrate efforts to tackle with the biodiversity and climate crises (Pörtner et al., 2021). With this synthesis, we aim to develop a common and consistent language for integrated research and better communications about Brazil's grassy ecosystems, while also improving recognition of the ecology, evolution, and conservation of these ecosystems.

Beyond climate: multiple drivers define distribution of grassy ecosystems

Classical models of climatic zones assume that under a given climate one main vegetation type exists. However, recent work suggests that the distribution of grassy

ecosystems is only partially governed by current climate (e.g., Bond, 2019; Pausas and Bond, 2019; Dantas and Pausas, 2020). Past or present fire, grazing, waterlogging and edaphic constraints have also been underlined as critical factors for the existence of grassy ecosystems (e.g., Veldman et al., 2015; Bond, 2019). In recognition that some climatic regimes allow for the existence of forest-grassland mosaics, Whittaker (1975) defined an 'Ecosystem Uncertainty Climate Zone' that spans over large parts of the globe (Bond, 2005). Bond (2005) argues that ecosystems in these regions are 'consumer-controlled': herbivores, fire or both are the driving forces that prevent – over evolutionary relevant periods – these systems to reach their (theoretical) climate-defined state (see also Vera, 2000; Hoffmann et al., 2012; Pausas and Bond 2019).

When plotting grassy ecosystems from different regions in Brazil on the classical climate envelope map of major ecosystem types, many of them fall out of the expected distribution and even out of the 'Ecosystem Uncertainty Climate Zone' originally proposed by Whittaker (1975, Fig. 1). Natural grassy ecosystems in Brazil occur even under very high levels of annual precipitation in the Atlantic Forest and in the Amazon basin, suggesting that drivers beyond climate are required to explain their distribution. This finding is in line with the idea of alternative states, a perspective that can integrate climate drivers with processes mediated by fire and herbivory, rather than consider these processes as external factors that 'reset' succession (see Pausas and Bond, 2019). In many transitional regions, forest and grassy mosaics are thus considered alternative stable states (*sensu* Beisner et al., 2003) driven by a combination of disturbances and climatic and edaphic factors, also modulated by historical processes and human actions (Simon et al., 2009; Staver et al., 2011a; Hirota et al., 2011; Innes et al., 2013; Henderson et al., 2016). In light of the alternative stable state framework, the existence of large areas of savannas in the Amazon (de Carvalho and Mustin, 2017; Devecchi et al., 2020) can be explained based on ecological theory and allows for an appropriate consideration of them in conservation.

(Figure 1 here)

In many, if not most grassy ecosystems, it is difficult to disentangle the relative roles of different drivers that shape them or that are responsible for their development and maintenance (Fuhlendorf and Engle, 2004). For instance, climate influences productivity and phenological patterns of grasslands, which in turn have effects on the role of disturbance in the system (see e.g., Milchunas et al., 1988; Lezama et al., 2014). At the landscape scale, geomorphology, soil features and even relatively small topographic differences can be decisive in defining vegetation types. Consequently, and mosaics of different physiognomies, including forest patches, can be found throughout Brazil's grassy ecosystems. Thus, complexity is an inherent feature of grassy ecosystems, and this is probably a major reason for their high biodiversity.

Brazil's major grassy ecosystems

In the following, we present Brazil's major grassy ecosystem types (Fig. 2 and 3, Tab. 1). We classify them based on their principal physiognomic features based on the literature, and not based on vegetation composition data which still presents major data gaps for many regions (Menezes et al., unpublished results). Lists of typical plant families and species in the different ecosystems can be found in Suppl. Material 3.

(Figure 2 here)

(Figure 3 here)

(Table 1 here)

Savannas

In Brazil, savannas – grassy ecosystems under seasonal tropical climate with an upper layer of scattered shrubs and trees in varying density – occur across a broad range of climatic conditions, with annual average temperature from 18 to 28°C and rainfall from 800 to above 3,000 mm, but usually with a long (i.e., six months in the core region) dry season (Oliveira-Filho and Ratter, 2002). Savannas are the dominant vegetation within the Cerrado, but also occur in the Amazon, Pantanal, Atlantic Forest and Caatinga. Within their climatic range, savannas predominantly occupy nutrient-poor soils (Furley and Ratter, 1988), mainly oxisols or quartz

sand soils, while seasonal (tropical dry) forests tend to occur on richer limestone soils (Oliveira-Filho and Ratter, 2002; Bueno et al., 2018). Close to watercourses, where moisture levels in the soil remain higher during the dry season or are permanently waterlogged, savannas are either replaced by gallery forests or grassy wetlands. Plant species in the savanna are mostly shade-intolerant perennials, with robust, often woody, underground organs, which permit vigorous resprouting and flowering after fire (Pilon et al., 2021). Savannas exhibit high levels of endemism (>40% for the Cerrado, Myers et al., 2000; BFG, 2022b) and have high species richness in the herbaceous layer, with dominance of C₄ grasses. Shrubs and trees either possess sclerophyllous leaves that can maintain constant minimum leaf water potential across the seasons and/or are deciduous during the dry season.

Interacting with climate and soil, fire is a key factor shaping mosaic savanna landscapes, in which savanna and forest ecosystems may co-occur, depending on the frequency and intensity of fires (Staver et al., 2011b; Abreu et al., 2017; Bueno et al., 2018). By limiting tree growth and preventing forest expansion, fire defines plant community composition and structure (Ribeiro et al., 2019). In contrast to African savannas, famous for their diverse large mammals, large native grazing and browsing animals are practically inexistent in South American savannas, since most megafauna went extinct 50.000 to 12.000 years ago (Hansen and Galetti, 2009).

Savannas in the Cerrado

Brazil's savannas are mostly concentrated in the plateaus of Central Brazil in the core of the Cerrado (Fig. 3b), under Köppen's Aw climate (Tropical savanna climate according to Peel et al., 2007, or tropical climate with dry winters according to Alvares et al., 2013), where grassy ecosystems originally covered 158 million ha. In the Cerrado, mosaics of different vegetation types with varying degrees of woody species cover occur (see Table 2 and Fig. 4), ranging from open grassland without trees ('*campo limpo*', Fig. 4a), open savannas ('*campo sujo*' or '*campo cerrado*', Fig. 4b) and 'true' savanna ('*cerrado sensu stricto*'), to Cerradão, a closed woodland no longer considered a savanna, as the flammable grass layer has been suppressed by tree shade (Ribeiro and Walter, 2008), and forests, mostly along water courses. In the Cerrado,

grasslands are often found where the soils are too shallow or periodically waterlogged, which hinders tree establishment and growth (Leite et al., 2018), or as a result of very high (annual) fire frequency (Guidoni-Martins et al., 2021). Additional distinct savanna physiognomies are the *campos de murundu*, typical of floodplains of Central Brazil, where countless termite mounds, often covered by woody vegetation, are distributed over a grassy matrix (Oliveira-Filho, 1992; Marimon et al. 2012) and the *veredas* (Fig. 4c), grassy wetlands that occur in permanently or seasonally waterlogged sites where the herbaceous stratum has a peculiar hydrophilic flora (Moreira et al., 2015; Silva et al., 2017), often, but not necessarily, including palms such as *Mauritia flexuosa* L.f. and *Mauritiella armata* (Mart.) Burret.

The Cerrado, one of the world's biodiversity hotspots (Myers et al., 2000), is the most diverse savanna of the world (Colli et al., 2020; see also Murphy et al., 2016). Its diverse flora presents fire-adapted traits whose evolution coincided with the expansion of C₄ grasses worldwide in the late Miocene and early Pliocene (Simon et al., 2009). Based on woody species composition, the Cerrado has been divided into five distinct floristic provinces, with the Amazonian savannas (see below) as an additional province with many shared species (Bridgewater et al., 2004); the most frequent tree species are shared among these regions. In contrast, Amaral et al. (2017) identified nine phytogeographic regions associated to two core regions, based on species distribution modeling of more than 5,000 plant herbs and shrubs: while also separating northern and southern Cerrado, their results differ considerably from studies that considered the woody component (Bridgewater et al. 2004; Francoso et al. 2020), emphasizing the need to use herbaceous plants, not just trees, to classify savanna ecosystems.

Savannas in the Amazon

The Amazon region holds some 12.9 million ha of grassy ecosystems (de Carvalho and Mustin, 2017). Their drought-resistant, fire-adapted vegetation with scattered, tortuous trees and shrubs surrounded by a more or less continuous herbaceous layer dominated by grasses and sedges (Pires and Prance, 1985) has a similar appearance to the Cerrado savannas, but they occur under Af and Am climate types (Alvares et al., 2013). As in the Cerrado, Fabaceae constitute an important component of forb diversity across the Amazon savannas, but

Asteraceae, a large species-rich family in central Brazil, is poorly represented in these Amazonian savannas (Flores and Rodrigues, 2010; Rocha and Costa Neto, 2019; Siniscalchi et al., 2021). The Amazonian savannas usually occur on sandy or stony soil, on slightly elevated areas such as ridge tops and small arenitic plateaus, i.e., on sites where soil conditions and exposure amplify the water deficits of the dry season (Borghetti et al., 2020).

Three major stretches of Amazon savannas correspond to the Rio Branco savannas, the Sipaliwini–Parú savannas and the Amapá savannas (de Carvalho and Mustin, 2017). The first occur in northern Roraima, which is the largest area of Amazonian savannas, with 43,000 km² (Barbosa et al., 2007). Savannas in this region are known as *lavrados* (Miranda and Absy, 2000) and extend to adjacent Guyana; together they are termed Rio Branco-Rupununi savannas (Borghetti et al., 2020). Rio Branco savannas are under increasing pressure from mechanized agriculture (soybean, irrigated rice) and invasive tree species (Barbosa et al., 2007; Barbosa and Campos, 2011, Souza et al., 2018). In Pará state, we find the Sipaliwini–Parú savannas, which cover 15,453 km² in Brazil and Suriname (van Donselaar, 1968; de Carvalho and Mustin, 2017). Also known as savannas of the Tiryíós, these areas are protected indigenous lands unlike other largely unprotected Amazonian savanna sites (Rodrigues et al., 2006; de Carvalho and Mustin, 2017). The savannas of Amapá occur in the eastern region of the state in two blocks along a north/south oriented strip of 13,027 km² (de Carvalho and Mustin, 2017; Amaral et al., 2019; Borghetti et al., 2020). Similar to the Rio Branco savannas, these physiognomies are severely threatened by the expansion of soybean (Hilário et al., 2017).

Other Amazonian savanna patches are found on Marajó Island (Pará State), where they are known as *campos tesos* and have a long history of water buffalo and cattle grazing (Lisboa, 2012); recently, these savannas are subject to increasing conversion to rice plantations (Meirelles Filho, 2017). Finally, savannas also occur in eastern Amazonia, from the Santarém/Monte Alegre region to Oriximiná and Óbidos (Egler, 1960; Amaral et al., 2019; Devecchi et al., 2020) and in southern Amazonia, in Mato Grosso and Rondônia, where the Campos Amazônicos National Park has been established.

Savannas in the Caatinga

The Caatinga is the driest of Brazil's phytogeographic domains, with large areas receiving less than 800 mm of rainfall per year, concentrated in a few months (Moro et al., 2016). It is mostly covered by typical *caatinga* vegetation, a deciduous forest or shrubland whose herbaceous layer is only present during the short rainy season. While we recognize that the *caatinga* forests and woodlands can support high richness of annual herbs, we do not consider *caatinga* to be grassy ecosystems, due to shrub and tree dominance and discontinuous herbaceous cover. In some regions, however, the Caatinga does harbor small savanna areas (Fig. 3c) that are probably remnants of larger savannas that formed during Pleistocene climatic fluctuations (Bueno et al., 2017; Costa et al., 2018) and that persist today due to frequent fire and edaphic factors (de Castro Oliveira et al., 2019). While many woody Caatinga species can colonize these areas, in large savanna patches on highlands like the Araripe Plateau or the Chapada Diamantina, the flora is mostly composed by species that also occur in savannas of the Cerrado; these sites have greater similarity with the Cerrado flora of central Brazil than with adjacent Caatinga woodlands (Nepomuceno et al., 2021).

In the coastal zone of the Caatinga, patches of coastal savannas occur (Moro et al. 2011, 2015, Fig. 2). These coastal areas receive slightly more annual precipitation and are more strongly seasonal than the core areas of the Caatinga. Soils are different as well, with most savannas occurring on sedimentary terrains with latosols. Consequently, the climatic and edaphic conditions of these coastal savannas are more similar to the Cerrado than most areas of the Caatinga. This may explain the large number of Cerrado species in coastal zones of the Caatinga, which form typical savanna, while in other areas we find coastal grasslands (see below) or coastal forests (Moro et al., 2015).

Hyperseasonal savannas and grasslands in the Pantanal

The Pantanal is a Quaternary sedimentary basin of 150,000 km², formed by a mosaic of fluvial megafans and plains (Assine, 2010; Assine et al., 2015). Climatic conditions are tropical, with dry winter and rainfall ranging from 1,000 to 1,400 mm/year, concentrated during the summer (Köppen's Aw climate). In the Pantanal, seasonal flood pulses determine ecological patterns and processes (Junk et al., 2015) and lead to three main types of habitat defined by

the interaction of topography and vegetation on a large scale: (1) Flood-free elevations with woody vegetation, including dry forests; (2) Seasonally flooded plains with grasslands and savannas (Fig. 3d), with flooding periods ranging from a few weeks to six months (Barbosa da Silva et al., 2020); and (3) depressions with permanent water bodies dominated by macrophytes (Pott et al., 2011). Grasslands and savannas cover approximately 31% of the Pantanal's area (Silva et al., 2000). They are amphibious habitats ('wet-dry-savannas') with an alternation between an aquatic and a terrestrial phase (Nunes da Cunha and Junk, 2015) with a dominant grassy stratum, woody plants in variable abundance, and occupied by aquatic macrophytes during the flooding period (Schessl, 1999; Barbosa da Silva et al., 2020). Different herbaceous communities related to specific flooding regimes have been identified for the Pantanal (Allem and Valls, 1987; Schessl, 1999, Pott et al., 2011; Barbosa da Silva et al., 2020). As the Pantanal is recent in geological terms, it is poor in endemic species (Pott et al., 2011). Most grassy ecosystems in the Pantanal are under cattle grazing throughout the year, with fire serving as a management tool to facilitate resprouting of forage grasses after the dry season. Thus, in the Pantanal, grazing, fire, and the flooding regime interact to maintain the typical features of the vegetation; after long dry periods, as in 2020, wildfires can take catastrophic dimensions (Pivello et al., 2021). As the flooding regime impedes intensive agriculture, the Pantanal region is less affected by land use change (Fig. 5), even though natural grasslands are increasingly replaced by non-native pasture.

Amazonian white sand grasslands and shrublands

In the Brazilian Amazon, names such as *campina*, *campinarana*, Amazonian *caatinga* or white-sand savannas have been traditionally associated with different vegetation physiognomies on sandy soils (Ducke and Black, 1953; Anderson, 1981; Pires and Prance, 1985; Huber, 1988). These areas are collectively referred as to white sand ecosystems (Adeney et al., 2016; Capurucho et al., 2020) and encompass open, savanna-like physiognomies (*campinas*, i.e., grasslands and shrublands, Fig. 3a) that generally form an intricate gradient to the closer, thin-trunked forests (*campinaranas*, i.e., white sand forests). Amazonian white sand grasslands and shrublands cover an area of 51,200 km² in Brazil and generally occur at sites with the

longest water-saturation (Bongers et al., 1985; Adeney et al., 2016). The region of the upper Rio Negro, including areas south of its largest tributary, the Branco River, has been long recognized for the widespread occurrence of white sand ecosystems (Ducke and Black, 1953). However, small to large patches of these ecosystems are found throughout the Brazilian Amazon, mostly occurring in areas with more than 2,000 mm of rainfall per year (Adeney et al., 2016). Because the white sand soils are porous and have a low capacity to retain water, plants may be subjected to severe low water availability during the dry seasons (Anderson, 1981). The extremely nutrient-poor white-sand soils are characterized by low organic matter content and high acidity (Damasco et al., 2012; Adeney et al., 2016). During the rainy season, the white-sand ecosystems in the central Amazon generally have an impeded drainage mostly due to podzolization, leading to the long-term soil saturation and flooding (Junk et al., 2011; Adeney et al., 2016). Along the Rio Negro basin, where white-sand soils possibly originated from megafan sedimentary processes or aeolic palaeodune deposits, poor drainage of sandy soils and water infiltration of periodically flooded river margins led to flooding of large plains (Zular et al., 2019; Rossetti et al., 2019; Capurucho et al., 2020). In addition to hydrologic and edaphic constraints, occasional fires shape the occurrence of distinct sclerophyllous physiognomies of white sand ecosystems at local scales (Anderson, 1981; Adeney et al., 2016). For instance, in the floodplains of the middle Rio Negro such open, herbaceous physiognomies expand where wildfires recurrently entered into forests (Flores and Holmgren, 2021).

While dense grasslands covered by a low number of tall species of Cyperaceae and Poaceae occur at some sites, the occurrence of scattered trees and shrubs distributed over a grassy or non-gramineous matrix of herbaceous genera of Xyridaceae, Rapateaceae, Eriocaulaceae, ferns, and lichens (Anderson, 1981; Huber, 2006) is common. White sand shrublands and grasslands usually have a lower species richness in comparison to adjacent tropical forests and the Amazonian savannas, but these ecosystems nonetheless harbor many endemic species (Anderson, 1981; Vicentini, 2004; Costa et al., 2019). However, there are still many gaps in the characterization of vegetation and flora of these ecosystems since they encompass remote and heterogeneous species assemblages under a wide range of physical conditions (Vicentini, 2004; Perigolo et al., 2017).

Campo rupestre

Campo rupestre (Fig. 3f) occurs in less than 0.8% of the Brazilian continental area, yet it is home to more than 5,000 plant species (nearly 15% of Brazil's flora). *Campo rupestre* has the highest endemism levels in Brazil (40%; BFG, 2015), extremely high species turnover among areas (Neves et al., 2018; Zappi et al., 2019; Andrino et al., 2020) and high diversification rates (Vasconcelos et al., 2020). Concentrated in the Cerrado (but also present in the *Caatinga* and other regions, Fig. 2), *campo rupestre sensu lato* is defined as a montane (above 800 m), megadiverse, grassy–shrubby, fire-prone vegetation mosaic on nutrient-poor, usually sandy or stony soils associated with quartzite, sandstone, limestone, or ferruginous outcrops, sometimes including grasslands exposed to seasonal waterlogging (Silveira et al., 2016). Geographically, *campo rupestre* is mostly associated with the Espinhaço Range in Minas Gerais and Bahia and disjunct mountain ranges in Goiás (Giulietti et al., 1997), but also occurs on small, isolated mountains in 13 other Brazilian states (Miola et al. 2021), where the elevation often is lower than 800 m but exposed rocks create the ideal condition for their establishment (see e.g. Pires and Prance (1985) and Viana et al. (2016) for *campo rupestre* in the Amazon). Miola et al. (2021) have mapped the geographic distribution of *campo rupestre* and have found its occurrence across all Brazilian biomes, except the Pampa. However, even for sites in the Pampa with rock outcrops, as in parts of the Serra do Sudeste, the term *campo rupestre* has been used (Ab'Saber, 2003).

The *campo rupestre* areas in its core region – Minas Gerais, Bahia, Goiás and Tocantins states – are complex in terms of physiognomy, and the delimitation of different vegetation types is not easy, since they may also contain patches of savanna, gallery forests and hilltop forests (Zappi et al., 2017). *Campo rupestre sensu stricto* are the often disjunct, grassy–shrubby patches found in mosaic with other vegetation types adjacent or on rock outcrops, usually at elevations above 800 m a.s.l., and also includes vegetation types associated with banded ironstone formation, such as itabirites and cuirasses, locally known as *canga* (Jacobi et al., 2007; Viana et al., 2016). Often, ericoid shrubs and treelets are embedded in a matrix of more continuous grasslands dominated by grasses, sedges and graminoid Xyridaceae, Eriocaulaceae,

Cyperaceae and Rapateaceae monocots; these systems thus are not always ‘grassy’ in the strict sense. Exposed rock outcrops within the *campo rupestre* are dominated by species of Velloziaceae, Bromeliaceae, Cactaceae and Orchidaceae. The *campo rupestre* bears similarities with the *campos de altitude* (see below) in terms of physiognomy but occurs on different geological substrate and generally under a more seasonal climate than *campos de altitude*.

A multitude of factors are responsible for the diverse physiognomy of *campo rupestre* and their extremely high biodiversity (Vasconcelos et al., 2020). Mountain tops with shallow and nutrient-poor substrate, high proportion of rock outcrops and thus low water soil water holding capacity, paired with high insolation and exposure are strong filters that favor genera and species adapted to these conditions (*Vellozia*, *Barbacenia*, *Paepalanthus*). Soils are extremely impoverished, as they developed from ancient and nutrient-poor rocks under extreme weathering (Silveira et al., 2016). While they are considered resilient to fire (Le Stradic et al., 2018), the role of fire in evolution, development, and maintenance of *campo rupestre* is unclear. *Campo rupestre* is physiognomically and functionally similar to the fynbos in the Cape Floristic Region and the kwongan in Southwestern Australia Floristic Regions, but there are analogies also to other old and nutrient-poor landscapes (Mucina, 2018).

The vegetation on the summits of the iconic tabular quartzite mountains in the Guyana region – also known as *tepui* – is also treated here within the *campo rupestre sensu lato* concept, although considered a biogeographic province in the Guyana region – the Pantepui (Huber 1994; Rull et al. 2019a). While concentrated in Venezuela, some important tepuis are found in Brazil, at the northern border of the states of Roraima and Amazonas, including Brazil’s and Pantepui’s highest elevation, the Pico da Neblina, reaching 2994 m. In general, montane shrublands, grasslands, and open saxicolous plant communities dominate on tepuis, but broadleaved grasslands on peat, sclerophyllous woodlands, and montane forests also compose the unique landscape of the tepuis. Some characteristic plant families of the Pantepui are the herbaceous Rapateaceae, Xyridaceae, and Sarraceniaceae (with their endemic genus *Heliophora*), and the woody Bonnetiaceae (Berry and Riina, 2005; Huber, 2006). Taxonomic similarities with the flora of *campo rupestre* of the Espinhaço range (Giulietti and Pirani, 1988) suggest a past connection between these areas, exemplified by disjunctions in the distribution

of some taxa, such as Rapateaceae (*Cephalostemon*), Eriocaulaceae (*Paepalanthus*), Xyridaceae (*Xyris*, *Abolboda*), Poaceae (*Apochloa*, *Dichantherium*), and Melastomataceae (*Marcetia*, *Microlicia*). The tepuis are also known for housing representatives of ancestral lineages of vascular plants of South America (Barbosa-Silva et al. 2020).

Campos de altitude

The term *campos de altitude* has been used to describe grassy-shrubby, island-like patches in forest-grassland mosaics found in the granitic-gneissic mountains of the Atlantic Forest domain along Brazil's eastern coastline, such as Serra da Bocaina (Fig. 3g), Serra do Caparaó, Serra Geral, Serra da Mantiqueira, Serra do Mar and Serra dos Órgãos, under oceanic climate with possibility of winter frosts. Authors differ in their definition of *campos de altitude* (see discussion in Vasconcelos, 2011). Safford (1999), suggesting the term 'Brazilian Páramo', uses the most restrictive concept with a lower limit of 1,800 m a.s.l. (but see e.g. Roderjan et al. (2002) and Garcia and Pirani (2005) for *campos de altitude* further to the south). Common use of the term usually does not include the highland grasslands on the Southern Brazilian plateau (*Campos de Cima da Serra*, part of the *Campos Sulinos*; Table 1) that also are at lower elevation (but see Longhi-Wagner et al., 2012). We suggest – following the widespread understanding of the term in botanical and ecological studies – that the grassy ecosystems in the mountains of the Atlantic Forest be called *Campos de altitude*, without including the grasslands in the southern part of Brazil that occur under contrasting climatic and edaphic conditions and differ in terms of physiognomy (see below).

Campos de altitude are thought to be relicts from a former much larger geographic distribution, currently isolated and shrinking due to the expansion of the surrounding cloud forest (Safford, 2007; Fiaschi and Pirani, 2009). The remaining grassland islands are often located on mountaintops, on shallow soils, where grasses, sedges, forbs, and rare dwarf trees share the space with rocky outcrops. However, there are *campos de altitude* also on deep soils in the absence of rocks outcrops (Modenesi et al., 1982; Garcia and Pirani 2005). While sharing some similarities in terms of physiognomy, the *campos de altitude* are distinct from *campo rupestre* in terms of floristic composition and biogeographic affinities: the former have more

floristic links with the Patagonian and Andean regions and with the highland grasslands in southern Brazil (Alves and Kolbek, 2010; Vasconcelos, 2011). Roughly two thirds of the genera found in these highland grasslands are of tropical ancestry, while the remaining coming are from temperate zones or other widespread origins (Safford, 2007). These grassland islands harbor a flora with extremely high endemism, corresponding to 20% of endemism of the Atlantic Forest domain (Ribeiro and Freitas, 2010).

(Table 2 here)

(Figure 4 here)

Campos Sulinos: The South Brazilian grasslands

The southern part of Brazil, including the states of Paraná, Santa Catarina and Rio Grande do Sul, is distinct from most of Brazil in terms of climate as it is not subject to rainfall seasonality, but to temperature seasonality (Köppen's Cfa and Cfb, humid subtropical without dry season and hot or warm summers, depending on elevation; Alvares et al., 2013). Landscapes are marked by the presence of two distinct main vegetation types: forests, either seasonal forest or, in higher and thus cooler regions, mixed broadleaf forest dominated by the conifer *Araucaria angustifolia* (Bertol.) Kuntze (Araucaria Forest), and grasslands without the tree component typical of savannas. The grasslands in the three southern states are collectively referred to as '*Campos Sulinos*' ('South Brazilian grasslands'; see e.g., Overbeck et al., 2007, Table 1), and can be divided into three major regions: The *Pampa* grasslands in the South, the South Brazilian highland grasslands (with different regional denominations in Portuguese) in northern Rio Grande do Sul, Santa Catarina and Paraná states, and the '*Campos Gerais*' in Paraná which, in the northern part, in the Tibagi region, are in a zone of transition with savannas of the Cerrado. Plant community data support the division of the (lowland) Pampa and the highland grasslands (Andrade et al., 2019), corresponding to the biogeographic division of the region into Pampean and Paraná provinces (Cabrera and Willink, 1980); studies that evaluate the similarities of these two regions to the Campos Gerais are still missing. The

lowland and highland divisions are also supported by phylogenetic analyses of plant genera that have diversified in this region (Fregonezi et al., 2013; Acosta et al., 2016; Barros et al., 2020).

A characteristic of South Brazilian grasslands is the coexistence of C₃ and C₄ grasses. The tropical C₄ grasses dominate in terms of cover, but especially in winter and early spring, the C₃ grass component is highly relevant for domestic cattle. Grasslands in the region developed under the presence of large grazing animals and fire. Fossil records of large grazing animals are abundant since the Pliocene and until the megafauna extinctions about 10,000 years ago (Lopes et al. 2020). Currently, grasslands are almost entirely under grazing from domestic herbivores (mostly cattle and sheep), which leads to the selection of plant species adapted to grazing (Cayssials and Rodríguez, 2018), and contributes to the maintenance of typical and high biodiversity (e.g., Ferreira et al., 2020). When grazing and fire are absent, the vegetation quickly becomes dominated by tall growing tussock grasses and shrubs, mostly Asteraceae, shifting from *campo limpo* to *campo sujo* (Table 2), and when in the vicinity of forest, pioneer trees and shrubs may colonize the grasslands (Carlucci et al., 2011; Dechoum et al., 2018; Schinestsck et al., 2019; Sühs et al., 2020). The potential role of fire in these ecosystems under current climatic conditions is unclear: while on the one hand the accumulated biomass from C₄ grasses is highly flammable, we do not know much about the frequency of natural ignition events. Palaeoecological studies indicate the presence of fire in the region over the past 40,000 years, and the arrival of indigenous people appears to have increased fire frequency (Behling et al., 2004). The palaeoecological evidence also provides clear information about the strong environmental changes the region underwent over the past millennia, from a cold and dry steppe climate at the Last Glacial Maximum to current warm and humid climate that permits forest development.

Pampa grasslands

The Brazilian Pampa, covering only 2% of Brazil, has a diverse geology reflected in soil heterogeneity and thus includes regions with open, slightly undulated landscapes to regions of low mountains, often with shallow soils and rock formations, covered by mosaics of grassland and low forests with many rock outcrops; in addition, we find wide river floodplains. Grasslands

in the Pampa (Fig. 3j) are almost entirely grazing lands grazed by domestic animals; relatively high stocking rates are responsible for dominance of prostrate grasses; when grazing pressure is low, taller grasses and shrubs become more abundant (Andrade et al., 2019). The Pampa grasslands are part of the *Rio de la Plata* grassland region that include Uruguay and the northeastern part of Argentina, as defined by Soriano et al. (1992).

Extended palm groves, the *butiazais* (Tab. 2 and Fig. 4d), can form a conspicuous type of landscape in the Pampa (Marchi et al., 2018; Sosinski et al., 2019). They are locally formed by one palm species, such as *Butia yatay* (Mart.) Becc., *B. lallemantii* Deble & Marchiori or *B. odorata* (Barb. Rodr.) Noblick, over a continuous herbaceous layer. Another recognized ecosystem in the Pampa is the *Espinilho* in the extreme western part of the region (Marchiori and Alves, 2010). Here, the vegetation has an upper layer of *Prosopis affinis* Spreng. (popular name: ‘inhanduvá’; restricted to the Southwestern Pampa) and *Vachellia caven* (Molina) Seigler & Ebinger (popular name: ‘espinilho’; a more wide-spread species) and constitutes the easternmost part of the Espinal province that forms an arc around the Rio de la Plata grasslands, separating it from the drier vegetation further to the west (Lewis et al., 2009). As discussed by Marchiori and Alves (2010), the term ‘Inhanduvá park’ would be more appropriate due to the presence of this species specifically in the region.

South Brazilian highland grasslands

Natural vegetation on the South Brazilian plateau, formed by igneous rocks, mostly consists of mosaics of grassland and Araucaria Forest (Fig. 3i). These grasslands receive different regional names: *Campos de Cima da Serra* or *Campos do Planalto das Araucárias* (Rio Grande do Sul and Santa Catarina; Boldrini, 2009), *Campos de Guarapuava* and *Campos de Palmas* (both in Paraná; Maack, 1981); we pragmatically suggest the term ‘South Brazilian highland grasslands’ as a collective term. The cool winters in this region with Cfb climate, with high frequency of frosts (Araujo Frangipani et al., 2021), result in the dieback of aboveground biomass (mostly of C4 grasses) which is then often removed by farmers by prescribed burns at the end of winter. This, together with the relatively low stocking rates, in consequence of the unproductive winter periods, leads to the dominance of tussock grasses and a much lower

proportion of rhizomatous or stoloniferous grasses (dominant in the lowland Pampa further to the south) that are not adapted to recurring fires (Overbeck et al., 2007). Where grasslands are not grazed and where fires are prevented, they may be subject to slow processes of forest expansion from the forest border and to the establishment of large populations of grassland shrubs (Oliveira and Pillar, 2004; Dechoum et al., 2018), but sites with long-term fire exclusion are rare. While it is unclear what a natural fire regime would be today, the flora as such indicates that fire was a relevant process in shaping the vegetation (Overbeck et al., 2018). It is interesting to note that *Araucaria angustifolia*, the characteristic conifer tree of the Araucaria forest that readily colonizes grassland also shows structural adaptations to fire, such as thick bark and high crown ration (Overbeck et al., 2018). Locally, we also find *butiazais* in the region, mostly with the threatened species *Butia eriospatha* (Mart. ex. Drude) Becc., *B. exilata* Deble & Marchiori and *B. witeckii* K. Soares & S. Longhi (Calambás-Trochez et al., 2021).

Campos Gerais

The Campos Gerais (Fig. 3h) are located on the eastern edge of the Second Paraná Plateau, formed by sedimentary rocks of the Paraná basin that result in a diversity of soil types, from very shallow to deep, structured, and well-drained soil (Moro and Carmo, 2007). Grasslands are found in mosaic with gallery forests, forest patches and Cerrado savannas (Maack, 1948; Roderjan et al., 2002), usually on poor and sandy soils that, together with fire and, more recently, grazing contributes to the maintenance of the grasslands (Moro and Carmo, 2007). The grasslands of Campos Gerais are homogeneous in terms of vegetation physiognomy, but floristically very diverse, in response to substrate, soil depth, drainage and topography (Moro and Carmo, 2007; Silva et al., 2016), also harboring high endemism levels, such as of the dwarf palms *Butia microspadix* Burret and *Butia pubispatha* Noblick & Lorenzi, found scattered in grasslands (Calambás-Trochez et al., 2021). In the northern portion of the Campos Gerais region, a transition to the Cerrado in terms of flora and physiognomy occurs. However, no general analysis of similarities to grassy ecosystems further to the North and the South exists.

Grassy ecosystems in coastal regions

Large areas of Brazil's coastal region were formed after successive marine regressions and transgressions following sea level changes during the Quaternary period, which allowed the formation of beach plains, ridges, dunes and interdunes along the long Brazilian coast (Araujo and Henriques, 1984; Martin et al., 1997). In Brazil, the term *Restinga* is used to denominate an assemblage of coastal ecosystems on sandy substrate with floristically and physiognomically distinct plant communities (Falkenberg, 1999), which includes herbaceous plant communities as well as assemblages dominated by shrubs or trees (Fig. 3e), with widely varying canopy coverage (Silva et al., 2010). Often, these physiognomies may follow a zonation towards the ocean-continent, with an increase in species richness, woodiness and height of the vegetation following an increase in the distance from the sea and a decrease in the influence of salinity and wind, corresponding to a reduction of ecological stress (Scarano, 2002; Bona et al., 2020). Within these *Restinga* complexes, we find different grassy ecosystems such as coastal dune sequences with a successional sequence of different vegetation types, influenced by topographic position and dune dynamics (Pfadenhauer, 1980; Moro et al., 2015). Open coastal ecosystems occur from the mouth of the Parnaíba river in the Northeast to the mouth of the Chuí river in Southern Brazil. In semiarid northeastern Brazil, shrublands, savannas and grasslands develop on the coastal plains and dunes (e.g., Moro et al., 2015, Soares et al., 2021).. In southern Brazil, grasslands that extend over considerable areas in the coastal plain (Menezes et al., 2015) differ floristically from the grasslands of the Pampa (Andrade et al., 2019). The structurally and floristically heterogeneous coastal and *Restinga* ecosystems in general have not been mapped in more detail and beyond the local scale (but see da Silva Menezes et al., 2016, and da Silveira et al. 2022). Thus, our map (Fig. 2) gives only an approximation, at least for part of these regions, of the original distribution of these environments that include different vegetation types, not all of them grass-dominated.

Anthropogenic impact on Brazil's grasslands and savannas

Brazil has lost 46% of the original distribution of its grassy ecosystems by 2019 (Fig. 5 and 6). Vast areas of grassy ecosystems have been converted to agricultural land or non-native

tree plantations. In Brazil's major grasslands and savanna regions, native vegetation has been replaced extensively by planted pastures with non-native and often invasive grass species (Ferreira et al., 2013; Parente et al., 2019; Sano et al., 2020; Souza et al., 2020). In the Cerrado, only 57% of native vegetation remains, of which 69 million ha are grassland and savanna, with a strong recent agricultural expansion in northern regions (Sano et al., 2020). Intensive agriculture is also rapidly encroaching on the *Campos Sulinos* (Fig. 6c; Cordeiro and Hasenack, 2009; Baeza and Paruelo, 2020; Souza et al., 2020), even though grassy ecosystems still are the basis for livestock production (Sparovek et al., 2007). *Campo rupestre* regions are threatened by mining expansion (Salles et al., 2019; Souza-Filho et al., 2019). Of the remaining areas with grassy ecosystems, many are severely impacted by human activities (Fig. 6). A general problem is the presence of invasive species, today widespread across Brazilian grasslands and savannas (for example, Guido et al., 2016; Assis et al., 2021). Productive invasive grasses, such as those of the genus *Urochloa*, are widely used for planted pastures, especially in the Cerrado, Pantanal and Amazon, exposing native grassland and savanna remnants to biological invasions. These alien species outcompete native grasses and therefore alter vegetation composition and dynamics (Damasceno et al., 2018). The spread of invasive species poses (Fig. 6b, 6d) risks for the already underprotected grassy ecosystems in Brazil (Overbeck et al., 2015).

The scientific debate on grassland conservation and restoration will be facilitated by clearer use of terms that consider the extent of human impact on grasslands (Table 3). The term 'pasture', for instance, is commonly used to refer to artificial (e.g., fertilized, overseeded, improved) grasslands, yet, grazed native grasslands are also referred to as 'pastures' (Ávila et al., 2019; Jaurena et al., 2021). While planted pastures can be important to avoid further land conversion and maintain cattle grazing (Dick et al., 2021; Jaurena et al., 2021), they are generally monocultures of commercial and non-native species and should be referred to as agricultural land (see also Table 3). However, often natural grassland and pastures planted with one or few non-native species (e.g., pastures with *Urochloa* or other forage species) are categorized under same form of land use (grazing land). There are vast differences in the biodiversity, ecology, and ecosystem service delivery of such different types of grazing land, and yet these different grazing systems can be difficult to distinguish using remote sensing

techniques, thus undermining the appreciation of natural grasslands and their huge value in terms of hosting biodiversity and providing ecosystem services. This leads to further subsuming of ecologically valuable grasslands and grassy systems under either the umbrella term 'agriculture' or makes these kinds of grassy systems even disappear from the radar in policy terms.

Furthermore, a distinction between primary (i.e., old-growth grassland *sensu* Veldman et al., 2015) versus secondary grassland would more clearly highlight conservation value and restoration need. Primary grasslands are grasslands that were never replaced by other land uses (Table 3), while secondary grasslands developed after other land uses were abandoned. In the Cerrado, after use for livestock grazing or forestry, there is a successful recovery of the woody component, but the native grassy layer fails to recover (Cava et al., 2018; Haddad et al., 2021). For the *Campos Sulinos*, it has been shown that secondary grasslands differ from primary ones in terms of plant species composition and ecosystem processes (e.g., Koch et al., 2016; Leidinger et al., 2017). This is analogous to recent research underlining that historical legacies of land use influence soil microbial dynamics in ecosystems (Fichtner et al., 2014), or the susceptibility to extreme weather events (Mausolf et al., 2018). For the *campo rupestre*, it has been shown that recovery after disturbance is extremely slow (Le Stradic et al., 2014). The distinction between primary and secondary grasslands is fundamental from a conservation perspective (see Table 4): restoration of the latter is important, conversion of the first should be avoided. To aid conservation efforts at a time when the extent of grassy ecosystems is rapidly declining, clearer terminology that emphasizes human use needs to be more widely adopted.

(Figure 5 here)

(Figure 6 here)

(Table 3 here)

Knowledge gaps and research needed to foster adequate strategies in conservation and restoration of the Brazil's grassy ecosystems

Here we present the first synthetic view of Brazil's major grassy ecosystems and briefly discuss the main ecological drivers that shape their distribution and physiognomy. Historically, grassy ecosystems have been considered an 'anomaly' or even 'aberration' by plant ecologists (Pausas and Bond, 2019). This is because their distribution cannot be explained chiefly by climate, which has long been considered to be the most important factor determining vegetation across the globe (Bond, 2019). Further, they lose visibility for being subsumed under more general terms like 'pasture' that also are used for human-created systems. The consequences of these misperceptions are clearly reflected in Brazilian conservation policies that have focused on fire suppression and management exclusion, threatening grassy ecosystems and their high biodiversity (Durigan and Ratter, 2016). Further, grassy ecosystems are highly vulnerable to global change (e.g., Hofmann et al., 2021). Yet, these ecosystems generally achieve less attention in the media and conservation of them has less policy support (Bardgett et al., 2021).

Recognizing the role of endogenous disturbances (*sensu* Buisson et al., 2019) – such as fire and grazing – in maintaining biodiversity and ecosystem functioning is key to developing appropriate strategies for conservation and restoration of grassy ecosystems. This is even more important as tree planting is promoted worldwide to increase carbon stocks to mitigate climate change. While there is an urgent need to manage ecosystems to store more carbon and cause climate cooling, the focus on trees continues to threaten grassy ecosystems that, when 'restoration' involves tree planting, are actually being degraded to forests (Temperton et al., 2019; Veldman et al., 2019). In contrast, the potential of grassland ecosystems to provide important ecosystem services (e.g., water supply or carbon stocks; Conant et al., 2017; Klink et al., 2020) is poorly recognized in the conservation and restoration debate (Zhao et al., 2020). In the case of Brazil, this may be due in part to large data gaps for these grassy ecosystem services. Apparently, grassland ecosystems still have an image problem worldwide as well as in Brazil, which impedes implementing effective conservation and natural climate solutions.

We recognize that further work is needed to refine vegetation mapping and classification (see Box 2 for a summary of key research needs). For instance, the IBGE vegetation map, which forms the basis for our map (Fig. 2), currently uses terminology that is

misleading or imprecise. In particular, the term '*estepe*' (English: steppe) is applied by IBGE to refer to the sub-humid grasslands in southern Brazil, while in the international literature the term is generally used to refer to semi-arid grassland ecosystems under climatic conditions that limit forest growth (e.g., Paruelo et al., 2015; Werger and van Staalduinen, 2012). Further, the category '*formações pioneiras*' (English: pioneer formations) used by IBGE lumps together very different ecosystem types, from forests to wetlands to various grassy ecosystems, reinforcing the misconception of grassy ecosystems as early successional vegetation (see. Suppl. Mat.).

Terminology aside, more detailed vegetation maps with higher resolution and ground information on ecosystem quality (or degree of degradation) will be critical for conservation and restoration planning and thus public policy. While remote sensing technology certainly will see important advances in the near future, we should be aware that this alone will not be sufficient: field work is necessary to validate data from remote sensing, especially to map degraded grassy ecosystems and to inform conservation and restoration programs. In Brazil's grassy ecosystems, specific types of plant communities have been identified and characterized only for a few regions (e.g., Pantanal: Pott et al., 2011; Barbosa da Silva et al., 2020); for many regions, studies on plant community ecology are still scarce, and data are far from sufficient for detailed classification (see also Menezes et al., 2022). Defining specific communities or habitats requires comprehensive datasets (see e.g., Willner et al., 2017; Marcenò et al., 2018; Bland et al 2019). Their mapping will allow conservation to become much more targeted to specific and particularly threatened habitat types. Additionally, field mapping is necessary to distinguish native grassland and savanna from degraded forest.

Box 2: Research needs on Brazil's grassy ecosystems

- Map and classify different grassy ecosystems using remote sensing with extensive on-the-ground validation. Current classifications, e.g., IBGE's 1:250.000 vegetation maps, are very coarse in spatial scale and imprecise with regard to plant community composition.

- Expand field sampling of the plant species composition of grassy ecosystem, focused on the herbaceous layer, ideally prioritizing regions that have received little attention from botanists and ecologists in the past.
- Establish standardized sampling methodologies for ecosystem processes and services to foster comparative studies in grassy ecosystems.
- Develop tailored methods to evaluate the conservation status of grassy ecosystems, through for example, mapping of ecosystem degradation states and restoration priorities.
- Use the results of comparative ecological studies across Brazil's ecosystems to develop best practices for conservation and restoration that are adequate to the specificities of grassy ecosystems, not only forests.

The classification and description of the savanna and grasslands presented here is only a first step toward a better understanding of Brazil's grassy ecosystem and the drivers of their diversity and vegetation structure. We expect that a common and shared terminology and understanding, as proposed here, will stimulate more integrative research that will be fundamental to developing improved conservation strategies for the multitude of grassy ecosystems in Brazil. Next steps include coalescing a database of biotic and abiotic features of grassy ecosystems. This will allow comparison among systems based on quantitative data and analysis of internal gradients in species composition as well as environmental and historical drivers. This should then make it possible to propose refined classification systems and to develop targeted conservation and restoration strategies.

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Figure and table captions

Figure 1: The Whittaker diagram of world biomes (from Whittaker, 1975) with Whittaker's original Ecosystem Uncertainty Climate Zone (red dash-dotted line) and colored dots representing Brazil's grassy ecosystems. Brazilian grassy ecosystems occur throughout a broad range of global biome types, including zones outside the Ecosystem Uncertainty Climate Zone. Sites are coded according to the main types presented in Table 1 and Fig. 2 (see Suppl. Material 1 for data sources; note that Amazonian white sand grasslands and shrublands and savannas in the Caatinga are not included in the figure). The distribution of Brazil's grassy ecosystems in the Whittaker diagram reinforces the relevance of non-climate factors in shaping the distribution of grassy ecosystems across large parts of Brazil.

Figure 2: Brazil's grassy ecosystems are spread over all regions of the country. A) Brazil's major open ecosystems mapped based on Institute of Biogeography and Statistics's (IBGE) 1:250.000 vegetation map; (B) Map of the potential distribution, based on modelling, of *campo rupestre*, following Silveira et al. (2016); (C) Indication of regions with presence of highland grasslands, following Alves et al. (2014). (D) Pampa, South Brazilian highland grasslands and *Campos Gerais* forming, together, the *Campos Sulinos* (South Brazilian grasslands). See Table 1 for definitions of major grassy ecosystems, and Suppl. Material 2 for details on mapping. Abbreviations in A indicate biomes according to the Brazilian IBGE (2019) classification: AM - Amazon, CA - Caatinga, CE - Cerrado, MA - Atlantic Forest, PN - Pantanal, PM - Pampa.

Figure 3: Major grassy ecosystems in Brazil: (A) White sand grasslands and shrublands in the Amazon (Photo: Floresta Estadual de Trombetas in Pará, Daniela Zappi); (B) Savannas in the Cerrado (Photo: Parque Nacional da Chapada dos Veadeiros in Goiás, Alexandre Sampaio); (C) Savannas in the Caatinga (Photo: Fortaleza in Ceará, Marcelo F. Moro); (D) Hyperseasonal savannas and grasslands in the Pantanal (Photo: Mato Grosso, Gerhard Overbeck); (E) Grassy ecosystems in coastal regions (Photo: Parque Natural Municipal das Dunas da Lagoa da Conceição in Santa Catarina, Michele Dechoum); (F) Campo rupestre (Photo: Serra do Cipó in Minas Gerais, Fernando Silveira); (G) Highland grasslands (Photo: Serra da Bocaina in São Paulo, Giselda Durigan); (H) Campos Gerais (Photo: Parque Estadual do Guartela in Paraná, Marcos Carlucci); (I) South Brazilian highland grasslands (Photo: Parque Estadual Tainhas in Rio Grande do Sul, Gerhard Overbeck); (J) Pampa grasslands (Photo: Valério Pillar). Savannas in the Amazon (see Fig. 2) are not pictured. Typical plant families and species for the major grassy ecosystems are listed in Suppl. Material 3.

Figure 4: Some grassy ecosystems may change their structure rapidly depending on the disturbance intensity and frequency, such as campo limpo (A) and campo sujo (B) or are hardly mappable in national or regional vegetation maps, because they are scattered in the landscape, such as *veredas* (C) and *butiazais* (D). Photos: A – Parque Nacional Chapada das Mesas, Maranhão; B and C – Chapada dos Veadeiros, Goiás; D – *Butiazal* in São Miguel Farm, Rio Grande do Sul. Photos: A, B and C – Alexandre Sampaio, D – Ênio E. Sosinski Jr.

Figure 5: Brazil's major grassy ecosystems have experienced rapid and extensive loss in recent decades. On the left, original (i.e., potential natural) and remaining distribution (2019 data; MapBiomias, 2021) of grassy ecosystems, based on IBGE's 1:250.000 map (Fig. 2). On the right, transition pathways from 1985 to 2019 (data from MapBiomias, 2021). 'Pastures' here indicates planted pastures, not natural grassland under grazing.

Figure 6: Anthropogenic impact on grassy ecosystems: (A) *Campo rupestre* degraded by erosion; (B) Savanna in the Cerrado invaded by an exotic grass (*Urochloa* sp.); (C) Grassland converted to soy plantation (left side of the fence) in the *Campos Sulinos*; (D) Invasion of exotic pine tree (*Pinus* sp.) over coastal grassland. Photos: A – Serra do Cipó, Minas Gerais; B – Chapada dos Veadeiros, Goiás; C – Jari, Rio Grande do Sul; D – Parque Natural Municipal das Dunas da Lagoa da Conceição, Santa Catarina. Photos: A – Fernando Silveira, B – Alexandre Sampaio, C – Luciana Menezes, D – Michele Dechoum.

Table 1: Brazil's major grassy ecosystem types (see also Fig. 2 and 3). Brazilian terms (first column) derive mainly from particular geographic regions /biome (sensu IBGE) types within Brazil or refer to altitude. Typical plant families and species for the major grassy ecosystems are listed in Suppl. Material 3.

Table 2: Specific physiognomies within the major grassy ecosystem types presented in Table 1. The terms listed here refer to terms used, sometimes only locally, for specific expressions of the major grassy ecosystems presented in Table 1 and Figures 2 and 3. We indicate main ecological drivers responsible for them.

Table 3: Suggested terminology to indicate human influence on Brazil's grassy ecosystems. Terms in Portuguese and English used for different grassland types, their definition, main type of current management (marked with 'X') and occurrence in Brazilian biomes. (X) indicates that management is not very common across the Brazilian ecosystems, but may occur occasionally.

Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐ The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

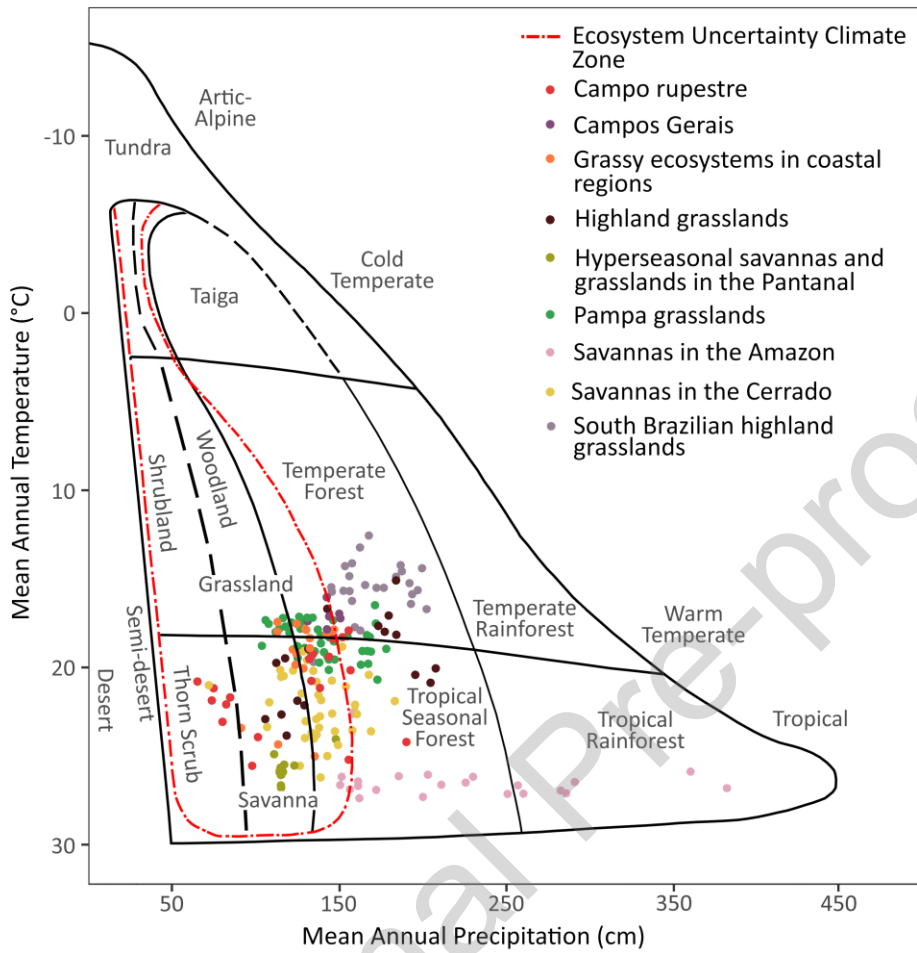


Fig 1

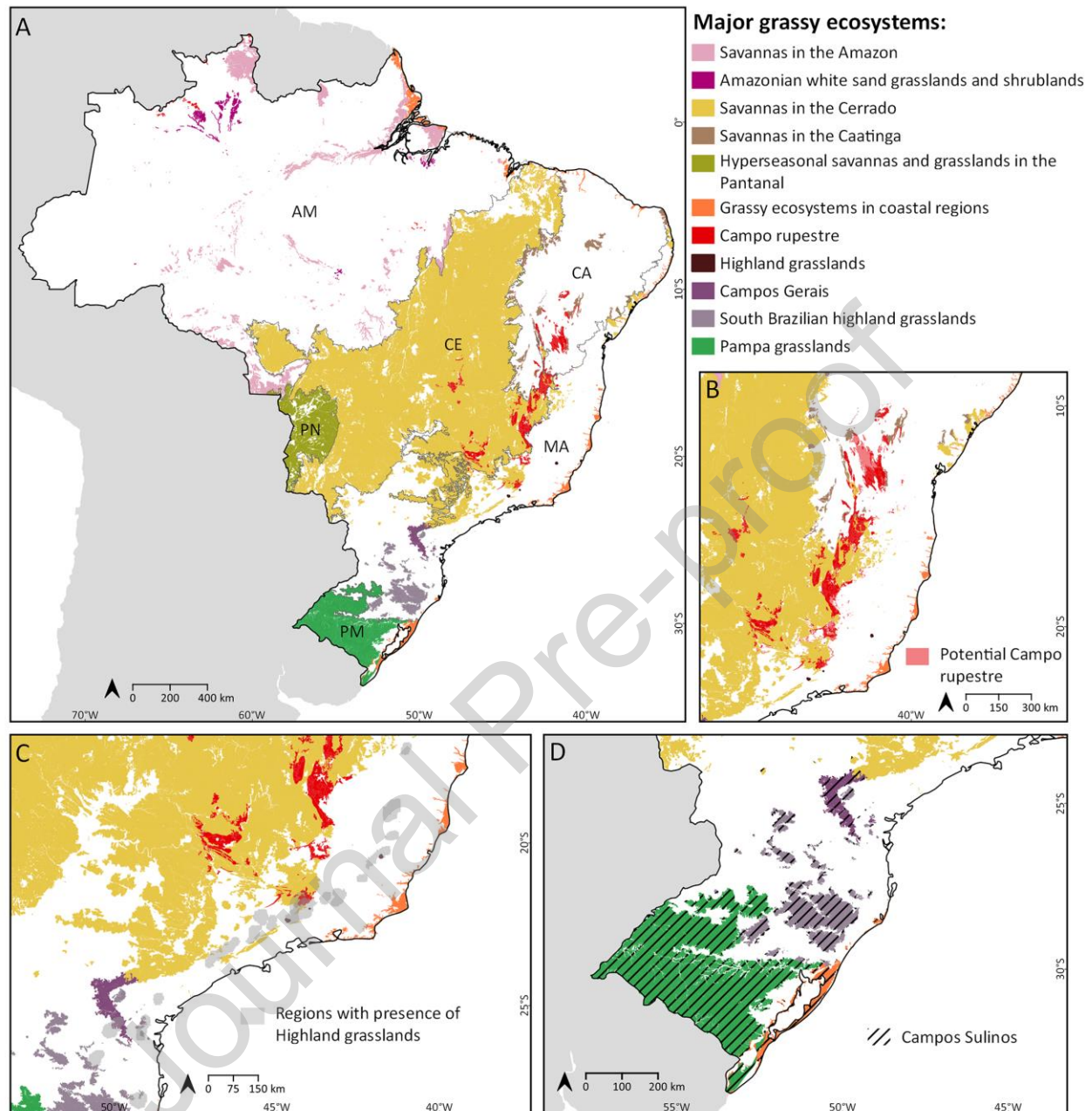


Fig 2

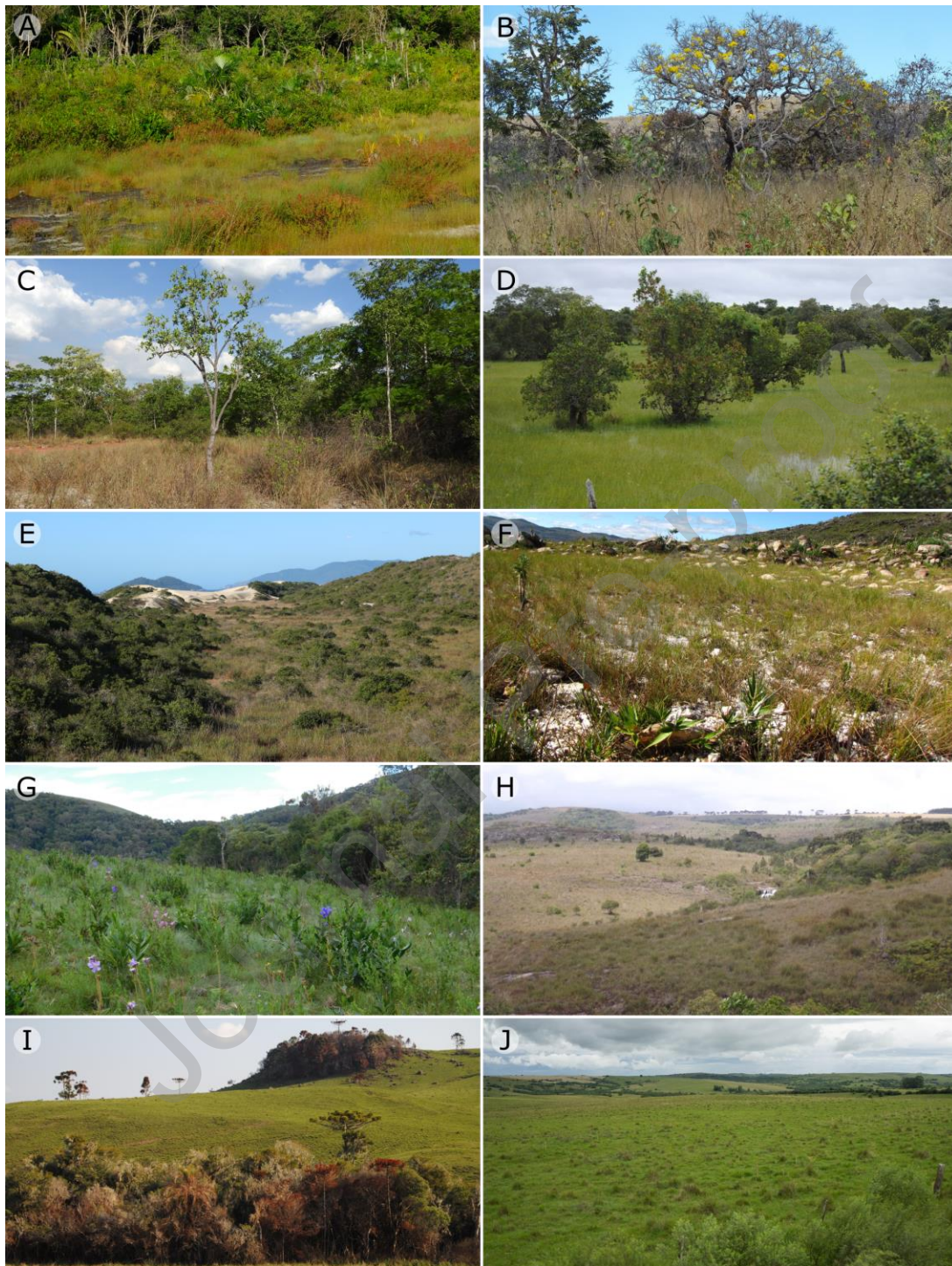


Fig 3

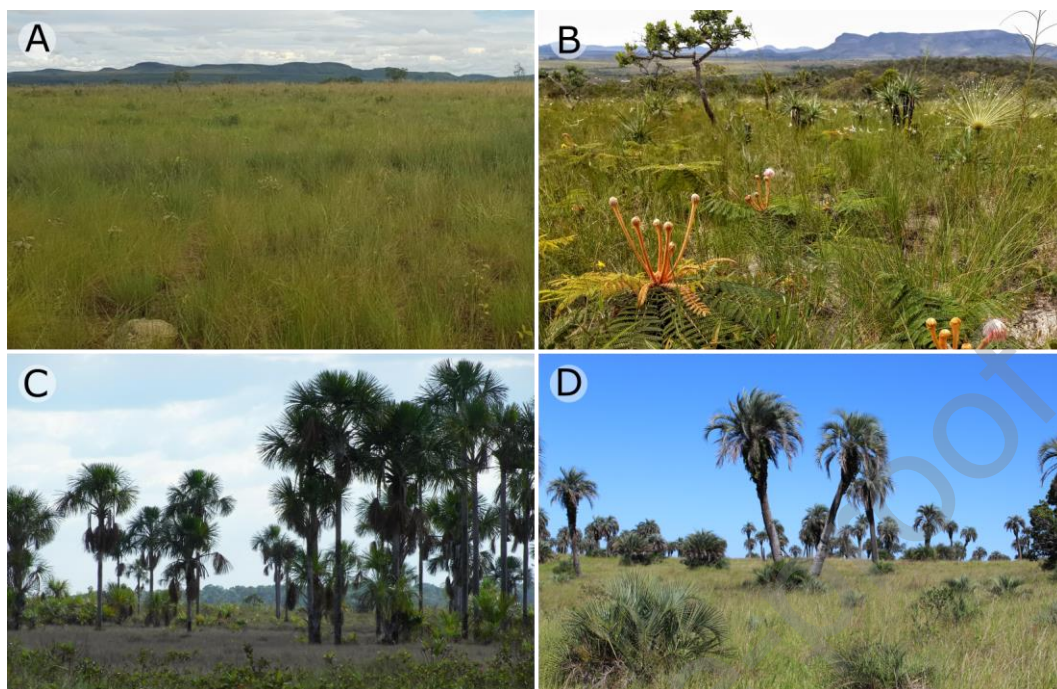


Fig 4

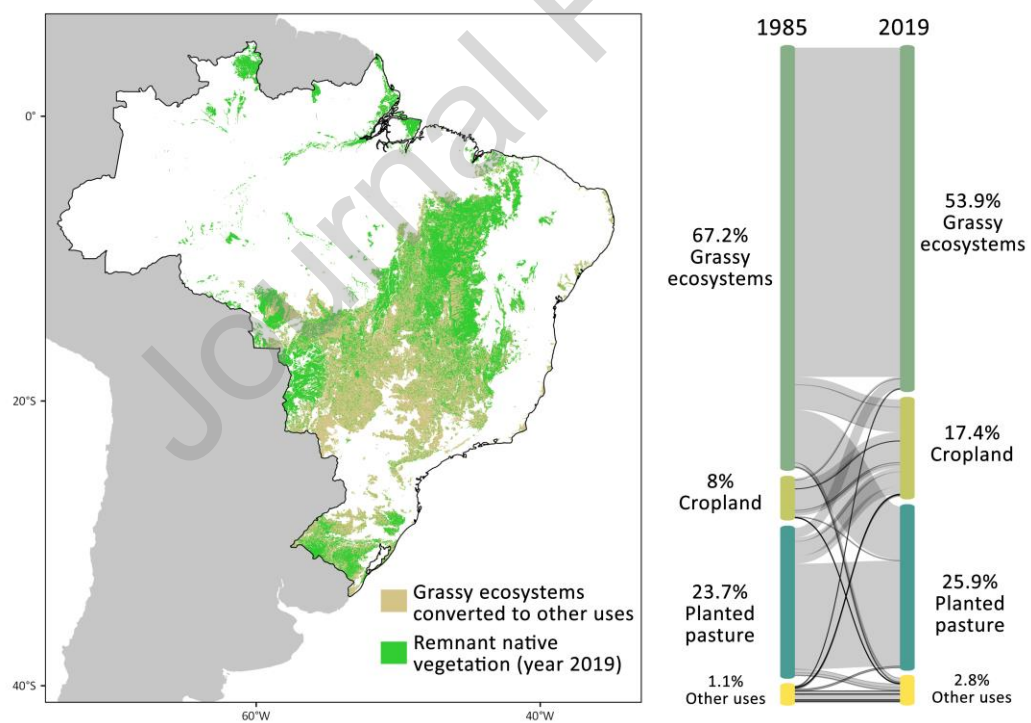


Fig 5

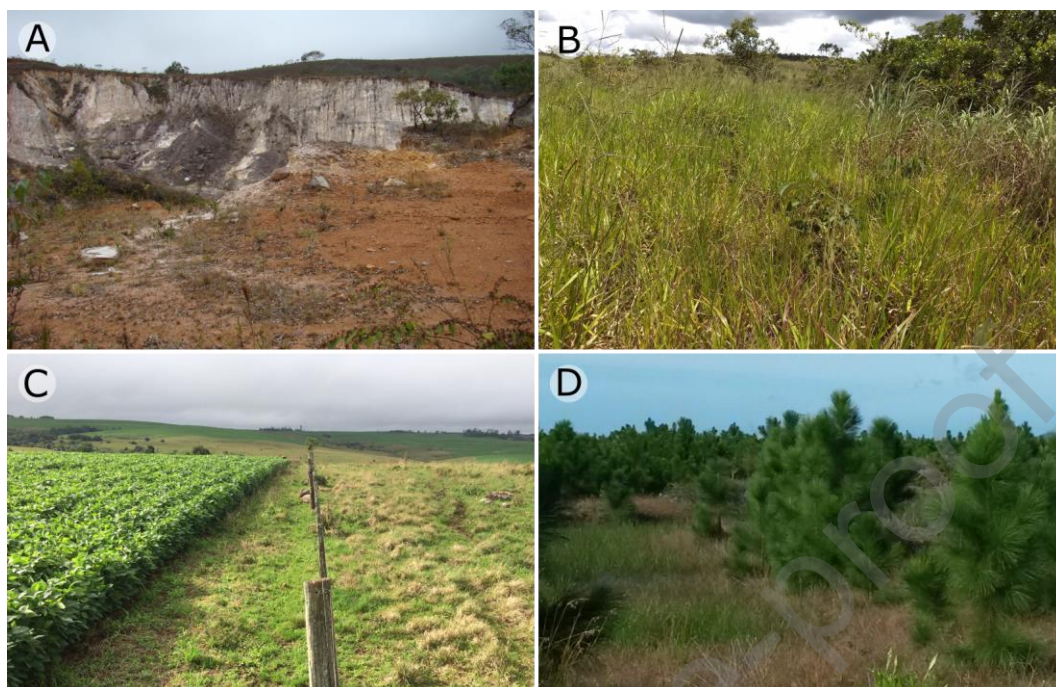
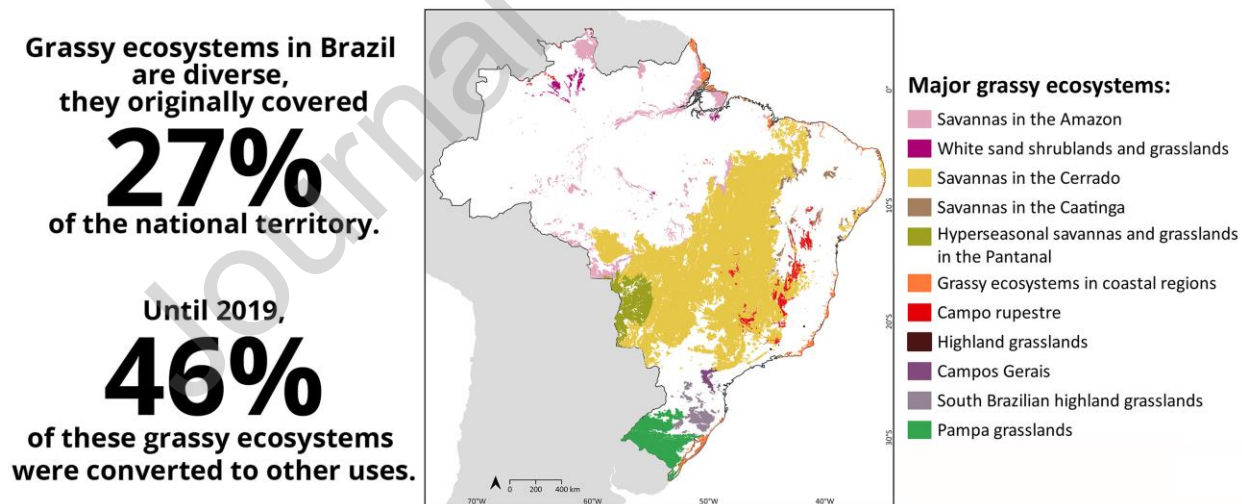


Fig 6



Graphical abstract

Highlights

- 27% of Brazil's natural vegetation are grasslands and savannas
- Brazil's grassy ecosystems remain undervalued in conservation: 46% have been converted to other uses
- Eleven major regions of grassy ecosystems can be identified across Brazil
- Disturbances (e.g., fire, grazing) are key determinants of Brazil's grassy ecosystems
- Efforts are needed to map grassy ecosystems and develop conservation strategies