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INVITED REVIEW

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Geoclimatic drivers of diversification in the largest arid and semi-arid environment of the Neotropics: Perspectives from phylogeography

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Abstract

The South American Dry Diagonal, also called the Diagonal of Open Formations, is a large region of seasonally dry vegetation extending from northeastern Brazil to northern Argentina, comprising the Caatinga, Cerrado, and Chaco subregions. A growing body of phylogeography literature has determined that a complex history of climatic changes coupled with more ancient geological events has produced a diverse and endemic-rich Dry Diagonal biota. However, the exact drivers are still under investigation, and their relative strengths and effects are controversial. Pleistocene climatic fluctuations structured lineages via vegetation shifts, refugium formation, and corridors between the Amazon and Atlantic forests. In some taxa, older geological events, such as the reconfiguration of the São Francisco River, uplift of the Central Brazilian Plateau, or the Miocene inundation of the Chaco by marine incursions, were more important. Here, we review the Dry Diagonal phylogeography literature, discussing each hypothesized driver of diversification and assessing degree of support. Few studies statistically test these hypotheses, with most support drawn from associating encountered phylogeographic patterns such as population structure with the timing of ancient geoclimatic events. Across statistical studies, most hypotheses are well supported, with the exception of the Pleistocene Arc Hypothesis. However, taxonomic and regional biases persist, such as a proportional overabundance of herpetofauna studies, and the under-representation of Chaco studies. Overall, both Pleistocene climate change and Neogene geological events shaped the evolution of the Dry Diagonal biota, though the precise effects are regionally and taxonomically varied. We encourage further use of model-based analyses to test evolutionary scenarios, as well as interdisciplinary collaborations to progress the field beyond its current focus on the traditional set of geoclimatic hypotheses.

KEYWORDS
Caatinga, Cerrado, Chaco, dry diagonal, phylogeography, South America

1 | INTRODUCTION

The South American Dry Diagonal (DD), also known as the Diagonal of Open Formations, encompasses the largest continuous area of seasonally dry vegetation in the Neotropics, extending from northeastern Brazil to northern Argentina, and occupying over 3,000,000 km^2 (Prado & Gibbs, 1993; Vanzolini, 1963; Werneck, 2011). The DD separates the two main humid tropical forests in South America: the Amazon Rainforest in the northwest and the Atlantic Forest in the east and southeast. A steep latitudinal gradient and a complex history of geoclimatic events – marine incursions, tectonic uplift, and climatic fluctuations – have divided the DD into three traditionally recognized subregions: (i) the Cerrado, with the world's largest tropical savanna, in central Brazil; (ii) the Caatinga, with the world's largest seasonally dry tropical forest (SDTF), in northeastern Brazil; and (iii) the Chaco, a semi-arid plain in Bolivia, Paraguay and northern Argentina (Figure 1a). These regions are not uniform vegetation domains; rather, they are intricate mosaics of phytophysiognomies dispersed along gradients of other vegetation types such as grasslands, savannas and woodlands. The Cerrado domain is composed mainly of not only savannas, but also SDTFs, seasonal grasslands, gallery forests, campos rupestres, and other vegetation types (Oliveira-Filho & Ratter, 2002). Within the Caatinga, SDTFs dominate extensive areas while also including humid tropical forests in elevated terrains alongside savannas and campos rupestres situated on plateaus (de Queiroz et al., 2017). Similarly, the Chaco domain predominantly features dry forest interspersed with savannas and humid forests. However, in contrast to the SDTFs of the Caatinga, the Chaco experiences periodic frosts and shares floristic affinities with temperate vegetation, resulting in a mixture of subtropical and temperate characteristics (Pennington et al., 2000). High floristic diversity, endemism and differentiation across the DD suggest that few species are widespread and shared across the different regions (DRYFLOR et al., 2016). Although all three DD subregions are characterized by xeric environments and steep dry seasonal periods (Neves et al., 2015), they differ in their specific climatic and edaphic conditions, geological histories, and associated biotas. For example, though all subregions have dry and wet seasons, rainfall in the Caatinga is highly sporadic, and monthslong absolute droughts are frequent. Climatically, the Chaco's temperatures are much more extreme than those of the other DD subregions, from below freezing in winter and up to 48.9°C (the South American record) in summer (Werneck, 2011). Because of this diversity and complexity, the debate over which geographic and climatic factors have been most important in shaping DD biodiversity is contentious (Jaramillo, 2023).

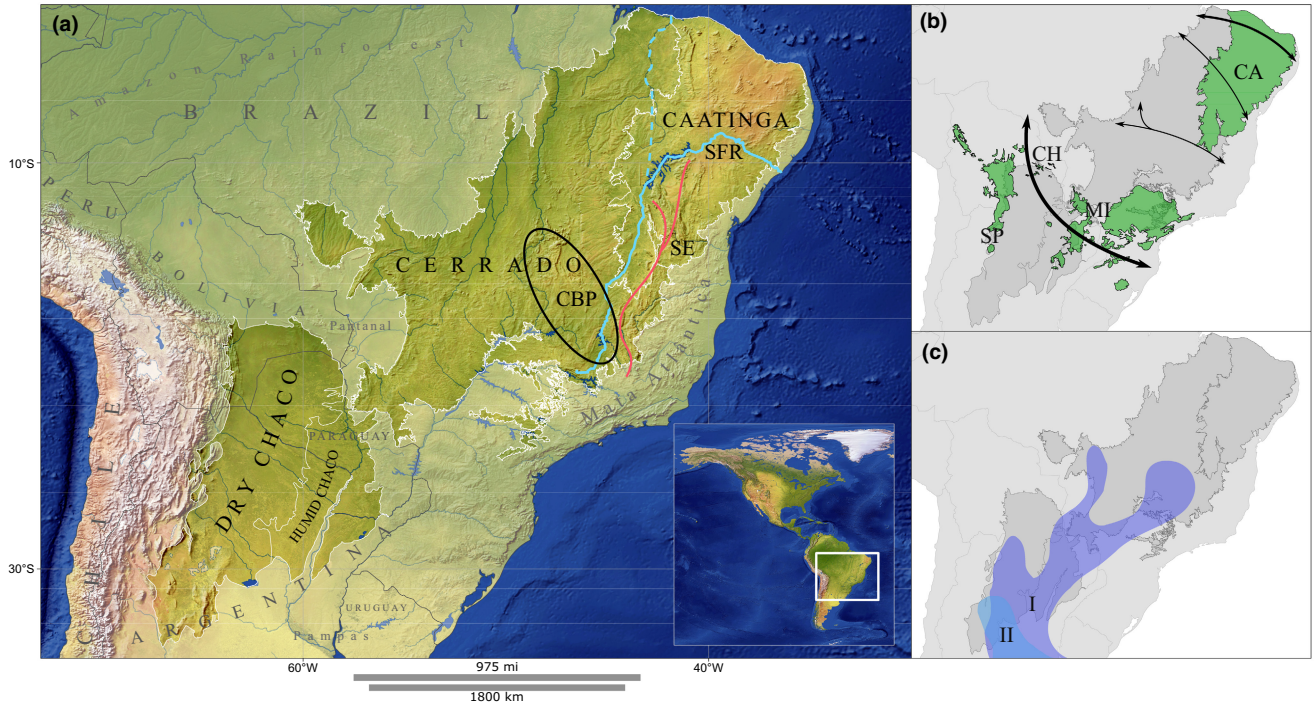

FIGURE 1 The South American Dry Diagonal (DD). (a) DD subregions and important geographical features. The rough extent of the Central Brazilian Plateau (CBP; black) and the spine of the Serra do Espinhaço (SE; red) are shown. The São Francisco River (SFR) is drawn in solid cyan, while its hypothesized paleocourse, partially following the course of the Parnaíba after Grabert (1968), is drawn in dashed cyan. (b) Pleistocene Arc Hypothesis and hypothesized Amazon–Atlantic Forest connections (black arrows; adapted from Ledo & Colli, 2017). Present-day SDTF nuclei, hypothesized to have been connected as the Pleistocene Arc, are drawn in green (adapted from Goncalves et al., 2019). CA, Caatinga; CH, Chiquitanía; MI, Misiones; SP, Subandean Piedmont. (c) Hypothesized Miocene marine incursions, adapted from Hernández et al. (2005). The first incursion (I) occurred ~15–13 mya. The second incursion (II) occurred ~10–5 mya. A 'clean' version of map (a) is provided for community use in the Supplementary Data S1.

The modern DD subregional assemblages are thought to have developed recently relative to the surrounding rainforest biomes, alongside global aridification events linked to glacial cycles (Azevedo et al., 2020; Pennington et al., 2009). The modern Caatinga arose from ~10–2.5 mya, probably due to a combination of aridification, erosional exposure of nutrient-rich crystalline soils and the immigration of plant communities from the Cerrado and neighbouring SDTF isolates in the Atlantic Forest (Fernandes et al., 2022). The Caatinga's primary watercourse, the São Francisco River, was shaped by these geoclimatic changes, which in turn likely shaping the Caatinga biota in the Pleistocene (Rodrigues, 1986, 2003). Meanwhile, the Cerrado vegetation assemblage probably originated with the global expansion of C4 grasslands after 10 mya, with most lineages arising after 4 mya (Edwards et al., 2010; Jaramillo, 2023; Simon et al., 2009). The history of the Cerrado is further characterized by the uplift of the underlying Central Brazilian Plateau and its subsequent erosion through the Neogene and beyond. The resulting landscape compartmentalization potentially shaped diversification in the region (Ab'Saber, 1983; da Silva, 1997). Finally, the Chaco was most likely formed from a combination of Pleistocene cooling and aridification (Ortiz-Jaureguizar & Cladera, 2006), Pleistocene fluvial deposition (Iriondo, 1993), Andean uplift (Gregory-Wodzicki, 2000), and vast marine incursions in the late Neogene (~10 mya). These marine incursions are suspected to have driven diversification in the Chaco via displacement and allopatry (Brusquetti et al., 2018). The entire DD was also affected by the strong climatic fluctuations of the Pleistocene, which in turn may have driven the formation of temporary rainforest corridors that connected Amazonia, the Yungas, and the Atlantic Forest while forming barriers to dispersal in the DD itself (Sobral-Souza et al., 2015; Trujillo-Arias et al., 2017). Importantly, the DD subregions are not the only arid or semi-arid environments of South America – in fact the term 'Arid Diagonal' is sometimes used to describe another such region stretching from coastal Peru to Patagonia (Abraham et al., 2020). However, being continuous and affected by similar geoclimatic forces, the Caatinga, Cerrado, and Chaco form a coherent and tractable system of study and are the focus of this review.

The DD is very biodiverse, with many endemic species (Azevedo et al., 2016; da Silva et al., 2017; Klink & Machado, 2005; Neves et al., 2015). The richest subregion is the Cerrado, one of 35 global biodiversity hotspots, boasting at least 10,000 plant species, of which nearly half are endemic (Mittermeier et al., 2011). The Caatinga harbours at least 3150 species of plants, 23% of them endemic (da Silva et al., 2017), while the Chaco has ~3400 plant species, 11% of which are endemic (Baumann et al., 2016). However, the biodiversity of the DD and the processes generating it have only recently seen significant attention from researchers. For example, Vanzolini (1963, 1974) and later Vitt (1991) regarded the fauna of the region as depauperate, with low endemism and overall diversity. Increased sampling and the advent of molecular phylogenetics in the past two decades have revealed a vast underestimation of DD biodiversity. Numerous lineages once thought to belong to a single widespread taxon are now known to comprise multiple species (Bezerra et al., 2020; Collevatti et al., 2009; Domingos et al., 2014; Oliveira et al., 2015; Recoder et al., 2014), and other species new to science have also been described (Barboza et al., 2011; Jansen et al., 2009; José da Silva, 2014; Teixeira Jr. et al., 2013).

Here, we review the growing DD phylogeography literature, which suggests that a set of geoclimatic events drove the formation of DD biodiversity. These include the aforementioned (i) Pleistocene climatic fluctuations; (ii) historical corridors between the Amazon Rainforest and Atlantic Forest; (iii) the establishment of the São Francisco River in the Caatinga; (iv) the uplift of the CBP in the Cerrado and (v) marine incursions in the Chaco. We identified 142 DD phylogeography studies, most of which address one or more of these hypotheses (Table S1 and Appendix S1). In this review, we offer an overview of DD phylogeography studies in terms of the geoclimatic hypotheses they investigate and discuss trends, issues and possible future directions in the field.

2 | LITERATURE SURVEY

We conducted our literature survey of DD phylogeography studies in multiple sessions between July 2021 and August 2023 by searching Google Scholar with the keyword 'phylogeography', in combination with 'dry diagonal', 'diagonal of open formations', 'open diagonal', 'cerrado', 'caatinga', and 'chaco'. Some studies were additionally identified among the references of other studies. We identified 142 studies fitting our criteria, which were geographic and methodological. We counted a study as a 'Dry Diagonal study' if it was at least partially conducted with samples collected from one or more of the Caatinga, Cerrado, and Chaco subregions. Some studies also include samples from Amazonia or the Atlantic Forest (e.g. Fonseca et al., 2021); these studies were still included so long as the balance of samples and discussion was at least equal between DD and non-DD regions. To qualify as a 'phylogeography study', a given manuscript must be conducted with genetic data from many samples across a relatively large area and utilize phylogeographic methods. As such, we did not include studies that focused on small areas (i.e. landscape genetics studies), on niche modelling exclusively (i.e. did not use genetic data) nor phylogeny and associated methods exclusively (i.e. did not use phylogeography methods). Support for a given hypothesis is generally stated within the discussion of the associated study, though it is important to note that most studies (70%) did not perform explicit hypothesis *tests*. In these cases, hypothetical support is based on the endorsement of the hypothesis by that study's authors, given their results and knowledge of the DD literature. For additional details on the literature survey methodology, see Appendix S1.

3 | CLIMATIC DRIVERS OF DIVERSIFICATION IN THE DRY DIAGONAL

3.1 | Pleistocene climate fluctuations

Climatic change during the Pleistocene likely explains the most recent speciation events, accounting for the regional distribution of communities through to the Holocene. In South America, the

Pleistocene Refuge Hypothesis (Haffer, 1969) posits that repeated glacial cycles during the Pleistocene led to fragmentation of the Amazon Rainforest into isolated refugia, facilitating allopatric speciation of rainforest-adapted taxa. This hypothesis is supported by some studies (Garzón-Orduña et al., 2015), whereas others have shown that many South American lineages arose earlier, in the Neogene, due to geoclimatic processes such as Andean uplift (Bush & de Oliveira, 2006; Hoorn et al., 2010; Rull & Carnaval, 2020; Turchetto-Zolet et al., 2013). A similar Pleistocene versus Neogene dichotomy emerges from the DD-specific literature (Collevatti et al., 2020; Colli, 2005), though the exact hypothesized mechanisms of speciation differ.

In the Cerrado, the majority of phylogeographic studies have overwhelmingly demonstrated demographic or evolutionary responses to Pleistocene climate change, mostly in plants (Figure 2) (Buzatti et al., 2017; Collevatti et al., 2015; Fiorini et al., 2020; Leal et al., 2019; Ramos et al., 2007; among many others – see Fava et al., 2020, for a contradictory case). A meta-analysis by Collevatti et al. (2020) found that the effects of Pleistocene climate fluctuations in plants are reflected primarily as intra-specific diversity, with the actual origin of major lineages occurring during the Neogene due to geological events. Discordant demographic responses during the Pleistocene are observed among plants, with some species expanding (Bonatelli et al., 2014; Leal et al., 2019) and others contracting (Collevatti et al., 2015; Collevatti, Ribeiro, et al., 2012; de Lima et al., 2014) or even remaining stable (Lima et al., 2017). Some Cerrado plants exhibit an east–west pattern of lineage differentiation (northeast–southeast in a few cases) (Correa Ribeiro et al., 2016; Leal et al., 2019; Ramos et al., 2007; Resende-Moreira et al., 2017). No physical barriers seem to account for this phylogeographic break, which has been linked to historical range shifts of Cerrado vegetation during Pleistocene climate changes.

In animals, most Cerrado phylogeography studies focus on reptiles and amphibians, which also show contradictory responses. Frogs generally show refugial isolation in the older Pleistocene and population expansion in the more recent Pleistocene due to the end of the last glaciation (Arantes et al., 2023; Camurugi et al., 2021; Miranda et al., 2019; Prado et al., 2012; Vasconcellos et al., 2019). Similarly, Werneck, Nogueira, et al. (2012) demonstrated that squamate reptiles persisted and diversified in Pleistocene refugia located on Cerrado plateaus (Ab'Saber, 1983). However, further research has revealed little genetic divergence between stable and unstable regions (Santos et al., 2014; Werneck, Gamble, et al., 2012). Older, Neogene diversification events (Domingos et al., 2014; Guarnizo et al., 2016; Machado et al., 2014; Werneck et al., 2009) suggest that Pleistocene refugia might have had limited effects on reptile

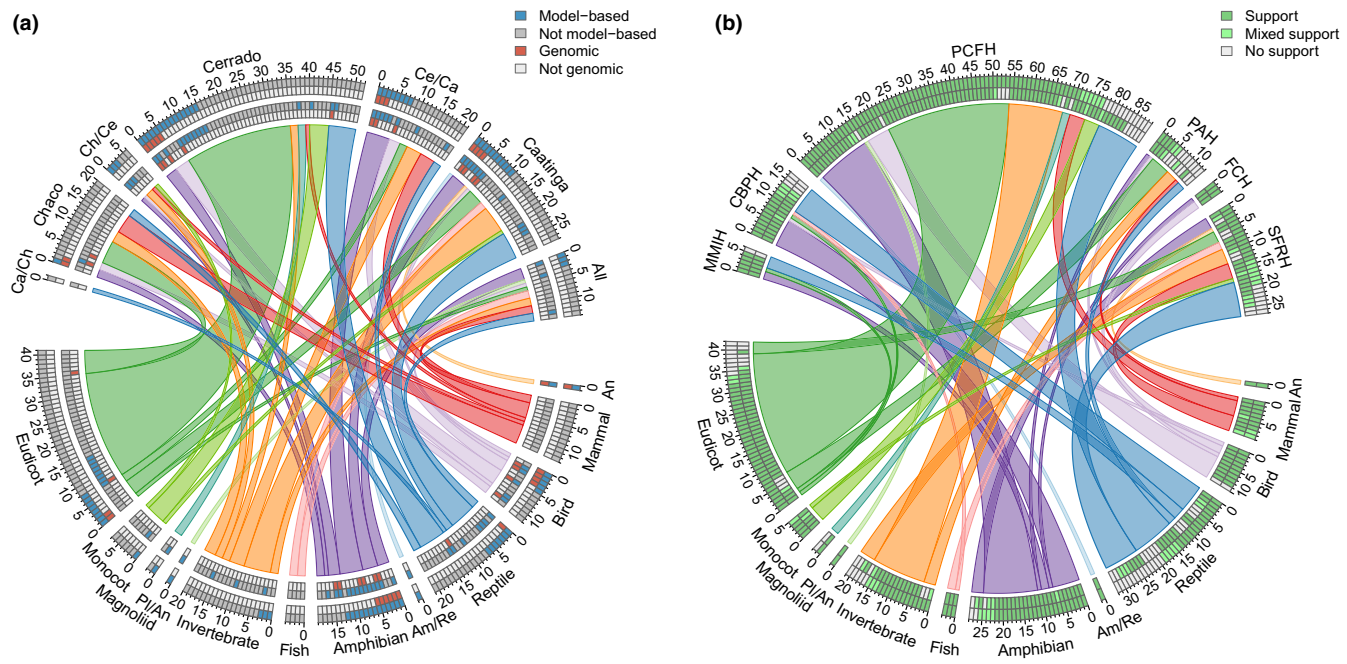

FIGURE 2 Circos plots visualizing the DD phylogeography literature, constructed with the R package circlize v0.4.15 (Gu et al., 2014). (a) Relationships between focal taxonomic groups and focal subregions (or combinations thereof), as well as the quantity of model-based studies and studies using genome-scale data for each category. The outer ring of cells represents the total number of model-based and/or genomic studies for a given category; the inner ring represents totals for the corresponding ribbon. (b) Relationships between focal taxonomic groups, DD biogeographic hypotheses, and the corresponding degree of support. The outer layer of the ring of cells shows the total number of addressed hypotheses (*not* studies; studies may address ≥1 or 0 hypotheses) showing full support, mixed support, or no support for the given category, while the inner layer pertains to the corresponding ribbon. Am, Amphibian; An, Animal; Ca, Caatinga; CBPH, Central Brazilian Plateau Hypothesis; Ce, Cerrado; Ch, Chaco; FCH, Forest Connections Hypothesis; MMIH, Miocene Marine Incursion Hypothesis; PAH, Pleistocene Arc Hypothesis; PCFH, Pleistocene Climatic Fluctuations Hypothesis; Pl, Plant; Re, Reptile; SFRH, São Francisco River Hypothesis.

population structure and diversity, despite the small number of affirmative studies. For Cerrado reptiles, the effects of Pleistocene climate change may therefore be limited to demographic changes. Other animal taxa studied in this context have generally shown demographic changes and/or changes in population structure in response to Pleistocene climatic fluctuations (mammals: Di-Nizo et al., 2022; González-Ittig et al., 2022; birds: Corbett et al., 2020; Lima-Rezende et al., 2019; Luna et al., 2017; Rocha et al., 2020; Souza et al., 2022; invertebrates: Andrade-Souza et al., 2017; Barrios-Leal et al., 2019; Fernández Campón et al., 2021; Franco & Manfrin, 2013; Françoso et al., 2016; Moraes et al., 2009).

The Caatinga's formation occurred during the Neogene and Pleistocene, with an SDTF flora assembling in the region as regional aridification and the exhumation of Paleo-Mesozoic sediments promoted environmental heterogeneity (Fernandes et al., 2022). The Pleistocene Caatinga contracted during dry glacial maxima as global moisture was locked into ice sheets closer to the poles, expanding again during interglacial periods (Werneck et al., 2011). The main onset of diversification in the Caatinga flora probably occurred during or after the Pliocene, in parallel with the diversification of other SDTF isolates in South America (Colli-Silva et al., 2021), such as the Subandean Piedmont and Misiones (Figure 1b), though they probably developed in isolation from each other (see later section). Just over half (13/24) of studies on the effects of Pleistocene climatic fluctuations on Caatinga taxa are focused on herpetofauna. As with the Cerrado, Caatinga amphibians in general demonstrate demographic change and changes in population structure in response to Pleistocene climatic change (Camurugi et al., 2021; Gehara et al., 2017; Oliveira et al., 2021; Thomé et al., 2016; Thomé & Carstens, 2016; Thomé, Carstens, Rodrigues, Alexandrino, & Haddad, 2021; Thomé, Carstens, Rodrigues, Galetti Jr, et al., 2021), while reptiles have responded more strongly to Neogene geological events (Fonseca et al., 2018; Oliveira, Martinez, et al., 2018; Passoni et al., 2008; Werneck et al., 2015; but see Camurugi et al., 2022). However, synchronous population expansions in both Caatinga reptiles and amphibians have been detected in the late Pleistocene (118–224 kya), potentially coinciding with an expansion in Caatinga habitat (Gehara et al., 2017). Studies on insects (Andrade-Souza et al., 2017; Barrios-Leal et al., 2019; Bonatti et al., 2014; Maia et al., 2022; Miranda et al., 2017) and plants (Balbino et al., 2018; Caetano et al., 2008) also generally show Pleistocene climate change effects. The exact patterns and mechanisms of Pleistocene climate change in the Caatinga are still unclear (Colli-Silva et al., 2021); the proposed Pleistocene Arc Hypothesis (Prado & Gibbs, 1993) is a popular explanation but has seen only mixed support in phylogeographic studies (see later section).

Like other ecoregions in southern South America, the Chaco experienced pulses of expansion and retraction during Pleistocene glaciations that may also have influenced its biodiversity patterns (Ortiz-Jaureguizar & Cladera, 2006). Of the few available studies, consistent patterns include minimal population structure (Brusquetti et al., 2019; Camps et al., 2018; Delgado et al., 2021; Ferreiro et al., 2023; Robiatti et al., 2021) and species-specific demographic responses to glaciations. Some forest-associated species seem to have expanded during glacial maxima (Camps et al., 2018; Trujillo-Arias et al., 2017; Vergara et al., 2017), while other species expanded during interglacials (Bartoleti et al., 2017; Brusquetti et al., 2019; González-Ittig et al., 2022; Scaldaferro et al., 2023). Additional phylogeographic studies of Chaco species are needed to assess the importance of Pleistocene glaciations in the region's history. Recent phylogeographic studies on various taxa (Byrne et al., 2022; Ferreiro et al., 2023; Giudicelli et al., 2022; Gonzalez et al., 2023; González-Ittig et al., 2022; Sánchez-Restrepo et al., 2023; Scaldaferro et al., 2023) all demonstrated significant effects of Pleistocene climate fluctuations.

When testing the effects of Pleistocene climate fluctuations, one should expect populations in less stable areas to show larger population size changes and less overall genetic diversity compared to populations in more stable ones (e.g. Carnaval et al., 2009). Testing for Pleistocene population change in a coalescent framework, such as with FastSimCoal (Excoffier & Foll, 2011), Momi (Kamm et al., 2020) or PipeMaster (Gehara et al., 2020), would show support for this hypothesis. Additionally, paleoclimatic models should provide parallel predictions of genetic diversity and genetic distances between samples (e.g. Camurugi et al., 2021; Oliveira, Martinez, et al., 2018; Vasconcellos et al., 2019).

3.2 | Campos rupestres, the Serra do Espinhaço, and Pleistocene climatic fluctuations

Campos rupestres (rupestrian grasslands) are a unique vegetational assemblage associated with higher elevation in Brazil. This phytogeographic unit is mainly characterized by a mosaic of rocky mountaintop islands from 900 m to more than 2000 m above sea level (Silveira et al., 2016), sharing substrate, climate and floristic elements (e.g. grassy-shrubby vegetation and mild temperatures) that differ from the surrounding Cerrado, Caatinga and Atlantic Forest (Alves et al., 2014). Although much of the campos rupestres are technically found within the bounds of the DD, their character is different with enough endemicity to merit their own detailed review; here, we provide only a brief overview of the effects of Pleistocene climate fluctuations on this system. In the DD, campos rupestres are primarily found in the Serra do Espinhaço, a mountain range extending approximately 1200 km from northern Bahia to southern Minas Gerais, parallel to the upper São Francisco River (Figure 1). Campos rupestres in the Serra do Espinhaço act as a sky-island system (Oliveira et al., 2021; Santana et al., 2023; Vasconcelos et al., 2020), harbouring a megadiverse and highly endemic biota relative to the surrounding areas, associated with diversification processes decoupled from lowland Cerrado and Caatinga assemblages (Colli-Silva et al., 2019; Leite et al., 2008; Rapini et al., 2008; Silveira et al., 2016). Highest rates of diversification in the sky islands are timed to the Pleistocene, though major endemic lineages mostly originate in the Miocene (Carvalho et al., 2021; Inglis & Cavalcanti, 2018; Ribeiro et al., 2014; Vasconcelos et al., 2020). Pleistocene climatic fluctuations likely

favoured dispersal and isolation events within and between these isolated patches, shaping the demographic histories of endemic campos rupestres species (Barres et al., 2019; Collevatti, de Castro, et al., 2012; Dantas-Queiroz et al., 2021, 2023; Oliveira et al., 2021). In general, Pleistocene climatic fluctuations induced population expansion in campos rupestres taxa due to climatic cooling as forests retracted to lower altitudes. During wetter and warmer interglacial periods, forests expanded to higher altitudes, isolating campos rupestres at higher elevations. Consequently, the effects of genetic drift on small and disjunctly distributed populations during periods of isolation would promote the diversification of many endemic lineages restricted to single mountaintops, as observed in frogs (Nascimento et al., 2018; Oliveira et al., 2021; Oswald et al., 2022) and plants (Dantas-Queiroz et al., 2023; Silva et al., 2020). Many DD taxa are descended from common ancestors that diversified within the campos rupestres (likely in the Miocene), rendering the Serra do Espinhaço an ancient cradle of biodiversity.

3.3 | The Pleistocene Arc Hypothesis

The Pleistocene Arc Hypothesis (PAH) posits that a continuous SDTF occupied much of the DD during the Last Glacial Maximum (LGM) before fragmenting into the present-day Caatinga and other non-DD SDTF isolates, such as the Misiones, Piedmont, and Chiquitanía (Figure 1b) (Goncalves et al., 2019; Pennington et al., 2000; Prado, 2000; Prado & Gibbs, 1993). Similarly to the Pleistocene Refuge Hypothesis, the PAH supposes that climate-induced fragmentation of formerly continuous habitat resulted in allopatric diversification within refugia. Previous phylogeographic studies on SDTF plants by Caetano et al. (2008) and Collevatti, Terribile, et al. (2012), as well as a genome-scale bird study (Corbett et al., 2020), supported the PAH. On the other hand, paleoclimatic modelling by Werneck et al. (2011) suggested that SDTFs had a more limited extent during the LGM and have since expanded in area, contrary to expectations under the PAH. Colli-Silva et al. (2021) found ambiguous support for the PAH with palaeoclimatic modelling, with disjunct SDTF plant species responding differently to Pleistocene climate fluctuations. Some studies have shown that divergences in some SDTF taxa are older than the hypothesized age of the Pleistocene Arc (Garcia et al., 2011; Hernández et al., 2022; Lanna et al., 2018; Magalhaes et al., 2014), and others have shown evidence of post-LGM expansion sensu Werneck et al. (2011) (de Melo et al., 2016; Franco & Manfrin, 2013; Vieira et al., 2015). Currently, the majority of PAH-focused studies do not support it (69%). As the most historically unstable region in South America (Costa, Hampe, et al., 2018), the Caatinga did undergo cycles of expansion and contraction, but this does not necessarily imply that it joined with other SDTFs in a continuous Pleistocene Arc.

Phylogeographic evidence for the PAH would constitute Pleistocene divergences between sister lineages in disjunct SDTF isolates (Figure 1b). Demographic modelling should show divergence without migration and population contraction at the time of divergence, and genetic distances should relate to resistance in non-SDTF environments, which should form barriers to dispersal. Until more phylogeographic studies of Caatinga and SDTF taxa show such patterns, the generality of the PAH across taxa remains unlikely.

3.4 | Ecological speciation and potential hybrid zones in the DD

Ecological speciation occurs when selective pressures cause populations to adapt to distinct environmental conditions (Burbrink & Ruane, 2021; Nosil, 2012; Pyron et al., 2015). Encompassing three ecologically distinct subregions arranged in a NE–SW latitudinal gradient, the DD is sufficiently heterogeneous that we should expect ecological speciation to occur there, either between DD subregions (Fonseca et al., 2018) or between the DD and adjacent environments (Rodríguez-Cajarville et al., 2022). The Caatinga–Cerrado transition in particular appears to induce ecological speciation in several taxa via environmental polarity (rather than secondary contact). This ecotone occurs from east (Caatinga) to west (Cerrado) along a N–S axis just west of the middle São Francisco River (Figure 1). Several herpetofaunal studies have indicated population structure delimited by the Caatinga–Cerrado transition (Fonseca et al., 2018; Oliveira et al., 2015; Teixeira Jr. et al., 2016; Thomé, Carstens, Rodrigues, Alexandrino, & Haddad, 2021; Werneck, Gamble, et al., 2012). The presence of admixed individuals in most of these studies implies that genetic divergence could be occurring in the presence of gene flow (Thomé, Carstens, Rodrigues, Alexandrino, & Haddad, 2021). Some studies have found support for a demographic model of divergence with migration (Fonseca et al., 2018; Oliveira et al., 2015), which is the expected model in the case of adaptation across an environmental gradient. Since recent divergence relative to population size can also account for the presence of admixed individuals, statistical support for migration provides evidence for identifying this type of speciation; its prevalence in other DD taxa remains to be seen. Overall, this phenomenon is not yet sufficiently well studied in DD taxa to merit its inclusion as a major hypothesis in this manuscript.

Ecological divergences may also occur between the DD and neighbouring environments such as the Amazon Rainforest, Atlantic Forest or Andes Mountains. For example, Rodríguez-Cajarville et al. (2022) identified divergence with gene flow across the Chaco–Andes ecotone in the bird *Phytotoma rutila*. Other cases of bird sister lineages in the Cerrado and Atlantic Forest, with minimal gene flow, may represent divergences at more complete stages of isolation (Bolívar-Leguizamón et al., 2024; Cabanne et al., 2011). The Vanishing Refuge Model (Vanzolini & Williams, 1981) may particularly apply to these and similar cases of potential ecological speciation between DD biomes and the neighbouring rainforests, as the relative spatial organization of these regions is known to be temporally dynamic (Ledo & Colli, 2017). The Vanishing Refuge Model suggests that climatic instability generates diversity by exposing peripheral populations to new environments, subjecting them to divergent selection and resulting in sister lineages occupying adjacent

but different environments. However, the only genetic study of the Vanishing Refuge Model, conducted on a lizard found in both coastal Atlantic Forest and forest isolates within the Caatinga, found mixed support for this hypothesis (Damasceno et al., 2014).

Hybrid zones between diverging lineages can form due to differential fitness along an environmental gradient (Barton & Gale, 1993; Barton & Hewitt, 1985; Burbrink & Ruane, 2021). Some DD studies with widespread taxa show admixed individuals between genetic clusters corresponding to the Caatinga and Cerrado; however, in the absence of sufficient spatial sampling depth, whether these individuals are isolated cases or constitute potential hybrid zones cannot be verified, let alone their widths, or degrees of coincidence among different species. Characterizing hybrid zones in this way can have important implications for our understanding of ecological speciation or secondary contact in the DD. For example, determining the width of the zone (i.e. the region across which alleles are exchanged) relative to the actual spatial cline (i.e. the region across which the environmental gradient occurs), and identifying which alleles diffuse across it, might demonstrate which traits change across the zone, and consequently the role of selection in determining those changes. Oliveira et al. (2015) showed that genetic variation in whiptail lizards was correlated with climate, but future studies with whole genomes can implement gene ontology-based and GWAS methods to determine the actual genes affected, and identify potential genomic islands of speciation. This will further help disentangle the effects of environmental gradients from simple isolation by distance. Ultimately, comparisons across taxa may identify common mechanisms of selection and hybridization, allowing for more generalized knowledge of ecological speciation in the DD.

4 | HISTORICAL CONNECTIONS BETWEEN THE AMAZONIAN AND ATLANTIC FORESTS AS BARRIERS FOR DRY-ADAPTED TAXA

Climatic fluctuations during the Pleistocene may have contributed to the subsectioning of the DD subregions with the formation of forest connections/corridors between the Atlantic and Amazonian rainforests (Coelho, Camurugi, et al., 2022; Dal Vechio et al., 2018; Sobral-Souza et al., 2015). Paleontological evidence of humid cycles in South America supports the Plio-Pleistocene expansion of rainforest connections crossing the DD (Figure 1b) (Cheng et al., 2013; Ledo & Colli, 2017; Melo Santos et al., 2007). The subsequent disconnection of the rainforests corresponds to the expansion of DD habitats, resulting in the formation of disjunct rainforest lineages (Batalha-Filho et al., 2013; Costa, 2003; Dal Vechio et al., 2018; Gehara et al., 2014; Prates et al., 2016). For example, studies of disjunctly distributed birds suggest ancient forest connections between the Atlantic Forest and central Andean rainforests (Yungas) through the Cerrado and/or Chaco (Trujillo-Arias et al., 2017, 2019).

Forest connections drove the diversification of DD taxa as well as rainforest taxa, primarily by allopatry and niche conservatism. Some frogs and snakes restricted to mesic, high-altitude forest enclaves surrounded by dry vegetation in the Caatinga (brejos de altitude) are more closely related to Amazonian than DD species (Mângia et al., 2018; Roberto & Loebmann, 2016), indicating that the enclaves are relics of ancient forests. The saffron-billed sparrow *Arremon flavirostris* likely colonized gallery forests in the Chaco and Cerrado through intermittent rainforest connections (Trujillo-Arias et al., 2017). Additionally, the Caatinga four-eyed frog *Pleurodema diplolister* shows north–south genetic structure, the boundary possibly coherent with a putative trans-Caatinga forest corridor (Thomé et al., 2016). The proximity of such divergent habitats to each other may also have promoted diversification via the Vanishing Refuge Model (Vanzolini & Williams, 1981). However, allopatry and stabilizing selection (i.e. niche conservatism) seem to be more important for understanding the relationship of rainforests and the DD subregions in generating biodiversity.

Uncertainty in the geographic location of the hypothesized forest connections makes predicting and testing their spatial effects on DD species difficult. The forest connections may have acted as physical barriers within the DD, leading to populations structured on either side of hypothetical wet forest corridors (Pinaya et al., 2019; Thomé et al., 2016). In this case, it is expected that a demographic model of divergence without migration, plus population contraction, would be supported, since isolation would coincide with a reduction in habitat availability, followed by expansion after the connections disappeared. Because of the dynamic nature of this process, isolation could be recurrent with opportunities for secondary contact after expansion, potentially forming areas of high genetic diversity. Thomé et al. (2016) represents the most comprehensive and exemplar test of whether the forest connections acted as barriers to date.

Alternatively, the forest connections may have been composed of forest galleries, facilitating dispersal between rainforests and fragmenting the DD, but not necessarily acting as hard barriers (André et al., 2022; Leal et al., 2019, 2021; Trujillo-Arias et al., 2017). Despite the lack of a contemporary barrier to gene flow in the region, an east–west divergence during the Pleistocene observed in tree populations in the central Cerrado (54–43°W) underscores the possibility of a barrier there (Buzatti et al., 2018; Correa Ribeiro et al., 2016; Leal et al., 2019, 2021; Ramos et al., 2007; Resende-Moreira et al., 2017). This potential phylogeographic break could offer an opportunity to investigate the role of forest corridors in the formation of the DD biota. In this scenario, one should expect high genetic diversity in stable areas that were not replaced by forest galleries.

5 | THE SÃO FRANCISCO RIVER AS A PUTATIVE BARRIER IN THE CAATINGA

The Riverine Barrier Hypothesis is one of the oldest and most enduring biogeographic hypotheses of South America, beginning with Wallace's (1854) proposal that the Amazon River acts as a barrier to species on either side. The hypothesis has been proposed for

rivers in the DD, including the Tocantins in the Cerrado (Werneck, Gamble, et al., 2012) and the Paraná-Paraguay system at the eastern boundary of the Chaco (Kopuchian et al., 2020). However, the São Francisco River (SFR) is by far the most prominent in discussions of the Riverine Barrier Hypothesis as applied to the DD. The SFR is the fourth longest river in South America and drains most of the Caatinga (Figure 1a). It was originally proposed to form a biogeographic barrier for several reptile species pairs inhabiting opposite margins of the river (Rodrigues, 1986, 1993, 1996, 2003; Rodrigues & Juncá, 2002) and has since been extended to other taxa. Rodrigues (1996) proposed that the formerly endorheic SFR (i.e. not flowing into the ocean) became exorheic (flowing into the ocean) at the end of the Würm glaciation ~12 kya (Ab'Saber, 1969; Tricart, 1974), traversing the Caatinga to divide formerly continuous habitat and promote vicariance. The São Francisco River Hypothesis (SFRH) has remained a popular explanation for Caatinga biodiversity patterns, especially in herpetological studies, which are disproportionately represented in explorations of the SFRH (Figure 2b).

The geological literature on the SFR's history is very limited, with considerable uncertainty around the origin of the river and the timing of events relevant to the development of the Caatinga and its biota (Thomé, Carstens, Rodrigues, Alexandrino, & Haddad, 2021). The endo-exorheism theory (Ab'Saber, 1969; Tricart, 1974) of SFR paleocourse change at the end of the most recent glaciation (~12 kya) remains uncorroborated. Most other studies that discuss the paleocourse change infer a much older event, wherein the SFR trended eastward, from an ancient south–north paleocourse along the present-day course of the lower Parnaíba, to its modern course (Figure 1a). This was possibly due to erosion in the São Francisco basin (Grabert, 1968) and/or neighbouring uplift events (Mabesoone, 1994; Potter, 1997). The estimated ages of this event range from mid-Eocene (Karner & Driscoll, 1999) to mid-Miocene (Potter, 1997; Valadão, 1998) to mid-Pleistocene (~0.45 mya) (Mabesoone, 1994). Mabesoone (1994) also inferred an endorheic period (Figure 3), and is most often cited in SFRH studies.

Phylogeographic support for the SFRH has generally been based on inferring divergence times for sister lineages separated by the river and associating them with one of the suggested paleocourse changes listed earlier. Because of the variation in ages of suggested paleocourse changes, the divergence times 'supporting' the SFRH vary considerably as well. Divergences, including Mio-Pliocene (Almeida et al., 2020; Passoni et al., 2008; Werneck, Gamble, et al., 2012), Plio-Pleistocene (Costa, Amorim, & Mattos, 2018; do Nascimento et al., 2011), early Pleistocene (Bruschi et al., 2019; Faria et al., 2013; Oliveira, Martinez, et al., 2018; Siedchlag et al., 2010), and late Pleistocene (Coutinho-Abreu et al., 2008; Fegies et al., 2021), either highlight the inconsistency in associating genetic divergence with SFR geology or indicate that the barrier is older, with species entering the region at different times since its origin (Figure 3; Table 1). Few studies used model- or simulation-based tools to unambiguously identify SFR-based vicariance (Almeida et al., 2020; Bruschi et al., 2019). However, some model-based studies recovered shallow structure with ongoing gene flow across the SFR (Coelho, Guillory, & Gehara, 2022; Oliveira, Martinez, et al., 2018; Thomé, Carstens, Rodrigues, Alexandrino, & Haddad, 2021) or negligible structure/high gene flow across the SFR (Miranda et al., 2016; Oliveira et al., 2015; Thomé, Carstens, Rodrigues, Galetti Jr, et al., 2021).

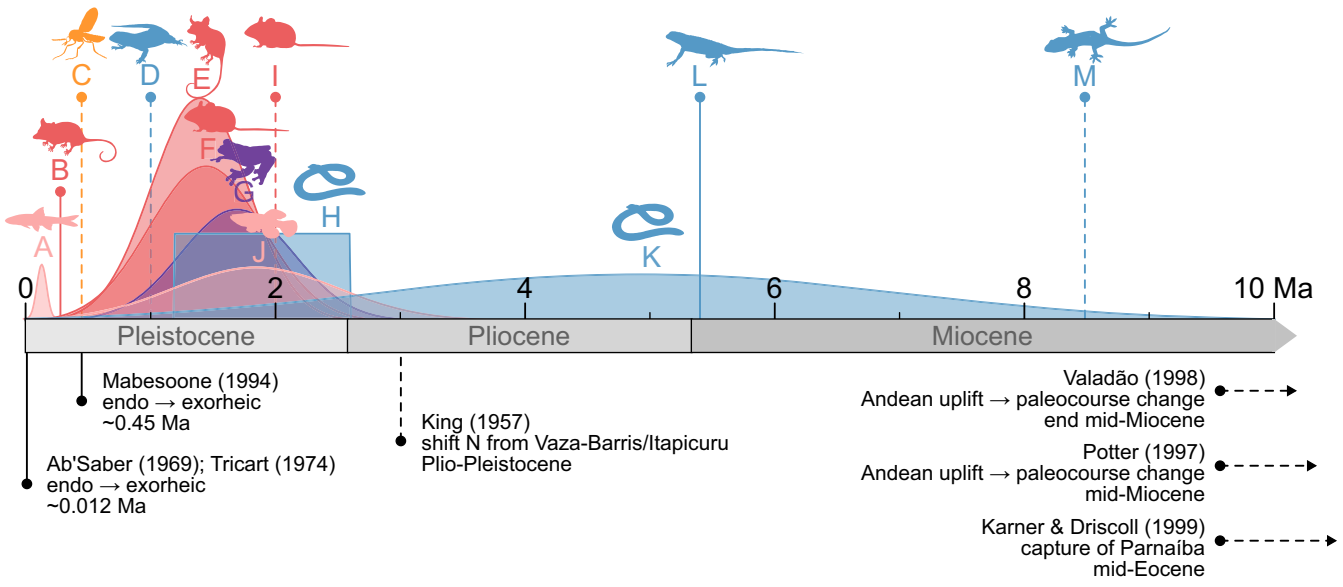

FIGURE 3 Timeline of São Francisco River Hypothesis (SFRH)-related animal divergence events (above timeline) and geological hypotheses (below). Note that the geological hypotheses almost certainly did not all occur: the timeline shows hypothesized events, not an agreed-upon geological history. Only divergence events treated as unambiguously supporting the SFRH are shown. Temporal uncertainty is displayed for those taxa where it was provided. Dashed lines correspond to rough estimates provided by the authors rather than exact dates, while solid lines correspond to exact estimates provided by the authors sans uncertainty. Letters A–M correspond to the studies listed in Table 1.

Just under half (13/27) of SFRH-focused studies show mixed or negative support for the SFRH (Figure 2b). For example, Lanna et al. (2020) found that the SFR's proposed north–south paleocourse had no effect on the population structure of the gecko *Lygodactylus klugei*, while its modern course may have led to shallow mitochondrial DNA (mtDNA) divergence. Other studies found genetic structure between sites along the SFR (i.e. upstream vs. downstream) rather than across it (Machado et al., 2014), or no population structure at all (Andrade-Souza et al., 2017; Balbino et al., 2018; da Conceição Lazarino et al., 2023). Notably, few studies have tested the SFRH on plant species. While the SFR was rejected as a barrier to gene flow in two of these plant-focused studies (Balbino et al., 2018; Moreira & Fernandes, 2013), two others did identify population structure concordant with the SFRH (Menezes et al., 2016; Souza et al., 2018). The remaining SFRH studies focus on animals, and over half of those on reptiles and amphibians, which commonly show strong to mixed effects of the SFR (Figure 2b), especially arid-adapted or fossorial species that may have lower vagility than less specialized taxa. In most species, the SFR is likely to act as a soft barrier that permits some gene flow while leading to weakly structured lineages on either bank (Coelho, Guillory, & Gehara, 2022; Fegies et al., 2021; Oliveira, Martinez, et al., 2018; Werneck et al., 2015), especially if the SFR has fluctuated in width and the steepness of its banks (i.e. its strength as a barrier) over time.

High support for a model of divergence (with high or low migration), temporally concordant with the SFR's paleocourse change, would offer the best support for the SFRH. However, divergence times seen in the literature fit the proposed paleocourse change times poorly (Figure 3). Resistance across the river should predict genetic distances more strongly than other factors such as climate change or topography. Unfortunately, without new geological studies to demystify the SFR's origin and paleocourse, it remains difficult to derive generally consistent theories that are temporally conguent regarding the effect of the river on Caatinga biodiversity.

6 | THE ROLE OF THE CENTRAL BRAZILIAN PLATEAU IN STRUCTURING THE CERRADO

The uplift of the Central Brazilian Plateau (CBP) is frequently cited as a driver of diversification in the Cerrado, but the geological origins of the plateau are poorly understood. The CBP comprises the highlands of central and southeastern Brazil, covering most of the Cerrado at altitudes ranging from ~100 to 1670 m (Figure 1a). Relevant phylogeography studies typically cite Del'Arco and Bezerra (1989) in support of a late Neogene to early Pleistocene plateau uplift event. There are several proposed mechanisms by which the CBP may have structured populations. Some studies find evidence of allopatry between sister lineages isolated to either side of the CBP (Oliveira, Gehara, et al., 2018) or on and adjacent to it (i.e. altitudinal segregation) (Ishihara et al., 2022). Other studies propose that a system of sub-plateaus and intervening riverine depressions, formed by incision after the CBP's initial uplift, contributed to diversification and population structure, between either related populations on different sub-plateaus (Mittan et al., 2022) or related populations on the sub-plateaus and in the riverine depressions (Camurugi et al., 2021). Collectively, we refer to this group of hypotheses as the Central Brazilian Plateau Hypothesis (CBPH).

The principal uplift of the CBP is thought to have occurred through the Neogene, followed by peripheral subsidence and sub-plateau formation in the Plio-Pleistocene. The most frequently cited sources in support of these events are da Silva (1997) and Colli (2005), who themselves cite older geological literature, the most important being Del'Arco and Bezerra (1989) (but see also Ab'Saber, 1983; Brasil & Alvarenga, 1989; Cole, 1986). The authors of modern phylogenetics and phylogeography studies pertaining to the CBP have generally asserted that late Neogene to early Pleistocene divergence dates (~18–2 mya) demonstrate the CBP's effect on population structure (Figure 4) (e.g. Costa et al., 2017; Domingos et al., 2014; Santos et al., 2014). However, Del'Arco and Bezerra (1989) propose a more protracted scenario than these studies suggest, consisting of Paleogene wet/dry cycles that first promoted valley and plateau formation in the central Brazilian highlands via intense erosion, including Eocene pediplanation (i.e. plain formation from erosional scarp retreat) and Oligocene fault reactivations and uplifts, forming the essential definition of the Cerrado landscape. Late Neogene (Mio-Pliocene) and Pleistocene wet/dry cycles further defined the modern system of plateaus and depressions. As such, the uplift of the CBP being a specifically late-Neogene phenomenon may be overstated, with the landscape instead having formed throughout the Cenozoic.

Despite uncertainty around the timing of the CBP uplift and associated events, many CBP phylogeography studies have undeniably recovered late Neogene divergences between pertinent taxa (Figure 4). As with the SFRH, there is a strong herpetological bias in CBPH studies (Figure 2b). Two studies of frogs revealed highly concordant divergences ~3.5 mya between lowland lineages separated by the CBP to its northeastern and southwestern margins (Oliveira, Gehara, et al., 2018; Porto et al., 2022; G and E in Figure 4). Thus, the CBP may itself form an allopatric barrier, as suggested in earlier studies (Lanna et al., 2018; Recoder et al., 2014; Werneck, Gamble, et al., 2012). The elevational difference between the plateau and the surrounding lowlands may also have segregated sister lineages on and off the plateau. Ishihara et al. (2022) and Costa et al. (2017) both identified this pattern, though at very different time periods – the former among populations of a lizard in the Plio-Pleistocene, the latter between killifish genera well within the Miocene. The CBP has seemingly structured Cerrado diversity at multiple taxonomic scales throughout the Neogene. However, it should be noted that this vicariant effect may result from correlated environmental factors such as temperature. A concordant divergence time is only preliminary evidence for the CBPH; other ecological hypotheses, and the prevalence of gene flow between sister lineages, should also be explored.

Other studies have asserted that compartmentalization of the CBP via river incision contributed to diversification in Cerrado taxa, with sister lineages occupying either adjacent sub-plateaus or

TABLE 1 List of phylogeographic studies claiming to unambiguously corroborate the SFRH, with corresponding taxa and divergence times.

	Study	Taxon	Divergence time
A	Oliveira-Silva et al. (2023)	*Characidium bahiense* (fish)	0.139 mya (0.065–0.227)
B	Fegies et al. (2021)	*Cryptonanus agricolai* (possum)	0.28 mya
C	Coutinho-Abreu et al. (2008)	*Lutzomyia longipalpis* s.l. (fly)	~0.45 mya
D	Werneck et al. (2015)	*Tropidurus semitaeniatus* group (lizard)	~1 mya
E	Faria et al. (2013)	*Gracilinanus agilis* (possum)	1.40 mya (0.63–2.36)
F	do Nascimento et al. (2013)	*Thrichomys* spp. (rodent)	1.45 mya (0.35–2.39)
G	Bruschi et al. (2019)	*Pithecopus nordestinus* (frog)	~1.5 mya (0.8–2.6)
H	Siedchlag et al. (2010)	*Calyptommatus/Nothobachia* spp. (lizard)	~1.2–2.6 mya[a]
I	do Nascimento et al. (2011)	*Calomys expulsus* (rodent)	~2 mya
J	Costa, Amorim, and Mattos (2018)	*Hypsolebias/Cynolebias* spp. (fish)	1.13–2.57 mya (0.54–3.76)[a]
K	Almeida et al. (2020)	*Amphisbaena pretrei* (lizard)	4.9 mya (0.715–9.7)
L	Passoni et al. (2008)	*Eurolophosaurus* spp. (lizard)	~5.4 mya
M	Werneck, Gamble, et al. (2012)	*Phyllopezus pollicaris* (lizard)	Late Miocene

Note: Letters in the first column correspond to points of interest in the timeline of Figure 3.
[a]Multiple divergence dates across multiple taxa.

adjacent plateaus (500–1700 m) and depressions (100–500 m) (da Silva, 1997). This latter scenario is called the Plateau–Depression Hypothesis (PDH) in the literature, and specifically predicts older lineages on plateaus and younger sister lineages in intervening riverine depressions (Werneck, 2011). However, no studies have specifically tested this prediction. To our knowledge, only a taxonomic study of teiid lizards has identified reciprocal monophyly between plateau and depression lineages (Giugliano et al., 2013). Instead, as with the previously discussed role of the CBP as an allopatric barrier, most phylogeographic studies simply claim that late Neogene divergence times indicate that CBP compartmentalization structured their focal taxon, which formerly occupied the CBP highlands more uniformly (Amaral et al., 2021; Arantes et al., 2023; Domingos et al., 2014; Guarnizo et al., 2016; Miranda et al., 2019; Mittan et al., 2022; Prado et al., 2012). A few earlier phylogenetics studies also identified this pattern (Machado et al., 2014; Maciel et al., 2010). Camurugi et al. (2021) identified an analogous yet opposite pattern in which a lowland frog distributed through the riverine depressions of the CBP was probably structured by the higher altitude plateaus, albeit with significant gene flow. Both that study and Lima-Rezende et al. (2019) inferred late Pleistocene divergence times (Figure 4; letters A and B), indicating that subsidence-induced diversification in the CBP may still be ongoing. On the other hand, the CBP's uplift and compartmentalization have apparently not affected some squamate reptiles, which show significant gene flow and/or a lack of elevational differentiation (Fonseca et al., 2018; Ledo et al., 2020; Santos et al., 2014).

Overall, the underlying geology of the CBP and its effects on Cerrado biodiversity remain poorly understood. Determining the exact mechanisms of divergence and diversification in CBP-related taxa will require direct hypothesis testing. High support for a model of divergence with or without migration would support the CBPH, but idiosyncratic divergence dates are perhaps unavoidable. Genetic structure could in fact represent a climatic barrier rather than a physical one, so divergence times may be associated not with the barrier's appearance, but with the actual dispersal across the barrier, conditioned by climate, vegetation and species-specific traits. Given the diversity of divergence times seen in the literature (Figure 4), this is currently the most likely scenario. Overall, the difficulty of disentangling the influences of climate versus elevation will likely remain a challenge to explorations of the CBPH (Table 2).

7 | MIOCENE MARINE INCURSIONS IN THE CHACO

The inundation of much of Miocene South America by seawater has been a frequently cited driver of biodiversity since the inception of the idea nearly three decades ago (Hoorn, 1993). Geological evidence

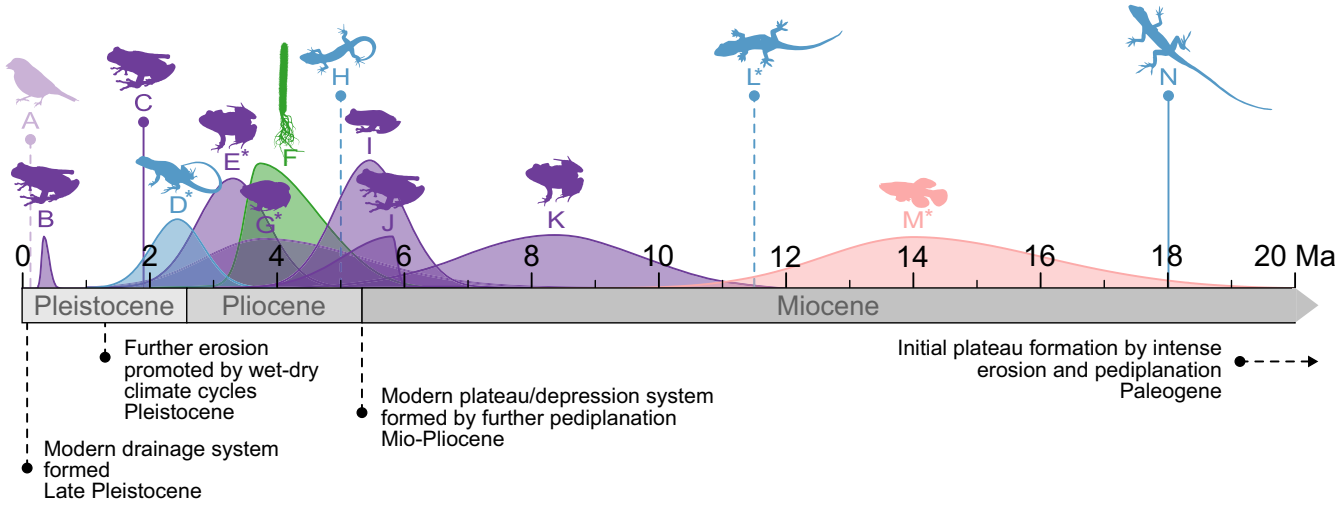

FIGURE 4 Timeline of CBPH-related divergence or diversification events (above timeline) and sequence of relevant geological events proposed by Del'Arco and Bezerra (1989) (below timeline). Temporal uncertainty is displayed for those taxa where it was provided. Dashed lines correspond to rough estimates provided by the authors rather than exact dates, while solid lines correspond to exact estimates provided by the authors sans uncertainty. Letters A–N correspond to the studies listed in Table 2. Divergence events marked with an asterisk (*) are hypothesized to have occurred because of allopatric isolation on either side of the CBP, or on versus off of it, rather than CBP compartmentalization in accordance with the Plateau–Depression Hypothesis.

suggests marine incursions extended southward from the Caribbean along the east Andean versant, eastward across the Amazonian basin to the North Atlantic and southeast across the Paraná basin into the South Atlantic around 10 mya (Hoorn et al., 2010; Webb, 1995). The extent, timing, and frequency of the incursions remain uncertain (Jaramillo et al., 2017). The incursions are thought to have isolated the Guianan and Brazilian Shields both from the Andes and each other, promoting extinction in the intervening lowlands (the Amazon and Paraná basins) and isolation/diversification on the shields. This was followed by dispersal into the lowlands after the incursions receded (Räsänen et al., 1995). The distributions of several South American lineages are proposed to have been shaped by this mechanism (Aleixo, 2004; Garda & Cannatella, 2007; Giugliano et al., 2013; Maciel et al., 2010; Noonan & Wray, 2006; Ribas et al., 2005; Werneck et al., 2009).

Of the DD subregions, the Chaco would have been most affected by Miocene marine incursions, which are considered a primary influence on its geoclimatic history (Hernández et al., 2005); the Cerrado and Caatinga are largely located on the Brazilian Shield and were mostly spared from flooding. The Chaco likely experienced two or three periods of marine inundation, potentially localized to southern South America as the ephemeral 'Paranaense Sea', from ~13 to 10 and ~10 to 5 mya (Figure 1c) (Hernández et al., 2005; Ortiz-Jaureguizar & Cladera, 2006; Ruskin et al., 2011). Studies of fossil rodents (Candela et al., 2012) and phylogenetic studies of fairy armadillos (Delsuc et al., 2012), geckos (Morando et al., 2014; Werneck, Gamble, et al., 2012), and plants (Acosta et al., 2016; Aguilar et al., 2020; Moré et al., 2015) indicate a role for vicariance via the Paranaense Sea.

Phylogeographic evidence for the effects of Miocene marine incursions on Chaco taxa is rare. However, Brusquetti et al. (2018) determined that the three species of the frog *Lepidobatrachus* diverged through the late Miocene ~15–8 mya, coinciding with multiple instances of the Paranaense Sea. Furthermore, they showed evidence of recent population expansion, as expected after the sea's final recession. Long-term persistence of northern populations of *Lepidobatrachus llanensis* near the Michicola Arch, a highland that would not have been flooded during the marine incursions, offers further evidence for vicariant effects of the Paranaense Sea. The southern/southwestern Chaco, Asunción Arch and Rio de la Plata Craton are proposed as additional refugia, though evidence for this beyond a single *Lepidobatrachus* fossil from the Mio-Pliocene (Nicoli, 2015) is lacking. Future phylogeographic studies in the Chaco may corroborate these findings in other taxa. A promising example is a study on the tree frog *Scinax squalirostris* (Abreu-Jardim et al., 2023), which used demographic modelling and approximate Bayesian computation to identify a phylogeographic break dated to the late Miocene, likely corresponding to the end of a marine incursion. However the substantial age of this phenomenon may limit the amount of demographic information researchers can retrieve from genetic data. It might therefore be necessary to resort to methodologies more appropriate for exploring biogeography at deeper timescales, such as BioGeoBEARS (Matzke, 2014), when exploring the Miocene marine incursions. It is still expected that elevation will predict genetic diversity, with high-elevation areas showing higher genetic diversity relative to recently colonized lower elevation areas that were formerly inundated (Fagundes et al., 2007).

8 | DISCUSSION

8.1 | Trends in DD phylogeography studies

Significant progress in DD phylogeography has been made in the past two decades, with at least 142 studies published as of August 2023 (Table S1; Figure 5). One of the most noticeable trends is the

proportional dominance of studies featuring herpetofauna: nearly one third (41/142) of DD phylogeography studies focus on reptiles and/or amphibians. A greater number of studies ($n = 50$) are plant focused (41 of those in eudicots), but with ~20,000 plant species across the DD (Collevatti et al., 2020) versus 500–1000 reptile and amphibian species (Álvarez et al., 2009; de Albuquerque et al., 2012; Nogueira et al., 2011; Valdujo et al., 2013), a proportional bias is evident. The over-representation of reptiles, amphibians, and plants in the DD literature may be due to the relative ease of collecting samples across phylogeographic scales (as opposed to mammals or birds), and relatively complete taxonomic knowledge bases (as opposed to invertebrates). More studies in other groups such as birds (currently $n = 12$) or invertebrates (currently $n = 20$) would greatly benefit the field. The distribution of studies among DD subregions is also biased: only 14% (20/142) of studies focus exclusively on the Chaco (21 other studies include Chaco samples, but are not focused on it exclusively) (Figure 2a). Given the urgency of Chaco conservation amid ongoing deforestation (Cuyckens, 2021), phylogeographic study of this region should be prioritized.

A conceptual divide between animal and plant researchers pervades the DD phylogeography literature, wherein animal studies explore whether Neogene versus Pleistocene events drove DD biodiversity patterns, while the vast majority of plant studies (82%; 41/50) focus on Pleistocene climatic fluctuations or the related PAH (Figure 2b). Most of these plant studies were conducted in the Cerrado, which hosts 80% (40/50) of DD plant phylogeography studies, 88% (35/40) of which were focused on the PCFH (Figure 2a). There are some exceptions (Aguilar et al., 2020; Menezes et al., 2016), including the meta-analysis by Collevatti et al. (2020) that explicitly explores the relative importance of Neogene versus Pleistocene events on Cerrado plants, but animal studies comprise the bulk of those exploring the effects of older geoclimatic phenomena on DD biodiversity. Importantly, all DD taxa evolved under the same environmental conditions and geoclimatic events – only their responses to these phenomena differed. We encourage both researchers of all taxonomic specialties to explicitly test hypotheses such as those corresponding to the CBP and SFR.

The DD phylogeography literature has yet to broadly adopt genome-scale data (Figure 2a), which would allow for more robust hypothesis testing and demographic inference. Sequencing at the genomic scale offers far greater resolution than mtDNA or microsatellite studies for inferring population characteristics of interest like effective population size and gene flow and the geoclimatic processes underlying them (McGaughran et al., 2022). Inferring phylogenies from many loci further obviates concerns over incomplete lineage sorting, to which single-locus studies are particularly vulnerable (Liu et al., 2015). In our review, 10% (14/142) of DD phylogeography studies have used genome-scale datasets, primarily RADseq (Figure 2a; Table S1). The high cost of next-generation sequencing is almost certainly the main hurdle preventing the widespread adoption of these newer technologies in DD phylogeography, particularly considering the decreases in Brazilian science funding over the past decade (Oliveira et al., 2020; Overbeck et al., 2018). Further reductions in the cost of genome-scale or even whole-genome sequencing will hopefully allow more DD researchers to harness their power for inferring phylogeographic patterns.

DD researchers should also use more advanced analytical methods to improve the power of their inferences. Less than one third (41/142) of DD phylogeography studies have used some sort of model-based method (Figure 2a; Table 3), most of these published in the past 5 years. This could also include performing trait-based analyses that account for the phenotypic and ecological properties of the organism, such as regressing ecological variables against genetic distances (Paz et al., 2015; Vasconcellos et al., 2019; Zamudio et al., 2016) or using demographic and evolutionary simulations that can be further combined with approximate Bayesian computation (Csilléry et al., 2010) or machine learning (Fonseca et al., 2021) to directly test phylogeographic hypotheses (Hickerson et al., 2010). An inherent challenge in phylogeography, given the impossibility of designing randomized experiments across evolutionary timescales for most taxa, is to clearly outline expectations for these hypotheses. Ideally, integrated temporal and spatial expectations should be explored. However, due to theoretical challenges and computational limitations, spatial and temporal questions have generally been explored separately. As such, phylogeographic methods can generally be separated into two main categories. First, explicit time/implicit space methods are mostly based on coalescent theory (Kingman, 1982), fitting empirical data to simulated demographic scenarios representing expectations under proposed hypotheses (Csilléry et al., 2010). These methods can be (and for the most part, have been) used to test any of the geoclimatic hypotheses discussed in this review. Second, implicit time/explicit space methods are founded in the population genetics theory pertaining to isolation by distance (Slatkin, 1993; Wright, 1943). These methods, including multiple matrix regression (MMR) and generalized dissimilarity modelling (GDM), usually test for the power of distance matrices derived from the landscape (e.g. pairwise geographic distance) in predicting the variance of a genetic distance matrix. Explicit time/implicit space and implicit time/explicit space methods can be considered perpendicular to each other and may be used in combination to integrate spatial and temporal genetic patterns and processes. Additionally, a 'third class' of forward-time genetic simulator is emerging (Currat et al., 2019; Messer, 2013), with wide implications for the field despite their (as-yet) steep learning curves.

A full review of phylogeographic methods is far beyond the scope of this manuscript; we simply wish to emphasize the importance of considering both spatial and temporal dimensions. We previously made methodological suggestions throughout the manuscript for testing each hypothesis considered in the review (see also Table 4). Rather than using these model-based approaches, most DD phylogeographic studies rely instead on phylogenetic inference, divergence time estimation, population structure characterization, and/or niche modelling. The

TABLE 2 List of phylogeographic studies claiming to corroborate the CBPH, with corresponding taxa and divergence times.

	Study	Taxon	Divergence/ diversification time
A	Lima-Rezende et al. (2019)	*Neothraupis fasciata* (songbird)	Last Interglacial
B	Camurugi et al. (2021)	*Boana raniceps* (frog)	0.340 mya (0.257–0.522)
C	Mittan et al. (2022)	*Boana* aff. *multifasciata/albopunctata* (frog)	1.9 mya
D	Ishihara et al. (2022)	*Enyalius capetinga* (lizard)	2.43 mya (1.49–3.43)
E	Porto et al. (2022)	*Pseudopaludicola mystacalis* (frog)	3.3 mya (2.1–4.9)
F	Amaral et al. (2021)	*Cereus* spp. (cactus)	3.67 mya (3.31–5.8)
G	Oliveira, Gehara, et al. (2018)	*Dermatonotus muelleri* (frog)	3.79 mya (1.85–7.22)
H	Domingos et al. (2014)	*Gymnodactylus amarali* (lizard)	~5 mya
I	Arantes et al. (2023)	*Dendropsophus rubicundulus* (frog)	5.45 mya (4.38–6.65)
J	Prado et al. (2012)	*Boana albopunctata* (frog)	5.8 mya (3.6–5.9)
K	Miranda et al. (2019)	*Physalaemus cuvieri* (frog)	8.32 ± 2.93 mya
L	Werneck, Gamble, et al. (2012)	*Phyllopezus pollicaris* (lizard)	~11.5 mya
M	Costa et al. (2017)	*Cynolebias/Simpsonichthys* (fish)	14 mya (10–19)
N	Guarnizo et al. (2016)	*Anolis meridionalis* (lizard)	18.01 mya

Note: Letters in the first column correspond to points of interest in the timeline of Figure 4.

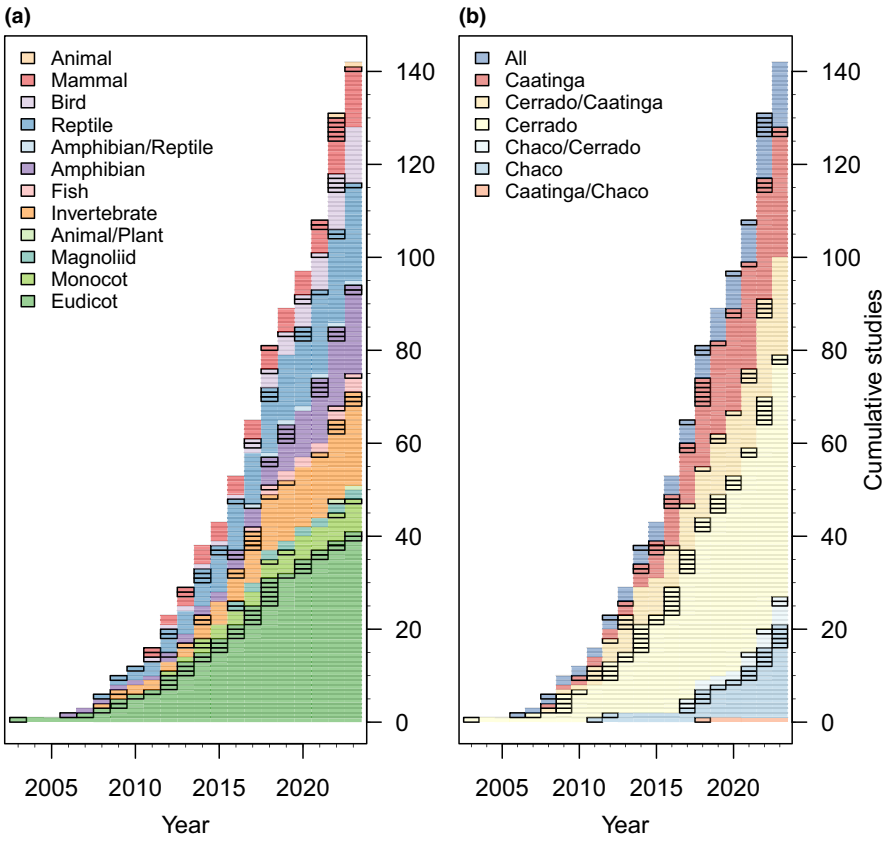

FIGURE 5 Timelines describing the accumulation of Dry Diagonal phylogeography studies as of August 2023, with respect to (a) taxonomic group(s) and (b) study subregion(s). Black-bordered boxes represent new studies published in the corresponding year. After their initial year of publication, studies are represented as borderless boxes to show the accumulation of studies over time.

evidence these methods provide in relating phylogeographic to geoclimatic patterns is circumstantial – they are agnostic to one or the other. On the other hand, explicit time/implicit space and implicit time/explicit space methods allow direct hypothesis testing. For example, Gehara et al. (2017) compared the efficacy of four demographic models with various degrees of synchrony in population expansion in Caatinga herpetofauna, demonstrating a community-wide response to potential landscape reorganization in the Caatinga during the late Pleistocene. A similar model-based approach was performed by Bonatelli et al. (2022), testing the effects of Pleistocene climate changes in different species of plants, lizards, frogs, spiders, and insects distributed within the DD. Results demonstrated discordant demographic patterns even within taxonomic groups. Some temporally concordant expansion and contraction events were detected during the middle-to-late Pleistocene, supporting the role of climatic change in shaping genetic diversity.

A potential issue for the DD phylogeography literature is the fixation on testing the same set of geoclimatic hypotheses. The field risks becoming a self-perpetuating isolate where old ideas are tested and debated for decades with no real resolution in sight. For example, the PAH, proposed three decades ago (Prado & Gibbs, 1993), is still investigated despite fewer than half of relevant studies supporting it (Figure 2b), including only one of three model-based studies (Table 3). On the other hand, the other geoclimatic hypotheses have seen much higher support. It may no longer be necessary to frame studies as 'tests' of the SFRH (for example) in general; rather they can be presented as determining whether a well-studied barrier affects the study taxon, as it has been previously found to affect many others. In general, the prevailing hypothesis-centred practice may encourage the shoehorning of tests for geoclimatic phenomena into studies to which they may only appear at first to apply, rather than encouraging the development of more creative explanatory hypotheses for DD biodiversity patterns. Some possible diversification drivers briefly discussed earlier, such as the role of rainforest corridors between the Amazon and Atlantic Forest, or the influence of ecological transition zones, are poorly explored in DD taxa, comprising rich avenues for future research. Additionally, it is key to also investigate the underlying geology and paleoclimate of the DD

TABLE 3 Support for DD biogeographic hypotheses from model-based studies.

	# studies	# model-based studies	# model-based studies that are supportive
PCFH	89	29/89 (33%)	25/29 (86%)
PAH	13	3/13 (23%)	1/3 (33%)
FCH	3	2/3 (67%)	2/2 (100%)
SFRH	27	9/27 (33%)	7/9 (78%)
CBPH	17	7/17 (41%)	5/7 (71%)
MMIH	6	2/6 (33%)	2/2 (100%)

Note: Note that some studies may have more than one hypothesis test; as such the table is better interpreted as counting the number of times a hypothesis was tested rather than an absolute number of studies.

Abbreviations: CBPH, Central Brazilian Plateau Hypothesis; FCH, Forest Connections Hypothesis; MMIH, Miocene Marine Incursion Hypothesis; PAH, Pleistocene Arc Hypothesis; PCFH, Pleistocene Climatic Fluctuations Hypothesis; SFRH, São Francisco River Hypothesis.

TABLE 4 Genetic expectations under the primary DD phylogeography hypotheses.

Hypothesis	Expectations
PCFH	• Support for out-of-refuge models where ↓ stability predicts ↑ ΔN_e and ↓ genetic diversity (Carnaval et al., 2009) • Support for demographic models with Pleistocene ΔN_e • Paleoclimatic models predict genetic diversity across space (see Vasconcellos et al., 2019) • Synchronicity in expansion times of co-distributed species (see Gehara et al., 2017)
PAH	• Sister relationships between disjunct species in isolated SDTF nuclei • Pleistocene divergence times • Model support for divergence w/o migration, with ↓ N_e at time of divergence • Resistance across intervening non-SDTF habitats predicts genetic distance • Pleistocene ↓ N_e in non-SDTF populations (see Thomé, Carstens, Rodrigues, Alexandrino, & Haddad, 2021)
FCH	• Model support for divergence w/o migration, and with ↓ N_e at the time of divergence, then recent ↑ N_e (see Thomé et al., 2016) • Potential admixture/hybridization after population expansion
SFRH	• Model support for divergence (migration determines 'hardness' of barrier) (see Coelho, Camurugi, et al., 2022; Coelho, Guillory, & Gehara, 2022) • Divergence times concordant with paleocourse change • Temporal concordance in divergence times of co-distributed species • Resistance across SFR predicts genetic distance
CBPH	• Model support for divergence (migration determines 'hardness' of barrier) (see Oliveira, Gehara, et al., 2018) • Elevational resistance predicts genetic distance
MMIH	• ↑ elevation areas predict ↑ genetic diversity (see Brusquetti et al., 2018) • Miocene divergence times • Support for out-of-refuge models with range expansion to ↓ elevation areas

for a richer understanding of their effect on genetic diversity. The most recently published phylogeography article on the SFRH, for instance, still cites geological literature from 25 years ago (Oliveira-Silva et al., 2023). In this case, essentially nothing has been published about the SFR's hypothesized paleocourse changes since then, but that may not be true for the other geoclimatic events often cited as biodiversity drivers in the DD. To better understand the historical biogeography of the DD, biologists should work with climatologists and geologists to encourage and develop new integrated avenues of study.

9 | CONCLUSION

The DD biota was shaped by a combination of Neogene and Pleistocene factors, but the responses of individual taxa are largely idiosyncratic, determined by both local geoclimatic events and organismal traits. The origins of many deep divergences – mostly known from herpetofauna – are related to Neogene events such as the uplift of the Central Brazilian Plateau and multiple marine incursions in the southern DD. The paleocourse change of the São Francisco River also isolated lineages in many Caatinga species. Pleistocene climatic fluctuations shaped phylogeographic histories as well through vegetation shifts, refugium formation, and rainforest connections through the DD, though the evidence for some specific theories such as the PAH is currently weak.

Many phylogeographic studies on the DD have been published, especially in the last decade, though the region is still understudied compared to the South American rainforests. One significant avenue for advancing DD phylogeography lies in using genome-scale and whole genome data, which has thus far seen limited use (though a recent increase in studies using these types of data is encouraging). We also advocate using model- and simulation-based techniques to directly test phylogeographical hypotheses. We advise testing the established DD phylogeographic hypotheses using comparative phylogeography methods with a broader range of taxa (Beaumont et al., 2010) – most explorations of Pleistocene climatic fluctuations, for instance, focus on plants, while tests of vicariant events disproportionately feature herpetofauna. On the other hand, we note that disrupting an endless cycle of testing decades- old geoclimatic hypotheses based on outdated and critically unexamined literature is necessary to progress our understanding of the formation of biodiversity in this region. The DD is not only scientifically overlooked, but conservationally as well; as the evolutionary histories of DD taxa become clearer, researchers will not only better understand this unique region, but better enable its protection.

AUTHOR CONTRIBUTIONS

WXG and MG conceived the manuscript. WXG designed the figures and led the writing with guidance from MG. FMM and FEAC assisted with the literature survey and writing. The other authors contributed to writing and offered additional perspectives.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All data used to support the conclusions of this review are contained in the Supporting Information.

BENEFIT-SHARING STATEMENT

Benefits from this research accrue from the sharing of our data in the Supporting Information.

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