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LUANA MARIA DEOCLÉCIO DA SILVA

FILOGEOGRAFIA COMPARADA E PREDITIVA NA DIVISÃO
LESTE-OESTE DO CERRADO: TESTE DE DIVERGÊNCIA
SIMULTÂNEA E IDENTIFICAÇÃO DE CARACTERÍSTICAS
PREDITORAS DE QUEBRA FILOGEOGRÁFICA

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DO CERRADO: TESTE DE DIVERGÊNCIA SIMULTÂNEA E IDENTIFICAÇÃO
DE CARACTERÍSTICAS PREDITORAS DE QUEBRA FILOGEOGRÁFICA

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RESUMO

O Cerrado é uma vasta formação de savana no Brasil central e que atualmente está incluído na lista dos principais *hotspots* de biodiversidade do planeta. Apesar do reconhecimento de sua relevância biológica, os processos biogeográficos que moldaram a diversificação de sua biota em diferentes níveis taxonômicos ainda são pouco conhecidos. Um padrão relativamente comum inferido em diferentes espécies do Cerrado é uma quebra filogeográfica no Planalto Central Brasileiro, separando no sentido leste-oeste, populações de diferentes espécies animais e vegetais. Neste trabalho, nós combinamos a filogeografia comparada com a estrutura preditiva do aprendizado de máquina para investigar a existência de eventos síncronos entre pares de espécies/populações que apresentam o padrão filogeográfico relatado e identificar características preditoras dessa divergência. A primeira etapa do trabalho consistiu no levantamento de todos os artigos sobre estudos filogeográficos realizados no Cerrado, do qual, 33 artigos foram criteriosamente selecionados. A quebra filogeográfica leste-oeste foi identificada através da construção de árvores filogenéticas e/ou quando foi relatada pelos autores dos artigos. Nós utilizamos a inferência Bayesiana de eventos evolutivos compartilhados para estimar o tempo e a sincronicidade da divergência em oito pares de táxons, compreendendo plantas, artrópodes, lagartos e sapos. Finalmente, construímos um modelo estatístico de floresta aleatória usando informações bióticas e abióticas para identificar os melhores preditores da quebra filogeográfica em questão. Nós identificamos que a congruência espacial está associada a sincronia temporal em plantas, principalmente relacionada aos eventos climáticos do Pleistoceno que antecederam o Último Máximo Glacial. Dentro dos animais, nós identificamos múltiplos pulsos de divergência que coincidem com os eventos geológicos do Neógeno e as oscilações climáticas quaternárias. Nosso modelo estatístico previu que as variáveis bióticas relacionadas à capacidade de dispersão, fluxo gênico e preferência de habitat, podem ter tido um papel fundamental na estruturação da quebra leste-oeste das linhagens do Cerrado central, consistente com as contribuições relativas das forças extrínsecas e intrínsecas que impulsionam as respostas dos organismos.

Palavras-chave: Biogeografia, Filogeografia Comparada, Variação Genética, Cerrado, Aprendizado de Máquina, Inferência Bayesiana.

ABSTRACT

The Cerrado is a vast savanna formation in central Brazil currently included in the list of the main global hotspots for biodiversity conservation. Despite the recognition of its biological relevance, the biogeographic processes that shaped the diversification of its biota at different taxonomic levels are still poorly understood. A relatively common pattern inferred in different Cerrado species is a phylogeographic break in the Brazilian Central Plateau, separating populations of different animal and plant species in an east-west direction. In this work, we combine comparative phylogeography with the predictive framework of machine learning to investigate the existence of synchronous events between species/population pairs that show the reported phylogeographic pattern and identify predictive variables of this divergence. The east-west phylogeographic break was determined through the construction of phylogenetic trees and when the authors of the articles reported the east-west division. We used Bayesian inference of shared evolutionary events to estimate the timing and synchronicity of divergence in eight taxa pairs comprising plants, arthropods, lizards, and frogs. Finally, we build a random forest statistical model using biotic and abiotic information to identify the best predictors of the phylogeographic structure. We identified that spatial congruence is associated with temporal synchrony in plants, mainly related to Pleistocene climatic events that preceded the Last Glacial Maximum. We identified multiple divergence pulses within animals that coincide with Neogene geological events and Quaternary climatic oscillations. Our statistical model predicted that biotic variables related to dispersal ability, gene flow, and habitat preference played a crucial role in structuring the east-west break of the central Cerrado lineages, consistent with the relative contributions of extrinsic and intrinsic forces that drive the responses of organisms.

Keywords: Biogeography, Comparative Phylogeography, Genetic Variation, Cerrado, Machine Learning, Bayesian Inference.

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1. INTRODUÇÃO GERAL

1.1. Padrões biogeográficos da América do Sul

A América do Sul ocupa a maior parte da região Neotropical e apresenta biomas extremamente diversos, com espécies que foram alvo de histórias biogeográficas altamente complexas (Turchetto-Zolet *et al.*, 2013). O continente também mostra padrões geomorfológicos complexos, como grandes planícies fluviais (por exemplo, a bacia Amazônica) e extensas cadeias de montanhas (por exemplo, a cordilheira dos Andes). Nas últimas décadas, muito esforço tem sido feito para elucidar os processos que deram origem à biodiversidade sul-americana, com viés para estudos em áreas florestais, como as Florestas Amazônica e Atlântica (Wright, 2002; Mittelbach *et al.*, 2007; Turchetto-Zolet *et al.*, 2013, Cannon & Lerdau, 2015; Usinowicz *et al.*, 2017, Rull, 2020). A maioria das hipóteses biogeográficas que explicam padrões de diversificação na região é baseada em eventos vicariantes, dentre os quais pode-se destacar o soerguimento dos Andes (Chapman, 1917), os refúgios pleistocênicos (Haffer, 1969; Vanzolini & Williams, 1970) e os rios como barreiras (Wallace, 1854). Para as formações de vegetação aberta como a Caatinga, o Cerrado e o Chaco, as hipóteses sugeridas estão fortemente relacionadas às mudanças climáticas do Pleistoceno, como a hipótese do Arco Pleistocênico (Prado & Gibbs, 1993, Toby Pennington *et al.*, 2000) e a formação dos corredores florestais que podem ter conectado áreas florestais por meio das áreas abertas (Ledo & Colli, 2017, Pinaya *et al.*, 2019).

O continente é atravessado diagonalmente, do nordeste do Brasil ao norte da Argentina, por um amplo cinturão de vegetação aberta denominado de “diagonal” de formações abertas (Vanzolini, 1963). Três áreas biogeográficas compõem essa região: a Caatinga, um núcleo de florestas tropicais sazonalmente secas no nordeste brasileiro; o Cerrado, um mosaico de fitofisionomias de savana no Brasil central; e, o Chaco, uma formação de vegetação seca no nordeste da Argentina, oeste do Paraguai e sudeste da Bolívia. Em comum essas três formações se caracterizam por uma intensa sazonalidade climática, com vegetação adaptada ao estresse hídrico e biotas especializadas (Werneck, 2011). Inicialmente, pesquisadores sugeriram que essas formações possuíam baixos níveis de diversidade de espécies e endemismo (Vanzolini, 1963). Entretanto, estudos têm demonstrado que as formações da diagonal de áreas abertas além de apresentarem uma

biodiversidade muito maior do que afirmada anteriormente, constituem um importante centro neotropical de endemismo (Müller, 1973; Colli *et al.*, 2002; Nogueira *et al.*, 2011, Antonelli *et al.*, 2018). Somado a isso, por estar localizada entre a Amazônia e a Floresta Atlântica, esse corredor de vegetação aberta atua como barreira efetiva para o intercâmbio biótico entre esses dois grandes domínios (Fouquet *et al.*, 2013; Ledo & Colli, 2017, Pinaya *et al.*, 2019).

O Cerrado é uma vasta savana tropical localizada no Brasil central, ocupando principalmente planaltos de blocos cristalinos e sedimentares, cuja descontinuidade é marcada por uma extensa rede de vales e depressões periféricas (Brasil & Alvarenga, 1989). Além de sua fronteira com a Caatinga no nordeste do Brasil, a região possui extensas fronteiras com a Amazônia ao norte e a Floresta Atlântica ao leste. O Cerrado brasileiro é a savana mais diversa do mundo, principalmente em termos de número de espécies vegetais presentes, além de apresentar altos níveis de endemismo (Klink & Machado, 2005). Embora a importância biológica do Cerrado seja reconhecida, nos últimos anos mais de 50% de sua área natural foi substituída por pastagens e terras agrícolas (Machado, 2004; Klink & Machado, 2005), tornando-o um dos principais *hotspots* globais para a conservação da biodiversidade (Myers *et al.* 2000). Apesar de tal relevância, ainda existem lacunas de conhecimento sobre a biogeografia histórica do Cerrado para serem preenchidas.

Entre as hipóteses propostas para a diversificação dos organismos do Cerrado, os ciclos de contração e expansão como consequência das mudanças climáticas do Pleistoceno têm sido sugeridos como principal mecanismo de diversificação (Ratter *et al.*, 1997, Bueno *et al.*, 2017; Buzzati *et al.*, 2018). Estudos moleculares recentes mostraram que as flutuações climáticas foram responsáveis pela estruturação da diversidade genética em alguns táxons, como plantas (Ramos *et al.* 2007; Bonatelli *et al.* 2014; Collevatti *et al.* 2015; Vittorino *et al.* 2018), invertebrados (Moraes *et al.*, 2009; Bartoletti *et al.*, 2017) e lagartos (Werneck *et al.*, 2012). Os eventos geológicos durante o Neógeno também são evocados para explicar parte da diferenciação genética intraespecífica, incluindo a divisão entre florestas úmidas e áreas abertas na América do Sul, o soerguimento andino e eventos de vicariância associados a transgressões marítimas e o soerguimento do Planalto Central brasileiro (Raven & Axelrod, 1974; Gentry, 1982; Giugliano *et al.*, 2007; Werneck *et al.*, 2009; Maciel *et al.*, 2010; Werneck *et al.*, 2012). Muitos estudos destacam que o soerguimento final do Planalto Central brasileiro (7-5

Ma), que aumentou a heterogeneidade da paisagem no Cerrado, teve um papel fundamental na diversificação de pequenos vertebrados que vivem no domínio (Domingos *et al.*, 2014; Giugliano *et al.*, 2013; Guarnizo *et al.*, 2016; Camarugi *et al.*, 2021).

As conexões entre a Amazônia e a Mata Atlântica através do Cerrado têm sido cada vez mais elucidadas. Corredores florestais que ligam essas formações se estabeleceram mais de uma vez ao longo do tempo, tanto no Último Período Interglacial (LIG) quanto no Último Máximo Glacial (LGM) (Ledo & Colli, 2017) (Fig. 1a). Além dessas conexões, há evidências de dois padrões de migração de floresta tropical montanhosa através do Cerrado, conectando o sul/sudeste ao nordeste do Brasil e a Amazônia com uma terceira rota curta que se estende de um deles (Pinaya *et al.*, 2019). A principal hipótese é que esses corredores eram de fato transectos de microrefúgios de vegetação montanhosa que se estabeleceram durante o período mais frio e úmido do evento Heinrich Stadial 1 (HS1; 18.1–14.7 kcal yr BP) e possivelmente em períodos glaciais anteriores (Pinaya, *et al.*, 2019) (Fig. 1b).

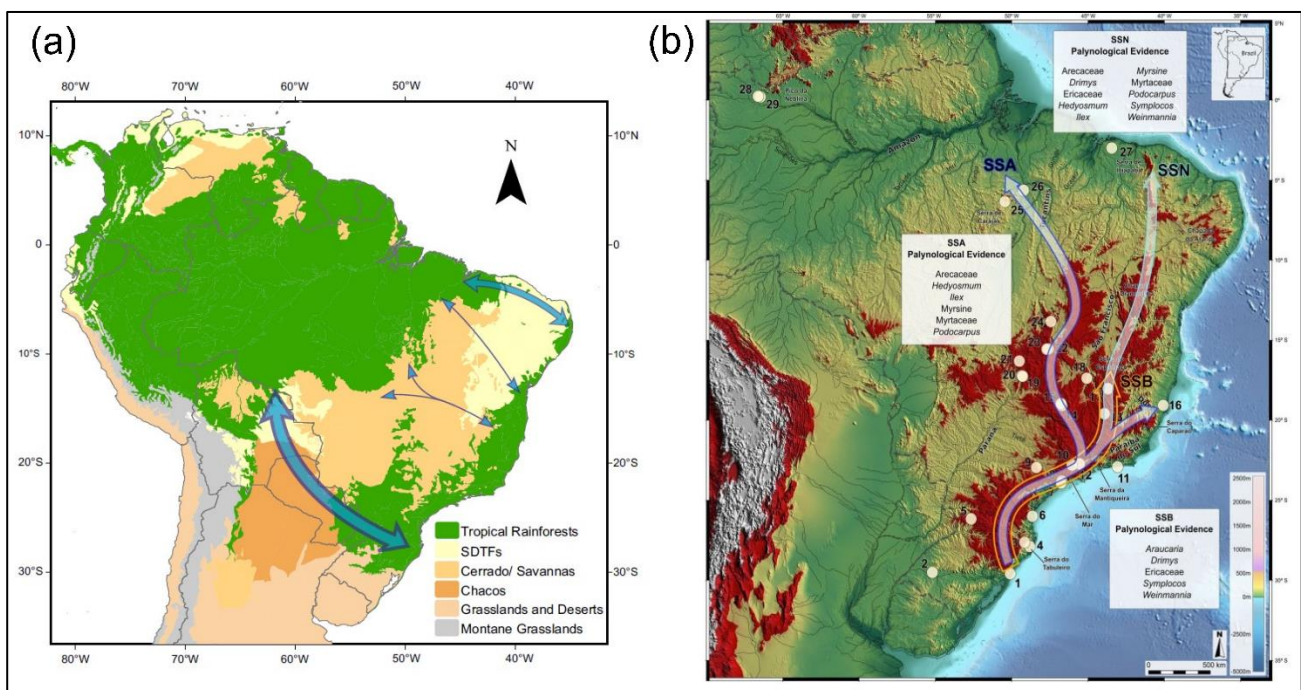


Figura 1. Corredores de migração através do Cerrado conectando: (a) a Amazônia e a Floresta Atlântica, retirado de Ledo & Colli (2017); (b) o sul e sudeste do Brasil ao nordeste e a Amazônia, retirado de Pinaya *et al.* (2019).

1.2. Barreiras biogeográficas

Há muito se reconhece que a distribuição geográfica das espécies tem implicações diretas para a compreensão de processos evolutivos (Wallace, 1876). As barreiras biogeográficas são conhecidas por limitar a dispersão e o fluxo gênico entre populações, atuando como um importante mecanismo de diversificação intraespecífica (Avice, 2000). Outro princípio importante das barreiras biogeográficas é que elas podem impulsionar a diversificação de múltiplas espécies simultaneamente, gerando uma distribuição geográfica coincidente de linhagens divergentes e/ou espécies que coabitam a paisagem (Wallace, 1876). O isolamento geográfico pode ser iniciado por barreiras físicas como cadeias de montanhas e rios (Avice, 2000) ou por barreiras ocultas influenciadas por mudanças climáticas históricas, como os períodos glaciais e interglaciais durante o Pleistoceno (Hewitt, 2000). Identificar tais barreiras pode contribuir para explicações sobre respostas de linhagens co-distribuídas a um evento histórico compartilhado e sua relação com características da paisagem, fenótipos e relações ecológicas com outras espécies (Pyron & Burbrink, 2010; Zamudio *et al.*, 2016; Satler & Carstens, 2017)

A filogeografia comparada fornece um importante meio de elucidar a influência relativa de eventos históricos compartilhados entre múltiplas espécies co-distribuídas (Avice *et al.*, 1987). Uma abordagem comum é inferir a estrutura genética da população e estimar parâmetros em um contexto geográfico que dedica atenção especial às barreiras biogeográficas. Nesse contexto, as congruências nas histórias demográficas entre as espécies sugerem uma resposta compartilhada com as mudanças na paisagem (Avice *et al.*, 1987, Sullivan *et al.*, 2019), enquanto padrões idiossincráticos são indicativos de uma resposta independente (Papadoulous *et al.*, 2018). Ainda que os padrões espaciais comuns possam indicar uma história semelhante, a informação temporal é necessária para demonstrar uma resposta compartilhada no tempo (Edwards & Beerli, 2000). Isso pode ser feito estimando os tempos de divergência de cada espécie para a comparação (Carstens *et al.*, 2005; Smith *et al.*, 2012) ou usando modelos probabilísticos para estimar o número de eventos de divergência (Hickerson *et al.*, 2006, 2007; Oaks, 2019).

A inferência de divergências espaço-temporais congruentes em vários táxons co-distribuídos forneceu evidências importantes do impacto de barreiras biogeográficas ocultas na distribuição atual da diversidade genética (Avice *et al.*, 2000; Edwards *et al.*, 2017). No entanto, estudos comparativos revelaram que populações co-distribuídas

podem responder de forma e em momentos diferentes às mesmas barreiras geográficas ou ambientais (Kropf *et al.*, 2003; Carstens *et al.*, 2005; Eldridge *et al.*, 2014). Essas observações levantaram a necessidade de investigar quais características do organismo e características ambientais locais podem prever os padrões filogeográficos idiossincráticos (Zamudio *et al.* 2016). Nesse contexto, estudos de filogeografia mais recentes têm usado modelos preditivos, como aprendizado de máquina supervisionado para investigar associações entre características e respostas idiossincráticas (Espíndola *et al.* 2016; Sullivan *et al.*, 2019; Bonatelli *et al.* 2022).

1.3. Divergência Leste-oeste no Cerrado Central

Estudos filogeográficos prévios de plantas amplamente distribuídas no Cerrado revelaram altos níveis de divergência genética entre populações e linhagens geneticamente estruturadas (Ramos *et al.*, 2007; Collevatti, Rabelo & Vieira, 2009; Novaes *et al.*, 2010). Recentemente, Resende-Moreira *et al.* (2017) relataram a existência de dois grupos genéticos de *Byrsonima coccolobifolia*, traçando uma ruptura longitudinal na área central do Cerrado, um grupo leste e outro oeste (Fig. 2c). Esta estrutura assemelha-se ao observado para outras espécies arbóreas do Cerrado, tais como, *Hymenaea stigonocarpa* (Fig. 2d) (Ramos *et al.*, 2007) e *Annona coriacea* (Fig. 2b) (Ribeiro *et al.*, 2016). A quebra leste-oeste em plantas é geralmente associada às mudanças históricas da vegetação do Cerrado durante as oscilações climáticas do Pleistoceno (Ramos *et al.*, 2007; Ribeiro *et al.*, 2016; Resende-Moreira *et al.*, 2017).

Além das espécies amplamente distribuídas, o mesmo padrão de quebra filogeográfica no Planalto Central Brasileiro foi observado em espécies restritas aos campos rupestres, como *Lychnophora ericoides* (uma espécie arbustiva) (Collevatti, Rabelo & Vieira, 2009) e o complexo *Pilosocereus aurisetus* (cactos colunares) (Fig. 2a) (Bonatelli *et al.*, 2014; Perez *et al.*, 2016). Dados genéticos sugerem que as populações dessas espécies, atualmente encontradas em múltiplos enclaves de vegetação xerofítica, são relíquias de uma distribuição mais ampla dos períodos glaciais do Pleistoceno. De modo geral, a quebra filogeográfica leste-oeste não corresponde a barreiras físicas óbvias; em vez disso, acredita-se que a localização da barreira varie entre as espécies com uma zona de sobreposição entre aproximadamente 54-43°W de longitude. Apesar dos esforços, a maior parte dos estudos filogeográficos realizados na região basearam-se

apenas na distribuição dos padrões de diversidade genética dentro de uma única espécie (Ramos *et al.*, 2007, 2008; Prado *et al.*, 2012; Santos *et al.*, 2014; Ribeiro *et al.*, 2016).

Até o presente momento, nenhum estudo comparativo foi realizado buscando compreender quais fatores e características de vida podem ter influenciado a resposta intraespecífica para o estabelecimento do atual padrão leste-oeste de distribuição das espécies do Cerrado Central. Considerando os aspectos apresentados anteriormente esta dissertação está organizada em formato de artigo que será posteriormente publicado em um periódico de alto impacto nas áreas de Biogeografia, Ecologia Molecular ou Genética Evolutiva, o qual está descrito abaixo:

- No Capítulo I, utilizamos dados genéticos em estudos filogeográficos de táxons do Cerrado, características dos organismos e dados climáticos para investigar a quebra filogeográfica leste-oeste relatada. Usamos a inferência Bayesiana de eventos evolutivos compartilhados em espécies co-distribuídas nesta região para testar os seguintes cenários alternativos: (I) um único evento síncrono ou (II) múltiplos eventos de divergência. Também integramos dados filogeográficos com características de organismos, taxonomia e dados climáticos para investigar variáveis preditivas da quebra filogeográfica leste-oeste.

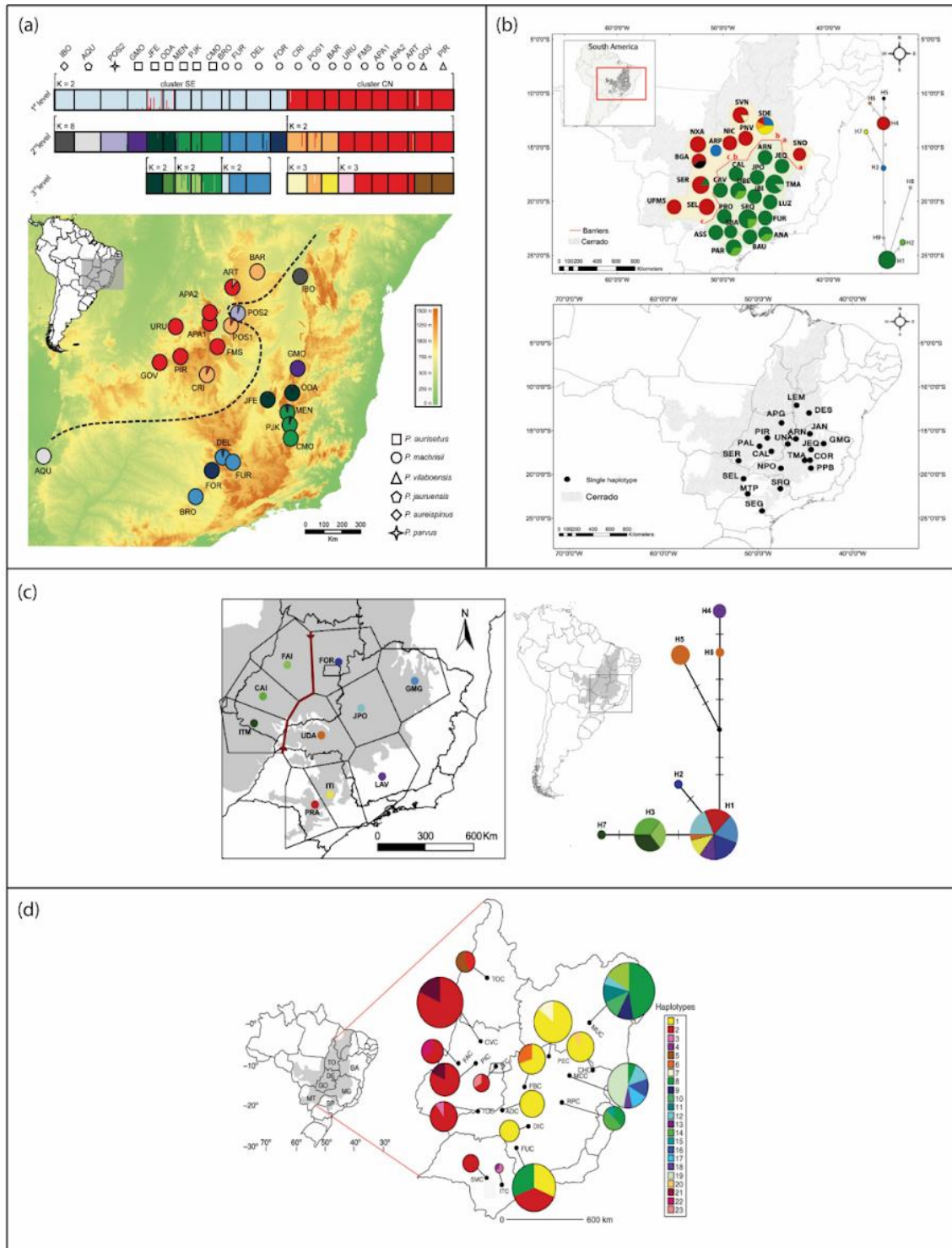


Figura 2. Resultados de estudos prévios evidenciando a quebra filogeográfica Leste-oeste em espécies vegetais do Cerrado. (a) complexo *P. aurisetus*, retirado de Bonatelli *et al.* (2014). (b) *A. coriacea*, retirada de Ribeiro *et al.* (2016). (c) *B. coccolobifolia*, retirado de Resende-Morera *et al.* (2017). (d) *H. stigonocarpa*, retirado de Ramos *et al.* (2007).

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CAPÍTULO I

Comparative and predictive phylogeography of east-west disjunction in central Cerrado: species responses to hidden barriers.

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Abstract: Biogeographic barriers are known to limit the gene flow between populations, acting as an important mechanism for intraspecific diversification. Comparative phylogeography has provided important means to elucidate how multiple co-distributed species responded to a common historical event, such as hidden barriers caused by climatic events. Here we reuse sequence data and accessed organismal traits and climate data a long-term term barrier for many species inhabiting the Cerrado domain: the so-called east-west phylogeographic break. We combined a Bayesian inference for evolutionary events and predictive classification approaches to interrogate the congruence of divergence time within plant and animal species and which traits and environmental features can predict their phylogeographic structure. We identified that spatial concordance is associated with temporal synchrony in plants during the Pleistocene. Within animals, we estimated several divergence pulses that coincide with Neogene geological events and Pleistocene climatic oscillations, suggesting a complex biogeographic process and the association of intrinsic/biotic factors in the maintenance of the observed phylogeographic structure. Finally, taxonomy and biotic variables related

to dispersal and connectivity largely predict the species' responses to east-west break. Our findings suggest that the modern east-west disjunction shared by many taxa of the central Cerrado is a relic of complex biogeographic processes associated with abiotic and biotic factors.

Keywords: Biogeography, Comparative Phylogeography, Hidden Barriers, Genetic Variation, Cerrado, Machine Learning, Bayesian Inference.

Introduction

Biogeographic barriers limit the dispersion and gene flow between populations, acting as an important mechanism for intraspecific diversification. Another essential principle of biogeographic barriers is that they are regularly expected to drive the diversification of multiple species simultaneously, generating a coincident geographical distribution of divergent lineages co-inhabiting the landscape (Wallace, 1876). Identifying such barriers may contribute to explain how multiple co-distributed species may respond to shared historical events and investigate how these responses correlate with landscape features, phenotypes, and ecological relationships with other species (Proches, 2006; Pyron & Burbrink, 2010; Zamudio *et al.*, 2016; Satler & Carstens, 2017).

Physical barriers are simple to identify when there is a sharp geographic boundary between divergent genetic groups, such as mountain ranges or rivers (Avice, 2000). However, it can be more challenging to identify hidden barriers caused by past changes in environmental conditions (e.g., glacial-interglacial oscillations during the Pleistocene) when obvious physiographic features are no longer evident (Edwards, 2017). Such barriers can be detected indirectly by finding deep phylogeographic structure in co-distributed taxa, especially if the compared species share similar ecological tolerances and are distantly related in the tree of life (Di Virgilio, Laffan & Ebach, 2012). Methodological advances in model selection approaches have enabled explicit tests of co-divergence across evolutionary lineages (Overcast *et al.*, 2017; Bagley *et al.*, 2018; Oaks, 2019), opening new opportunities for inference of such hidden barriers (e.g., Satler & Carstens, 2017).

The inference of congruent spatiotemporal divergences across multiple co-distributed taxa has provided substantial evidence for the impact of hidden biogeographic

barriers on the current distribution of genetic diversity (Avise *et al.*, 2000; Edwards *et al.*, 2017). However, several comparative studies have found that co-distributed populations of different species respond differently and at different times to the same geographic or environmental barriers (Kropf *et al.*, 2003; Carstens *et al.*, 2005; Eldridge *et al.*, 2014). These observations have encouraged scientists to investigate which organismal traits and local environmental features can predict idiosyncratic phylogeographic patterns (Satler *et al.*, 2016; Zamudio *et al.*, 2016; Edwards *et al.*, 2022). More recent phylogeographic studies have used predictive models, such as supervised machine learning to investigate associations between traits and idiosyncratic responses (Espíndola *et al.*, 2016; Sullivan *et al.*, 2019; Bonatelli *et al.* 2021).

The Cerrado domain is a vast neotropical savanna formation, occupying the highlands of central Brazil, recognized as a global biodiversity hotspot (Myers *et al.* 2000). It is predominantly a woodland-savanna composed of a mosaic of grassland, dry forests, and humid forests along water courses (Eiten, 1972; Ribeiro & Walter, 2008). The domain occupies mainly plateaus of crystalline or sedimentary blocks, whose discontinuity is marked by an extensive network of valleys and peripheral depressions (Brasil & Alvarenga, 1989). The existence of multiple phylogeographic datasets of widely distributed species across the Cerrado provides a case for investigating the impact of common biogeographic events on this biodiversity hotspot. A growing catalog of species and independent evolutionary lineages have been proposed for different taxa based on the observation of a deep phylogeographic structure in the central Cerrado, splitting lineages in a roughly east-west direction (Ramos *et al.*, 2007; Ribeiro *et al.*, 2016; Resende-Moreira *et al.*, 2017). This pattern has been referred to as the “east-west divergence” in central Brazilian Cerrado (Resende-Moreira *et al.*, 2017). In this case, the break does not correspond to obvious physical barriers; instead, the lineages are thought to turn over approximately between 54-43° W longitude. The east-west break has been associated with historical range shifts of the Cerrado vegetation during the Quaternary climate changes (e.g., Ramos *et al.*, 2007; Bonatelli *et al.*, 2014, Ribeiro *et al.*, 2016; Resende-Moreira *et al.*, 2017). However, comparative analysis of taxa that share this phylogeographic pattern and the life history traits influencing the intraspecific response have not yet been explored.

Here we reuse sequence data available for a set of distinctive co-distributed species and accessed organismal traits and climate data from the Cerrado taxa to

investigate the east-west phylogeographic break. We combined comparative phylogeographic and predictive classification approaches to interrogate the congruence of time divergence within plant and animal species and which traits and environmental features can predict this phylogeographic structure. We use Bayesian inference to test the alternative scenarios of a single, synchronous versus multiple events of divergence in co-distributed species. We also integrate phylogeographic data with organismal traits, taxonomy, and climate data to investigate predictive variables of the east-west phylogeographic break. We hypothesize that there is support for a synchronous diversification correlated to a shared biogeographic event in central Cerrado. The non-temporal synchrony would be associated with idiosyncratic characteristics of each species. This approach may provide a better understanding of biogeographic and evolutionary events shaping diversification across the Cerrado domain. It also may provide valuable information about abiotic and biotic correlates of diversification in this region that can be further explored.

Materials and Methods

Empirical Data

We performed a systematic survey in the “Web of Science®” database for phylogeographic studies to evaluate the available genetic data for plant and animal taxa from the Cerrado region matching the phylogeographic break investigated in this work. We checked for articles published from 1987 (date considered the birth of phylogeography as a discipline: *Avise et al.*, 1987) until July 14, 2021, using keyword searches for topic: “phylogeography*” AND “Cerrado”. Articles were included in our analyses if they met the minimum criteria: (i) sampling of species/lineages distributed in the Cerrado region, delimited in this work between coordinates 11.000°S to 23.000°S and 43.000°W to 54.000°W (hereinafter referred to as “central Cerrado”) (Fig. 1); and, (ii) sampling of populations of a single species or closely related species, ensuring that only phylogeographic works with empirical data were used. We restricted our analyses only to the populations sampled within the central Cerrado, i.e., samples outside this quadrant were discarded. This procedure was adopted to reduce the influence of additional phylogeographic structures possibly present in species with wider distribution occurring beyond the investigated east-west break region.

We retrieved all articles that met the minimum criteria specified above and identified those records that included GenBank accessions. For articles that included accessions, we retrieved mitochondrial (mtDNA) and chloroplastic (cpDNA) genetic data from GenBank. The inclusion of only cytoplasmic genetic data was adopted to homogenize the substitution models and rates of markers and increase the robustness of the analyses.

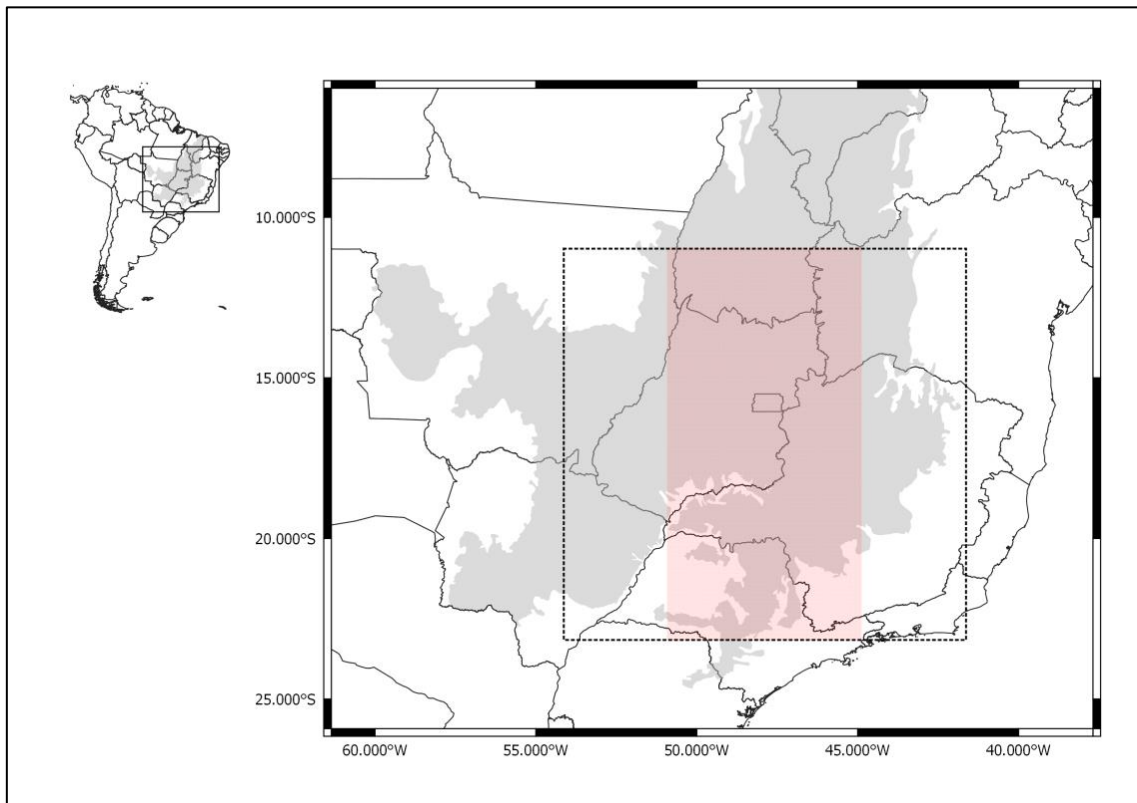


Figure 1. Map of the central region of Brazil investigated in this study, with the “central Cerrado” delimited with a dashed line and the east-west phylogeographic break region delimited by the area in red. The gray area shows the distribution of the Cerrado domain (Ab'Saber, 2003).

Examining the spatial east-west phylogeographic structure

To classify each taxon according to the presence or absence of an east-west phylogeographic break, we followed two different criteria and datasets according to the methodology applied: (i) for comparative phylogeography (i.e., inference of shared divergence events), the classification was done by inspecting the topology of

phylogenetic trees (see below). This criterium was defined particularly for taxa whose phylogenies follow an east-west division, enabling assign the samples in each geographic group and test the synchrony of divergence events; (ii) for predictive phylogeography (i.e., identification of predictive variables), the classification was based on the inspection of phylogenetic trees or according to the east-west division proposed by the authors of the original studies. As our predictive approach does not incorporate genetic data, we were able to adopt all studies matching our minimum criteria, regardless of whether or not genetic data were available. This was defined to maximize the number of taxa analyzed and to increase the predictive power of subsequent analyses.

We inferred maximum-likelihood trees to classify each species as showing or not a topology congruent with the east-west phylogeographic break. Species with trees showing a phylogenetic east-west division were classified as having the presence of a break. Due to the possible low variation in molecular markers for some species exhibiting, the phylogenetic trees may have unresolved (polytomies) or poorly supported sections, as well as a lack of reciprocal monophyly between east and west clades. In those cases, well-supported monophyly on at least one side of the break was considered sufficient to classify the divergence. The species classified as absent of break were those whose phylogenies did not show an east-west division or presented other phylogeographic patterns (e.g., northern-southern or southwest-northeast oriented structure). We generated the sequence alignments through MAFFT using the SuperCRUNCH v.1.2.1 tool (Portik & Wiens, 2020). The selection of nucleotide substitution models was performed using the Bayesian Information Criterion (BIC) implemented in ModelFinder (Kalyaanamoorthy *et al.*, 2017). To infer a maximum likelihood phylogeny for each species, tree searches were conducted in IQ-TREE (Nguyen *et al.*, 2015) under the best substitution model for each marker and the ultrafast bootstrap percentage computed with 1000 replications. The input files were reduced to one population sequence per haplotype to avoid unnecessary redundancy and complexity in the data. Phylogenetic relationships among haplotypes were visualized using Figtree v.1.4.3 (Rambaut, 2010).

Inference of shared evolutionary events

We used the *ecoevolity* program (Oaks, 2019; Oaks *et al.*, 2019), a recently developed full-likelihood Bayesian approach, to estimate the timing and synchronicity of the divergence between pairs of populations that shared the east-west phylogeographic break. *Ecoevolity* assumes that each species consists of a pair of isolated populations and uses the Dirichlet process before estimating the number and timing of divergence events and assigning pairs to the events (Oaks, 2019). Based on the results of the phylogenetic trees, we used as input the intraspecific genetic data that presented the phylogeographic pattern of interest. In addition, we separated each alignment into eastern and western populations, with eight pairs of comparisons assessed by *ecoevolity*. We divided our dataset into three categories according to the taxonomic classification: Arthropods (two pairs), Lizards + Frogs (four pairs), and Plants (two pairs) (Table 1).

To estimate shared divergence events, the *ecoevolity* program incorporates prior distributions on population size and divergence times (T). To use empirical values to increase the accuracy of the analysis, we estimated each of these parameters separately for each taxon. We inferred the effective population size (N_e) by estimating the composite parameter θ using DnaSP v.6.0. (Rozas *et al.*, 2017). For haploid and uniparental loci, as assumed to be cpDNA and mtDNA markers, N_e was calculated as $\theta/2\mu$ (Oaks, 2019). The divergence times between east and west lineages were inferred by estimating the time of the most recent common ancestor (TMRCA) using a Bayesian Markov Monte Carlo (MCMC) method implemented in BEAST v.2.6.3 (Drummond & Rambaut, 2007). We used a Yule Model prior and a relaxed lognormal clock for each analysis. We calibrated the time estimates using a normal prior distribution on the mtDNA and cpDNA substitution rates used in the original articles. When this information was unavailable, we used commonly used rates for related species (Appendix 2). We conducted two independent runs for each taxon, based on 50.000.000 generations, with samples taken every 1.000 generations. We use Tracer v.1.7.1 (Rambaut, Drummond, Xie, Baele, & Suchard, 2018) to evaluate stationary posterior distributions, effective sample sizes (ESS > 200), and convergence between runs.

Table 1. Taxa used to investigate shared divergence events across eastern and western lineages from central Cerrado. For multilocus datasets, sequence alignment length is given in nucleotide base pairs (bp), and the length of each gene is in parentheses, in the same order genes are listed at left.

	mtDNA genes	cpDNA genes	Length (bp)	<i>Ntotal</i> (east/west)	Source
Arthropods					
<i>Parawixia bistrata</i>	COI	-	712	9 (7/2)	Fernández Campón <i>et al.</i> (2021)
<i>Simulium hirtipupa</i>	COI	-	651	50 (11/39)	Andrade-Souza <i>et al.</i> (2017)
Lizards+Frogs					
<i>Norops meridionalis</i>	ND2	-	1015	41 (2/39)	Guarnizo <i>et al.</i> (2016)
<i>Polychrus acutirostris</i>	Cytb	-	838	19 (14/5)	Fonseca <i>et al.</i> (2018)
<i>Hypsiboas lundii</i>	ND2	-	1032	34 (28/6)	Vasconcelos <i>et al.</i> (2019)
<i>Leptodactylus frogs</i>	H1	-	2198	15 (10/5)	Carvalho <i>et al.</i> (2020)
Plants					
<i>Pilosocereus aurisetus</i>	-	trnT-trnL, trnS-trnG	1452 (311/1141)	102 (69/33)	Bonatelli <i>et al.</i> (2014)
<i>Byrsonima coccolobifolia</i>	-	trnS-trnG, trnH-trnK	2435 (740/1695)	49 (15/34)	Resende-Moreira <i>et al.</i> (2017)

Ntotal, total number of individuals; -, missing data.

Each analysis using the *ecoevolity* program (Arthropods, Lizards/Frogs, and Plants) was performed with different prior combinations: (1) for the concentration parameter (α), which is used by the Dirichlet process to determine prior probability in shared divergence events, we used values that place approximately 50% of the prior probability into independent divergences for all species; (2) for the event time prior (T),

which specifies the prior over the divergence times, we used converted values that correspond to the average of the divergence times of each species estimated using BEAST; and, (3) for the effective population size, we use the estimated N_e values calculated from θ . Details on the specific prior settings are provided in Appendix 3. To scale effective population sizes and divergence times by the mutation rate, we set the mutation rate parameter to 1. Thus, we obtained time in the expected number of substitutions per site. We ran five independent analyses of 150,000 generations for each dataset, sampling every 100th generation. We checked for convergence and calculated median values for parameters of interest in Tracer v.1.7.1 (Rambaut *et al.*, 2018), with 10% burn-in. Posterior distributions for the number of divergence events and marginal divergence times were summarized using two tools distributed with *ecoevolity*: *pyco-sumevents* and *pyco-sumtimes*. Graphics were produced using the accompanying Python package ‘*pycoevolity*’ v.0.2.4 (Oaks *et al.*, 2019) with the burn-in of 101 samples for each log file.

Predictor variables of phylogeographic break

We built a Random Forest classifier (Liaw & Wiener, 2002) to evaluate the importance of each sampled variable (see below) for predicting the presence or absence of the east-west phylogeographic break in the studied taxa. The analysis was performed with the ‘*randomForest*’ package (Liaw & Wiener, 2002) available in the R program. We divided our dataset into three subsets: (A) plants + animals; (B) animals; and (C) plants. To compose our base of putative predictor variables, we compiled geographic, climatic, taxonomic, and organismal trait data extracted from each sampled location. For all analyses, we extracted information from latitude, longitude, altitude, and solar radiation (from SOLARGIS) (Cebecauer & Suri, 2016). Climatic data were extracted from WorldClim (Fick & Hijmans, 2017), including all 19 bioclimatic variables. For organismal trait variables, we compiled the information from the literature about ‘traits’ shared by all taxa in each dataset. Details of the taxon-specific traits of each subset and their biological relevance in predicting the break are provided in Appendix 4. Taxonomic classifications (class, order, and family) were also used as a proxy for life-history traits exhibiting high phylogenetic signals that may not have been explicitly considered in our predictive model. All the variables and their information are listed in Appendix 5.

We constructed classifiers for each subset (plants/animals, animals, and plants) with and without the taxonomic classification of species as a predictor variable. We performed this procedure to assess the impact of unsampled traits of each taxonomic group to predict the response variable. Model accuracy was estimated from out-of-bag values and by cross-validation using a confusion matrix. The importance of each predictor variable was assessed by measuring the Mean Decrease in Accuracy (MDA) of the prediction after the removal of each variable in the predictive function.

Results

Empirical Data

Our search of the Web of Science® repository retrieved 126 articles, excluding five reviews. After excluding 93 articles that did not meet the requirements of the current study, 33 articles were selected to be included in our analyses (Appendix 1). Taxa that met our criteria included the following groups: plants (17), frogs (5), lizards (4), flies (3), birds (2), spiders (1), and monkeys (1). Of these, 25 (75.75%) articles published the mtDNA and cpDNA sequences on Genbank, and the remainder did not. Articles involving parasitic species (e.g., an arachnid, *Amblyomma sculptum*, and a bed bug, *Euschistus heros*) were excluded from our analyses, as the distribution of these species may be much more dependent on the distribution of their hosts than on environmental variables.

Examining the spatial east-west phylogeographic structure

According to the results of the phylogenetic trees, of the 25 taxa examined, eight showed population structure with two well-evidenced genetic groups whose division coincides with the east-west break (Appendix 1). These taxa were classified as having an east-west division; the 17 remaining taxa showed no structure or had unclear results. Following our second classification criterium, we classified an addition of six taxa whose original articles declared the east-west phylogeographic break across the central Cerrado. Therefore, for the predictive analysis, our dataset was composed of 33 taxa, with 14 (42,4%) classified as having the presence of structure and 19 (57,6%) as the absence.

Inference of shared evolutionary events

For the arthropods *Parawixia bistrinata* and *Simulium hirtipupa*, our *ecoevolity* results supported the two pairs of populations diverging independently (Fig. 2a). For the spider *P. bistrinata*, the divergence event occurred between Pliocene Piacenzian [upper 95% credible interval (CI) = 2.9 Mya] and the Pleistocene Calabrian ages (lower 95% CI = 1.2 Mya) (Appendix 6a). The divergence between populations of the Diptera *S. hirtipupa* was inferred as occurring between the Pleistocene Calabrian and Chibanian ages (median: 0.73 Mya, 95% CI = 1.15 to 0.4 Mya) (Appendix 6a).

For lizards and frogs, the *ecoevolity* analyses strongly rejected the hypothesis of shared divergence (Fig. 2b). Nonetheless, the overlap in 95% confidence intervals for frog populations (*Hypsiboas lundii* and the *Leptodactylus complex*) suggest a shared divergence between these species (Appendix 6b). Therefore, we performed separate *ecoevolity* runs for these two lineage pairs to examine whether there was any clustering of divergence events. The species-specific test showed clear evidence for concordant divergence across the frogs, taking place between the Pliocene Piacenzian and the Pleistocene Gelasian ages (median: 2.5 Mya, 95% CI: 1.8 - 3.3 Mya) (Fig. 3). Apart from this synchronic event, *N. meridionalis* lineages diverged at the Miocene Tortonian age (median: 7.5 Mya, 95% CI: 9.8 - 5.3) and *P. acutirostris* during the Pliocene Zanclean age (median: 4.0 Mya, 95% CI: 5.7 - 2.6) (Appendix 6b).

For plants, the posterior probabilities and the Bayes factor support the model of synchronous divergence between the tree *Byrsonima coccolobifolia* and the cactus *P. aurisetus* (Fig. 2c). Using the slow evolutionary rate of cpDNA (0.0011 subs/site/Myr, Wolfe *et al.* 1987), these species diverged synchronously between the Pleistocene Calabrian and Chibanian ages (median: 0.5 Mya, 95% CI: 0.24 - 1.8) (Appendix 6c), while using the fast evolutionary rate (0.0029 subs/site/Myr) the divergence occurred between the Pleistocene Chibanian and Stage 4 Pleistocene ages (median: 0.2 Mya, 95% CI: 0.09 - 0.32) (Appendix 6d).

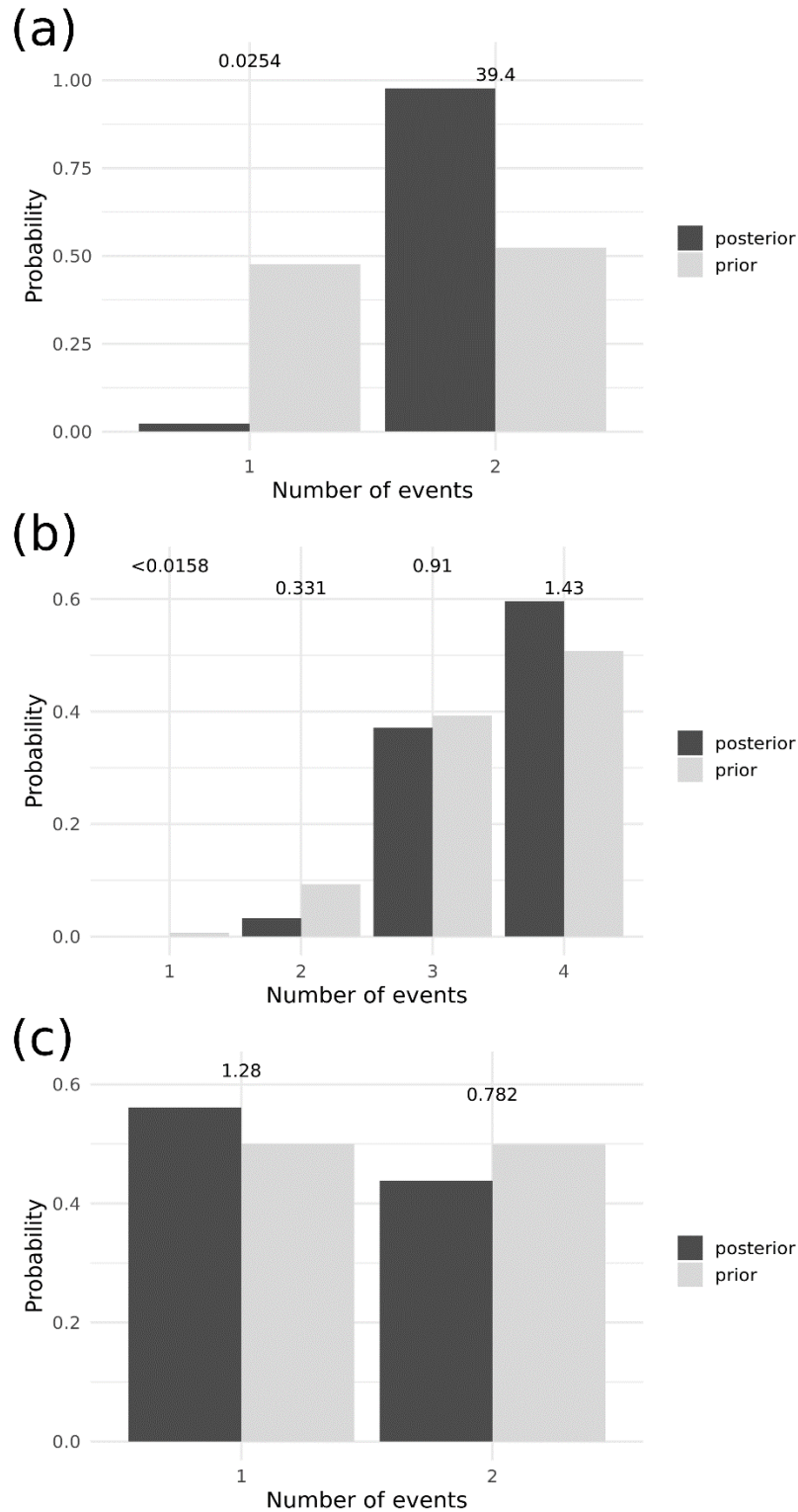


Figure 2. Approximate prior and posterior probabilities distributions of numbers of inferred divergence events across (a) arthropods (population pairs=2), (b) lizards and frogs (population pairs =4), and (c) plants (population pairs =2). Prior probabilities are in light gray, and posterior probabilities are in dark gray. Bayes factors for each number of divergence times are given above the corresponding bars.

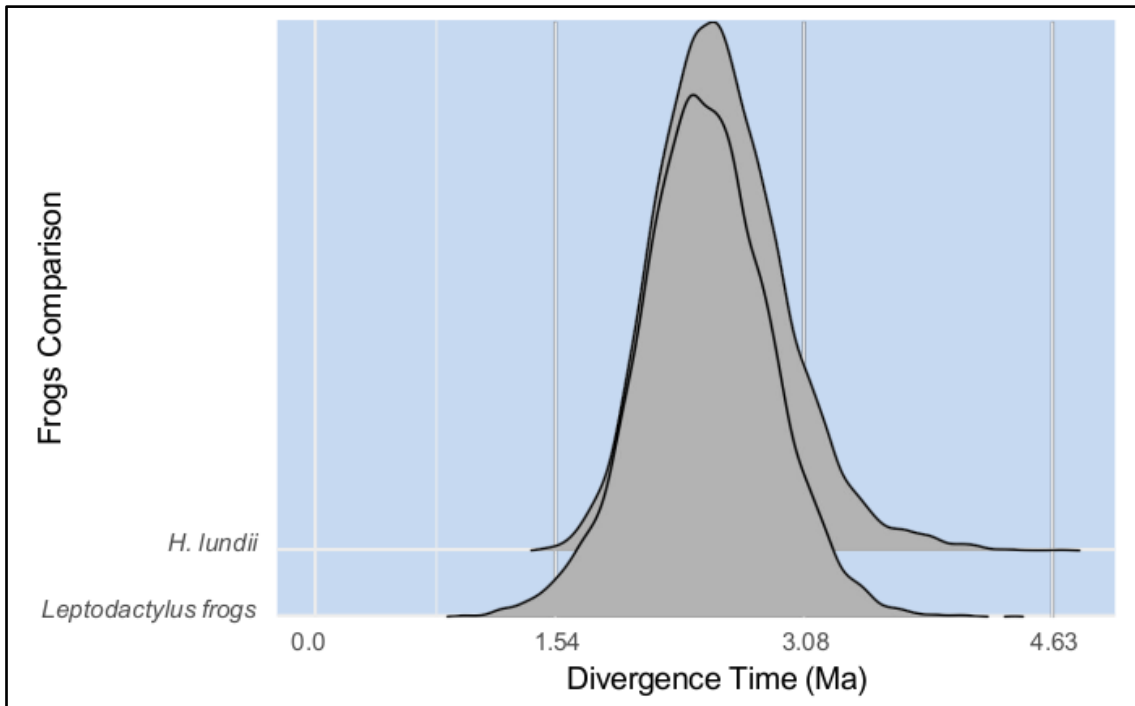


Figure 3. Approximate marginal posterior distributions of divergence times (in Million Years Ago) for each pair of frog populations.

Variable correlates of the phylogeographic break

When taxonomy was used, RF models accurately predicted the responses of the east-west phylogeographic break in all taxa (subset A, 86.8%), animals (subset B, 90.8%), and plants (subset C, 97.2%). In the general analysis (A), taxonomy (family and order ranks) had the highest measures of MDA, followed by organismal traits (dispersion means and phytophysionomy) (Fig. 4a). In the animal-specific analysis (B), family rank was again the most important variable, followed by the trophic level, order rank, and phytophysionomy measured by MDA (Fig. 4b). The most important predictor for plants was organismal traits, represented by pollination syndromes and dispersal vectors, followed by taxonomy (order and family ranks) (Fig. 4c).

The removal of taxonomic variables drastically reduced the correct prediction to 9.06% for all taxa datasets, 17.4% for the animals, and 1.7% for plants. In this scenario of low predictability, the organismal traits had the highest measures of MDA. In the classifier with all taxa, dispersion means, and phytophysionomy were the most important predictors (Fig. 5a). Trophic level and movement ability were the most critical for animals

(Fig. 5b), while pollination syndromes and dispersal vectors were the best predictors for plants (Fig. 5c).

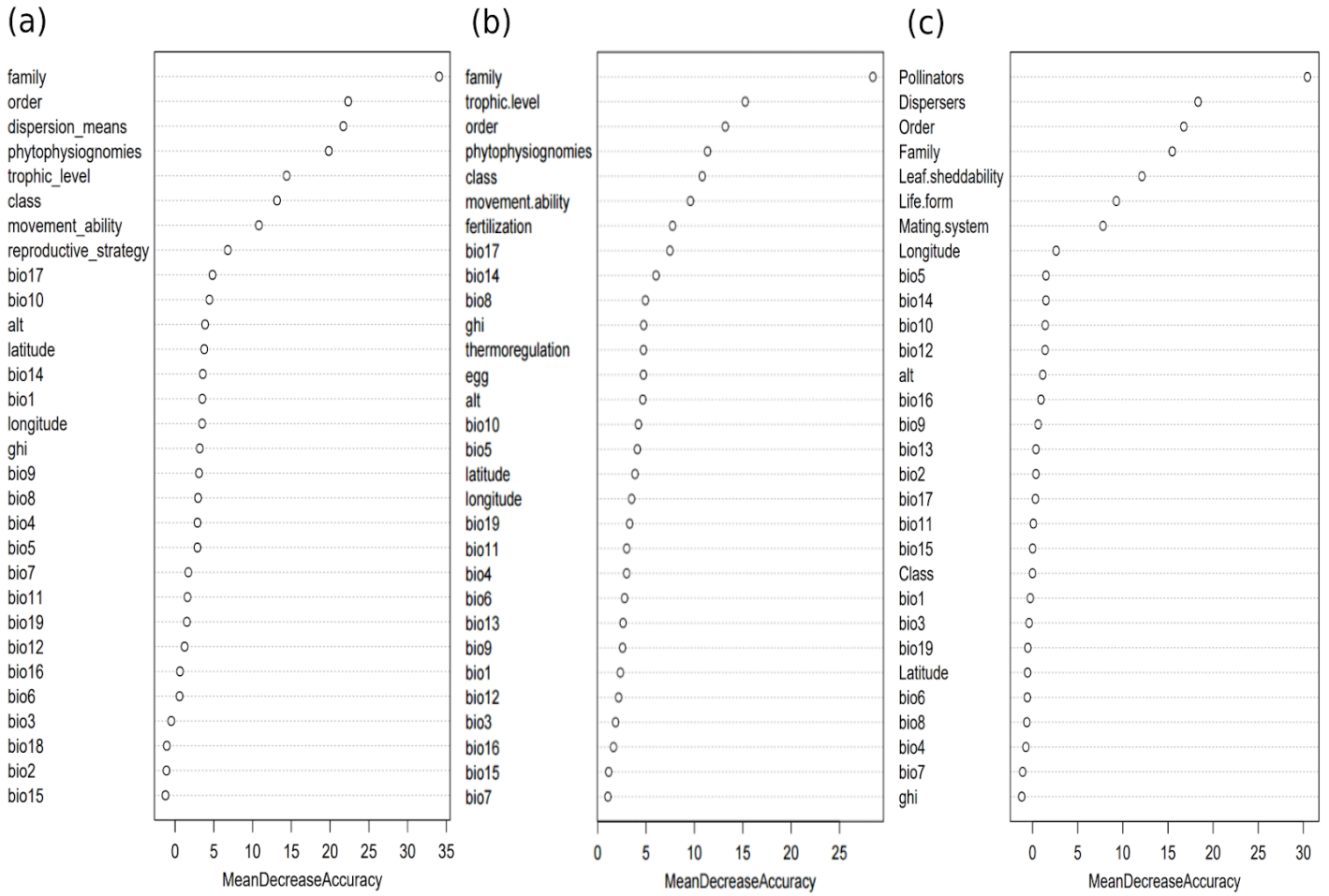


Figure 4. Variable importance (with taxonomy) for predicting the east-west phylogeographic break responses of (a) animals+plants, (b) animals, and (c) plants based on the Mean Decrease in Accuracy (MDA).

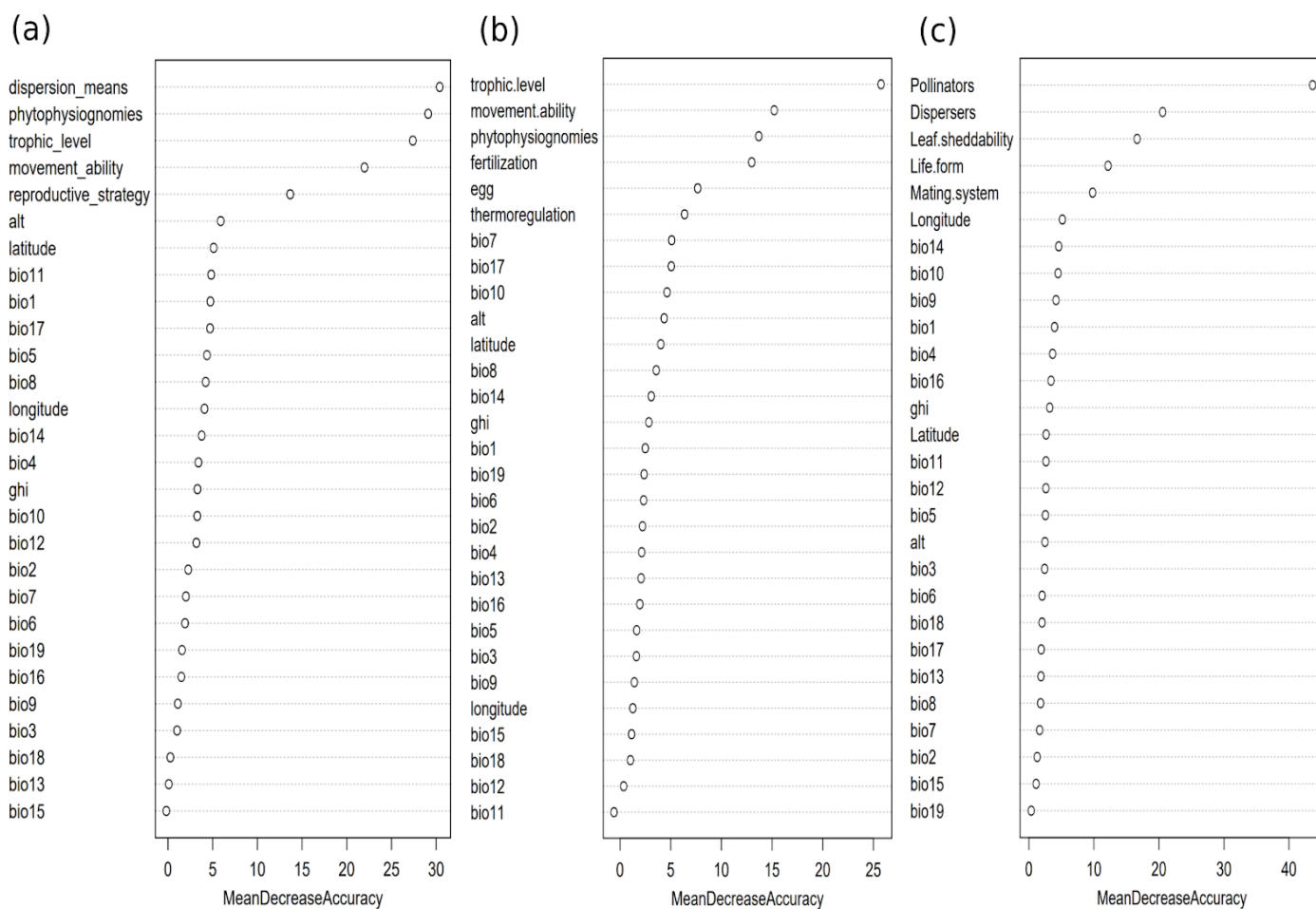


Figure 5. Variable importance (without taxonomy) for predicting the east-west phylogeographic break responses of (a) animals+plants, (b) animals, and (c) plants based on the Mean Decrease in Accuracy (MDA)

Discussion

We used a new full-likelihood Bayesian approach (Oaks, 2019) to investigate temporal patterns of diversification of several Cerrado plant and animal species co-distributed along an east-west phylogeographic break. We also evaluated the predictive variables likely correlated with the intraspecific responses of our focal species. We found evidence of a synchronous pulse of diversification between two plant species pairs, suggesting Pleistocene glaciation effects on establishing the shared phylogeographic

structure. Further, several aspects of our results indicated that the animal species experienced independent divergence events during the Miocene Tortonian to Pleistocene Chibanian ages. Finally, we identified traits associated with dispersion and population connectivity, such as pollination syndromes and dispersal vectors, as the main biotic correlates of this phylogeographic break in plants. For animals, taxonomy was the most important variable. We discuss the implications of these findings and suggest some future directions for Cerrado phylogeography.

Synchronous divergence in plants during the Pleistocene

By applying statistical tests for shared evolutionary events in the community, we recovered a signal of synchronous diversification between the eastern and western lineages of the tree *B. coccolobifolia* and the cactus *P. aurisetus*. Unlike *B. coccolobifolia*, a tree species widely distributed in the Cerrado, *P. aurisetus* is restricted to rocky areas. Therefore, the synchrony between these species may not be evidence of a single common barrier. Despite the limited availability of published data (chloroplast loci only), our study provides insights into the Quaternary diversification process in Brazilian savannas. The split between lineages occurred during the Pleistocene Chibanian age suggesting that the climatic events of this period could have had some influence on this diversification. This result is consistent with another study of the rocky savanna plants, where an east-west split was also found with divergence times dating to the mid-Pleistocene (Collevatti *et al.*, 2009). The strong spatial and chronological congruence of east-west divergence between phylogenetically distant taxa suggests a contribution of common causes in this divergence, such as multiple hidden barriers caused by past climatic changes in the Pleistocene.

According to our estimates (using slow evolutionary rates), the time of synchronous divergence between the western and eastern lineages (*B. coccolobifolia* and *P. aurisetus*) coincides with the Interglacial period known as the Cromer Interglacial (620-455 ka). This period was followed by the Kansan Glaciation, the most severe Pleistocene glaciation that lasted from 455-300 ka (Gibbard and van Kolfschoten, 2005; Ehlers *et al.*, 2018). Repeated climatic oscillations provided substantial opportunities for population split and admixture through time, affecting distinct populations in possibly idiosyncratic responses. Our sampling relies on available phylogeographic studies and

thus is not representative of the whole Cerrado biodiversity. However, our results support the role of these earlier glacial periods in synchronous divergence across eastern and western lineages in the central Cerrado. Considering the knowledge gaps in the Cerrado, we encourage more collection and availability of genetic data in the region.

Neogene and Quaternary effects in asynchronous divergence in animals

A model of asynchronous divergence (i.e., multiple pulses) is supported for arthropods, frogs, and lizards, suggesting the role of Miocene, Pliocene, and Pleistocene events affecting the east-west phylogeographic break. Thus, the phylogeographic patterns we observed in central Cerrado are likely driven by a combination of Neogene geological events and Pleistocene climatic fluctuations. Across two lizard species, *N. meridionalis* and *P. acutirostris*, with eastern and western populations, *ecoevoluty* estimated two discrete pulses of divergence during Miocene Tortonian and Pliocene Zanclean ages, respectively. In this case, the population divergence can be explained by vicariance events associated with the final stages of the Central Brazilian Plateau uplift (CBP, approx. 7-5 Ma) (Del'Arco & Bezerra, 1989; Saadi *et al.*, 2005). Our estimates have been consistent in terms of the relative impact of the CBP as a major soft vicariance barrier within Cerrado range, as suggested for other Cerrado vertebrates (e.g., Giugliano *et al.*, 2013; Domingos *et al.*, 2014; Guarnizo *et al.*, 2016; Camarugi *et al.*, 2021). In other words, it is possible that the fragmentation of populations started after the topographic reorganization of the Cerrado during the Miocene, and different intrinsic/biotic factors may have controlled the maintenance of the observed genetic structure.

We found one synchronous pulse of divergence between frog species pairs (*H. lundii* and the *Leptodactylus* complex) during the Pliocene Piacenzian, and the Pleistocene Gelasian ages, likely associated with climatic oscillations and landscape heterogeneity found within the Cerrado. In this case, the phylogeographic break does not coincide with an evident topographic barrier (large rivers or rivers basins); nonetheless, it could be associated with the landscape compartmentalization of Cerrado, as previously observed in a frog (*Leptodactylus* complex, Rocha *et al.* 2020), a lizard (*Micrablepharus atticolus*, Santos *et al.* 2014) and a tanager (*Neothraupis fasciata*, Lima-Rezende *et al.* 2019). The divergence times pre-date the LGM events, so it may be that the common phylogeographic structure arose through a long persistence of isolated lineages or connected by low gene flow since the Pliocene Piacenzian and the Pleistocene Gelasian

ages. In addition, our results align with paleoclimate evidence showing a strong association between stable areas and genetic clusters, suggesting that climatic oscillations have been an important force in maintaining the congruent genetic structure in frogs (Rocha *et al.*, 2020).

Across two arthropod species pairs, we did not find support for a shared split across the eastern and western lineages. However, the pulses of asynchronous divergence overlap cycles of range shifts in dry vegetation during the Pliocene Piacenzian age and throughout the Pleistocene (Prado & Gibbs, 1993; Pennington *et al.*, 2009). These results are in line with other fly studies that have shown the relative influence of Pleistocene climatic fluctuations shaping the genetic structure of open vegetation taxa (Moraes *et al.*, 2005). In conclusion, within animals, we found that spatial concordance is not associated with temporal synchrony. Instead, multiple events of divergence, which coincide with Neogene geological events and Quaternary climatic oscillations, suggest a complex biogeographic process and the association of intrinsic/biotic factors in maintaining the congruent genetic structure and asynchrony.

The role of hidden barriers in the temporal congruence of the east-west break

The Cerrado area of ca. 2 million km² in central Brazil acts as a dry barrier separating the Amazon from the Atlantic rainforests. Despite this isolation, many studies suggest that the Pleistocene glacial-interglacial phases could have favored the occurrence of migration routes connecting these rainforests through the Cerrado (Ledo & Colli, 2017; de Oliveira *et al.*, 2020). In addition, Pinaya and collaborators (2019) evaluated all palynological records from Brazil covering the period known as Heinrich Stadial 1 (HS1; 18–14.7 cal ka BP) and identified the presence of three main migration routes of montane rainforest taxa connecting the south/southeast of Brazil to the northeast and the Amazon. Here, we highlight that the multiple incursions of rainforest through the central Cerrado promoted important changes in the geographic distribution of the species during LGM and previous climatic events. Based on our results, most taxa that shared the east-west phylogeographic break presented divergence times dating between Pleistocene Gelasian and Chibanian ages. Therefore, we suggest that the repeated fragmentation of the Cerrado landscape during this period may have acted as a hidden barrier to dispersal, favoring the

initial fragmentation of populations into western and eastern lineages, later reinforced during the LGM, and possibly maintained since then by low gene flow.

Predictor variables for east-west division

Our findings from analyses using a predictive framework suggested that organismal traits have played a key role in structuring east-west genetic variation and divergence across Cerrado plant species. However, our predictive model identified that taxonomic classification was the most critical variable when animals were included (i.e., general and animal species-specific analysis). Taxonomic classification has already been recovered as the primary variable in other works using this same algorithm (Espindola *et al.*, 2016, Smith *et al.*, 2018, Bonatelli *et al.*, 2022). Therefore, these results suggest that our RF modeling may be highly dependent on the taxonomy, possibly because this variable encapsulates relevant traits, including dispersion means, that are not directly quantified. This is also reflected in the decrease in the analysis accuracy when taxonomy was removed, a fact that occurred in all situations.

When the taxonomy was removed, we observed a low predictability scenario in both general and animal species-specific analysis. Under this circumstance, dispersion means and phytophysionomy appear as the most critical predictors in our general analysis. Despite the low predictive accuracy of the model, this information suggests that these organismal traits might be considered in future studies. Within “phytophysionomy”, we evaluated habitat preferences represented by categorical variables such as widely distributed, rock areas, forest, savanna, grassland, or forest/savanna (Appendix 3). These results strengthen that habitat preferences of both fauna and flora may have played a key role in determining differences in temporal genetic divergence, possibly linked to the landscape heterogeneity of Cerrado and intraspecific responses to environmental change (Rocha *et al.*, 2020). Within animals, among those variables with low predictive capacity, trophic level and the ability of organisms to move across landscapes were the most important predictors. The type of locomotion is closely linked to taxonomy (e.g., birds and flight or reptiles and walking). Therefore, this can reinforce the importance that taxonomy had in previous analyses. It is recognized that movement ability influences the differentiation between populations (Medina *et al.*, 2018), primarily affecting

populations' dispersal capacity and genetic differentiation (Claramunt *et al.*, 2012, Ikeda *et al.*, 2012, Schiebelhut & Dawson, 2018).

Within plants, removing the taxonomy did not drastically reduce the predictive power of the analysis, and the most important correlates were pollinators and dispersers, traits deeply linked to dispersal potential. We highlight the fundamental role of ecological variables in maintaining the strong and congruent genetic structure observed in plants. Since changes in climatic conditions during the Pleistocene may have contributed to the genetic fragmentation of western and eastern lineages, this structure may have been maintained by limited seed dispersal in species such as *B. coccolobifolia* and *P. auriscetus*, with zoochorous dispersion syndromes (Bonatelli *et al.*, 2014; Resende-Moreira *et al.*, 2017). The opposite is also true; the east-west split seems subtler or even missing in some anemochorous taxa (Novaes *et al.*, 2010; Collevatti *et al.*, 2012, 2015). This finding highlights the role of pollinators and dispersers as important predictors of an east-west phylogeographic break in plants across the central Cerrado.

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Appendix 1. Animal and plant datasets used in this study.

Citation for the source of genetic data	Taxon	Taxonomic group	Genetic data	East-West break	Source (break)	RF	<i>Ecoevolity</i>
Andrade-Souza <i>et al.</i> (2017)	<i>Simulium hirtipupa</i>	Arthropod	ok	present	phylogeny	x	x
Bonatelli <i>et al.</i> (2014)	<i>Pilosocereus aurisetus complex</i>	Plant	ok	present	author+phylogeny	x	x
Collevatti <i>et al.</i> (2012)	<i>Tabebuia impetiginosa</i>	Plant	ok	absent	author+phylogeny	x	-
Faria-Santos <i>et al.</i> (2017)	<i>Nasutitermes corniger</i>	Insect	ok	absent	author+phylogeny	x	-
Fava <i>et al.</i> (2020)	<i>Leptolobium dasycarpum</i>	Plant	ok	absent	author+phylogeny	x	-
Fiorini <i>et al.</i> (2019)	<i>Mandirola hirsuta</i>	Plant	ok	absent	author+phylogeny	x	-
Fonseca <i>et al.</i> (2018)	<i>Polychrus acutirostris</i>	Plant	ok	present	phylogeny	x	x
Guarnizo <i>et al.</i> (2016)	<i>Norops meredionalis</i>	Lizard	ok	present	phylogeny	x	x
Leal <i>et al.</i> (2019)	<i>Pitcairnia lanuginosa</i>	Plant	ok	absent	author+phylogeny	x	-
Ledo <i>et al.</i> (2020)	<i>Colobosaura modesta</i>	Lizard	ok	absent	author+phylogeny	x	-
Lima <i>et al.</i> (2017a)	<i>Eugenia dysenterica</i>	Plant	ok	absent	author+phylogeny	x	-
Lima <i>et al.</i> (2017b)	<i>Complexo de espécies Sapajus</i>	Monkey	ok	absent	author+phylogeny	x	-
Moraes <i>et al.</i> (2005)	<i>Drosophila gouveii</i>	Arthropod	ok	absent	author+phylogeny	x	-
Novaes <i>et al.</i> (2010)	<i>Plathymenia reticulata</i>	Plant	ok	absent	author+phylogeny	x	-
Novaes <i>et al.</i> (2013)	<i>Dalbergia miscolobium</i>	Plant	ok	absent	author+phylogeny	x	-
Oliveira <i>et al.</i> (2018)	<i>Dermatonotus muelleri</i>	Frog	ok	absent	author+phylogeny	x	-
Prado <i>et al.</i> (2012)	<i>Hypsiboas albopunctatus</i>	Frog	ok	absent	author+phylogeny	x	-
Resende-Moreira <i>et al.</i> (2017)	<i>Byrsonima coccolobifolia</i>	Plant	ok	present	author+phylogeny	x	x
Santos <i>et al.</i> (2014)	<i>Micrablepharus atticolus</i>	Lizard	ok	absent	author+phylogeny	x	-
Trujillo-Arias <i>et al.</i> (2017)	<i>Arremon flavirostris</i>	Fly	ok	absent	author+phylogeny	x	-

Vasconcelos <i>et al.</i> (2019)	<i>Hypsiboas lundii</i>	Frog	ok	present	author+phylogeny	x	x
Carvalho <i>et al.</i> (2020)	<i>Leptodactylus frogs</i>	Frog	ok	present	phylogeny	x	x
Camurugi <i>et al.</i> (2020)	<i>Boana raniceps</i>	Frog	ok	present	author	x	-
Rocha <i>et al.</i> (2020)	<i>Lepidocolaptes angustirostris</i>	Fly	ok	present	author	x	-
Fernandez-Campon <i>et al.</i> (2021)	<i>Parawixia bistrinata</i>	Arthropod	ok	present	phylogeny	x	x
Buzatti <i>et al.</i> (2017)	<i>Qualea multiflora</i>	Plant	missing	absent	author	x	-
	<i>Qualea parviflora</i>	Plant	missing	absent	author	x	-
Buzatti <i>et al.</i> (2018)	<i>Qualea grandiflora</i>	Plant	missing	present	author	x	-
De Melo <i>et al.</i> (2016)	<i>Tabebuia roseoalba</i>	Plant	missing	absent	author	x	-
Ramos <i>et al.</i> (2007)	<i>Hymenaea stigonocarpa</i>	Plant	missing	present	author	x	-
Ramos <i>et al.</i> (2008)	<i>Hymenaea courbaril var. stilbocarpa</i>	Plant	missing	present	author	x	-
Resende-Moreira <i>et al.</i> (2018)	<i>Byrsonima crassifolia</i>	Plant	missing	absent	author	x	-
Ribeiro <i>et al.</i> (2016)	<i>Annona crassiflora</i>	Plant	missing	present	author	x	-
Vitorino <i>et al.</i> (2018)	<i>Handroanthus ochraceus</i>	Plant	missing	absent	author	x	-

x, presence; -, absence

Abbreviations: RF, Random Forest

Appendix 2. Substitution rates used in BEAST and *ecoevolity* estimates.

Specie	Molecular Maker	Mutation rate (subs/site/Myr)	Source
<i>Parawixia bistrata</i>	Mitochondrial	0.0115	Brower (1994)
<i>Simulium hirtipupa</i>	Mitochondrial	0.0115	Brower (1994)
<i>Norops meridionalis</i>	Mitochondrial	0.00325	Macey <i>et al.</i> (1998)
<i>Polychrus acuticostris</i>	Mitochondrial	0.00325	Macey <i>et al.</i> (1998)
<i>Hypsiboas lundii</i>	Mitochondrial	0.00325	Macey <i>et al.</i> (1998)
<i>Leptodactylus frogs</i>	Mitochondrial	0.00325	Macey <i>et al.</i> (1998)
<i>Pilosocereus auriscetus</i>	Chloroplastidial	0.0011 (slow) 0.0029 (fast)	Wolfe <i>et al.</i> (1987)
<i>Byrsonima coccolobifolia</i>	Chloroplastidial	0.0011 (slow) 0.0029 (fast)	Wolfe <i>et al.</i> (1987)

Appendix 3. Specific prior settings for *ecoevolity* analyses.

Clade	Species-pairs	Concentration prior		Population size (Ne)	Event time prior
		Prior type	Value		
Arthropods	2	Independent	1.0	Gamma (shape = 2.0, scale = 0.005)	Exponential (rate=50)
Plants	2	Independent	1.0	Gamma (shape = 5.0, scale = 0.0003)	Exponential (rate = 2000)
Lizards + Frogs	4	Independent	7.71475	Gamma (shape = 2.0, scale = 0.02)	Exponential (rate = 100)
Frogs	2	Independent	1.0	Gamma (shape = 2.0, scale = 0.007)	Exponential (rate = 100)

Appendix 4. The relative importance of species-specific traits used in the RF.

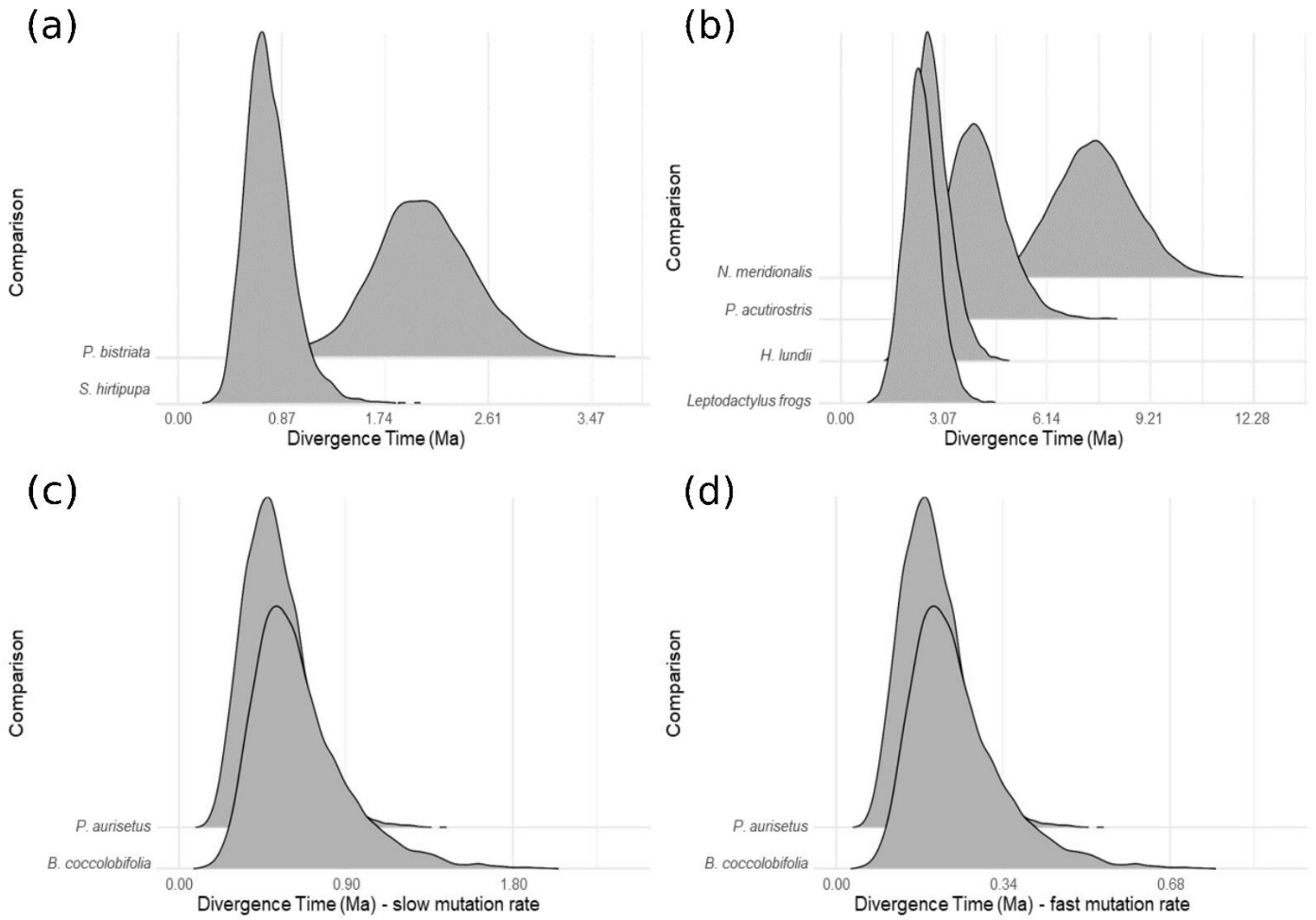
Biotic variable	Subcategories	Importance predictor
Trophic level	Producer	each predicted to confer the resource use in response to phylogeographic structure
	herbivore	
	omnivore	
	carnivore	
Movement ability	sessile	each predicted to confer the ability to move across the landscape in response to phylogeographic structure
	flying	
	terrestrial	
	swimmer/terrestrial	
Reproductive strategy	outcrossing	each predicted to confer the gene flow response to phylogeographic structure
	asexual	
	both	
Phytophysiognomies	widely distributed	each predicted to confer the habitat preference response to phylogeographic structure
	forest	
	grassland	
	savanna	
	rock areas	
	forest/savanna	
Dispersion means	self	each predicted to confer the dispersion propensity response to phylogeographic structure
	animals	
	wind	
Thermoregulation	ectotherms	each predicted to confer the physiology response to phylogeographic structure
	endotherms	
Fertilization	internal	each predicted to confer the reproduction systems response to phylogeographic structure
	external	
Egg	oviparous	each predicted to confer the embryonic development response to phylogeographic structure
	viviparous	
Dispersal vectors	wind	each predicted to confer the dispersal capabilities response to phylogeographic structure (plant species-specific)
	mammals	
	birds	
	birds/bats	
	none	
Pollination syndromes	bats	each predicted to confer the dispersal capabilities response to phylogeographic structure (plant species-specific)
	bees	
	beetles	
	moths	
	hummingbirds	
	bees/wasps	
	moths/bats/hummingbirds	
Life form	shrub	each predicted to confer the life form response to phylogeographic structure
	tree	
	herbaceous	
Mating system	outcrossing	each predicted to confer the gene flow response to phylogeographic structure
	asexual	
	self-compatible	
Leaf sheddability	mixed	each predicted to confer the leaf sheddability response to phylogeographic structure
	deciduous	
	semi-deciduous	
	perennial	
	none	

Appendix 5. Predictor variables used in this study and their relative subsets. (A) animals + plants, (B) animals, and (C) plants.

Variables	Subcategories	Subset		
		A	B	C
Geographic	Latitude	x	x	x
	Longitude	x	x	x
	Altitude	x	x	x
	Solar radiation	x	x	x
Climatic	BIO1 = Annual Mean Temperature	x	x	x
	BIO2 = Mean Diurnal Range (Mean of monthly (max temp - min temp))	x	x	x
	BIO3 = Isothermality (BIO2/BIO7) (×100)	x	x	x
	BIO4 = Temperature Seasonality (standard deviation ×100)	x	x	x
	BIO5 = Max Temperature of Warmest Month	x	x	x
	BIO6 = Min Temperature of Coldest Month	x	x	x
	BIO7 = Temperature Annual Range (BIO5-BIO6)	x	x	x
	BIO8 = Mean Temperature of Wettest Quarter	x	x	x
	BIO9 = Mean Temperature of Driest Quarter	x	x	x
	BIO10 = Mean Temperature of Warmest Quarter	x	x	x
	BIO11 = Mean Temperature of Coldest Quarter	x	x	x
	BIO12 = Annual Precipitation	x	x	x
	BIO13 = Precipitation of Wettest Month	x	x	x
	BIO14 = Precipitation of Driest Month	x	x	x
	BIO15 = Precipitation Seasonality (Coefficient of Variation)	x	x	x
	BIO16 = Precipitation of Wettest Quarter	x	x	x
	BIO17 = Precipitation of Driest Quarter	x	x	x
	BIO18 = Precipitation of Warmest Quarter	x	x	x
	BIO19 = Precipitation of Coldest Quarter	x	x	x
Taxonomic	Class	x	x	x
	Order	x	x	x
	Family	x	x	x
Biotic	Trophic level	x	x	-
	Movement ability	x	x	-
	Reproductive strategy	x	-	-
	Phytophysiognomies	x	x	-
	Dispersion means	x	-	-
	Thermoregulation	-	x	-
	Fertilization	-	x	-
	Egg	-	x	-
	Dispersal vectors	-	-	x
	Pollination syndromes	-	-	x
	Life form	-	-	x
	Mating system	-	-	x
	Leaf sheddability	-	-	x

x, presence; -, absence.

Appendix 6. Approximate marginal posterior distributions of divergence times (in Million Years Ago) for (a) arthropods, (b) lizards and frogs, (c) plants (slow mutation rate), and (d) plants (fast mutation rate).



2. CONCLUSÕES GERAIS

Nós conduzimos os primeiros testes para a diversificação simultânea de plantas e animais que compartilham a quebra filogeográfica leste-oeste ao longo do Cerrado Central. Em particular, com a ajuda de métodos filogeográficos comparativos, nosso estudo explorou a fascinante diversidade abrigada no Cerrado e identificou que a concordância espacial está associada à sincronia temporal em plantas, mas não em animais. Em outras palavras, a sincronia do evento de divergência em plantas está associada principalmente aos eventos Pleistocênicos que antecedem o LGM. Entretanto, dentro dos animais, nós estimamos diversos pulsos de divergência que coincidem com os eventos geológicos do Neógeno e as oscilações climáticas do Pleistoceno, sugerindo um processo biogeográfico complexo e a associação de fatores intrínsecos/bióticos na manutenção da quebra filogeográfica observada. Finalmente, nós defendemos que estudos comparativos investigando processos determinísticos mediados por “traits” devem ser incentivados, principalmente em regiões com diversidade exuberante e com uma gama de hipóteses distintas para explicar a diversificação dos organismos.