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A synthesis of the biogeographic history of Brazil's phytogeographic domains

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Abstract. In this study, we provide a comprehensive and updated overview of the biogeographic history of several Brazilian phytogeographic domains: the Amazon Rainforest, Brazilian Atlantic Forest, Caatinga, Cerrado, Pampa, and Pantanal. We also outline the main hypotheses that were proposed to explain the distribution patterns and endemism of taxa within these domains. The tropical forests, specifically the Amazon Rainforest and the Brazilian Atlantic Forest, were likely continuous during the Eocene optimum. However, global cooling and increased aridity in the late Eocene and part of the Oligocene led to the fragmentation of these extensive tropical forests. This fragmentation resulted in the creation of the dry diagonal, which includes the Cerrado, Caatinga, Pantanal, and Chaco regions. The dry diagonal served as a geographic barrier, promoting the formation of the Brazilian Atlantic Forest to the East and the Amazon Rainforest to the West. Despite this barrier, forest corridors likely existed between these domains, playing a crucial role in the segregation of the Caatinga from the Cerrado. The Caatinga is the most recent of these domains, having formed in the early to mid-Holocene. The lineages characteristic of the Cerrado likely diversified between the Miocene and early Pliocene.

Keywords: Amazon Rainforest, Brazilian Atlantic Forest, Caatinga, Cerrado.

INTRODUCTION

Brazil is the largest country in the Neotropical region (and the fifth largest in the world), covering over 8.5 million km^2 (IBGE 2024). This vast geographic area encompasses a rich biota and is considered one of the most biodiverse countries on the planet (Fiaschi and Pirani 2009). It also includes distinct phytogeographic domains (Fig. 1) such as the Amazon Rainforest and the Brazilian Atlantic Forest (both tropical humid forests), the Cerrado (tropical savannas), the Caatinga (seasonally dry tropical forests), the Pampa (grasslands of Southern Brazil), and the Pantanal (seasonally flooded wetland) (Fiaschi and Pirani 2009; Fiaschi et al. 2016). This article aims to provide a comprehensive and updated overview of the biogeographic history

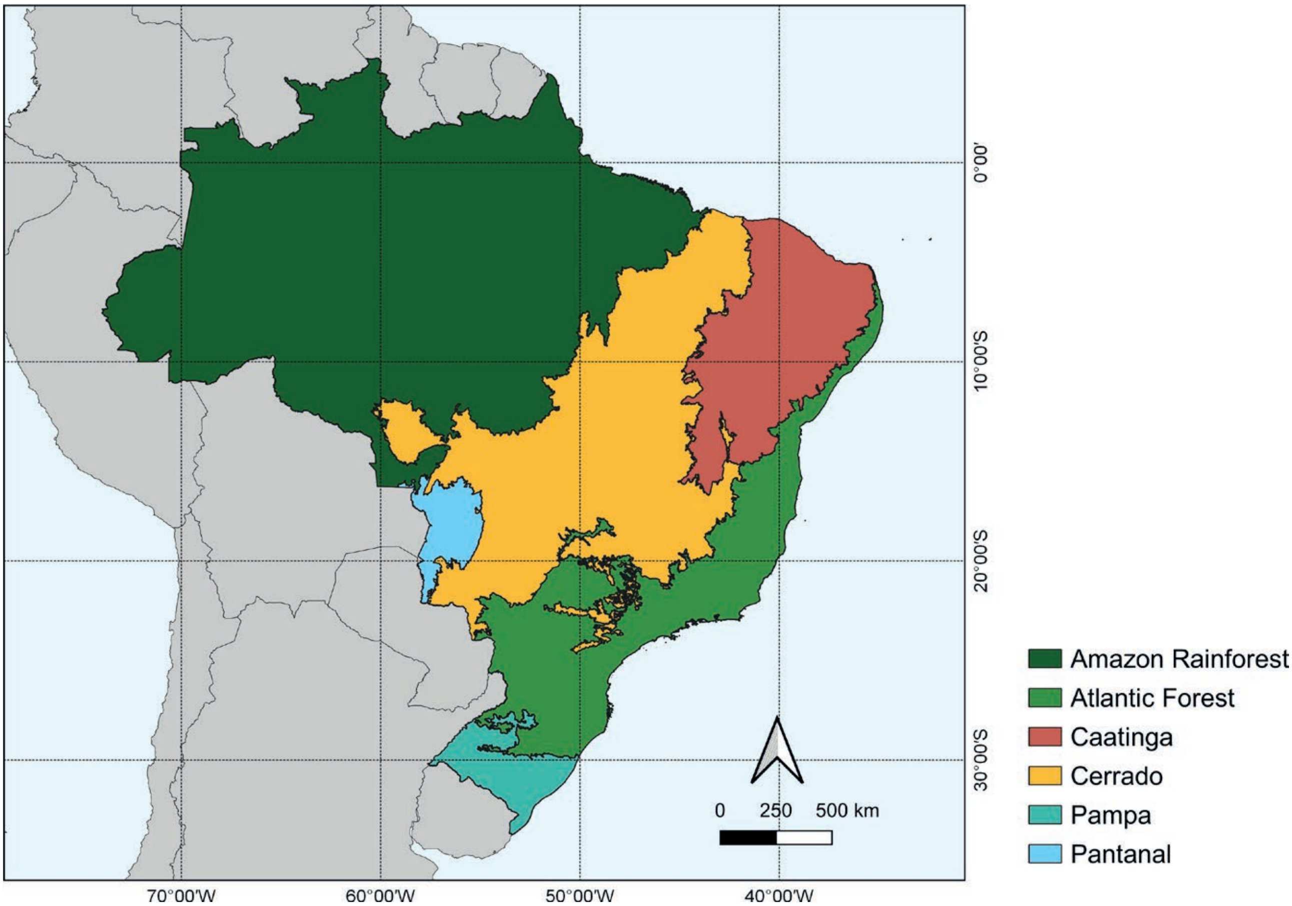

Figure 1. The phytogeographic domains of Brazil.

of these Brazilian phytogeographic domains. Additionally, we will discuss the main hypotheses that have been developed to explain the distribution patterns and endemism of species within these areas.

AMAZON RAINFOREST

The Amazon Rainforest is the largest tropical forest on the planet and one of the most biodiverse regions in the world (Nores 2020). This phytogeographic domain covers approximately 5.5 million km^2, extending from the Atlantic coast to the foothills of the Andes. It extends across nine countries, with more than half of this area located in Brazil, where it encompasses over 40% of the national territory (IBGE 2024). The Amazon Rainforest has long attracted scientific interest due to its immense biodiversity, which is home to approximately 12,800 species of vascular plants in Brazil alone (Flora do Brasil, 2020). In this sense, Antonelli et al. (2018) identified Amazon as the most important source area of species in the Neotropical region. However, the biogeographic history of this domain remains a subject of debate, with no clear consensus (Cracraft et al. 2020). Below, we present the main hypotheses proposed to explain the extraordinary biodiversity of the Amazon.

In 1969, Jürgen Haffer (geologist and ornithologist) published a study on bird distribution patterns in the Amazon, hypothesizing that climatic fluctuations during the Pleistocene could explain the observed patterns (Rull 2020). According to Haffer (l.c.), the forests were fragmented into isolated patches, or refuges, during glacial periods (which were drier/arid). On the other hand, non-forest vegetation expanded and dominated the region (Bush and Oliveira 2006; Leite et al. 2015; Fiaschi et al. 2016; Rull 2020). Thus, speciation would have occurred within these isolated refuges. During interglacial phases (more humid), the forests would have expanded and coalesced again, while non-forested areas retracted (Bush and Oliveira 2006; Leite et al. 2015; Rull 2020). This cycle is thought to have repeated multiple times throughout the Pleistocene, shaping the distribution patterns observed today (Haffer identified nine areas of endemism as potential candidates for these refugia) (Rull 2020). To support this hypothesis, Haffer used climate data from Africa during a glacial period (100 to 20 thousand years ago) to argue that the Amazon basin experienced similar arid conditions. He suggested that "seas" of savannas surrounded isolated forest "islands," creating the genetic isolation necessary for speciation (Bush and Oliveira 2006, Fiaschi and Pirani 2009). This explanation later became known as the Pleistocene refugia hypothesis.

Many studies on different groups of organisms (including butterflies, frogs, lizards, and various plant taxa) have supported the predictions of the refugia hypothesis (Fiaschi and Pirani 2009; Antonelli and Sanmartín 2011; Rull 2020). As a result, this model has become a dominant paradigm in the scientific community (Rull 2020). However, by the late 1980s, Quaternary paleoecological data began challenging this view, revealing insufficient evidence for widespread Amazonian aridity during the last glacial maximum (21 thousand years ago) (Baker et al. 2020; Rull 2020). Furthermore, palynological and paleoenvironmental modeling-based analyses have documented the Amazon rainforest's continuity and stability during this period, contradicting key predictions of the refugia hypothesis (Fiaschi and Pirani 2009; Antonelli and Sanmartín 2011; Baker et al. 2020; Rull 2020).

More recently, calibrated molecular phylogenies have provided further evidence against the hypothesis, suggesting that the diversification of many Amazonian lineages dates back to the Neogene rather than resulting from a sudden wave of Pleistocene-driven speciation (Bush and Oliveira 2006; Fiaschi and Pirani 2009; Antonelli and Sanmartín 2011; Baker et al. 2020). Another major critique argues that the proposed refugia (interpreted as centers of endemism) may be artifacts of biased sampling rather than actual historical refuges (Fiaschi and Pirani 2009; Hoorn et al. 2010; Antonelli and Sanmartín 2011). Thus, this hypothesis has been increasingly debated and rejected by many researchers (Baker et al. 2020).

Recent data show that precipitation levels during the Last Glacial Maximum in Eastern Amazonia were similar to modern values for that region, although lower than contemporary precipitation levels in Western Amazonia (precipitation decreased during periods of greater summer insolation) (Baker et al. 2020). In contrast, Western Amazonia remained as humid as it is today (precipitation increased during periods of greater summer insolation) (Baker et al. 2020). These findings highlight distinct climatic histories between Eastern and Western Amazonia (Cracraft et al. 2020).

Moreover, several studies have shown the long-term stability of tropical rainforests from Western to central Amazonia during the Quaternary (Costa et al. 2017; Baker et al. 2020; Cracraft et al. 2020). However, evidence suggests periodic expansions and contractions of forest-savanna ecotones in Southern and Eastern Amazonia (Werneck et al. 2011; Costa et al. 2017; Baker et al. 2020; Rull 2020). Episodes of forest expansion may have even created ecological corridors (forming a mosaic landscape alongside seasonally dry tropical forests in Northeastern Brazil) connecting the Amazon and the Brazilian Atlantic Forest (Baker et al. 2020). Thus, the available evidence strongly indicates that the Amazon basin was never arid during the last glacial cycle, meaning it was not fragmented by open vegetation; pollen records further confirm that most of the region has remained forested throughout this period (Colinvaux et al. 2000; Werneck et al. 2011).

Another hypothesis was proposed to explain the high biodiversity of the Amazon, known as the disturbance-vicariance hypothesis. This hypothesis suggests that the composition of the forests changed due to the dispersal and migration of montane species (particularly emphasizing the role of the Andean elevation) during the cooling period, along with a moderate reduction in precipitation and a decrease in atmospheric CO_2 during the glacial period (Baker et al. 2020; Rull 2020). During this time, there was significant competition between the taxa that were arriving from the montane environments and those that were already established in these lower areas, which may have led to specialized adaptations (Nores 2020). However, not all paleoecologists accepted this view, and Haffer's hypothesis remained more widely acknowledged (Rull 2020).

The museum hypothesis has also been considered. According to this assumption, the high Amazonian biodiversity would be explained by the stability of the forests since the Miocene. Consequently, extinction would be reduced due to high environmental stability, and there would be an accumulation of lineages over time (Rull 2020).

The river barrier hypothesis suggests that the ancestral populations of species were fragmented and isolated as the Amazon River network developed during the Neogene and early Quaternary periods, promoting allopatric speciation (Cazé et al. 2016; Rull 2020). This idea is old, dating back to 19th-century naturalists, but it was only in the 1960s that it was formalized as a hypothesis (Cazé et al. 2016; Nores 2020). Thus, it is now considered that the large Amazonian rivers and river systems formed because the elevation of the Andes produced isolation (reduction of gene flow) and differentiation of taxa due to the fragmentation of their distribution areas (Nores 2020).

The marine transgression hypothesis suggests that during the rise in sea levels (around 100 meters) between the Tertiary and Quaternary periods, the Amazon and other tropical forests became fragmented into numerous islands and archipelagos. Thus, plant and animal species would have diversified due to geographic isolation (Nores 2020). As sea levels decreased, these forests were able to expand again (Nores 2020). According to this hypothesis, we would expect a geographic coincidence between the areas of endemism and the regions that were once isolated due to the rise in sea levels (Nores 2020).

More recently, Neogene events began to be highlighted as the main drivers of Amazonian diversification, which became known as the Neogene hypothesis (Rull 2020). These events include the Andean orogeny and the closure of the Isthmus of Panama. The paradigm shift from the Pleistocene refugia hypothesis to the Neogene hypothesis was somewhat radical; however, many scholars consider that both hypotheses are not opposed and/or exclusive (Rull 2020).

In addition to historical hypotheses, some studies examined ecological factors to explain the immense diversity of the Amazon Rainforest. These factors include greater energy availability, a higher number of ecological niches, increased productivity and net primary resources, as well as greater competition and more ecological opportunities (Cracraft et al. 2020).

In general, studies indicate that many clades of Amazonian plant groups emerged between the end of the Cretaceous period and the beginning of the Paleocene, approximately 58 million years ago (Antonelli et al. 2018; Cracraft et al. 2020). The Cretaceous floras of the New World are not well understood, but some research suggests that modern plant families became established in the Paleocene and were abundant and widespread during the Eocene (Cracraft et al. 2020). Despite the various hypotheses already proposed, it seems that the Amazonian biodiversity originated from multiple drivers and mechanisms (Rull 2020), indicating a complex evolutionary history.

BRAZILIAN ATLANTIC FOREST

The Brazilian Atlantic Forest domain once covered more than 1.3 million km^2, which is approximately 15% of Brazil's national territory, from the State of Rio Grande do Norte to Rio Grande do Sul state, along the Brazilian coast (Nores 2020; IBGE 2024). The width of this domain varies significantly, expanding inland in some regions of the Southeast, Eastern Paraguay, and Argentina (Fiaschi and Pirani 2009). This domain encompasses a range of 25 degrees of latitude and reaches altitudes exceeding 2 thousand meters (Fiaschi and Pirani 2009). The Brazilian Atlantic Forest comprises areas of tropical and subtropical forests, as well as several types of smaller vegetation, such as mangroves, restingas, high-altitude fields, and rocky outcrops (Fiaschi and Pirani 2009; Peres et al. 2020; Reginato and Michelangeli 2020).

The Brazilian Atlantic Forest is recognized as a hotspot due to its high species richness (it has approximately 16,500 species of vascular plants [Flora do Brasil 2020]) (Guedes et al. 2020; Peres et al. 2020), high levels of endemism, and the growing anthropogenic threats that have increasingly reduced and fragmented the forests (Martini et al. 2007). Several biogeographic studies have been carried out in the Brazilian Atlantic Forest, mainly seeking to understand the areas of endemism (hence the greater emphasis on this topic in the discussion below). Below, we will briefly discuss these biogeographic studies.

Multiple centers of endemism, based on various groups of organisms, have been proposed for the Brazilian Atlantic Forest (Fiaschi and Pirani 2009). The number of these centers varies according to the organisms studied and the issues addressed, which influences the selection of these areas (Fiaschi and Pirani 2009). There are studies with plants, reptiles, birds, mammals, termites, and harvestmen, which point to the segregation of the Brazilian Atlantic Forest into two blocks, North and South; with the separation between these portions being located between the States of Bahia and Rio de Janeiro, respectively (Guedes et al. 2020; Peres et al. 2020). Most of the work carried out in this phytogeographic domain points to the "break/separation" around the Rio Doce valley, located in Espírito Santo state (Fiaschi and Pirani 2009; Guedes et al. 2020; Nores 2020; Peres et al. 2020; Reginato and Michelangeli 2020).

Several explanations have been proposed for the "break" observed around the Rio Doce valley. The first, and perhaps most intuitive, suggests that the Rio Doce acts as a geographic barrier, which reduces gene flow by segregating populations that reside on opposite banks of the river (Peres et al. 2020; Reginato and Michelangeli 2020). The second explanation is based on climatic factors due to the area's proximity to the Tropic of Capricorn (Peres et al. 2020; Reginato and Michelangeli 2020). The second explanation has been more accepted for plants, although it remains a topic of debate. It is noted that the rivers of the Brazilian Atlantic Forest are relatively narrow compared to those in the Amazon, making them less effective as barriers for species with high dispersal capabilities, which is typical for many plants (Peres et al. 2020).

Despite this, differences in community composition between the Northern and Southern portions of the Brazilian Atlantic Forest are supported by evolutionary studies, which have recovered entire clades that occur exclusively within each region (Fiaschi and Pirani 2009). However, the relationships between Northern and Southern lineages appear to vary considerably among taxonomic groups (Peres et al. 2020).

The Northern Brazilian Atlantic Forest extends from the State of Rio Grande do Norte to Espírito Santo state and has two centers of endemism: Pernambuco and Bahia (center and coast) (Silva et al. 2004; Fiaschi and Pirani 2009; Nores 2020). The Northern portion presents some influences from the Amazon Rainforest, thus, it is stipulated that connections occurred between these domains in the Cenozoic (Fiaschi and Pirani 2009). The Southern Brazilian Atlantic Forest, in turn, extends from the State of Espírito Santo to Santa Catarina state and has an extensive center of endemism that coincides with the Serra do Mar and Serra da Mantiqueira mountains (Silva et al. 2004; Fiaschi and Pirani 2009; Nores 2020). Taxa from the Southern portion appear to receive more influence from the Andes (Fiaschi and Pirani 2009).

The Pernambuco area of endemism was first described for birds and includes a region of evergreen, semi-deciduous, and deciduous forests along the Brazilian Atlantic Ocean coast (North of the São Francisco River, including the States of Alagoas, Pernambuco, and Paraíba) (Peres et al. 2020). This area of endemism has also been supported by plant data (Peres et al. 2020).

The area of endemism of Bahia has also been described based on bird data. This region encompasses the slopes of Chapada Diamantina, the plateaus of central Bahia, and the Northern Minas Gerais state, including evergreen, semideciduous, and deciduous forests (Martini et al. 2007; Peres et al. 2020). Data on vascular plants and butterflies also support this area of endemism (Peres et al. 2020). The coast of Bahia state, characterized by evergreen vegetation, can also be recognized as a center of endemism. It has been identified as such for several groups, including woody plants, ferns, harvestmen, and birds (Peres et al. 2020; Souza et al. 2021). In some groups of invertebrates, such as flies, harvestmen, butterflies, beetles, spiders, hemipterans, and heteropterans, this center of endemism may extend to the South bank of the São Francisco River or the North of Espírito Santo state (Peres et al. 2020).

The Serra do Mar area of endemism encompasses a habitat gradient that ranges from montane, submontane, and floodplain forests to restingas. Research on various species, including woody plants, amphibians, birds, ferns, mammals, butterflies, and snakes, supports this area of endemism (Peres et al. 2020; Souza et al. 2021; Della and Prado 2024). However, the limits of this area vary depending on the specific group being studied. For instance, for woody plants, amphibians, and birds, the area extends from the State of Santa Catarina to central Espírito Santo state. In contrast, studies focusing on vertebrates, butterflies, and snakes identify the area extending only from the State of Santa Catarina to Rio de Janeiro state. For ferns, Souza et al. (2021) defined two distinct regions: The first encompasses a small part of the Northern coast of Paraná state and the Southern coast of São Paulo state, while the second covers the Northern portion of São Paulo and Rio de Janeiro states, and a small part of the Minas Gerais state. Additionally, the Southern region of Brazil (i.e., the area that encompass the States of Paraná, Santa Catarina, and Rio Grande do Sul) has also been recognized as a center of endemism, coinciding with the occurrence of Araucaria forests, based on findings from studies involving birds, moths, butterflies, amphibians, harvestmen, and snakes.

Various hypotheses have been proposed to explain the biodiversity patterns in the Amazon Rainforest, and similar concepts have been applied to taxa from the Brazilian Atlantic Forest. In this sense, the Pleistocene refuge hypothesis has already been used to explain the areas of endemism and the distribution patterns of taxa in the Brazilian Atlantic Forest (Dantas et al. 2011; Peres et al. 2020). Paleoclimatic models suggest climate stability (with high humidity) in the Northern region of the Brazilian Atlantic Forest during the last glacial maximum (Carnaval and Moritz 2008; Peres et al. 2020) and in the areas of endemism of Pernambuco and Bahia states (Costa et al. 2017). In the Southern portion, the impact of climate fluctuations and, mainly, of the arid phases of the Pleistocene seem to have been greater (compared to the Northern region) (Carnaval and Moritz 2008). This makes the hypothesis of restricted humid refugia during glacial periods the focus of much debate (Peres et al. 2020). These models also suggest that montane species along the coast of Brazil may have expanded their ranges during cold phases of the Quaternary, despite currently having limited distributions confined to small areas (Peres et al. 2020). On the other hand, lowland taxa show signs consistent with a scenario of range contraction during colder periods (Peres et al. 2020). Fossils also indicate that the Southern Brazilian Atlantic Forest was subject to drastic climate fluctuations in the Pleistocene, which promoted the replacement of forests by fields in short periods, until the climate changed to more favorable conditions, when the forests expanded (Costa et al. 2017; Peres et al. 2020).

The river barrier hypothesis has also been considered, given the limits of areas of endemism and the North-South segregation of the Brazilian Atlantic Forest

(Dantas et al. 2011). Rivers can act as barriers, reducing gene flow, as has been verified for lizards, frogs, and snakes in the Brazilian Atlantic Forest (Dantas et al. 2011). Despite this, the rivers of the Atlantic Forest in Brazil are not as wide as those in the Amazon Forest, which questions the real role of rivers as physical barriers for many taxa with greater dispersal capacity (Peres et al. 2020). However, it is expected that the formation of river basins acted as barriers at some point in the past (Peres et al. 2020).

The neotectonic hypothesis considers that the Atlantic margin of the South American plate is tectonically passive, though changes have occurred and continue to occur, leading to the formation of faults and fractures that reshape the landscape (Dantas et al. 2011; Peres et al. 2020). The uplift of Brazil's coastal mountains (called Serra do Mar) promoted significant changes, particularly in the Southeastern region (Peres et al. 2020). Notable among these changes are shifts in precipitation that began in the Pliocene epoch, approximately 5.6 million years ago. These shifts have had a profound impact on the distribution of wet and dry habitats, contributing to the fragmentation of the Brazilian Atlantic Forest (Dantas et al. 2011).

The Serra do Mar and Serra da Mantiqueira may have acted as refuges and centers of endemism and diversification for Neotropical organisms (Guedes et al. 2020). High-altitude grasslands developed on the tops of these mountains, which share some floristic similarities with the Andean Páramos (Fiaschi and Pirani 2009; Andrade et al. 2016; Guedes et al. 2020). In these mountainous regions, the different geomorphological and climatic attributes, as well as geographic isolation, appear to influence the observed gradients in species richness today (Reginato and Michelangeli 2020). Biotic connections, or exchanges/dispersals, between the Andes and the Southeastern mountains (such as the Southern route through Patagonia) have been proposed to explain the disjunction of many taxa (Guedes et al. 2020). In addition, other explanations have been developed, such as fragmentation due to the uplift of the Andes during the Miocene, marine transgressions in the Miocene, and aridity in Patagonia and the Chaco since the end of the Miocene (Luebert et al. 2020).

The ecological gradient hypothesis considers the gradual transition between humid forests and drier vegetation (e.g., Cerrado and Caatinga) (Silva et al. 2004; Dantas et al. 2011). Thus, as each region presents distinct ecological characteristics, it is expected that different selective pressures will lead to divergence among organisms (Dantas et al. 2011). Observations of various species, including rats, birds, and snakes, indicate that their distribution correlates with specific humidity and temperature zones. This suggests that environmental gradients play a significant role in the evolution of these groups (Dantas et al. 2011). Additionally, recurrent marine progressions and introgressions in the glacial period may have significantly influenced the dynamics of the biota by promoting the isolation of certain taxa (Leite et al. 2016).

The biogeographic history of the Brazilian Atlantic Forest, as well as the Amazon Rainforest, is quite complex. As seen above, several mechanisms and events may have been responsible for generating the enormous biodiversity present in this phytogeographic domain. Despite this, we still do not have clarity about which events were most important or highlighted.

CAATINGA

The Caatinga phytogeographic domain extends over approximately 850,000 km^2 (corresponding to approximately 11% of the national territory) along the Northeastern region of Brazil (Fiaschi and Pirani 2009; Thomé et al. 2016; Silva and Souza 2018; IBGE 2024). The Caatinga comprises the largest area of seasonally dry tropical forests in the Neotropical region. This domain has approximately 5,100 species of vascular plants (Flora do Brasil 2020). It occurs on fertile soils with high nutrient content and moderate to high pH; however, it suffers from severe drought for at least five months a year (which determines its geographic distribution) (Cole 1960; Werneck 2011; Werneck et al. 2011; Thomé et al. 2016; Florentín et al. 2018; Silva and Souza 2018; Collevatti et al. 2020). The Caatinga is very different from the Cerrado, as it consists mainly of trees and thorny shrubs, which lose their leaves during the dry season; it also has succulent plants, such as cacti and bromeliads, and low-growing herbs, which emerge after the rain (Cole 1960; Pennington et al. 2000; Costa 2003; Werneck 2011; Werneck et al. 2011; Florentín et al. 2018; Reginato and Michelangeli 2020). In addition, the Caatinga vegetation is intolerant to fire (Simon et al. 2009; Azevedo et al. 2020). Within this phytogeographic domain, there are so-called "brejos de altitude", which are interpreted as enclaves of humid forest in higher areas (Costa 2003).

The floristic composition of the Caatinga shows strong links with other seasonally dry tropical forest centers in the Neotropics, such as Missiones (along the Paraguay and Paraná River basins), Piedmont (Southwestern Bolivia and Northwestern Argentina), the Caribbean coast of Colombia and Venezuela, the Andean dry valleys, and the centers located in Central America, along the Pacific coast and in Mexico; but not with the Chaco and the Cerrado (Fiaschi and Pirani 2009; Côrtes et al. 2015).

The history of the distribution of the Caatinga is poorly understood (Thomé et al. 2016); in some places, the boundaries with other phytogeographic domains are clear, and in others, there may be extensive and gradual ecotones, suggesting a state of constant flux. Thus, Prado and Gibbs (1993) proposed the inclusion of the Caatinga in the definition of seasonally dry tropical forests, and based on the distribution of tree species, they established the Pleistocene arc hypothesis. This hypothesis states that seasonally dry tropical forests formed a continuous arc throughout the Neotropics. These forests would have extended into the Amazon, infiltrating the Andean region and establishing connections with the Caribbean (Prado and Gibbs 1993). This would have happened in the Pleistocene, during the glacial period, when the climate was drier and colder; and during this period, the humid tropical forests would have contracted (Pennington et al. 2000; Caetano et al. 2008; Côrtes et al. 2015; Thomé et al. 2016; Florentín et al. 2018). Later, with the increase in temperature and humidity, this arc was fragmented and would have given rise to the various nuclei of seasonally dry tropical forests that exist today in the Neotropics (Thomé et al. 2016). Thus, the species of seasonally dry forests must have originated through vicariance (Pennington et al. 2000). This hypothesis was observed in studies with plants, bees, and lizards and was accepted for several decades (Werneck 2011).

Some authors, however, have proposed long-distance dispersal events to explain the disjunct distribution of many taxa in seasonally dry tropical forests (Caetano et al. 2008; Antonelli and Sanmartín 2011; Thomé et al. 2016). More recently, Werneck et al. (2011) and Costa et al. (2017) modeled paleoenvironments in the Neotropics and found that the distribution of seasonally dry tropical forests was further fragmented during the last glacial maximum. Thus, the previously predicted expansions of seasonally dry forests into areas now occupied by the Amazon were not confirmed (Thomé et al. 2016). Furthermore, modeling results show that the Caatinga is one of the most unstable areas in South America (Costa et al. 2017). Despite this, there are still studies that support a wide and continuous distribution of seasonally dry tropical forests in the past, such as Collevatti et al. (2020).

Pollen records indicate that in certain regions, humid tropical forests have replaced the Caatinga during multiple periods of increased humidity (Thomé et al. 2016). It seems that drought conditions, similar to those experienced today, emerged during the Holocene, which suggests the relatively recent development of this phytogeographic domain (Thomé et al. 2016; Costa et al. 2017). Furthermore, modeling studies indicate that the Caatinga only expanded during the Holocene (Werneck et al. 2011). Some authors have even proposed the formation of a humid forest corridor in the late Pleistocene, connecting the Amazon Rainforest and the Brazilian Atlantic Forest, crossing the Caatinga through the Chapada Diamantina (Thomé et al. 2016). In this case, the "brejos de altitude" would be considered remnants of this past humid tropical forest (Thomé et al. 2016).

Dated phylogenies of common lineages in South American seasonally dry tropical forests suggest an origin that predates the Pleistocene (throughout the Paleogene and Neogene) (Côrtes et al. 2015; Florentín et al. 2018). Therefore, it appears that the Caatinga does not represent a remnant of this supposedly more extensive forest existing at the last glacial maximum, as proposed by the Pleistocene arc hypothesis (Côrtes et al. 2015).

Furthermore, studies have already verified some areas of endemism in the Caatinga. For animals, eight areas are recognized: Borborema Plateau, Campo Maior Complex, Ibiapaba-Araripe Complex, Northern Sertaneja Depression, Southern Sertaneja Depression, São Francisco Dunes, Chapada Diamantina Complex, and Raso da Catarina (Werneck 2011). For plants (Fabaceae), only seven of these eight areas already highlighted are recognized, the only exception being the Borborema Plateau (Werneck 2011).

CERRADO

The Cerrado is a phytogeographic domain that covers more than two million km^2, located in Brazil (mainly in the central region), reaching Bolivia and Paraguay (Simon et al. 2009). It is the second largest domain in Brazil by land area, covering approximately 20% of the national territory, surpassed only by the Amazon Rainforest (Werneck 2011; IBGE 2024). Cerrado presents several types of vegetation, from fields (with many C4 grasses), with sparse cover of shrubs and small trees, to an almost closed forest with a height of 12 to 15 meters (Cerradão) (Pennington et al. 2000; Fiaschi and Pirani 2009; Azevedo et al. 2020; Collevatti et al. 2020; Reginato and Michelangeli 2020). Another important type of vegetation in the Cerrado is the riparian forests, found along the rivers, which contain several species of tropical forests (Pennington et al. 2000). The soil of the Cerrado is acidic and has low availability of calcium and magnesium, in addition to having high levels of aluminum, and is generally well drained (Cerrado vegetation is intolerant to flooding) (Pennington et al. 2000). Fire plays a crucial role in this ecosystem, and many plant species have developed adaptations such as thick bark and cork, xylopodia, and the ability to resprout after fire (Pennington et al. 2000). Studies have shown that the vegetation of the Cerrado had already developed these adaptations to fire even before human activity was known in the region, which demonstrates the natural origin of this phytogeographic domain (Pinheiro and Monteiro 2010).

The distribution of savannas around the world is influenced by the seasonality of precipitation (Azevedo et al. 2020). In the case of the Cerrado, various factors contribute to this seasonality, including the geography of South America, its latitudinal position, and the orientation and elevation of the Andean mountains (which determine the transport of moisture across the continent) (Azevedo et al. 2020). In addition, some authors consider that CO_2 levels may have played a critical role in the expansion of Neotropical savannas. This is because grasses cannot compete with trees under high CO_2 levels or in cases of low water stress (Azevedo et al. 2020). Over the Cenozoic era, CO_2 levels fluctuated significantly: they were high during the Paleocene, promoting the expansion of forests, decreased during the Oligocene, rose temporarily in the Miocene, and then dropped drastically in the Pleistocene (Azevedo et al. 2020).

The Cerrado is recognized as a global biodiversity hotspot (with 12,700 species of vascular plants [Flora do Brasil 2020]) due to the high number of endemic plants and the anthropogenic changes it has undergone (Simon et al. 2009, Collevatti et al. 2020). The highest levels of endemism are found along the mountains of the Espinhaço Range (Minas Gerais and Bahia) and the Chapada dos Veadeiros (Goiás) (Fiaschi and Pirani 2009). Most endemic species occur in rocky fields above 900 meters, where low, herbaceous, or shrubby vegetation predominates in sandy or stony soils (Fiaschi and Pirani 2009, Andrade et al. 2016). These mountains are ancient but have been remodeled over time, so the current elevations (500–1,700 meters) were obtained from the Upper Tertiary to the Lower Quaternary (Werneck 2011).

Within the Cerrado, open vegetation is considered older than forests (Werneck 2011). Furthermore, it is believed that the highest and most continuous plateaus (Central Plateau of Goiás and Chapada dos Guimarães) may have formed a single, large Cerrado refuge during the Pleistocene. The lower plateaus and peripheral depressions, on the other hand, should have been drier than today and could have been dominated by xeric vegetation (such as the Caatinga) or by cooler and drier vegetation (such as the Pampas and Monte) (Werneck 2011).

Many studies have developed hypotheses about the origin and diversification of Cerrado vegetation based on phylogenies of representative taxa of this domain. In this sense, Simon et al. (2009), Bouchenak-Khelladi et al. (2014), and Azevedo et al. (2020) commented that, probably, several groups of grasses and legumes originated between 32 and 25 million years ago, with most of the lineages of these families being present since the beginning of the Miocene. As for the diversification of these groups, it is estimated that it occurred between the Miocene and the beginning of the Pliocene, from 10 to 4 million years ago (Simon et al. 2009; Azevedo et al. 2020). Della and Prado (2025) found that species of the genus *Ormopteris* (Pteridaceae), which are very common in the Cerrado, are relatively recent, having emerged within the last 1.3 million years. Magri et al. (2025) discovered that *Vellozia*, a common genus in the Campos Rupestres of the Cerrado, emerged and diversified during the Oligocene, occupying the Southern region of the Espinhaço Range in the Lower Miocene.

Furthermore, evidence from charcoal particles and pollen suggests that grasses and legumes became ecologically dominant only between 4 and 8 million years ago. Thus, the idea that Cerrado lineages evolved in response to the increase in C4 grasses and fire is reinforced by the presence of adaptations to the latter (Simon et al. 2009). A time lag between the origin and expansion (dominance) of savannas in South America can also be observed (Bouchenak-Khelladi et al. 2014; Stromberg 2011; Azevedo et al. 2020).

Studies have shown that taxa characteristic of savannas (which exist worldwide) are, in general, recently derived from ancestors present in humid or dry forests (Simon et al. 2009). Since the Cerrado is delimited by several other phytogeographic domains, the Amazon Rainforest, Brazilian Atlantic Forest, Caatinga, and Chaco, these domains may have contributed to the recruitment of Cerrado lineages (Simon et al. 2009), as demonstrated by Antonelli et al. (2018). Thus, the lineages existing today in the Cerrado appear to be the product of more recent diversifications and with few endemic genera (Simon et al. 2009).

Furthermore, paleoenvironmental modeling suggests that savannas have existed since the Middle Miocene, while environmental conditions suitable for forests and open ecosystems not analogous to savannas dominated the continent in earlier times, mainly from the Paleocene onwards (Beerling and Osborne 2006; Stromberg 2011; Werneck 2011; Costa et al. 2017; Azevedo et al. 2020). This shows us that the savannas of South America are not the oldest ecosystems on the continent, as previously believed (Pinheiro and Monteiro 2010; Azevedo et al. 2020). Furthermore, molecular phylogenies show a much older origin for forest taxa; for example, the radiation of Malpighiales occurred in the mid-Cretaceous, between 112 and 94 million years ago, and the origin of palm trees around 100 million years ago (Azevedo et al. 2020). Thus, South America can be considered a land of ancient forests and relatively young savannas (Azevedo et al. 2020).

The first open vegetation in South America is believed to have emerged around the middle Eocene, in the Southern portion of the continent, as indicated by phytoliths, herbivore macrofossils, and pollen data (Azevedo et al. 2020). Furthermore, data showing the decline in CO_2 at the end of the Oligocene, which precedes the Miocene cooling, and the estimated ages for the divergence of animal clades typical of this domain, support this idea (Azevedo et al. 2020).

PAMPA

The Pampa phytogeographic domain covers an area of 176,496 km², representing 2.1% of the national territory (IBGE 2024). It occupies more than half of the state of Rio Grande do Sul and extends into Argentina and Uruguay (Roesch et al. 2009). The region is characterized by a rainy climate with no dry season, but with negative temperatures during winter (IBGE 2024). Although the Pampa domain is predominantly composed of grasslands, other phytogeographic formations are also present, such as savanna, steppe, steppic-savanna, coastal vegetation, transition areas, and patches of seasonal deciduous and semi-deciduous forests (Roesch et al. 2009; Baez-Lizarazo et al. 2023).

It is estimated that between 3,000 and 4,000 plant species occur in the Pampa (Overbeck et al. 2007; Roesch et al. 2009; Fiaschi and Pirani 2009). Despite this high diversity, the relative abundance of species is low, and around 8% are endemic (Fiaschi and Pirani 2009; Roesch et al. 2009; Baez-Lizarazo et al. 2023). The main botanical families found in the Brazilian Pampa are Poaceae, Asteraceae, Cyperaceae, Fabaceae, Apiaceae, Oxalidaceae, Verbenaceae, and Iridaceae (Roesch et al. 2009).

Studies have shown that the flora of the Pampa is generally connected to other South American vegetation formations. Baez-Lizarazo et al. (2023) found that most dispersal events into the Pampa originated from the Atlantic Forest, the Andes, the Cerrado, or the Chaco. Although the Pampa is largely dominated by grasses and other herbaceous taxa, the presence of trees and woody plants is notable, especially in riparian forests. Authors such as Rambo (1954), Cabrera (1976), and Waechter (2002) had already highlighted that part of the Pampa flora is shared with the Cerrado, the Chaco, and the Andes. Most dispersal events from these domains into the Pampa occurred during the late Miocene and from the Pliocene onward (ca. 5 mya) (Baez-Lizarazo et al. 2023). In contrast, dispersal events from the Pampa to other regions have been less frequent and are mostly concentrated in the last 2 million years (from the Pleistocene onward) (Baez-Lizarazo et al. 2023). This suggests that lineage exchange between the Pampa and these other domains is asymmetrical, with most events occurring toward the Pampa. This pattern supports the idea that the Pampa may function as a macroevolutionary sink (Baez-Lizarazo et al. 2023).

Baez-Lizarazo et al. (2023) also found that some lineages diversified within the Pampa, such as: Amaryllidaceae (*Nothoscordum*), Apiaceae (*Eryngium*), Apocynaceae (*Oxypetalum*), Asteraceae (*Perezia*, *Stenachaenium*, *Hypochaeris*, *Sommerfeltia*, *Microgyne*), Cactaceae (*Frailea*, *Parodia*, *Gymnocalycium*), Euphorbiaceae (*Croton*, *Tragia*), Iridaceae (*Herbertia*, *Cypella*, *Sisyrinchium*), Solanaceae (*Calibrachoa*, *Petunia*), Orchidaceae (*Bipinnula*), and Poaceae (*Distichlis*, *Hordeum, Nassella*). These cladogenetic events mostly occurred within the last 5 million years, with a higher concentration during the Pleistocene (the last 2.6 million years).

The results obtained by Baez-Lizarazo et al. (2023), along with fossil evidence, indicate that the herbaceous vegetation of the Pampa was present since the Middle Miocene and remained dominant until after 7 mya (Ortiz-Jaureguizar and Cladera 2006). From the Pliocene to the Pleistocene (5.32–2.58 mya), grasslands and steppes dominated the region, likely associated with a rich megaherbivore fauna and cooler, drier climatic conditions (Ortiz-Jaureguizar and Cladera 2006). Starting in the Pleistocene, macrofossil and palynological records indicate a drastic change in the taxonomic and ecological composition of the Pampa flora, with the onset of more humid and stable climatic conditions and an increase in non-grass pollen (Baez-Lizarazo et al. 2023).

Thus, the current Pampa can be interpreted as a relic of the region's drier past climates, which allowed grasses to dominate the landscape (Baez-Lizarazo et al. 2023). However, the present climate is suitable for forest development (Roesch et al. 2009; Baez-Lizarazo et al. 2023). Abiotic stress on tree growth, along with biomass consumption by fire and herbivores, has been suggested as an explanation for the absence of forest vegetation in the region (Baez-Lizarazo et al. 2023).

PANTANAL

The Pantanal phytogeographic domain covers an area of 150,355 km², representing 1.8% of the national territory (Mato Grosso and Mato Grosso do Sul states) (IBGE 2024). It comprises a predominantly flat and low-lying region, surrounded by escarpments of the edge of the Paraná Sedimentary Basin and the Serra da Bodoquena to the East, and by the Chapada dos Parecis and the Serra de Cuiabá to the North. To the South, the Pantanal is bordered by the Apa River, and to the west, it extends into Bolivia and Paraguay, with smaller portions, especially in the latter (Junk and Cunha 2016). It is recognized as the largest continuous floodplain on Earth (Alho 2008). The annual floods, due to their large extent and long duration, cause significant changes in both the biotic and abiotic environments and are essential for the existence of the Pantanal (Alho 2008). Unlike other phytogeographic domains, it is the only one whose delimitation is not based on vegetation formations or phytophysiognomies.

The origin of the Pantanal can be attributed to the sub-horizontal subduction of the Nazca Plate beneath the South American Plate between the Paleogene and Neogene periods (approximately between 66 and 2.6 million years ago) (Rocha et al. 2022). This tectonic process promoted uplift and differential subsidence of the terrain, creating a depressed area between elevated blocks, corresponding to the current sedimentary basin where the Pantanal developed (Rocha et al. 2022). The subduction movement led to the formation of faults and rift-like structures, which facilitated sediment accumulation and the subsequent formation of the floodplain (Rocha et al. 2022). Later, alternating cycles of dry and wet periods during the Late Pliocene and Early Pleistocene likely contributed to the formation of a geomorphologically complex landscape in the Upper Paraguay Basin, now occupied by the Pantanal (Junk and Cunha 2016).

The Pantanal can be considered a hypersseasonal savanna, meaning a savanna subject to prolonged flooding (Junk and Cunha 2016). Its flora is closely related to that of the Cerrado (Junk and Cunha 2016), but it also includes species from the Amazon, the Chaco, and dry forests—phytogeographic domains that border the Pantanal. Some authors consider the Pantanal to be an extension of the Chaco, a semi-arid region that spans parts of Argentina, Paraguay, and Bolivia.

The vegetation of the Pantanal includes approximately 1,900 species of phanerogamic plants (Alho 2008). There are very few endemic species in the region, and it is estimated that the 6,000 years following the last intense dry period were not sufficient to generate endemism (Junk and Cunha 2016). Furthermore, the speciation process in the Pantanal may be hindered by the flood pulse, which "forces" mobile species to move between the floodplain and the river areas, while water currents passively transport propagules—or less mobile species—from one area to another (Junk and Cunha 2016). This mobility results in constant gene flow and prevents speciation that would otherwise occur through spatial isolation of populations (Junk and Cunha 2016). Thus, it can be concluded that the flora of the Pantanal is composed of widely distributed species originating from more or less adjacent phytogeographic domains, such as the Cerrado, seasonally dry forests, the Chaco, the Amazon, and the Atlantic Forest (Pott et al. 2011).

INTEGRATING THE BIOGEOGRAPHIC HISTORY OF THESE PHYTOGEOGRAPHIC DOMAINS

Studies indicate that until the end of the Paleocene and beginning of the Eocene (i.e., until ca. 34 mya), the climate was predominantly warmer and wetter than the current one, suggesting the presence of extensive and continuous tropical forests in South America (Ortiz-Jaureguizar and Cladera 2006; Werneck 2011; Collevatti et al. 2020; Peres et al. 2020). In the Eocene, according to climate reconstructions, there were tropical temperatures in up to two-thirds of South America, indicating that tropical forests were still dominant, in addition to being more diverse than those existing in the Paleocene and Holocene (Wilf et al. 2003; Burnham and Johnson 2004; Jaramillo et al. 2006; Ortiz-Jaureguizar and Cladera 2006). During the late Eocene and Oligocene (or until the Pleistocene, when the dry diagonal would have been fully formed), global episodes of cooling and drought occurred, which favored the formation and expansion of open vegetation in the Southern and Central regions of the continent (Thode et al. 2019; Peres et al. 2020). This led to the development of a diagonal strip of open and dry vegetation, known as the South American dry diagonal (also called "the greater South American disjunction") (Werneck 2011; Lohmann et al. 2013; Fiaschi et al. 2016; Thode et al. 2019; Peres et al. 2020). Although the formation of the dry diagonal began at this time, the dominance of the Cerrado and Caatinga is much more recent.

This dry diagonal led to the formation of the Brazilian Atlantic Forest to the East and the Amazon Rainforest to the West, which thus became separated (Peres et al. 2020). Therefore, the dry diagonal may have acted as a barrier to the migration of species between these two forests, explaining the floristic differences between them (Werneck 2011; Fouquet et al. 2012; Pedro 2014; Côrtes et al. 2015; Fiaschi et al. 2016; Collevatti et al. 2020). Several phylogenetic studies show that the dry diagonal acted as a strong geographic barrier for plants and animals that occur in tropical forest domains (Côrtes et al. 2015; Azevedo et al. 2020). One example is the work of Thode et al. (2019) carried out with *Amphilophium* (Bignoniaceae), a group of Neotropical lianas. Based on a dated phylogeny, the authors found the formation of two distinct clades, one with species from the Amazon Rainforest and the other with species from the Brazilian Atlantic Rainforest, and that the estimated time of divergence of these clades coincides with the period of formation of the dry diagonal.

Despite this, several studies have suggested that the Brazilian Atlantic Forest and the Amazon Forest were reconnected several times in the past, thus seeking to explain the disjunction of the taxa (Sobral-Souza et al. 2015; Capurucho et al. 2018; Collevatti et al. 2020; Peres et al. 2020). These connections may have occurred through Northeastern Brazil, in areas currently occupied by "brejos de altitude" (Costa 2003; Capurucho et al. 2018; Peres et al. 2020), or through the riparian forests existing in the South-Central Cerrado, or even through forests associated with the Paraná and Paraguay rivers (Southern Brazil), in the latter case connecting the Brazilian Atlantic Forest to the Southeastern Amazon Forest (Costa 2000; Peres et al. 2020). These connections may have occurred at different times, with the connection between the Southern Brazilian Atlantic Forest and the Southeastern Amazon and the one through the Cerrado being the oldest (dating back to the Middle/Upper Miocene, between 16–5.3 mya); the connections through the Northeast are estimated to have occurred between the Pliocene and Pleistocene, between 5–1 mya (Capurucho et al. 2018; Nores 2020; Peres et al. 2020). Since reconstructions have shown that the Eastern Amazon suffered a more intense drought (this region appears to be less stable), it is assumed that the corridors between the Brazilian Atlantic Forest and the Amazon Forest through the Southern region were the most stable and long-lasting. Nores (2020) also hypothesized that the Tocantins, São Francisco, and Jequitinhonha Rivers may have played an important role in the connections between the Brazilian Atlantic Forest and the Amazon Forest. Furthermore, phylogenetic studies also point to the hypothesis of past contact between the Southern Brazilian Atlantic Forest and the Andean tropical forests (Peres et al. 2020).

Thus, since the Cerrado and Caatinga have a more recent origin, the migration of species from tropical forests to savannas and seasonally dry tropical forests may have shaped the high diversity of these phytogeographic domains (Collevatti et al. 2020). Antonelli et al. (2018) found that lineages adapted to drought are more likely to evolve from lineages adapted to humidity than vice versa, so there are few observed transitions from dry to humid vegetation. Fine and Lohmann (2018) commented on the possibility that humid forest taxa have developed characteristics (or adaptations) associated with dry conditions within the humid areas themselves, that is, even before migrating to these dry areas.

Modern wetter climatic conditions in Central Brazil, with periods of seasonal drought, were established in the Holocene (Pinheiro and Monteiro 2010; Collevatti et al. 2020). With the increase in humidity in the Cerrado region, the leaching process became more intense, which promoted the expansion of the Cerrados and, consequently, the retraction of tropical forests, which never recovered the rich and extensive forest cover they had during the Pliocene (Pinheiro and Monteiro 2010).

Furthermore, many paleomodeling studies have found that tropical dry forests experienced a gradual southward expansion during the Holocene, with a large gap in central Brazil, where Cerrado vegetation had already established itself (Werneck et al. 2011). However, this expansion was much smaller than that proposed by the Pleistocene arc hypothesis, and it was also more recent. The last glacial maximum was probably too dry and cold to sustain large extensions of dry forests (Werneck et al. 2011). After this expansion phase, dry forests showed small fluctuations until reaching their current distribution (Werneck et al. 2011). Humid forest corridors connecting the Amazon and Atlantic forests may likely have segregated the Caatinga from the Cerrado.

Still based on paleoenvironmental modeling and using fossil pollen, Costa et al. (2017) found high stability over the last 30,000 years in Southwestern Amazonia, the Brazilian Atlantic Forest, and parts of the Cerrado. Furthermore, the climate of Western Amazonia was probably continuously humid, supporting the presence of tropical forests, and Southeastern Brazil, in turn, was colder and drier during glacial periods. This caused the grasslands and *Araucaria* Forests to spread Northward, replacing the Brazilian Atlantic Forest and savannas at latitudes up to 20 degrees South (which retreated southward only after the glaciation) (Collevatti et al. 2020). There is also evidence that during the last glacial maximum, there were wetter conditions in parts of the Caatinga (Werneck 2011).

The history of Brazilian phytogeographic domains is quite complex, characterized by numerous hypotheses that aim to explain the significant diversity and distribution patterns of various taxa (Fiaschi and Pirani 2009). Additionally, many criticisms have been raised against these hypotheses; some have been accepted for certain taxa, whereas others have been refuted, making the biogeographic history of these domains a subject of ongoing debate (Colli-Silva and Pirani 2019). This situation highlights the need for new studies involving different groups of organisms to establish congruence in results across various taxa.

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