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Climate Change in the Brazilian Cerrado: A Looming Threat to Terrestrial Biodiversity

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ABSTRACT

Over the past 5000 years, the predictable climate seasonality of the Brazilian Cerrado has played a crucial role in shaping the life history strategies of species and the structure of ecological communities of this global biodiversity hotspot. However, this biome is becoming hotter and drier, with a notable lengthening and intensification of the dry season. Declining rainfall results from three key factors: the expansion of the South Atlantic Subtropical Anticyclone, warming of northern tropical Atlantic waters, and reduced evapotranspiration during the dry season due to widespread land conversion. The evapotranspiration drop also plays a pivotal role in regional warming and higher vapor pressure deficit. Climatic change already affects the physiology, phenology, and reproduction of the Cerrado plants, while also driving community-level alterations, such as woody encroachment and ant–plant–herbivore interaction outcomes. Dry season lengthening is likely to reduce the biomass and alter the dynamics of microbial communities, with negative effects also extending to invertebrates and other groups. The pronounced warming reduces the amount and duration of dewfall, an important water source for insect pollinators and other animals with low vagility during periods of drought. Concerning vertebrates, the most suggested impact is the loss of specialist or endemic species, with restricted distributions, and the expansion of generalist species, lowering the levels of β- and γ-diversity across the region and

making communities poorer and more homogenized. In summary, climate change is actively reshaping Cerrado communities, and species' survival will largely depend on their phenotypic plasticity, evolutionary response, and dispersal capabilities.

This article is categorized under:

Assessing Impacts of Climate Change > Observed Impacts of Climate Change

Climate, Ecology, and Conservation > Observed Ecological Changes

Trans-disciplinary Perspectives > Regional Reviews

1 | Introduction

The Brazilian Cerrado (hereafter called Cerrado) is the second-largest biome in Brazil (the term "biome" is used here only in line with Brazil's legal framework), recognized as a global biodiversity hotspot harboring thousands of endemic species (Klink and Machado 2005). It spans around 2 million km^2, comprising a dynamic mosaic of vegetation, including forests, savannas, and grasslands composed of a broad spectrum of species with different growth forms transitioning into one another in the landscape (Figure 1). While climate broadly defines the Cerrado boundaries, fire, competitive interactions, and edaphic factors interact and shape the different vegetation types at local scales (Mistry 1998). The climate is characterized by elevated temperatures and seasonal rainfall distribution, with wet summers and dry winters, which remained stable throughout the Late Holocene (from 5000 years ago to the present) (Behling and Hooghiemstra 2001; Ledru et al. 2006). The duration and intensity of wet and dry seasons impact the biotic communities by alternating water availability, controlling plant phenology/reproduction, and mediating intra and interspecific interactions (Calixto et al. 2021; Rossatto and Franco 2017).

The Cerrado is seriously threatened by human activities. Agricultural and pasture expansion, and thousands of anthropogenic wildfires annually, have caused widespread habitat loss (Strassburg et al. 2017). Regional climate change amplifies these pressures, interacting with land-use change and fire regimes to further threaten biodiversity. These impacts, predicted over two decades ago through simulations of the massive removal of native vegetation combined with increased concentration of greenhouse gases (Costa and Pires 2010; Hoffmann and Jackson 2000), are now confirmed by observational data. The primary goals of our study are: (i) to synthesize the most recent understanding of the processes driving climate change in the Cerrado, and; (ii) to project the potential impacts of these changes on the region's diverse terrestrial biodiversity across different taxonomic groups. This synthesis is essential for informing effective conservation and land management strategies, enabling stakeholders to anticipate ecological shifts, prioritize vulnerable species and habitats, and implement targeted mitigation and adaptation measures to safeguard the Cerrado's unique ecosystems and biodiversity in the face of ongoing climate change. For comparison purposes, we used the same annual division proposed by Hofmann et al. (2023), with four distinct seasons according to rainfall distribution: wet season (WS; December–March), the beginning of the dry season (BDS; April–May), the dry season (DS; June–September), and the beginning of the wet season (BWS; October–November).

2 | Regional Climate Change in Cerrado

Currently, the most evident alteration caused by climate change in the Cerrado is the lengthening and intensification of DS, resulting from atmospheric warming coupled with reduced rainfall (Figure 2). This rainfall reduction varies regionally, ranging from 5% to 15% of total annual precipitation, and three main factors contribute to this trend (Campos and Chaves 2020; Hofmann et al. 2023). First, changes in regional rainfall appear to have begun in the late 1960s (Hofmann et al. 2023), coinciding with rising sea-level atmospheric pressure in the South Atlantic due to the expansion of Hadley cell circulation (Choi et al. 2014). These shifts are likely linked to increasing greenhouse gases and declining stratospheric ozone, significantly altering Southern Hemisphere atmospheric circulation, especially the South Atlantic Subtropical Anticyclone (SASA) (Reboita et al. 2019). SASA intensification/expansion results in higher sea level pressure and strengthened zonal winds, leading to atmospheric moisture transfer from the Cerrado to other regions (Hofmann et al. 2023). These changes inhibit vapor condensation and cloud formation, reducing precipitation and rainy days (Figure 3a). While alterations in atmospheric circulation due to SASA affect the Cerrado year-round, they are most pronounced during the DS and BWS, when the anticyclone is stronger and closer to the Brazilian coast (Hofmann et al. 2023).

A second factor attributed to the decline in Cerrado rainfall is a change in atmospheric circulation caused by the warming of the northern tropical Atlantic Ocean. This phenomenon weakens moisture transport from the sea to South America, reducing atmospheric water vapor, particularly in the central and northern Cerrado near the Amazonian border (Espinoza et al. 2016; Marengo et al. 2022). The third factor is a reduction in vapor supply due to decreased evapotranspiration, which may seem counterintuitive given rising air temperatures and evaporative demand (Figure 3b). However, models predicting the climatic consequences of native vegetation suppression in the Cerrado have confirmed this decline during DS and BWS through field measurements and remote sensing (Oliveira et al. 2005). The primary cause is reduced rooting depth from land-use changes, along with increased albedo, reduced leaf area, and turbulence caused by pastures and crops (Costa and Pires 2010). Converting Cerrado forests and savannas to pasture and cropland can reduce evapotranspiration by 20% to 45%, depending on the transition type (Rodrigues et al. 2022). During DS and BWS, native vegetation's evapotranspiration significantly exceeds that of agricultural areas, as tree root systems can access deeper soil water (Oliveira et al. 2005). With water bodies covering less than 1% of the Cerrado and limited soil moisture in dry pastures and fallow crops during the DS, increased evaporation due to higher air demand does not offset the decline in transpiration from the loss of native

(b)

Cerrado Terrestrial Biodiversity

- Cerrado is often regarded as the most biodiverse savanna in the world.

- Number of species living in the Cerrado is unknown, but Brazilian governmental agencies assume it exceeds 320,000.

- 12,829 plants species and 4,613 endemics (Silva et al. 2022; Jardim Botânico do Rio de Janeiro, 2024).

- More than 95,000 invertebrate species (estimated number) (EMBRAPA, 2024).

- 204 amphibians species and 124 endemic species (Aguiar et al. 2015; Vieira-Alencar et al. 2024).

- 278 reptiles species and 129 endemic species (Aguiar et al. 2015; Vieira-Alencar et al. 2024).

- 856 birds and 28 endemic species (Silva and Santos 2005; Lopes and Silva 2024).

- 251 mammals species and 42 endemic species (Aguiar et al. 2015; Vieira-Alencar et al. 2024).

Cerrado Phytophysiognomies

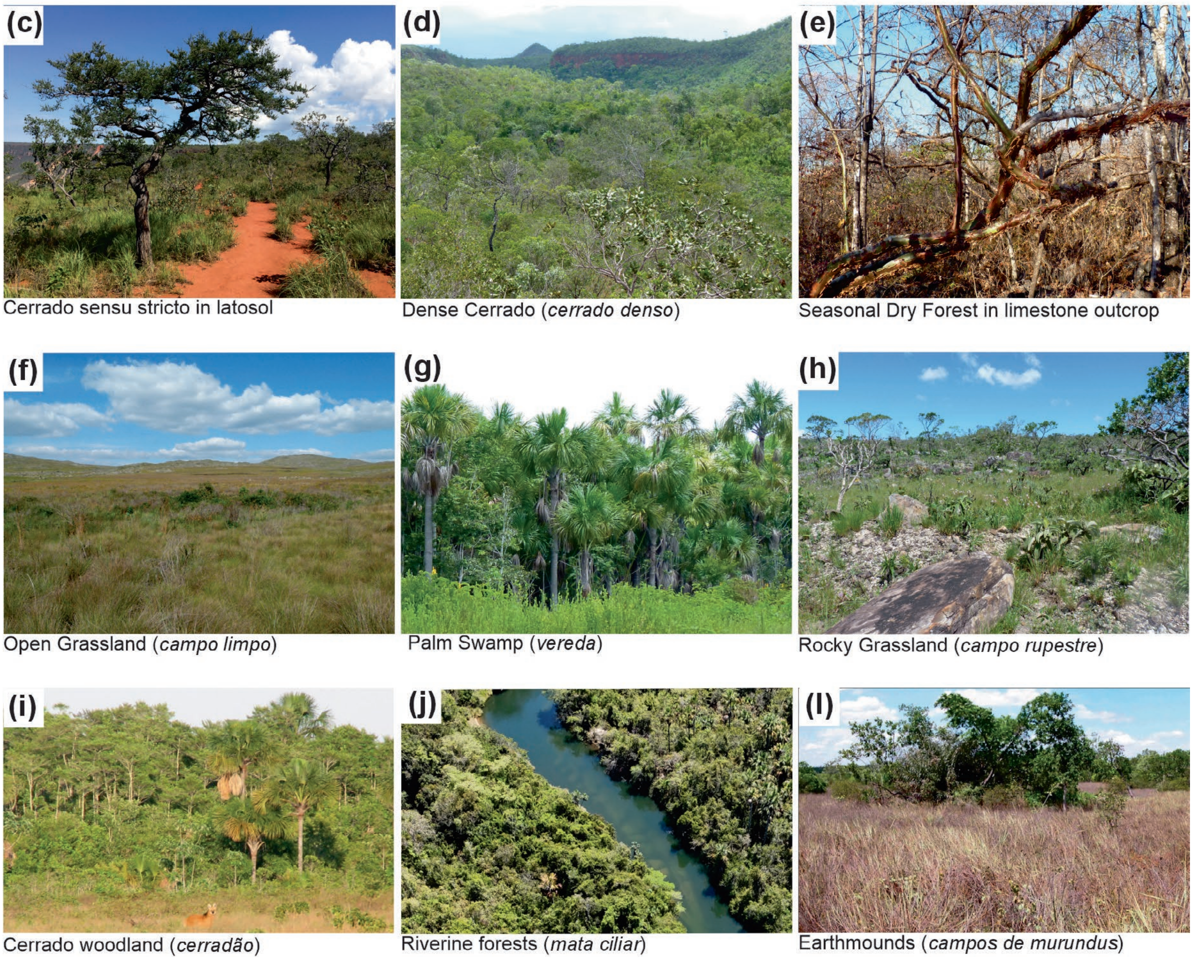

FIGURE 1 | Legend on next page.

FIGURE 1 | Location of the Brazilian Cerrado, its terrestrial biodiversity, and main phytophysiognomies. (a) Official limits of the Cerrado and other Brazilian biomes. (b) Cerrado terrestrial biodiversity information compiled in the recent literature. (c) Cerrado sensu stricto vegetation in the Jalapão State Park, state of Tocantins. (d) and (e) Dense Cerrado (*cerrado denso*) and Seasonally Dry Forest (*mata seca*) areas, recorded near Mambaí municipality, state of Goiás. (f) Open Grassland (*campo limpo*) vegetation in the Serra da Canastra National Park, state of Minas Gerais. (g) Palm Swamp (*vereda*) in Sesc Serra Azul Park, state of Mato Grosso. (h) Rocky Grassland (*campo rupestre*) area, recorded near Chapada dos Veadeiros National Park, state of Goiás. (i) Cerrado woodland (*cerradão*) vegetation in the Emas National Park, state of Goiás. Riverine forests (*mata ciliar*) vegetation, recorded in Porto Cajueiro Private Natural Heritage Reserve, state of Minas Gerais. Earthmound fields (*campos de murundus*) in the Sete Cidades National Park, state of Piauí (photo provided by Mario Barroso Ramos Neto).

vegetation. Therefore, the effects of the second and third factors converge to diminish the regional air moisture content, reinforcing the effects of SASA changes and prolonging the DS duration.

Beyond its effects on the hydrological cycle, the suppression of native vegetation also acts as a radiative forcing by altering energy budget components (Costa and Pires 2010). This reduction in evapotranspiration plays a crucial role in regional warming by decreasing latent heat flux, which increases the energy available for sensible heat flux, resulting in significant rises in surface and air temperatures (Loarie et al. 2011). Long-term temperature data reveal distinct warming trends for nocturnal and diurnal periods, reflected in minimum and maximum temperatures. Minimum temperatures have gradually increased since the 1960s, likely linked to the intensification of the global greenhouse effect, while maximum temperatures have sharply risen since the 1980s, coinciding with significant agribusiness expansion in the region (Hofmann et al. 2021). Diurnal and nocturnal warming are more pronounced during DS and BWS, with monthly rates ranging from 0.3°C to 0.7°C per decade. These periods are the same ones in which a reduction in regional evapotranspiration is observed, which is attributable to the expansion of pastures and crops (Spera et al. 2016). Regional warming has also caused an increase in vapor pressure deficit, as well as a reduction of relative humidity over recent decades (Hofmann et al. 2021). Both are a consequence of air expansion with increasing temperature, which is why they are greater during BWS, when warming is more pronounced. The Cerrado warming has also increased dew point depression at night, hampering vapor condensation on the surface and potentially reducing the amount and duration of dewfall (Hofmann et al. 2021).

The increased vapor pressure deficit, coupled with decreased rainfall, has extended the duration of water deficit months in the Cerrado. A recent study comparing contemporary climate data with geochemical proxies in speleothems revealed that the ongoing drying trend has been unprecedented over the past 700 years (Stríkis et al. 2024). Studies have documented the environmental consequences of climate change, noting that declining rainfall and rising agricultural water use have resulted in fewer floods and more droughts in the Cerrado (Chagas et al. 2022). An analysis of a 33-year time series across 81 river basins found reduced water flow in 71 basins (Salmona et al. 2023). The adverse effects of climate change are particularly pronounced during severe droughts when heatwaves reduce soil moisture, terrestrial water storage, evapotranspiration, and primary productivity (Lopes Ribeiro et al. 2021; Rossi et al. 2023). Such droughts often correlate with strong El Niño events or periods of anomalous warmth in the Tropical North Atlantic (Marengo et al. 2022). In 2023, a strong El Niño year, most of the Cerrado experienced its warmest start to spring in at least 63 years (Perkins-Kirkpatrick et al. 2024).

Regarding projections for the end of the 21st century, climate model forecasts indicate an amplification of regional climate change currently in progress. There is robust evidence that increasing the concentration of greenhouse gases will intensify the Hadley circulation, induce atmospheric moisture divergence, and reduce the tropospheric relative humidity in the tropics (Lau and Kim 2015). Therefore, this process will probably increase the tropospheric and surface dryness of Cerrado (Cattelan et al. 2024). Considering only the most pessimistic scenario generated by the Intergovernmental Panel on Climate Change (SSP5-8.5), the CMIP5/CMIP6 model's projections for the Cerrado suggest slightly increased precipitation during the WS and a reduction in other periods, especially during BWS (Cattelan et al. 2024; Ortega et al. 2021). Furthermore, the forecasts show a clear warming trend with an average increase of 6°C by the end of the 21st century, with the strongest projected temperature rise in South and Central Americas predicted to occur during Cerrado's BWS (Ortega et al. 2021).

3 | Impacts on Terrestrial Biodiversity

3.1 | Vegetation

The increased temperatures, vapor pressure deficit, reduced rainfall, and prolonged DS in the Cerrado will likely impose strong selective pressure on plant physiology, affecting their persistence. Species' responses will depend on their capacity to adapt to a hotter, drier environment, influenced by genetic composition and phenotypic patterns (Franco et al. 2014; Souza et al. 2016). Phenotypic plasticity will be critical for species' survival, influencing geographical ranges and, consequently, the distribution and boundaries of vegetation types (Valladares et al. 2007). In the Cerrado, leaf fall peaks in the DS (Rossatto 2013). However, many native plants renew their foliage at the end of DS and during the BWS, when the effects of climate change are more intense, and the atmosphere's evaporative demand is at its maximum (Giambelluca et al. 2009). Bud break and leaf expansion in the DS can only occur if the plant is fully hydrated. Trees and other growth forms can do this because of their physiological mechanisms to deal with the high evaporative demand and the water shortage imposed by rainfall seasonality. The mechanisms involved are tight stomata control of transpiration, water storage tissues, deep root systems, and mechanisms linked with hydraulic safety and an efficient water transport system to keep

Wet Season (December-March)

	Climate Normal 1961-1990	Climate Normal 1991-2020	Diference
Mean Temperature (°C)	23.9	24.7	+0.8
Maximum Temperature (°C)	30.0	30.8	+0.8
Minimum Temperature (°C)	20.0	20.7	+0.7
Relative Humidity (%)	78.5	76.1	-2.4
Total Evaporation (mm)	357.1	425.5	+70.4
Total rainfall (mm)	878.1	858.4	-19.7

Beginning of Dry Season (April-May)

	Climate Normal 1961-1990	Climate Normal 1991-2020	Diference
Mean Temperature (°C)	22.8	23.6	+0.8
Maximum Temperature (°C)	29.6	30.5	+0.9
Minimum Temperature (°C)	18.2	18.9	+0.7
Relative Humidity (%)	74.3	71.0	-3.3
Total Evaporation (mm)	209.1	251.2	+42.1
Total rainfall (mm)	148.6	142.8	-5.8

Dry Season (June-September)

	Climate Normal 1961-1990	Climate Normal 1991-2020	Diference
Mean Temperature (°C)	22.1	23.1	+1.0
Maximum Temperature (°C)	30.2	31.3	+1.1
Minimum Temperature (°C)	16.1	16.9	+0.8
Relative Humidity (%)	60.9	55.7	-5.2
Total Evaporation (mm)	686.5	866.4	+179.9
Total rainfall (mm)	89.2	71.0	-18.1

Beginning of Wet Season (October-November)

	Climate Normal 1961-1990	Climate Normal 1991-2020	Diference
Mean Temperature (°C)	24.3	25.4	+1.1
Maximum Temperature (°C)	31.0	32.4	+1.4
Minimum Temperature (°C)	19.8	20.7	+0.9
Relative Humidity (%)	70.5	64.4	-6.1
Total Evaporation (mm)	261.5	340.9	+79.4
Total rainfall (mm)	310.7	289.1	-21.6

FIGURE 2 | Legend on next page.

FIGURE 2 | Change in the climate variables recorded in the Brazilian Cerrado in the last two normal climates (i.e., 1991–2020 and 1961–1990) during the wet season, the beginning of the dry season, the dry season, and the beginning of the wet season. Seasonal values of mean temperature, maximum temperature, minimum temperature, relative humidity, and total evapotranspiration were calculated from the arithmetic mean of normal data from 45 meteorological stations (Table S1) published by the National Institute of Meteorology (INMET 2024). Total rainfall seasonal values were extracted from Hofmann et al. (2023), representing the arithmetic mean of 70 rainfall stations of the Brazilian Cerrado. The Wet Season photograph was taken in Emas National Park, in the state of Goiás (photo by Mario Barroso Ramos Neto). The Beginning of Dry Season was captured in Jalapão State Park, Tocantins (photo by Igor Pfeifer Coelho). The Dry Season image was photographed near the Serra da Mesa Dam, in northern Goiás. The Beginning of Wet Season photo was taken in the Serra do Ouro Grosso, Minas Gerais (photo by Ruy José Válka Alves). The orange and red leaves on the ground are from *Andira humilis*, an underground tree.

pace with the transpiration rates without causing an excessive drop in leaf water potential, which would induce cavitation and loss of xylem conductivity (Goldstein et al. 2008).

Phenological responses to DS prolongation and increased vapor pressure deficit remain poorly understood. However, reduced rainfall during the DS and WS transition will undoubtedly affect plant water balance and soil water recharge, while the evapotranspiration of native plants will tend to increase drastically (Christoffersen et al. 2014). As the plant water potential gradually drops (i.e., becomes more negative), cavitation should spread widely within xylem conduits, decreasing water supply to the foliage and increasing the risk of tissue dehydration (Bucci et al. 2008). Under severe dehydration, vegetative tissues may experience irreversible cellular damage and death. Tighter control of plant water loss would then be crucial for plant survival, and water leaks by leaf cuticles or through the bark, which represent a small fraction of the water lost by transpiration, can become increasingly important (Machado et al. 2021; Oliveira et al. 2003). The limited available information suggests that xylem vulnerability to drought-induced cavitation may become widespread in Cerrado trees under a changing climate scenario, as has been found for the Atlantic Forest species (Hollunder et al. 2024). In the Amazonia and Cerrado, valley arboreal species are more susceptible to drought-induced embolism than those on hillsides (Mattos et al. 2023). Additional research is needed on grasses, herbs, and small shrubs, which are vital to plant dynamics. While vulnerability to hydraulic failure is closely tied to a plant's ability to resist xylem embolism, the presence of large water reservoirs or access to deep, moist soil layers may serve as alternative mechanisms to mitigate the risk of hydraulic failure (Liu et al. 2021; Loram-Lourenço et al. 2022).

Tighter stomatal control of transpiration comes at the cost of reducing CO_2 uptake by the foliage, selecting for an increase in water use efficiency, expressed as the amount of carbon assimilated per unit of water loss (Goldstein et al. 2008). However, transpiration is an important mechanism of leaf cooling for Cerrado plants (Bucci et al. 2008). With the DS extension and the rise of vapor pressure deficit, young leaves would need tighter control of stomatal apertures, and higher leaf temperature would inevitably be exposed as they are to the high irradiances that prevail in this period. This scenario could negatively affect leaf carbon balance due to higher rates of respiration and photorespiration and increase the risk of photo inhibition and thermal damage to the leaf tissues (Franco and Lüttge 2002). While the rising CO_2 levels of the atmosphere might partially offset the impacts on the plant carbon balance of tighter stomatal control of transpiration, a higher risk of thermal injury would be inevitable (Figure 4).

The response of Cerrado plants to escalating temperatures remains uncertain, mainly because the limited existing research on thermotolerance is restricted to trees (Araújo et al. 2021; Silva and Rossatto 2022). In the Cerrado, forest species are less thermotolerant than trees from open savannah formations, where tree photosynthesis is drastically affected when leaf temperature reaches 48°C to 52°C (Silva and Rossatto 2022). Damages imposed by high temperatures on photosynthesis can affect plant persistence, leading trees to lose leaves more frequently. These thermotolerance traits have been reported for tree species with sufficient available water. Under drought, as the stomatal aperture is limited, leaf temperature can further increase, and damage could be substantially larger, leading to widespread mortality of tree canopies. Together with warming, DS prolongation can have additional impacts on plant reproduction. Higher temperatures and heat waves may impair flower and seed production, seedling establishment, and species regeneration and persistence in the environment (Abeli et al. 2012). A pioneering in situ experiment investigating the effects of increased temperature on the inflorescences of *Byrsonima pachyphylla* (Malpighiaceae), a Cerrado native, found no impact on viable pollen production but reported a significant decline in fruit production (Werkmeister et al. 2024). These findings have implications for the reproductive success and long-term persistence of *B. pachyphylla*, potentially affecting interspecific relationships within the community.

Rising CO_2 levels in the atmosphere could impact the Cerrado plant community in other ways besides regional warming. Woody encroachment is a widespread phenomenon in African savannas and has been linked to CO_2 enrichment as a key driver of this process, despite other factors such as overgrazing and land degradation also playing significant roles (Devine et al. 2017; Tabares et al. 2020). Remote sensing data and field observations show woody encroachment in the Cerrado northern region and transition areas with the Amazonia and the Pantanal (Rosan et al. 2019). In addition to increased atmospheric CO_2, woody encroachment in the Cerrado is linked to fire suppression and land-use abandonment (Pellegrini et al. 2016; Rosan et al. 2019). Conversely, studies in African savannas suggest that longer and more frequent dry spells during the growing season may benefit grasses, which can rapidly recover when moisture becomes available, while tree growth is generally limited to specific times of the year (Wigley et al. 2024). Although Cerrado trees exhibit similar growth patterns (Rossatto et al. 2009), changes in vegetation may be more subtle due to the high diversity and functional variety of ground-layer species, despite the dominance of C4 grasses and numerous tree species (Rossatto and

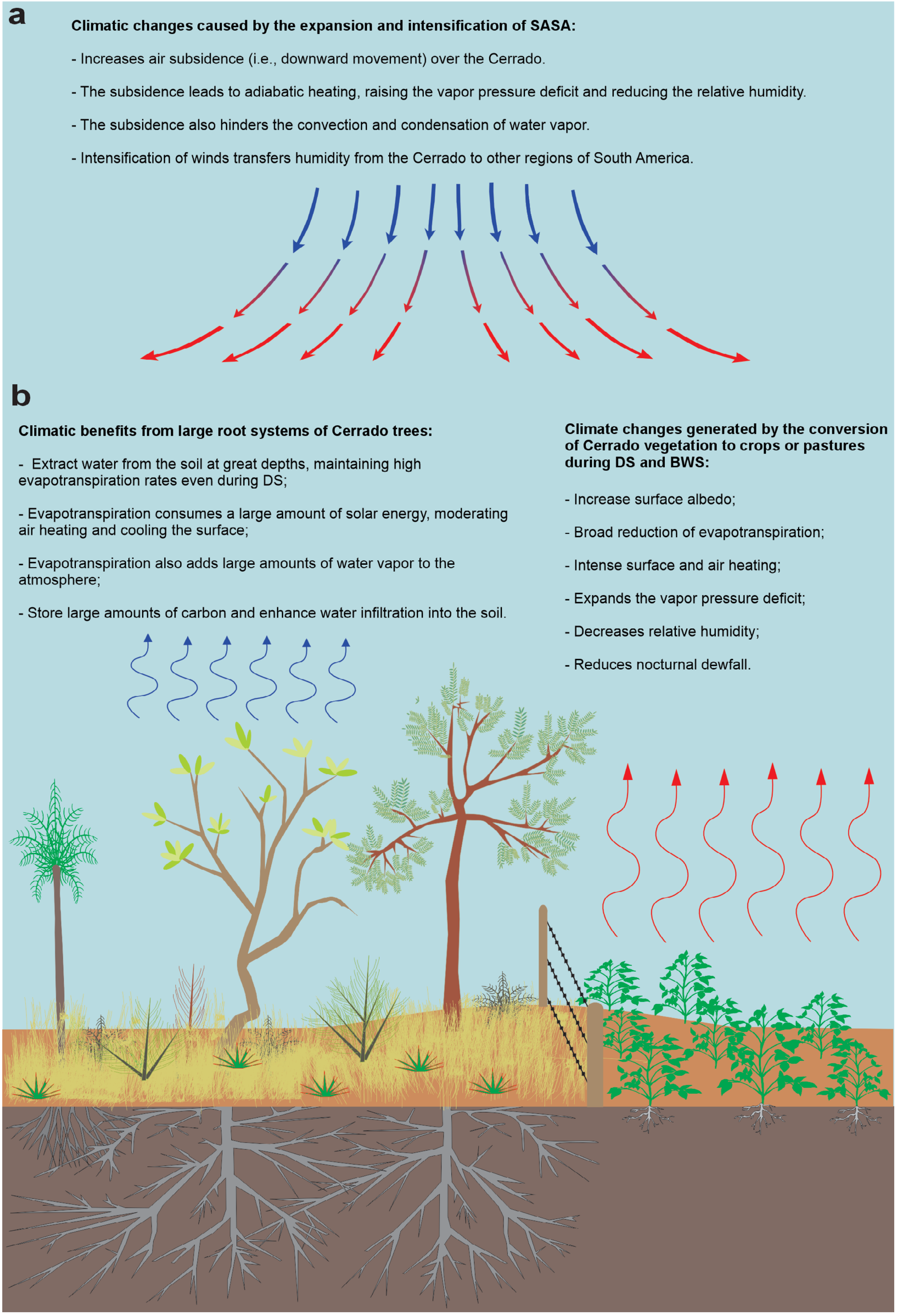

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FIGURE 3 | Schematic representation of the main climate changes that impact the Brazilian Cerrado. (a) Synthesis of the main climate changes driven by the expansion and intensification of the South Atlantic Subtropical Anticyclone (SASA) in the Cerrado. Atmospheric circulation changes intensify the air subsidence over the Cerrado, leading to adiabatic heating, a decrease in relative humidity in the cloud-forming atmospheric layers (1.5 to 5.5 km above sea level), and a hindrance of deep convection. Consequently, there is a rainfall reduction, especially between June and October, lengthening the Dry Season in most subregions of the Cerrado. (b) Synthesis of the main climate changes driven by Cerrado native vegetation conversion to crops or pastures during the Dry Season (DS) and at the Beginning of the Wet Season (BWS). Land use and land cover changes impact the hydrological cycle and energy budget components. The drastic reduction in regional evapotranspiration recorded during DS and BWS causes surface and air warming, expanding the vapor pressure deficit.

Franco 2017). Regardless of whether the Cerrado becomes more open or woody, climate changes are likely to impact ecosystem productivity, recovery after disturbances, and CO_2 sequestration potential. Regional climate change may also influence the invasion of exotic plants. Ecological niche simulations indicate that native species are expected to decrease in range due to warming, while invasive grasses may either be less affected or even expand their range (Ferreira et al. 2022; Simon and Pennington 2012).

Due to the vastness of the Cerrado and the regional variations in climate change, plant responses may vary by location. Physiological traits related to water use and temperature tolerance suggest a general trend of increased tree mortality, particularly in drier areas like the Caatinga border, if species lack plasticity to withstand prolonged DS and higher temperatures (Anderegg et al. 2013; Taccoen et al. 2022). At the landscape level, wetter vegetation types—such as gallery forests, wet grasslands, and *veredas*—would suffer from reduced river flows and soil moisture in areas with significant rainfall declines (Gonçalves et al. 2022). On a broader scale, boundaries with other biomes could shift: Cerrado species might expand northward toward the Amazonia, as seen in the past (Bueno et al. 2017), while Caatinga species could move southwestward into the Cerrado. In the south, the Cerrado may retreat to lower latitudes due to increased rainfall in southern Brazil (Hofmann et al. 2023).

3.2 | Soil Microbial Communities

Throughout the Cerrado, contrasting vegetation physiognomies and differences in soil characteristics result in natural variations in soil microbial biomass, respiration, and activity (Rocha et al. 2019). However, transitioning from the WS to DS consistently decreases microbial biomass C and N (Carvalho et al. 2018; Nardoto and Bustamante 2003). The absence of available water during the dry season explains the high abundance of microbial genes related to the cell wall, capsule synthesis, and sporulation, suggesting dormancy during this period. Water-saturated soils in the WS present high oxygen concentrations, which, coupled with a high content of genes related to amino acids, DNA, and protein metabolism, indicate that these dormant microbial communities proliferate when water is available (Pereira de Castro et al. 2016). Increased soil moisture in the WS boosts organic matter from plant debris, stimulating microbial biomass (Eaton and Chassot 2012) and enzyme activities like FDA, urease, dehydrogenase, β-glucosidase, and phosphatase (Carvalho et al. 2018). This heightened microbial activity enhances biogeochemical cycles, particularly C and N, and improves nutrient availability for plant growth, especially K and P.

The typical functioning of below-ground soil communities will be impacted by climate change. Altered water regimes and prolonged dry periods will reduce microbial biomass and alter the dynamics of microbial communities, especially in the upper 5–10 cm of soil. Prokaryotic groups like Solibacteres, Acidobacteriia, and Chloroflexi, associated with the DS, will remain dominant for longer, while WS groups like Alphaproteobacteria and Sphingobacteria will have a shorter influence (Pereira de Castro et al. 2016). Both bacterial groups drive C and N cycling, crucial for biogeochemical processes. However, increased microbial biomass and activity will elevate greenhouse gas emissions, such as CO_2, CH_4, and N_2O (Siqueira-Neto et al. 2021). Prolonged water stress in the DS could further disrupt microbial dynamics and native vegetation growth.

3.3 | Invertebrates

The Cerrado has a high diversity and endemism of invertebrates, including gastropods, onychophorans, chelicerates, and insects (Diniz et al. 2022; Lemes et al. 2020; Salvador et al. 2017). Heterogeneity of habitats contributes to high values of beta diversity in different physiognomies (Brown and Gifford 2002; Freire Jr. et al. 2024), especially in ecotones with other Brazilian biomes (Beirão et al. 2017). However, research on invertebrates here has been taxonomically biased and limited to sites close to the main research groups (Lewinsohn et al. 2005). Many groups remain poorly understood, and significant biodiversity may be lost before it is even documented. This lack of knowledge about the ecological roles of these organisms in Cerrado ecosystems limits our ability to project the impacts of climate change accurately.

Daytime and nighttime warming will likely affect invertebrates, altering their daily activity rhythms or prompting them to disperse to higher altitudes or latitudes (Battisti et al. 2005; Speights et al. 2017). The ability of these organisms to adjust their distribution will depend on their behavioral plasticity and dispersal abilities. Additionally, many species rely on complex interactions with other organisms, such as specialized herbivorous insects (Bellaver et al. 2022). Their survival will hinge on resource availability in new areas or the ability to exploit alternative resources in newly colonized regions. However, empirical data on how regional warming affects the daily activity patterns and distribution of Cerrado invertebrates is still limited.

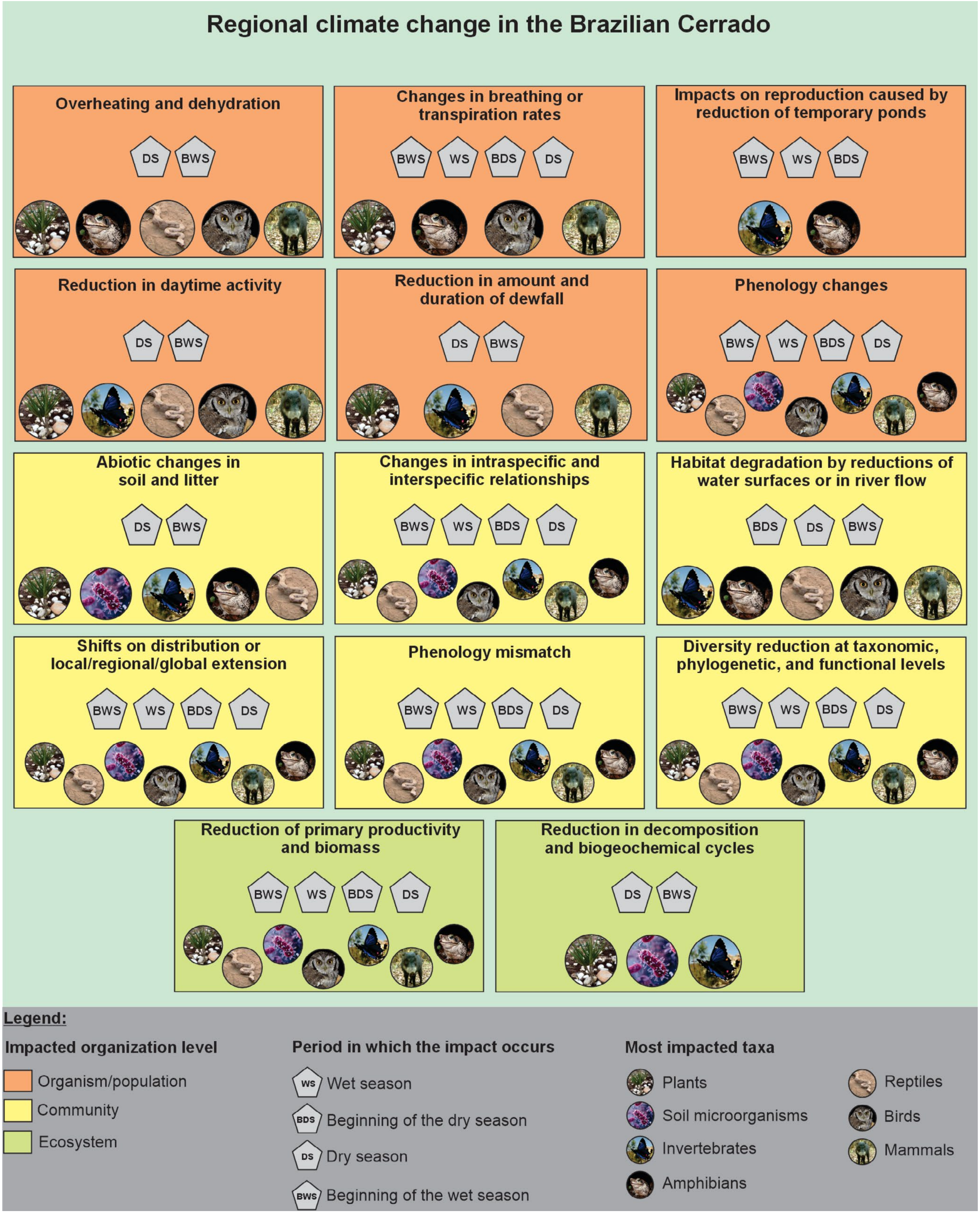

FIGURE 4 | Summary of the main impacts of regional climate change on terrestrial biodiversity in the Brazilian Cerrado. These impacts are shown in the different levels of ecological organization, indicated by the color of the rectangles. Pentagons identify the seasons of the year when each impact is most intense, while circles identify the most affected taxonomic groups.

Cerrado invertebrates tend to show seasonal patterns in reproduction, abundance, and diversity, peaking from late DS to mid WS (Oliveira et al. 2021; Silva et al. 2011). In general, the rising temperatures and the first rains trigger the resurgence of insect activity after DS. Therefore, the pronounced environmental alterations observed during the BWS may impact the seasonal cycles of invertebrates in regions most affected by climate change. The reduction in rainfall and frequency of rainy days will likely alter the mesic and wetland ecosystems, potentially impacting their invertebrate communities. *Veredas*, gallery forests, and riverine ecosystems are critical habitats for various invertebrates, including damselfly species (Machado and Bedê 2015; Vilela et al. 2023), and serve as refuges for other invertebrates during the DS. These areas support higher biodiversity than the surrounding drier regions (Araújo et al. 2024; Freire Jr. et al. 2024). In the Cerrado, endemic species of wetland ecosystems with restricted distribution and top predators with aquatic larvae are highly threatened by changes that render their habitats unsuitable. For instance, the only known specimens of the world's largest diving beetle were collected in this biome, but the species is now believed to be extinct (Hendrich et al. 2019). Nocturnal warming is likely to decrease the amount and duration of dewfall. Dew is an important water source for invertebrates with low vagility during the DS, such as honeybees and other pollinators (Joachimsmeier et al. 2012). Moreover, climate change affects above and belowground invertebrates differently, particularly species that live in leaf litter and are less tolerant of moisture loss and rising temperatures (Parr and Bishop 2022). In the case of soil invertebrates or those that lay eggs in the soil, increased environmental unpredictability and long periods of drought should select individuals with adaptations to these conditions, potentially leading to the extinction of populations with less phenotypic plasticity (Martins et al. 2016).

These possible changes in community composition and structure may jeopardize the wide range of ecosystem services provided by invertebrates. Some physiognomies, such as *campo de murundus* (earthmound fields), are created by the action of social insects (Martin et al. 2018). Invertebrates, particularly ants, are crucial for nutrient cycling in *campos rupestres* (rocky fields), as demonstrated in studies of various African savannas (Fernandes et al. 2024; Parr et al. 2016). Ecosystem engineering produced by wood-boring beetles and shelters created by gall-inducers influence the community structure of invertebrates on plants (Pereira et al. 2024; Priest et al. 2021). Sources of liquid foods, such as extrafloral nectaries of plants and honeydew-producing insects on vegetation, attract ants that facilitate or restrict the occurrence of herbivorous insects on plants (Oliveira and Freitas 2004). These communities are typically seasonal, following pulses of resource availability, and are affected by abiotic factors such as water availability (Calixto et al. 2021). Cerrado's stable seasonal precipitation shaped adaptive strategies, especially in endemic taxa; many species have univoltine life cycles, with a long larval stage and a short reproductive period, which are generally associated with resources available in narrow phenological periods (Furtado 2004). In this sense, invertebrate communities of the Cerrado are characterized by seasonal cycles and synchrony between consumers and prey (Silva et al. 2011; Vilela et al. 2018). Changes in plant phenology should affect all trophic levels, including herbivorous insects and their natural enemies that depend on specific resources, such as insects that eat young leaves (Furtado 2004; Muniz et al. 2012).

3.4 | Amphibians and Reptiles

Amphibians and reptiles comprise the extant lineages of ectothermic tetrapods, with anurans and squamates the most diverse groups within their classes. The Cerrado is home to an impressive diversity of those taxa, many of which have restricted distributions (Vieira-Alencar et al. 2024). Though sharing ecological similarities, primarily related to size and thermal physiology, differences in natural history, morphology, physiology, and behavior likely lead to varied responses to climate change (Deutsch et al. 2008). Taxonomic diversity, phylogenetic distance, and specializations of the Cerrado's herpetofauna (Colli et al. 2002) indicate a broad range of responses to climate change (Winter et al. 2016). Amphibians possess moist, permeable skin, rely on cutaneous respiration, have non-amniotic eggs, and often undergo a larval stage (with eggs and tadpoles typically aquatic) (Duellman and Trueb 1994). So, the natural history of most species is closely tied to water availability and seasonality. Amphibians are the most threatened vertebrate class, and 41% are globally at risk. Climate change has been responsible for 39% of increased extinction risks in the past 20 years (Luedtke et al. 2023). Reptiles possess scaly, less permeable skin, rely on pulmonary respiration, and lay terrestrial amniotic eggs without a larval stage, making them generally less sensitive to humidity and water availability fluctuations. However, many species are diurnal and heliothermic, making them more vulnerable to rising air temperatures. Overall impacts of climate change on reptiles remain less certain, but 21% are globally threatened (Cox et al. 2022). About 5 amphibians and 11 reptiles (respectively 2.5% and 4% of the richness of each group in the Cerrado) are officially threatened (ICMBio 2025).

As ectotherms, amphibians and reptiles rely heavily on environmental temperatures for their physiological functions, making them more vulnerable to temperature fluctuations than endotherms (Deutsch et al. 2008). Our understanding of thermal tolerances, water-conserving behaviors, and other ecophysiological traits is still limited, and observational evidence of climate change impacts is scarce (Winter et al. 2016). Nonetheless, we can expect direct and indirect effects on the Cerrado's herpetofauna, influencing individual organisms and entire communities, with consequences for ecosystems due to their vital roles in food chains. Direct impacts are likely to arise from temperature and water availability changes, while indirect effects may involve shifts in food resources and habitat conditions.

Amphibians and reptiles typically cope with extreme climatic conditions by reducing or halting their activity to avoid exposure to lethal temperatures. As temperatures rise, we anticipate significant impacts on their daily and seasonal activity patterns due to their thermoregulatory needs. Projected warming in the Cerrado may extend the duration of temperatures nearing or exceeding the thermal tolerance limits of many species, particularly during the daytime. Diurnal species, like most lizards and Colubridae snakes, may be more affected by rising temperatures than crepuscular or nocturnal species, like most amphibians, Viperidae, Dipsadini, and Pseudoboini snakes.

Diurnal amphibians are rarer in the Cerrado compared to rainforest biomes (Ribeiro et al. 2020). Similarly, terrestrial or arboreal species, such as Teiidae, Polychrotidae, and Leiosauridae lizards, Colubridae snakes, and Hylidae treefrogs, may be more affected by warming temperatures than fossorial or cryptozoic species, like many Dipsadidae snake lineages, Amphisbaenidae worm lizards, and microhylid frogs. Fossorial or semi-fossorial amphibians and reptiles are common in the Cerrado, likely a consequence of the region's fire, rainfall, and temperature regimes (Colli et al. 2002). Fossorial behavior and other reproductive specializations (as burrowed foam nests) may offer some protection against climate change. Predicting the full impact of climate change requires data on thermal tolerances and preferences. A study examining voluntary thermal maximum temperatures (VTMax) for 53 amphibians and reptiles from the Cerrado and Atlantic Forest found that lizards generally exhibit higher VTMax than amphibians and snakes (Díaz-Ricaurte et al. 2022). Additionally, Atlantic Forest species had higher VTMax than those from the Cerrado, indicating that the herpetofauna of the Cerrado may be more vulnerable to the projected temperature increases. Other studies have modeled the impact of climate change in the Cerrado, projecting deleterious effects on the suitability for viviparous lizards (Machado et al. 2023), psammophilous squamates (Oliveira et al. 2024), and a fossorial snake (Vasconcelos 2014).

Rainfall and temperature shape the phenology of herpetofauna in the Cerrado. Most anurans reproduce during the WS in temporary water bodies within open areas (Vasconcellos and Colli 2009). As warming intensifies during the DS and BWS, many species may face challenging thermal conditions at the start of their reproductive cycles. However, reduced water availability is likely to have an even greater impact. Decreased rainfall and fewer rainy days are expected to shorten the reproductive season and diminish population output, particularly for amphibians. Prolonged and explosive breeders will experience different impacts; prolonged breeders are more vulnerable to shorter seasons, while explosive breeders may have fewer reproductive opportunities (Ribeiro et al. 2020; Ulloa et al. 2019). Additionally, higher temperatures and lower humidity could reduce the availability of temporary ponds critical for amphibian reproduction. Alves-Ferreira et al. (2022) tested the influence of life history and biogeographic characteristics on the response of Cerrado anurans to climate change. They found a potential reduction in geographic distribution for 70% of the species, with a stronger impact in species inhabiting higher-altitude areas and the western Cerrado (Alves-Ferreira et al. 2022).

Indirect effects, while harder to predict due to uncertainties and synergistic interactions, can be equally significant (Blaustein et al. 2010). Changes in prey availability and habitat alterations are expected to be among the most impactful indirect consequences of climate change. Most adult amphibians and squamates are predators, with amphibians, small lizards, Amphisbaenidae, and some snakes primarily feeding on invertebrates, while most snakes prey on small vertebrates. Shifts in prey availability will likely affect biotic suitability for many species. Changes in landscape structure and vegetation composition in the Cerrado will also impact herpetofauna, particularly habitat specialists such as lizards found in rock outcrops, sandy soils, or forest patches (Colli et al. 2002), as alterations in habitat availability or microclimatic conditions significantly affect these species. Despite uncertainties due to limited data, climate projections suggest severe shifts in habitat suitability, species distribution, richness, and phenology for Cerrado amphibians and reptiles in the coming decades.

3.5 | Birds

Cerrado bird species exhibit distinct geographic distribution patterns, ranging from endemics with restricted ranges to widely distributed species (Lopes and Silva 2024). The extent of a bird's range distribution partly reflects its tolerance to more extreme portions of the thermal gradient (i.e., generalist versus specialist species), which significantly influences its capacity to adapt to climate change (Cohen et al. 2023). Cerrado birds are facing increasingly intense and warmer drought periods during DS and the BWS. Consequently, diurnal species must shorten their activity duration or continue being active during higher temperatures, likely leading to high thermoregulatory costs that can affect the fitness and survival of birds (Cunningham et al. 2013; McKechnie and Wolf 2010), although physiological changes in native species still lack empirical observations in the Cerrado. The rainfall reduction in the Cerrado already impacts species dependent on wetlands, such as *Mergus octosetaceus* due to the decrease in water-covered surfaces in natural habitats.

Adding to the physiological effects, regional climate change will likely interact synergistically with habitat loss, impacting the species distribution, potentially leading to a restructuring of bird assemblages (Pearce-Higgins et al. 2015; Şekercioğlu et al. 2012). Climate niche modeling and future greenhouse gas emissions scenarios indicate significant shifts in bird range sizes. In optimistic scenarios, widely distributed species are projected to maintain 34% to 85% of their current distributions (Borges and Loyola 2020). In contrast, pessimistic scenarios predict drastic reductions in range sizes for all species (Hidasi-Neto et al. 2022). A study on 26 Cerrado bird species revealed that changes in range size vary depending on habitat specialization, with dispersal scenarios ranging from a 5% increase to an 80% decrease (Marini et al. 2009b). Notably, the greatest potential losses in range size under full dispersal were anticipated for species dependent on grassland and forest habitats. Endemics could also experience losses of over half of their current distribution area by 2099, as predicted for *Myiothlypis leucophrys* (loss of 74%), *Syndactyla dimidiata* (−61%), *Geositta poeciloptera* (−68%), *Taoniscus nanus* (−59%), and *Nothura minor* (−57%), for example (Marini et al. 2009a). In most cases involving endemic and rare species, the core shift in range size has been projected toward the southeastern Cerrado, where higher latitudes and elevation result in lower temperatures. However, these predicted shifts are concerning, as the southeastern region has one of the lowest proportions of remaining native vegetation in the Cerrado, coupled with a minimal representation of protected areas (Marini et al. 2009b).

Projections using individual species distribution models also suggest an increase in overall bird species richness in the northern region and a reduction in the southern Cerrado (Hidasi-Neto et al. 2022). In both cases, community homogenization may occur due to local extensions and invasions (Kortz and

Magurran 2019). In general, endemic, rare species with restricted range sizes, or those that occupy specific niches, are identified as the most sensitive to climate change in the Cerrado (Borges et al. 2019; Borges and Loyola 2020; Hidasi-Neto et al. 2022). Borges and Loyola (2020) projected that four endemics (*Cercomacra ferdinandi, Paroaria baeri, Pyrrhura pfrimeri*, and *Synallaxis simoni*) will be entirely outside refuge areas under future climate scenarios. On the other hand, the ability to disperse in highly anthropized landscapes can be a critical issue, exacerbated by factors like philopatric behavior, as known for Psittacidae (Vilaça et al. 2024). Thus, the establishment of new reserves that accommodate species in these projected conditions is crucial for the conservation of the Cerrado bird assemblage (Marini et al. 2009b).

3.6 | Mammals

The most striking potential effect of climate change on the over 200 species of mammalian fauna of the Cerrado is biotic homogenization. Expected changes in rainfall and increased wildfires, combined with habitat loss, will likely reduce mammal species richness, leading to local extinctions. Hidasi-Neto et al. (2019) anticipate that amidst this overarching decline, the Cerrado will exhibit nuanced patterns of phylogenetic overdispersion and clustering, alongside a pervasive trend of functional overdispersion within non-volant mammals. While some sites may experience a decline in diversity, the loss of specific species could lead to an increase in phylogenetic or functional divergence. Temporal and spatial shifts in species composition are anticipated, with heightened taxonomic turnover expected in the Northern Cerrado. Conversely, Southern Cerrado faces biotic homogenization, with mammalian communities expected to become increasingly similar taxonomically, phylogenetically, and functionally. Rising temperatures and declining rainfall are anticipated to alter activity patterns and niche overlap (temporal and spatial) among potentially competing species or predator–prey pairs (Hofmann et al. 2016). These changes are likely to produce unpredictable effects on the interacting species.

Extinctions may arise from two mechanisms: severe declines in population sizes leading directly to extinction and range shifts wherein species vacate their historical distribution ranges. Climate change can disrupt the reproductive cycles and phenology of Cerrado mammals. The anticipated decrease in precipitation during the BWS is expected to alter the phenology of plants and insects, with cascading effects across all trophic levels. Predicted changes in the distribution and abundance of plants may affect food availability for mammals (Losada et al. 2024), leading to changes in feeding behavior (Habeck and Lindroth 2013). This can intensify competition for limited resources and ultimately influence population dynamics and assemblage (Magioli et al. 2019). Mammalian reproductive patterns are intricately linked to the seasonal availability of food resources (Bronson 1989) because parturition ideally takes place during periods of favorable environmental conditions, as the demands of lactation, a unique mammalian trait, impose significant costs on maternal time and energy (Speakman 2008). Indeed, female energetic requirements more than double during lactation across several lineages (Gittleman and Thompson 1988). Strikingly, the reproductive patterns of Cerrado mammals are greatly correlated with rainfall patterns. In didelphids, energetically demanding phases such as lactation and weaning are confined to periods of ample food availability coinciding with the WS (Lopes and Leiner 2015). Some species follow semelparous life cycles, typically linked to habitats exhibiting strong seasonality and predictability (Zangrandi and Vieira 2023). Under climate change, the synchronization between reproductive demands and food availability becomes increasingly precarious (Simmonds et al. 2020). Shifts in precipitation patterns and altered seasonality could disrupt the delicate balance between resource availability and reproductive cycles, threatening the survival of species reliant on such synchronization (Dong and Anderson 2022). The inability to adapt reproduction to changing environmental conditions may elevate the extinction risk for marsupials and other species with similar ecological requirements. Several Cerrado frugivore bats exhibit seasonal bimodal polyestry with parturition and lactation concentrated during the WS, when fruit abundance and diversity are highest (Willig 1985). Regardless of environmental conditions, most bats are monotocous, so in the Cerrado, most females will generate at most two juveniles per year. The shortened duration of the WS may result in the loss of one of the yearly reproductive events, leading to a fast decline in population replacement rate (Racey 1982).

Climate change may drive species to adjust their ranges. Our predictions indicate that moisture-dependent vegetation types (e.g., gallery forests and *veredas*) will suffer from decreased river flow and soil moisture, especially in areas with significant rainfall declines. This may force species reliant on these habitats to go extinct or disperse to suboptimal sites. Small non-volant mammals endemic to the Cerrado are projected to suffer losses due to a decline in suitable habitats (Evaldt et al. 2024). Similarly, while Cerrado bats may encounter suitable climate conditions approximately 281 km southeast of their current ranges by 2050, failure to adapt to these new habitats could result in significant range contractions, with 36 species potentially losing over 80% of their distribution (Aguiar et al. 2016). The maned wolf, *Chrysocyon brachyurus*, a key mesocarnivore in the Cerrado, is projected to lose at least 33% of its range by 2050 (Torres et al. 2013).

The homogenization of the mammalian fauna across the Cerrado should trigger a cascade of effects, notably disrupting food chains and impacting ecosystem services. For example, mammals hold pivotal roles in seed dispersal and pollination (Wolowski et al. 2019), and top and mesopredators are known to regulate herbivory pressure on vegetation (Elmhagen et al. 2010). Consequently, the loss or displacement of those species could profoundly affect the structure and composition of vegetation. Moreover, mammals significantly contribute to nutrient cycling through grazing, defecation, and decomposition (Hobbs 1996). The absence of key species will disrupt essential processes, leading to imbalances in nutrient cycling and soil fertility. Mammal diversity in the Cerrado plays a crucial role in ecosystem services related to disease control, including disease surveillance, pest management, and carrion disposal (Vale et al. 2023). Climate-driven shifts in mammal assemblages are expected to have profound effects on the structure of the mammalian virome (Carlson et al. 2022). Increased cross-species viral transmission events are predicted, raising the risk of zoonotic viruses emerging. High-risk zoonoses may find new hosts, increasing the likelihood of spillover into human populations (Carlson et al. 2022). This heightened zoonotic transmission potential raises concerns about disease outbreaks in both humans and wildlife, exacerbating human-wildlife conflicts.

3.7 | Communities and Biotic Interactions

Despite limited research, growing evidence indicates that climate change is driving major shifts in ecological communities and biotic interactions in the Cerrado (Calixto et al. 2021; Franco et al. 2014; Vasconcelos et al. 2018; Vilela et al. 2018). Climate effects on community dynamics are scale-dependent (Bastazini et al. 2021). In the Cerrado, at broader spatial scales, recent projections suggest that communities tend to become more homogenized due to the loss of specialist species and the expansion of non-native generalist species, lowering the levels of β- and γ-diversity across the region (Hidasi-Neto et al. 2019). At more refined scales, climate change is also projected to restructure local communities (Vasconcelos et al. 2018), further suggesting a homogenization of species diversity across the region. This homogenization in species composition and lower levels of β-diversity are likely to simplify biotic interactions across space. However, most of our knowledge comes from predictive stacked individual species distribution models (e.g., Borges and Loyola 2020; Hidasi-Neto et al. 2019). Thus, the lack of proper and empirical assessment of ecological community data is evident, highlighting the need for thorough and explicit empirical community assessments.

Woody plant encroachment is an example of how regional climate change can drive high levels of species turnover and changes in vegetation structure in northern Cerrado (Rosan et al. 2019). This process leads not only to the loss of biodiversity associated with open formations but also to the reduction of wetland areas (Gonçalves et al. 2021), significantly altering species composition and the set of biotic interactions across spatial scales in the region. However, our understanding of how biotic interactions are being restructured in the Cerrado in response to climate change remains highly limited. The available information is restricted to insect-plant interactions and reveals substantial shifts in biotic relationships, underscoring a significant yet overlooked ecological reorganization within the complex Cerrado ecosystems (Braga and Diniz 2022; Calixto et al. 2021; Vilela et al. 2018). Phenological changes have already affected mutualist and antagonist interactions in ant–plant–herbivore interactions, a ubiquitous and widespread ecological interaction across the Cerrado (Calixto et al. 2021; Vilela et al. 2018). Future climate scenarios are also expected to adversely impact caterpillars and their tritrophic interactions, particularly during the late DS (Braga and Diniz 2022).

Changes in population-level responses are predicted to alter ecological community composition, species richness, and patterns of relative species abundance in other regions (Bastazini et al. 2021; Bergamin et al. 2024; Scheffers et al. 2016). Ultimately, these changes will reorganize the complex network of biotic interactions due to new conditions in temporal (e.g., phenological matching) and spatial (e.g., range) overlaps of interacting species (Bartley et al. 2019). Positive and negative feedback loops may emerge, emphasizing the complex nature of climate change impacts on higher levels of ecological organization.

4 | Conclusion

The Cerrado is becoming hotter and drier due to large-scale climate shifts, such as the expansion of Hadley cells and the warming of the northern tropical Atlantic, combined with the widespread suppression of native vegetation driven by the expansion of Brazil's agricultural frontier. The most evident alterations are regional warming, higher vapor pressure deficit, rainfall volume drop, and lengthening of DS. Climate change already impacts terrestrial biodiversity in several ways, altering physiological processes and species' reproductive success. Thus, climate change is reshaping ecological populations and communities and their interactions, leading to biotic homogenization across the region, with potentially concerning consequences for ecosystem functioning. We emphasize that some of these impacts are interrelated with, or amplified by, other anthropogenic drivers, such as land-use changes. The lack of long-term biodiversity monitoring limits our ability to understand and mitigate these impacts fully. We believe that the effectiveness of biodiversity conservation policies and climate mitigation/adaptation strategies in the Cerrado will depend on a transformative shift in current food production systems coupled with large-scale ecosystem restoration.

Author Contributions

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

Related WIREs Articles

A First Assessment of Greenhouse Gas Emissions From Agricultural Peatlands in Canada: Evaluation of Climate Change Mitigation Potential

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** Identification and location of weather stations from the National Institute of Meteorology (INMET) used to calculate the mean values presented in Figure 2. Monthly data from the most recent two climate normals for all these meteorological stations are published and freely available on the INMET website (https://portal.inmet.gov.br/normals). Where: WMO is World Meteorological Organization; Mean Temp. is Mean Temperature; Max. Temp. is Maximum Temperature; Min. Temp. is Minimum Temperature; Evapor. is evaporation obtained with Piche evaporimeter.