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6	A New Tropical Savanna PFT, Variable Root Growth and Fire Improve Cerrado
7	Vegetation Dynamics Simulations in a Dynamic Global Vegetation Model
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Abstract

The Cerrado, South America's second largest biome, has been historically underrepresented in Dynamic Global Vegetation Models (DGVMs). Therefore, this study introduces a novel Plant Functional Type (PFT) tailored to the Cerrado biome into the DGVM LPJmL-VR-SPITFIRE. The parametrization of the new PFT, called a Tropical Broadleaved Savanna tree (TrBS), integrates key ecological traits of Cerrado trees, including specific allometric relationships, wood density, specific leaf area (SLA), deeprooting strategies, and fire-adaptive characteristics. The inclusion of TrBS in LPJmL-VR-SPITFIRE led to notable improvements in simulated vegetation distribution. TrBS became dominant across Brazil's savanna regions, particularly in the Cerrado and Pantanal. The model also better reproduced the above- and belowground biomass patterns, accurately reflecting the "inverted forest" structure of the Cerrado, characterized by a substantial investment in root systems. Moreover, the presence of TrBS improved the simulation of fire dynamics, increasing estimates of burned area and yielding seasonal fire patterns more consistent with observational data. Model validation confirmed the enhanced performance of the model with the new PFT in capturing vegetation structure and fire regimes in Brazil. Additionally, a global-scale test demonstrated reasonable alignment between the simulated and observed global distribution of savannas. In summary, the integration of the TrBS PFT marks a critical advancement for LPJmL-VR-SPITFIRE, offering a more robust framework for investigating the interaction of above- with belowground ecological processes, fire disturbance and the impacts of climate change across the Cerrado and other tropical savanna ecosystems that together account for approximately 30 % of the primary production of all terrestrial vegetation.





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1. Introduction

The Cerrado, a biome of global importance and recognized as the world's most biodiverse savanna, faces numerous challenges that threaten its rich biodiversity and the vital ecosystem services it provides (Myers et al., 2000; Sano et al., 2019; Schüler and Bustamante, 2022). The alarming deforestation rates, driven by agricultural expansion, and the impacts of climate change, which are already exacerbating droughts and altering fire dynamics, are the two main drivers of degradation, impacting water availability and vegetation dynamics in this biome (Strassburg et al., 2017; Gomes, et al., 2020a; Rodrigues et al., 2022). Climate change impacts in Brazil are already evident. A study by INPE to the First Biennial Transparency Report (MCTI, 2024) reveals an increase of approximately 20% in the number of consecutive dry days in Brazil in recent decades, particularly in the North, Northeast, and Central regions of the country. Similarly, Feron et al., (2024) demonstrated an increase in the frequency of compound climate events involving heat, drought, and high fire risk in key regions of South America, including the Amazon. A significant increase in maximum and minimum temperatures was also observed in the Brazilian Cerrado between 1961 and 2019, along with a reduction in relative humidity (Hofmann et al., 2021). In this context, vegetation modeling emerges as an essential tool for understanding and predicting the Cerrado's responses to these pressures. Dynamic Global Vegetation Models (DGVMs), such as the Lund-Potsdam-Jena managed Land model (LPJmL), aim to simulate changes in vegetation, fire, water and carbon fluxes depending on climate and land use (Cramer et al., 2001; Thonicke et al., 2010; Baudena et al., 2015; Moncrieff et al., 2016; Schaphoff et al., 2018; Drüke et al., 2019; Martens et al., 2021). In order to reduce complexity, common DGVMs classify vegetation into so-called Plant Functional Types (PFTs), which are groups of plants that show similar responses to external drivers and



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growth form, phenology and photosynthetic strategy (Wullschleger et al., 2014). Parameterization of PFTs should therefore capture the most important characteristics of certain vegetation types while balancing complexity. Specifically in savannas, vegetation is often characterized by small trees and shrubs that grow deep roots and are well adapted to fire and drought, all of which distinguish them from the trees in moist and seasonal tropical forests (Ratnam et al., 2011). However, many DGVMs, including LPJmL, lack a dedicated savanna PFT, leading to significant inconsistencies in model projections (Foley et al., 1998; Hughes, Valdes and Betts, 2006; Clark et al., 2011; Neilson, R. P. 2015; Drüke; et al., 2019). This omission often results in the underestimation of savanna vegetation extent and fire occurrences, while overestimating above-ground biomass and the extent of tall tropical forest formations, as demonstrated in simulations for South America (Cramer et al., 2001; Drüke et al., 2019), or a depiction of savanna vegetation as tropical grasslands which do not encompass the coexistence of grasses, shrubs and trees. DGVMs are, nevertheless, widely used to simulate future transitions between the Amazon and the Cerrado biomes, often predicting an abrupt shift from forest to grassland under climate change (Malhi et al., 2009; Swann et al., 2015). However, this oversimplification neglects the intricate ecological gradient that spans diverse vegetation types, from open forests to woody savannas with varying tree cover densities. This lack of precision in modeling has broader implications for understanding the Cerrado's role in climate mitigation and adaptation, including nature restoration. For example, restoring the entire 20 million hectares of the identified priority areas for restoration in the Cerrado could remove up to 1.77 million tons of carbon from the atmosphere (Schüler and Bustamante, 2022). Beyond carbon sequestration, savannas play

resemble their ecological function. PFTs are, in general, distinguished by their allometry,





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a crucial role in preserving water resources and biodiversity, acting as natural buffers against climate change and enhancing ecosystem resilience (Oliver et al., 2015; Salazar et al., 2016; Syktus and McAlpine 2016; Bustamante et al., 2019). With its highly seasonal climate and diverse mosaic of grasslands, savannas, and forest formations, the Cerrado is particularly significant for mitigating and adapting to climate change (Ribeiro and Walter 2008; Bustamante et al., 2019; Schüler and Bustamante 2022). Accurately representing savanna-type vegetation in DGVMs will not only improve projections of the Cerrado's vulnerability to climate change but also help identify high-risk areas and guide the development of effective conservation, restoration, and management strategies. For instance, improved models, acknowledging savanna-specific characteristics, could inform studies investigating biome transitions and ecological tipping points, fire management measures, support agricultural adaptation, and optimize water resource management, ensuring the Cerrado's resilience in the face of environmental challenges. We therefore introduce a new Cerrado specific PFT which we call "Tropical Broadleaved Savanna tree" e (TrBS) that entails the biome's unique characteristics into a state-of-the-art version of the LPJmL model (LPJmL-VR-SPITFIRE). LPJmL-VR-SPITFIRE explicitly simulates variable tree rooting strategies (Sakschewski et al., 2021) and employs the prossed-based fire model SPITFIRE (Thonicke et al., 2010; Oberhagemann et al., 2025), while being based on the latest LPJmL version (LPJmL 5.7; Wirth et al., 2024). In this study, we test our new approach by modeling the Potential Natural Vegetation (PNV) distribution for the entire Brazil and validate our results against observational datasets. This model improvement provides a robust basis for studies exploring the impact of climate change on vegetation dynamics in the Cerrado region. This model is expected to show significant improvements in biomass estimate, vegetation type distributions, and fire dynamics in tropical regions.





2. Methods

2.1 Study region

position, the Cerrado has ecotones with four of the other five Brazilian biomes: Amazon, Caatinga, Atlantic Forest and Pantanal (Fig. 1).

Brazil spans over 850 million hectares, extending from approximately 5°N to 35°S (IBGE, 2024). Due to its size, the country encompasses a wide range of climatic conditions, from subtropical and semi-arid regions to tropical wet environments (Table S1). The Cerrado, the second-largest vegetation formation in South America, covers about 23% of Brazil (~2 million km²), primarily in its central region (IBGE, 2024). Recognized as both a savanna and a global biodiversity hotspot, its seasonal precipitation regime is closely tied to the South American Monsoon System (Myers at al., 2000; Grimm, Vera and Mechoso, 2004). Its climate is predominantly classified as tropical savanna (Aw) according to the Köppen-Geiger classification system, characterized by a rainy season from October to April and a dry season from May to September (Peel et al., 2007; Oliveira et al., 2021). Annual rainfall ranges from 600 mm to 2,000 mm, with the highest averages near the Amazon border and the lowest near the Caatinga, and the mean annual temperature is 20.1°C (Sano et al., 2019).

Our study region encompasses all of the Brazilian territory, focusing on the distribution

of its six biomes, with special attention to the Cerrado biome. Because of its central





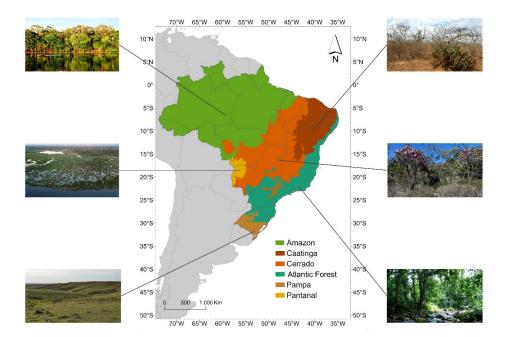


Fig. 1: Map representing the distribution of Brazilian biomes according to IBGE (2024) and photos showing their general appearances. Amazon photo by Andre Deak, Pantanal photo by Leandro de Almeida Luciano, Pampa photo by Ilsi Boldrini, Caatinga photo by Matheus Andrietta, Cerrado photo by Jéssica Schüler, and Atlantic Forest photo by Tânia Rego.

Historically, the biome is subject to periodic fires, especially in the grassland and savanna formations, highly influencing the evolution of its vegetation (Simon et al., 2009; Simon and Pennington 2012). Currently, fires predominantly occur at the end of the dry season, during September and October (Gomes et al., 2020; MapBiomas Fogo 2024). The vegetation in the Cerrado can be classified into three main vegetation formations: Forests, Savannas and Grasslands. Forestations predominantly consist of trees forming a continuous canopy, typically found on deeper soils (Ribeiro and Walter 2008). Savanna formations are defined by the presence of both arboreal and herbaceous-shrub strata with





a canopy cover ranging from 5% to 70% and tree heights reaching 8 m on average (Ribeiro and Walter 2008). Finally, grassland formations consist of shrubs and sub-shrubs intermixed with herbaceous strata (Ribeiro and Walter 2008).

2.2 Model description

The LPJmL-VR-SPITFIRE model is a fire-enabled DGVM that integrates the latest version of the DGVM LPJmL (LPJmL 5.7, Wirth et al., 2024) with the most recent improvements of the SPITFIRE fire regime model (Thonicke et al., 2010; Oberhagemann et al., 2025), together with the variable-roots (VR) developed by Sakschewski et al., (2021). This model framework enables the simulation of global vegetation dynamics, including fire influence, fire disturbance (Schaphoff et al., 2018; Drüke et al., 2019).

LPJmL simulates the growth and productivity of both natural and managed vegetation, considering water, carbon, and energy fluxes, and represents vegetation through PFTs (Schaphoff et al., 2018). The model accounts for factors such as climate, soil, water, and nutrient availability to simulate the distribution, biomass, and productivity of PFTs, and has been validated against observational data on productivity, biomass, evapotranspiration and PFT distribution on the global scale (Schaphoff et al., 2018). We briefly outline only the most important features of the LPJmL-VR-SPITFIRE model version, while referring to Schaphoff et al., (2018) for the general LPJmL model description.

Variable roots: In the original LPJmL model, a PFT-specific shape parameter β defines tree rooting depth and fine root biomass distribution (Jackson et al., 1996). To better reflect the diversity of rooting strategies of tropical trees, Sakschewski et al., (2021) introduced a range of possible rooting strategies (shallow to deep rooted trees) per PFT, that can coexist or outcompete each other. Unless constrained physically by soil depth or by available resources, actual rooting depth is scaled with tree height via a logistic root growth function,





180 and new carbon pools (root sapwood and heartwood) represent the plant's investment in 181 growing coarse roots (Sakschewski et al., 2021). A long-term selection of the best suited rooting strategies amongst each PFT is mediated by a modified tree establishment 182 183 approach, where the most successful rooting strategies can produce more saplings. 184 Water-stress mortality: Tree mortality in LPJmL depends on tree longevity, growth 185 efficiency and heat stress (Schaphoff et al., 2018). In this study, a new mortality component 186 reflecting mortality risk due to water stress has been included. This newly integrated water 187 stress mortality depends on tree phenology (phen) (Forkel et al., 2014, applied in 188 Schaphoff et al., 2018), leaf senescence due to water stress (phenwater) and PFT-specific 189 parameters representing water stress resistance (c_{res}) and sensitivity to drought (c_{sens}). 190 $mort_{water} = c_{sens} \cdot phen \cdot (1 - phen_{water} - c_{res})$ (1) c_{sens} is a PFT-specific parameter that determines the overall sensitivity to drought stress. 191 192 Phen represents the actual phenological state of a tree, ranging from 0 (no leaf cover) to 1 193 (full leaf cover). This term accounts for the fact that trees with lower phenology (i.e., more dormant trees) experience reduced water stress mortality. The expression $(1 - phen_{water})$ 194 195 represents the intensity of leaf senescence due to low water availability (Forkel et al., 196 2014), indicating that periods of reduced water availability lead to higher drought-induced mortality. c_{res} defines a threshold below which drought-induced leaf senescence does not 197 198 significantly impact tree survival. 199 This model refinement allows for a more accurate representation of PFT-specific sensitivity to water stress. Coupled with the variable rooting scheme, LPJmL-VR-200 201 SPITFIRE allows trees to optimize the trade-off between carbon investment in deep roots 202 and aboveground growth, providing a survival advantage under drought conditions. The 203 PFT-specific parameters are found in Table 1.





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SPITFIRE is a process-based fire model that simulates wildfire occurrence, spread, and behavior, while considering fuel availability, fuel composition and weather conditions to simulate ignitions, rate of spread and flame intensity (Thonicke et al., 2010). By coupling SPITFIRE into LPJmL-VR (LPJmL-VR-SPITFIRE), SPITFIRE can simulate the influence of fire on vegetation dynamics. Vegetation properties simulated by LPJmL-VR, such as PFT composition and litter fuel moisture, determine the simulation of fire spread and intensity which in turn influence post-fire vegetation conditions. SPITFIRE considers both human-induced and natural ignitions, with the likelihood of these ignitions developing into fires depending on the fire danger index of the modelled grid cell. Fires then spread depending on factors such as dead and live fuel composition, wind speed, and fuel moisture. We adopted the VPD (water vapor pressure deficit)-dependent calculation of the fire danger index (Drüke et al., 2019; Gomes et al., 2020b) and the most recent updates to the fire spread functions (Oberhagemann et al., 2025). Both the fire danger index and rate of spread calculations include PFT-specific parameters that reflect different vegetation related properties that affect ignition, fire duration and propagation. Fire-related tree mortality is calculated considering PFT specific bark thickness (influencing cambial damage) and scorch height (influencing crown mortality). Furthermore, with the recent updates, SPITFIRE allows for multi-day fires and considers moisture of the live grass share. SPITFIRE feeds back to the vegetation components by calculating fire effects on the vegetation, such as fuel combustion and post-fire tree mortality (Drüke et al., 2019; Oberhagemann et al., 2025).

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2.3 Parameterization of a new Savanna tree PFT

The Cerrado trees exhibit considerable morphological and physiological differences compared to other tropical forest trees growing in closed canopy and wet environments.





Tree functional traits such as allometry, wood density, specific leaf area (SLA), rooting depth, bark thickness, among others, contribute to a distinctive vegetation structure and functioning, which are highly adapted to periodic drought and fire regimes. To incorporate these characteristics into the LPJmL-VR-SPITFIRE model, we used a combination of literature data and field observations to derive and calibrate the relevant parameters for the new Tropical Broadleaved Savanna tree (TrBS) parametrization. A summary of all parameters and data sources used is provided in Table 1 and 2, with detailed explanations below.

2.3.1 Allometry and growth form

The tree allometry is defined through a diameter distribution that follows an asymptotic pattern, where height increases at a slower rate as diameter grows larger, with most trees remaining under 10 meters in height (Fig. S2A and C). A similar trend is observed in the relationship between diameter and crown area: trees initially grow in diameter, subsequently expanding their crown until crown growth reaches a plateau (Fig. S2B and D). This observed growth pattern is implemented by allometric relationships using PFT-specific allometric parameters within the LPJmL model (Schaphoff et al., 2018; Eqn. S1; Eqn. S2). To ensure an accurate representation of TrBS's tree growth, we analyzed field data to estimate maximum height, maximum crown area, and their relationship with stem diameter (Table S2). Using these field measurements, we derived the allometric constant values that best aligned with the observed data, by fitting the allometric equations to the data (Fig. S2). Details about site location, data collected, and their references can be found on Table S2.

Despite variations of wood density and SLA due to factors such as soil quality, temperature, and water availability, trees in more arid environments typically develop denser wood with lower SLA values (indicating thicker leaves), an adaptation to water





scarcity and mechanical stress (Scholz et al., 2008; Terra et al., 2018, Souza et al., 2024). While we based our wood density value on literature (Souza et al., 2024), the SLA values used in the development of TrBS PFT were estimated from field data collected from 71 individuals of 26 species (Table 1, Table S2).

Table 1: Allometry, drought mortality and rooting parameters used to define the new Tropical Broadleaved Savanna Tree (TrBS) PFT, along with the corresponding values for the Tropical Broadleaved Evergreen Tree (TrBE), and Tropical Broadleaved Raingreen Tree (TrBR). References cited apply exclusively to TrBS PFT. Details about the field survey data are available on Table S2. Additional information on TrBE and TrBR parameters, as well as parameters not included in this table, can be found in Schaphoff et al., (2018).

Parameter	Tropical Broadleaved Evergreen tree	Tropical Broadleaved Raingreen tree	Tropical Broadleaved Savanna tree	Reference
SLA (mm ² .mg ⁻¹)	9.04	14.71	7.36	Field survey (Table S2)
Wood density (g.cm ⁻³)	0.44	0.44	0.6	Souza et al., (2024)
Max. height (m)	100	100	10	Field survey (Table S2)
Max.crown area (m²)	25	15	10	Field survey (Table S2)
Parameter in allometry function (<i>K-allom 1</i>)	100	100	153	Field survey (Table S2)





Parameter	Tropical Broadleaved Evergreen tree	Tropical Broadleaved Raingreen tree	Tropical Broadleaved Savanna tree	Reference
Parameter in allometry function (<i>K</i> -allom 2)	40	40	12	Field survey (Table S2)
Parameter in allometry function (<i>K-allom 3</i>)	0.67	0.67	0.52	Field survey (Table S2)
Maximum leaf-to-root- mass-ratio scaling parameter	1	1	0.7	
(lr_{max}) Vertical root distribution parameter (β_{root})		0.9925, 0.9950, 0. 0.9981, 0.9986, 0.9		Sakschewski et al., (2021)
Shape parameter in logistic root growth function (<i>k</i> _{root})	0.02	0.02	0.07	Saboya and Borghetti (2012)

2.3.2 Root growth and belowground carbon allocation

Rooting depth is a crucial adaptation for the Cerrado species, enabling access to deep water reserves during prolonged dry periods (Oliveira et al., 2005; Tumber-Dávila et al., 2022). Due to its high investment in belowground structures, the Cerrado is often referred to as an 'upside-down forest,' storing approximately five times more carbon below-ground (in roots and as soil carbon) than above-ground (Terra et al., 2023). While deep roots are a well-documented feature of the Cerrado plants, rooting strategies vary widely among species. To try to reflect this diversity in rooting strategies in LPJmL-VR-SPITFIRE we allowed for 10 different root distributions (β_{root} parameter) per PFT. We chose the same range of β_{root} values for TrBS PFT as for the other PFTs, to allow a spectrum of shallow,





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intermediate and deep rooting strategies to compete. From β_{root} the depth where 95% of root biomass are found (D95) can be calculated (see Sakschewski et al., 2021). Studies show that the Cerrado tree seedlings invest more in root growth compared to shoot growth as a strategy to access water deeper in soil during the dry season (Hoffmann, Orthen and Franco 2004; Saboya and Borghetti 2012). We reflect this by modifying the shape parameter of the logistic root growth function (k_{root} , Table 1), to allow TrBS to reach deeper rooting depths already earlier in their lifecycle (Fig. 2), enhancing the underground competitiveness of these savanna trees. In LPJmL-VR-SPITFIRE, carbon allocation to coarse woody roots is represented by separate root sapwood and heartwood carbon pools, introduced in addition to the fine root carbon pool (Sakschewski et al., 2021). Due to the necessary balance between root and stem sapwood investment (Pipe Model approach; Shinosaki et al., 1964), and the relationship between tree height and rooting depth, deep root growth for TrBS saplings represents a trade-off between above- and belowground growth. The ratio between the leaf and the fine root biomass in the model depends on the model internally calculated water stress index (ω), where more root biomass is built under water stress, and is constrained by the lr_{max} (maximum leaf-to-root-mass-ratio) scaling parameter (Table 1; Schaphoff et al., 2018). We set lr_{max} to 0.7 to allow TrBS to invest relatively more into root biomass than the other tropical tree PFTs, where lr_{max} was set to 1 (Schaphoff et al., 2018).





Fig. 2: Logistic growth function scaling rooting depth to tree height, shown for a soil depth of 20m for the different PFTs (TrBE = tropical broadleaved evergreen, TrBR = tropical broadleaved raingreen, TrBS = Tropical Broadleaved Savanna).

2.3.2 Phenology

The Cerrado exhibits pronounced precipitation seasonality, which shapes the phenology of its vegetation. Deciduous and semi-deciduous species display leaf dynamics in which leaves shed during the dry season, peaking in July, and sprout during the transition to the rainy season in September (de Camargo et al., 2018). Despite the dominance of deciduous and semi-deciduous species (74%), the community rarely experiences complete defoliation, retaining at least half of its foliage in most years (de Camargo et al., 2018). This seasonal pattern is also evident in the Leaf Area Index (LAI) of trees. LAI values drop from around 1 in the rainy season to approximately 0.6 on the peak of the dry season (Hoffmann et al., 2005).

The degree of foliation in LPJmL-VR-SPITFIRE is given by the phenology status, which is updated daily (ranging from 0 = no leaves to 1 = full leaf cover) and derived by multiplication of four limiting functions, namely a water-limiting (f_{water}), light-limiting (f_{light}), cold-limiting (f_{cold}) and heat-limiting (f_{heat}) function (Schaphoff et al., 2018;



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Forkel et al., 2014). The shape parameters of f_{water} were chosen to reflect a behaviour intermediate between the evergreen and the raingreen PFT (Fig. S3), and thereby reflects the general phenological behaviour of the Cerrado community as explained above; f_{heat} , f_{cold} and f_{light} were set to the same values as for TrBE. 2.3.4 Fire dynamic and vegetation adaptation Approximately 6 million hectares burned in the Cerrado in 2023 (MapBiomas Fogo 2024), with 98% of these fires attributed to human activity (Schumacher et al., 2022). At local and landscape scales, fire dynamics are influenced by factors such as fuel availability, ignition sources, topography, and climatic conditions (Gomes, Miranda, and Bustamante 2018). In the Cerrado, fire behavior is closely tied to seasonal cycles and one key factor determining its behavior is the vapor pressure deficit (VPD) (Gomes, et al., 2020b; Oliveira et al., 2021). VPD is the measure of the difference between the vapour pressure of the moisture present in the air and the maximum vapour pressure the air can hold, being influenced by temperature and relative humidity. In the Cerrado, the VPD varies seasonally, with average values around 0.3 to 0.7 kPa in the rainy season and 1.4 to 2.0 kPa in the dry season (Cattelan et al., 2024). Higher VPD dehydrates plant biomass, especially from grasses, making it more flammable and susceptible to fire (Gomes, et al., 2020b). The VPD affects the rate of spread and intensity of the fire, with higher VPD resulting in faster and more intense fires in a given fuel bed (Gomes et al., 2020b; Oliveira et al., 2021). In LPJmL-VR-SPITFIRE, the fire danger index depends on VPD and is scaled via a PFT-specific factor α VPD, where higher values of α VPD increase fire danger. We calibrated a VPD to achieve good agreement between observed and modelled burnt area. A higher αVPD for TrBS than for TrBE and TrBR was chosen, because the fuel produced by the Cerrado trees burns more readily, compared to the fuel dropped by trees in the moist forests (dos Santos et al., 2018).





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Because of its fire-prone environment, the Cerrado trees exhibit several adaptations that enable them to survive fire damage. These include belowground organs that promote resprouting after fire, thick bark that insulates and protects internal tissues, robust terminal branches, leaves concentrated at branch tips, and persistent stipules that safeguard apical buds, all minimize fire damage (Simon et al., 2009; Simon and Pennington 2012). Fireinduced tree mortality in LPJmL-VR-SPITFIRE results from combined effects of cambial and crown damage (Oberhagemann et al., 2025). PFT-specific parameters for bark thickness were chosen to fit the relationship between stem diameter and bark thickness shown in Hofmann et al., (2009) (Fig. S3; Table 2). Scorch height, the highest point at which flames reach and affect the vegetation, is calculated from fire intensity and a PFT specific scaling factor (F; see Eqn. S5), which also depends on tree crown length relative to its height (Thonicke et al., 2010; Oberhagemann et al., 2025). The Cerrado trees have relatively long crowns compared to their total height, with a ratio of 0.53 (Table 2). While this exposes them to crown scorch, the above-mentioned adaptations result in an overall lower mortality risk from crown scorch, and we therefore adjusted the parameter F accordingly (Table 2).

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Table 2: Fire parameters used to define the new Tropical Broadleaved Savanna Tree (TrBS) PFT, along with the corresponding values for the Tropical Broadleaved Evergreen Tree (TrBE) and Tropical Broadleaved Raingreen Tree (TrBR) PFTs. References cited apply exclusively to TrBS PFT. SPITFIRE parameters for TrBE and TrBR are taken from (1) Thonicke et al., (2010), and (2) Drüke et al., (2019).





Parameter	Tropical Broadleaved Evergreen tree	Tropical Broadleaved Raingreen tree	Tropical Broadleaved Savanna tree	Reference
Leaf Longevity (years)	1.6	0.5	1	Cianciaruso et al., (2013); Souza, J. P. (2012)
Sensitivity to drought (c sens)	100	100	10	
Water stress resistance (c _{res})	0.1	0.1	0.1	
Water limitation factor (wscal _{min})	0	0.35	0	
αVPD	6	6	10	
Crown length parameter	0.3334 (1)	0.10 (1)	0.53	Field survey (Table S2)
Scorch height parameter (F)	0.193 (2)	0.0799 (2)	0.13	
Bark thickness par1/par2	0.0301/0.0281 (1)	0.1085/0.212 (1)	0.135/0.2820	Hoffmann et al., (2009)

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2.4 Simulation protocol

To evaluate the performance of the newly implemented TrBS PFT, two simulation runs were conducted: one including TrBS PFT (hereafter 'Savanna' simulation) and the other experiment excluding it (hereafter 'No Savanna' simulation). Both simulations covered





371 the period from 1901 to 2019, with a 5000-year spin-up phase, and utilized identical 372 environmental input data in a 0.5° horizontal resolution. The model spin-up was simulated from bare ground using climate input from 1901-373 374 1930 (with pre-industrial pCO2 = 276.59 ppm), which was repeated for 5000 years, to 375 allow carbon pools to reach equilibrium with climate. The transient simulation then ran 376 from 1901 to 2019. For model validation, we analyzed the last 30 years of the transient 377 run. Because we aim to evaluate the establishment and general characteristics of the new 378 TrBS PFT, all simulations were conducted for potential natural vegetation (PNV) only, 379 with no simulation of human land use to focus on geographical distribution of vegetation 380 and fire. While LPJmL-VR-SPITFIRE features the latest model updates regarding the nitrogen cycle (Bloh et al., 2018) and biological nitrogen fixation (Wirth et al., 2024), we 381 382 switched the nitrogen limitation off as it was beyond the scope for this study. 383 The LPJmL-VR-SPITFIRE model uses daily climate input, including air temperature, precipitation, wind speed, humidity, and long- and shortwave radiation. These datasets 384 385 were sourced from ISIMIP3a (https://data.isimip.org/10.48364/ISIMIP.664235.2), which combines GSWP3 data (1901-1978) and W5E5 data (1979-2019). Atmospheric CO₂ 386 387 concentration data were derived from the TRENDY project (Friedlingstein et al., 2023). Soil texture data were obtained from the Harmonized World Soil Database 388 389 (Nachtergaele et al., 2009). Soil depth in LPJmL-VR-SPITFIRE was defined using the 390 lower water table depth values provided by the SOIL-WATERGRIDS dataset (Guglielmo 391 et al., 2021). 392 Ignition sources for the SPITFIRE model are based on population density (Klein Goldewijk et al., 2011) for human ignitions, and lightning occurrence data from the 393 394 OTL/LIS dataset (Christian et al., 2003) for natural ignitions.





2.5 Model validation

For each of our simulation outputs, we selected appropriate Brazilian or global datasets to validate the modeled results from LPJmL-VR-SPITFIRE. All spatial analysis and comparisons between the validation data and model outputs were conducted in R, utilizing the ncdf4, terra, raster and sf packages. The analysis focused on the mean values of the last 30 years of the simulations (1990-2019). Details of each validation dataset are provided below.

2.5.1 Vegetation distribution

To validate the modeled distribution of the vegetation in Brazil, represented by the foliar projected coverage (FPC) of each PFT, we used Brazil's original vegetation distribution by IBGE (2017). The original IBGE map was a very detailed Shapefile, with specific variation of each major vegetation group, that would have complicated the comparison with the FPC and limited number of PFTs. For this reason, we aggregated the vegetation classes into 13 vegetation types following the attribute table of IBGE's product (Fig. 4). After that, we converted the Shapefile into a raster file using the function rasterize from the terra package in R.

To evaluate the distribution of the new TrBS PFT, as well as the other tropical PFTs, we overlaid the FPC output with the corresponding classification from IBGE. For this

comparison, we selected only grid cells where the respective FPC \geq 0.3 and matched the class in the IBGE dataset, generating a map that identifies under-, over-, and correctly simulated PFT coverage.



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2.5.2 Above- and belowground Biomass, evapotranspiration and productivity The above- and belowground biomass (AGB and BGB) validation maps were produced by the team from the Fourth National Communication to the United Nations Convention of Climate Change, here referred to as QCN (MCTI 2020). These maps were produced considering the distribution of Brazil's original vegetation (IBGE 2017) and estimating AGB and BGB using specific equations and field data that best fit each vegetation type. From these maps we derived a BGB:AGB ratio map to validate the structural characteristics of TrBS PFT. For better comparison, we calculated the Spearman Correlation between the two modeled scenarios of BGB:AGB and the QCN validation using the stats package from R software. For evapotranspiration (ET) and gross primary productivity (GPP), the mean annual distribution of the last 30 simulation years (1990-2019) were compared to reference datasets (GPP: Carvalhais et al., 2014; ET: ERA-Interim-Land, Balsamo et al., 2015) and evaluated via the Normalized Mean Squared Error (NMSE) and Pearson correlation (as described in Sakschewski et al., 2021). 2.5.3 Burned Area The Burned Area validation map was produced using the annual burned coverage product from MapBiomas Fogo 3.0 (2023) database. This product gives a 30 m resolution presence-absence map of areas in which fire occurred for a time series from 1985 to 2023. The burned area was calculated from the burned coverage for a 0.5° grid, covering all the Brazilian territory, for each year from 1990 to 2018. Then, from resulting annual burned area maps, we calculated the mean burned area for all selected time series. All calculations





and map generation from the MapBiomas dataset were performed using the Google Earth 439 440 Engine platform. 441 For the spatial distribution of annual burned area, we created a map of the human landuse fraction based on MapBiomas 9.0 land-use data (MapBiomas, 2023), using the mean 442 443 value from 1990 to 2019 (Fig. S5). Since our simulation considers only potential natural 444 vegetation (PNV), we weighed the burned area, in both the validation data and model 445 output, to account for fire occurrences in human-managed land. 446 The validation of the monthly burned area for the Cerrado biome was conducted using 447 the MapBiomas Fogo 3.0 dataset (2023). The burned area validation was also weighed by the natural land-cover of the corresponding year. This dataset was used to assess the 448 449 accuracy of the simulated seasonal burned area patterns in the Cerrado. The comparison 450 between the simulated scenarios and the MapBiomas data was evaluated using Normalized 451 Mean Squared Error (NMSE), Willmott's index, R², and p-value statistics from the 452 respective R packages kerntools, hydroGOF and stats (Drüke et al., 2019). 453 For carbon emission by fire (FireC), our validation is based on the Global Fire 454 Emissions Database (GFED4), which derives its fireC emission maps using its own burned 455 area data (van der Werf et al., 2017). GFED4 combines satellite observations of burned 456 area with biogeochemical modeling to estimate emissions of CO₂, CO, CH₄, and other 457 trace gases. Given the strong link between burned area and fire emissions, we apply the 458 same land-use fraction weighting approach as for burned area to ensure consistency in our 459 analysis.





3. Results

3.1 Vegetation distribution

The inclusion of TrBS PFT has significantly altered the distribution and abundance of key vegetation types across Brazil, particularly the Tropical C₄ grasses and TrBE PFTs. In simulations without TrBS, C₄ grass dominates across northeastern and central Brazil, occupying the whole Caatinga biome, most of the Cerrado and northern Atlantic Forest (Fig. 3).

TrBS establishes itself predominantly in the Cerrado and Pantanal biomes, aligning with regions classified as savanna vegetation by IBGE (Figs. 3 and 4). Pockets of TrBS also appear in northern portions of the Amazon biome, where patches of savanna-like vegetation can occur, and Atlantic Forest regions where seasonal forest is present (Fig. 3 and 4). The presence of TrBS results in a contraction of C₄ grass, which retreats mostly to the Caatinga biome, where they almost entirely dominate due to Caatinga's dry environment, while grass and savanna vegetation coexist in Pantanal, northern and eastern Cerrado (Fig. 3).



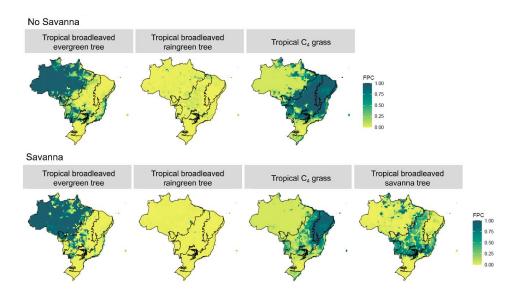






Fig. 3: Foliar Projected Cover (FPC) of the Plant Functional Types (PFT) for Tropical Broadleaved Evergreen Tree, Tropical Broadleaved Raingreen Tree, Tropical C₄ Grass and Tropical Broadleaved Savanna Tree in Brazil under two model configurations: 'No Savanna' and 'Savanna'.

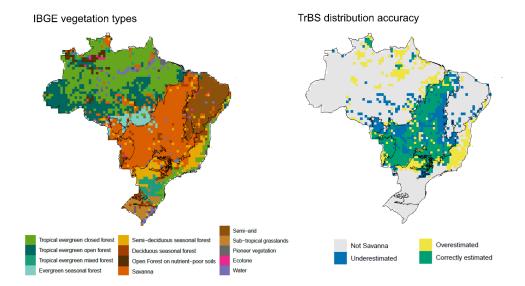


Fig. 4: Maps showing the Brazilian vegetation types according to IBGE (left) and TrBS PFT distribution accuracy (right) in comparison with the savanna vegetation class from IBGE. A threshold of 30% FPC cover was used to determine distribution accuracy.

3.2 Above- and belowground Biomass and vegetation structure

The inclusion of TrBS PFT significantly improved the simulated above- and belowground biomass patterns across Brazil compared to simulations without it. By better capturing the characteristic small trees with extensive belowground structures of the Cerrado, TrBS PFT led to an improved representation of the 'upside-down forest' in central Brazil (Fig. 5). As a reflection of the distinct allocation strategies of the Cerrado





vegetation, the biomass ratio (BGB:AGB) was also clearly improved in the Savanna scenario (Fig. 5). Although the simulated values did not fully match those observed in the QCN validation, as shown by the Spearman correlations (QCN vs. Savanna: 0.27; QCN vs. No Savanna: -0.16), the introduction of TrBS resulted in a more accurate simulation of carbon allocation across Brazil. Normalized Mean Error (NME) and correlation of modelled ET and GPP across Brazil were in a similar range for both simulations in comparison to the reference data (Fig. S9; Table S3).

TrBS PFT also improved the representation of tree height gradients, with tall trees, above 20 m, in the Amazon transitioning to slightly shorter trees in the southern Amazon and reaching approximately 7 m in the Cerrado (Fig. 5; Fig. S7). Additionally, the model now captures a gradient in rooting depth (D95), with shallower roots in the Amazon, deepening towards the southern Amazon and Cerrado (Fig. 5; Fig. S7). This pattern is further supported by a higher D95:height ratio in the Cerrado, aligning with the characterization of its vegetation as an 'upside-down forest,' where rooting depth can exceed tree height.





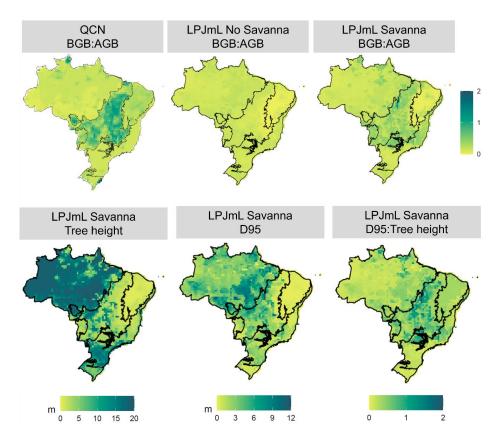


Fig. 5: FPC-weighted BGB:AGB below- and aboveground biomass ratio (BGB:AGB) from LPJmL simulations and QCN validation product (top row), and FPC-weighted tree height and D95, and their ratio (D95:Tree height) from LPJmL 'Savanna' simulation (bottom row).

3.3 Fire dynamics

The introduction of TrBS PFT significantly influenced burned area patterns across biomes. LPJmL-VR-SPITFIRE generally underestimated burned areas in the 'No Savanna' simulation, particularly in the Cerrado and Amazon regions, while overestimating them in the Caatinga (Table 3; Fig. 6). With the inclusion of the new TrBS PFT, the burned area estimates in the Cerrado increased, surpassing the values recorded in





the MapBiomas Fogo in the central Cerrado, but still underestimating burned area in the northern region (Fig. 6). In contrast, the Amazon continued to show underestimations of burned areas, likely due to the general assumption of higher human-caused ignitions in rural areas not capturing the real motivations to set fire. Despite these regional discrepancies and given the SPITFIRE improvements applied to both model configurations, the inclusion of TrBS PFT and its adjusted parameterisations led to a clear improvement in the total burned area estimates for Brazil (Table 3).

Table 3: Total burned area for all Brazilian biomes simulated by LPJmL-VR-SPITFIRE for 'Savanna', and 'No Savanna' scenarios, and the validation data from MapBiomas Fogo. The values are in Thousand hectares (Kha).

	Savanna (Kha)	No Savanna (Kha)	MapBiomas (Kha)
Cerrado	6660.7	2597.21	7748.43
Amazon	405.67	44.48	4991.57
Atlantic Forest	89.69	5.82	130.83
Caatinga	2937.68	2818.43	345.6
Pantanal	203.84	5.33	558.55
Pampa	1.15	1.15	11.89
Brazil	10298.73	5472.42	13786.89





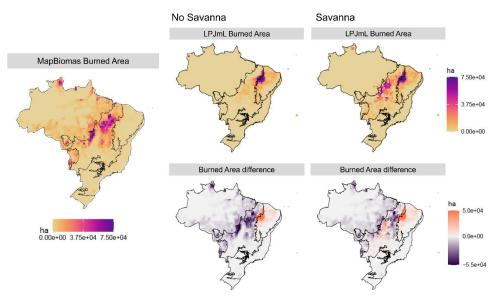


Fig. 6: LPJmL simulations of burned area in Brazil for 'No Savanna' and 'Savanna'

scenarios (top row), the validation data by MapBiomas Fogo (left), and the respective

difference between simulated results and MapBiomas Fogo validation (bottom row).

We could also observe an improvement in the seasonal patterns of the burned area in the Cerrado Biome with the incorporation of TrBS PFT (Fig. 7). The Savanna scenario, compared to the MapBiomas data, shows an NMSE of 0.39 with an R² of 0.45, and a Willmott index of 0.81, indicating that the model has a good fit. The No Savanna scenario has a slightly higher NMSE (0.83) and Willmott index (0.86), and a lower R² (0.40) compared to MapBiomas, suggesting that removing TrBS reduces the overall model's ability to represent observed seasonal fire patterns.





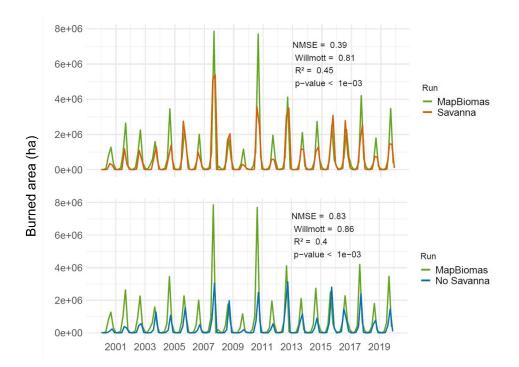


Fig. 7: Total monthly burned area, for the Cerrado Biome, from 2000 to 2019 for two LPJmL simulation scenarios: Savanna' (top) and 'No Savanna' (bottom) in comparison with the monthly burned area product from MapBiomas Fogo.

Carbon emission by fire (FireC) patterns reflect directly the burned area patterns (Fig. 8). Overall, the introduction of TrBS did not improve emission estimates in Brazil as most of the emission comes from southeastern Amazon, which has its burned area highly underestimated by our model. Fire-related emissions in the Cerrado, on the other hand, were overestimated in the Savanna scenario, especially in the central portion of the biome, which is linked to the spatial burned area patterns.





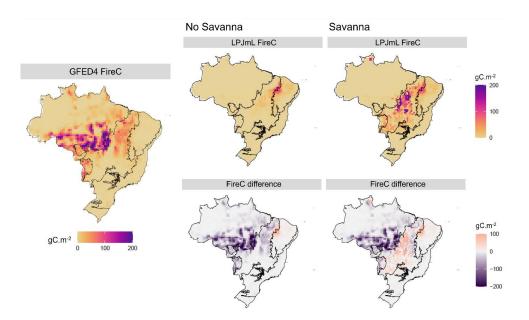


Fig. 8: LPJmL simulations of Fire carbon emission in Brazil for No Savanna and Savanna scenarios (top row), the validation data by GFED4 (left), and the respective difference between simulated results and GFED4 validation (bottom row).

3.4 Extrapolation to the global scale

Since the LPJmL-VR-SPITFIRE model will also be run on a global scale in future applications, the parameterization of the new PFT was tested in a global simulation using the same climate input data set as for the Brazilian simulations. Although TrBS PFT was specifically adapted to the Cerrado tree data, we found high agreement in the simulated global savanna distribution compared to a reference dataset (Hengl et al., 2018). The results are shown in Supplementary Fig. S8.



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4. Discussion

4.1 Advancing in Savanna Modeling

SPITFIRE model significantly enhances the representation of vegetation and fire dynamics in Brazil. TrBS improved simulations of carbon allocation, particularly below- to aboveground biomass ratio, and better represented fire behavior, namely the spatial distribution and temporal dynamics of burned area. Key features of the Cerrado, that also apply to tropical savannas in general, are now well represented: a vegetation that is adapted to seasonal drought environments by accessing water with deep root systems and allocating more resources belowground and can cope with or even depends on regular occurring fires. This update moves the capability of LPJmL-VR-SPITFIRE beyond the previous binary classification of tropical rainforests and grasslands, allowing for a more nuanced depiction of ecological transitions, such as the Amazon-Cerrado interface. By incorporating savanna vegetation, the model facilitates more realistic investigations into the future dynamics of these biomes and allows for a more critical evaluation of restoration efforts within this specific vegetation type. A model limited to representing only 'forest' and 'grasslands' will fail to capture the significance and vulnerabilities inherent in savanna ecosystems like the Cerrado. Other DGVMs have struggled earlier to accurately depict the savanna biome (Whitley et al., 2017; Baudena et al., 2015), as many of them oversimplify root dynamics, specific phenology and vegetation-fire feedback. In particular, the role of rooting depth, which is often constrained to shallow values in DGVMs, has a significant impact on the competition between forest, savanna vegetation and grasses, as shown by Langan et al., (2017) for South America. The introduction of root growth and rooting depth diversity in the LPJmL model (Sakschewski et al., 2021) can therefore be considered key to improving savanna

The introduction of a savanna-specific Plant Functional Type in the LPJmL-VR-





597 modeling, as it allows vegetation adaptation to water scarcity, especially when subdividing 598 the PFTs into different rooting strategies. Importantly, the competition for water between savanna trees and grasses can also be better depicted when partitioning of access to water 599 600 resources is considered (Whitley et al., 2017; Baudena et al., 2015). 601 The SPITFIRE model provided a process-based calculation of ignition, fire spread and 602 tree fire mortality that is central to better reproduce typical Cerrado and savanna biome 603 characteristics. However, the often-extensive use of fire for land management purposes in 604 savannas (and, for example, also the edges of Amazonia) is not explicitly reflected in 605 SPITFIRE, as the model only considers a function of population density to calculate 606 ignition risks. Recent attempts to better reflect anthropogenic fire management (Perkins et al., 2024) could help further improve Cerrado fire modeling. Given the increasing pressure 607 608 on the Cerrado and already observed shifts in fire regimes (da Silva Arruda et al., 2024), this is key to enabling simulations of future trajectories in the region. While accurate fire-609 vegetation dynamics are crucial for realistic biome distribution simulations, they are 610 611 insufficient if key vegetation characteristics, such as deep root water uptake, are not 612 adequately represented (D'Onofrio et al., 2020, Baudena et al., 2015). 613 We parameterized the savanna tree PFT using field and literature data specific to the 614 Brazilian Cerrado region and achieved a good fit between modelled and observed savanna 615 distribution. Other modeling studies, for example Moncrieff et al., (2016), have encountered challenges to capture the Cerrado extent due to missing processes. 616 617 Extrapolations of model parametrization that were specifically evaluated for one savanna 618 region, here the Cerrado, often leads to inaccuracies, given the distinct climate, species composition, and fire-vegetation interactions in each of the savanna-type regions (Solbrig 619 620 et al., 1996; Lehmann et al., 2014; Moncrieff et al., 2016). Nevertheless, to assess the 621 robustness of our parameterization, we conducted a global simulation and found that the





parameterization developed for the Brazilian savanna performed well in simulating global tropical savanna distributions (Fig. S7). Future work could also include an assessment to better capture main functional differences between each savanna-type region.

4.2 Challenges in Representing the Cerrado Dynamics

Despite these advancements, several challenges remain in capturing the complex vegetation dynamics of the Cerrado. Although our simulations already produce a mix of savanna trees and grasses in the northern Cerrado, one key issue is achieving a realistic balance and dynamic feedback between tree and grass cover. Achieving a more realistic vegetation structure is challenging with representing tree and shrub individuals as generalized representatives of each PFT, even though differentiations by rooting depth were incorporated in LPJmL-VR-SPITFIRE. Building on the knowledge gained in this study a gap-model framework that simulates individual trees and also incorporates trait diversity such as the LPJmL-FIT model (Sakschewski et al., 2015; Thonicke et al., 2020), could offer a more accurate representation of tree-grass coexistence in the near future.

Our analysis focused on depicting the overall distribution and performance of the new savanna PFT across Brazil. A detailed, site specific validation of carbon and water fluxes, the seasonality of leaf cover and productivity might complement the results of this study. In this context, further model refinement could be undertaken, such as implementing shade intolerant PFTs in the model (Ronquim et al., 2003; Lemos-Filho et al., 2010). Additionally, a notable limitation observed in our simulations is the overrepresentation of C4 grasses in the Caatinga biome, which contrasts with the known vegetation characteristics of the region. The Caatinga is a semi-arid biome characterized by diverse vegetation physiognomies, including succulents and small shrub vegetation, with a predominance of seasonal dry tropical forests rather than extensive grasslands (de Queiroz





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et al., 2017). In follow-up work with LPJmL-VR-SPITFIRE, it should be determined which PFT combination is closest to this complex real-world vegetation. As discussed for the tree-grass coexistence in the previous paragraph, Caatinga vegetation modeling would benefit from an individual tree approach (as in LPJmL-FIT) rather than the average individual approach of the LPJmL model. Addressing this will be important for improving model realism and its applicability to drier tropical ecosystems, as well as enhancing its performance in representing fire patterns in the region. Fire impacts on the vegetation are a key process that maintains savannas' open-canopy structure. Our parameterization of the savanna tree PFT resulted in a vegetation type that is readily burning, while being well protected against lethal damage from fire. However, resprouting mechanisms, which are crucial for post-fire recovery (Souchie at al. 2017) are not yet implemented explicitly in the vegetation model but would improve the simulation of vegetation recovery. The amount of fuel available for burning is another key area of ongoing model development, as it strongly influences fire spread and intensity. In the most recent SPITFIRE version that we used in this study, the live grass moisture calculation was substantially improved (Oberhagemann et al., 2025), better reflecting seasonal dynamics of fuel availability of grass vegetation. However, currently live woody materials are not parametrized as part of the burnable matter in SPITFIRE, but this is potentially important in Cerrado (Oliveira et al., 2021). In Savannas, there is often extensive use of fire for land management purposes. Specifically, in the Cerrado, fire in natural areas is associated with the use of fire for deforestation, with fire escaping to natural areas and also with pasture management; in areas of mechanized agriculture and planted forests, owners rather protect the areas against fire. The underestimation in burned area observed in southeastern Amazon is also a product

of such land-use change practices, especially the usage of fire to manage large extension





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of pasturelands in Amazon (MapBiomas Fogo, 2024) which could possibly escape and damage adjacent tropical rainforest (Cano-Crespo et al., 2015). The SPITFIRE model does not explicitly account for different fire management regimes but scales ignitions to human population density. This might explain the lack of fire at the edges of Amazonia in our simulations and also complicates validation of burned area and fire carbon emissions from our PNV simulations. We therefore weighed both validation data and model output by the human landuse fraction from MapBiomas to exclude grid cells with extensive human land use from the analysis. The most recent version of LPJmL incorporates the nitrogen cycle (von Bloh et al., 2018), along with mechanisms of biological nitrogen fixation (BNF, Wirth et al., 2024). Soils in the Cerrado are characterized by acidity, high aluminum concentrations, and nutrient scarcity (Bustamante et al., 2006; 2012), requiring vegetation to develop specific adaptations that confer a competitive advantage in these nutrient-poor conditions. Future advancements should leverage these model enhancements to incorporate nitrogen and other nutrient constraints, enhancing ecological realism to specifically address this aspect to the complex ecological interactions. Beyond the factors already discussed, rootable soil depth significantly influences vegetation dynamics. However, determining the maximum depth roots can physically penetrate is challenging, as they can grow into bedrock and access groundwater, but are also limited by high soil density and low oxygen availability. In our simulations we used the water table depth of Guiglemo et al., (2021) as a proxy for rootable soil depth, which allows deep rooting over large parts of the Cerrado, in line with observations of deep rooting vegetation. While this method provides reasonably spatial variable maximum rooting depths, LPJmL-VR-SPITFIRE does not simulate an actual water table. In reality, deep-rooted trees can tap groundwater, but LPJmL-VR-SPITFIRE assumes free drainage,





preventing this interaction. Consequently, some areas may experience artificially shallow rooting depths (e.g. Amazonian floodplains) without the benefit of accessing deeper water reserves, a factor that could become important, especially when running future simulations with the model. Considering these aspects in future work, especially global studies, could further improve the representation of belowground competition and resulting spatial vegetation distribution.

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5. Conclusion

The parameterization of the new Tropical Broadleaved Savanna PFT (TrBS) in LPJmL-VR-SPITFIRE significantly improves the representation of the Cerrado biome, the secondlargest vegetation formation in South America, in terms of belowground vs aboveground competition, vegetation dynamics and fire. By inclusion of variable rooting strategies along with recent process-based fire modeling, and a new drought mortality function, we present a model that is suited to study complex ecological interactions of the sensitive Cerrado biome that are rapidly changing under ongoing climate change. Here, we combined literature and observational data to parameterize the TrBS PFT and to adjust parameters of tree and root allocation functions, among others. Introducing a dedicated vegetation type for tropical savannas and combining with variable rooting strategies will equip DGVMs to make more precise assessments of recovery, reforestation, and regeneration strategies in these unique ecosystems. By refining the modeling of savanna dynamics, this study provides a valuable foundation for improving conservation strategies, land-use planning, and climate mitigation efforts in fire-prone landscapes such as the Cerrado. The introduction of a savanna-specific PFT with deeper rooting depth not only led to a more realistic allocation of carbon belowground but also enabled the model to reproduce the iconic "upside-down forest" structure of the Cerrado. This structural realism



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also translated into better representation of vegetation distribution, fire regimes, and their seasonal patterns. These results underscore the importance of incorporating trait diversity, particularly rooting strategies, into DGVMs. Building on this progress, future work, such as extending this savanna-specific PFT to individual-based models like LPJmL-FIT, can further enhance our understanding of post-fire recovery dynamics interacting with functional diversity and more clearly distinguish the intrinsic ecological behavior of tropical savannas from that of tropical forests. 6. Code and Data Availability The LPJmL-VR-SPITFIRE model is open-source and available at [link will be added in future]. Field survey data used in this study are available from the corresponding author upon reasonable request. All other relevant data supporting the findings of this study are available from the authors or included in the supplementary materials. 7. Competing interests One author is a member of the editorial board of journal "Biogeosciences". 8. Author contributions *J.S.: Data curation, Formal analysis, Visualization, Writing – original draft *S.B.: Methodology and Software, Formal analysis, Visualization, Writing – original draft W.v.B.: Methodology and Software, Writing – review and editing M.Bi.: Methodology and Software, Writing – review and editing B.S.: Conceptualization, Writing – review and editing L.O.: Writing – review and editing





K.Th.: Supervision, Writing – review and editing

M.Bu.: Supervision, Writing – review and editing

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